

PHYSIOLOGICAL ECOLOGY OF FOSSORIAL MAMMALS:
A COMPARATIVE STUDY

By

LUIS C. CONTRERAS

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Luis C. Contreras

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Chairman: B.K. McNab
Major Department: Zoology

This study evaluates the significance of some physiological characteristics and their interpretation as adaptations to fossorial living mammals.

An intraspecific study of the energetics in the South American rodent Spalacopus cyanus from low altitude and high temperature and from high altitude and low temperature indicates that the basal rate of metabolism is low in animals from both populations, but it is lower in the larger animals from high altitudes (74 vs 85% of the value expected from the Kleiber relation). Minimal thermal conductance is low in both populations (80 and 85%, respectively). Tolerance to high ambient temperature is the same in both populations; however, it is attained by a low rate of metabolism at high altitude and by a small body mass at low altitude. These characteristics are interpreted as adaptations to reduce overheating, especially in the warmer burrows at low altitude.

In studying the thermal and metabolic response to low temperature and oxygen pressure, it was found that interspecifically the critical oxygen pressure was lower in fossorial than in surface dwelling mammals. Even though the basal rate of metabolism and body mass did not set P_c , they may be of importance in reducing respiratory stress, because the development of hypoxia and hypercapnia is directly proportional to these factors.

Fossorial mammals scale basal rate of metabolism according to the function $\dot{V}_{bO_2}/M_b = 9.752 M_b^{0.493}$. This function yields lower values than expected by the Kleiber relation at body masses larger than 74.5 g and higher values at small masses. The combination of this relationship and minimal thermal conductance determines a temperature differential between body temperature and the lower limit of thermoneutrality independent of body mass. Species that do not fit this pattern at small masses have low basal rates of metabolism, high minimal thermal conductances, live in warm environments, and are poor thermoregulators.

These characteristics are interpreted mainly as adaptations to reduce overheating. Although alternative hypotheses, e.g., that these modifications are related to hypoxia and hypercapnia, low food availability, and the high cost of burrowing, should also be considered.

CHAPTER ONE INTRODUCTION

One of the difficulties in comparative studies is that organisms living in nature are exposed to multiple uncontrolled variables and to their interactions. Fossorial mammals seem to offer a good opportunity for these kinds of studies, because they live in relatively stable and well characterized environments (Rosenmann 1959, Kennerly 1964, McNab 1966, Studier and Baca 1968, Studier and Proctor 1971, Arieli 1979). Moreover, fossoriality has evolved in several different taxa; i.e., marsupials, edentates, insectivores, and rodents; thus, by studying them we can distinguish the characteristics related to fossoriality from those independent of it. Several morphological characteristics in these animals have been indisputably attributed to this mode of life (Eloff 1951, Dubost 1968, Hildebrand 1974, Topachevskii 1969/1976).

[Several respiratory and energetic characteristics of these animals, such as low critical oxygen pressure, low rate of metabolism, and body size, have been proposed as adaptations to hypoxia and hypercapnia (Baudinette 1972, Arieli et al. 1977, Arieli and Ar 1981b), to overheating (McNab 1966, 1979), to low food availability (Jarvis 1978), or to the high cost of burrowing (Vleck 1979, 1981).] These

propositions have generated some controversy, because the same characteristics have been attributed to different selective forces.

The aim of this study was to evaluate the significance of these characteristics and proposed explanations in fossorial mammals. First, I compare the energetics of two populations of the South American rodent Spalacopus cyanus. One of them lives at 70 m altitude in a warm habitat near the Pacific Ocean, the other lives at 2500 m altitude in a colder ambient in the Andean Mountains of central Chile. Second, I studied the metabolic and thermal response of this and other fossorial mammals to low temperature and oxygen pressure to see if these animals show a greater tolerance to hypoxia than other mammals, and if they do, whether this lower sensitivity is related to their rate of metabolism. Third, I present new data on the energetic parameters of 11 fossorial rodents from South America, North America, and Africa, and I discuss these data and others found in the literature in relation to body size and distribution.

CHAPTER TWO
BIOENERGETICS OF THE FOSSORIAL SPALACOPUS CYANUS (OCTOCONTIDAE:
RODENTIA) FROM TWO ALTITUDES

Introduction

A fossorial existence has developed independently in several mammalian orders; e.g., marsupials, insectivores, rodents, and edentates. Adaptations to fossoriality include several physiological as well as morphological characteristics. [The microenvironment faced by fossorial mammals is relatively stable, characterized by high relative humidity, small temperature variation, low oxygen tension, and high carbon dioxide tension] (Rosenmann 1959, McNab 1966, Studier and Baca 1968, Studier and Proctor 1971, Arieli 1979, MacLean 1981).

Several respiratory characteristics of fossorial mammals have been regarded as adaptations to the hypoxic and hypercapnic atmosphere of their burrows (Detweiler and Sporri 1957, Bartels et al. 1969, Quillam et al. 1971, Darden 1972, Chapman and Bennet 1975, Lechner 1976, Ar et al. 1977, Arieli and Ar 1979, 1981a, b). In general, all of these studies indicate a high H_b-O_2 affinity, low P_{50} , high O_2 capacity, high buffering capacity of blood pH, reduced sensitivity to CO_2 , low respiratory frequency, small respiratory dead space, low tissue PO_2 , and low heart rate.

The energetics of fossorial mammals have been studied by several authors; however, there has been no complete agreement on the data or in their interpretation. In the first comparative study on energy

expenditure of fossorial mammals, McNab (1966) included five species of herbivorous rodents. [Low metabolic rate and high thermal conductance, together with a small body size, especially when living in a constantly warm environment, were interpreted as adaptations to reduce the probability of overheating.] This interpretation has also been extended by MacMillen and Lee (1970) to burrowing mammals in general. However, Gettinger (1975) and Vleck (1979) questioned McNab's data and interpretation. These comments have been answered by McNab in two papers. The first one includes new data not only on fossorial herbivorous rodents, but also on fossorial insectivores, thus extending the body mass (M_b) and food habits range of the species examined (McNab 1979). The second paper concerns the methods used to estimate the minimal thermal conductance (McNab 1980).

From this new set of data (McNab 1979), a more complex pattern emerged. [The basal rate of metabolism is lower than expected if M_b is greater than 80 g, but it is higher if M_b is lower than 60 g, unless they inhabit an extremely constant and warm environment. This pattern indicates that bioenergetic adaptations to fossoriality include (1) maintenance of a small temperature differential between body temperature and the lower limit of thermoneutrality independent of body mass by matching the mass sensitivity of the basal rate to that of the minimal thermal conductance; (2) reduced basal metabolic rate; (3) standard to high thermal conductance; and (4) small body mass.]

In the present study the bioenergetic characteristics of two populations of the fossorial Spalacopus cyanus (Octodontidae) are estimated to evaluate the significance of these parameters as

adaptations to fossoriality in different environments. One population is from low altitude, ca. 70 m, close to the Pacific Ocean, the other is from higher altitude, ca. 2500 m, in the Andean Mountains of central Chile. Spalacopus cyanus is distributed from 30°S to 37°S along the coast of Chile, and it is also found above 2000 m altitude in the Andes between 33°S and 34°S (Osgood 1943, Mann 1978). The animals from the mountains are larger than those from the coast but have the same chromosomal characteristics (Reig et al. 1972).

Methods

Live animals were trapped during August with snare traps in Con-Con, Valparaiso (32°56'S, 71°31'W; ca. 70 m) and from Farrellones, Santiago (33°20'S, 70°11'W; ca. 2500 m). The animals were shipped by air to Gainesville, Florida. They were kept in heterosexual pairs in steel cages of about 60 x 80 cm filled with about 30 cm of humid dirt where they could dig their burrows. Ambient temperature was between 20 and 23°C. The room had windows and the photoperiod was not controlled. They were fed mainly rabbit food, sweet potatoes, and carrots ad libitum.

Oxygen consumption measurements in eight individuals from low land and nine from the mountains were made at different ambient temperatures with an open flow system, utilizing either a paramagnetic Beckman G-2 or an Applied Electrochemistry oxygen analyzer. Carbon dioxide and water vapor were absorbed from the gas stream after the metabolic chamber and before the flow rate being measured. Ambient temperature (T_a) was controlled by submerging the ca. 3 liter metabolic chamber in a thermoregulated water bath, and T_a was

measured with a mercury thermometer or a thermocouple located on the interior top of the chamber. Room air was pumped into the metabolic chamber at a flow rate between 600 and 750 ml/min. Each run lasted at least 2 h. All runs were made during daytime between 0800 and 1800 hours. The animals were left without food between 2 and 12 h before measurements, except for the 24 h continuous runs in which the animals were provided with food within the chamber. Body temperature (T_b) and body mass (M_b) were measured at the beginning and end of each run.

Oxygen consumption was calculated using the equation

$$\dot{V}_{O_2} (\text{cm}^3 \text{ O}_2/\text{g h}) = 27.257 (\Delta P_{O_2} F_R P_b) / T M_b$$

where ΔP_{O_2} is the fractional change in oxygen content, in the gas stream between the entrance into and the exit from the metabolic chamber, F_R the flow rate (ml/min), P_b the barometric pressure (mm Hg), T the temperature of gas stream at the site of the flow rate measurement ($^{\circ}\text{K}$), and M_b the body mass (g). The mean of the two lowest periods lasting at least five minutes was considered to represent the value for that run.

Mean basal rate of metabolism (\dot{V}_{bO_2}) was estimated from measurements of minimal oxygen consumption within the zone of thermoneutrality. The minimal thermal conductance was calculated from the relationship $C_m = \dot{V}_{O_2} / (T_b - T_a)$ for each measurement of oxygen consumption below the limit of thermoneutrality. This method solves the problem of extrapolation to a higher T_b than actually is measured, when the minimal thermal conductance is calculated by the regression method (McNab 1980). The calculated thermal conductance

reflects the "wet" or total thermal conductance. The \dot{V}_{bO_2} and C_m were compared to the expected values from the allometric equations of Kleiber (1961) and McNab and Morrison (1963), respectively.

Burrow, ground surface, and air temperatures at both localities were measured in summer and winter.

Statistical t-tests were performed to test for the differences between the obtained values for $\% \dot{V}_{bO_2}$ and $\% C_m$ from the expected values based on body mass after angular transformation. Statistical z-tests were used to test for differences in body size between different sexes in each locality and within sexes in different localities. Variation around means are expressed as ± 1 standard error (SE).

Results

The rate of oxygen consumption over a 24 h period shows the absence of a circadian or photoperiodic effect in individuals from both populations (Fig. 2-1). Periods of rest are spaced by about 15 min to 1.5 h.

The bioenergetic characteristics of Spalacopus taken from the coast and from the mountains are shown in Table 2-1. Animals from both populations are good thermoregulators at T_a between 2 and 32°C. Body temperature is not significantly different $P > 0.05$; Figs. 2-2, 2-3; Table 2-1) between these populations. The \dot{V}_{bO_2} is low in both populations, but is significantly lower in individuals from the mountains than in those from the coast (Table 2-1). The minimal thermal conductance below 20°C is equally low in both populations (Table 2-1, Figs. 2-4, 2-5).

Figure 2-1. Rate of oxygen consumption over 24 h period in S. cyanus from high altitude. The same pattern is observed in lowland individuals. The dark bars represent period of darkness.

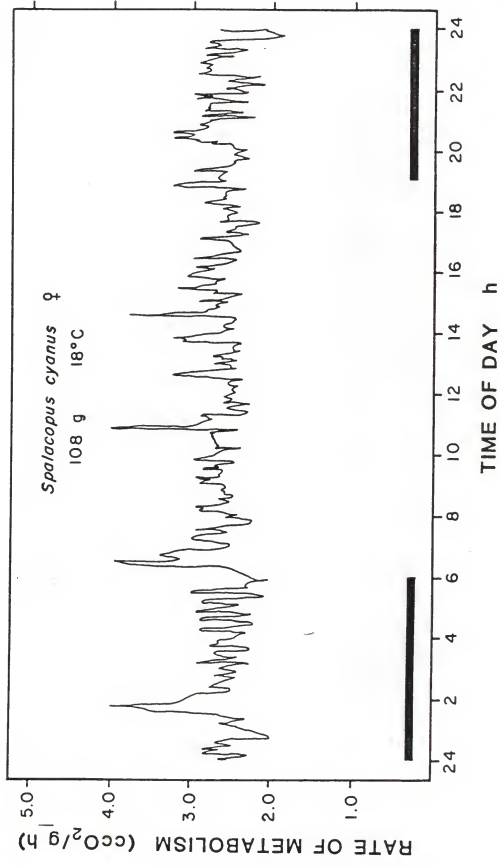


Table 2-1. Bioenergetic parameters of Spalacopus cyanus from two altitudes.

Altitude m	Summer g Burrow	\dot{V}_{bO_2}				C_m				T_b	T_1	ΔT_1	ΔT_m	Reference		
		T	x \pm SE	n/N	Z	P	x \pm SE	n/N	Z						P	
2500	136	15	0.754 \pm 0.026	15/9	74.1	<<0.001	0.0737 \pm 0.0015	32/9	84.8	<<0.001	0.87	36.4	26.4	10.0	4.2	This study
70	83	26	0.956 \pm 0.024	16/8	84.6	<<0.001	0.0877 \pm 0.0023	29/8	80.2	<<0.001	1.06	36.7	26.0	10.7	4.3	This study
?	185		0.790 \pm 0.020	19/2	85.0		0.0800 \pm 0.0020	21/2	109		0.78	36.4	26.5	9.9	4.5	McNab 1979

\dot{V}_{bO_2} = Basal metabolic rate ($cm^3 O_2/g h$).

C_m = Minimal thermal conductance ($cm^3 O_2/g h ^\circ C$).

n/N = Number of measurements/ Number of different animals.

Z = Percentage of the expected value based on body mass.

F = $\Sigma V_{bO_2} / \Sigma C_m$.

T_b = Body temperature, $^\circ C$.

T_1 = Lower limit of thermoneutrality, $^\circ C$.

ΔT_1 = Temperature differential between T_b and T_1 , $^\circ C$.

ΔT_m = Temperature differential between T_b and ambient temperature above thermoneutrality.

Figure 2-2. Rate of oxygen consumption and body temperature in S. cyanus from high altitude (Farellones) versus ambient temperature.

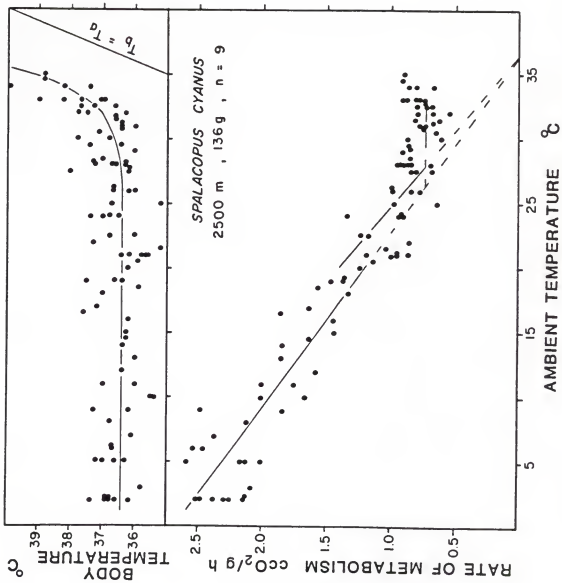


Figure 2-3. Rate of oxygen consumption and body temperature in *S. cyanus* from low altitude (Con-Con) versus ambient temperature. Closed and open circles were obtained with an open and closed system, respectively.

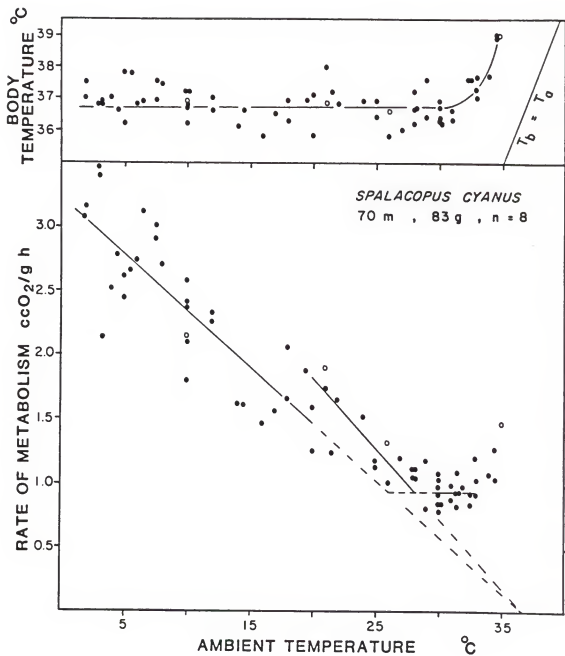


Figure 2-4. Wet thermal conductance in Spalacopus cyanus from low altitude (Con-Con) versus ambient temperature.

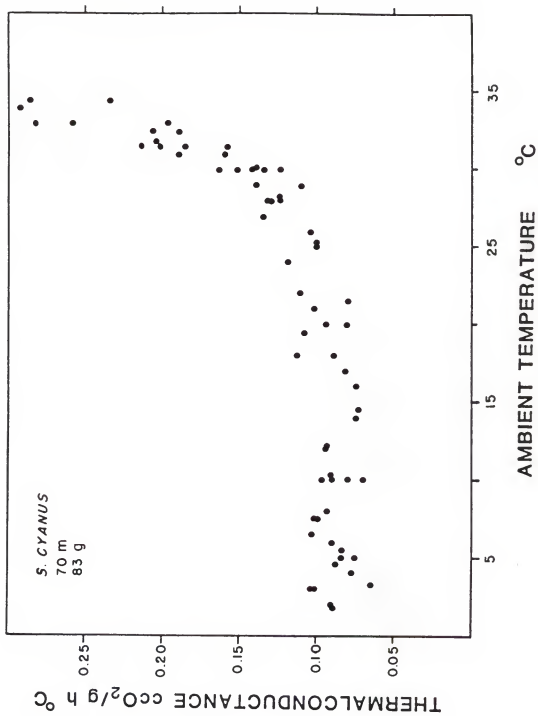
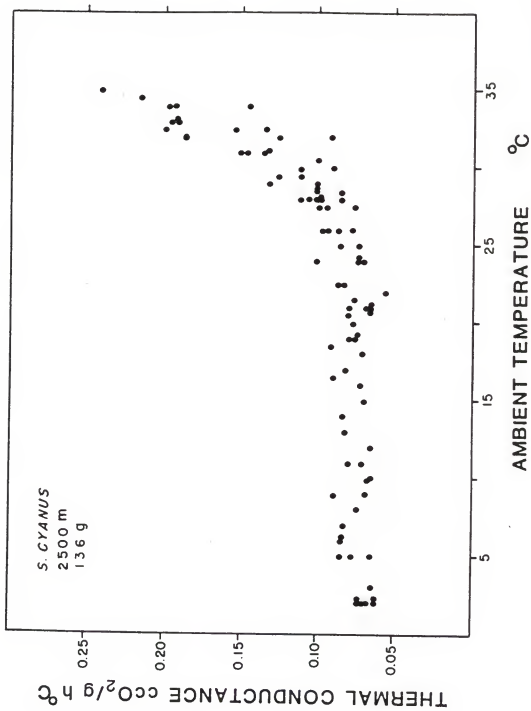


Figure 2-5 Wet thermal conductance in Spalacopus cyanus from high altitude (Farrellones) versus ambient temperature.



Comparing the M_b of animals trapped in the field (Table 2-2) we can see, first, that there is significant sexual dimorphism in individuals from the lowlands but not in those from high altitude; and, second, that females and males from low altitude have a body size equal to 71.3% and 83.9%, respectively, of the high altitude animals of the same sex.

In Figures 2-6 and 2-7 the environmental temperatures measured at both localities in winter are plotted. Average burrow temperatures in winter are 4° and 11°C for the mountain and coastal populations, respectively. Note that burrow temperature, as well as temperatures measured at 10 cm deep in the ground, shows a greater daily fluctuation at the coastal site. Average summer burrow temperatures are 15 and 26°C at the mountain and low altitude sites, respectively.

Discussion

Activity Pattern

The activity pattern of S. cyanus over 24 h lacks a circadian or photoperiod effect (Fig. 2-1), as is characteristic of fossorial forms such as Geomys bursarius (Vaughan and Hansen 1961), Thomomys bottae (Vleck 1979), T. talpoides (Andresen and MacMahon 1981), Arvicola terrestris (Airoidi 1979), and Scalopus aquaticus (Arlton 1936). This pattern is manifested in the activity observed in captive animals, as well as in the field, except during the warmer hours of the summertime when activity decreased, making trapping less successful.

Basal Metabolic Rate

Previous measurements on the bioenergetic characteristics of S. cyanus have been done in two captive animals from the coastal region

Table 2-2. Body mass of Spalacopus cyanus from two altitudes.

Altitude (m)	Male		Female
2500	118.3 \pm 7.3	NS	112.5 \pm 7.7
	0.04		0.01
70	99.3 \pm 2.2	0.001	80.2 \pm 3.2

Values represent mean \pm SE, (g).

T-test was used to test for differences.

Figure 2-6. Environmental temperatures of the habitat of S. cyanus at high altitude during winter.

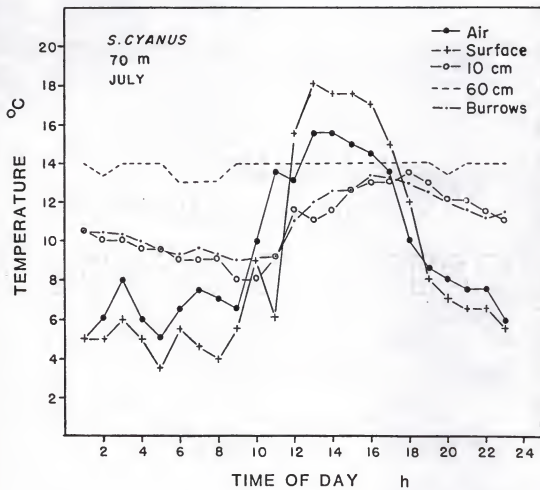
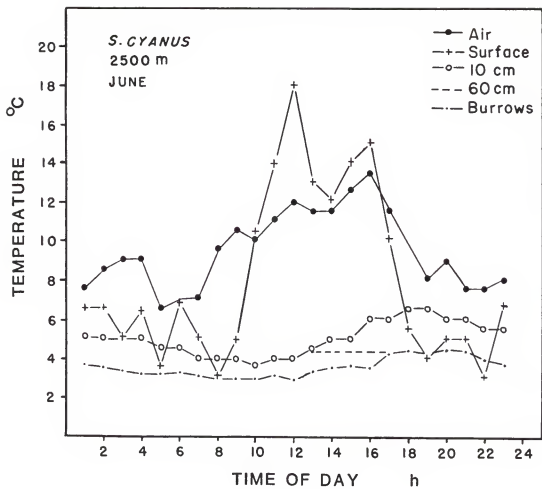


Figure 2-7. Environmental temperatures of the habitat of S. cyanus at low altitude during winter.

|



Sample size was seven individuals for each sex at each locality. (McNab 1979). However, these animals had an extremely large M_b never found in nature, not even in the largest animals from high altitude. Because of this, even though there are similarities in the values (Table 2-1), the discussion will consider only the data from this study.

The values of \dot{V}_{bO_2} found in individuals of S. cyanus from both populations are significantly lower than expected from the Kleiber relation, and they are significantly lower in the individuals from high altitude and cooler sites (Table 2-1). In general, these low values are in accordance with those of other fossorial mammals. Looking at this parameter alone, other things being equal, according to the thermal stress hypothesis (McNab 1966, 1979), we should expect a lower \dot{V}_{bO_2} at low altitude because burrow temperature is higher there. However, other things are seldom, if ever, equal, especially in the field. McNab (1979) proposed that fossorial mammals scale \dot{V}_{bO_2} to body mass to a function different from the Kleiber relation ($\dot{V}_{O_2}/M_b = 3.42 M_b^{-.25}$) with an exponent between -0.50 to -0.40, intercepting the Kleiber relation at about 80 g. Thus, we should expect a greater difference between the observed and expected values from the Kleiber relation as body mass increases above 80 g, which is the case for S. cyanus studied here.

Minimal Thermal Conductances

Minimal thermal conductance in fossorial mammals living in cool burrows (< 20°C) are generally equal to the standard values (McNab 1979). The lower minimal thermal conductances of S. cyanus found in

this study probably can be related to a seasonal change similar to the one described for Geomys pinetis (Ross 1980). If so, higher values should be expected during the summer, especially at low altitude.

The correlation of thermal conductance with ambient temperature (Figs. 2-4, 2-5) is probably related to postural changes in the shape of the animal. At low T_a the animals frequently adopted a more spherical shape, reducing the surface to volume ratio. At high T_a the animals usually adopted a position maximizing the exposed surface. Blood circulation to the tail and feet, denoted by the color of the skin, also increased with increasing T_a . The same behavior has been observed in the genera Thomomys and Ctenomys (personal observation). Evaporative cooling is of no significance to heat dissipation in Geomys, Spalax, Heterocephalus (McNab 1966), or Thomomys (Gettinger 1975). Spalacopus was never seen to spread saliva on the fur. Spreading of saliva on the entire body has been observed to occur and to be of importance in Tachyoryctes and Heliophobious (McNab 1966). There is a question whether this avenue of heat loss is important in nature, given the high relative humidity in burrows.

The Temperature Differential

The combination of \dot{V}_{bO_2} , C_m , and M_b determines the temperature differential between T_b and T_a at the lower limit of thermoneutrality (T_1) by the equation

$$\Delta T_1 = 3.42 F M_b + 0.25$$

(McNab 1974), where F is equal to the ratio between the \dot{V}_{bO_2} and C expressed as percentage of the expected values based on M_b .

Nevertheless, animals from these two populations have a similar ΔT_1

(10.0 and 10.7°C). However, these values are obtained by different means. The individuals from high altitude have a small F value, produced mainly by a low \dot{V}_{bO_2} . Individuals of the population on the coast have a small M_b and an F ratio close to unity (Table 2-1). Because a small ΔT_1 is related to high temperature tolerance (McNab 1979), individuals from the two populations should show a similar tolerance to high T_a ; this is actually the case (Figs. 2-2, 2-3).

According to the thermal stress hypothesis of McNab (1966, 1979), we should expect the individuals from the lower and warmer place to show a greater tolerance to high T_a . However, two factors should be considered regarding this disagreement. First, the animals from low altitude do not face a constant and warm environment. Thus, if they could reduce the F ratio or M_b to a greater extent, they could become poor thermoregulators at the low T_a found during winter. A second factor may be that the lower \dot{V}_{bO_2} of individuals from high altitudes and lower burrow temperature may be thought of as an adaptation to a lower oxygen partial pressure given by the combination of fossorial habits and high altitude. Even though the lower \dot{V}_{bO_2} of the high altitude S. cyanus is possibly related to a lower oxygen tension, it cannot explain the larger body size of those animals because the total requirements for oxygen increase with body mass. If the level of the rate of metabolism is actually an adaptation to low oxygen tension, we should expect a positive correlation between this level and the critical oxygen pressure, not only intraspecifically, but also interspecifically.

Vleck (1979, 1981) interpreted the low metabolic rate and small body size in fossorial mammals in warmer environments as adaptations to the high cost of obtaining food by burrowing, the cost being higher when soil friability and food availability are low. Undoubtedly, the cost of burrowing is high; however, fossorial mammals do not get all their food from underground. Thomomys bottae and Spalacopus cyanus feed on the surface vegetation around the opening of their burrows.

Several points suggest that the thermal stress hypothesis (McNab 1966, 1979) is more likely than the cost of burrowing hypothesis (Vleck 1979) to explain the observed characteristics in S. cyanus. According to the cost-of-burrowing model, we should expect a larger M_b in more friable soils than in hard soils. This is not the case for S. cyanus. Individuals with smaller M_b are found mainly in friable sandy soils along the coast and, to a much lesser extent, in hard clay soils in the ravines around the Central Valley (Contreras, personal data). Larger individuals are found only in the Andean Mountains above 2000 m altitude and always in hard clay soils. An alternative explanation would be a much larger plant productivity in the hard soils or a very small plant productivity in the sandy soils. The high population densities at both sites indicate that food availability is unlikely to be low in either environment.

A similar pattern of body size differences and soil type was found along an altitudinal transect of 758 m in the Beartooth Mountains, Wyoming, for Thomomys talpoides (Tyron and Cunningham 1968). In this case the larger M_b was claimed to relate to higher protein content in the stomachs of the individuals. However, the relation was not a

strict one, food availability was essentially the same along the transect, and the study did not consider seasonal fluctuation or food storage.

The opposite trend was found for T. bottae (Davis 1938). In this case M_b decreased with altitude and was claimed to relate to food availability; however, sample sizes per locality were very small, and there were no actual measurements of food availability.

Another indication making the thermal stress hypothesis more likely is that S. cyanus individuals show sexual dimorphism of M_b only at low altitude, the warmer sites. During pregnancy and lactation females would have an increase in heat production due to an increment in M_b , as well as by hormonal stimulation (Kleiber 1961). This increase in heat production would more likely represent overheating problems at low altitude because of higher burrow temperature, and smaller females would thrive better than larger ones at low altitudes.

Clearly, a long term ecological study of S. cyanus living in contrasting habitats is highly necessary to describe the actual characteristics and relationships of the individuals to the environment in which they live. A study of this type has been done in Thomomys talpoides (Andresen and MacMahon 1981). However, they considered only different successional stages within a given local area, thus thermal factors were more or less the same in the different stages. In that case, the animals responded to differences in food availability by a change in population density.

CHAPTER THREE
METABOLIC AND THERMAL RESPONSE OF FOSSORIAL MAMMALS
TO LOW TEMPERATURE AND OXYGEN PRESSURE

Introduction

Fossorial mammals spend most of their life underground in microenvironments characterized by darkness, high relative humidity, small temperature fluctuations, and hypoxic and hypercapnic atmospheres (Rosenmann 1959; Kennerly 1964; McNab 1966; Studier and Baca 1968; Studier and Proctor 1971; Baudinette 1974; Arieli 1979; MacLean 1981). Adaptations to these conditions are found in diverse taxa, e.g., marsupials, insectivores, edentates, and rodents.

Proposed adaptations include low basal rates of metabolism (\dot{V}_{bO_2}) and standard to high minimal thermal conductances (C_m) (McNab 1966; 1979; Gorecki and Christov 1969; Bradley et al. 1974; Nevo and Shkolnik 1974; Bradley and Yousef 1975). The low rates of metabolism are considered adaptations to the hypoxic and hypercapnic conditions of their burrows (Baudinette 1972; Arieli et al. 1977; Arieli and Ar 1981b) in attenuating respiratory anoxia or acidosis. McNab (1966) argued that this interpretation is unlikely because burrow oxygen tensions (P_{O_2}) are usually above values where rates of metabolism are affected and also because fossorial mammals are insensitive to hypoxia and hypercapnia. The only measured critical oxygen pressure (P_c) for

a fossorial mammal (Spalax ehrenbergi) indicates that these animals have lower P_c than non-fossorial mammals, and their rates of metabolism did not differ from expected values based on body mass (M_b) (Arieli et al. 1977).

The aim of this study was to determine whether fossorial mammals have a lower sensitivity to low P_{O_2} than surface dwellers; and if they do, whether this characteristic is related to the level of the rate of metabolism.

Methods

Animals. Three adult male eastern moles, Scalopus aquaticus (Talpidae), were caught near Gainesville, Florida. They were kept in glass aquaria with moist soil and were fed canned dog food, worms, and crickets.

Five and six adult cururos Spalacopus cyanus (Octodontidae) from 70 and 2500 m altitude, respectively, were used in my experiments. Localities and conditions of captivity were indicated in Chapter Two.

One mole-mouse, Notiomys macronyx (Cricetidae), was collected at 700 m altitude, 18 km SE of Bariloche, Prov. Rio Negro, Argentina, by O.P. Pearson. The animal was fed canned dog food, worms, apples, mushrooms, grapes, oatmeal, and sweet potatoes ad libitum. It was kept in a large aquarium with moist soil within which it established tunnels.

Two common mole-rats Cryptomys hottentotus (Bathyergidae) were trapped in Pietermaritzburg, South Africa by G. Hickman. They were maintained in rat laboratory cages with sawdust. They were fed sweet

potatoes, carrots, and rabbit food pellets. They did not eat worms or dog food even when available.

Experiments. Basal rate of metabolism and minimal thermal conductance were estimated by measuring rates of oxygen consumption at different ambient temperatures using techniques described in Chapter 2. Body temperatures and body masses were measured at beginning and end of each run.

Subsequently, rates of metabolism and body temperatures were measured at 12, 10, 8, and 6% oxygen at 30, 20, and 10°C. In these cases oxygen-nitrogen mixtures, rather than atmospheric air, were pumped through the metabolic chamber. These experiments lasted 1 hour. The measurements allowed estimates of the critical oxygen tensions where \dot{V}_{bO_2} or T_b fell below values found at normoxic conditions (Rosenmann and Morrison 1974).

Results

Standard conditions

The parameters of energetics of the species studied as well as those obtained from the literature are given in Table 3-1. Notiomys macronyx maintains T_b about 36.8°C at temperatures below 31°C. At higher T_{as} , body temperature increases slightly (Fig. 3-1). Basal rate of metabolism in this species is 113.4% of the expected based on body mass (Kleiber 1932, 1961) and has a thermal conductance as expected for its size (McNab and Morrison 1963).

Cryptomys hottentotus maintains a relatively low body temperature (35.7°C) for a mammal while inactive at ambient temperatures up to 33-34°C (Fig. 3-2). Body temperature does not increase exponentially

Table 3-1. Bioenergetic parameters in some fossorial mammals.

Species	M_b	\dot{V}_{O_2}	\dot{V}_{O_2}	C	TC	T_b	Reference
<i>Scalopus aquaticus</i>	48	1.410 ± 0.053 (20/2)	109.0	0.1300 ± 0.0033 (12/2)	90.0	36.0	McClab 1979
<i>Notiomys macrourus</i>	62	1.360 ± 0.027 (11/1)	113.4	0.1308 ± 0.0025 (14/1)	103.0	36.8	This study
<i>Cryptomys hottentotus</i>	71	0.952 ± 0.0235 (16/2)	80.8	0.1380 ± 0.0041 (17/2)	116.8	35.7	This study
<i>Spalacopus cyanus</i>							
70 m	83	0.956 ± 0.024 (16/8)	84.6	0.0877 ± 0.0023 (29/8)	80.0	36.7	This study
2500 m	136	0.754 ± 0.026 (15/9)	74.1	0.0737 ± 0.0015 (32/9)	84.8	36.4	This study
<i>Spalax ehrenbergi</i>	186	0.99 ± 0.10 1	108.3	0.1070	145.9	35.5	Arieli et al. 1977

M_b = Body mass (g).

\dot{V}_{O_2} = Basal rate of metabolism, ($\text{ccO}_2\text{g}^{-1}\text{h}^{-1}$). Numbers in parentheses are number of measurements/number of different individuals

\dot{V}_{O_2} = Percent metabolic rate of $3.42 M_b^{-0.25}$

C = Minimal thermal conductance ($\text{ccO}_2\text{g}^{-1}\text{h}^{-1}\text{C}^{-1}$). Numbers in parentheses are number of measurements/number of different animals

TC = Percent minimal thermal conductance of $1.00M_b^{-0.50}$

T_b = Body temperature ($^{\circ}\text{C}$).

1. = Mean \pm standard deviation, other values are mean \pm standard error

Figure 3-1. Resting rate of oxygen consumption and body temperature of Notiomys macronyx as a function of ambient temperature. Thermal conductance is the average of each measurement below 20°C. Basal rate is the average value of measurements between 29 and 32.5°C.

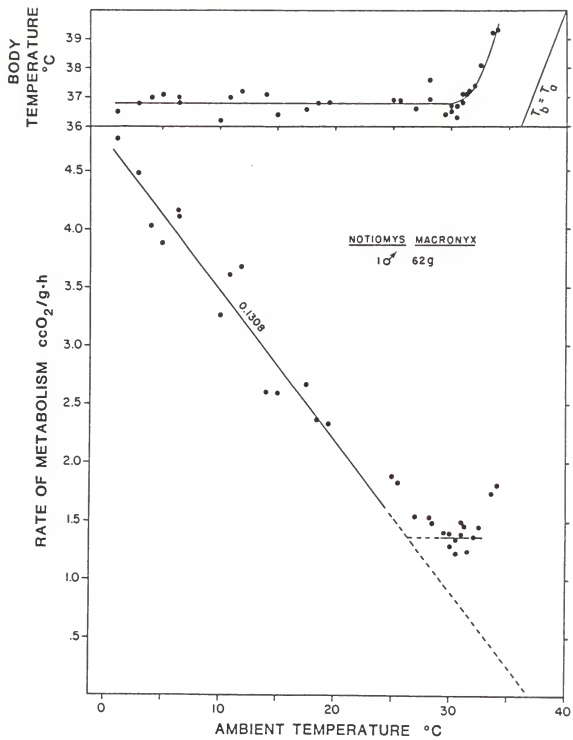
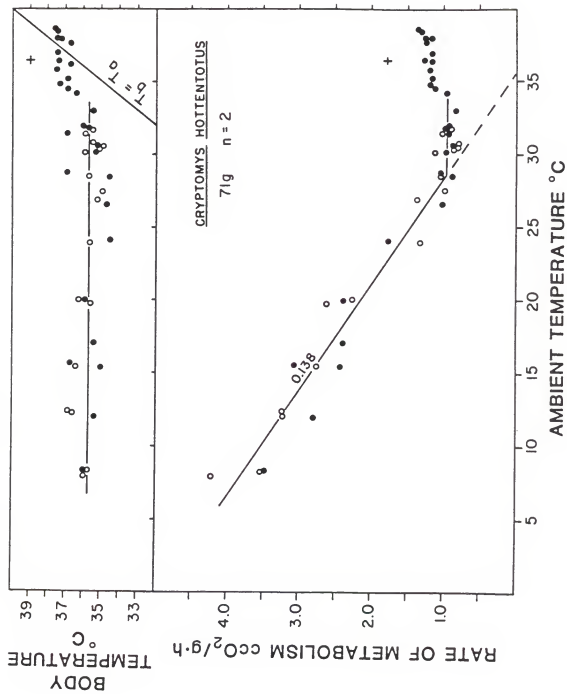


Figure 3-2. Resting rate of oxygen consumption and body temperature of Cryptomys hottentotus. Thermal conductance is the average of measurements below 27.5°C Ta. Basal rate of metabolism is the average of measurements between 28 and 34°C . Open and closed circles indicate different animals.



at temperatures above the thermoneutral zone as in most other mammals; it remains constant at about 37.5°C. During activity, however, body temperature greatly increases and the animals became hyperthermic (Fig. 3-2). A high rate of evaporative water loss coupled with a low basal rate of heat production and high thermal conductance may be important in the ability of C. hottentotus to maintain a low T_b at high ambient temperatures.

Response to low oxygen tensions

Critical oxygen pressures were determined by calculating linear equations relating ΔT_b and \dot{V}_{bO_2} to P_{O_2} below P_c (Fig. 3-3, 3-4, 3-5, 3-6, 3-7, 3-8, 3-9, 3-10, 3-11, and 3-12). These equations are given in Table 2. Note that the equation $\dot{V}_{bO_2} = b(\dot{V}_{O_2}) P_{O_2} + \text{intercept}$ could not be calculated for S. aquaticus or M. macronyx, because neither species showed a reduction in the rate of metabolism below normoxic values at any combination of P_{O_2} and T_a used (Fig. 3-4 and 3-6). Consequently, P_{cO_2} could not be calculated by extrapolating the equation to normoxic V_O . Both species did show a reduction in T_b when exposed to very low P_{O_2} and low T_a , thus allowing the calculation of P_{cT_b} (Fig. 3-3, 3-5; Table 3-2 and 3-3).

Critical oxygen pressure for body temperature generally is higher than for resting oxygen consumption. Maximal rates of oxygen consumption are, however, more sensitive to a low P_{O_2} than T_b ; these relationships are shown in Figures 3-3, 3-4, 3-5, and 3-6 for S. aquaticus and N. macronyx.

Table 3-3 shows the P_c for body temperature and resting \dot{V}_{O_2} for fossorial mammals. The P_{cO_2} values for S. aquaticus and M.

Figure 3-3. Change in body temperature (mean \pm SE) in Scalopus aquaticus at different combinations of T_a and P_{O_2} .

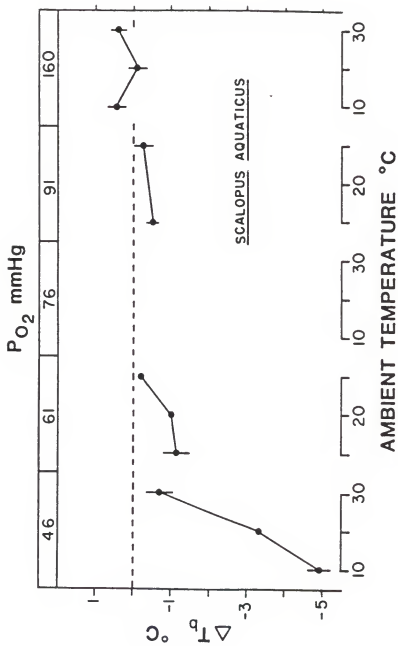


Figure 3-4. Resting rate of oxygen consumption (mean \pm SE) in Scalopus aquaticus versus P_{O_2} at different T_a . Upper curve is the highest rate of metabolism measured at 10°C.

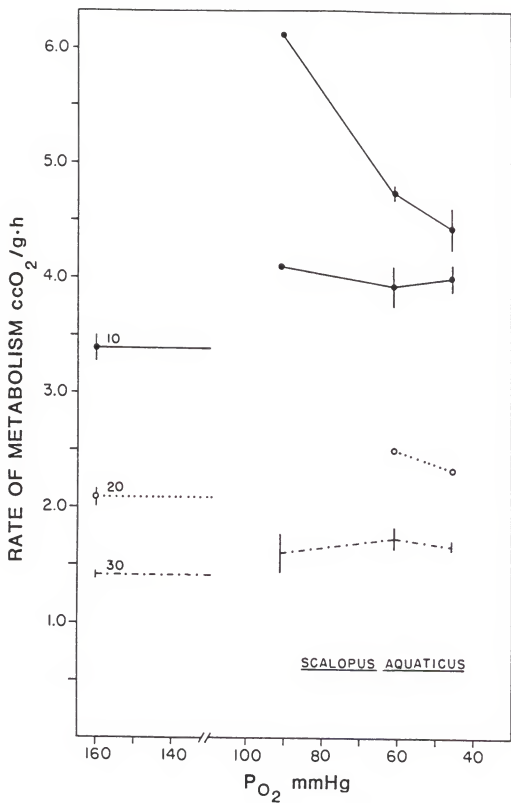


Figure 3-5. Change in body temperature (mean \pm SE) of Notiomys macronyx at different combinations of T_a and P_{O_2} .

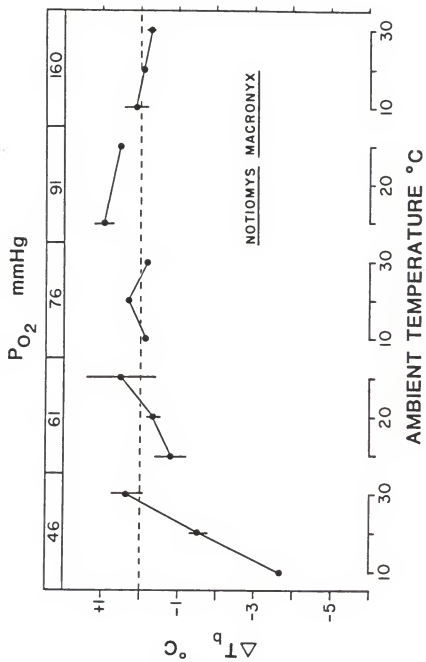


Figure 3-6. Resting rate of oxygen consumption (mean \pm SE) in *Notiomys macronyx* versus P_{O_2} at different T_a . Upper curve is the highest rate of metabolism measured at 10°C.

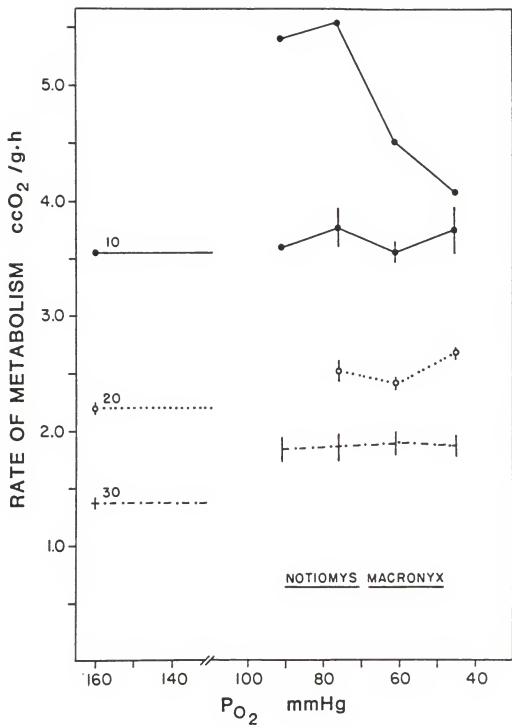


Figure 3-7. Change in body temperature (mean \pm SE) of Cryptomys hottentotus at different combinations of T_a and P_{O_2} .

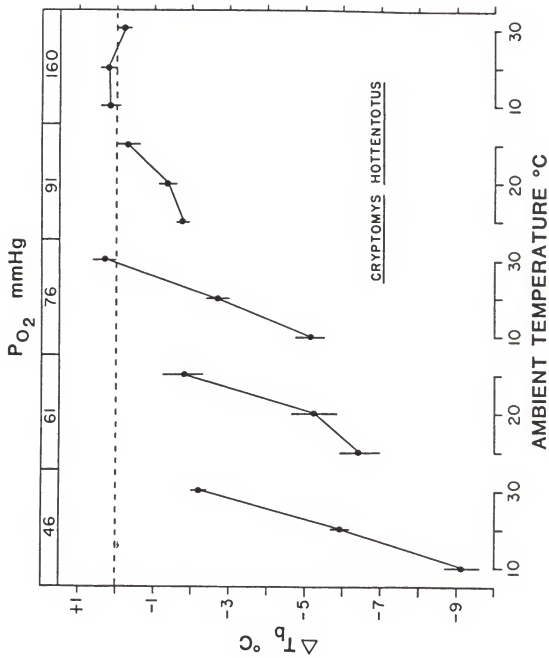


Figure 3-8. Resting rate of oxygen consumption (mean \pm SE) in Cryptomys hottentotus versus P_{O_2} at different T . Equations for lines below P_c are given in Table 3-2. For clarity, points at $30^\circ C$ are not connected by a line.

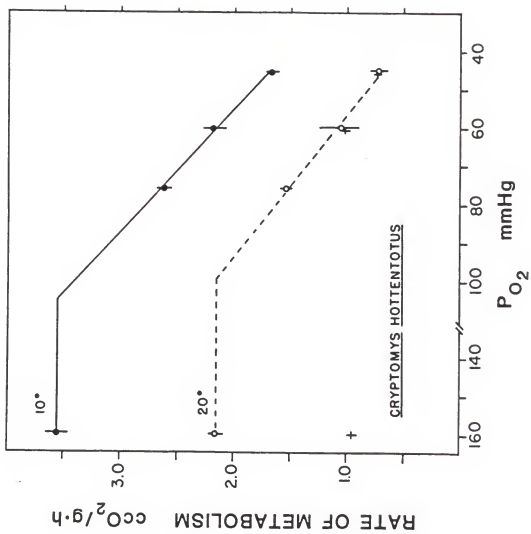


Figure 3-9. Change in body temperature (mean \pm SE) of Spalacopus cyanus from low altitude, at different combinations of T_a and P_{O_2} .

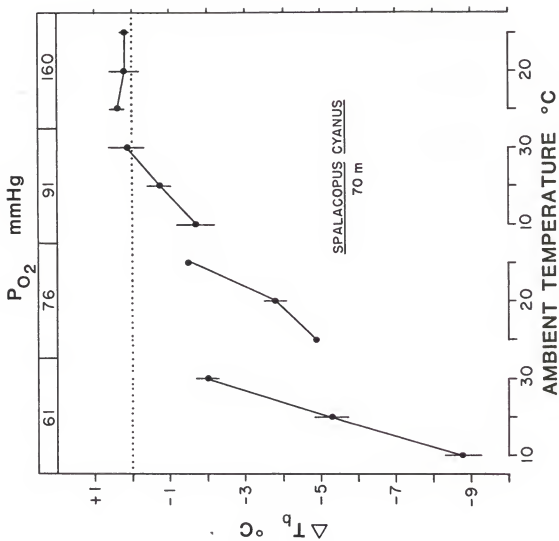


Figure 3-10. Resting rate of oxygen consumption (mean \pm SE) in Spalacopus cyanus from low altitude versus P_{O_2} at different T_a . Equations for lines below P_c are given in Table 3-2.

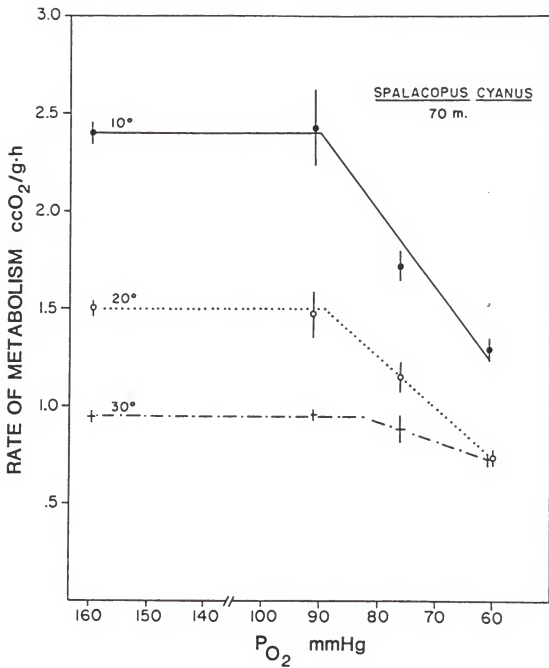


Figure 3-11. Change in body temperature (mean \pm SE) of Spalacopus cyanus from high altitude at different combinations of T_a and P_{O_2} .

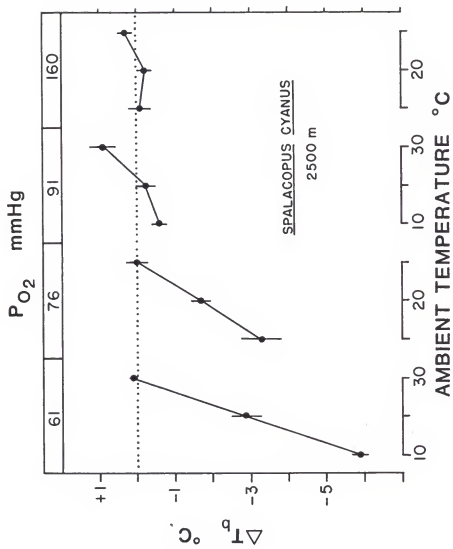


Figure 3-12. Resting rate of oxygen consumption (mean \pm SE) in Spalacopus cyanus from high altitude versus P_{O_2} at different T_a . Equations for lines below P_c are given in Table 3-2.

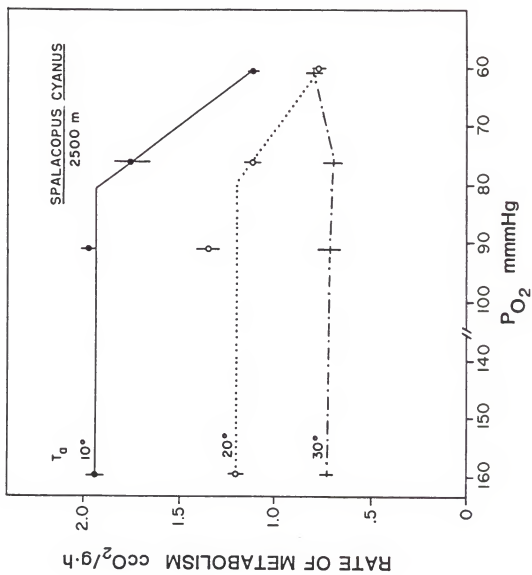


Table 3-2. Linear regression equations of T_b and \dot{V}_{O_2} versus P_{O_2} below values of normoxia in fossorial mammals.

Species	T_a	1. $\Delta T_b = b(T_b) \times P_{O_2} - \text{intercp.}$		n	r^2	p <		
		2. $\dot{V}_{O_2} = b(\dot{V}_{O_2}) \times P_{O_2} - \text{intercp.}$						
<u>Scalopus aquaticus</u>	10	1.	0.2489	16.38	5	0.998	.01	
	20	1.	0.1085	11.25	8	0.920	.01	
<u>Notiomys macronyx</u>	10	1.	0.1960	12.75	6	0.937	.01	
	20	1.	0.0822	5.33	5	0.912	.01	
<u>Cryptomys hottentotus</u>	10	1.	0.1585	16.38	7	0.974	.01	
		2.	0.0321	0.21	4	0.992	.01	
	20	1.	0.1085	11.25	8	0.920	.01	
		2.	0.0272	0.56	6	0.910	.01	
<u>Scalopus cyanus</u>	70 m	10	1.	0.2332	22.84	11	0.945	.01
		2.	0.0377	1.06	11	0.800	.01	
	20	1.	0.1544	15.05	11	0.876	.01	
		2.	0.0271	0.91	7	0.766	.01	
	2500 m	10	1.	0.1728	16.37	15	0.922	.01
			2.	0.3984	1.28	8	0.823	.01
		20	1.	0.0757	7.48	8	0.507	.05
			2.	0.0230	0.62	8	0.895	.01
<u>Spalax ehrenbergi</u> ¹	10	1.	0.2332	16.62				
		2.	0.0362	0.21				
	20	1.	0.0995	7.24				
		2.	0.0115	0.77				

1. From Arieli et al. 1977

Table 3-3. Critical oxygen pressures for resting rates of metabolism and body temperature for fossorial mammals.

Species	M _b (g)	N	T _a	P _{cT_b}	P _{cO₂}	Reference
<u>Scalopus aquaticus</u>	45.5	3	10	68.8	65.9 ¹	This study
			20	67.2		
<u>Notiomys macronyx</u>	62.0	1	10	65.1	62.0 ¹	This study
			20	64.9		
<u>Cryptomys hottentotus</u>	71.4	2	10	103.3	104.1	This study
			20	103.6	100.1	
<u>Spalacopus cyanus</u>						
70 m	95.9	5	10	97.9	91.9	This study
			20	97.5	89.1	
2500 m	137.8	6	10	94.7	80.7	This study
			20	94.5	79.4	
<u>Scalax ehrenbergi</u>	186.0	18 ²	10	71.3	65.0	Arieli et al. 1977
			20	72.8	82.0	

¹ Values calculated by the equation $P_{cO_2} = 1.0561 P_{cT_b} - 7.2900$ ($n = 6$, $r = .854$, $P < .01$) for $T_a = 10^\circ C$.

² Total number of animals captured, actual number of animals used in the experiments not given.

P_{cT_b} = Critical oxygen pressure below which body temperature falls below normal value, mm Hg

N = Number of animals used in the experiments.

T_a = Ambient temperature, °C.

P_{cO₂} = Critical oxygen pressure below which metabolic rate falls below normal value, mm Hg.

macronyx were estimated by using the equation

$$P_{cO_2} = 1.0561 P_{cT_b} - 7.29$$

($r^2 = 0.729$, $p < .01$, $n = 6$) at $T_a = 10^\circ\text{C}$ derived from the data given in Table 3-3.

Discussion

The relation of rate of metabolism and body temperature to P_{O_2} in fossorial mammals is similar to that of other mammals (Segrem and Hart 1967; Rosenmann and Morrison 1974, 1975; Arieli et al. 1977). Mammals can tolerate large reductions in P_{O_2} with no reduction in their rates of oxygen consumption or body temperatures. The critical oxygen pressure, below which there is a progressive reduction in \dot{V}_{O_2} and T_b , is proportional to the rate of metabolism (Segrem and Hart 1967; Rosenmann and Morrison 1975, 1976; Arieli et al. 1977). Consequently P_c is generally higher at a lower T_a . Surprisingly, Arieli et al. (1977) reported that P_{cO_2} for Spalax ehrenbergi is 17 mm Hg lower at 10°C than at 20°C (Table 3-3). It is difficult to explain this observation.

I found that the critical oxygen pressure for T_b is higher than for resting \dot{V}_{O_2} in fossorial mammals (Table 3-3); a similar conclusion can be derived from data given for Spalax ehrenbergi at 10°C (Arieli et al. 1977). The reduction in T_b indicates an increment in thermal conductance, probably due to locomotor activity to avoid hypoxic conditions. In the tundra vole (Microtus oeconomus), body temperature decreases at a faster rate, if the animal is active under hypoxic conditions (Rosenmann and Morrison 1974). Body temperature is generally more sensitive than \dot{V}_{O_2} to extreme

conditions. In mammals exposed to high T_a , body temperature increases above normal values before the rate of oxygen consumption.

Critical P_{O_2} for six highland and 15 lowland small mammal species has been reported by Rosenmann and Morrison (1975). They arbitrarily adjusted P_c values to 3.8 times standard rate of metabolism ($3.8 M_b^{-.27} \text{ cm}^3\text{O}_2/\text{g h}$). For comparison I adjusted the data from this study to 3.8 times the basal rate of metabolism (Table 3-4). The comparison showed that fossorial mammals had a P_c significantly lower than that found in both lowland mammals ($t = 5.10$, $n = 21$, $P < .001$) and highland mammals ($t = 2.63$, $n = 10$, $P < .05$). Undoubtedly this greater tolerance to low P_{O_2} is important to fossorial mammals, especially when active in closed burrows at low ambient temperatures and high altitudes.

The data on fossorial mammals at 10°C (Table 3-3) show independence of P_c with respect to body mass:

$$\log P_{cO_2} = -0.0392 \log M_b + 82.177$$

($r^2 = 0.015$, $P > 0.5$, $n = 6$). Despite a proposed correlation of the ability to extract oxygen at low tensions with body mass (Hall 1966). Similar results to this study were found for 21 species ranging from 8 to 481 g by Rosenmann and Morrison (1975); however, it is possible that in their study the influence on body size on P_c has been obscured by the standardization to 3.8 times basal rate of metabolism. Since larger species require a lower ambient temperature to reach a 3.8 times basal rate of metabolism than smaller species. Low rates of metabolism in fossorial mammals have been considered as an adaptation to low P_{O_2} (Baudinette 1972, Arieli et al. 1977, Arieli and Ar 1981b). Although

Table 3-4. Critical oxygen pressures (P_c) for fossorial mammals adjusted to 3.8 basal rate of metabolism according to Rosenmann and Morrison (1975).

Species	\dot{V}_{bO_2}	$\dot{V}_{O_2} 10^{\circ}C/\dot{V}_{bO_2}$	$3.8 - (\dot{V}_{O_2} 10^{\circ}C/\dot{V}_{bO_2}) \times 13$	$P_c (3.8\dot{V}_{bO_2})$	Reference
<u>Scalopus aquaticus</u>	1.41	2.397	18.24	84.0	This study
<u>Notiomys macronyx</u>	1.36	2.578	15.89	78.0	This study
<u>Cryptomys hottentotus</u>	0.952	3.725	0.97	105.1	This study
<u>Spalacopus cyanus</u>					
70 m	0.956	2.45	17.56	109.5	This study
2500 m	0.754	2.581	15.9	96.6	This study
<u>Spalax ehrenbergi</u>	0.99	2.756	13.6	78.0	Arieli et al. 1977

\dot{V}_{bO_2} = Basal rate of metabolism ($ccO_2 g^{-1}h^{-1}$).

there is a correspondence between the rate of metabolism and P_c at the intraspecific level, no correlation is found interspecifically among fossorial mammals between the rate of metabolism and P_c , irrespective of whether rate of metabolism is expressed per unit body mass:

$$P_{cO_2} = -39.75 (\dot{V}_{bO_2}) + 120.8 \quad (r^2 = .362, P > 0.10, n = 6)$$

or on total body size:

$$P_{cO_2} = -0.1603 (\dot{V}_{bO_2} M_b) + 93.9 \quad (r^2 = .1737, P > 0.20, n = 6)$$

A larger number of species was considered from Rosenmann and Morrison (1975) (Table 3-5) to determine whether the lack of correlation was peculiar to fossorial mammals or due to small sample sizes. These data also indicate that no correlation exists between P_c and the rate of metabolism at the interspecific level when expressed per unit body mass:

$$P_{cO_2} = -1.500 (3.8\dot{V}_{bO_2}) + 130.7 \quad (r^2 = 0.142, P > .20, n = 14)$$

or on total body size:

$$P_{cO_2} = 0.0086 (3.8\dot{V}_{bO_2} M_b) + 118.2 \quad (r^2 = 0.079, P > .20, n = 14)$$

I conclude that fossorial mammals do show a greater tolerance to low P_{O_2} , however this greater tolerance is related neither to body mass nor to the rate of metabolism at the interspecific level. The critical P_{O_2} as measured here is the response of the whole individual to low P_{O_2} . Specific values are the result of a combination of several physiological characteristics, such as small respiratory dead space (Darden 1972), high blood oxygen-affinity (Hall 1965, 1966; Bartels et al. 1969; Baudinette 1974; Ar et al. 1977; Quilliam et al. 1971; Lachner 1976), low heart rate (Arieli and Ar 1981a), short tissue

Table 3-5. Basal rate of metabolism (\dot{V}_{bO_2}), critical oxygen pressure (P_C) for metabolism for some of the species studied by Rosenmann and Morrison (1975).

Species	\dot{V}_{bO_2} ^a	M_b	P_C	Reference
<u>Octodon degus</u>	0.811	181	139	12, personal data
<u>Acomys cahirinus</u>	1.10	49	131	16
<u>Spermophilus parryii</u>	0.68	472	131	2, 4, 15
<u>Glaucomys volans</u>	1.217	67	128	9, 10
<u>Baiomys taylori</u>	1.95	8	127	6
<u>Microtus oeconomus</u>	2.50	36	123	2
<u>Meriones unguiculatus</u>	1.412	48	123	3, 7, 11, 17
<u>Dicrostonyx rubricatus</u>	1.83	52	123	2, 15
<u>Clethrionomys rutilus</u>	3.00	33	122	14
<u>Cavia porcellus</u>	0.581	481	117	Personal data
<u>Mus musculus</u> (feral)	1.80	19	116	13
<u>Mus musculus</u> (white)	1.76	35	116	13
<u>Peromyscus maniculatus</u>	1.908	21	109	5, 8
<u>Microtus pennsylvanicus</u>	1.93	29	97	1

1, Bradley 1976; 2, Casey et al. 1979; 3, Contreras 1984a; 4, Erikson 1956; 5, Hayward 1965; 6, Hudson 1965; 7, Luebert et al. 1979; 8, McNab and Morrison 1963; 9, Muul 1968; 10, Neumann 1967; 11, Robinson 1959; 12, Rosenmann 1977; 13, Rosenmann and Morrison 1974; 14, Rosenmann et al. 1975; 15, Scholander et al. 1950; 16, Shkolnik and Borut 1969; Weiner and Gorecki 1981.

Body mass (M_b) and P_C from Rosenmann and Morrison (1975).

a Average from estimated values.

diffusion distance (Arieli and Ar 1981**b**), and high myoglobin concentration in skeletal muscles (Ar et al. 1977; Lachner 1976), each of which permits these animals to tolerate hypoxic conditions.

Low P_c values of fossorial mammals permit them to tolerate lower P_{O_2} environments than surface dwelling mammals. Even though low rates of metabolism are not important in setting P_c , they may reduce respiratory stress from low O_2 and high CO_2 tension because the development of hypoxic and hypercapnic conditions in burrows is directly proportional to rate of metabolism (Withers 1978**b**, MacLean 1981). The combination of low P_c and low $\dot{V}O_2$ may have special relevance to colonial species with large body mass that live in clay humid soils at high altitude, since these conditions enhance hypoxia and hypercapnia in burrow microenvironments (Withers 1978**b**; Wilson and Kilgore 1978; Arieli 1977; MacLean 1981).

CHAPTER FOUR
ENERGETICS OF FOSSORIAL MAMMALS AND ITS RELATION
TO BODY MASS AND DISTRIBUTION

Introduction

Mammals usually avoid environmental fluctuations in their environment by adjusting their activity pattern and/or by living in comparatively constant microenvironments. Fossorial mammals of many different taxa, e.g., marsupials, insectivores, edentates and rodents, spend most of their life in burrows. Their food, invertebrates, roots and tubers, is contained in the soil and they excavate tunnels to obtain it. They are seldomly, if ever, seen above ground, except in some species during breeding, dispersal, or flooding of their burrows.

Burrow microenvironments are characterized by darkness, high relative humidity, small temperature fluctuations, and hypoxic and hypercapnic atmospheres (Rosenmann 1939, Kennerly 1964, McNab 1966, Studier and Baca 1968, Studier and Proctor 1971, Baudinette 1974, Arieli 1979, McLean 1981).

Several physiological as well as morphological (Dubost 1968) characteristics of these animals have been proposed as adaptations to this way of life. Other studies have analyzed the respiratory adaptations to hypoxia and hypercapnia (Darden 1972, Hall 1965, Bartels et al. 1969, Baudinette 1974, Ar et al. 1977, Quilliam et al. 1971, Lechner 1976, Arieli and Ar 1981a, b). Early studies on the energetics

of fossorial mammals indicated that they are characterized by a low basal rate of metabolism and a standard to high thermal conductance (McNab 1966, Gorecki and Christov 1969, Bradley et al. 1974, Bradley and Yousef 1975, Nevo and Sholnik 1974).

Low basal rate of metabolism has been interpreted as an adaptation to hypoxic and hypercapnic conditions of their burrows (Baudinette, 1972, Arieli et al. 1977, Arieli and Ar 1981b). Fossorial mammals indeed have a lower critical oxygen pressure than surface-dwelling mammals, however this critical oxygen pressure bears no relation to the rate of metabolism at the interspecific level.

The interaction of low basal rate of metabolism, high minimal thermal conductance and small body size has been interpreted as a to reduce overheating (McNab 1966, MacMillen and Lee 1970, Ross, 1980) when digging, especially in warm burrows. However, the low basal rate of metabolism and low body temperature of the golden-mole Chrysochloris asiatica have been interpreted as a consequence of a "primitive" physiology (Withers 1978). A final interpretation of the low basal rate of metabolism and small body size of this animal relates them to the high energy expenditure involved in food searching by digging (Vleck 1979, 1981, Andersen 1982). Even though all these hypotheses intend to explain low rates of metabolism and small body size, it has been found lately that fossorial mammals at body mass less than 80 g tend to have higher rates of metabolism than expected (McNab 1979).

Here I present and analyze new data on the energetics of fossorial mammals, together with the data available in the literature, in relation to body size, food habits, and distribution.

Methods

Animals. Three Scapanus latimanus were caught in mole live traps (Yates and Schmidly 1975) along a small stream on the Stanford University campus, Santa Clara Co., California in June, 1982.

Two Aconaemys fuscus were trapped alive using leg traps Oneida Victor No. 0, with the edges cushioned by Tygon tubing. They were trapped 3 km east of Laguna Malleco, Parque Nacional Tolhuaca, IX Region, Chile, in November, 1982. For description of the habitat see Greer (1966).

Four Ctenomys sp. (Gallardo 1979) were caught in the same way as A. fuscus in Longuimay and Liucura, Prov. Malleco, IX Region, Chile (30° 27'S, 71° 17'W and 38° 30'S, 71° 10'W) in November, 1982. For description of the habitat refer to Greer (1966).

Six Ctenomys maulinus bruneus were caught in Cordillera de Las Raices, Prov. Malleco IX Region, Chile (38° 26'S, 71° 27'W) at 1650 m altitude in December, 1980. These animals were caught in open volcanic sands as well as in Nothofagus-Araucaria forest.

Six Ctenomys fulvus were trapped in the vicinities of San Pedro de Atacama, II Region, Chile (22° 25'S, 68° 15'S) at 2436 m during September 1982. Two other individuals tentatively assigned to Ctenomys fulvus were collected in La Ola, III Region, Chile (26° 30'S, 69° 05'W) by the side of a stream at 4,000 m during September, 1982. The climate in this locality, as in San Pedro de Atacama, is a high altitude desert (Cagri and Hajek 1976).

Four individuals of Thomomys bottae melanotus were trapped near Bishop, Owen's Valley, Inyo Co., California (37° 25'N, 118° 25'W) in April, 1982.

Four T. bottae bottae were trapped on the Stanford University Campus (37° 30'N, 122° 12'W) in May, 1982.

Two T. townsendii beckmani were collected in Valmy, Humbolt Co., Nevada (40° 50'N, 117° 15'W) during May-June, 1982.

All rodents were maintained in individual cages provided with sawdust or moist dirt. The rodents were fed sweet potatoes, carrots, green grass, and rabbit food pellets ad libitum. The moles were fed earthworms and canned dog food. Ambient temperature was about 20° with no control of the photoperiod.

Ambient temperatures were recorded in the field in most of the cases.

Experiments.--Rates of oxygen consumption were measured at different ambient temperatures. Oxygen consumption of the animals from Chile was measured in a closed system. The animals were placed in a stainless steel chamber with CO₂ and water absorbents. The chamber was submerged in a thermoregulated water bath, connected to an automatic manometric respirometer and this in turn to a recorder (Morrison 1951). Each animal measurement lasted for at least 3 hours and the lowest value of about 8 to 13 min was considered.

Measurements on Scapanus and Thomomys were made in an open system, using an Applied Electrochemistry Oxygen Analyzer. Each run lasted at least two hours, and the average of the lowest two values lasting at least five min was considered. All values were corrected for STDP and a respiratory quotient equal to 0.8 was assumed in the calculations. Body mass and body temperature were recorded at the beginning and at the end of each run.

In the case of Ctenomys maulinus and C. fulvus measurements were also made with an open system as described in Chapter Two.

Minimal thermal conductance was calculated as the average of each individual measurement of oxygen consumption, usually below 20° C ambient temperature (McNab 1980). When minimal thermal conductance reported in the literature was calculated by linear regression and did not extrapolate to body temperature at \dot{V}_{O_2} equal to zero, it was recalculated according to McNab (1980).

Results

A summary of the data on the energetics of the species studied here, as well as that found in the literature, is presented in Table 4-1. A species by species interpretation is given in this section.

Scapanus latimanus is a good thermoregulator, the average body temperature (T_b) equals 37.1° C at ambient temperatures (T_a) between 6 and 30° C. At higher T_a s body temperature increased to 37.6 at 34° C T_a , when the animal was at rest. However, when the animal was active, it became hyperthermic (Fig. 4-1). This species has a basal rate of metabolism (\dot{V}_{bO_2}) as expected from body mass (100.3%) (Kleiber 1932, 1961). Minimal thermal conductance (C_m) was lower than expected from body mass (87.4%) (McNab and Morrison 1963). These values are similar to those reported for Scalopus aquaticus (McNab 1979). Neither of these two species clearly distinguishes between physical and chemical thermoregulation, as is shown by the high \dot{V}_{O_2} values near the lower limit of thermoneutrality (Fig 4-1).

Table 4-1. Parameters of energetics in fossorial mammals.

Species	V_{b02}		$\bar{x} \pm SE$	n/N	$\bar{x} \pm SE$	C_m	$\bar{x} \pm SE$	n/N	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	ΔT_1	T_1	T_b	F	$\bar{x} C_m$	References
	$\bar{x} \pm SE$	n/N																	
Insectivores:																			
<u>Blarina brevicauda</u>	21	2.50			156.0	0.235			108.0	1.45	38.5	29.0	9.5						Platt 1974
<u>Chrysochloris asiatica</u>	33	1.20 \pm 0.08	9/		84.1	0.144			82.6	1.02	32.5	24.2	8.4						Withers 1978
<u>Scalopus aquaticus</u>	48	1.41 \pm 0.053	20/2		109.0	0.130 \pm 0.0033	12/2		90.0	1.21	36.0	26.0	10.0						McNab 1979
<u>Scapanus latimanus</u>	61	1.25 \pm 0.024	8/2		100.3	0.112 \pm 0.002	14/2		87.4	1.15	37.1	25.9	11.2						This study
<u>Amblysomus hottentotus</u>	70	1.21			102.3						33.5								Kuyper 1979
<u>Talpa europaea</u>	100										36.2								Poczopko and Chrzanoski 1966
Rodents:																			
<u>Pitymys pinetorum</u>	25	1.98 \pm 0.07	22/		129.0	0.191 \pm 0.006	40/		97.0	1.33	38.3	29.7	9.2						Bradley 1976
	26	2.60			172.0														Pearson 1947
<u>Heterocephalus glaber</u>	35?	0.66			47.0	0.339			200.0	0.24	32.8	30.9	1.9						Jarvis 1978
	39	0.66 \pm 0.024	20/		48.0	0.387 \pm 0.0145	22/		242.0	0.20	32.1	30.5	1.6						McNab 1966
<u>Hottomys macronyx</u>	62	1.36 \pm 0.027	11/1		113.4	0.131 \pm 0.0025	14/1		103.0	1.10	36.8	26.7	10.1						This study
<u>Cryptomys hottentotus</u>	71	0.95 \pm 0.024	16/2		80.8	0.138 \pm 0.0041	17/2		116.8	0.69	35.7	28.5	7.2						This study
<u>Thomomys umbrinus</u>	85	0.85			75.0	0.121			112.0	0.67	34.6	26.5	8.1						Bradley et al. 1975

Table 4-1 continued.

<u>Heliphobius argentocinerus</u>	88	0.85 ± 0.043	8/	76.0	0.139 ± 0.0050	20/	130.0	0.58	35.1	30.0	5.1	McNab 1966
<u>Spalacopus cyanus</u>	83	0.96 ± 0.023	16/8	84.6	0.088 ± 0.0023	29/8	80.0	1.06	36.7	26.0	10.7	This study
	136	0.75 ± 0.026	15/9	74.1	0.074 ± 0.0015	32/9	84.8	0.87	36.4	26.4	10.0	"
	185	0.79 ± 0.020	19/2	85.0	0.080 ± 0.0020	21/2	109.0	0.78	36.4	26.5	9.9	McNab 1979
<u>Spalax ehrenbergi</u>	104	1.03		96.0								Nevo and Shkolnik 1974
	117	0.85		82.0								"
	121	0.62		60.0								"
	124	0.87		85.0								"
	128	0.86		85.0								"
	186	0.99 ± (0.01 SD)		108.3	0.107		145.9	0.74	35.5	26.3	9.3	Arieli et al. 1977
<u>Thomomys talpoides</u>	106	1.03		97.0	0.099		106.0	0.95	35.5	25.0	10.5	Bradley et al. 1974
	111	1.33		126.0	0.101		106.0	1.19	36.9	25.0	11.9	Gettinger 1975
<u>Aconaemys fuscus</u>	112	1.08 ± 0.017	13/2	103.5	0.090 ± 0.0019	18/2	94.6	1.09	37.3	25.3	12.0	This study
<u>Ctenomys sp</u>	117	0.82 ± 0.018	12/3	78.1	0.073 ± 0.0016	12/3	81.7	0.96	36.4	25.3	11.1	"
	197	0.66 ± 0.019	8/1	71.9	0.057 ± 0.017	11/1	81.1	0.89	36.4	24.7	11.6	"
<u>Geomys pinetis</u>	126	0.90 ± 0.04		87.7	0.126 ± 0.005		141.4	0.62	36.1	29.0	7.1	Ross 1980
	136	1.03 ± 0.04		103.0	0.130 ± 0.005		151.6	0.68	35.1	27.2	7.9	"
	144	0.74		75.0	0.112 ± 0.003		134.4	0.56	35.9	29.3	6.6	"

Table 4-1 continued.

Species	\bar{M}_b		\bar{V}_{b02}		$\bar{z}V_{b02}$	C_m		ΣC_m	F	T_b	T_1	ΔT_1	References
	\bar{x}	\pm SE	\bar{x}	\pm SE		\bar{x}	\pm SE						
150	0.69	\pm 0.10	70.2	0.104	\pm 0.004	127.4	0.55	35.4	28.8	6.6	"		
157	0.91	\pm 0.05	94.0	0.116	\pm 0.006	145.4	0.65	34.5	26.7	7.8	"		
162	0.85	\pm 0.5	89.0	0.095	\pm 0.002	120.9	0.74	36.1	27.1	9.0	"		
200	0.71	\pm 0.019	26/	0.065	\pm 0.002	19/	92.0	0.85	36.3	26.0	10.3	McNab 1966	
178	0.63		67.0	0.079		105.0	0.63	36.0	24.0	12.0	Gorecki and Christov 1969		
201	0.74	\pm 0.011	11/	0.066	\pm 0.002	16/	94.0	0.87	36.6	25.0	11.6	McNab 1966	
191	0.79	\pm 0.029	20/	0.090	\pm 0.0028	25/	124.0	0.69	35.9	26.5	9.4	"	
111	0.97	\pm 0.049	8/4	0.089	\pm 0.0025	19/4	93.3	1.00	37.3	26.4	10.9	This study	
143	0.84	\pm 0.030	21/	0.079		94.6	0.90	36.0	25.4	10.6	Vleck 1979		
143	0.85	\pm 0.029	9/2	0.074	\pm 0.0022	5/2	88.4	0.97	37.4	25.8	11.5	This study	
262	0.61	\pm 0.023	7/2	0.059	\pm 0.0006	8/2	94.0	0.77	37.4	27.0	10.3	"	
197	0.70		10/7	0.121		16/7	170.0	0.45	35.0	30.0	5.0	Bradley and Yousef 1975	
215	0.87	\pm 0.019	9/2	0.056	\pm 0.0017	11/6	82.0	1.19	36.2	20.7	15.5	This study	
249	0.76	\pm 0.025	9/2	0.059	\pm 0.0017	13/2	91.4	0.97	37.6	24.6	13.0	"	
275	0.64	\pm 0.037	15/6	0.050	\pm 0.0074	25/6	81.6	0.89	35.6	22.7	12.9	"	
300	0.63	\pm 0.015	13/2	0.046	\pm 0.0013	13/2	79.2	0.98	36.6	22.9	13.7	"	
344	0.50	\pm 0.029	11/5	0.054	\pm 0.0012	39/5	100.0	0.63	36.0	27.0	9.0	McNab 1979	
490	0.45		2/	0.056		2/	124.0	0.50	35.2	27.2	8.0	Morrison and McNab per. com.	

Table 4-1 continued.

<i>Aplodontia rufa</i>	630	0.44 ± 0.011	11/3	64.0	0.039 ± 0.0006	25/3	98.0	0.66	38.0	26.5	11.5	McNab 1979
	1120	0.54?		91.0	0.030		100	0.91?	38.0	20.0?	18.0?	Kinney 1971

M_b = Body mass, g.

\dot{V}_{bO_2} = Basal rate of metabolism, cm^3O_2/g h.

$2\dot{V}_{bO_2}$ = Basal rate of metabolism as a percentage of the Kleiber relation, $3.42 M_b^{-0.25}$.

C_m = Minimal thermal conductance, cm^3O_2/g h °C.

F = $2\dot{V}_{bO_2}/C_m$.

T_b = Body temperature, °C.

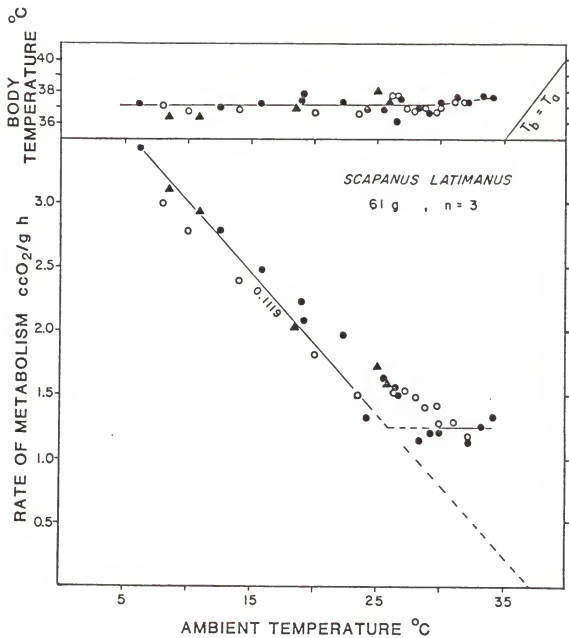
T_1 = Lower limit of thermoneutrality, °C.

ΔT_1 = Temperature differential between T_b and T_1 , °C.

n/N = Number of measurements/ number of animals.

$\%C_m$ = Minimal thermal conductance as a percentage of $1.00 M_b^{-0.50}$ (McNab and Morrison 1963).

Figure 4-1. Rate of metabolism and body temperature versus ambient temperature in Scapanus latimanus. Different symbols represent different animals (3). The open circle at 33.2°C ambient temperature represent an active animal. Mean \dot{V}_{O_2} was calculated between 30 and 34°C. Minimal thermal conductance is indicated by the slope of the line below thermoneutrality. The numerical value of slope is indicated in the graph.



A temperature range of 19.5-26° C was found in the superficial burrows of S. latimanus (ca. 4-6 cm deep) in which these animals were captured. At the same time the temperature range was 12-29° C in the air, 15-36° C at the ground surface, and 20.5-22.2° C at 25 cm deep in the ground. The ground was very humid.

Aconaemys fuscus had an average $T_b = 37.3^\circ \text{C}$ at air temperatures between 6 and 32° C; T_b increased slightly with T_a (Fig. 4-2). They have a V_{bO_2} and C_m close to expected (103.5 and 94.6%, respectively). Frequent rainfall and snowfall are common in the range of A. fuscus. The temperature range in the air was -3 to 18° C; at 20 cm deep in the ground it was 13.5 to 14° C.

Ctenomys sp. maintains an average $T_b = 36.4^\circ \text{C}$ up to 32° C (Fig. 4-3). This species presented a low V_{bO_2} (78-72%) and low minimal thermal conductance (81%). The temperature at 18 cm in the ground was 13° C.

Ctenomys maulinus bruneus maintains an average T_b equal to 36.7° C below 26° C ambient temperature (Fig. 4.4). Body temperature increased sharply at higher T_a . This species has the highest V_{bO_2} of any Ctenomys (94.7%), and the lowest lower limit of thermoneutrality. Ctenomys m. bruneus also shows the least tolerance of high ambient temperature (Fig. 4.4). Minimal conductance is low (82%). Temperatures of 10.7 and 14.5° C were recorded in burrows at 25 and 21 cm deep. The following temperature profile of the ground was also found at 17:30 h on 11 December 1980: Air, 15.2° C; surface, 18° C; 10 cm, 16° C; 20 cm, 14.5° C; 30 cm, 13; and at 50 and 70 cm deep,

Figure 4-2. Rate of metabolism and body temperature versus ambient temperature in *Aconaemys fuscus* from Parque Nacional Tolhuaca, Malleco, IX Region, Chile. Different symbols represent different individuals (2). Mean $\dot{V}bO_2$ was calculated between 28.5 and 33°C. The value given on the line below thermoneutrality is the C_m .

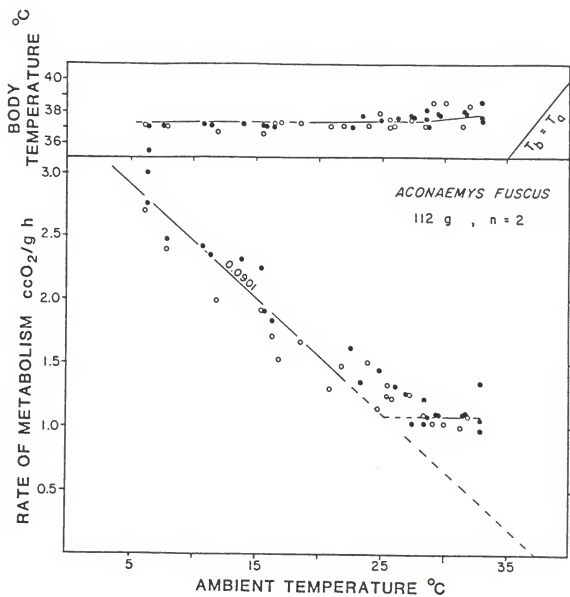


Figure 4-3. Rate of metabolism and body temperature versus ambient temperature in Ctenomys sp. from Malleco Prov., Chile. Different symbols represent different individuals (4). Mean $\dot{V}bO_2$ was calculated between 29 and 32.5°C T_a . The value of the slope of the line below thermoneutrality is C_m .

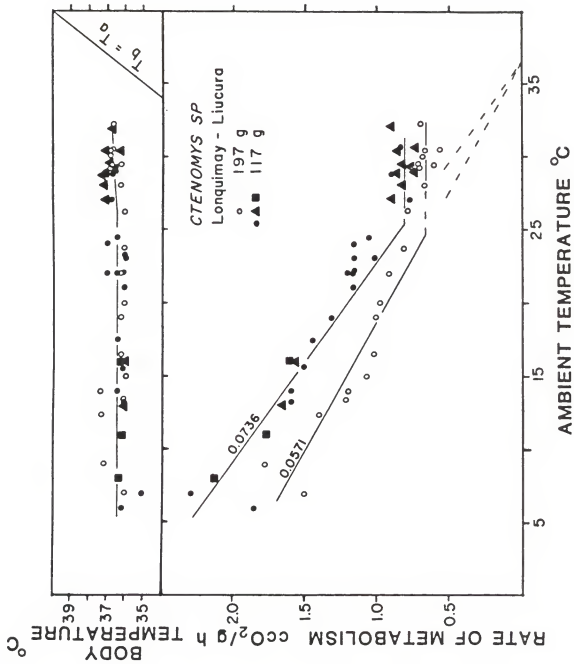
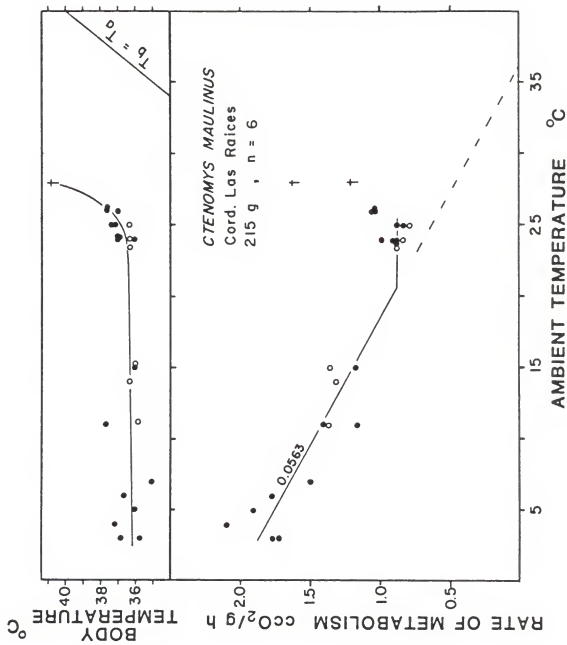


Figure 4-4. Rate of metabolism and body temperature versus ambient temperature in Ctenomys maulinus bruneus from Cordillera de Las Raices, Malleco Prov., IX Region Chile. Closed circles are measurements obtained in a closed system, open circles were obtained in open systems. Crosses represent values obtained at 1.5 and 2.0 hours after an experiment done at 28°C. T_a: the animals died shortly after the experiment.



11° C. Burrow cores were found on the surface of the ground after snow had melted indicating snow-ground interface activity by these animals. The ground at Cordillera de Las Raices is usually covered by snow 6-7 months a year and upon occasion for as much as 10 months.

Ctenomys fulvus, in contrast to C. maulinus, inhabits the extremely arid Atacama Desert. This species maintains a slightly lower T_b up to 25° C T_a ; body temperature increases at T_a higher than 30° C (Fig 4-5 and 4-6). Basal rate of metabolism is 77% of expected. Minimal thermal conductance is also low. Ambient temperatures in the C. fulvus habitat are shown in Table 4-2. Burrow temperatures ranged between 9 and 16.5° C. During February they range between 19 and 25° C (Rosenmann 1959).

Thomomys bottae melanotus from Owens Valley, Cal. had an average T_b equal to 37.3° C at air temperatures below 30° C (Fig. 4-7). Basal rate of metabolism and C_m are slightly lower than expected (93.6 and 93.3%, respectively).

Small T. b. bottae from Stanford University campus have a lower V_{bO_2} and it is even lower in the larger individuals from the same locality (96.3 and 72.4%, Table 4-1, Fig. 4-8). The opposite is true for C_m : it is lower in the smaller animals (88.4% and 94%, Table 4-1, Fig. 4-8). Vleck (1979) reported measurements on T. bottae from southern California that are similar to the values reported here on T. b. bottae with the same body size (Table 4-1). Burrow temperatures for T. b. bottae ranged between 22.8 and 25.5° C. At 20 cm deep, soil temperature was 22.3-25.6° C. Surface temperature varied between 14.4 to 45.0° C.

Figure 4-5. Rate of metabolism and body temperature versus ambient temperature in Ctenomys fulvus from San Pedro de Atacama, Atacama Desert, Chile. Closed circles and open circles are measurements obtained in closed and open systems, respectively. The value on the line below thermoneutrality is C_m .

Figure 4-6. Rate of metabolism and body temperature versus ambient temperature in individuals tentatively assigned to *Ctenomys fulvus* from La Ola, III Region, Chile. Closed and open circles are different individuals. The two highest measurements at 33°C T_a are at 14 and 18 min after the animal became active. The value on the line below thermoneutrality is C_m.

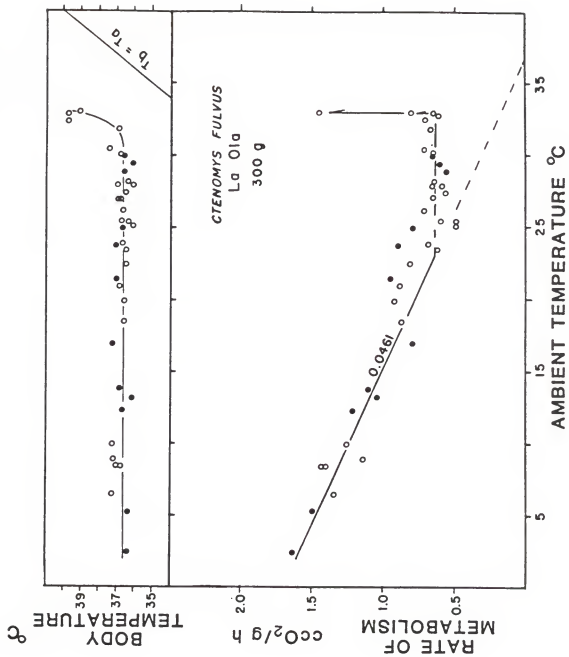


Table 4-2. Ambient temperatures in *Ctenomys fulvus* habitat between San Pedro de Atacama and Solor, II Region, Chile, 20 September, 1982.

Time	T° air	Surface	Burrow		30 cm deep
10:25			8.9	16.1	13.5
11:30			11.2	16.0	13.5
12:15	21.0	50.6	11.6	16.1	14.0
13:00	23.9	51.0		16.2	14.5
13:48			12.9		
14:19	25.0	48.7		16.2	15.5
15:46	24.3		13.8	16.5	16.7
16:57		30.0	13.4	16.3	17.5
17:26	21.0				
22:00	11.1	6.1		16.2	17.5

Figure 4-7. Rate of metabolism and body temperature versus T_a in Thomomys bottae monticola from Owens Valley, California. Minimal thermal conductance is given on the line below thermoneutrality. Mean \dot{V}_{bO_2} was calculated between 28 and 30°C T_a .

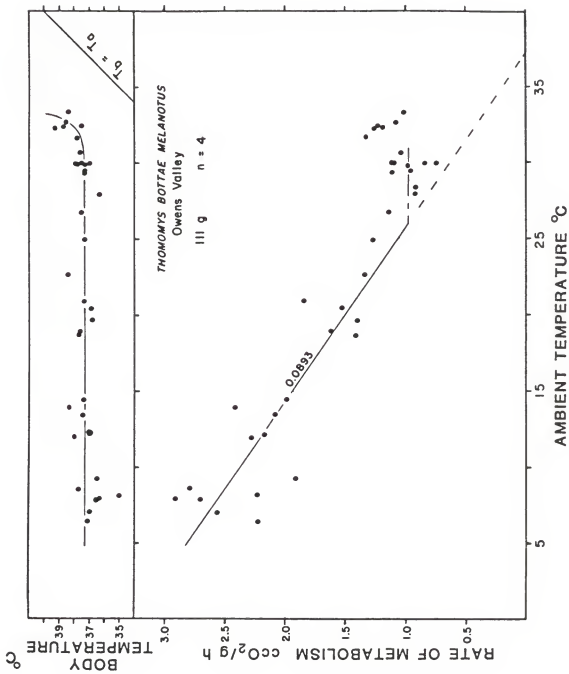
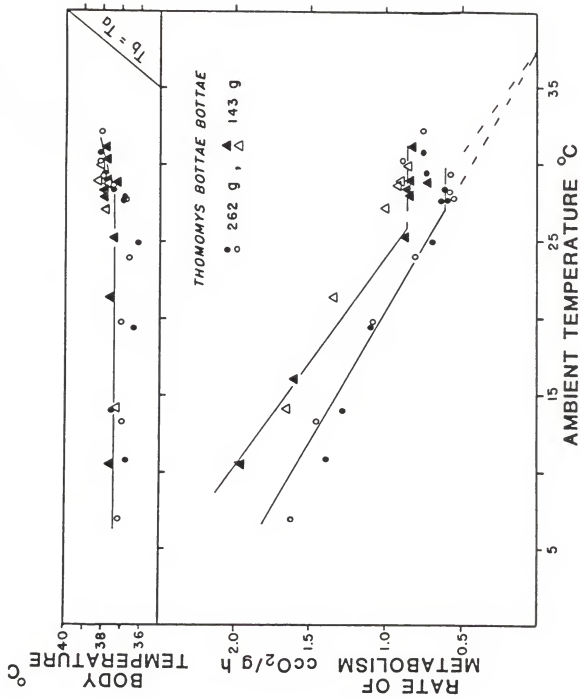


Figure 4-8. Rate of metabolism and body temperature versus \dot{m}_b in four Thomomys bottae bottles from the Stanford University campus, California. Different symbols represent different individuals. Minimal thermal conductances are given on the lines below thermoneutrality.



T. townsendii backmanii maintains an average T_b equal to 37.5°C at air temperatures below 30°C , above which T_b sharply increases. Basal rate of metabolism is 88.5% and C_m is 91.4% (Fig. 4-9). Environmental temperatures taken on 26th June, 1982 at 09:30 h at Valmy, Nevada were as follows: air, 23.6°C ; surface, 39°C ; at 5.5 cm deep, 22.4°C ; and at 9 cm, 19°C .

Discussion

The basal rate of metabolism. McNab (1979) found that his previous conclusion (McNab 1966) that fossorial mammals have a low basal rate of metabolism only holds for animals with a body mass greater than 100 g. The difference between measured values and those expected from the Kleiber relationship increases as body mass increases. When fossorial mammals have a body mass smaller than 80 g, basal rate of metabolism is higher than expected by the Kleiber relation, unless they live in warm environments (T_a 25°C). McNab (1979) proposed that these animals scale basal rate of metabolism in a manner that is different from the Kleiber relation, the exponent falling between -0.50 and -0.40. Linear regression of the data in Table 1 (except H. glaber, C. asiatica, and A. hottentotus, see later) shows that this is actually the case:

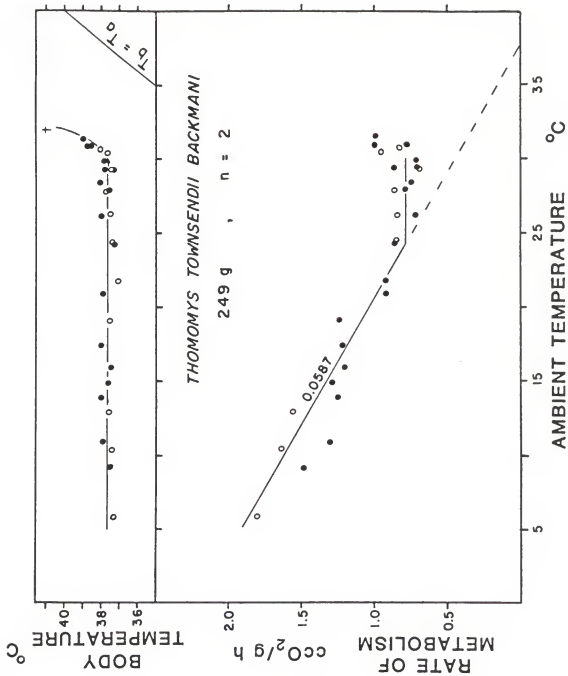
$$\log_{10} \dot{V}_{\text{bO}_2}/M_b^1 = -0.493 \log_{10} M_b + 0.981 \quad n=45 \quad r^2=0.840 \quad (4-1)$$

or

$$\dot{V}_{\text{bO}_2}/M_b = 9.752 M_b^{-0.493} \quad (4-2)$$

This pattern is independent of phylogeny. At small mass, both the insectivore Elarina and the rodent Pitimys, or the mole Scalopus and the cricetid mole-mouse Notiomys, have similarly high basal rates of

Figure 4-9. Rate of metabolism and body temperature versus T_a in Thomomys townsendii backmani from Humboldt, Co., Nevada. Different symbols are different individuals (2). The cross at $32^{\circ}\text{C } T_a$ indicates that the animal died soon after the experiment. The value given on the line below thermoneutrality is the minimal thermal conductance.



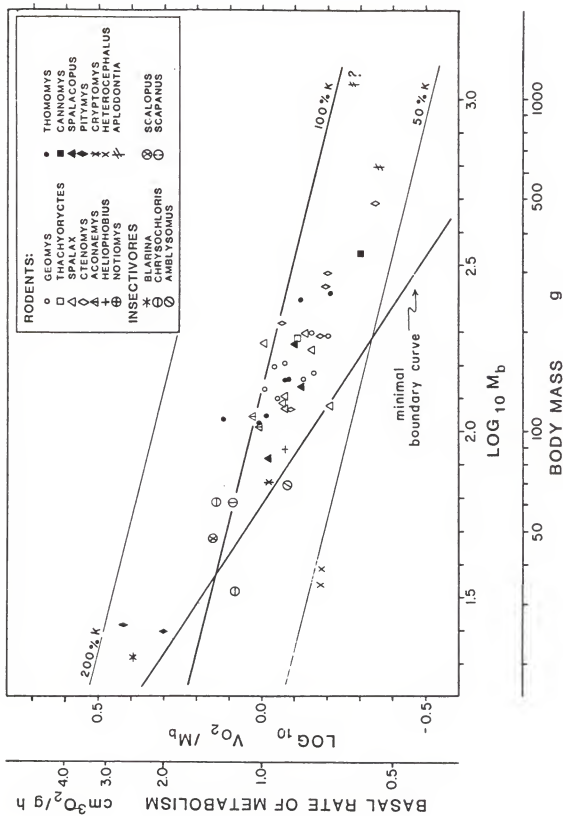
metabolism. On the other hand, both the South American caviomorphs Scalacopus and Ctenomys, and the North American Thomomys have lower basal rates of metabolism with increasing body mass (Fig. 4-10).

Exceptions to this pattern are found among fossorial mammals with body mass lower than 80 g inhabiting warm burrows. The extreme case is represented by the naked mole-rat Heterocephalus glaber (Fig. 4-10). As will be shown, poor thermoregulation is produced by combining a small body size and a low basal rate of metabolism in these animals.

McNab (1983) proposed mean and minimal boundary curves for endothermy relating basal rate of metabolism and body mass (Fig. 4-10). These equations $\dot{V}_{bO_2} / M_b = 21.53M_b^{-0.67}$ and $\dot{V}_{bO_2} / M_b = 15.56M_b^{-0.67}$, respectively, intercept the Kleiber relation at 80 and 37.7 g. Thus, at a small body mass a mammal should have a basal rate of metabolism higher than predicted by the Kleiber relation to be a good thermoregulator. Mammalian species whose basal rate of metabolism falls below this minimal boundary curve are poor thermoregulators and may enter into daily torpor. Among fossorial mammals this is the case for H. glaber, C. asiatica and A. hottentotus (Fig. 4-10).

Even though burrow temperatures show much less daily fluctuation than above ground ambient temperatures, some fossorial species experience considerable fluctuations throughout the year (Ross 1980). It has been widely noticed that fossorial mammals become less active during the warmer seasons (Wilks 1963, Genelly 1965, 1980, Arieli 1979, Nevo et al. 1982, Contreras 1984a). In addition to this behavioral change, fossorial mammals also show a physiological adaptation to high

Figure 4-10. Basal rate of metabolism versus body mass in fossorial mammals. The three parallel lines represent percentages of the Kleiber relationship (Kleiber 1961). The other line is the mean boundary curve for endothermy (McNab 1983). The linear regression for fossorial mammals excluding *Chrysochloris*, *Heterocephalus*, *Amblysomus*, and the large *Aplodontia* is $\log_{10} \dot{V}_{b02} / M_b = -0.493 \log_{10} M_b + 0.989$, $n = 45$, $r^2 = 0.840$, or $\dot{V}_{b02} / M_b = 9.753 M_b^{-0.493}$.



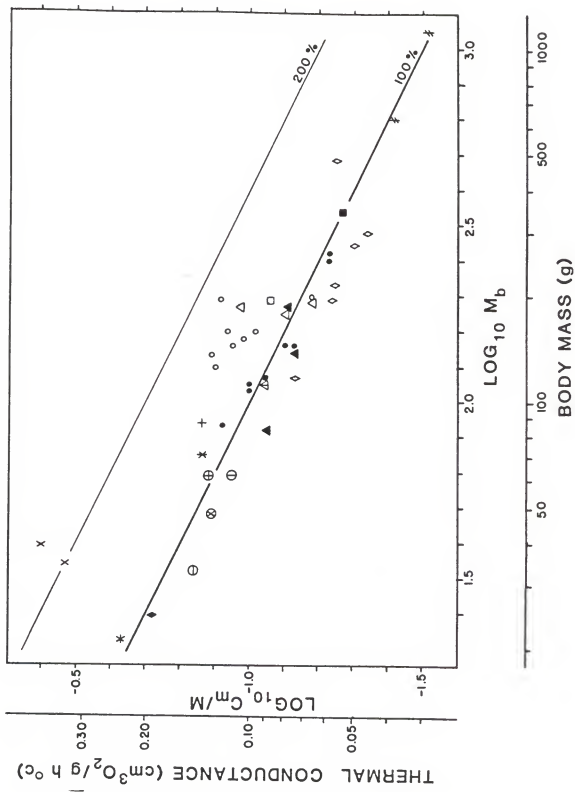
T_a by reducing the rate of metabolism. Geomys pinetis in northern central Florida has a basal rate of metabolism equal to about 97% of expected from mass during winter, decreasing to about 71% during the summer (Ross 1980).

The minimal thermal conductance. Fossorial mammals that live in burrows with temperatures below 20° C have a minimal thermal conductance close to the expected value based on body mass. However, it is high when they live in warm environments ($T_a > 25^\circ$ C). This is the case for Heterocephalus glaber (Burrow $T^\circ = 30-31^\circ$ C) (McNab 1966, Jarvis 1978), Heliophobius argentocinerus ($T^\circ = 26^\circ$ C) (McNab 1966), and Geomys pinetis ($T^\circ = 27^\circ$ C) (Ross 1980) (Fig. 4-11).

Minimal thermal conductance, as with the basal rate of metabolism may be adjusted with season, especially in those species with large yearly fluctuations in burrow temperature and especially in species that face high summer burrow temperatures. In Geomys pinetis minimal thermal conductance increases from 127% in winter to 159% in the summer (Ross 1980).

The temperature differential and the effectiveness of thermoregulation.--Fossorial mammals, when at rest, usually can maintain normal body temperature at ambient temperatures up to about 30° C. However, when active these animals store heat, even at ambient temperatures as low as 5° C (Ross 1980), and body temperature may reach lethal levels as ambient temperatures higher than 28° C (Fig. 4-1, 4-4, and 4-6). The thermoregulatory ability of a mammal at any ambient temperature will depend upon the balance established between the rate of heat production and rate of heat loss. Basal rate of metabolism and

Figure 4-11. Minimal thermal conductance versus body mass in fossorial mammals. The lines represent the expected values according to McNab and Morrison (1963). Symbols as in Figure 4-10.



minimal thermal conductance are both functions of body mass and in conjunction they will determine the temperature differential between body temperature and the temperature at the lower limit of the thermoneutral zone (McNab 1974), assuming that a species conforms to both scaling functions:

$$\frac{\dot{V}_{bO_2}}{\Delta T_1} = \frac{3.42 M_b^{-0.25}}{3.42 M_b^{+0.25}}$$

If a mammal shows deviations from the expected values in the observed basal rate of metabolism or in minimal thermal conductance, the observed ΔT_1 will also deviate from values expected according to equation 4-3. To account for these deviations a factor F can be incorporated in equation 4-3, such that F is equal to the fractional expression of the percentage observed values of the basal rate of metabolism and minimal thermal conductance ($F = \dot{V}_{bO_2} / \%C_m$):

$$\Delta T_1 = 3.42 F M_b^{+0.25}$$

In fossorial mammals the combination of low rates of metabolism, high thermal conductances and/or small body masses, should lead to small ΔT_1 . The significance of ΔT_1 for fossorial mammals rests on its relationship to the temperature differential that a mammal maintains between body temperature at high ambient temperatures (McNab 1979). Thus, animals with small ΔT_1 are able to tolerate higher ambient temperatures because they maintain a lower T_B at high ambient temperatures.

As was previously shown, fossorial mammals scale the basal rate of metabolism according to equation 4-2, rather than to the Kleiber relation. In this case:

$$\Delta T_1 = \frac{9.752 M_b^{-0.493}}{1.00 M_b^{-0.50}}$$

$$\Delta T_1 = 9.752 m_b^{+0.007} \quad (4-5)$$

From equation 4-5 it can be seen that in fossorial mammals ΔT_1 is essentially independent of body mass (Fig. 4-12).

The temperature differential at the lower limit of thermoneutrality (ΔT_1) is directly related to the effectiveness of thermoregulation, and even though a small ΔT_1 permits a mammal to tolerate high ambient temperatures in burrows, it leads to poor thermoregulation at low ambient temperatures. Because fossorial mammals scale basal rate of metabolism according to equation 4-2, and ΔT_1 is independent of body mass (equation 4-5), ΔT_1 does not decrease at small body mass, and generally does not fall below the values predicted from the minimal boundary curve. As a consequence small fossorial mammals are good thermoregulators and able to live in cold environments. Species that do not fit this pattern have a small ΔT_1 , are poor thermoregulators and are restricted to warm environments. Among fossorial mammals this is the case for Heterocephalus glaber (McNab 1966, Jarvis 1978), Chysochloris asiatica (Withers 1978), Heliofobius argentocinerus (McNab 1966) and Geomys bursarius (Bradley and Yousef 1975).

In this context, the low basal rate of metabolism and poor thermoregulation of the golden mole Chysochloris asiatica may be an adjustment to burrowing in warm environments and not as a consequence of a primitive physiology (Withers 1978). Note that the naked mole rat also has a poor capacity for temperature regulation, and it is related to warm burrows, and not to phylogeny. If this interpretation is

Figure 4-12. Temperature differential between body temperature and the lower limit of thermoneutrality versus body mass in fossorial mammals. Data taken from Table 1. Symbols as in Figure 4-10.

correct we should expect even poorer thermoregulation in the Grant's desert golden mole Eremitalpa granti, because it is smaller and probably inhabits warmer burrows than C. asiatica (Walker et al. 1964). However, better thermoregulatory capacity should be expected in the large golden mole Chrysothalpa, unless they have an extremely low basal rate of metabolism ($< 50\%$ at 200 g), which is unlikely because they live in forested areas (Walker et al. 1964), presumably with cooler burrow temperatures.

[The temperature differential is also adjusted in animals with large body mass] however in this case ΔT_1 values tend to be lower than predicted by the $3.42M_b^{-0.25}$ curve reducing heat storage (Fig. 4-12), i.e. there is an adjustment at both small and large body masses.

Other alternatives have been proposed to explain changes in body size and for low rates of metabolism in fossorial mammals. The large body size in Thomomys talpoides on a 758 m altitudinal transect in the Beartooth Mountains, Wyoming, was claimed to relate to higher protein content in the stomachs of the individuals (Tyron and Cunningham 1968). However, the relation was not a strict one, food availability was the same along the transect, and no seasonal fluctuations were considered. In that case body mass was larger in shallower soils in contra-position to the claim that small body size is related to shallow soils (Davis 1938, Kennerly 1959).

[Food limitation has been indicated to explain not only small body size and low rate of metabolism but also coloniality] in Heterocephalus glaber (Jarvis 1978). [These characteristics have also been considered adaptations to optimize energy gain given the high cost of burrowing]

(Vleck 1979, 1981, Andersen 1982). In general, available data are in agreement both with the thermal-stress hypothesis and the cost-of-burrowing hypothesis, because plant primary productivity usually decreases as ambient temperature increases. Vleck (1979), although realizing that the hypotheses are not mutually exclusive, thinks that small body size and low rates of metabolism may be favored in less productive habitats by the economics of foraging rather than by the thermal-stress hypothesis. He claims (Vleck 1979, 1981) in opposition to the thermal-stress hypothesis that body size in Geomys bursarius, compared to G. personatus (Kennerly 1959), and in Thomomys quadratus, compared to T. bottae (Davis 1938), is correlated to habitat productivity rather than to soil temperature. However, G. personatus is actually larger than G. bursarius and lives in more xeric environments (Kennerly 1959) with presumably lower food availability. In the case of T. quadratus and T. bottae, differences in body size were claimed to relate to food availability (Davis 1938); however, the number of individuals caught per locality was few, there were no measurements of food availability, and the altitude difference was small (Davis 1938).

Even though, as Vleck (1982) points out, the largest members of the family Geomyidae are found at low latitudes in Central America, this observation does not necessarily contradict the thermal-stress hypothesis. To evaluate this apparent contradiction, it is necessary to know the energetic characteristics of these animals and the actual burrow temperatures that they face. Among these Central American gophers the largest individuals are found in at higher altitudes with

lower ambient temperatures, like the Mexican high Central Plateau. Body size decreases at lower altitudes where the ambient is humid and warmer. Moreover, thermal conductance is expected to be very high at lower altitudes and warmer environments, because they have sparse and coarse pelage on the dorsum and are almost naked on the ventral side (Mendez 1970, and personal observation of the specimens from Guatemala at the Florida State Museum). If Vleck is correct that these gophers face high burrow temperatures and high plant productivity, this combination would be an exception to his general suggestion that high plant primary productivity occurs at lower temperatures.

Many organisms in nature respond to a given problem with different solutions in different environments. When explaining interspecific differences we principally rely on correlations and associations. In this case, it is very likely that not only the thermal stress (McNab 1979), the cost of burrowing (Vleck 1981), or the hypoxia and hypercapnia (Contreras 1984b), but also the historical factors (Smith and Patton 1980) must be considered for us to have a global understanding of the observed patterns in fossorial mammals.

CHAPTER FIVE
CONCLUSIONS

- 1.- In Spalacopus cyanus the basal rate of metabolism is lower than expected both in individuals from warm burrows at low altitude (85%) and from cool burrows at high altitude (79%). However, basal rates are lower in the larger animals from high altitude.
- 2.- Minimal thermal conductance is 80% of the value expected from mass at high altitude and 85% of expectations at low altitude.
- 3.- The combination of the basal rate of metabolism, minimal thermal conductance, and body size in Spalacopus determine a similar temperature differential between body temperature and the lower limit of thermoneutrality (10.0 and 10.7°C). Similar temperature differentials, and consequently similar tolerances to high ambient temperature, are attained by a low metabolic rate at high altitudes, and by a smaller body size at lower altitudes.
- 4.- Fossorial mammals have a lower critical oxygen pressure than surface dwelling mammals.
- 5.- Interspecifically the setting of the critical oxygen pressure is not related to rate of metabolism or to body size in either fossorial or surface dwelling mammals at masses between 8 and 481 g.

- 6.- Low rates of metabolism and small body size, although not setting the critical oxygen pressure, may reduce respiratory stress by hypoxia or hypercapnia.
- 7.- Basal rate of metabolism in fossorial mammals scales to body mass according to the function $V_{bO} / M_b = 9.752 M_b^{-0.493}$. This equation intercepts the Kleiber relation at 74.5 g; thus, at larger sizes the basal rate is lower than expected by the Kleiber relation and is higher at smaller body masses.
- 8.- Minimal thermal conductance is high in those animals living in warm environments (25°C).
- 9.- The combination of the basal rate of metabolism, minimal thermal conductance, and body mass determine the temperature differential maintained by an endotherm with the environment; this differential is independent of body mass in fossorial mammals.
- 10.- Fossorial mammals that fall below the temperature differential curve derived from the minimal boundary curve (McNab 1983) are poor endotherms and are restricted to warm environments.
- 11.- This energetic pattern of fossorial mammals is interpreted as a result of adaptations to reduce overheating and to maintain endothermy at small masses when living in cool environments.

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BIOGRAPHICAL SKETCH

Luis Carlos Contreras Casanova was born in Santiago, Chile, on 23 October 1953. He completed secondary education at Liceo de Aplicacion No. 3 de Hombres, Santiago, in 1970. He spent the first half of 1970 in Michigan, U.S.A., as a Youth for Understanding exchange student.

In June 1977 he obtained the degree of Licenciatura en Biología, at the Facultad de Ciencias, Universidad de Chile. His thesis was on the "Annual Reproductive Cycle in the Male Octodon degus Molina."

Since November 1977 he has been working at the Universidad de Chile. In September 1979 he commenced graduate studies at the University of Florida. After completion of his Ph.D. degree he will continue work at the Departamento de Ciencias Ecologicas, Facultad de Ciencias Basicas y Farmaceuticas, Universidad de Chile.

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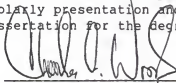
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Professor of Zoology

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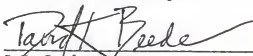
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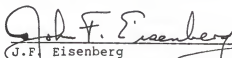
C.A. Woods
Professor of Zoology

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D.K. Beede
Assistant Professor of
Dairy Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



J.F. Eisenberg
Professor of Forest Resources
and Conservation

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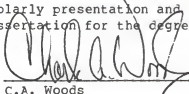
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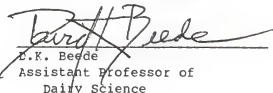
J.F. Anderson
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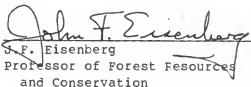
C.A. Woods
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



E.K. Beebe
Assistant Professor of
Dairy Science

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J.F. Eisenberg
Professor of Forest Resources
and Conservation