

AN ABSTRACT OF THE THESIS OF

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Title: THE THERMAL REGULATION, MICROCLIMATE, AND
DISTRIBUTION OF THE MOUNTAIN BEAVER,
APLODONTIA RUFA PACIFICA MERRIAM

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An investigation was undertaken to determine the role that temperature might play in limiting the distribution of the mountain beaver, Aplodontia rufa. A field study was carried on from August, 1965, through August, 1966, in the coast mountains of Benton County, Oregon, and consisted of measuring the annual temperature cycle of the burrows in conjunction with air temperatures taken at a height of six cm above the soil surface. A laboratory study was conducted to determine the effects of ambient temperature on body temperature, metabolic rate, thermal conductance, insensible water loss, and heart rate.

The burrow system was characterized by a cool and stable microclimate. The temperature above the soil showed a maximum annual fluctuation of 40.5° C, the temperature within the burrows varied 18.3° C, with a weekly variation in burrow temperature of

not more than 4° C. Annual range in mean burrow temperature was from 2° to 14° C.

The mean body temperature of Aplodontia, over an ambient temperature range of from 4° to 29° C was 37.6° C. Free-living animals had a mean body temperature of 38.0° C. Hyperthermia began at ambient temperatures above 29° C and a lethal body temperature of approximately 42° C was reached after a two hour exposure to temperatures between 32° and 35° C.

Aplodontia lacked a thermoneutral zone and minimal metabolic rates were recorded at high ambient temperatures when the animals were hyperthermic. Under conditions of heat stress, mean metabolic rates were 65 percent of the values predicted by Kleiber's equation. These animals were lethargic, their respiration rates decreased to as low as 18 per minute with minimal heart rates between 60 and 100 beats per minute. The mean minimal recorded heart rates, based on body weight, were 38 percent of that predicted.

Aplodontia had a minimal thermal conductance of 0.195 cal/g/hr/° C which could only be increased by a factor of 1.84. Winter animals had an effective insulation 1.23 times that of summer animals. This raised the lower critical temperature of summer animals by 4° C (19° to 23° C). Aplodontia required a six degree thermal gradient to dissipate its minimal heat production.

Insensible water loss could only be increased by a factor of 2.3

over the ambient temperature range of 12° to 31.5° C. At the latter ambient temperature, evaporative heat loss accounted for only 22 percent of Aplodontia's total heat loss.

The results of this investigation indicated that high environmental temperatures may act as an important limiting factor in the distribution of the mountain beaver which lacks adequate mechanisms to avoid heat stress.

The Thermal Regulation, Microclimate, and
Distribution of the Mountain Beaver,
Aplodontia rufa pacifica Merriam

by

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THE THERMAL REGULATION, MICROCLIMATE, AND
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INTRODUCTION

The Problem

The ultimate goal in studying the ecology of any species is the determination of the factors which are responsible for distribution and abundance of the species in time and space. In reality, the attainment of this goal is probably impossible since the activity and interaction of factors in time and space can be infinitely variable. The variability of factors in time is especially critical since the present distribution of any species is dependent upon its past evolutionary history. This history, which includes interactions with past environments, must be inferred from the knowledge of modern forms used in conjunction with a usually inadequate fossil record. Regardless of the feasibility of attaining the ultimate goal, most ecological studies, whether they are at the species or community level, are concerned with the factors which control the distribution and abundance of organisms.

There are numerous approaches which can be used to analyze these factors. In this study, the mountain beaver, because of its unique characteristics, was studied from a physiological

point of view in an attempt to establish the functional capabilities of the animal within its environment and to determine the extent to which this affects distribution. This species is unique because it is considered to be the most primitive living rodent and has apparently shown very little morphological change since the Miocene. Aplodontids have been restricted to western North America since they appeared in the Eocene. This limited distribution has been a source of puzzlement to numerous zoologists. Within this limited but diverse geographical area, the mountain beaver appears to be even further limited to a cool-moist environment. Another important characteristic of Aplodontia is the fact that it is a semi-fossorial rodent with a highly stable microclimate which is readily measurable.

Since a cool-moist climate appears to be a prerequisite for the presence of Aplodontia, the influence of this type of environment on the mountain beaver should be investigated. There are at least three possible reasons why the mountain beaver is restricted to this environment. These are: (1) A dependency on food plants that are restricted to this type of an environment; (2) A water balance problem; and/or (3) A thermal regulation problem.

A dependency on a specific group of food plants seems unlikely since Aplodontia can be maintained in the laboratory on a variety of foods such as apples and lettuce. Nungesser and Pfeiffer (1965) have suggested that the limited ability of this species to concentrate urine

is responsible for its restricted distribution. Aplodontia does require a high water intake but it can survive in the laboratory without free water if it has access to succulent vegetation. Since this species is found in areas which lack free water, free water is evidently not a necessity in this species' environment. It is probable that if free surface water is lacking, succulent vegetation must be present for survival.

Because of the lack of previous study and because of the importance of a mammal's ability to regulate its body temperature, the thermoregulatory adaptations of Aplodontia provide the basis for this research.

In order to evaluate the role that thermal regulation might play in the distribution of Aplodontia, two major questions have to be answered: What are the thermoregulatory capacities of this species and what are the thermal properties of its environment, especially the thermal patterns of its burrow systems? The answers to these questions should form the basis for predicting the type of thermal environments in which Aplodontia can survive.

A mammal's ability to thermoregulate is dependent on a complex set of adaptations which have evolved in response to natural selection. This set of adaptations have not evolved in isolation but in conjunction with the sum total of all adaptations that characterize a given species. Therefore, in the evaluation of the role that thermal

regulation might play in limiting the distribution of Aplodontia in time and space, it will be necessary to briefly review the evolution and life history of this species as well as the specific adaptations concerned with thermal regulation.

The problems encountered in studying this species are the same for any mammal. Their metabolic responses must be dealt with under abnormal laboratory conditions. For reasons of time and the availability of animals, only one of the seven subspecies of Aplodontia could be examined so that many of the conclusions must be tentative until further investigations are completed.

Review of the Literature

Evolution

The mountain beaver is the only living species of the rodent superfamily Aplodontoidea, whose fossil history dates back to the late Uintan of the Eocene epoch. It contains two families, Aplodontidae and Mylagualidae. According to Shotwell (1958), the family Mylagualidae was derived from aplodontid stock in the late Oligocene or early Miocene. The mylagaulids, however, declined during the early Pliocene and have apparently been extinct since the Hemphillian (late Pliocene) (Shotwell, 1958).

The early Miocene or late Oligocene was a period of great diversification for the aplodontids. There are at least six genera of aplodontids recognized from this period: Allomys, Haplomys,

Meniscomys, Niglaradon, Pipestoneomys, and Selelledon (Shotwell, 1958, and Romer, 1966). Only Allomys has been found outside of North America.

During the mid and late Miocene two more North American aplodontid genera appeared, Liodontia and Tardontia. From Europe during this same period, two other genera, Ameniscomys and Sciurodon have been described, but their relationship to the aplodontids remains in doubt (Shotwell, 1958).

North America, therefore, has been the center of the evolution of the superfamily Aplodontoidea. Shotwell (1958) has correlated the historical biogeography of the North American aplodontids and mylagaulids with the major climatic and vegetation changes that took place in Western North America during the Tertiary Period. He indicates that the modern genus Aplodontia, whose fossil record dates back to the Pleistocene, was most likely derived from some Liodontia ancestry during the late Pliocene, and that there has been very little morphological change in the Liodontia-Aplodontia line since at least the Barstovian of the late Miocene.

During the late Miocene, both families were found only in areas dominated by the Western American element of the Arcto-Tertiary Geoflora, the mylagaulids, with the more xeric component of the West American element and the aplodontids with the more mesic component. The fossil distribution of both families shows little

change during the early and middle Pliocene. The mylagaulids, however, became highly specialized during the late Miocene and did not survive the Hemphillian while the aplodontids remained conservative and have apparently shown little morphological or habitat change since the Barstovian.

Taxonomy

The first description of the mountain beaver occurs in the journal of Lewis and Clark, from which the name Anisonyn rufa was given by Rafinesque (1817). In 1829 Richardson proposed the name Aplodontia leporina after he had examined some skins and skulls from Oregon that were collected by David Douglas in 1826 (Thwaites, 1904). From this point the description and taxonomy becomes increasingly confused until Taylor, in 1918, revised the genus Aplodontia and recognized only nine valid taxa. The number of subspecies was further reduced to the present recognized number of seven by Dalquest and Scheffer (1945) and Hall and Kelson (1959).

Distribution

A distribution map of Aplodontia is given in Figure 1. The overall distribution of Aplodontia varies from sea level along the Pacific Coast states to at least 9,700 feet in the head of Lyell Canyon in Yosemite National Park (Taylor, 1918). Ingles (1965) states that

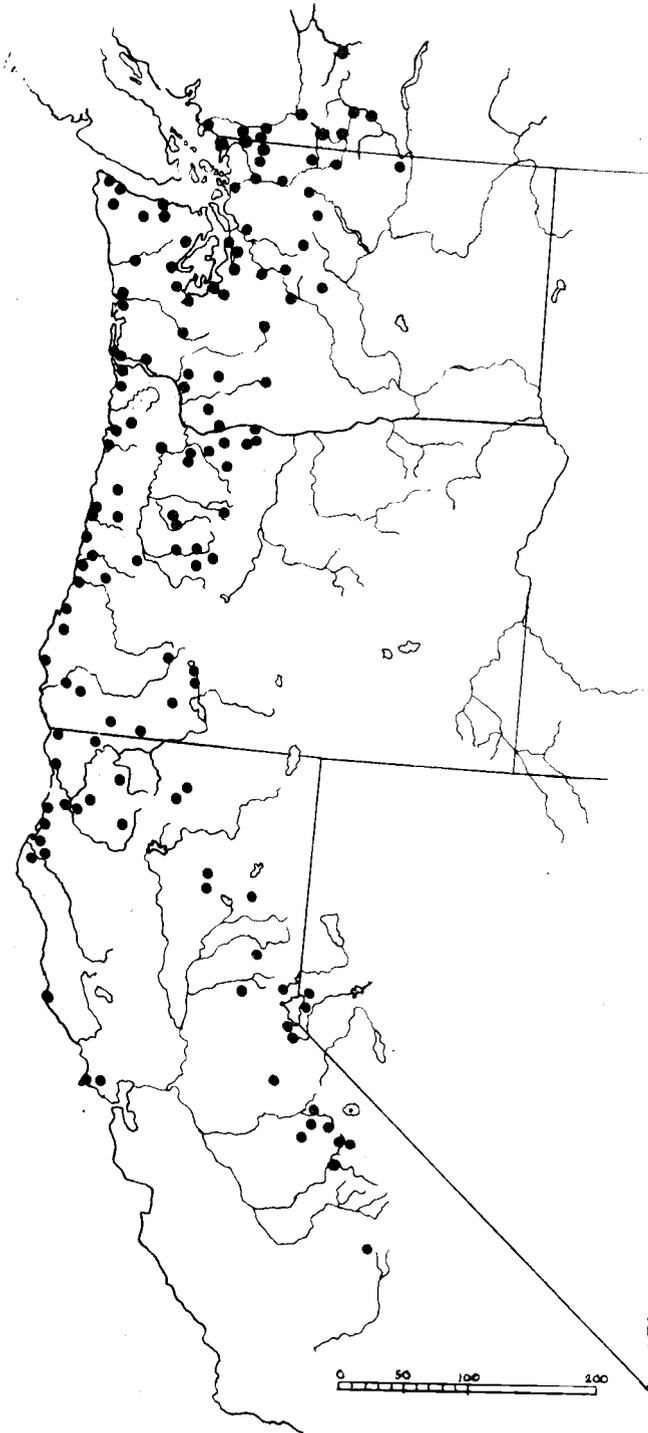


Figure 1. The distribution of *Aplodontia rufa* based on collection records made over the last 90 years.

the mountain beaver is a successional species found in the Transitional, Canadian, and Hudsonian life zones of the Pacific Coast states. Within these zones the mountain beaver is usually found in clearings at the edge of coniferous forests, in clear cut areas, on road-side clearings and along stream sides, especially on steep slopes with a tangle of vegetation (Dalquest, 1948). Crouch (1964) found the greatest abundance of Aplodontia on west or northwest facing slopes. In general, the mountain beaver is always found in cool, moist environments in areas with moderate to dense vegetation. The availability of free ground water appears to be important (Dalquest, 1948; Nungesser and Pfeiffer, 1965), but it does not appear to be limiting for there are sites in western Washington that have high populations but do not have free water.

Natural History

Information concerning the life history of the mountain beaver is scattered throughout the literature. The most comprehensive investigations can be found in the works of Anthony (1916), Camp (1918), Taylor (1918), Scheffer (1929), and Voth (1968). Godin (1964) has summarized much of the literature concerning Aplodontia.

Burrow Systems

The best descriptions of mountain beaver burrow systems can

be found in the works of Anthony (1916), Camp (1918), and Voth (1968). Voth found five types of underground chambers: nest, feeding, refuse, fecal pellet, and earth-ball storage. He found that the nest, feeding, and refuse chambers are usually at the lowest level of the burrow system. The ceiling of the nest complex usually is at least 50 cm below the surface of the soil (Voth, 1968). The nest chamber, usually filled with dry vegetation, has a horizontal diameter of between 50 (Camp, 1918) and 60 cm (Hubbard, 1922) and a vertical height of 36 cm (Voth, 1968). The ceiling of the nest-feeding chamber complex has been found to be covered with a coat of clay that appears to seal out water (Nelson, 1918, and Voth, 1968). Due to a relative humidity of nearly 100 percent, the vegetation stored in the feeding chamber remains as wet as it was when stored by the mountain beaver (Voth, 1968). Except when being used for plant storage, the nest-feeding chamber complex is always closed off from the rest of the burrow system by earth or rock plugs sometimes called "baseballs" (Voth, 1968).

The main tunnel complex of a burrow system radiates in all directions with tunnel diameter varying between 10 to 20 cm in diameter. Voth (1968) found two types of tunnels on his study site; deep tunnels, 100 cm below the surface, and shallow tunnels, under approximately 50 cm of soil. Most of the shallow tunnels examined by Anthony (1916) were at a depth of about 25 cm.

Food Habits

The most comprehensive study is the work done by Voth (1968). He studied a population of the Pacific Mountain Beaver, A. rufa pacifica in the immediate vicinity of the present study. He determined that the mountain beaver relied heavily on ferns for a food source with sword (Polystichum munitum [Kaulf.] Presl.) and bracken (Pteridium aquilinum [L.] Kuhn) fern comprising about 83 percent of the annual diet. Ferns made up 36.8 percent of the total dry weight productivity of the area.

Voth (1968) examined a single frond from each of these ferns and found that the wet weight of the Pteridium frond was about 6.5 times that of the Polystichum frond (233 g versus 36 g). The pinnae accounted for 42 percent of the wet weight of the Polystichum frond and 61 percent of that of the Pteridium frond. The pinnae of both species had a 72 percent water content. Because of its large size, the single Pteridium frond yielded about 9.5 times more dry weight material in terms of pinnae than did the Polystichum frond. This led Voth to conclude that the pinnae of a single Pteridium frond would provide about 108 kilocalories of energy whereas a single Polystichum frond would only yield about 11 kilocalories.

Polystichum was utilized throughout the year while Pteridium was used heavily when it was available during the summer months

(late May through September) (Voth, 1968). Pteridium is a unique food item for any mammal. It is classified as an undesirable forage species for cattle and it appears to be the leading cause of "Fern Staggers", a disease seen in livestock (Evans et al., 1958). Weswig, Freed and Haag (1946) found that laboratory rats died in 30 days when fed a diet containing 40 percent bracken fern. Voth also reports that in feeding experiments, Aplodontia readily devoured thistles (Cirsium vulgare [Savi] Airy-Shaw and C. brevistylum Cronq.) and nettle (Urtica gracilis Ait.) without any apparent discomfort. It would seem that the mountain beaver has an enviable "food niche," eating primarily plant species that are either poisonous or unpalatable for other mammals.

Behavior

The mountain beaver has between six and seven activity periods during a given 24 hours (Ingles, 1959). The longest rest period of 4:15 hours occurred during the day while the longest activity (2:45 hours) period was at night. Ingles estimated that Aplodontia had about eight or nine active hours and 15 to 16 at rest, with about 40 percent of its active period occurring during the day and about 60 percent at night. Voth (1968) agreed with Ingles except that his animals showed additional activity periods during the twilight hours, one about dawn and the other about dusk. Voth has estimated that

73 percent of the animal's active time involves feeding and foraging.

Voth explained this large time block by the evidence that the mountain beaver harvested almost everything in his environment. Orr (1949) noted stacks of vegetation as deep as 60 cm outside of burrow systems.

According to Voth, Aplodontia harvests at least 2.5 times the material that it ingests. It harvests whole plants or large parts of plants which it takes back to its burrow entrance and places in large piles. This type of harvesting procedure insures that an ample supply of forage will be available in the immediate vicinity of a burrow opening at times when exposure of the animal above the ground is dangerous.

Reproduction and Population Dynamics

Pfeiffer (1958) found that the reproductive potential for Aplodontia is quite low for a rodent. Very few females breed before they are two years old. Dalquest (1948) states that the litter size is usually two to three and, rarely, four. This is small for a rodent. The breeding season usually begins in late February or early March and the gestation period is between 28 and 30 days (Pfeiffer, 1958, and Scheffer, 1929). Lactation probably does not extend for more than two months following parturition (Pfeiffer, 1958). This would mean animals born in April would be able to start foraging for

themselves in June. Voth (1968) found lactating females as early as the 24th of April and as late as the 28th of June. The earliest record of a juvenile being caught was the 25th of June.

Very little is known concerning the population dynamics of Aplodontia. Camp (1918) found a population density of about ten per acre and Voth (1968) found in his study that a two-hectare site contained 58 burrow systems; 44 of these systems were being actively used, indicating about nine animals per acre. Voth found that the population was at its low point around the 15th of March, with 22 per hectare, and that the summer high population was 41 per hectare or approximately 16 animals per acre.

Physiology

Water Balance

Physiological studies concerning the mountain beaver have been meager. Pfeiffer and his associates have played the dominant role in this field. They (Pfeiffer et al., 1960, and Nungesser et al., 1960) were the first to describe the renal morphology of Aplodontia. These works were quickly followed with functional studies (Pfeiffer, Braun and House, 1962, and Dolph, Braun and Pfeiffer, 1962) which showed that the mountain beaver has very limited powers of concentrating urine. A water balance study by Nungesser and Pfeiffer (1965)

demonstrated that Aplodontia takes in approximately 33 percent of its body weight in water daily and that its urinary output accounts for the majority of this water load. They also suggest that the limited distribution of Aplodontia in wet, western slopes of the Pacific Coast may be a result of the animal's inability to concentrate urine. The possibility that the neurohypophyseal hormone of the mountain beaver differs from other mammals is indicated by the study of Greenbaum and Dicker (1963) which shows that the liver and kidney mitochondria of the mountain beaver do not swell when incubated in the presence of either lysine-8-vasopressin or lysine-8-vasotocin as in the case with rat mitochondria.

Thermal Regulation

The direct effect of heat upon living organisms is well known, and the thermal limits of many organisms have been described (Prosser and Brown, 1961, and Altman and Dittmer, 1966). All living organisms have a specific temperature zone in which survival is possible. The exact limits of this zone are not firmly fixed and can vary depending on the organism's past thermal history and thermal adaptations. The temperature zone is bounded by a high and low lethal temperature, temperatures at which survival is impossible after exposure for a given length of time.

Closely associated with the physical death of an organism which

occurs at the high and low lethal temperatures is the concept of ecological death. Ecological death describes the condition in which an organism can survive a given ambient temperature (T_A) indefinitely but is incapable of carrying out many of the normal activities which are vital to the survival of the individual or species to which it belongs. Such activities could be escaping from predators or reproducing. For example rats adapted to high ambient temperatures, maintain their body temperature (T_B), and survive for months but do not mate and reproduce (Gelineo, 1940). Hyperthermia has been shown to decrease fertility in sheep, bulls, and guinea pigs (Dutt, 1960). Maqsood and Reineke (1950) have concluded that high ambient temperatures can induce a hypothyroidal state in mammals which suppresses sexual development. Moore and Quick (1924) and Cowles (1945) had previously discovered the increase in sterility of male mammals subjected to high environmental temperatures. In mammals, therefore, it can be seen that the laboratory-determined upper lethal temperature is probably higher than the ecological lethal temperature.

It is now common knowledge that living organisms, like inanimate objects, tend to come into a thermal equilibrium with their environment through radiation, conductance, and convection. However, some animals, unlike an inanimate object, tend to maintain a constant T_B which is independent of their thermal environment. The terms

homeotherm and poikilotherm were first used by the German zoologist Bergmann in 1847 to differentiate between animals which maintain a constant T_B from those which lack this control (Brody, 1945).

The nature of body heat in homeotherms was first recognized as being the result of the oxidations of body substances in the classic work of Lavoisier and Laplace (1780). The development of a closed-circuit metabolic system by Regnault and Reiset in 1849 opened the door for future research. The more versatile open-circuit system was developed by Pettenkofer and Voit in 1862 and this apparatus was used by Rubner (1883) when he first demonstrated the "surface area law" for homeotherms on the basis of studying the metabolic rates of dogs. Richet (1889) worked with rabbits and came to the same conclusion that metabolic rate varied as to surface area and not body weight. Brody (1945) and Kleiber (1961) both have given credit for the theoretical formulation of the surface area law to Sarrus and Rameaux around 1840.

In the early 1900's a diversity of metabolic techniques were developed with a resultant emphasis on animal energetics and animal nutrition. The open-circuit gravimetric method developed by Haldane in 1892 was used by many to evaluate the metabolism of small mammals. In 1905, Atwater and Benedict published a description of a closed-circuit system that would allow the determination of an animal's respiratory quotient. Most of the research during the early

to mid 1900's was devoted to medical application of calorimetry with Du Bois (1927) being a guiding force in this field. A constant battle continued over the "surface area law." The literature concerning the surface area law is large and at times absurd, for there have been arguments over the third decimal place of the fraction power to which the animal's weight should be raised in predicting metabolic rate (Gordon, 1968, and Kleiber, 1961).

The study of thermal regulation in mammals other than man is a relatively new area of investigation. The idea of regulatory mechanisms is usually traced back to Claude Bernard (1878) when he stated that: "La fixité du milieu intérieur est la condition de la vie libre" (Brody, 1964, p. 244). The term homeostasis was applied to this concept by Cannon in 1932 and the concept remains as one of the most important physiological principles. The adaptations associated with thermal homeostasis in mammals was first systematically studied by Scholander et al. (1950a, 1950b, and 1950c). Even though Hardy and Soderstrom (1938) applied Newton's Law of Cooling to heat loss in man, Scholander et al. (1950b) were the first to apply this law to a large group of diverse mammals and to discuss its evolutionary significance. According to the biological application of this law, heat loss depends on the thermal conductivity of an animal's body and the thermal gradient that exists between the body and the environment. If the body temperature is to remain constant

as in a homeotherm, heat production must equal heat loss. This establishes four major variables in the regulation of T_B : (1) Body temperature; (2) Metabolic rate; (3) Thermal conductance; and (4) Thermal gradient.

Body Temperature. The normal T_B of mammalian homeotherms usually falls between 36° and 39° C (Prosser and Brown, 1961). The T_B of a homeotherm is not constant; it can vary with time of day, exercise, feeding, maturity, reproductive conditions, and age (Klieber, 1961).

Most mammals have a diurnal pattern of T_B . Irving (1964) indicated that the circadian temperature rhythm in man results in a 1.5° C fluctuation with the low point occurring during sleep just before dawn. Smith and Criss (1967) have shown a fluctuation of 2.1° C in Peromyscus polionotus. This is similar to the results of Morrison and Ryser (1962) with Zapus hudsonius. The mouse opossum, Marmosa, has a diel temperature cycle of 2.5° C (Morrison and McNab, 1962).

A special case of a variable T_B has been reported for the camel. This animal shows a maximum fluctuation in T_B under conditions of water stress. It has been shown to become hyperthermic during the day and to cool during the night. The maximum change in T_B that has been reported in this species has been 7° C, a change from 41° C

to 34° C (Schmidt-Nielsen et al., 1957).

Although seasonal variations in T_B of homeothermic mammals seldom occurs (Prosser and Brown, 1961) some exceptions have been noted. Wilks (1963) reported that the T_B of Geomys bursarius was 38° C in the summer and 36° C during the winter. Knorre and Knorre (1953) noted that elk have a lower T_B in the winter than summer, and Morrison (1962) reported that the Australian bandicoot, Thylacis obesulus, showed about a 2° C drop in T_B in the summer when it was exposed to cold during the day.

Exercise can elevate body temperature. It has been shown in man that during a long-distance race, man's T_B can increase to 41° C (Newburgh, 1959). Irving and Krog (1955) have indicated that body temperatures can increase in small mammals during exercise and this problem is well known to all who have tried to take the rectal temperature of a small mammal. Apparently, exercise under cold environmental conditions can lead to a decrease in T_B . Hart (1951) demonstrated that an active mouse at low environmental temperatures (10° C) had a lower T_B than a non-active mouse. The cause of this decrease appears to lie in a decrease in the insulation of the active mouse. Tucker (1965a) suggests that the increase in conductance is due to the increase in air movements over the lightly furred skin which is exposed during periods of activity.

Heterothermic mammals are well known for their variable T_B .

Monotremes and marsupials have been characterized as being "primitive" based on their low and variable T_B (Martin, 1903, and Robinson, 1954). Recent work by Schmidt-Nielsen, Dawson and Crawford (1966) indicates that the echidna, although possessing a low T_B (30.7°C) is still a good thermoregulator over the T_A range of from 0 to 25°C . Sloths, anteaters, and armadillos are heterothermic placental mammals with lower than normal body temperatures (Wislock and Enders, 1935). Johansen (1961b) investigated the armadillo, Dasypus novemcinctus, and concluded that the degree of thermostatic control limits the efficiency with which this species can maintain homeothermy. He also states (p. 141) that: "The low resting body temperature may extend its tolerance to heat."

Heterothermic mammals capable of torpor present a special series of adaptations. There is extensive literature covering torpor in small mammals. The complexity in the field stems from the fact that it is found in diverse groups of mammals with quite different phylogenetic backgrounds. There is still a great deal of debate as to whether torpor is a primitive condition or represents specific adaptations (Hudson and Bartholomew, 1964; Hudson, 1967; Cade, 1964; Eisentraut, 1960; and McNab, 1966 and 1969).

Semper (1881) and Kleiber (1961) mention the early work done by Horvath (1876) in establishing that mammals capable of hibernation can withstand a T_B of three degrees centigrade whereas

non-hibernators die at a T_B of 19°C . Martin (1903) was one of the first men to examine the relationship between T_A and T_B in primitive mammals. Much of the early knowledge concerning mammalian hibernation is summarized in the works of Rasmussen (1916), Johnson (1931), and Benedict and Lee (1938).

Six families of rodents (Cricetidae, Dipodidae, Gliridae, Heteromyidae, Sciuridae, and Muridae) contain some species that are capable of hibernation and/or estivation (Cade, 1960; Fertig and Edmonds, 1969). There are numerous species found in the order Chiroptera which are capable of deep torpor (Hock, 1951, and McNab, 1969). The order Insectivora contains hibernators and another, Carnivora, has species which show some signs of winter torpor (Hoffman, 1964). Bartholomew and Hudson (1962) and Morrison and McNab (1962) have shown that some marsupials are capable of estivation. The echidna is also capable of torpor but is not a true winter hibernator (Schmidt-Nielson, Dawson, and Crawford, 1966). Kayser (1965) indicates that some doubt exists about the existence of winter torpor in Lemuridae or in other primitive primates.

The value derived by a mammal from either winter torpor or summer torpor has been pointed out by many investigators (Kayser, 1965, Folk, 1966, and Gordon, 1968). Tucker (1965b) has shown, with Perognathus californicus in estivation at 15°C , that ten hours

of estivation uses 19 percent of the energy which would normally be used to maintain a standard T_B if not estivating. Through the use of a theoretical model he was able to demonstrate that the entrance into torpor could be explained by a simple decrease in the animal's metabolic rate.

Metabolism. The possible adaptive nature of the basal metabolic rate of homeotherms has been long debated. Benedict (1938) felt that the basal metabolic rate of any given species was constant. Benedict rejected the value of comparing the body weights and metabolic rates of different species of mammals on the basis that any seeming similarity was artificial. He stated (p. 179):

It seems, therefore, unjustifiable to apply mathematics to the pooled end-result of the activities of millions of cells each highly differentiated, with different energy potentialities and actuated by different stimuli.

Opposing Benedict's views, Brody (1945) and Kleiber (1961) supported metabolic rate-body weight relationships as being an important tool in energetic research. Kleiber (1961), in discussing the linear relationship that exists between the logarithms of metabolic rate and body weight of different mammalian species stated (p. 203):

Whether or not such a relationship has physiological significance depends on the physiologist, just as it depends on the listener whether he hears a symphony or a series of noises.

Kleiber felt that there was a sound theoretical basis for relating metabolic rate to the rates of heat transfer and blood circulation. He

proposed the following theory which integrates both of these relationships (p. 215):

In natural selection, those animals prove to be better fit whose rate of oxygen consumption is regulated so as to permit the more efficient temperature regulation as well as the more efficient transport of oxygen and nutrients.

Scholander et al. (1950a, b, and c) concluded from their investigations of arctic and tropical mammals that body temperature and basal metabolic rates were not adaptive. Scholander, in 1955, vigorously opposed Bergmann's rule on the basis that it was the thermal properties of an animal's surface and not the surface area which was important in thermal regulation.

More recent investigations have indicated that, contrary to Scholander's views, metabolic rate may be adaptive in mammals. McNab and Morrison (1963) found that xeric species of Peromyscus had a lower metabolic rate and a greater insulation than did more mesic species. Murie (1961), however, found the reverse to be true in lowland and desert races of Peromyscus maniculatus which had a higher metabolic rate at thermoneutrality than did races from higher altitudes. There were no differences observed in pelage insulation. McNab (1966) in working with the metabolism of fossorial rodents, came to the conclusion that metabolic rate could be adaptive. He stated that the cost and level of temperature regulation could be determined by the interaction of body weight, basal rate

of metabolism, and thermal conductance. In his work with bats (McNab, 1969) he further supported the adaptive nature of metabolic rates but increased the importance of body size. He stated (p. 249):

Therefore, the ratio M_b/C appears to determine the dependence of T_b on ambient temperature and the precision of thermoregulation, as well as the level of regulation.

The importance of body size and thermal regulation was also pointed out by Brown (1968) in his work with two species of woodrats, Neotoma cinerea and N. albigula. Brown was able to demonstrate adaptive modifications (body size and insulation) of temperature regulation in populations of these species which inhabited different thermal environments. Brown (p. 44) stated:

The data on N. cinerea suggests that Bergmann's rule may describe an important pattern of temperature adaptation within certain species or genera of small homeotherms because the advantages of an altered surface-to-mass ratio may be reinforced by changes in insulation that tend to accompany changes in body size.

Some mammals show a metabolic rate that is significantly lower than the predicted rate based on body size. Semi-desert and desert mammals have been found by numerous Russian investigators to have low metabolic rates (Gelineo, 1964). Similar observations have been made in this country on arid species found in the following genera: Baiomys (Hudson, 1965); Microdipodops (Bartholomew and MacMillen, 1961); Neotoma (Lee, 1963); Perognathus (Tucker, 1962 and 1965a; Morrison and Ryser, 1962); Citellus (Hudson, 1964); Dipodomys

(Dawson, 1955); and Peromyscus (McNab and Morrison, 1963; MacMillen, 1965). Hudson and Bartholomew (1964), in a review of estivation, indicated the adaptive significance of a low metabolic rate in desert forms in the following statement (p. 545):

A reduced metabolic heat production would, however, be adaptive for those diurnal animals exposed to extremely high ambient temperatures where survival time might be prolonged because of the reduction in the heat to be dissipated.

McNab (1966) was also able to show that many fossorial rodents had a basal metabolic rate that varied from 90 to 40 percent of the predicted values. These reductions in basal rates were thought to be directly related to the mean burrow temperatures of the individual species.

Seasonal variation in the metabolic rates of mammals have also been noted. The literature has been reviewed by Prosser (1955) and Hart (1957 and 1963). Inherent in these reviews is the fact that both metabolic and insulation adjustments are common seasonal phenomena in mammals. Gelineo (1964) felt that the basal metabolic rates of homeotherms constantly adapts to the changing thermal environment of the organisms. The literature concerning seasonal variation is often very contradictory. Gelineo (1964) pointed out that within the same species: (1) metabolic rate can remain the same throughout the year; (2) It can be higher in the summer than in the winter; and (3) It can be higher in the winter than in the summer. He felt that

differences apparently are due to such variables as the animal's thermal history, degree of excitement, sexual condition, and the presence of food within the digestive tract.

Another important variable is that responses of animals maintained in the laboratory tend to differ from those kept in outdoor enclosures. Working with white rats, Héroux et al. (1959) found that in animals maintained outside, winter rats had a lower metabolic rate and a greater pelage insulation with lower surface temperatures than they did in the summer. In contrast to this, they reported that similar rats maintained in the laboratory under cold conditions showed an increase in metabolic rate, a warmer surface temperature, and conductance identical to laboratory rats kept under warm conditions. Hart (1964) also indicated that the hormonal picture differs between natural and laboratory acclimated animals. He reported that the rat under natural conditions, tends to have an elevated adrenal activity and low thyroid function during the winter whereas cold acclimated rats show the opposite response.

Despite the conflicting literature, some generalizations can be made concerning seasonal variations in metabolic activity. Mammals with a body size greater than about five kilograms exhibit very little seasonal metabolic changes but show a marked difference in insulation (Scholander et al., 1950, and Irving, 1964). Small mammals have limited ability to undergo insulation changes due to the

interference with locomotion (Irving, 1964). Small mammals adapt to cold environments by seeking moderate microclimates and increasing their resistance to cold by increasing their heat production capabilities (Hart, 1964). Krog, Monson, and Irving (1955) have shown a six fold increase in basal metabolic rate in cold acclimated rats exposed to -40°C . In adapting to low environmental temperatures, shivering thermogenesis (Swift, 1932) is replaced by non-shivering thermogenesis (Depocas, 1961). Non-shivering thermogenesis appears to be under the control of the sympathetic nervous system (Carlson, 1960). Noradrenaline appears to be an important hormone in increasing metabolic capabilities (Depocas, 1960). The noradrenaline content of the adrenal gland is increased in cold acclimated mammals (Des Marais and Dugal, 1951) and has been shown to greatly increase the metabolism of cold acclimated and winter rats although it has very little effect on warm acclimated and summer rats (Hsieh and Carlson, 1957, and Héroux, 1961). There is also some indication that there is an increase in thyroid activity in cold acclimated mammals (Des Marais and Dugal, 1955, and Lachiver and Petrovic, 1960).

Thermal Conductance. In thermal regulation studies, the term "thermal conductance" indicates the rate at which heat is transferred from an organism to its environment per degree centigrade of the thermal gradient between these two. It does not indicate the way in

which the heat is transferred and therefore encompasses heat loss by radiation, conduction, convection, and evaporation.

The adaptive nature of thermal conductance is well documented in mammals. The reciprocal of conductance represents insulation (Scholander et al., 1950a), therefore, a mammal with a high conductance is poorly insulated.

Scholander et al. (1950a) were the first to show the excellent correlation between body weight and pelage insulation in arctic mammals weighing less than five kilograms. They studied 18 species of arctic mammals and 16 species of tropical mammals and found the pelage insulation of arctic species increased with fur thickness whereas the insulation of tropical forms was generally poor and showed very little relationship to thickness. This relationship has been expanded by Morrison (1960) and Herreid and Kessel (1967) to include a wide variety of non-arctic mammals. Both have derived almost identical equations for predicting thermal conductance based on body weight. Irving (1964) drew the conclusion that mammals weighing less than five kg could not adapt to cold environments by changes in pelage insulation because the necessary length of fur would interfere with normal locomotion.

Seasonal changes in insulation which constitute another form of conductance adaptation have been reported for numerous mammals. Huestis (1931) and Sealander (1951) reported that Peromyscus

maniculatus had more dense pelage in the winter than during the summer. Hart and Héroux (1953) found Peromyscus to be better insulated during the winter months. Héroux, Depocas, and Hart (1959) found the rat to have greater insulation during the winter but seasonal variation in the weight of pelage has not been found (Héroux and Campbell, 1959). Arctic red fox and the porcupine were shown to have seasonal changes in insulation due to modification of fur but this could not be demonstrated in Tamiasciurus hudsonicus (Irving, Krogh, and Monson, 1955). Mustela vison (Bassett and Lewellyn, 1949) and the ferret (Harvey and MacFarlane, 1958) have been shown to have seasonal changes in both the density and growth of their pelage. The latter changes are probably due to the effect of seasonal photoperiod changes and not to temperature since Hammond (1952) was unable to demonstrate that cold had any effect on the pelage of the ferret, M. cicognani. Hart (1956) examined the seasonal variation of pelage in numerous species and found an increased insulation of from 12 to 51 percent during the winter. The larger increase was seen in the larger mammals. Hart (1964) doubted the physiological significance of seasonal pelage changes in small mammals. Héroux (1961) came to a similar conclusion after studying alterations in the growth, internal organs, and pelage of cold and warm acclimated mammals.

The adaptive nature of thermal conductance in small mammals

is still debated. For minimal conductance to be adaptive, the conductance value should deviate from that predicted on the basis of body size and be correlated with some specific environmental problem. McNab and Morrison (1963) found xeric species of Peromyscus to have a greater maximum and minimum thermal conductance than more mesic species and concluded that these were adaptive to desert conditions. Murie (1961) was unable to demonstrate any significant differences in conductance in Peromyscus under similar conditions. Musser and Shoemaker (1965) felt that in the large species of Peromyscus, weight-specific conductance was inversely related to body weight. Hayward (1965a) examined various races of Peromyscus maniculatus found in diverse climatic areas and concluded that their insulation and metabolic rate were correlated with body size and not their environment. Hayward's (1965b) work on the microclimate of these mice lead him to state (p. 349):

It is concluded that in non-hibernating small mammals such as Peromyscus the behavioral responses to environmental temperature stimuli (use of microclimate, nest building, huddling) are of such efficiency that the insulative (fur, peripheral circulation changes) and physiological (metabolic rate) adaptations to climatic temperature are much reduced in their importance.

The work of Brown (1968) has shown that the coastal and highland populations of Neotoma cinerea are better insulated than desert populations of both N. cinerea and N. albigula. He found that body size in N. cinerea is inversely correlated with environmental temperature

and concluded that this relationship in conjunction with the differences seen in insulation would indicate that Bergmann's rule may play an important role in climatic adaptation.

McNab, in studying fossorial rodents (1966) and bats (1969), has stressed the importance of the relationship between metabolic rate and conductance in the determination of body temperatures in homeotherms. He stated (1969, p. 249):

These three characteristics, then, are "secondary" in the sense that they depend upon parameters that are determined by the ecological relations of a mammal: basal rate of metabolism, conductance, and weight.

Contrary to his conclusions in 1966, that poor thermoregulation would result if the basal metabolic rate/conductance ratio fell below 0.6, McNab (1969) felt that a mammal can regulate its body temperature at any level as long as the appropriate balance between this ratio and body weight is maintained. McNab therefore feels that metabolic rate, conductance, and body weight can all be adaptive and that the nature of any specific adaptation is dependent on the ecological niche of the mammal.

It is well known that changes in insulation can be brought about by modifications in the peripheral circulation. Irving and Krog (1955) pointed out the importance of peripheral cooling in arctic birds and mammals. Scholander and Scheville (1955) were among the first to establish the value of vascular counter-current heat exchangers.

Scholander and Krog (1957) demonstrated the presence of counter-current heat exchangers in the extremities of the sloths, Bradypus griseus and Choloepus hoffmanni. Heat exchangers have been postulated in the sparsely furred tails of Ondatra (Johansen, 1961a), Castor (Steen and Steen, 1965), Geomys (McNab, 1966) and the white rat (Little and Stoner, 1968). The advantage of a low skin temperature during cold weather in a bare-skinned mammal has been demonstrated in the domestic pig by Irving et al. (1956). Irving (1956) estimated that a thermal gradient of 100 mm could exist between the surface and deep core of a large pig.

The importance of a good insulative cover in large mammals faced with conditions of high solar radiation has been demonstrated in the sheep by Lee (1950) and Priestley (1957). Schmidt-Nielson et al. (1957) have established the same situation in the camel. It is interesting to note that Waites (1961) has demonstrated the presence of thermal receptors in the bare surfaces of the scrotum and udders of ungulates. MacFarlane (1964) summarizes information regarding the survival of ungulates in arid environments.

The influence of behavior on conductance is a complex problem and difficult to quantify. A mammal can easily vary its exposed surface by making alterations in its posture. McNab and Morrison (1963) reported that Peromyscus can reduce its exposed surface to a factor of 0.7 by maintaining a curled position. The nature of the body

surface exposed is also important. The pelage of most mammals is not evenly distributed and numerous species which inhabit warm regions have sparsely furred or naked areas on the ventral portion of their bodies. The exposure or concealment of these areas in conjunction with peripheral circulatory modifications can greatly alter a mammal's conductance (Gordon, 1968). Hudson (1962) has shown that Citellus leucurus can facilitate heat loss by flattening itself against any cool soil surface in its desert environment.

The importance of panting and fanning has been demonstrated in the thermal regulation of bats by Reeder and Cowles (1951), Robinson and Morrison (1957), and Bartholomew, Leitner and Nelson (1964). The thermal conductance of a mammal can be greatly increased through the evaporation of water from its surface. Chew (1965), in his review of mammalian water metabolism, stated that salivation and the spreading of this saliva over the body surface is best developed in marsupials. This behavior pattern has also been reported in at least ten species of small rodents and numerous larger mammals (Chew, 1965).

The insulative value of small mammal nests has been described for several species. Scholander et al. (1950a) found that an unoccupied lemming's nest had an insulative value 1.5 times that of a lemming's fur. Pearson (1960) reported that a nest reduced the metabolic requirements of Reithrodontomys by 17 percent. Brown

(1968) determined that a coastal Neotoma cinerea could reduce its metabolic rate by 23 percent when confined to its nest at an environmental temperature of 6° C.

The formation of social groupings during periods of cold weather can decrease an individual mammal's thermal conductance and therefore its heat production. Muul's (1968) comprehensive study of Glaucomys volans demonstrated the value of both a nest and social huddling. He found that during the winter, a single flying squirrel's metabolic rate was reduced by 12 percent when it occupied a nest in a tree. If six of these squirrels were allowed to huddle together in that nest, the metabolic rate of each animal would be reduced by 66 percent. Social huddling has also been shown to reduce individual heat production in bats (Herreid, 1963, and McNab, 1969), Peromyscus (Nicholsen, 1941, and Sealander, 1952), Reithrodontomys (Pearson, 1960), and Microtus (Stark, 1963).

Thermal Gradient. The magnitude of the thermal gradient is determined by a mammal's T_B and the temperature of its environment. Since the variation of T_B in a mammalian homeotherm is usually very small, the most important variable is the temperature of its environment. The temperature of the environment is dependent primarily upon its thermal properties, the general climatic and weather conditions, and the time of day. All of these variables can be exploited by a mammal through the use of behavior so that an

adequate thermal gradient can be maintained. This aspect of mammalian thermoregulation has been neglected by most investigators.

It is well known that many species of ungulates, bats and marine mammals undergo seasonal migrations. The factors responsible for these seasonal movements are not well understood, but they appear to result in the animal being relocated in a more favorable environment (Gordon, 1968). Most mammals, however, are either too small and/or lack efficient means of traveling long distances so they cannot avoid seasonal changes in environmental conditions.

Within a given environment, mammals can maintain a suitable thermal gradient by adjusting their activity patterns. The nocturnal and crepuscular behavior of small mammals living in hot environments is well known (Schmidt-Nielsen, 1964, and Gordon, 1968). Gentry and Odum (1957) have shown that small rodents adjust their activity periods so that they occur during times of minimal thermal stress. The same conclusions were made concerning Microtus and Peromyscus by Hatfield (1940) and for the red squirrel by Pruitt and Lucier (1958). The recent work by Hammer (1969) indicates that the combined factors of wind and temperature modify the activity patterns of Peromyscus maniculatus during the times that it is usually inactive. No effect was seen during this species' normal nocturnal activity cycle.

Small mammals have the advantage of size in that they can seek a suitable microclimate within a given environment. Unfortunately, there has been too little sampling of mammalian microclimates and too much speculation concerning them. The lack of information concerning these microclimates is especially amazing since Geiger's (1957) classical book of microclimatology was first published in 1927.

Small mammals can utilize a microclimate to maintain the necessary thermal gradient by: (1) Taking advantage of variations in surface topography (depressions, rocks, etc.) and vegetation; (2) Using underground retreats; and (3) Construction of suitable surface or arboreal nests. Schmidt-Nielsen (1964) described the potential surface microclimates available to desert mammals such as the jackrabbit and camel. Hudson (1962) found that the diurnal ground squirrel, Citellus leucurus used shaded areas within its desert environment as an aid in thermoregulation. A generalized discussion of the importance of surface microclimates can be found in the work of Gordon (1968).

The importance of underground retreats in thermoregulation has been described by numerous investigators. Vorhies (1945) published some of the first data on the microclimate of the burrows of desert rodents. He found that while the deep burrow temperature of Dipodomys spectabilis was 86° F, the ground surface was 155° F and the air temperature 103° F. Kirmiz (1962) reported similar

findings for several species of jerboas living in the Egyptian deserts. Carpenter (1963) has shown that the summer burrow temperatures of Dipodomys agilis and D. merriami allow these two species to remain within their thermal neutral zones while resting in their burrows. McNab (1966) reported that the mean burrow temperatures of numerous fossorial mammals were below their lower critical temperatures. This has also been found in Perognathus californicus (Tucker, 1965a), Peromyscus eremicus (MacMillen, 1965), Microdipodops pallidus (Bartholomew and MacMillen, 1961), Reithrodontomys megalotis (Pearson, 1960), and Peromyscus (Hayward, 1965a and b).

Hayward (1965b) examined the burrow temperatures of Peromyscus living in diverse environments, from the Wyoming alpine to the Nevada desert. He found that the outside temperatures had a maximum annual fluctuation of 56° C while the burrow temperatures only varied by 26° C. Although the summer burrow temperatures differed according to habitat, the winter burrows in all areas were very similar (0° to 6° C). Hayward stated (p. 349):

In these mice, the use of a subterranean microclimate is of considerable temperature-adaptive significance and is a concomitant of small body size.

In the case of fossorial rodents, the importance of a burrow system in thermoregulation has been well documented by McNab (1966). He found that fossorial rodents have a low basal metabolic rate and

a high thermal conductance. The magnitude of these variations could be directly correlated with the mean summer burrow temperatures of each species. He was also able to demonstrate that the lethal ambient temperature of each species is directly related to their mean burrow temperature. It would appear that these thermoregulatory adaptations represent an addition to fossorial adaptations previously described for mammals by Shimer (1903).

Beside the insulative value of nests which has been previously discussed, nests can also modify the thermal gradient directly. Neumann (1967) found that flying squirrels become highly gregarious during the winter and as many as 20 individuals may inhabit one nest box. He reported that six animals huddled in a nest box raised the temperature in the box to between 23° and 32° C when the temperature outside was -5° C. Modification of the thermal gradient by surfaces nests in the summer has been reported by Brown (1968) in his work with woodrats. He concluded that the desert woodrats probably could not survive the summer if it were not for their nests. In a discussion of this problem, Brown stated (p. 45):

The microclimatic data suggest that in summer, when populations are high, individuals (particularly juveniles) may occupy marginal den situations where the daily temperatures approach or reach lethal levels. Dispersing juveniles may suffer significant mortality from occupying inadequate microenvironments and being unable to tolerate the resulting temperatures.

Snow cover during the winter months has been shown to be

important in providing an adequate thermal environment for small mammals during periods of severe cold (Formozov, 1963). Johnson (1951) recorded the temperature under one and a half feet of snow and found it to be 15° F while the air temperature varied between -40° and -50° F. Pruitt (1953, 1957, and 1959) has found that on the George Reserve in Michigan the burrows of small mammals had a seasonal temperature fluctuation of from -1° to 2° C in the winter and from 15° to 20° C in the summer. He indicated that the lack of snow cover during severe cold periods led to the death of small mammals. This is in agreement with what Formozov (1963) has found in Russia. Stephenson (1969) has recently reported the importance of snow cover for the beaver (Castor). He feels that 40 cm of snow cover is necessary to give a beaver in its lodge adequate protection during the winter. He monitored a beaver's lodge during January in Ontario, Canada, and found that while the average daily minimum and maximum air temperatures were -21 and -6.8° C, respectively, inside the lodge, with snow cover, they were 0.8° and 1.6° C.

Prospectus. It can be seen from this review of mammalian thermal regulation that, during the evolution of mammals, an almost unlimited array of thermoregulatory adaptations have evolved. Although many of these adaptations have been described, very little is known about their functional importance to a mammal outside of the laboratory. It should also be noted there is some indication that

mammals housed in the laboratory act considerably different than those maintained under more natural environmental conditions. In conjunction with these problems, the lack of adequate information concerning the microclimate of mammals has prevented the direct application of laboratory results from solving problems observed in the natural environment.

The most recent work by Porter and Gates (1969) should open up a new approach to the physiological ecology of mammals. Their mathematical model relates radiation, air temperature, and wind speed to body temperature in the determination of specific climate space in which a mammal can survive. With the development of adequate technology which will permit the measurement of the necessary parameters, and with an increased awareness of the microclimate of mammals, mammalian physiological ecology should move from the descriptive stage to one of synthesis with zoogeography.

METHODS AND MATERIALS

Field Methods

Study Area

In evaluating the thermal characteristics of the mountain beaver's environment it was of prime importance to choose a site that would typify mountain beaver habitat and have a high population of these animals. Other important considerations were accessibility throughout the year and proximity to the laboratory facilities. A site with all of these characteristics was chosen in July of 1965, on the north side of Marys Peak, Benton County, Oregon. The location is shown in Figure 2. A site map is shown in Figure 3. The study site lies in the southeast quarter of Section 8, Township 12 South, Range 7 West from the Willamette Meridian. The mean elevation is about 537 meters.

Access to the area is provided by an unpaved logging road that leaves Highway 20 1.6 kilometers southwest of Blodgett, Oregon. The road follows Mulkey Creek through land owned by the Thompson Timber Company of Corvallis. Approximately 6.4 kilometers up this road a branch of Bark Creek is crossed and the road forks, with a secondary logging road going west. This intersect of the main access road with the secondary road is the reference point for all

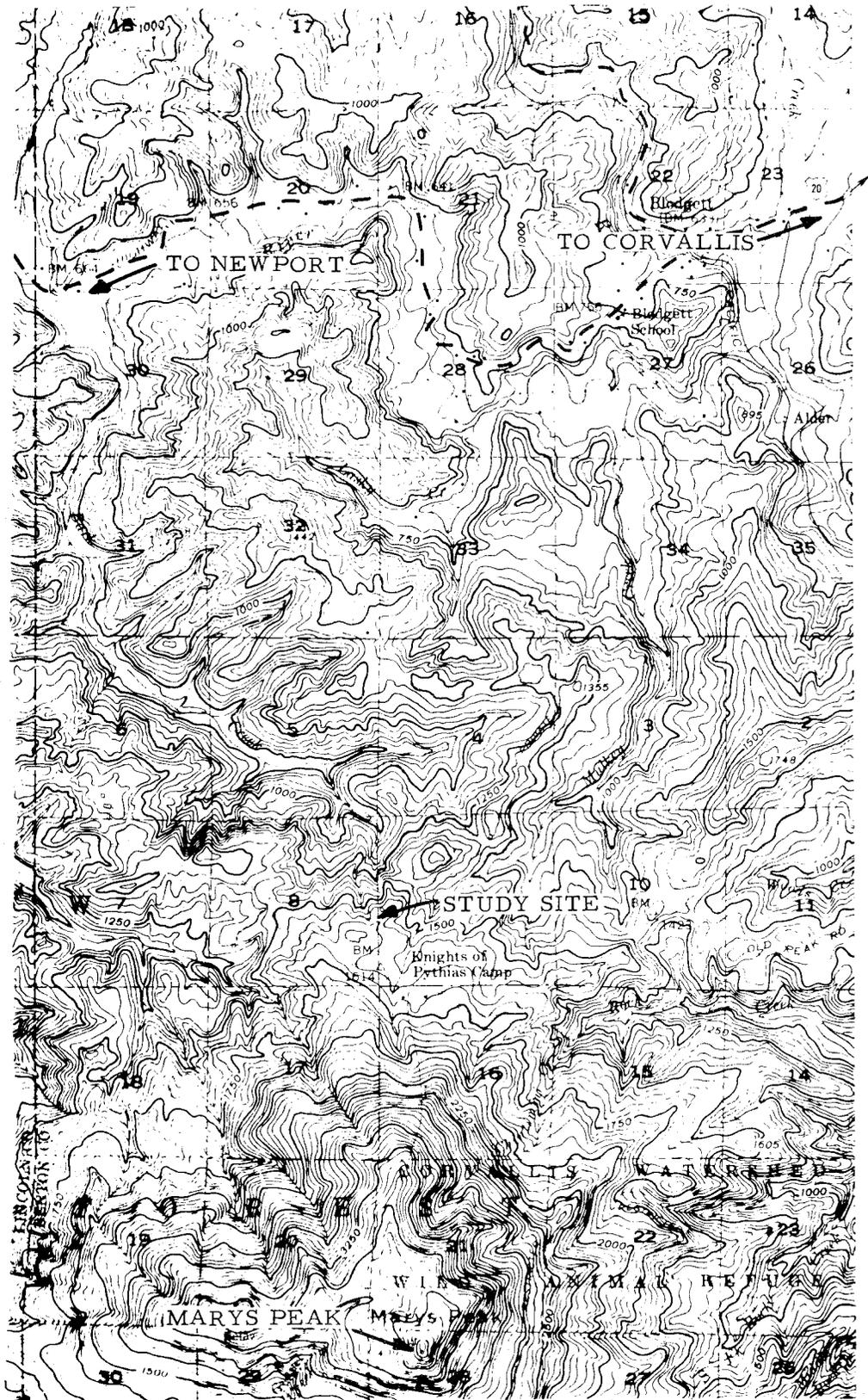


Figure 2. The location of the Marys Peak study site.

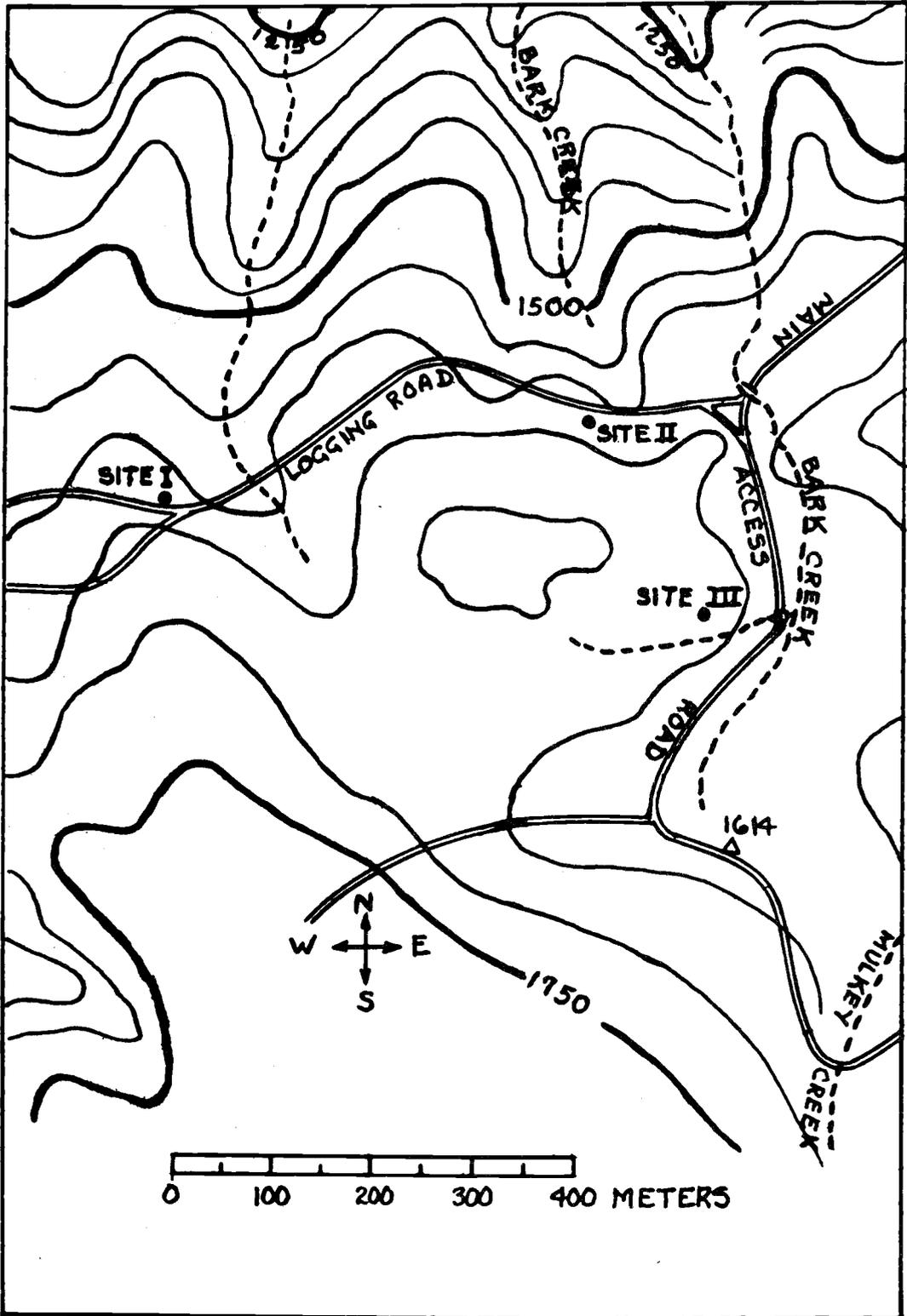


Figure 3. The location of the temperature recording stations on the Marys Peak study site.

measurements to the individual study stations.

The entire area was logged by the Thompson Timber Company in the 1940's. The area was characterized by secondary regeneration of Douglas fir (Pseudotsuga menziesii [Mirbel]Franco) with the presence of Western hemlock (Tsuga heterophylla [Raf.]Sarg.), Grand fir (Abies grandis [Dougl.]Lindl.), and Red alder (Alnus rubra Bong.). The open area had a wide variety of shrubs such as Red huckleberry (Vaccinium parvifolium Smith), Trailing blackberry (Rubus ursinus Cham. and Schlecht), Oceanspray (Holodiscus discolor [Pursh]Maxim), and Black elderberry (Sambucus racemosa L.). The herb layer was the best developed in the cool, open areas. Western brake-fern (Pteridium aquilinum) was the summer dominant in the herb layer, with Western sword-fern (Polystichum munitum), Bigsting nettle (Urtica dioica L.), and Common thistle (Cirsium vulgare) present over the cooler, open slopes. The forest floor was covered by Oregon oxalis (Oxalis oregana Nutt.) in the cool and moist areas, by California brome grass (Bromus carinatus Hook and Arn.) in the drier, open meadows, and by a composite of vegetation including Oxalis oregana, Montia sibirica (L.) Howell, Galium triflorum Michx., Trientalis latifolia Hook., and Viola glabella Nutt. on the cooler, open slopes.

Location and Description of Study Sites

Site I

Site I was located on a north-facing slope. It was six meters off the north side of the logging road which intersects the main access road 640 meters to the east (Figure 3). The site had a complete overstory of Red alder (Alnus rubra) with a few Douglas fir (Pseudotsuga menziesii) and Western hemlock (Tsuga heterophylla) dispersed throughout. The shrub layer was irregular in its distribution and was dominated by Salmon berry (Rubus spectabilis Pursh), and Devilsclub (Oplopanax horridum [J. E. Smith]Mig.). The herbaceous layer was dominated by ferns such as Western swordfern (Polystichum munitum) and Ladyfern (Athyrium filix-femina [L.]Roth), with Polystichum being by far the most abundant. The forest floor was covered by Oregon oxalis (Oxalis oregana) and mosses.

Site II

Site II was also located on a north-facing slope, and was ten meters off the south side of the logging road which intersects the main access road 160 meters to the east (Figure 3). This site lacked a tree overstory, although Pseudotsuga menziesii, Tsuga heterophylla, Alnus rubra, Sambucus racemosa, and S. cerulea Raf. were nearby. The shrub layer at this site was very diverse, containing species such

Holodiscus discolor, Rubus spectabilis, Vaccinium parvifolium, and Rubus ursinus. The herbaceous layer was also the best developed at this site being completely dominated by Pteridium aquilinum from late spring through the fall. Other important herbaceous species included Polystichum munitum, Cirsium vulgare, and Urtica dioica. The ground was covered by numerous species including Oxalis oregana, Galium triflorum, Digitalis purpurea L., Montia sibirica, Rumex acetosella L., Thalictrum occidentale Gray, and Trientalis latifolia.

Site III

Site III was in an open meadow on a southwest-facing slope. It was located 72 meters north of the point on the main access road which was 225 meters from the point where the logging road intersects with the main access road (Figure 3). This site lacked both shrub and overstory layers. The predominant grass in the meadow appeared to be Bromus carinatus. There was a scattering of Ros gymnocarpa Nutt., Vaccinium parvifolium, and Pteridium aquilinum throughout the meadow. Polystichum munitum was found near the forest edge of the meadow along with Alnus rubra.

Environmental Temperature

The environmental temperatures of the three sites located on Marys Peak were monitored from August 1, 1965, to September 3, 1966. Except for equipment failure or inaccessibility, temperatures were measured continuously. Dates of the temperature monitoring are given in Table 1.

Table 1. Dates during which the air and burrow temperature were monitored at Sites I, II, and III.

Site	Air Temperature	Burrow Temperature
I	Aug. 1, 1965, to Aug. 20, 1966	Sep. 1, 1965, to Aug. 20, 1966
II	Aug. 1, 1965, to Aug. 20, 1966	Aug. 1, 1965, to Aug. 20, 1966
III	Jan. 1, 1966, to Sep. 3, 1966	Oct. 1, 1965, to Sep. 3, 1966

The air temperature at each site was monitored with a portable, remote-reading, thermograph (Marshalltown Ink Stylus Model #1000-B, Electric Stylus Model #2200-B) equipped with seven-day recording charts. The recording unit was placed in a waterproof case; and the sensing element, which was attached to the unit by 1.8 m of wire, was suspended 6 cm above the ground in a well-ventilated and sun-shielded box (see Figure 4). The sensing element and its container were placed within 1 m of the opening of the burrow that was being monitored.

Each burrow temperature was measured by one of the following methods: (1) A recording thermograph (see above) with its heat

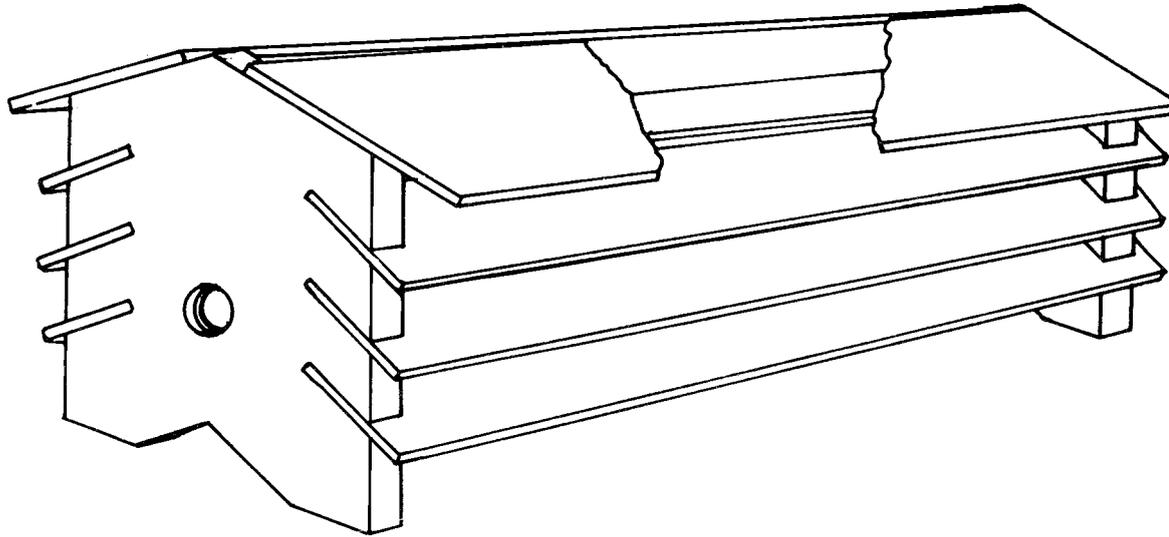


Figure 4. Ventilated and shielded container used to support thermal sensing probe of thermograph during the recording of air temperature six centimeters above the ground.

sensing element placed in the burrow at a distance of 50-60 cm, or (2) A maximum-minimum thermometer placed in the burrow at the same distance. The sensing element at Site I was under 18 cm of soil; at Site II, 15 cm of soil; and at Site III, 13 cm of soil.

Except for when weather would not permit access to the area, each site was checked weekly; and each temperature station was calibrated against a standard laboratory centigrade thermometer at the time that the charts were replaced.

Daily mean temperature for each month was determined by dividing each day into eight three-hour time intervals. The temperature of each of these intervals was read directly from the thermograph record. The sum total of all of the temperature readings for each of the three-hour periods were determined for each month and was divided by the total number of time periods. The mean daily maximum and minimum temperatures were determined by taking the sum of the daily maximum and minimum temperatures of each month and dividing that total by the total number of days in the month.

Animal Procurement and Housing

Animal Procurement

Thirteen male and four female animals were used in the laboratory studies. They were collected from areas immediately

surrounding Site I between January 12, 1966, and August 15, 1966. The live traps were manufactured by the Tomahawk Live Trap Company of Tomahawk, Wisconsin. These wire mesh collapsible traps were of single door (15 × 15 × 48 cm) and double door (15 × 15 × 61 cm) design. The single door traps were favored because they were less cumbersome.

In some cases the trap was placed at the opening of a burrow, thus becoming a continuation of the burrow. At other times the trap was set in the mountain beaver runway. In order to protect a trapped animal from the elements, old tar paper was used to cover the outside of all traps. Apples were used for bait and as a food source. Traps were set in the late afternoon or early evening and checked early the following morning.

When an animal was successfully trapped, the trap and the animal were transferred by automobile to the Forest Research Laboratory on the campus of Oregon State University. This was a distance of approximately 32 km from the trapping site. At the Forest Research Laboratory the animals were released directly into the holding pens without being handled.

Animal Housing

All animals were initially maintained in outdoor cages located at the Forest Research Laboratory. Each of the eight cages (0.7 ×

0.8 x 0.8 m) had a wooden frame which was covered with hardware cloth on all sides. The hardware cloth floors were covered with loose soil and sawdust. Each cage was provided with a wooden nest box which contained a center partition that divided this box into a nesting chamber and a feeding chamber.

The animals were provided with a diet of apples and lettuce, supplemented with fresh sword-fern, bracken fern, and Douglas fir branches. Water was provided in two-liter stoneware bowls.

Animals in the laboratory were temporarily maintained in one of two circular metal metabolism cages (diameter 62 cm). The cages had solid metal walls with hardware cloth floor and roof. A metal sliding door was located in the wall of the container and a metal hinged door in the roof. Each laboratory cage fitted on a funnel stand which permitted urine collection. The cages were located in a room that was subjected to normal day length via a window. The temperature varied from 20° to 25° C.

While animals were maintained in the metabolism cages, they were fed apples and lettuce. No free water was provided. Water balance was maintained on free water present in their food.

Laboratory Procedures

Metabolic Rate

Indirect calorimetry was used to determine the resting metabolic rate of Aplodontia, encompassing ambient temperatures of 4° to 34° C. These determinations were separated into winter and summer time periods. The animals for the winter period were collected between January 12, 1966, and March 25, 1966. The temperature range was 4° to 29° C. Experiments were carried out between February 23 and April 12, 1966. The mean weight of the ten animals (eight females and two males) was 681.7 ± 28.5 g (range 555-799 g). A total of 45 separate oxygen determinations, each of which was composed of three 30-minute trials were made.

Both oxygen consumption and carbon dioxide production were used in the determination of resting metabolic rates of summer animals. Seven animals (five female and two male) were caught between July 1 and August 15, 1966. These had a mean body weight of 742.7 ± 59.4 g (range 556-999 g). Measurements were made between July 12 and September 6, 1966. Oxygen consumption results are based on 32 experiments, each of which consisted of three separate 30-minute determinations with a temperature range of 10.6° to 34° C. Carbon dioxide results are based on 25 experiments, each of which consisted

of two 30-minute determinations. The gravimetric procedure used to determine carbon dioxide production is described with the insensible water loss procedure. Body temperature was monitored in all of the summer experiments using implanted thermal transmitters.

In comparing the results of these two methods, the data from each was converted to common units of calories per gram of wet body weight per day. An estimate of the respiratory quotient was determined from diet, which consisted of two parts apple and one part lettuce. The relative percentages of fat, protein, and carbohydrate for each foodstuff were taken from the Handbook of Biological Data (Spector, 1956). From this the relative percentage of each nutrient source was determined for the total diet: protein 10.6 percent, fat 3.3 percent, and carbohydrate 86.1 percent. This information was then converted into kilocalories per liter of oxygen or carbon dioxide using the caloric equivalents of nutrients from Kleiber (1961). Thus for this diet the energy equivalent of oxygen would be 4.94 Kcal/liter and of carbon dioxide would be 5.12 Kcal/liter under standard temperature and pressure and a R.Q. of 0.965.

A closed system respirometer was used to measure oxygen consumption (see Figure 5). The system consisted of an animal chamber (E), water bath (D), spirometer (J), electric kymograph (I), constant temperature apparatus (B), and a cylinder of compressed air (A).

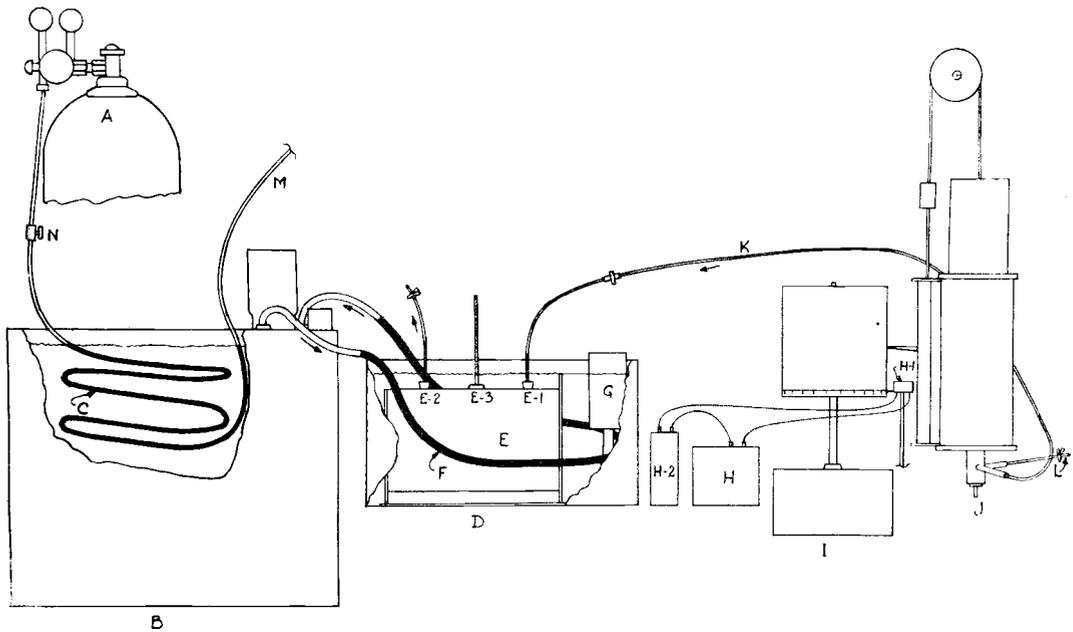


Figure 5. Closed system respirometer used to determine oxygen consumption in *Aplodontia*. A, compressed air cylinder; B, Aminco constant temperature unit; C, copper tubing for equilibration of air temperature; D, water bath; E, animal chamber with air ports (E-1 intake and E-2 outlet), thermometer (E-3), and carbon dioxide absorber; F, copper cooling coil for water bath; G, sump pump; H, electric timer assembly; I, kymograph; J, spirometer; K, input line to animal chamber; L, oxygen input line to spirometer; M, flushing line for animal chamber; N, needle valve.

The animal chamber (16.5 × 18.5 × 70 cm) was made from 1/4 inch acrylic plastic sheeting (Figure 6). It was equipped with intake (A), outlet (C), and temperature (B) vents. The entire structure was covered with black vinyl plastic. An observation window, which could be covered at will, was constructed of the same material. One end of the chamber was removable and served as the animal access way. This end was secured by brass nuts. The entire chamber had a removable tray (E) built from the same acrylic plastic. A hardware cloth screen (D) was placed over the removable tray.

A counter-balanced Phipps and Bird spirometer (Figure 5) was used as an oxygen reservoir. It had internal dimensions of 7.2 cm diameter and 34.3 cm in length and an approximate capacity of 1.4 liters.

A multi-speed electric kymograph, Harvard Apparatus Model #404 (Figure 5), was used to record the change in volume of the spirometer reservoir. It was run at a speed of 1.5 cm per minute. An electric timer, indicating minute intervals, was used to give a continuous time record.

The animal chamber was placed in a water bath (Figure 5), which was constructed of galvanized tin, insulated, and set in a wood frame. The temperature of the water bath was maintained with a copper coil (F) leading to the constant temperature unit (B). A sump pump (G) was used to circulate the water in the bath.

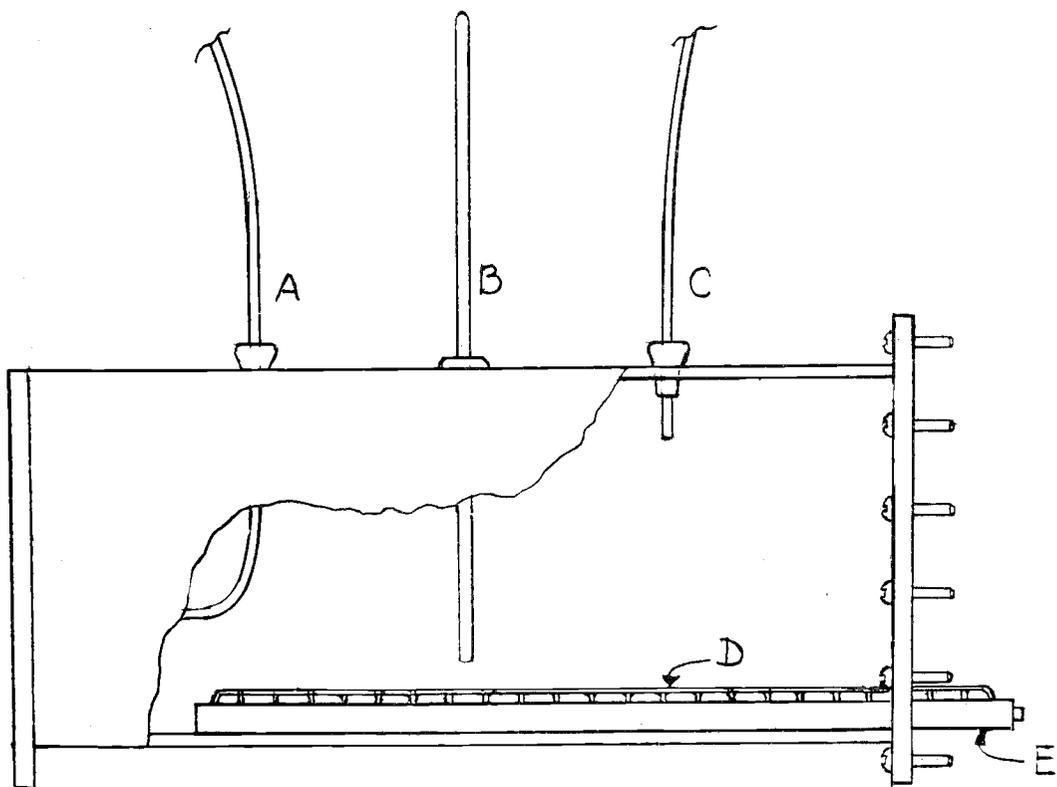


Figure 6. Animal chamber used in the determination of oxygen consumption. A, air intake port; B, thermometer; C, air outlet port; D, wire screen floor; E, removable tray.

An Aminco heating and cooling unit, American Instrument Co. Model #4-8600 (Figure 5), was used to maintain bath temperature. Water was circulated in a closed system. It flowed from the bath reservoir, through 1/2 inch copper tubing (F), to the water bath, and was then returned to the Aminco reservoir.

A cylinder of compressed air (Figure 5), equipped with a reducer valve (N), was used to flush the animal chamber between oxygen consumption runs and during the equilibration periods. Air was passed from the cylinder, through 3/16 inch tygon tubing, to a 1/2 inch copper coil (C), which was located in the reservoir of the Aminco unit. From the coil it flowed through more tygon tubing (M), to the input vent (E-1) located on the animal chamber, then through the animal chamber and finally out of the outlet vent (E-2).

Oxygen Consumption Procedure

In evaluating Aplodontia's normal resting metabolic rate, the animals were neither starved nor deprived of normal amounts of food and water prior to each oxygen consumption determination. They were taken directly from their outdoor or indoor cages and placed in a tared transfer cage. The cage was weighed and placed on the hardware cloth in the animal chamber.

This transfer cage (11 × 8 × 36 cm) was constructed out of galvanized wire fencing material. This material consisted of

overlapping wire (2 mm diameter), which formed rectangular spaces (2.5 × 5.0 cm). One end of the cage had a solid sliding metal door, while the other end was equipped with a wire hinged door. The entire cage weighed 335 g.

The removable tray (Figure 6-E) in the bottom of the animal chamber was furnished with indicating soda lime for absorption of carbon dioxide. The removable end of the chamber was secured, and the entire unit was submerged in a water bath. A 30- to 40-minute thermal equilibration period followed, during which air was supplied to the chamber from a tank of compressed air. The temperature of the air was adjusted to that of the bath by passing the air through copper coils in the Aminco reservoir prior to its passage through the chamber. The air temperature in the animal chamber was measured directly from a centigrade thermometer mounted in the top of the chamber. At the end of the equilibration period the compressed air was shut off, and the chamber was attached to the spirometer by way of plastic quick disconnects. Five minutes after the spirometer was connected the first 33-minute oxygen consumption determination was made. At the end of each run the chamber was flushed for 20-30 minutes with compressed air (flush rate approximately ten liters per minute), and the oxygen reservoir of the spirometer was refilled. Following this procedure, two or in a few cases three additional determinations were carried out,

whereupon the animal was removed from the animal chamber, reweighed, and returned to its cage. The rate of oxygen consumption was determined from the slope of the line on the kymograph record. Any activity of the animal resulted in pressure changes in the system and was reflected on the record by irregular movements. Resting metabolic rate was determined by taking the lowest oxygen consumption level which had been maintained for at least 15 minutes and which was preceded by at least a 30-minute inactive period (including flushing period). These were reduced to standard temperature and pressure conditions per gram of final wet body weight.

Insensible Water Loss and Carbon Dioxide Production Procedure

Water loss and carbon dioxide production were determined gravimetrically (Figure 7). Because it was necessary to observe the animals' behavior during this procedure, the following type of animal chamber was utilized. The chamber (E) consisted of a 5-gallon can (diameter 28 cm, height 33.6 cm) which had been filled with concrete to within 22.2 cm of the top. The concrete provided the necessary ballast. The lid of the can was equipped with a plastic plate (13 × 13 cm) which had five ports drilled in it to accommodate the various sensing leads and air vents. The inside of the chamber, including the cement floor, was sprayed with acrylic

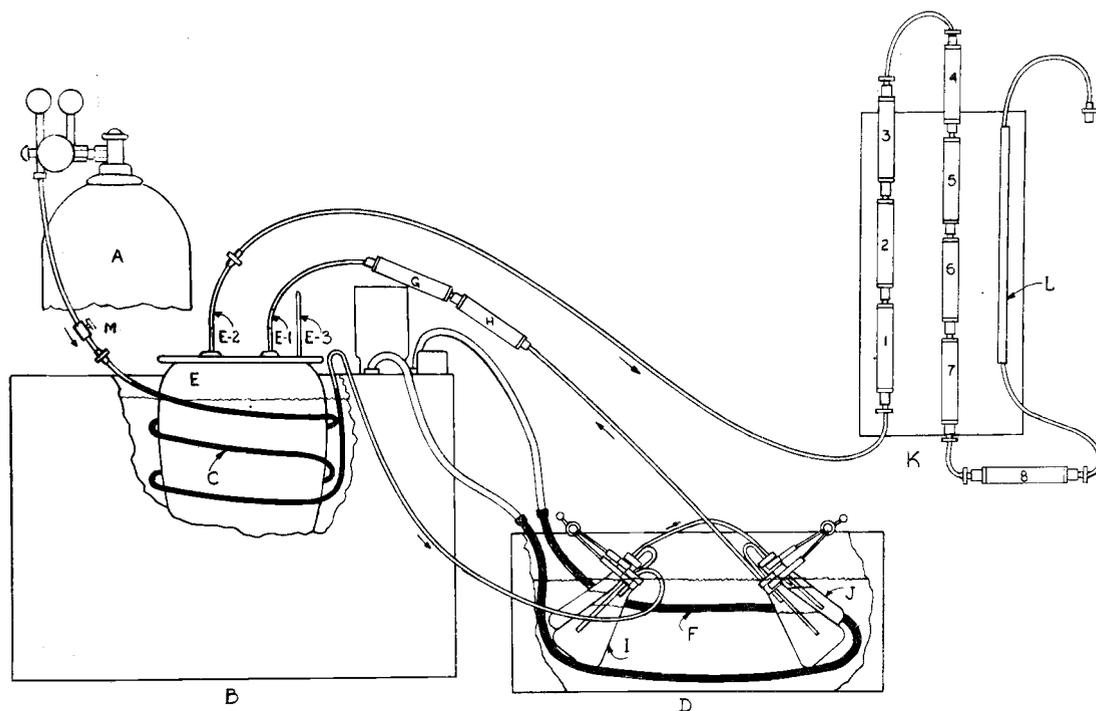


Figure 7. Insensible water loss and carbon dioxide production apparatus. A, compressed air cylinder; B, Aminco constant temperature unit; C, copper tubing for equilibration of air temperature; D, water bath; E, animal chamber with air ports (E-1 intake and E-2 outlet) and thermometer (E-3); F, copper cooling coil for water bath; G, silica gel water-absorbing tube; H, soda lime carbon dioxide absorbing tube; I, flasks containing 10 percent KOH for carbon dioxide removal; J, flasks containing silica gel for water removal; K, carbon dioxide and water absorbing chain; L, Manostat Predictable Flowmeter; M, needle valve.

plastic. A hardware cloth platform covered the bottom of the chamber. A mineral oil trap was used to prevent evaporation from excretory waste. This consisted of a 2 cm deep layer of oil at the bottom of the chamber beneath the false screen bottom.

The animal was placed in this chamber and the entire system was allowed to equilibrate for 30 to 40 minutes. During this time dry air passed through the chamber at the rate of approximately 1.1 liter per minute. A 30-minute water-loss determination followed this equilibration period. This was followed by a 40-minute air flushing period which, in turn, was followed by a second 30-minute water loss run. During each of the experimental periods air passed through the chamber at a rate of 630 ± 60 ml per minute. The air was first cleared of CO_2 by bubbling it through 10% KOH (I) and then dried by passing it through silica gel (J). The KOH and silica gel containers were placed in the water bath (D) to aid in temperature equilibration of the air in the chamber. After being dried the air was delivered to the chamber via a glass tube (E-1) that vented near the floor of the animal chamber. The air coming from the outlet vent (E-2) passed through an absorbing chain (K) which consisted of eight individual glass tubes fitted with rubber stoppers. These were equipped with plastic quick disconnect connectors. The first two tubes (1 and 2) contained silica gel, the next three soda lime (3, 4, and 5), the sixth silica gel, the seventh soda lime, and the eighth

silica gel. In addition to this chain, two pre-absorbers (H--one soda lime and G--one silica gel) were used to verify that the ingoing air was dry and free of CO_2 . The air was then directed through a Manostat Predictable Flowmeter (L) and finally vented to the atmosphere. The rate of air flow was controlled by a needle valve (M) that was located between the compressed air cylinder and the first KOH absorber. The absorbing tubes were weighed to the nearest 0.1 mg immediately prior to a water loss run and immediately after its completion on an analytical Mettler balance. Insensible water loss and carbon dioxide production were calculated from the lowest values determined during a single 30-minute run at any given ambient temperature.

During the entire procedure, the animal's body temperature was monitored. Respiration rate was periodically recorded during the run by direct observation of the animal's respiratory movements.

Body Temperature Procedure

Efforts to measure deep rectal temperature with a thermistor probe were unsuccessful. Abdominally implanted electronic transmitters (Figure 8) appeared to be the only practical method of monitoring body temperatures. The transmitters were based on the design of MacKay (1965, p. 208). Transmitters were relatively easy to construct, inexpensive, and reusable, although their effective range

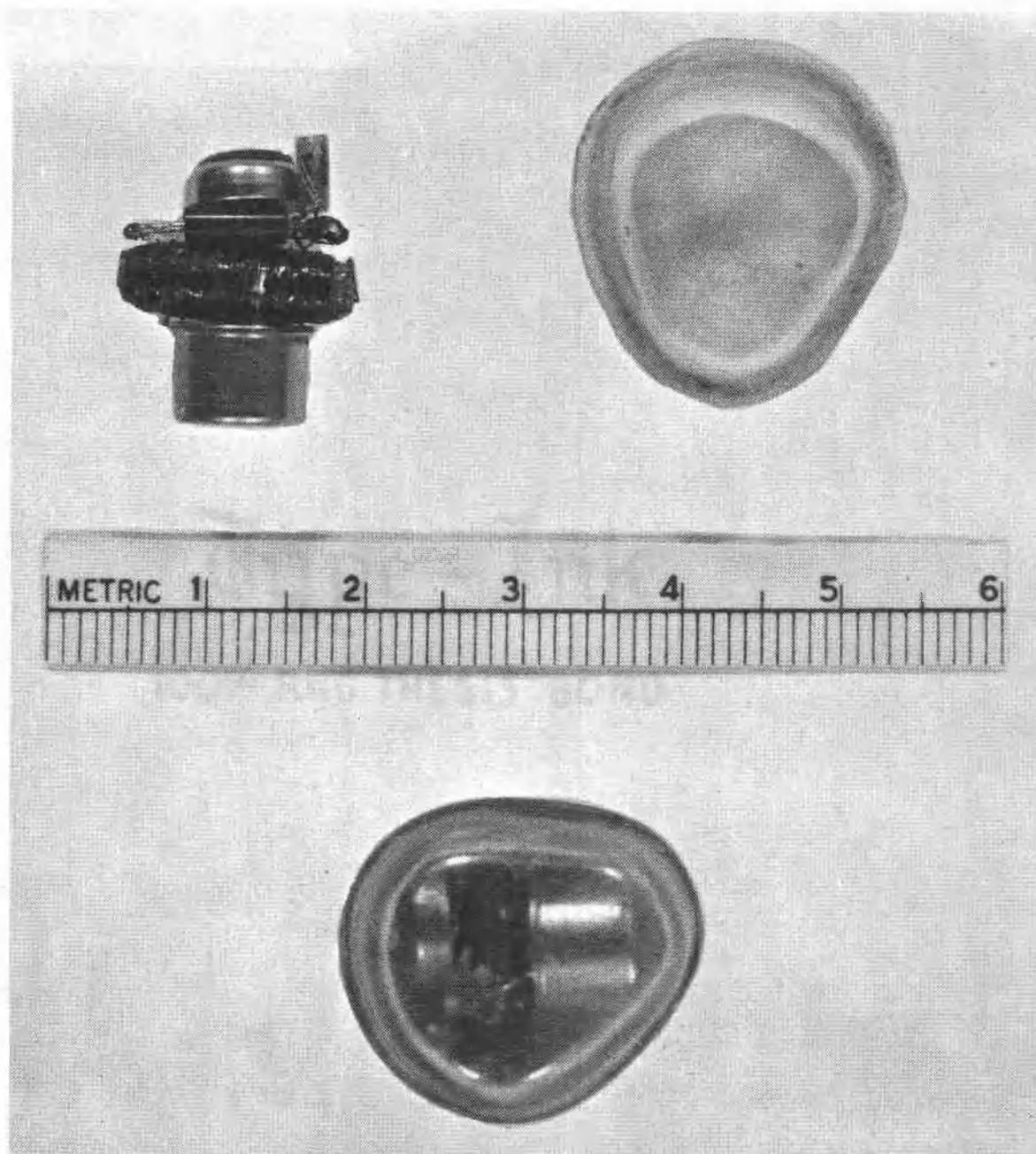


Figure 8. The body temperature transmitter.

was limited to approximately three feet. The schematic diagram is given in Figure 9.

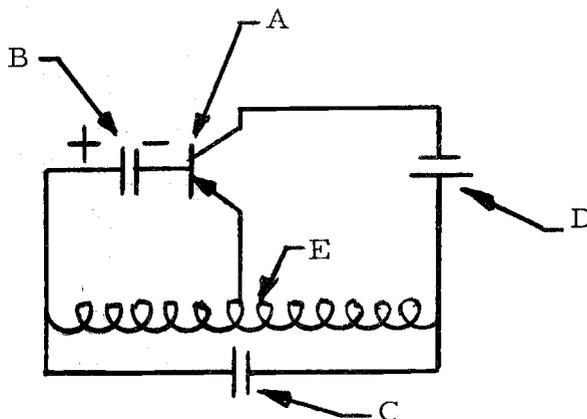


Figure 9. Schematic diagram of the body temperature transmitter. A, germanium transistor; B, tantalum capacitor; C, capacitor; D, Mallory battery; E, wire coil with center tap.

Components consisted of a temperature sensitive germanium transistor (Electronic Transistor Corporation Type 2N207A), a solid tantalum capacitor 225K, 2.2 uF, (Allied #43E4716), an NYT DC 461K, 470 pF capacitor (Allied #18Z049), a Mallory RM-312 1.4 volt battery (Allied #55Z950), and a coil of 400 wraps with a center tap constructed from size 32 plain enameled magnet wire. The coil determined the radio frequency and acted as an antenna. The germanium transistor served as the temperature sensor and as an oscillator.

A mold, the approximate size of the transmitter, was fabricated

out of plaster of paris. A cup was made by placing the mold beneath a Dental Omnivac Precision Vacuum adapter that, with a combination of heat and vacuum, covered the mold with clear Ominidental sheet resin, 0.08 inches in thickness. The transmitter was placed in the cup and a lid made of the same sheet resin material was fixed over it. The lid was fixed to the cup with Dental Walther's Special Nylon fiber acrylic and a catalyst of Acralite Fastcure Multipak. This gave a water-tight seal. As a precaution against formation of moisture within the cup, a few crystals of silica gel were placed in the cup before sealing. After the lid had dried, the sealed lip of the cup was rounded and sanded. The entire unit weighed approximately 4 grams and was slightly heart shaped.

Each unit was calibrated. For calibration each unit was placed in water, the temperature of which was measured by a centigrade thermometer graduated in 0.1°C and the rate of signals given by each transmitter was recorded. Since the signal rate increases with increasing ambient temperature, the number of signals given in 30 seconds, at the highest test temperature, was used as a counting constant. A calibration curve was then established by placing the ambient temperature (33° to 45°C) on the ordinate and the time (seconds) required to attain the counting constant on the abscissa. The sensitivity of the transmitters varied slightly, but temperature changes of 0.2°C could easily be distinguished. Each unit was

calibrated over three consecutive days; if no change was noted, the unit was implanted.

Before implantation the transmitters were soaked in zephrian solution. The site of the incision was shaved and washed with zephrian. Transmitters were placed in the abdominal cavity through a right flank incision of approximately 2 cm in length. The incision was closed in two layers using 3-0 surgical silk. Ether was used as a general anesthetic, and 70% alcohol was used as an instrument disinfectant. There were no post-operative complications, and all wounds healed normally. (This was verified by postmortem inspection at the end of the experiments.) The transmitters remained free in the abdominal cavity and caused neither inflammation nor adhesions. One animal was lost during the removal of a transmitter, but this death was caused by a respiratory reaction to the ether.

The life of a transmitter varied from three weeks to two months. The critical factor determining transmitter life was the amount of heat applied to the battery during construction of the unit. The transmitters were removed and re-calibrated when an animal was sacrificed or had died as a result of heat stress. It was noted that some transmitters tended to drift, i. e., they tended to increase their rate of signals per degree of temperature. This drift was linear and was corrected for by taking the rectal temperature manually and establishing a new calibration curve based on these findings.

These transmitters were used to measure the deep T_B during all summer experimental procedures. They were also used to monitor the T_B of free living animals in outdoor and laboratory cages. Readings were taken at various times of day and under various environmental temperatures.

Heart Rate Procedure

In evaluating the role that the cardiovascular system plays in the thermal regulation of the mountain beaver a series of four experiments were carried out. The purpose, in this instance, was to determine heart rate at high ambient temperatures. As the subject of these experiments, the mountain beaver was a difficult animal. Heart rate was determined by connecting three ECG leads to the animal and counting the electrical events of the heart on an oscilloscope screen.

Special handling procedures had to be used. The animals were anesthetized with ether and three standard ECG leads were attached to their backs with silver wound clips. The three leads were connected to the input termination and calibration switch box of a standard IMP-Scope (Heath-Kit Model EV-3). The animals were then allowed to recover from the anesthetic before any determinations were made. The recovery time was at least one hour for all animals. During this recovery period, it was necessary to place a slight heat stress (T_A 24° to 28° C) on the animals so that they would remain

calm and ignore the electrodes on their backs. (Even with these precautions, animal #21 pulled the leads off once and animal #22 removed them twice.) The T_A was then gradually increased while the animals' heart rate, body temperature, and respiration rate were monitored.

As soon as the animals were cooled they removed the electrodes, bit through the wire leads, or became so active that the electrical activity resulting from gross muscle contractions overrode the ECG signal and heart rate could no longer be determined. This made it impossible to determine the heart rate of the mountain beaver at low T_A 's.

RESULTS AND DATA

Terminology

Many of the common terms and symbols associated with studies of the metabolic patterns of homeotherms have been treated differently by various investigators. In order to avoid confusion, a number of these terms will be defined at this point. These definitions follow the work of Hudson and Brush, 1964, and MacMillen, 1965.

Hyperthermia. A term used to describe an animal's T_B when it exceeds the temperature normally seen when the animal is at rest in its thermal neutral zone.

Hypothermia. A term used to describe an animal's T_B when it falls below the value seen when the animal is at rest in its thermal neutral zone.

Thermal neutral zone. The range of T_A 's at which a resting animal can maintain its minimal metabolic rate while maintaining a normal T_B .

Upper critical temperature. The T_A above which the animal must increase its metabolic rate in order to dissipate metabolic heat so that it can maintain a constant T_B .

Lower critical temperature. The T_A below which the animal must increase its metabolic rate in order to prevent its T_B from falling below normal levels.

Newton's Law of Cooling. The rate of heat loss of a body per unit time is proportional to the temperature gradient that exists between the body and its environment. If an endotherm maintains a constant T_B , then heat loss must equal heat production. Substituting heat production for heat loss, the equation reads:

$$\text{metabolic rate (cal/g/hr)} = C (\text{proportionality constant}) \times (T_B - T_A) \quad (1)$$

C describes the conductance of the animal and will assume its lowest constant value at all T_A 's below the animal's lower critical temperature if the animal maintains its T_B constant. When metabolic rate is plotted against T_A , a straight line should fit the metabolic rate values below the animal's lower critical temperature; and the extrapolation of this line to zero metabolic rate should intersect the abscissa at a T_A equal to the normal resting T_B of the animal.

Conductance. The rate of heat transfer across the surfaces of an animal to its environment. This term describes total heat transfer and does not differentiate between heat lost by evaporation, conduction, convection, and radiation. The reciprocal of conductance represents insulation. The units for both terms are usually given as calories/gram of body weight/hour/degree centigrade difference between the animal's body temperature and the ambient temperature.

Torpor. The natural occurrence of hypothermia under conditions of moderate to low T_A 's. The animal's T_B and numerous

physiological parameters, such as metabolic rate, heart rate, and respiration rate, vary directly with the ambient temperature.

Aestivation. The condition of torpor occurring at moderate T_A 's and lasting from a few hours to several weeks.

Hibernation. The condition of torpor occurring at low T_A 's and usually lasting for a period of days or weeks.

Precipitation

The amount of precipitation at the study site from August 7, 1965, to August 17, 1966, is represented in Table 2.

Table 2. Precipitation (inches) at Marys Peak Study Site (August 7, 1965, to August 17, 1966).

	7 Aug	28 Aug	25 Sep	29 Oct	25 Nov	30 Dec	28 Jan
	28 Aug	25 Sep	29 Oct	25 Nov	30 Dec	28 Jan	26 Feb
Rain	0.92	0.28	5.05	11.99	13.83	14.10	8.58
Snow	--	--	--	--	19.0	1.5	2.0
	26 Feb	31 Mar	29 Apr	27 May	30 Jun	29 Jul	
	31 Mar	29 Apr	27 May	30 Jun	29 Jul	17 Aug	
Rain	15.60	2.51	1.42	1.27	0.87	0.0	
Snow	10.0	--	--	--	--	--	

These values were obtained from Bill Lovejoy (1966) who was engaged in a population study in this area during the same time period. A total of 76.42 inches of rain and 32.5 inches of snow fell on the study site during the year of this investigation.

The water equivalent of the 32.5 inches of snow was not measured, but a median value of 28.6 percent water equivalent is known based on 21 years of snow analysis on Marys Peak (Climatological Handbook, 1969, p. 245). This would add 9.3 inches of water for an annual precipitation of 85.77 inches of water.

The period of the greatest precipitation occurred between October 29, 1965, and March 31, 1966, when 84.4 percent (64.1 inches) of the total rain and all of the annual snow (32.5 inches) fell. The driest periods were from August 7, 1965, to September 25, 1965, and from June 30, 1966, to August 17, 1966, when only 2.7 percent (2.07 inches) of rain fell. Some form of precipitation occurred in every month of the year.

Environmental Temperature

A representative sample of the relationship between air and burrow temperatures is given in Figure 10. It represents the temperatures at Site III during the week of August 27 to September 3, 1966. The weekly means, as calculated from Figure 10, are seen in Table 3.

Table 3. Environmental temperatures ($^{\circ}\text{C}$) at Site III during the week of August 27 to September 3, 1966.

	Daily Mean	Mean Max.	Mean Min.	Max.	Min.
Air	12.5 $^{\circ}\text{C}$	27.0 $^{\circ}\text{C}$	3.3 $^{\circ}\text{C}$	33.3 $^{\circ}\text{C}$	1.7 $^{\circ}\text{C}$
Burrow	13.6 $^{\circ}\text{C}$	14.4 $^{\circ}\text{C}$	12.6 $^{\circ}\text{C}$	15.0 $^{\circ}\text{C}$	12.0 $^{\circ}\text{C}$

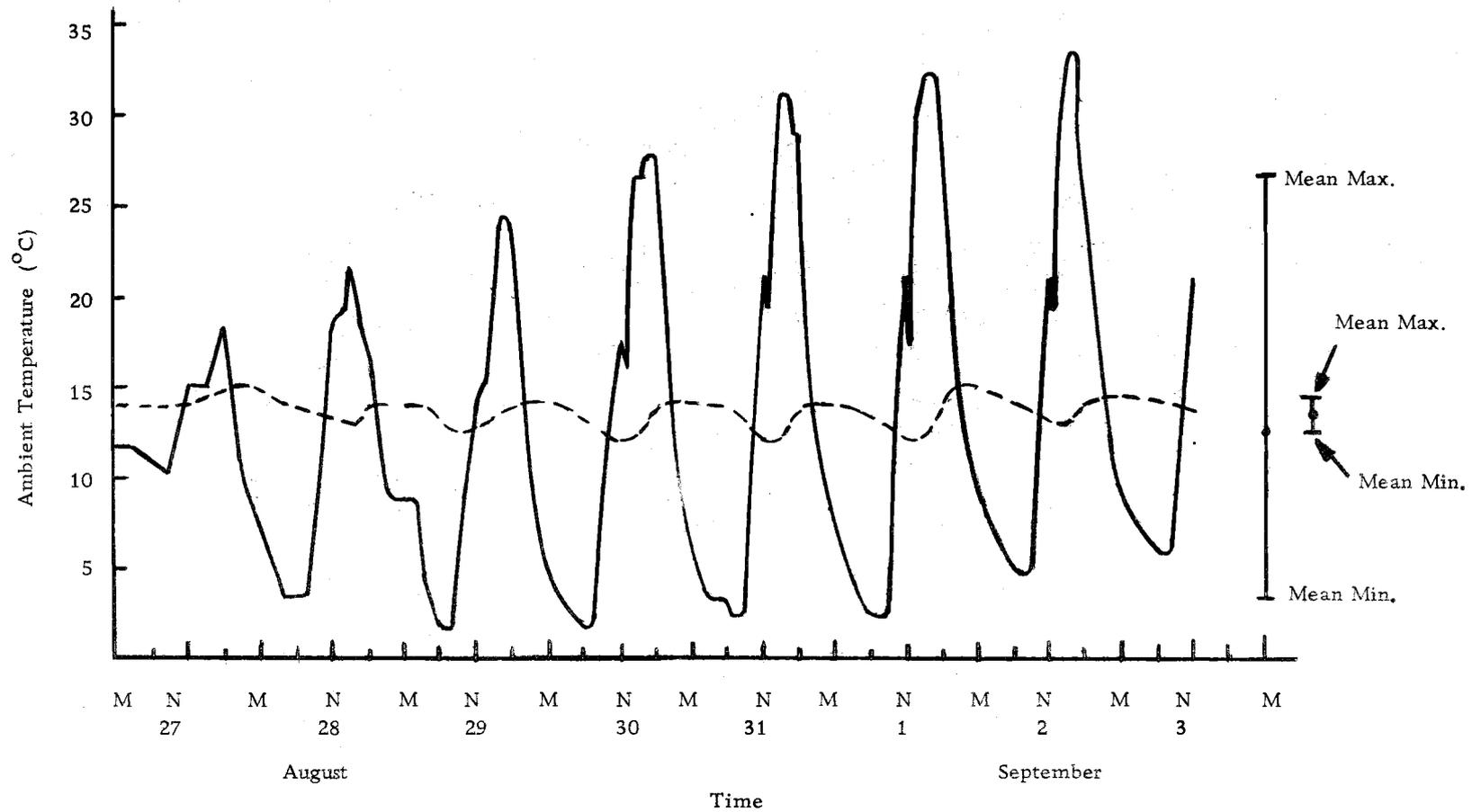


Figure 10. The relationship between the air and burrow temperatures at Site III during a week in the summer of 1966. The air temperature is represented by the solid line (—). The burrow temperature is shown by the dashed line (- -). The mean maximum and minimum temperatures are given to the right of the figure.

It should be noted that the daily peak burrow temperature lags about five to six hours behind the peak air temperature (7 to 10 p. m. versus 2 to 5 p. m.). This lag is also apparent in the daily minimum temperatures (air low, 6 to 9 a. m.; and burrow low, 11 a. m. to 2 p. m.). The burrow temperatures show very little daily variation (3°C maximum) even though the air temperature had a fluctuation of over 30°C .

Site I (North-facing Covered Slope)

Table 4 and Figure 11 summarize the temperature records at this site.

Air Temperature

The months of August were the warmest periods at this site with a daily mean of 14.7°C in 1965 and 16.6°C in 1966. The four warmest months were August, July, September, and June. August, 1965, was the only month having temperatures in excess of 25°C . Each of the four warmest months had temperatures in excess of 20°C . The coldest months were from December through March when the daily mean temperature did not exceed 3.8°C . December, the coldest month, had a mean daily temperature of 1.2°C and a minimum of -4.5°C . The range for the year shows a maximum of 27.8°C (August, 1965) and a minimum of -4.5°C (December, 1965); a range

Table 4. Environmental temperatures ($^{\circ}\text{C}$) at Site I (north-facing covered slope).

Month	Monthly Mean		Mean Maximum		Mean Minimum		Maximum		Minimum	
	Air	Burrow	Air	Burrow	Air	Burrow	Air	Burrow	Air	Burrow
Aug	14.7	14.2	18.1	14.5	12.0	13.9	27.8	16.0	8.5	12.0
Sep	11.5	12.0	14.0	12.2	9.4	11.6	20.0	13.5	3.9	10.0
Oct	10.8	10.9	12.0	11.1	9.4	10.6	17.5	12.8	2.8	9.0
Nov	5.8	--	6.8	--	5.0	--	11.1	10.5	-0.5	4.5
Dec	1.2	--	2.2	--	-0.5	--	9.4	5.0	-4.5	-5.0
Jan	2.8	3.1	4.1	3.4	1.9	2.8	6.1	5.5	-2.2	1.0
Feb	3.0	2.9	4.8	3.2	1.1	2.6	7.8	5.0	0.6	1.0
Mar	3.8	3.6	5.4	4.1	2.4	3.1	13.9	9.0	0.0	0.0
Apr	7.4	7.3	11.1	7.8	4.3	6.5	16.7	9.0	1.1	4.5
May	9.9	9.6	13.1	10.2	7.7	9.1	19.4	14.0	4.5	6.5
Jun	11.4	11.4	14.4	11.8	8.9	10.9	23.3	15.5	5.0	6.0
Jul	14.1	12.9	17.4	13.4	11.9	12.6	23.9	15.0	8.3	11.5
Aug (1-20)	16.6	--	20.4	--	14.1	--	23.9	14.5	11.1	10.6

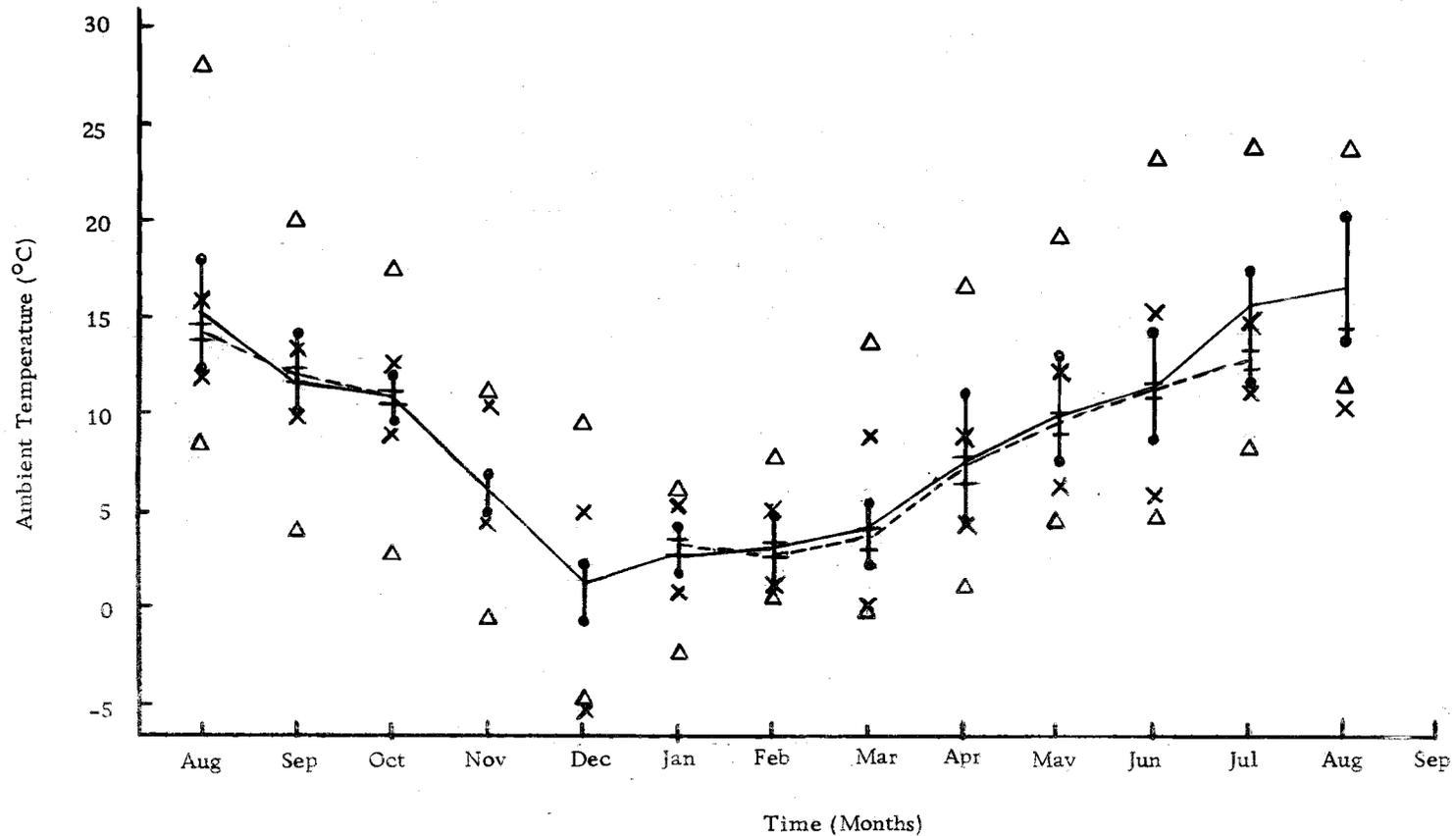


Figure 11. The annual temperatures recorded at Site I (North-facing covered slope). The mean air temperature is represented by the solid horizontal line (—). The mean maximum and minimum air temperatures are indicated by the solid circles on the vertical lines (●—●). The extreme air temperatures for each month are shown by the triangles (Δ). The mean burrow temperature is represented by the horizontal dashed line (---). The mean maximum and minimum burrow temperatures are indicated by the horizontal lines on the vertical lines (|—|). The extreme burrow temperatures for each month are shown by the X's.

of 32.3 °C.

Burrow Temperature

Burrow temperature at this site was almost identical to the air temperature in regards to daily mean, although it did fall about 2 °C below it during July and August, 1966. The warmest month was August, 1965, with a daily mean of 14.2 °C and a maximum of 16.0 °C. The coldest period was from December through March when the daily mean did not exceed 3.6 °C. December, the coldest month, had a minimum of -5.0 °C. From March through August the burrow showed a warming trend which closely followed that of the air. The greatest extreme temperature changes occurred in June with a maximum temperature fluctuation of 9.5 °C (15.5 ° to 6.0 °C). During this month, the air temperature showed maximum fluctuations of 18.3 °C (23.3 ° to 5.0 °C). During the same time period, the air temperature at Site II has a 28.3 °C fluctuation (32.2 ° to 3.9 °C) and the burrow a 12.2 °C variation (19.3 ° to 6.1 °C). The range for the year of 21 °C shows a maximum of 16.0 °C in August, 1965, and a minimum of -5.0 °C in December of 1965.

Site II (North-facing Open Slope)

Temperature records are summarized in Table 5 and Figure 12.

Table 5. Environmental temperatures (°C) at Site II (north-facing open slope).

Month	Monthly Mean		Mean Maximum		Mean Minimum		Maximum		Minimum	
	Air	Burrow	Air	Burrow	Air	Burrow	Air	Burrow	Air	Burrow
Aug	16.6	--	20.4	--	14.5	--	33.3	--	7.2	--
Sep	14.8	10.0	15.6	11.3	12.1	9.0	24.5	14.0	8.3	4.5
Oct	10.7	8.3	13.4	8.5	8.7	7.9	17.8	10.6	3.3	7.2
Nov	6.7	8.4	8.3	8.7	5.1	8.3	14.0	9.4	0.0	7.2
Dec	0.5	2.0	1.2	2.4	-0.1	1.7	6.0	8.0	-5.0	-1.7
Jan	--	2.9	--	3.3	--	2.6	6.7	5.6	0.6	0.0
Feb	3.8	3.2	4.8	3.5	2.8	2.9	7.8	5.0	0.0	1.1
Mar	5.3	3.2	7.0	3.8	3.8	2.6	17.2	7.8	1.1	0.0
Apr	10.5	6.2	13.8	7.4	5.5	5.1	20.6	9.4	2.2	2.8
May	--	9.8	--	11.6	--	8.7	27.2	16.1	2.2	6.1
Jun	14.0	10.6	22.9	12.2	9.5	9.2	32.2	18.3	3.9	6.1
Jul	15.3	12.6	22.1	13.5	11.5	10.1	28.3	17.8	0.5	7.8
Aug	17.0	13.4	25.0	15.5	13.4	11.8	29.4	20.0	11.7	8.9

(1-20)

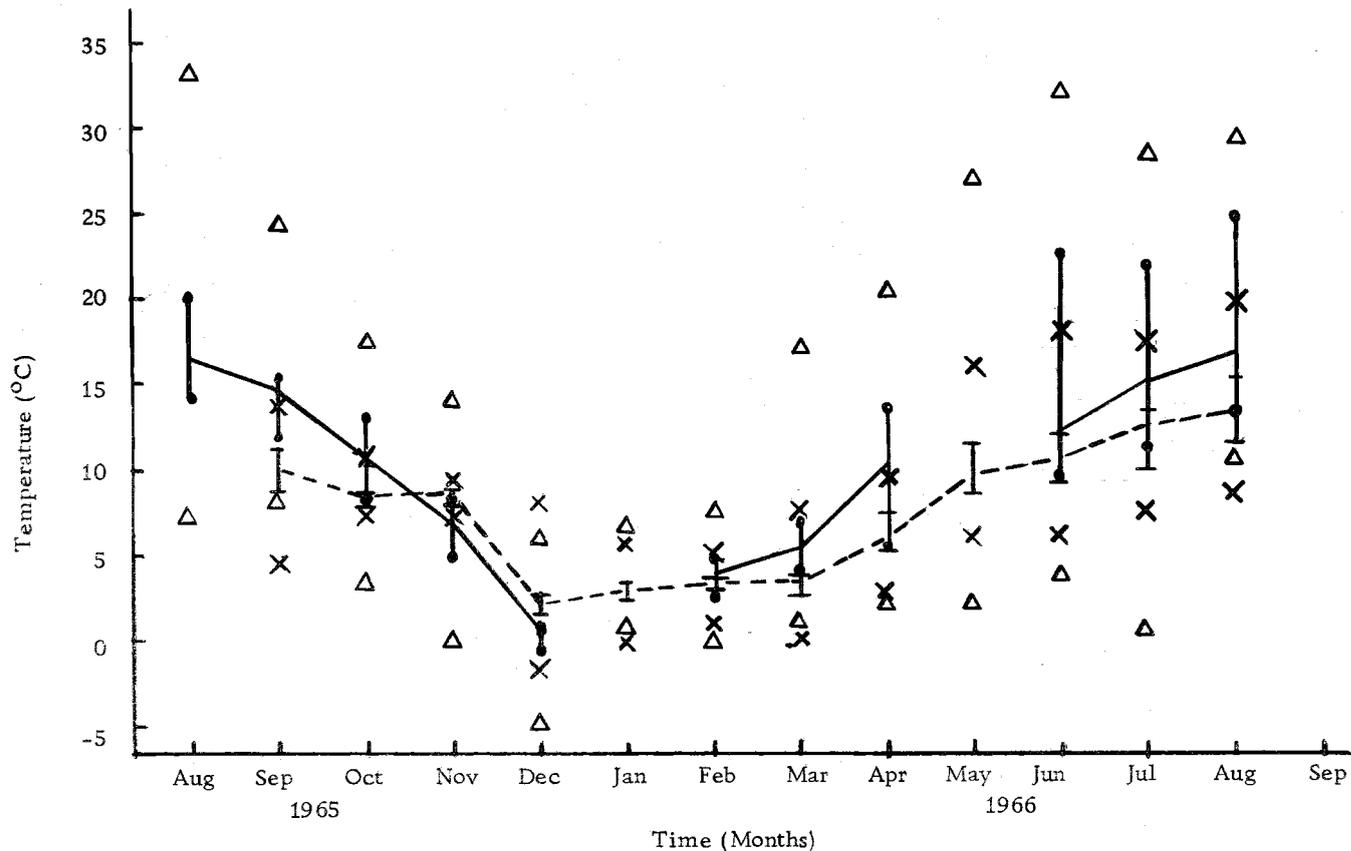


Figure 12. The annual temperatures recorded at Site II (North-facing open slope). The mean air temperature is represented by the solid horizontal line (—). The mean maximum and minimum air temperatures are indicated by the solid circles on the vertical lines (●—●). The extreme air temperatures for each month are shown by the triangles (Δ). The mean burrow temperature is represented by the horizontal dashed line (---). The mean maximum and minimum burrow temperatures are indicated by the horizontal lines on the vertical lines (|—|). The extreme burrow temperatures for each month are shown by the X's.

Air Temperature

The month of August was the warmest period during the study with a daily mean of 16.6°C in 1965 and of 17.0°C in 1966. The four warmest months, in order, were August, July, September, and June. Temperatures exceeding 25°C were recorded in May, June, July, and August. June, 1966, and August, 1965, were the only months to have temperatures above 30°C . The coldest four months were December, January, February, and March. December, the coldest month, had a daily mean temperature of 0.5°C and a minimum of -5.0°C . The range for the year shows a maximum of 33.3°C (August, 1965) and a minimum of -5.0°C (December, 1965); a range of 38.3°C .

Burrow Temperature

Burrow temperature follows that of the air with the warmest months being May through August with August the warmest with a daily mean of 13.4°C and a maximum of 20.0°C . The coldest period was December through March when the daily mean never exceeded 3.2°C . December, the coldest, had a daily mean of 2.0°C and a minimum temperature of -1.7°C . From October (1965) through March (1966) the mean daily burrow temperature did not vary more than 2.5°C from that of the air. In November and December the daily mean burrow temperature was actually higher than that of the air.

This was probably due to the slower rate of cooling of the ground than that of the air. During the spring and summer months, the burrow shows a progressive warming trend, going from a daily mean of 3.2°C in March to 13.4°C in August. This trend follows the air temperature but lags behind it. This lag can again be explained by the difference in thermal properties of air and soil. The range for the year shows a maximum of 20.0°C (August, 1966) and a minimum of -1.7°C (December, 1966). This is a range of 21.7°C .

Site III (South-facing Open Slope)

Table 6 and Figure 13 summarize the data collected at this site.

Air Temperature

Due to a limitation of temperature recorders, this site was not sampled until January, 1966. From January to August, 1966, the warmest month was June, which had a daily mean of 15.5°C and a maximum of 36.1°C . The four warmest months were June, July, August, and May (no data was collected for the month of September). January and March were coldest with minimum temperatures of -4.4°C . February and April were also very cold with minimum temperatures not exceeding -2.8°C . The daily mean temperatures showed an increasing trend from March (2.8°C) to June (15.5°C) but declined from June to August (14.1°C). This decline of the daily

Table 6. Environmental temperatures ($^{\circ}\text{C}$) at Site III (south-facing open slope).

Month	Monthly Mean		Mean Maximum		Mean Minimum		Maximum		Minimum	
	Air	Burrow	Air	Burrow	Air	Burrow	Air	Burrow	Air	Burrow
Jan	--	--	--	--	--	--	7.2	8.3	-4.4	0.0
Feb	--	--	--	--	--	--	13.3	6.7	-2.8	0.0
Mar	2.8	--	7.5	--	0.9	--	21.7	8.9	-4.4	-2.8
Apr	6.9	--	14.0	--	1.0	--	26.1	13.3	-3.3	2.8
May	12.1	--	23.1	--	5.8	--	32.2	13.3	1.7	3.3
Jun	15.5	--	28.1	--	6.9	--	36.1	14.5	2.8	10.0
Jul	15.0	--	26.8	--	7.2	--	34.0	15.0	2.2	8.0
Aug	14.1	13.2	29.3	14.1	6.1	12.4	36.1	15.5	1.7	10.5

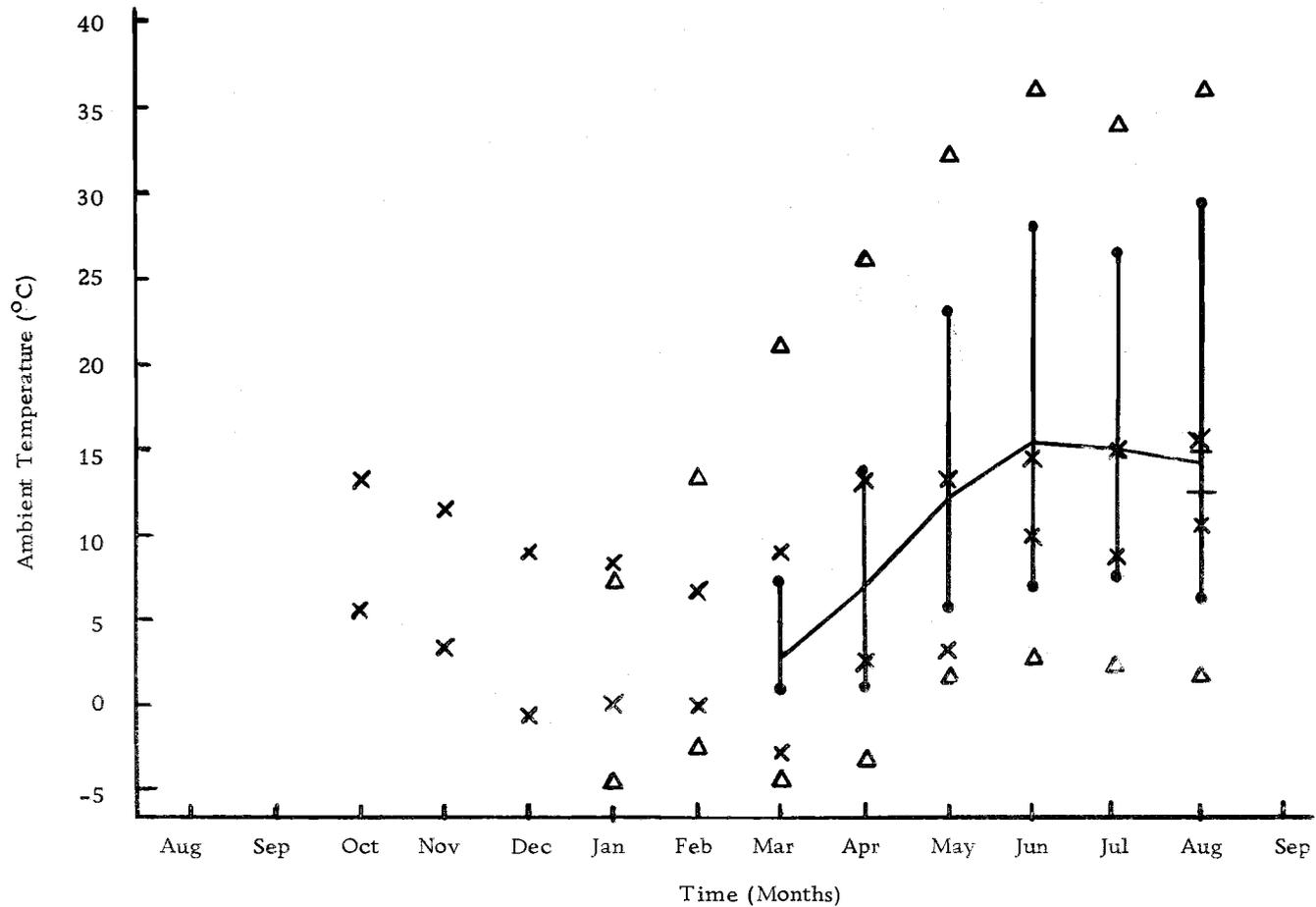


Figure 13. The annual temperatures recorded at Site III (South-facing open slope). The mean air temperature is represented by the solid horizontal line (—). The mean maximum and minimum air temperatures are indicated by the solid circles on the vertical lines (●—●). The extreme air temperatures for each month are shown by the triangles (Δ). The mean burrow temperature is represented by the horizontal dashed line (---). The mean maximum and minimum burrow temperatures are indicated by the horizontal lines on the vertical lines (|—|). The extreme burrow temperatures for each month are shown by the X's.

mean is a little misleading, since it reflects the lowering of night temperatures not seen at the other sites. These lowered night temperatures were probably caused by cool air flowing off Marys Peak and down the stream bed by which Site III was located. The other two sites were separated from Site III by a hill which would have blocked the flow of cold air.

April through August had temperatures exceeding 25°C , and May through August had temperatures above 30°C . A high temperature of 36.1°C was recorded in both June and August. The greatest monthly temperature variation, 34.4°C (36.1° to 1.7°C) occurred in August. The range of 40.5°C for the year shows a maximum of 36.1°C in August and June, 1966, and a minimum of -4.4°C in January and March, 1966.

Burrow Temperature

In lieu of a recording thermograph the temperature here was recorded with a maximum and minimum thermometer (except for the month of August, 1966). Based on weekly and bi-monthly measurements, the warmest month was August, 1966, which showed a maximum of 15.5°C and a minimum of 10.5°C . Six months showed a maximum temperature over 13.3°C . These were October, 1965, and April through August of 1966. Only two months, July and August, had maximum temperatures over 15°C . The greatest

temperature variation, 11.7°C , occurred in March. The three coldest months were January through March when the maximum burrow temperature did not exceed 8.9°C and the minimum temperatures were below 0°C . March had the lowest recorded temperature of a -2.8°C . The greatest annual variation of burrow temperature was 18.3°C (August high of 15.5°C and March low with -2.8°C).

Body Temperature

The body temperature data, T_B , are summarized in Table 7. These were obtained using abdominally implanted thermal transmitters in unrestrained animals while they carried out their normal activities in either the outdoor enclosures or the metabolic cages in the laboratory. The ambient temperatures, T_A , at which these animals were exposed during the T_B determination are also given. It should be noted that these temperatures were simply a measurement of the T_A at the time of the determination and do not signify any specific exposure time to any given temperature.

It can be seen from Table 7 that the mean T_B for the seven subjects was $38.0 \pm 0.10^{\circ}\text{C}$ for animals exposed to a range in T_A 's from 9.7° to 30.8°C , with a mean T_A of 21.6°C . A T_B of 38.0°C is well within the normal range for a normal homeothermic mammal (Prosser and Brown, 1961).

Figure 14 represents the T_B values of animals exposed to

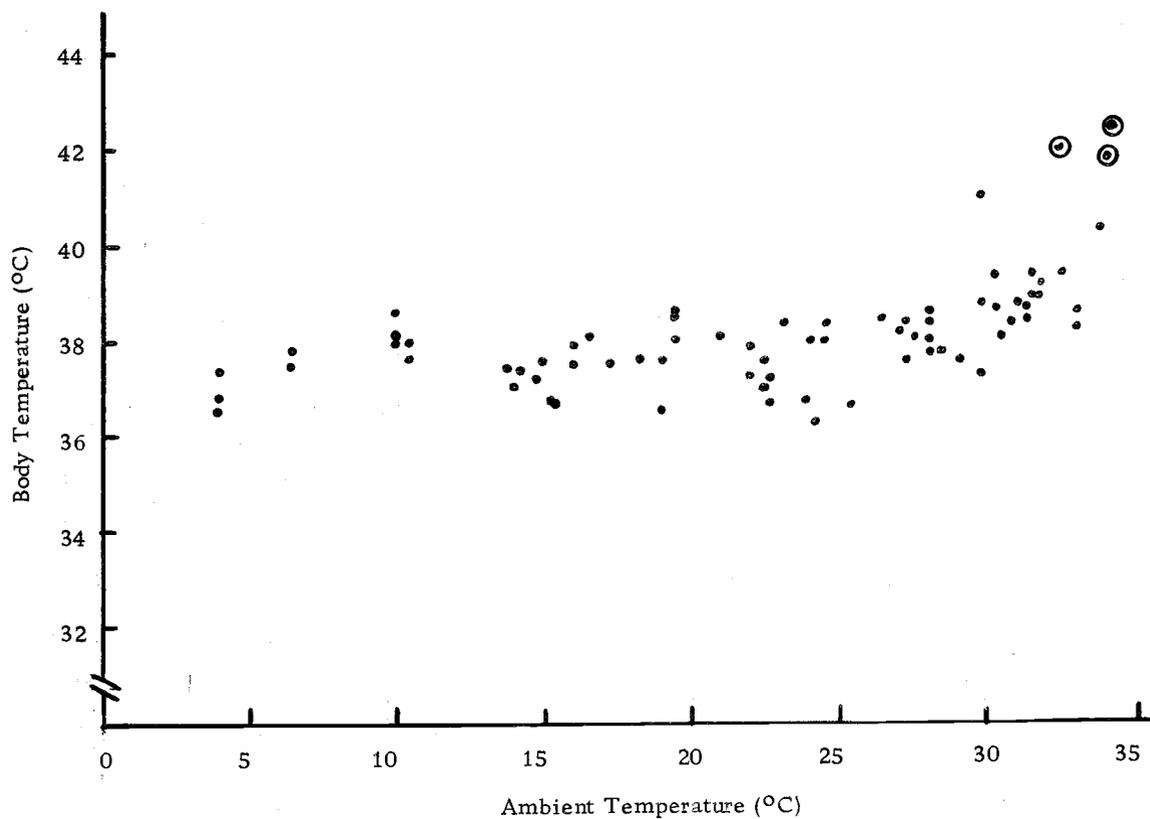
Table 7. Body temperatures of seven free-living animals as determined by telemetry.

Animal Number	Sex	Age Class*	Mean Weight ± S. E.	Mean Body Temperature ± S. E.	Range of Body Temperature	Mean Ambient Temperature	Range of Ambient Temperature***
16	female	4-5 yr	704 ± 3.9	37.8 ± 0.05 (72)**	36.5-38.6	22.4	19.0-25.5
17	male	3-4 yr	845 ± 10.2	38.2 ± 0.13 (22)	36.6-39.0	22.6	21.0-25.5
18	female	3-4 yr	645 ± 21.0	37.6 ± 0.07 (41)	36.7-38.6	21.7	12.5-30.8
19	male	over 6 yr	999 ± 10.8	38.3 ± 0.08 (15)	38.0-38.6	22.1	19.0-25.0
20	female	4 yr	676 ± 11.0	37.8 ± 0.07 (48)	36.2-38.7	21.3	9.7-30.8
21	female	2 yr	556 ± 4.5	38.1 ± 0.22 (15)	37.3-38.7	21.8	19.4-23.9
22	female	over 6 yr	775 ± 19.2	38.1 ± 0.09 (10)	37.7-38.6	19.6	9.7-30.3

*Age classes based on body weight (Voth, 1968, p. 41).

**Number of determinations for each body temperature given in parenthesis.

***The range of ambient temperatures at which the body temperatures were measured.



various T_A 's for at least a two hour period. This graph represents 70 determinations of T_B on animals confined in an animal chamber (see above). The animals started to become hyperthermic above a T_A of 30°C , and heat deaths appeared between ambient temperatures of 32°C and 35°C . When compared with other mammals, this is a low upper lethal temperature range (Folk, 1966). At the lowest T_A of 4°C a slight drop of T_B was seen, but the values are still within the range observed at much higher T_A 's. The mean T_B of the animals at T_A 's below 29°C was $37.6^\circ\text{C} \pm$ standard error of 0.4°C .

Metabolic Rate

The results of the winter experiments on metabolic rate are shown in Figure 15. The lower critical temperature, T_C , lies between 18°C and 19°C . If 19°C is taken as the lower T_C , the line fitted to all the points below this value by the method of least squares gives the equation:

$$\text{MR} = 150.04 - 4.05 T_A \quad (2)$$

(Standard error of estimate = 0.31, N = 7)

This line intercepts the abscissa at an ambient temperature of 37.2°C . At 19°C the mean metabolic rate of Aplodontia was 76.2 ± 1.8 cal/g/day.

According to the equation of Kleiber (1961):

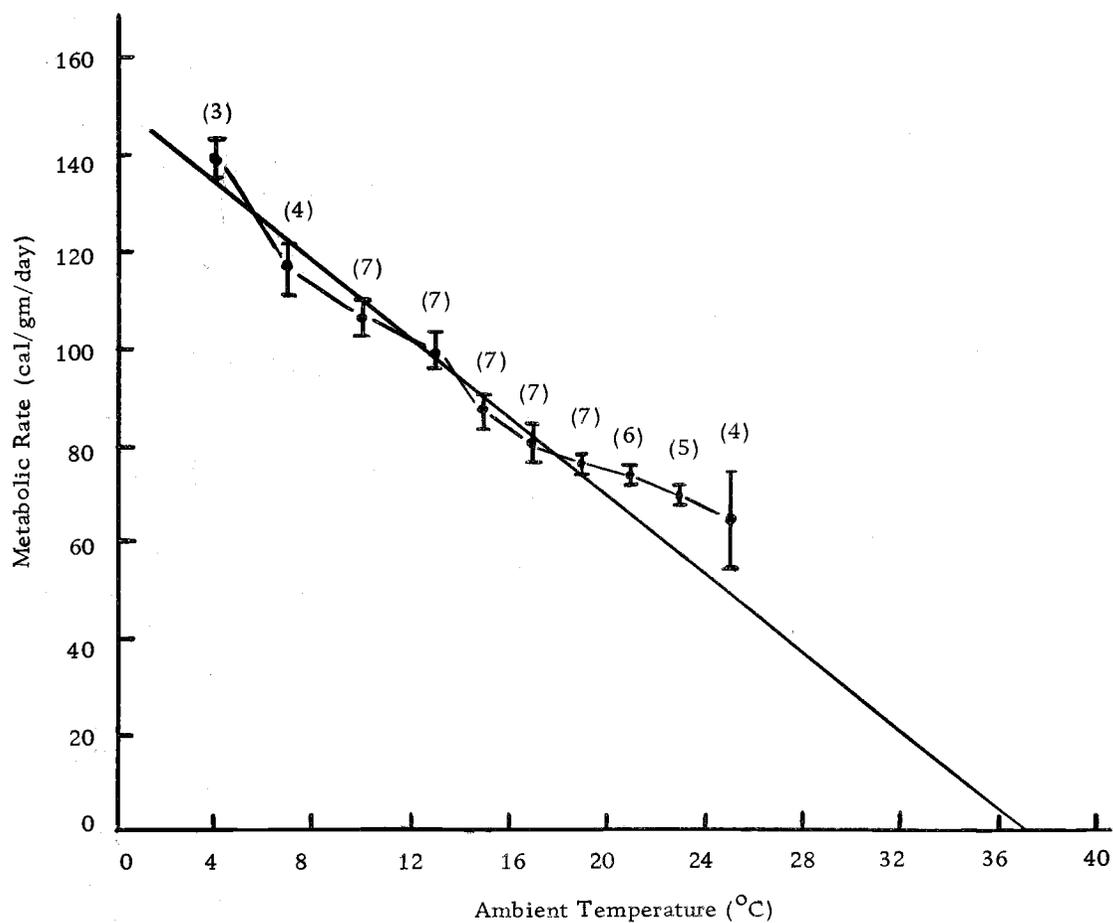


Figure 15. The winter metabolic rate of Aplodontia as a function of ambient temperature. The vertical bars represent \pm one standard error of the mean and the number of determinations for each point are given in parenthesis. The linear regression line is based on the values made at 19°C and below. The mean body weight of the animals was 682 g.

$$\text{MR (Kcal/animal/day)} = 70 W^{0.75} \text{ (weight in Kg)} \quad (3)$$

The basal rate of a 682 g mammal should be 52.5 Kcal/day or 77 cal/g/day. The experimental value at 19° C is therefore within one percent of the predicted figure. At 25° C the experimental value was 64.3 ± 9.8 cal/g/day which is 83.5 percent of the predicted value for a 682 g mammal.

Figure 16 shows the results of the summer metabolic rate determinations based on oxygen consumption and carbon dioxide production with the estimated R.Q. of 0.965. The data from oxygen and carbon dioxide experiments were pooled because the most divergent mean values were not statistically different even at the ten percent level of confidence ($15^\circ \text{C} = 1.16$, $n = 7$). The lower T_C of the summer animals appears to be between 22 and 23.0° C. The line fitted to all the data below 23° C by the method of least squares yields the equation:

$$\text{MR} = 182.46 - 5.14 T_A \quad (4)$$

(Standard error of estimate = 0.25, $N = 5$)

The predicted basal metabolic rate for a mammal weighing 743 g, according to Kleiber's equation, is 56.3 Kcal/day or 75.8 cal/g/hr. A summer Aplodontia had a metabolic rate of 65.7 ± 3.7 cal/g/hr. at 23° C which represents a value of 86.7 percent of the predicted value. At 32° C the mean resting value for the mountain beaver was

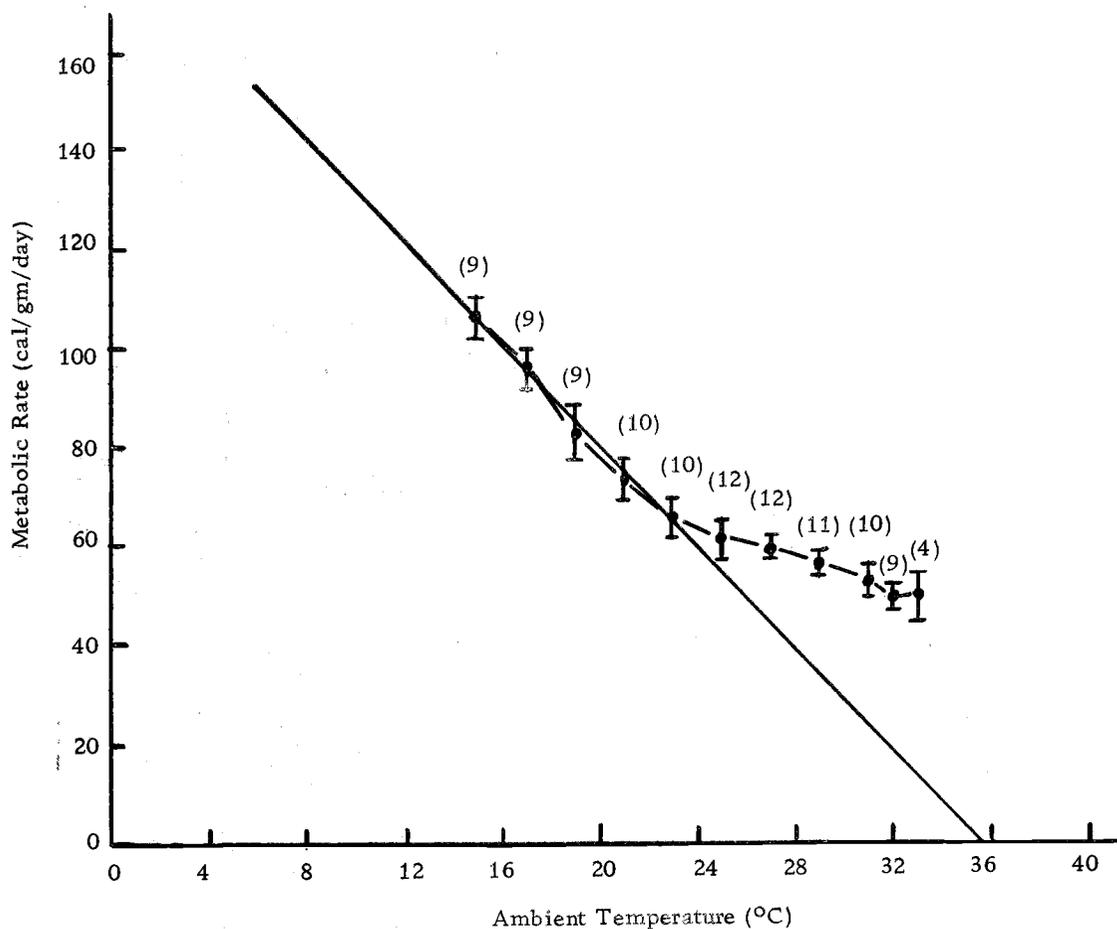


Figure 16. The summer metabolic rate of Aplodontia as a function of ambient temperature. The rates were determined by oxygen consumption and carbon dioxide production procedures. The vertical bars represent \pm one standard error of the mean and the number of determinations for each point are given in parenthesis. The linear regression line is based on the values made at 23°C and below. The mean body weight of the animals was 743 g.

49.2 ± 2.4 cal/g/hr or a value of 65.0 percent of the predicted figure.

Thermal Conductance

Conductance is a measurement of the transfer of heat from an animal to its environment. The reciprocal of conductance is insulation. Conductance is usually expressed in the amount of heat transfer (calories) per surface area (cm^2) per time interval (hour) per degree of temperature difference ($^{\circ}\text{C}$) between the animal and its environment. The amount of heat transferred is determined by the metabolic rate of the animal and any change in its body temperature.

If the animal's T_B increases, the amount of heat necessary to produce that increase must be subtracted from the total amount of heat produced by that animal in order to determine the true amount of heat that the animal is losing. If the animal's T_B decreases, then this heat loss must be added to its total metabolic heat production. In order to calculate the amount of heat gained or lost by a change in body temperature, the specific heat of the animal tissue must be known. The specific heat of a mammal's body has been determined by Hart (1951) to be 0.83. Therefore, the amount of heat gained or lost due to a change in body temperature is described by the following equation:

$$\text{Heat gained or lost (Kcal)} = \text{Mass (Kg)} \times \text{Specific heat (0.83)} \times \text{change in } T_B (^{\circ}\text{C}) \quad (5)$$

The surface area of an animal is very difficult to determine. This is especially true of the effective heat transfer surface area, since animals can modify surface area in thermal regulation. Usually the surface area is estimated using Meeh's equation:

$$S(\text{cm}^2) = 10W^{2/3} \text{ (weight in g)} \quad (6)$$

Surface area of the mountain beaver was not measured. Conductance in this paper will be expressed on the basis of body weight and not on surface area. Meeh's equation was not used because it has not been established that this equation describes the weight-to-surface area relationship of the mountain beaver's body.

Figure 17 represents the conductance values determined in the oxygen consumption and carbon dioxide summer experiments. The data were pooled because the results in these experiments were not significantly different. The values were based on the lowest metabolic rate determination at each T_A and were corrected for any change in T_B , as previously described.

The conductance below 21°C remains constant at $0.195 \text{ cal/g/hr}/^\circ\text{C}$. Conductance rises in a linear fashion from 21°C to 31°C . Above 31°C it undergoes an abrupt increase to a value of $.295 \text{ cal/g/hr}/^\circ\text{C}$ at 32°C . At 33.2°C the mean conductance, based on three animals, was $0.355 \text{ cal/g/hr}/^\circ\text{C}$. This represents a mean increase in conductance of 84 percent of basal at 18°C . All of the animals

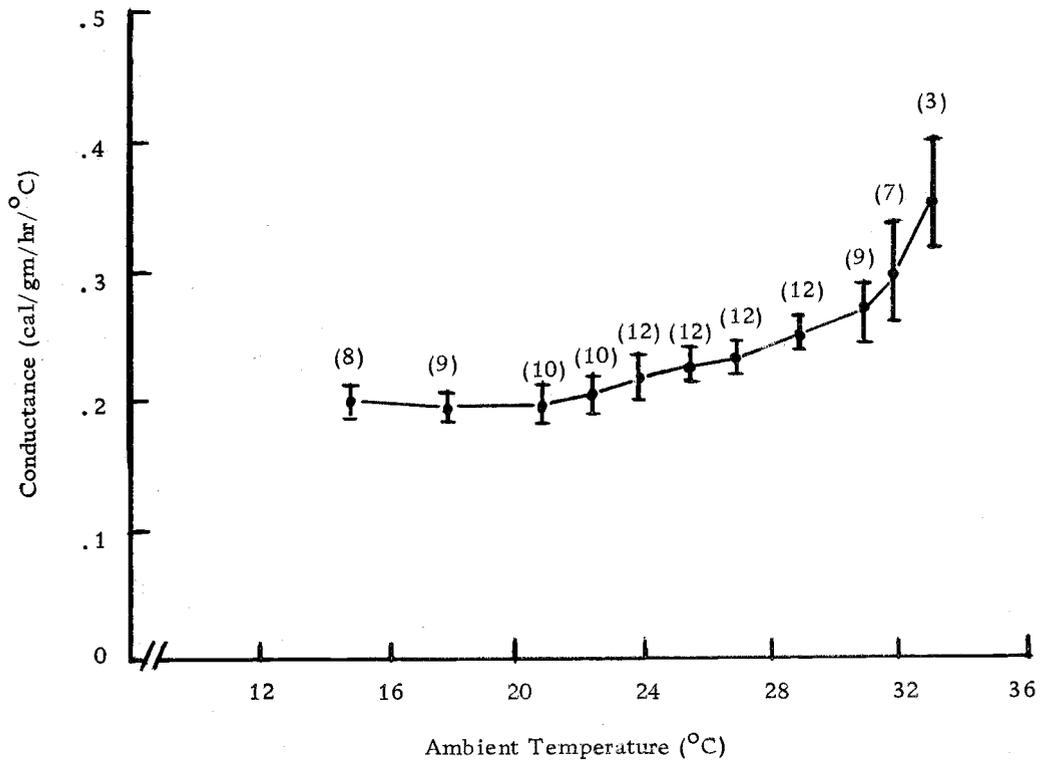


Figure 17. The thermal conductance of *Aplo dontia* as a function of ambient temperature. Measurements were made on summer animals. The vertical bars represent \pm one standard error of the mean and the number of determinations for each point are given in parenthesis.

became hyperthermic within two hours at T_A above 29°C . At T_A 's above 33°C , the animals rapidly became hyperthermic and active which, in turn, increased their hyperthermia. Deaths due to hyperthermia occurred within two hours at T_A 's between 32.5°C and 35°C when the animal's body temperature reached 42°C .

Metabolic Rate and Conductance Experiment Number 46

Figure 18 illustrates the results of an oxygen consumption experiment using a female mountain beaver (number 16) which weighed 673 g. In 72 determinations of the animal's T_B under free living conditions the mean was $37.8 \pm$ standard error of 0.05°C . Prior to the start of this experiment (at time 0), the animal had a T_B of 37.8°C . At that time the animal was being maintained in a metabolism cage at a T_A of 22.8°C . The animal was then placed in a transfer cage and secured in the respirometer chamber. Its T_B rose slightly to 38.2°C and then fell to 37.7°C within the next 0.27 hours. Following this period, the T_A was raised to 28.0°C . The animal at this point began to struggle violently within the respirometer chamber for the next 0.56 hour. During this time period, the animal's T_B rose in a linear fashion to 41.7°C (rate of 7.15°C/hr). Considering that the specific heat of a mammal's body is 0.83 (Hart, 1951) and that the animal weighed 673 g, this means that the animal was gaining heat at the rate of $0.83 \times 673 \text{ g} \times 7.15^\circ\text{C}$ per hour or 4.0 Kcal/hr.

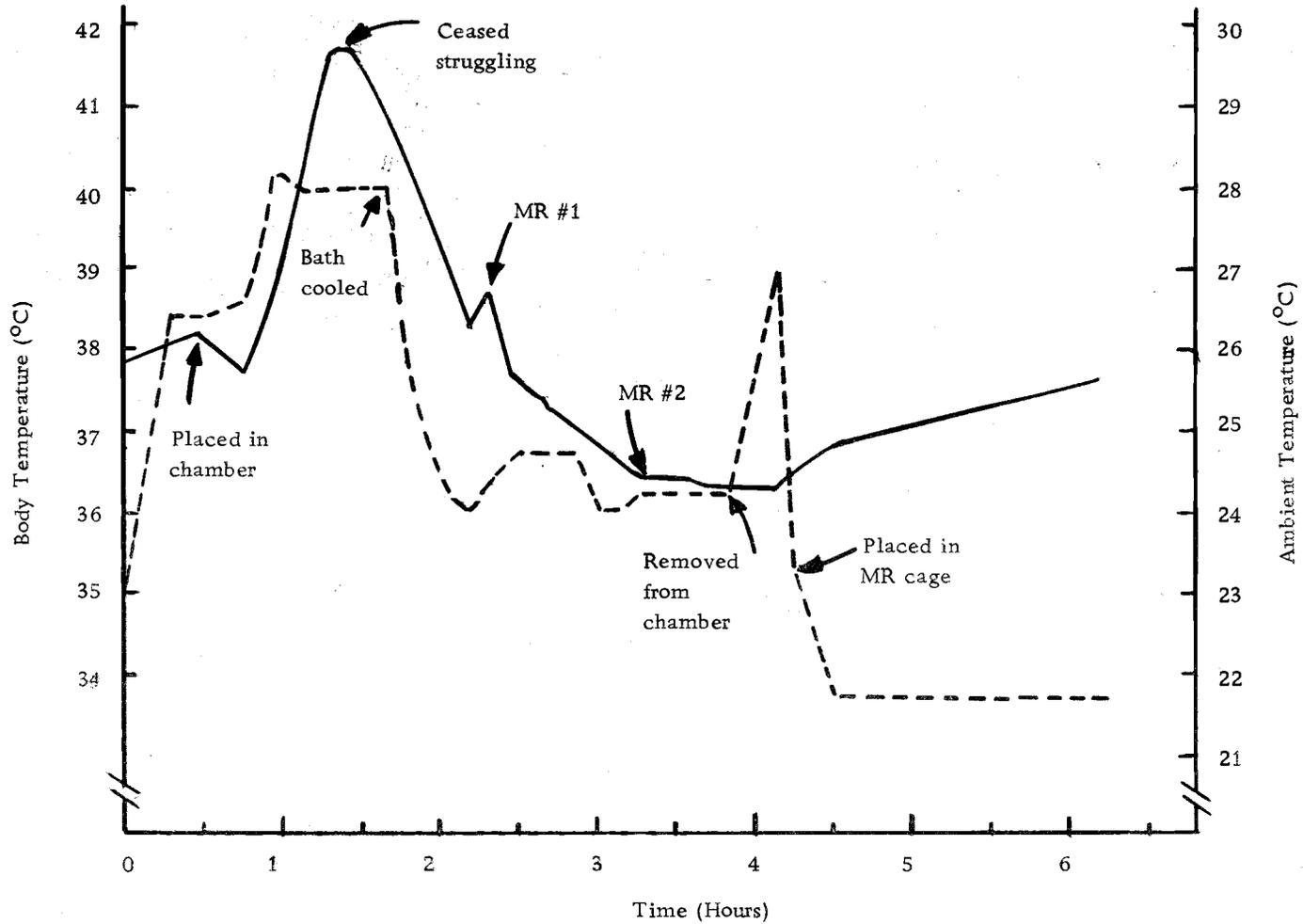


Figure 18. The effect of activity on the body temperature and metabolic rate of animal number 16. Body temperature is represented by the solid horizontal line (—) and ambient temperature by the dashed line (---). MR #1 and MR #2 indicate the beginning of two separate oxygen consumption determinations.

Once the T_B reached 41.7°C , the animal stopped its struggling and became very quiet. During the next 0.80 hours, the animal cooled at a rate of 4.25°C/hr .

One hour after the animal ceased struggling, a metabolic rate determination was made and found to be 37.2 cal/g/day . During this determination, the animal's T_B fell from 38.6 to 37.1°C . The 1.5°C drop in T_B represents a heat loss of 838 calories during the 30-minute metabolic rate determination or 60.0 cal/g/day . Therefore, the total rate of heat loss at this time was 97.2 cal/g/day at an average thermal gradient of 13.1°C for a thermal conductance of $0.310\text{ cal/g/hr}/^\circ\text{C}$.

A second metabolic rate determination was begun 0.66 hours after the completion of the first. During this 30-minute period, the animal's metabolic rate was 44.6 cal/g/day and its conductance was $0.167\text{ cal/g/hr}/^\circ\text{C}$. Its T_B fell 0.1°C , from 36.4 to 36.3°C .

According to Kleiber's metabolic rate equation, a 673 g mammal should have a basal rate of 77.3 cal/g/day . Therefore, the two metabolic rate determinations represent 48.1 percent and 57.8 percent of the predicted value.

Invisible Water Loss

Invisible water loss, as shown in Figure 19 was determined simultaneously with carbon dioxide production. These mean values

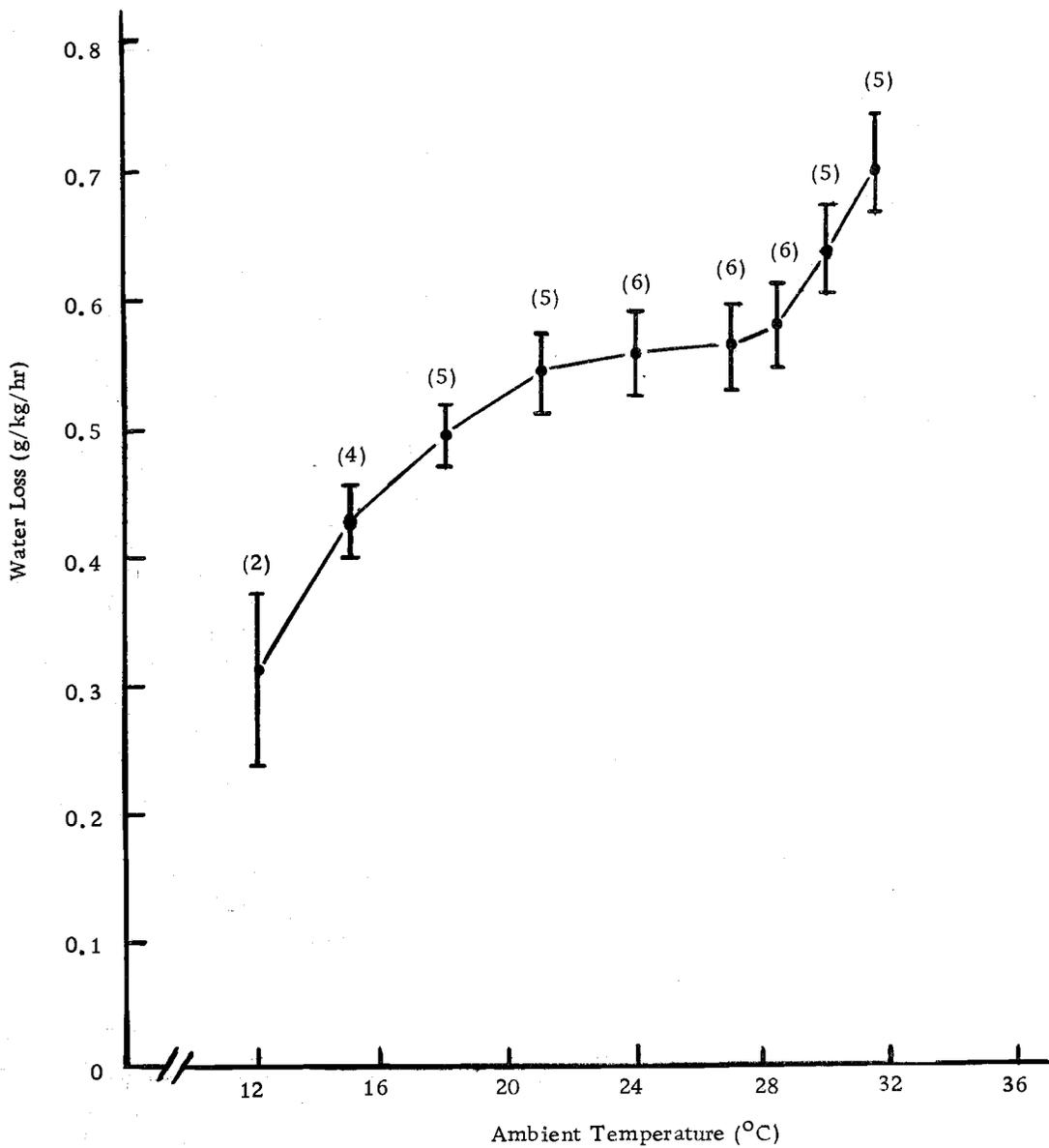


Figure 19. The summer insensible water loss of *Aplo dontia* as a function of ambient temperature. The vertical bars represent \pm one standard error of the mean and the number of determinations for each point are given in parenthesis. The mean body weight of the animals was 700 g.

were based on water loss during the 30-minute period when the animal maintained its lowest metabolic rate as measured by carbon dioxide production.

Chew (1965) gives the following equation to describe the relationship between body weight and insensible water loss at ambient temperatures from 18° to 29° C:

$$\text{Water loss (g/hr)} = 2.58 W^{0.826} \text{ (weight in Kg)} \quad (7)$$

In solving this equation for a mean body weight of 700 grams, the result is 1.922 g/hr or 2.75 g/kg/hr. Water loss values for the mountain beaver at temperatures between 21° C and 28° C were 0.552 g/kg/hr or 0.386 g/hr. This is 20.1 percent of the predicted value based on Chew's equation. Above 28° C the insensible water loss increases abruptly and by 31.5° C has reached a mean value of 0.699 g/kg/hr. Even so, this highest mean represents an increase of only 26.8 percent above that found at 21° C. The highest recorded value was only 0.769 g/kg/hr which is only 39.3 percent above the 21° C value and is 28 percent of that predicted by Chew's equation. Although these values appear quite low, they are within the range of other mammals. For example, a marmot weighing 1.83 kg had a water loss of 0.28 g/kg/hr at 17° C (Benedict and Lee, 1938), a 2.05 kg rabbit has a loss of 0.58 at 20° C and 0.72 g/kg/hr at 25° C (Nagayama, 1932), and a 100.1 g Dipodomys spectabilis has a loss of 0.70 g/kg/hr at 25° C (Schmidt/Nielsens, 1950).

Figure 20 also expresses water loss data but in terms of evaporative heat loss. One g of water is assumed to dissipate 580 calories of heat when evaporated. From 12° C to 28° C there was a linear increase in the percent of total heat lost by evaporation. Evaporative heat loss increased to a high mean value of 21.9 percent \pm 1.3 percent at 31.5° C. In this experiment the highest percentage of heat dissipation was 24.1 percent at 31.5° C. This figure shows a 5.3 increase in evaporative heat loss from 12° C (4.1 percent) to 31.5° C (21.9 percent) with only a 2.3 increase in water loss (Figure 19) over the same range. This apparent discrepancy is due to a 2.5 decrease in heat production.

Respiration

During oxygen and carbon dioxide determinations, the number of breaths per minute was determined by direct observation. At numerous times this was difficult because of the position of the animals with respect to the observation port of the animal chamber. Also, observations were stopped when it appeared that the animals were becoming agitated. The results of these observations can be seen in Figure 21. There was a decrease in the number of breaths per minute progressing from low to high ambient temperatures with an average of 40 (range 36 to 45) breaths per minute at 15° C and 23 breaths per minute at 32° C. The lowest rate observed, beginning

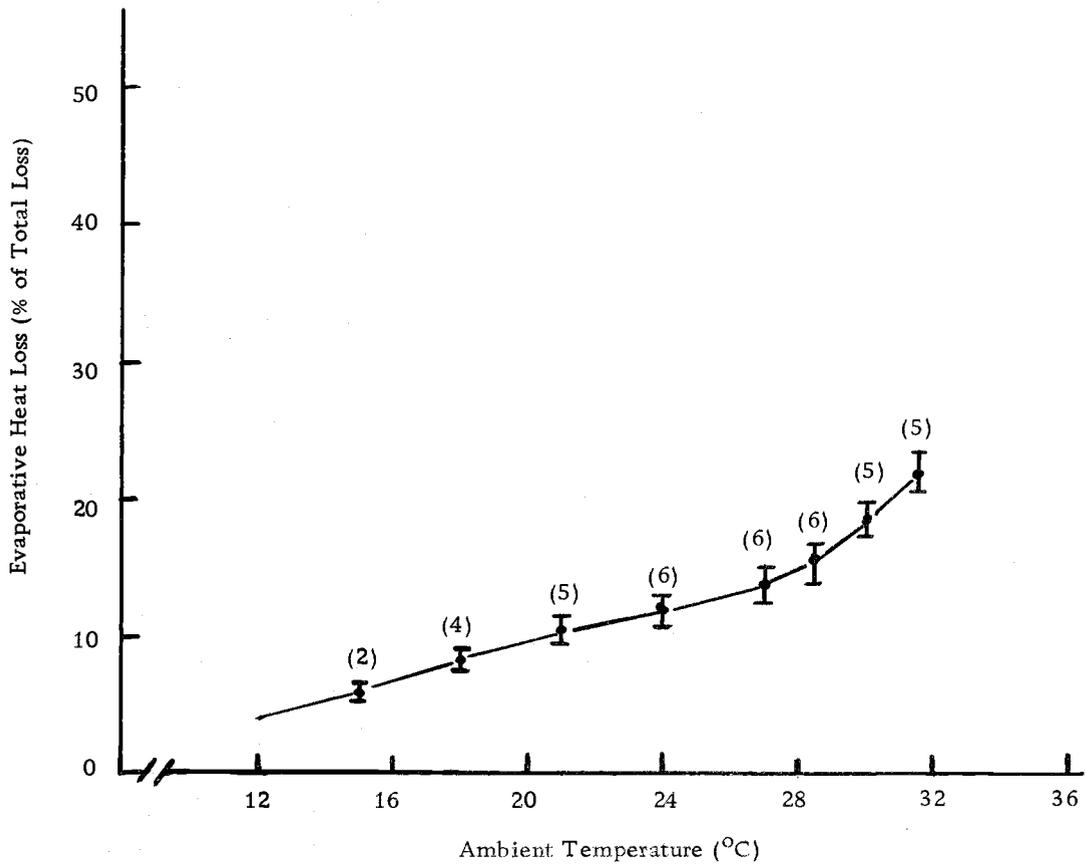


Figure 20. The effect of ambient temperature on evaporative heat loss in Aplodontia. The values are expressed as a percentage of total heat loss. The vertical bars represent \pm one standard error of the mean and the number of determinations for each point are given in parenthesis.

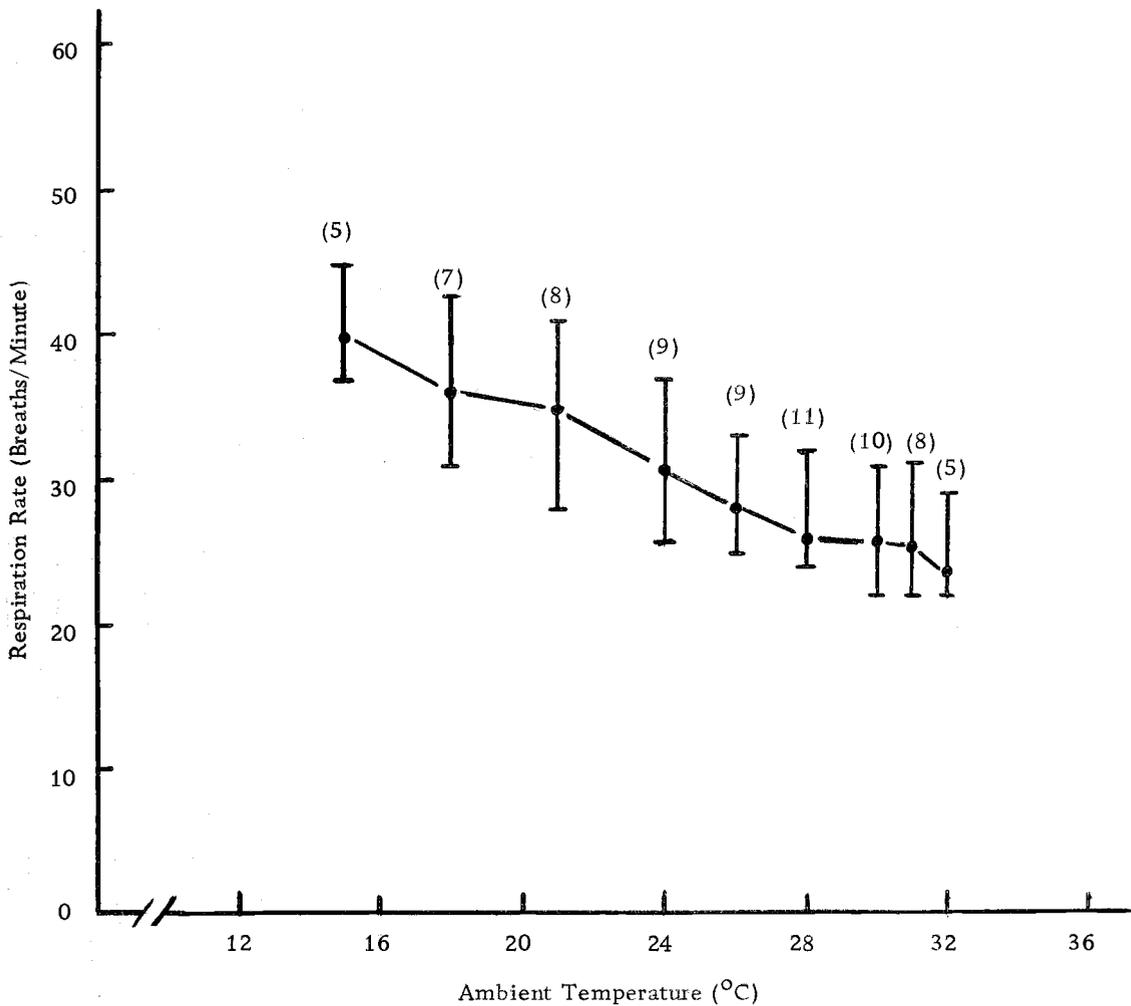


Figure 21. The respiration rate of *Aplodontia* as a function of ambient temperature. Each point represents a mean value of the number of breaths per minute recorded over a 30-minute observation period. The vertical bars represent the range of observations and the number of determinations for each point are given in parenthesis.

at temperatures above 24° C, was 18 breaths a minute and occurred in numerous animals for periods of 30-second duration. Respiration rate varied considerably during each 30-minute observation period and probably reflected normal variation of a confined animal as well as the technique used to measure the rate. Nevertheless, the figure reflects overall changes and especially at high ambient temperatures it indicates unusually low respiration rates for an animal of this size.

Heart Rate

Figures 22, 23, 24, and 25 show the results of the heart rate experiments on animals 16, 20, 21, and 22, respectively. The length of each experiment was determined primarily by the length of time the animal would tolerate the silver clip electrodes on its back. The predicted heart rate cited in the legend of each figure is based on Kleiber's (1961) equation relating heart rate to body size:

$$\text{Heart rate (beats/min.)} = 186 \times \text{weight}^{-0.25} \text{ (weight in kg)} \quad (8)$$

Although the time course and T_A 's varied between animals, some general trends are evident from these figures. The maximum recorded mean heart rates on the animals were quite similar, being, in order: 69 percent, 51 percent, 62 percent, and 51 percent of the predicted value. The mean minimum rates exhibited a similar relationship, being consecutively: 33 percent, 35 percent, 50 percent, and 36 percent of the predicted. Therefore, the mean maximum

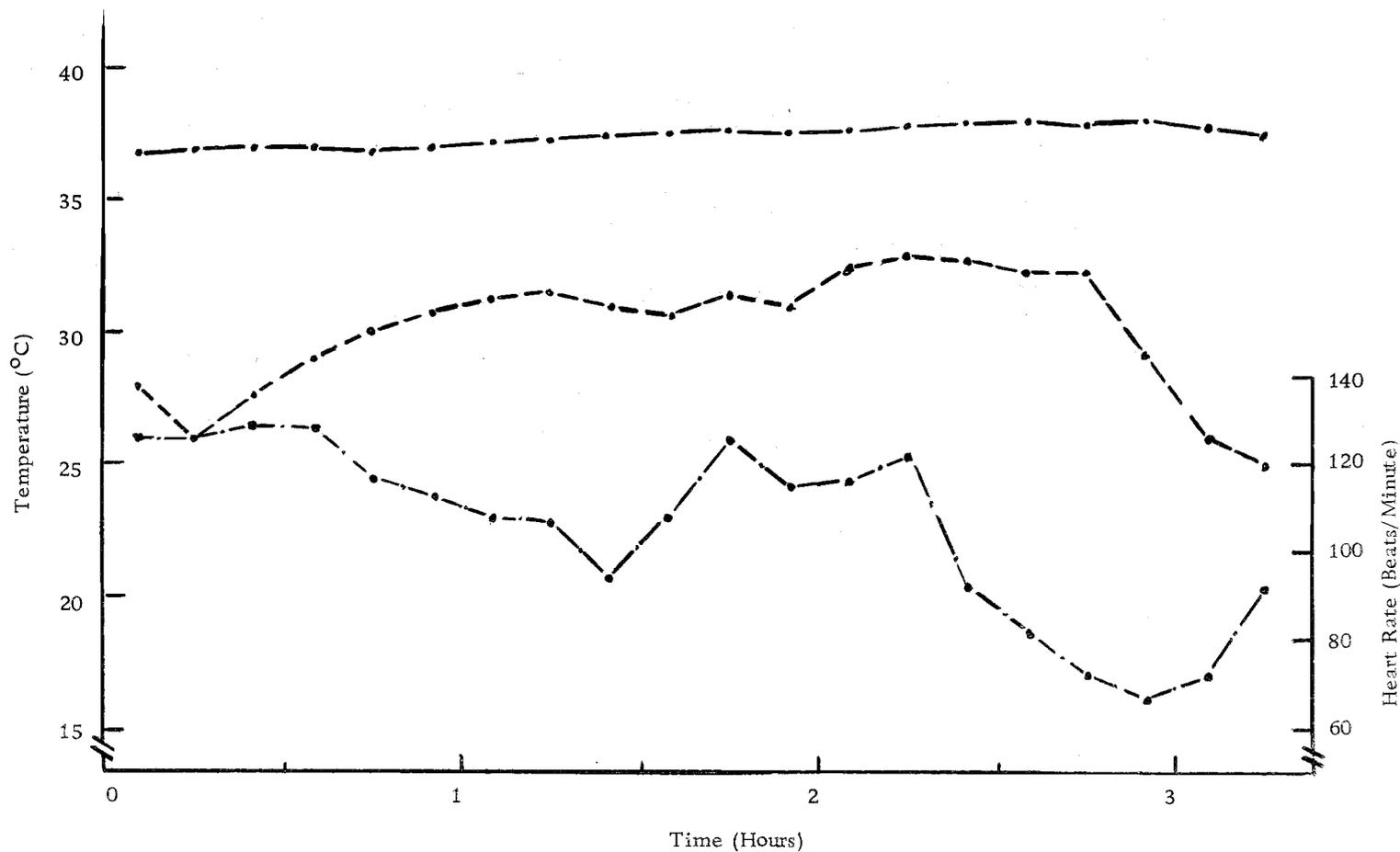


Figure 22. The relationship between heart rate, body temperature, and ambient temperature in animal number 16. Heart rate is indicated by the dashed line broken by a dot (---). Body temperature is represented by solid line (—) and ambient temperature by the dashed line (---). All points represent the mean value for each ten-minute observation period. The predicated heart rate (Kleiber's equation) for this animal was 201 beats per minute.

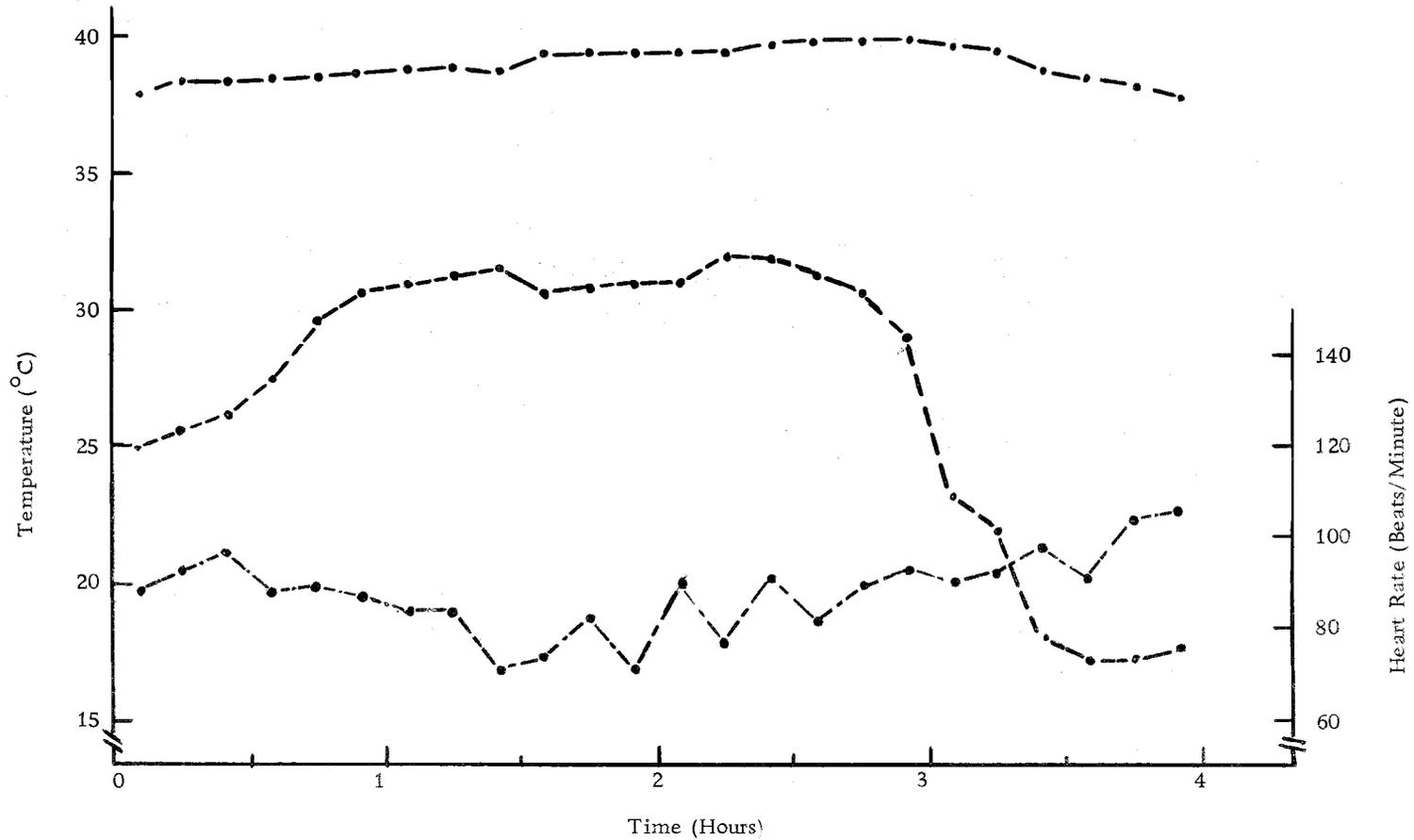


Figure 23. The relationship between heart rate, body temperature, and ambient temperature in animal number 20. Heart rate is indicated by the dashed line broken by a dot (---). Body temperature is represented by the solid line (—) and ambient temperature by the dashed line (---). All points represent the mean value for each ten-minute observation period. The predicated heart rate (Kleiber's equation) for this animal was 205 beats per minute.

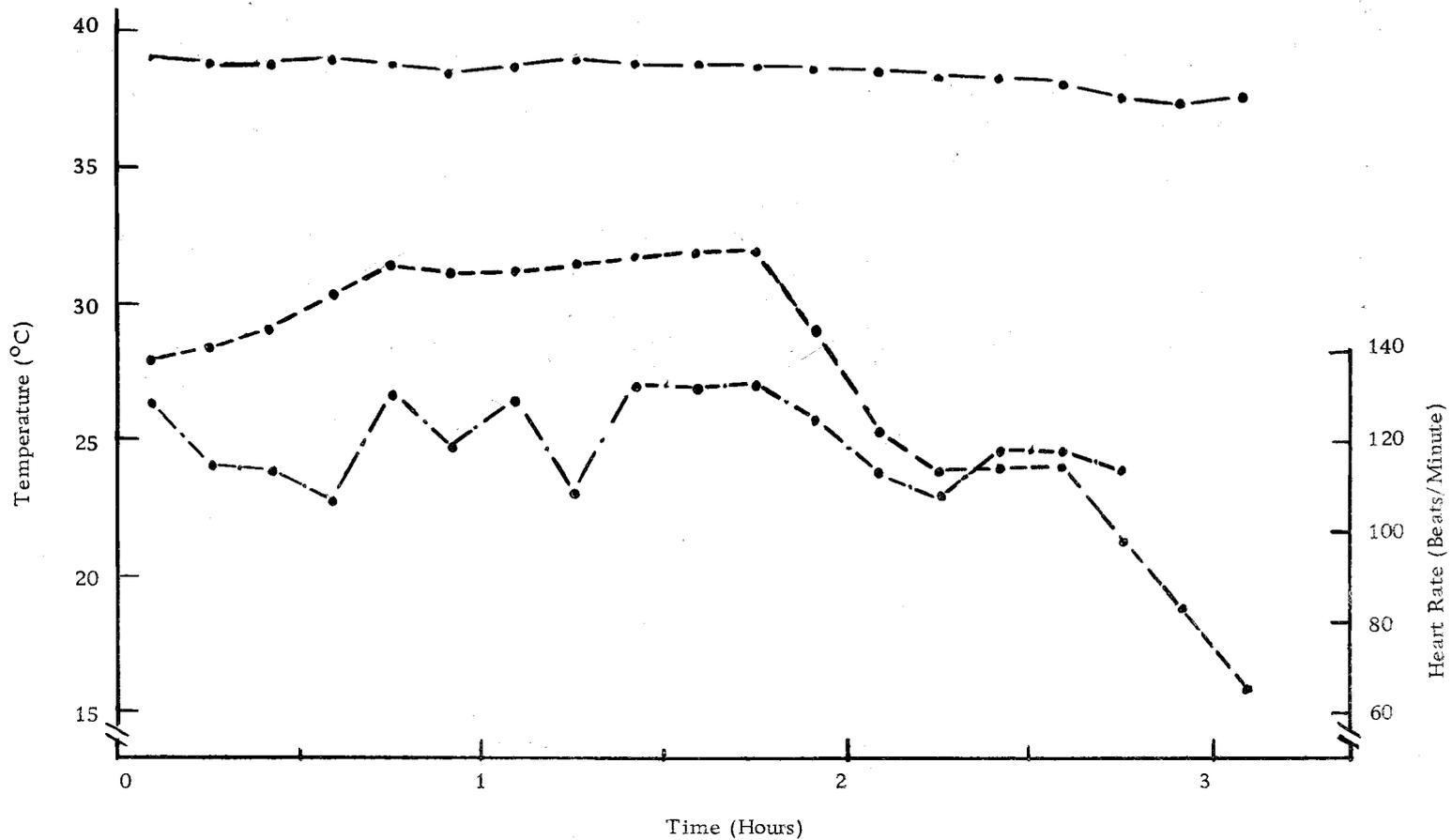


Figure 24. The relationship between heart rate, body temperature, and ambient temperature in animal 21. Heart rate is indicated by the dashed line broken by a dot (—•—). Body temperature is represented by the solid line (—) and ambient temperature by the dashed line (---). All points represent the mean value for each ten-minute observation period. The predicated heart rate (Kleiber's equation) for this animal was 214 beats per minute.

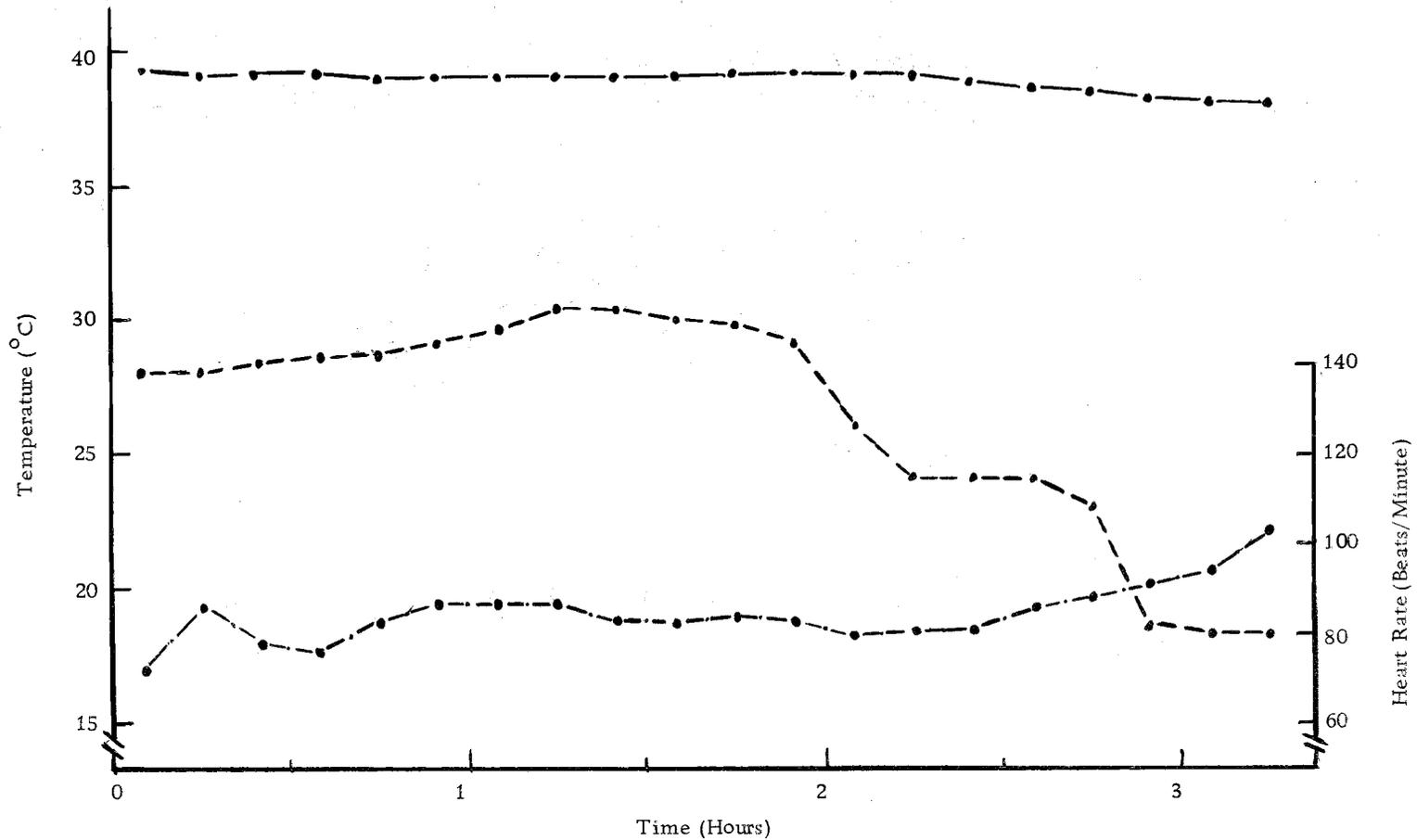


Figure 25. The relationship between heart rate, body temperature, and ambient temperature in animal number 22. Heart rate is indicated by the dashed line broken by a dot (---). Body temperature is represented by solid line (—) and ambient temperature by the dashed line (---). All points represent the mean value for each ten-minute observation period. The predicated heart rate (Kleiber's equation) for this animal was 203 beats per minute.

heart rate for these four animals was 58 percent of the predicted, while the mean minimum was 38 percent. Unfortunately, since this was the only procedure in which the animals would tolerate the recording electrodes, all of the heart rates were based on heat-stressed animals. Nothing is known of the heart rates of "normal" animals at T_A 's below stress values.

The body temperatures of the animals followed similar patterns throughout the heart rate experiments. Two of the animals, numbers 21 and 22, had a higher than normal initial T_B (39.1° and 39.3° C respectively). This was probably due to the fact that both had removed the clip electrodes, the former once and the latter twice, during the procedure. Animal 21 had to be anesthetized twice and number 22 was anesthetized three times before the experiment could be carried out. Animals 16 and 20 showed an increase in T_B once the thermal gradient between their bodies and the environment reached 6.5° and 7.5° C respectively. Animals 21 and 22 maintained a relatively constant high T_B at the minimal thermal gradient of 7° and 8.5° C respectively. All animals showed a decrease in T_B once the T_A was lowered near the end of the experiment. The T_B of number 16 fell 0.4° C, that of number 20 fell 2.0° C, of 21 fell 2.6° C, and the T_B of number 22 decreased 1.2° C.

In the two animals (16 and 20) which had a normal T_B at the start of the experiment, the heart rates decreased as T_A and T_B

increased. The two animals which were hyperthermic at the beginning of the experiment (21 and 22) maintained a relatively constant heart rate and T_B throughout the period of high T_A 's. Except for animal 21, which removed the electrodes before the termination of the experiment, all animals showed an increase in heart rate once the T_A was lowered and their T_B 's began to return to normal levels. It was impossible to continue following the increase in heart rate at low T_A 's. Once the T_A was lowered and the animals T_B had approached normal levels, the animals would become active and remove the recording electrodes.

DISCUSSION

Physical Environment

Numerous investigators have described the habitat of Aplodontia as being cool and moist (Godin, 1964; Ingles, 1965; Voth, 1968). Unfortunately, this description gives little information concerning the actual microclimate of the mountain beaver and the fact that a semi-fossorial form such as Aplodontia has a unique microclimate. The microclimate of Aplodontia can be divided into two main areas, that above the soil surface where it is engaged in foraging, and the area beneath the soil in the burrow system where it spends the majority of its time. Both of these environments have distinctive characteristics.

In terms of precipitation characteristics the 218 cm of water that fell on the study site is well within the Weather Bureau values. According to the Climatological Handbook (1969), the study site on Marys Peak is situated in an area which receives between 180 and 250 cm of annual precipitation. The July mean maximum temperature is between 27° and 28° C, and the January mean minimum lies between 0° and -2.5° C. It is well known, however, that Weather Bureau data seldom describes the microclimate of an animal (Geiger, 1957).

In this instance, the large amount of precipitation and its

associated cloud cover had a strong influence on the mountain beaver's microclimate. The presence of a cloud cover not only decreased the amount of incoming solar radiation but it also reduced the amount of heat lost from the soil, preventing low night temperature (Geiger, 1957). The presence of snow cover during the coldest months of the year (December through mid-March) is very important in moderating surface and burrow temperatures. The importance of snow cover has been well documented by Formozov (1946), Johnson (1951), and Pruitt (1953, 1957, 1959). Formozov (1946) reports that a snow cover of 20 to 25 cm has an important protective effect for small mammals. The surface of the ground under snow was on an average of 15°C higher than a surface lacking snow. He states that the daily minimum temperature in January and February may reach -48° to -41°C at the snow surface but only -19° to -15°C under the snow. Johnson (1951) reports temperatures of about -10°C under 46 cm of snow while the air temperature above the snow varied from a -40° to -46°C . Stephenson (1969) studied the winter temperatures of beaver lodges in Ontario, Canada, and found that 40 cm of snow gave adequate protection by keeping the lodge temperature just above 0°C while the air temperature outside reached -21°C . During this study the effect of snow cover was minimal because of the light snowfall. The heaviest snowfall occurred during the last week of December when about 36 cm fell.

The air temperature (6 cm above surface) at the study sites followed a predictable pattern. The mean temperature was similar at each site, even though there were large variations in the maximum and minimum temperatures. The south open slope had the greatest extremes, followed by the north open slope. The tree covered north slope exhibited the least variation. Obviously, the mean temperatures are a computation artifact and probably have very little meaning to the mountain beaver. The extreme thermal conditions, the time of their occurrence, and the length of time that these conditions persist are of real significance. It can be noted (Tables 4-6) that maximum air temperatures of 28° C were only encountered on the south slope in May through August, on the north open slope from June through August, and on the covered north slope in the months of June and July. Air temperatures exceeding 32° C were never seen on the covered north slope and were only encountered in June and August on the north open slope and from May through August on the south slope. Peak temperatures above 30° C were very transient and seldom occurred before 2 p.m. or lasted longer than five hours.

Winter minimum air temperatures of 0° C or lower were recorded at all sites from November through March (Tables 4-6). The south slope proved to be the coldest with minimal temperatures between -3° and -4° C occurring from at least January through April (no records before January). These minimum temperatures probably

play a very small role in the ecology of Aplodontia. They are not extremely cool and would be faced by the mountain beaver only when it left its burrow system.

The burrow itself is remarkably stable in regards to temperature (Tables 4-6). The mean burrow temperatures of all sites did not vary by more than 3° C during any month. The greatest daily variation in any burrow was less than 4° C. An annual trend in burrow temperatures can be seen with the lowest temperatures recorded in December, followed by a general warming trend with peak temperatures occurring in August. The greatest annual variation of temperatures in a burrow was 21.7° C and occurred on the north open slope where the minimum temperature in December was -1.7° C and the maximum temperature of 20° C occurred in August.

It should also be remembered that the burrow temperatures that were recorded represent readings at a mean soil depth of 15 cm. Voth (1968) found the nest chamber was at least 50 cm beneath the soil's surface. In June of 1969 an evaluation was made of the relationship between soil temperature and soil depth at all three of the study sites. It was found that at 50 cm the soil temperature was 1.5° C cooler than at 15 cm at the north covered slope (9.7° to 11.2° C), 2.4° C cooler at the north open slope (11.2° to 13.6° C), and 1.9° C cooler (11.7° to 13.6° C) at the south open slope. It would, therefore, appear that the nest chambers of Aplodontia would have a

summer temperature about 2° C cooler than the tunnels located 15 cm below the surface. The greater depth of the nest chamber would also lessen daily and seasonal temperature oscillations. In addition to this, it was noted that 77 percent of the thermal gradient that existed between the soil surface and a depth of 50 cm was reached at a soil depth of 15 cm.

The Importance of a Burrow System

A comparison of rodent burrow temperatures is given in Table 8. Unfortunately, there is very little information in the literature relating burrow depth and temperature with surface air temperature. It has been shown that air temperature within a burrow is essentially the same as the temperature of the soil surrounding it (Hayward, 1965b, and Smith and Criss, 1967). Rodents are listed in Table 8 in order of maximum burrow temperatures. It should be noted that the values for Aplodontia and the September values for jerboa are the only ones based on an entire month. The rest of the values are based on determinations made over a much shorter period, usually a single "typical" day. The burrow system of Aplodontia is obviously much cooler than others which have been investigated and represents a cool retreat from high summer air temperatures. It also offers a warm and stable thermal environment during the winter months.

Table 8. The microclimate temperatures of rodent burrows.

Species	Season (Month)	Burrow Depth (cm)	Mean	Air Max	Temperature °C			Source	
					Min	Mean	Burrow Max		
<i>Jerboa</i> sp	Warm (August)	75	--	35	22.5	--	33	29.5	Williams (Kirmiz, 1962)
<i>Peromyscus polionotus</i>	Warm (July)	54	--	50+	40.1	30.6	--	--	Smith and Criss, 1967
<i>Heterocephalus glaber</i>	Warm (March)	40	--	--	--	30.1	30.6	29.1	McNab, 1966
<i>Geomys bursarius</i>	Warm (July)	30	--	37	--	--	32	--	Wilks, 1963
<i>Thomomys bottae</i>	Warm (August)	30	--	--	--	--	30	28	Miller, 1948
<i>Jerboa</i> sp*	Warm (September)	100	28.6	29.2	26.8	26	26.8	--	Kirmiz, 1962
<i>Heliophobius kapeti</i>	Warm (March)	15-60	--	--	--	26	26.8	23.2	McNab, 1966
<i>Peromyscus maniculatus</i>	Warm	--	--	44	16.0	--	26.0	24.0	Hayward, 1965b
<i>Tachyoryctes splendens</i>	Warm (March)	15-25	--	--	--	23.2	25.3	21.4	McNab, 1966
<i>Geomys pinetis</i>	Warm (October)	30	--	--	--	22.2	23.1	21.2	McNab, 1966
<i>Peromyscus eremicus</i>	Warm (July)	60	23	--	--	17.7	18	17	MacMillen, 1965
<i>Aplodontia rufa</i> *	Warm (August)	13	14	36	1.7	13.5	15.5	10.5	This Study

*Monthly values. All others are based on single or daily measurements.

The insulative value of nests in the winter has been pointed out by numerous investigators. Cotton and Griffiths (1967) reported that with an ambient temperature of 0° C, the nest of a vole which contained an adult female was 13° C. Working with Reithrodontomys megalotis, Pearson (1960) found that while nesting, the metabolic requirements of this vole decreased by 17 percent, whereas, removing the hair from the animal increased its metabolic rate by 35 percent. The nest of coastal Neotoma cinerea allowed a reduction of 23 percent in metabolic rate at an ambient temperature of 6° C (Brown, 1968). Hudson (1964) discovered in his work with Citellus tereticaudus that the nest furnishes an environment 14° to 16° C warmer than ambient and that at an ambient temperature of 8° to 10° C, the animals had a metabolic rate that was basal for an animal at 24° C without the protection of a nest.

In summer Hayward (1965a and b) found that Peromyscus living in desert areas could maintain itself within its thermal neutral zone (burrow temperature 26° C) even though the surface air temperature reached 44° C. Vorhies (1945), Schmidt-Nielson (1964), and Carpenter (1963) have all stressed the importance of the summer burrow microclimate in regards to the survival of the members of the genus Dipodomys. Kirmiz (1962) found similar microclimate importance in the jerboas of Egypt. Brown (1968) postulates that the nest temperatures of the low desert forms of Neotoma albigula may be

important in their population dynamics and distribution. He recorded mean nest temperatures of 33 °C and a maximum of 36 °C. These desert woodrats assume an extended body position in response to temperatures above 32 °C and die after four hours of exposure to temperatures between 36 ° and 42 °C.

In addition to the insulative value of nests, numerous mammals form social groups during winter months and further reduce the energy expenditure necessary to maintain body temperature. Sealander (1952) reports that huddling increases the survival of Peromyscus exposed to low temperatures. Formozov (1966) cites that Ponugaeva found that social groupings of Microtus socialis had a metabolic reduction of 38 percent in the winter. Glaucomys volans form social aggregations from November through March. Muul (1968) studied the value of these social groupings and found that at an ambient temperature of -7.5 °C, the basal metabolism of a single Glaucomys was reduced by 12 percent when nesting. Three animals in the nest showed a 33 percent reduction, and six animals had a 66 percent reduction for a saving of 6.6 cal/g/hr per individual. Since Apodonia does not form social groupings, this form of metabolic adjustment is not available to it.

Another important characteristic of a burrow system is its rather high and constant humidity. Although this was not measured directly, it was noted that the soil in the runways was constantly

moist to touch. Jameson (1949) noted that the relative humidity in Microtus burrows was 100 percent. Stark (1963) in working with Microtus californicus found the relative humidity of burrows varied from 64 percent to 96 percent. McNab (1966) reported that the mean relative humidity of the burrows of Geomys pinetis was 99.4 percent. Kennerly (1964) found similar results with Geomys bursarius (mean 88 percent); and both men commented that the air in burrows was always nearly saturated with moisture, independent of temperature, and that this was maintained even when soil moisture reached one percent. Pruitt (1959) had earlier verified this condition when he constructed an artificial burrow and measured burrow humidity as he varied soil moisture. He found that the air in the burrow remained saturated until there was a complete lack of soil moisture. Even under desert conditions, the 40 cm deep burrows of the semi-arid rodent, Heterocephalus glaber, had a mean relative humidity of 95.6 percent (Range 92 to 100 percent) (McNab, 1966); and the burrows of the jerboa in the Egyptian Western Desert showed a daily variation of from 75 to 80 percent (Kirmiz, 1962). Considering the annual precipitation, the low environmental temperatures at the Marys Peak study sites, and the observations made by Voth (1968), it is probably safe to assume that the air in the burrows of Aplodontia is saturated with water vapor.

Thus, it can be seen that the mountain beaver lives in a rather

mild environment. Its burrow system and nest chamber offer a cool and moist refuge in the summer and a relatively warm and protected environment during the winter. The surface conditions undergo a greater amount of annual and daily variation, but periods of extreme heat are rather transient and limited to the exposed slopes, while severely cold temperatures seldom occur; and during the time of their most frequent occurrence, the presence of snow cover will normally moderate their influence on the mountain beaver.

Body Temperature

The mountain beaver has been shown to be a normal homeotherm over an ambient range of temperatures from 4° to 30° C. Free living forms had a mean T_B of $38.0^\circ\text{C} \pm 0.1^\circ\text{C}$ (Table 6), and experimental animals maintained a mean of $37.6^\circ\text{C} \pm 0.4^\circ\text{C}$ (Figure 15). The difference between these means probably reflects differences in behavior patterns. Temperatures of the experimental animals were taken after a period of inactivity of at least an hour. There was no attempt to standardize the activity patterns of the free living forms.

The only literature available concerning the T_B of Aplodontia are the observations made by Fisler (1965) on a single captured male animal. The rectal temperatures indicated that an inactive mountain beaver's T_B falls between 36° and 38° C. During "normal activity"

its T_B rose to a range between 37.5° and 38° C, and under "forced activity" it was between 38° and 38.5° C. He reported that once, after three hours of inactivity, his mountain beaver had a T_B of 34.4° C and that when disturbed, its temperature rose to 37.9° C within 30 minutes. This would mean a temperature rate increase of 7° C per hour. The arousal rate from torpor is normally found to be between 0.4° and 1.0° C per minute (Hudson, 1967, and Kayser, 1965); whereas, the warming of Fisler's mountain beaver was slightly less than 0.12° C per minute. The lowest T_B recorded in this study was 36.2° C. Four of the seven mountain beavers in this study whose body temperatures were measured in the outdoor pens had a mean minimum T_B of 36.5° C.

The lethal T_A for the mountain beaver is between 32° and 35° C. This is low for a mammal, although there are other mammals with similar characteristics. The primitive heteromyids, Liomys salvani and L. irroratus from Central America, for example, cannot survive at a T_A of 36° C (Hudson and Rummel, 1966). McNab (1966) found that Spalax leucodon, the blind mole-rat of the mideast, had a lethal T_A of 35° C; Geomys pinetus, the pocket gopher of southeastern United States and Tachyoryctes splendens, the root-rat of Africa, had lethal T_A 's between 35° and 37° C. Two other fossorial mammals with which he worked, Heliophobius kapeti, the mole-rat of east Africa, and Heterocephalus glaber, the naked mole-rat of the

semi-desert regions of Africa, had lethal T_A 's of from 37.5° to 38.5° C and 39° to 40° C, respectively. Sullivan and Mullen (1954) reported that Citellus barrowensis, which is about the same size as Aplodontia (mean weight 620 g), became heat prostrated at T_A 's above 25° C and could not survive 55 minutes at 30° C. Brown (1968) found that all individuals of Neotoma cinerea and N. albigula became hyperthermic at T_A 's above 32° C and that the coastal and highland forms of N. cinerea died at temperatures between 34° and 36° C.

McNab (1966) has further shown that the fossorial rodents with the lowest lethal T_A also live in a micro-environment with low mean summer temperatures (Table 8). For example, Geomys had an October burrow T_A of 22.2° C; Tachyoryctes, a March burrow T_A of 23.2° C; and Heliophobius, a March burrow T_A of 26° C. Heterocephalus, had a March burrow T_A of 30.1° C. Nothing is known of the microclimate of Spalax; but Reed (1958), in Iraq, found that the animal occurs in low elevations which have an annual rainfall of 17 inches or less and range upward to elevations of 5,500 feet, where the annual rainfall is somewhere between 50 and 90 inches. Spalax also occurs in the steppes of southwestern Russia, which has a climate similar to the Great Basin area of western North America. Aplodontia fits into this pattern very nicely. It has the lowest lethal T_A of any fossorial mammal and had a mean burrow temperature of 13.4° C during the warmest summer months, August, 1966.

Interaction of Microclimate and Temperature Regulation

Thermal regulation presents an endotherm with two major problems. An endotherm must withstand both low and high ambient temperatures. During cold weather the endotherm conductance can decrease and its oxidative metabolic heat production increase so that its T_B can remain stable. An alternate possibility has developed in some mammals in which homeothermism is temporarily abandoned and the energy expense of maintaining a high body temperature is no longer paid. This condition, known as winter torpor, has its energy advantages but also has the disadvantage of forcing inactivity for long periods of time. The mountain beaver did not show any signs of winter torpor. It is known to be active over all its range during the winter months (Hall and Kelson, 1959, and Ingles, 1965).

During the winter, under laboratory conditions, the metabolic rate of Aplodontia showed about a 1.9 fold increase between the ambient temperatures of 2° and 19° C (Figure 15). The environmental data shows that during the coldest month of the study (December, 1966) the mean burrow temperature was 2° C (Site II) with an extreme low of -1.7° C. It should also be noted that this burrow temperature represents a sample from the burrow system and not the nest chamber which is normally considerably deeper (Voth, 1968) and which would not be subjected to the temperature extremes found

in the burrow system.

According to Ingles (1959) the mountain beaver spends about eight or nine hours of the day being active and the rest in its nest chamber. Voth (1968) found that the ceiling of the nest chamber was at least 50 cm below the surface of the ground. Two nests that he excavated showed that a male's nest contained 6.8 kg of material which occupied a volume of 70 liters, and a nest of a female that contained 4.45 kg of material and which occupied a volume of 60 liters. The nest material in both cases consisted of dry vegetation. This large mass of dried vegetation, with air trapped between its fragments, would act as excellent insulation against heat loss for a resting mountain beaver. A 700 g mountain beaver would have a volume of about $1,200 \text{ cm}^3$, equivalent to a 25 cm cylinder with a diameter of 8 cm. This animal and its 60 liter nest, would make a sphere of about 61.2 liters. The sphere would have a radius of 24.4 cm with the mountain beaver contributing about 6.6 cm of the radius. The mountain beaver, therefore, would be surrounded by 17.8 cm of nesting material or about 12 times the depth of its own hair (hair length measured in study skins is about 1.5 cm long). This does not infer that the nest insulation is 12 times as effective as the animal's hair, but it does indicate that the animal is well insulated in the nest chamber and that this insulation must be at least as good in retarding heat loss as the animal's own hair. If this is true, then the mountain beaver

at rest in the nest chamber should be able to maintain a resting metabolic rate without becoming hypothermic. Thus, the mountain beaver can decrease its energy needs during the cold months by utilizing its relatively warm and protected burrow.

The other problem of maintaining a constant body temperature in the face of a heat stress is much more difficult to solve. As the T_A increases, the thermal gradient between the animal and its environment decreases. The animal is faced with a heat loss problem before the thermal gradient becomes zero. At the point at which the critical thermal gradient is reached, the animal will not be able to lose all of its metabolic heat fast enough and will begin to become hyperthermic. The magnitude of this critical thermal gradient can be estimated by "Newton's Law of Cooling," if the maximum conductance and the minimal metabolic rate are known. The cooling equation for the critical T_A at which normal body temperature can be maintained with minimal metabolism and maximal thermal conductance is solved as follows:

$$T_A = T_B - \frac{\text{Metabolic rate}}{\text{Conductance}} = 38.0^\circ \text{C} - \frac{2.05 \text{ cal/g/hr}}{0.355 \text{ cal/g/hr}/^\circ \text{C}} = 32.2^\circ \text{C} \quad (9)$$

This indicates that in order to prevent hyperthermia, the mountain beaver, under conditions of maximal conductance and minimal metabolism, requires a thermal gradient of about 6°C between its body

and its environment. If the predicted basal metabolic rate for summer animals (75.8 cal/g/day) is used, then Aplodontia would need a 9° C thermal gradient. This would mean that a mountain beaver would become hyperthermic at T_A 's above 29° C.

The mountain beaver has a microclimate within the burrow system that solves this heat problem. The warmest month of the study (August, 1966) showed a mean burrow temperature of 13.4° C with a high extreme of 20° C. The mean body temperature of the free-living mountain beavers was 38.0° C. Thus, the thermal gradient under the most severe conditions is still 18.0° C. It can be seen from the metabolic rate data that at 13° C in summer, the mountain beaver would probably be producing heat at the rate of 116 cal/g/day. This figure is about 1.8 times that at 23° C (66 cal/g/day). Thus, we have an animal that must almost double its resting metabolic rate in order to maintain its body temperature in its burrow during the hottest time of the year. From an energetics viewpoint, this is puzzling unless the insulative value of the nest chamber is considered. The metabolic rates are also based on resting animals, and a mountain beaver probably seldom rests in its burrow system when it is outside of its nest chamber.

When a mountain beaver leaves its nest chamber, it becomes active and may be engaged in feeding, food gathering, tunnel repair or extension, etc. Any of these activities will increase the animal's

energy utilization and, therefore, its metabolic rate and heat production. With our present technology it is almost impossible to accurately define the energy needs for the above mentioned activities in small mammals. We can, however, make some inferences based on other mammals. Hart and Héroux (1955), for example, showed that during exercise (running 1.3 mph) at 20° C, lemmings increased their metabolic rate 1.55 times and their heat conductance 1.45. Rabbits under the same conditions increased their metabolism 2.7 fold and conductance 2.48 times. In both species they found that insulation decreased with exercise and increased with a fall in temperature, both under conditions of rest and exercise. Tucker (1965a), in working with Perognathus californicus, reported that a curled posture reduced conductance by almost 50 percent at an ambient temperature of 30° C. He felt that this large reduction could not be simply due to an increase in surface area alone. Since Morrison and Tietz (1957) had shown that a curled position in small rodents decreased their surface by 25 to 33 percent and in dead rodents by 25 percent or less, Tucker (1965a) felt that the great change in conductance was due to the exposure of the thinly furred belly and inner limb surfaces. He further postulated that this would also account for the high conductance values seen by Hart in exercising rodents. Davis and Golley (1963) cite Catlett as reporting that Mus musculus increases its resting metabolic rate 1.19 fold during ingestive

activity, 1.88 times during investigative activity, and 2.28 fold during aggressive activity. No conductance information was given.

Pearson (1960) found in Reithrodontomys megalotis that activity seldom raised the animal's basal metabolic rate more than 50 percent.

An increase in metabolism by a factor less than two during activity such as investigation and digging should be well within the capacity of Aplodontia. This can be verified by evaluating animal number 16 in Figure 18. It can be seen that during the period of its greatest activity at the beginning of the experiment, its T_B increased 4°C in 0.56 hours. This animal was storing heat at the rate of 5.94 cal/g/hr. The mean thermal gradient between its body and the ambient air was 11.8°C . With a maximum conductance of 0.350 cal/g/hr/ $^\circ\text{C}$, this animal would be losing heat at the rate of 4.13 cal/g/hr; and with a minimal conductance of 0.193, its loss would be 2.27 cal/g/hr. Therefore, animal number 16 probably had a metabolic rate of between 10.17 and 8.21 cal/g/hr. A summer mountain beaver's lowest recorded mean rate occurred at 32°C and was 2.08 cal/g/hr. The range of the peak resting metabolic ratios would, therefore, fall between 4.89 and 3.95.

The fact that Aplodontia's burrow temperature is below its lower critical temperature is not unique. McNab (1966) found the ratio of minimal metabolism to basal metabolism, at the mean summer burrow temperatures, to be as follows for the fossorial rodents he

studied: Geomys, 1.42 at 22° C; Tachyoryctes, 1.48 at 23° C; Heliophobius, 1.44 at 26° C; and Heterocephalus, 1.64 at 30° C. If we consider the lowest recorded metabolic rate of the mountain beaver to be basal (at a T_A of 32° C), then at a burrow temperature of 13° C the ratio of minimal to basal metabolism would be 116/50 or 2.32. If the basal rate is taken at the lower critical temperature of 23° C, the ratio is 116/65 or 1.78. Thus, the mountain beaver shows a greater metabolic energy deficiency in its burrow than other fossorial rodents.

This difference in heat loss at mean summer burrow temperatures could be due to a greater amount of activity and thus a greater heat production in the mountain beaver than in other fossorial forms. This, however, seems unlikely since the other animals spend much more time and activity within their burrows. It could also reflect a lower conductance in the mountain beaver than in the other species. The minimal conductance of several fossorial forms has been determined by McNab (1966) (data expressed in cc of oxygen per gram per hour per ° C): Geomys, 0.075; Spalax, 0.068; Tachyoryctes, 0.080; Heliophobius, 0.128; and Heterocephalus, 0.45. The minimal conductance of the mountain beaver was 0.0363 cc/g/hr/° C. This means that the mountain beaver has a minimal rate of heat loss that is about one-half of that of the lowest fossorial form, Spalax. In other words, Aplodontia's insulation is about twice as effective. According to the

conductance equation of Morrison and Ryser (1951):

$$C (\text{cc/g/hr/}^\circ\text{C}) = 1.0 \text{ wt}^{-0.50} \text{ (weight in g)} \quad (10)$$

The conductance of a summer mountain beaver with a mean weight of 743 g should be 0.0367 cc/g/hr/°C. This figure is in close agreement with the experimental values. Thus, the mountain beaver does not have an unusually low conductance; rather, other fossorial animals have a conductance that is higher than "normal".

The environment of a burrow places certain restrictions on mammals. The mammal must have a "lower critical temperature"; that is, a few degrees above that of the burrow and also have a relatively high conductance in order to increase the loss of heat produced from metabolism to the environment of the burrow. A mammal such as the mountain beaver has a cool burrow even in the hot summer months and, accordingly, has a low conductance so that a constant T_B can be maintained with minimal metabolic cost in the face of a large thermal gradient. It might be said that the mountain beaver is a cold adapted form while the other fossorial rodents are warm adapted.

The mountain beaver does, however, face warm and even hot environments when it forages for food in the spring and summer and also during the time of dispersion of the population in the early summer. This is a special problem faced by the mountain beaver and not the other truly fossorial rodents which seldom leave the safety

of their burrow systems, although Howard and Childs (1959) indicated that during dispersal, the young of Thomomys bottae are forced out of the burrows onto the surface of the ground where they can be faced with lethal temperatures. According to Ingles (1959), the mountain beaver spends 40 to 50 percent of its active time during daylight hours and has its longest daylight activity period at 11:00 a. m. and 3:00 p. m. The author has seen mountain beaver active above the ground at noon and around 4:00 p. m. This occurred during the summer when the air temperature was above 30° C. What then are the mechanisms that allow this "cold adapted" animal to be active during times of high ambient temperatures?

From a physiological standpoint, if Aplodontia has to maintain any sustained level of activity, it is in trouble at T_A 's much above 28° C. This problem stems from the animal's apparent inability to modify its conductance (Figure 17). The ratio of mean maximum to mean minimum conductance in summer animals was 0.355/0.194 or 1.83. This means that the mountain beaver can increase its rate of heat loss less than two fold. (It must be remembered that conductance measures only total heat loss and does not give any specific avenues for heat loss). Based on the evaporative heat loss data, at 31.5° C (Figure 20) the mountain beaver loses only 22 percent of its metabolic heat through the evaporation of water. At 12° C this value is about four percent. This does not mean, however, that the

mountain beaver can increase its water loss 5.5 times, since at the high ambient temperatures the metabolism is markedly reduced. A more reliable picture of evaporative water loss can be seen in the absolute water loss data (Figure 19). The summer animals lost water at the rate of 0.43 g/kg/hr at 15° C. This increased to 0.54 g/kg/hr at 21° C where it leveled off until it began to rise again sharply around 29° C. The rate increased from about 0.57 g/kg/hr at 29° C to 0.70 g/kg/hr at 31.5° C. Thus, there was only a 1.64 fold increase in absolute water loss between 15° and 31.5° C. This low rate of water loss at high ambient temperatures is in agreement with observations made at these temperatures. The animals neither panted, salivated, nor drooled on themselves but remained very quiet while either sitting up or lying on their sides. This motionless attitude in response to high ambient temperatures has been called "heat lethargy" by Hudson (1964). This behavior has been described in numerous rodents such as Citellus tereticaudus (Hudson, 1964), Dipodomys (Dawson, 1955), and Perognathus (Tudker, 1965a). The lack of a panting or salivation response to high ambient temperatures is also not unique to Aplo-dontia. Similar observations have been reported for Microdipodops pallidus (Bartholomew and MacMillen, 1961); two heteromyids, Liomys salvani and L. irroratus (Hudson and Rummel, 1966); and Cercaertus nanus (Bartholomew and Hudson, 1962). Thus, it has

been shown that the mountain beaver has a limited ability to increase heat loss through evaporation at stressful ambient temperatures. This inadequate evaporative system is coupled with a renal system that is incapable of concentrating urine to any degree and thus promotes excess water loss through the kidney. Dicker and Eggleton (1964) found a maximum urine to plasma osmotic ratio of 1.4, whereas Nungesser and Pfeiffer (1965) found it to be between 2.0 and 2.4. They also found that the greatest number of nephrons in the kidney were of the cortical type and had very short loops which lacked the thin segment. Sixteen to 22 percent of all the nephrons were of the long-looped variety, and one-eighth to one-twelfth of these reached the area of cribrosa. Anatomically, the mountain beaver does have a countercurrent renal system that would lead to highly concentrated urine. Nungesser and Pfeiffer (1965) determined that the water intake for six caged animals, over a six-day period, was 327 ml/kg/24 hours (standard error 24 ml) while the urinary loss was 267 ml/kg/24 hours (standard error 25.7 ml). According to their data, their animals were taking in and losing, as urine, a volume of fluid equal to 34 percent and 28 percent, respectively, of their body weight per day. In August, 1964, in a similar seven-day study (unpublished data) based on two adult males (weight 988 and 826 g) it was found that mean daily water intake of Aplodontia rufa pacifica was 362 ml/kg. Urine output was 330 ml/kg/day, and the fecal water loss was 3.5

ml/kg/day. These animals were taking water in on an average of 40 percent of their body weight per day and losing water through their kidneys on the average of 36.4 percent of their weight per day and through their digestive tract at 0.4 percent per day. Thus, it can be seen that Aplodontia must either ingest a large amount of succulent vegetation or drink large amounts of water in order to maintain water balance.

Associated with this large urinary loss is a large urinary bladder. During the water balance experiments, the male which weighed 826 g, voided a measured volume of urine equal to eight percent of its body weight (66 mls). Nungesser and Pfeiffer (1965) discussing the mountain beaver's large urinary water loss and its geographical distribution, state that (p. 296):

The authors feel that this renal limitation is the principal factor which has resulted in their range being limited in geologic time to the wet western slopes of the American Pacific Northwest.

From the results of this study it appears that problems of thermal regulation are more likely to be responsible for the animal's limited distribution.

As shown above, the mountain beaver has a high urinary water loss and apparently lacks any mechanisms to utilize water in increasing its heat loss at high T_A 's. Another limitation associated with this is the lack of any specific behavioral mechanisms which would

increase heat loss. During the summer at high ambient temperatures (anywhere above 28°C) the animal becomes quiet and sits hunched over with its head pointed down toward its hind feet. At higher temperatures (above 30°C) the animal begins to nod and then falls over on its side. It does not pant or salivate, nor does it stretch itself out to increase its effective surface area. Occasionally, it would regain its feet and the sequence of events would begin again. If the body temperatures reached about 40°C , the behavioral patterns would change drastically. It would become very active and attempt to escape from the experimental chamber. It would claw and bite at the air intake line or thermometer. This activity would cause an increase in metabolic rate, and the added heat production would drive its T_B higher. Just before its T_B reached 42°C , it would collapse with irregular breathing associated with gross muscle spasms. Death occurred when the body temperature reached 42°C .

Some fossorial rodents have been shown to have special adaptations which permit survival at high ambient temperatures. The naked mole-rat, Heterocephalus glaber, owes its labile body temperature to its high conductance which results from its naked skin (McNab, 1966). This animal lives in burrow systems marked by their high mean temperature (Table 8). McNab (1966) has shown that Geomys pinetis depends on heat loss across its naked tail to prevent hyperthermia at high ambient temperatures. He has found that at an

ambient temperature at 35 ° C, 30 percent of a gopher's total heat loss occurs across the tail. The tail was shown to be 6.6 to 8.6 times more effective than other body surfaces in regard to heat loss. The larger geomyids (200 g) had the greatest dependency on tail heat loss with some dying from heat stress at an ambient temperature of 33 ° C. McNab suggested that the naked tail of Thomomys and the fossorial moles might also have a similar importance in thermal regulation. It is interesting to note that when the tail is removed from a large Geomys, the animal is essentially converted to the body configuration of Aplodontia. The low lethal T_A (33 ° C) is essentially the same for both Aplodontia and the large, tailless Geomys. Aplodontia does not appear to possess any special adaptations to increase its conductance at high T_A 's and so acts just like a tailless gopher.

As has been shown, when the T_A rises, the mountain beaver is placed in a heat budget bind. It lacks the mechanisms that will aid in heat dissipation when the temperature differential between its body and its environment becomes small. Since conductance cannot be appreciably increased, the only way in which T_B can be maintained below critical levels is for heat production to be reduced. A reduction in heat production means a decrease of activity. If the rate of heat production can be reduced so that the reduction rate equals the decrease in heat loss due to the reduction in the thermal gradient,

then T_B will remain constant. It should be noted that this type of mechanism has a limited value.

A mammal is constantly producing heat. The magnitude of this heat production is an expression of the intensity of the chemical reactions taking place in that mammal. Heat production ceases only when the chemical activities of the cells of the animal are stopped, which occurs only with death. There is, therefore, a lower limit to the reduction of metabolism and heat production. In the mountain beaver, the lowest recorded mean minimal metabolism occurred at an T_A of 32°C . It was $49.22 \text{ cal/g/24 hours} \pm 2.38$. The mean T_B of summer animals (mean weight 709 g) at this temperature was $38.8^\circ\text{C} \pm 0.4$. The predicted basal metabolic rate using Kleiber's equation was 76.31 cal/g/day . The mean minimal rate represents a value 64.5 percent of the predicted rate. The lowest mean metabolic rate, based on five carbon dioxide determinations is given in Table 9.

Table 9. The mean minimal metabolic rate of five Aplodontias.

Weight (g)	T_A $^\circ\text{C}$	T_B $^\circ\text{C}$	MR (cal/g/day)	Pred. MR (cal/g/day)	% of Pred.
697.0 ± 61	31.0 ± 0.6	38.6 ± 0.4	48.03 ± 2.88	76.63	62.7

Two of the animals gave their lowest metabolic rate at low ambient temperatures. Animal number 16 (weight 673 g) had a metabolic rate of 37.18 cal/g/day, 48.1 percent of its predicted rate, at a T_A of 24.7°C when its T_B was 37.4°C. The T_B fell 0.6°C during the 30-minute experiment. Animal number 17 (weight 860 g) had a MR of 51.48 cal/g/day, 70.8 percent of the predicted rate, at T_A of 21.8°C when its T_B was 37.8°C. The T_B fell 0.2°C during the 30-minute experiment.

The mean reduction of metabolic rate of 62.7 percent is correlated with the decrease of 57.4 percent in respiration rate (Figure 21), between the T_A 's of 14°C and 32°C. For short periods of time, at high T_A 's, respiration rates of 18 per minute were recorded. The heart rate data (Figures 22-25) shows a reduction of 30 to 50 percent of the normal predicted values based on Kleiber's heart rate equation. Unfortunately, the heart rate of Aplodontia at lower T_A 's is unknown. Lyman and Blinks (1959) were unsuccessful in recording the heart rate of intact mountain beavers, but they were able to determine that the isolated heart of Aplodontia stops beating at 10.6°C. This high "cut out" value indicates that the mountain beaver is incapable of torpor, for a prime prerequisite for torpor is the ability of the heart to function at low temperatures, although all mammals which possess this type of heart are not capable of torpor (Hudson, 1967).

The response to high T_A 's, therefore, involves a decrease in

metabolic rate in conjunction with a decrease in respiration and heart rate. This action allows Aplodontia to maintain a normal T_B until the temperature gradient between its body and the environment reaches about six degrees centigrade. At T_A 's above 28°C , this action must be associated with complete inactivity on the part of the animal. If this action takes place at low T_A 's, the animal's T_B will fall.

A low standard metabolic rate and torpor has been thought to be an adaptation to a low food supply (Hudson, 1967; Kayser, 1965; and Tucker, 1965b). Tucker (1966) has pointed out the value of torpor in Perognathus californicus and has shown that the length of torpor increases as the food supply diminishes. Hudson (1964) has stated that (p. 230): "A reduced metabolism, irrespective of its relationship to the capacity for hibernation, is adaptive to hot climates." Hudson (1967), in discussing the variation in torpidity patterns in small mammals, indicated that there was not always a positive correlation between low metabolism and daily torpor. He stated (p. 36):

Thus, there does not appear to be an invariable correlation between daily torpor and low basal metabolism. It is probable that when torpidity and a low metabolism are both adaptive to an animal's environment the two features are correlated, but not as a cause and effect relationship.

McNab (1966) has suggested that in fossorial forms a low metabolic rate and a high conductance is adaptive to the problems of preventing heat loads in an environment (burrow) which places limits on heat

loss by evaporation and convection.

Based on the results of this investigation, it would seem that Aplodontia follows the general pattern of the fossorial adaptations described by McNab (1966). The low conductance of Aplodontia probably is a reflection of the much cooler burrow system of this animal. A high conductance as found in the fossorial forms that McNab (1966) investigated would be disadvantageous for the mountain beaver. The low metabolic rate of Aplodontia does not appear to be as necessary to its survival in its burrow system as it is with the other fossorial forms studied. The low rates were only observed at T_A 's at least 10°C higher than its mean burrow temperatures. With at least a 24°C thermal gradient between its body and environment, the problem of heat stress within its burrow system seems unlikely.

It is obvious that if Aplodontia spent its entire life above the soil surface that its metabolic response to high T_A would not be effective. An animal which must become immobile in order to prevent hyperthermia at T_A 's above 32°C would be an easy prey for a multitude of predators. Even if this animal was forced to escape a predator, it would quickly become hyperthermic and die of heat stress in the process.

The metabolic rate response of Aplodontia is adaptive if the burrow system is considered as a heat sink. If a mountain beaver

forages during a day when the T_A is much above 28°C , the activity of foraging will most likely increase the animal's heat production so that it will become hyperthermic. Under laboratory conditions, Aplodontia did not show any escape reaction from hyperthermia until its T_B approach 40°C . Consider a 700 g mountain beaver foraging at a T_A of 30°C . If this activity would double the animal's resting metabolic rate at this temperature (110 cal/g/day) and if its conductance would increase to 0.400 cal/g/hr/ $^\circ\text{C}$, then the animal would have about 1.4 hours of foraging activity before its T_B would reach 40°C . At this time the animal could return to its burrow (14°C) and become quiescent. Its metabolic rate could decrease to the lowest value of 50 cal/g/day while maintaining the high resting conductance of 0.355 cal/g/hr/ $^\circ\text{C}$. Thus the mountain beaver would cool to its normal T_B of 38°C within 15 minutes. The burrow would serve as an admirable heat sink.

It should be noted that the mountain beaver's behavior of storing food immediately outside of its burrow openings can be considered an adaptation to high ambient temperature. The food could be gathered during acceptable ambient temperatures and then sorted and stored beneath the ground when the temperature became too warm with minimal exposure for the animal. This behavior pattern could also be developed to give minimal exposure to predators.

There is some evidence that the mountain beaver's inability to regulate its body temperature might be an important factor in its

distribution. While monitoring the movements of young Aplodontias, Dr. Wenkell Dodge of the Bureau of Sports Fisheries, Olympia Washington (personal communication, 1966) found indication that the animals were being forced out of their burrow systems in early summer (June and July) by the females. The young were being restricted above the soil surface from a few hours to several days. This is the same type of dispersion as has been reported for Thomomys by Howard and Childs (1959). Being trapped above the soil surface during a day which had an air surface temperature that exceeded 33 °C for several hours would be fatal to a young mountain beaver. Thus it would appear that Aplodontia's inability to regulate its body temperature at high T_A 's could be a vital factor in limiting the dispersion of the young and in so doing, limiting the distribution of the species.

Evolutionary Implications

If Aplodontia rufa pacifica can be considered physiologically typical of all the living Aplodontids, then a tentative hypothesis can be made concerning their evolution. The similarities of the subspecies habitats and lack of evidence concerning any major physiological differences between mammalian subspecies supports this assumption.

According to Simpson (1945) the aplodontids appeared during the Upper Eocene in North America. The Superfamily, Aplodontoidea,

contains Paramys the oldest known rodent from the Upper Paleocene (Simpson, 1945). The general climate during the early Tertiary was considerably milder than at present (Schwarzbach, 1963). Axelrod (1950 and 1956) has indicated that during the late Eocene and early Oligocene, the area encompassing fossil aplodontids was covered by the Neotropical Tertiary Geoflora. This flora indicates a rather subtropical climate with little extremes in temperature. It was during the Miocene that the mylagaulids diverged from the aplodontid stock (Shotwell, 1958). The main radiation took place during the mid-Miocene in the Great Basin area of North America. During this time, the Great Basin contained an Arcto-Tertiary flora with deciduous hardwoods and conifers; a rainfall of some 40-50 inches fell evenly throughout the year (Schwarzbach, 1963). The mylagaulids became associated with the dryer elements of the West American Element of this flora and spread throughout the mid-western states by the Pliocene. The aplodontids apparently remained associated with the more mesic West American Element, remaining in the general confines of the Great Basin (Shotwell, 1958). Shotwell, 1958, states that there has been very little change in the aplodontids after the late Miocene (Barstovian). The mylagaulids have been extinct since the mid-Pliocene (Hemphillian). Axelrod (1956) shows a progressive decline of the hardwood and coniferous forests in the northern Great Basin area with an increase in grasslands and other

elements of the Madro-Tertiary flora during the Pliocene. Perhaps the specialized mylagaulids could not keep up with the change in flora and climate. It is also noteworthy that possible competitors appeared during the time of the mylagaulid decline. According to Simpson (1945), the Miocene marked the appearance of Citellus and Thomomys, while Cynomys, Geomys, and Marmota first appeared in the Pliocene.

If we consider that the aplodontids of the late Miocene were structurally very similar to the present species, then it seems likely that they were also physiologically similar. If this assumption is true, then it seems likely that they were restricted to the cool and moist West American Element of the arcto-Tertiary Geoflora because of their thermal sensitivity. During the orographic activity during the Pliocene and Pleistocene, the moist West Element became more restricted to the Pacific Coast areas as the rain shadow effect became more pronounced. Because of the lack of early fossil deposits within the present distribution area of Aplodontia, it is not known whether the climatic changes forced them into this present area or simply restricted them to their present distribution.

As a result of the present study and the evolutionary history of the aplodontids, it seems reasonable to surmise that Aplodontia has had a long association with a cool and moist environment. The burrow systems of these rodents have provided protection from predators and climatic extremes. A moist environment has insured

an ample supply of succulent vegetation for maintaining water balance, and the cool environment has been a prerequisite because of their lack of adequate mechanisms to thermoregulate at high ambient temperatures.

CONCLUSIONS

From the data presented in this investigation, the following conclusions can be drawn:

1. The burrow system of Aplodontia presents a cool retreat during the summer and a relatively warm shelter during the winter months. The daily variation of temperature never exceeds 4°C , and the annual range in mean temperature is from 2° to 14°C .
2. The mean T_B of Aplodontia is 38°C and can be maintained over an ambient range of temperatures of from at least 4° to 29°C .
3. The lethal body temperature is about 42°C and is reached within two hours at T_A 's between 32.5° and 35°C .
4. Aplodontia lack a true thermal neutral zone. Lowest metabolic rates were recorded at high T_A during hyperthermia.
5. Winter animals show an effective insulation 1.23 times that of summer animals. Their annual summer molt results in a change in insulation which raises the lower critical temperature of summer animals by 4°C (19° to 23°C).
6. The animals minimal conductance of $0.195\text{ cal/g/hr}/^{\circ}\text{C}$ is normal for a mammal of their body size. However, this conductance can only be increased by a factor of 1.84.
7. The low maximum conductance is due to a lack of behavioral responses such as postural changes, panting, salivation, and to their

low insensible water loss. Insensible water loss can only be increased by a factor of 2.3 over the T_A range of from 12° to 31.5°C . Maximum evaporative heat loss accounts for only 22 percent of their total heat loss at 31.5°C .

8. Aplodontia respond to high T_A 's by a reduction of metabolic rate while maintaining a constant body temperature. Associated with this reduction in metabolic rate is a low heart and respiration rate. When a reduction in metabolic rate occurs at low ambient temperatures, the animal's T_B will fall but is normally regulated above 36°C .

9. The animals studied in this investigation showed a mean maximum reduction in metabolic rate of about 65 percent of their predicted rate, although one animal exhibited a rate 48 percent of the predicted. A low resting metabolic rate is adaptive to an animal which can retreat to a cool burrow system if it has become hyperthermic while foraging at high T_A 's.

10. It is proposed that Aplodontia's inability to thermal regulate at high ambient temperatures has played a major role in the restriction of the distribution of this species.

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