THE USE OF MORPHO——PHYSIOLOGICAL MEASUREMENTS TO INDICATE THE ENERGY STATE OF SMALL MAMMALIAN HERBIVORES

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INTRODUCTION

In order to exist endothermic vertebrates must use energy. The consequence of this is that they must find and process energy. These statements, by themselves, are rather tautological. However, the study of accumulation and allocation of energy as it relates to limits on life history tactics is valuable, for it gives us insights into what animals can and cannot do and how they are limited in when certain activities can occur. It is well known that most vertebrates which live in seasonal environments such as high, alpine, meadow ecosystems do not breed continuously nor are their food sources homogeneous throughout the year. It has been suggested by Goldberg et al. (1980) that certain sorts of molt patterns do not occur simultaneously with breeding in beach voles, *Microtus breweri*. These observations suggest that the ability of small mammals to accumulate energy and allocate that energy to reproduction (fitness) is limited and certain other energy-requiring processes (e.g. molt or growth) cannot occur when reproduction occurs or vice versa. Stenseth et al. (1980) have developed a model with which they suggest that energy may limit reproduction in small mammals. Thus there is an underlying tenet in small mammal ecology that the ability to accumulate energy and the avenues of allocation are important in determining whtt species can live where, when that species can breed, how many young it can prduce and these may be tied to various life history parameters such as food habits (McNab, 1980; 1986).

For these reasons energetics has been an important part of the study of small mammal ecology (Grodzinski and Wunder, 1975). This is particularly true for herbivores. They eat foods which are less energyy dense than those of carnivores and foods which are generally more difficult to digest. Also, the quality and abundance of their food will vary seasonally. Plants grow in summer and die back in fall and winter, translocating nutrients to roots (see Wunder et al., 1977).

Much of what I will discuss in this paper is limited to small herbivores. I do this because most of the data I have is limited to such forms and because I feel they are limited

Running Head: Morpho-physiological Indicators

more by energetics for the reasons I have just listed.

ENERGY BALANCE MODEL

In order to discuss how small herbivores might make adjustments in their balance of energy accumulation and allocation in order to meet different stressors in their environments, it is valuable to consider the pathways for balance. For that reason I present a descriptive model which I have discussed before (Wunder, 1978a). (Fig. 1). The thesis is quite simple. The amount of energy expended by a small herbivore must equal that accumulated or the animal will either: 1) heat or cool (imbalance of thermal energy) or 2) fatten or starve (imbalance of chemical energy). I depict the energy flow as a cascade because I feel that small homeotherms must allocate energy to different processes in a priority fashion (Wunder, 1978a). If they do not thermoregulate, they can do nothing else as they cannot behave. Secondly, they must gather energy by feeding as this is the feedback to balance their needs. When those first two needs are met then they can do other things. I suggest that when such a balance cannot be met or is tenuous they cannot breed; and, hence, timing for reproduction is limited. We know that increased needs for thermoregulation and/or reproduction will drive
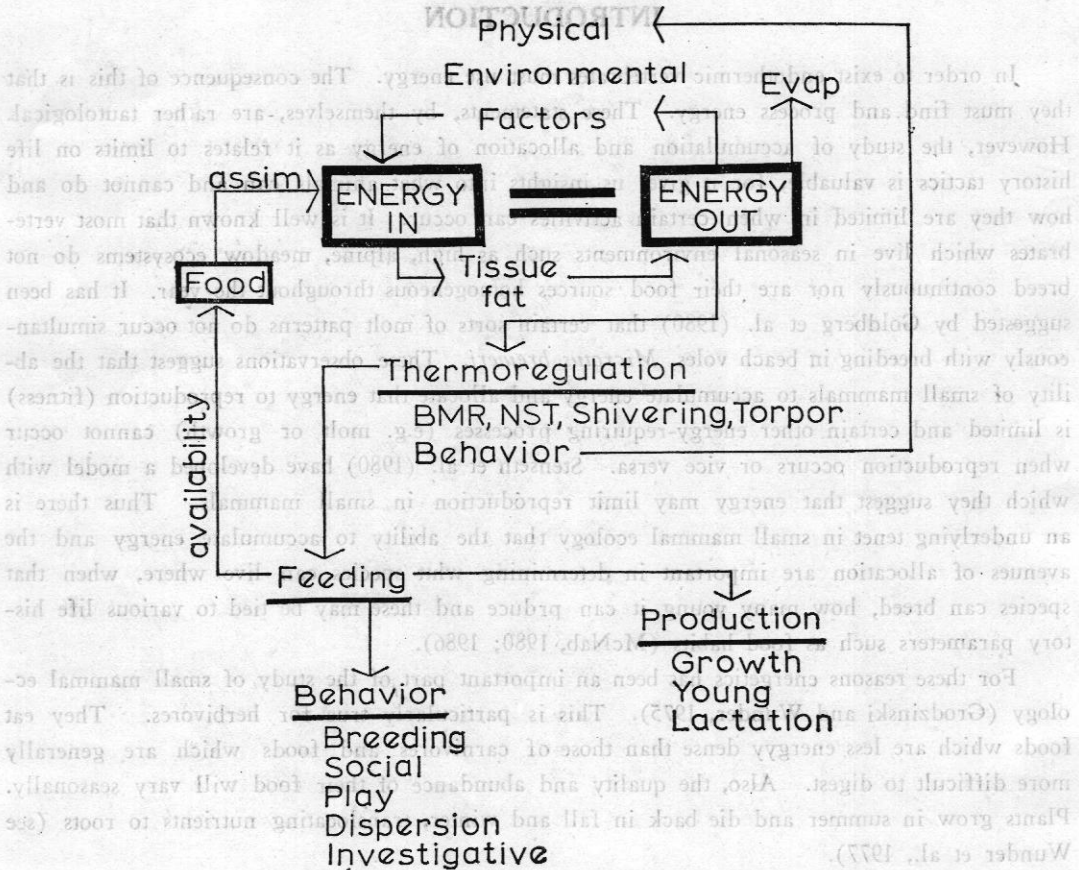

Fig. 1 A conceptual model of energy balance for a small mammal indicating a priority cascade for energy allocation. Lines represent both total energy flow and rate functions (from Wunder, 1978a, with permissoon). Abbreviations are: BMR, basal metabolism; NST, nonshivering thermogenesis; Evap, evaporation; assim, assimilation.

costs up and hence necessitate that the animals gather more energy per unit time, draw upon stores of chemical energy or both.

In order to meet increased energy demands small herbivores must accumulate more energy. We ecologists tend to think of food accumultion as a process which consists primarily of finding and handling food. This usually means getting food to the mouth. However, in herbivores, especially those which feed on material with substantial cell wall component, digestion may be limiting (Dement and Van Soest, 1985; Wunder, 1985; White, 1978).

It is well known to animal scientists that herbivores which feed upon leafy vegetation tend to keep the gut full processing that hard-to-digest food (Van Soest et al., 1983). It is also known that digestibility is related to how long food is kept in the gut (retention time). If energy needs increase, that means more food must be processed through the gut per unit time. If gut size remains constant, the retention time may decrease and; hence, digestibility could decrease reducing the net energy gained per unit time (Sibly, 1981; Wunder, 1985). The limits to passage rates of material through the gut and factors which affect those rates are discussed by Warner (1981). Recently it has been found that gut size of small birds (reviewed in Sibly, 1981) and mammals (Gross et al., 1985) changes in response to need.

APPLICATION

Given this brief overview of energy balance in small herbivores it is frustrating that we have few insights and even fewer data on how such forms actually interpret that world in which they operate. During winter we presume they are cold stresssed and must spend extra energy on thermoregulation. We presume they must eat dead vegetation with relative high cell wall content and must spend longer to digest it. However, we have few data to substantiate these suppositions. That it is cold is indicated by the fact that insulation usually changes seasonally (Irving, 1964; Bartholomew, 1977; Wunder, 1984). But with such changes in insulation to buffer the animals against a cold environment we do not actually know that they must continuously expend extra energy on thermoregulation. The insulation alone may counteract the cold. There are few measurements of energy expenditiure by animals in the field. Probably the best are those of Nagy (1985a, b), but he has not looked at seasonal patterns or animals found in cold, high alpine areas.

Over the past 10 years I have studied the ways in which small herbivores adjust to seasonal environments. I have been particularly interested in how small mammals can change their capacity for heat production and what cueing mechanisms are involved (Wunder, 1979; 1984); and, more recently, in how they change gut size to allow for assimilatin of more energy from the small intestine per unit time or for more fermentation of plant cell wall in the caecum per unit time (Gross et al., 1985). Much of this recent work is now in press or in the process of publication and I will draw heavily upon it. During these studies it occured to me that it would be valuable to have some measures of how small herbivores actually interpret the world in which they live and how they respond to that world.

Shvarts (1975), Vorontsov (1967) and Bashenina (1984) have pioneered in the use of morphophysiological characteristics to indicate what sort of habitat animals may be adapted to and to some extent how those animals adjust to certain environmental stressors. Some of the indicators they have used allow certain insights into the energy states of small mammals. More recently Schieck and Millar (1985) building on earlier studies of (Golley, 1960; Vorontsov, 1967; Barry, 1977) have shown that various measures of the guts of small mammals can be used to estimate food habits. However, they do not talk about how these might change in

relation to need. I present some new morphophysiological indicators below.

METHODS

Most of the data used in this paper come from the literature or papers in the process of publication. Pika (*Ochotona princeps*) were collected from Loveland Pass, Clear Creek County, Colorado. To sample for brown fat, four animals were collected by shotgun in January 1981. Two animals were collected in March 1981; and two were collected in December 1982. Four were collected alive using Tomahawk live traps in Spetember 1982. They were kept in the lab at 23°C in individual cages or natural photoperiod given water and food *ad libitum*. Food consisted of rabbit chow and material from their hay piles. However when cold acclimated, the "hay" had run out and they were given grass clippings (bluegrass) from my lawn. *Microtus ochrogaster* were captured near Horsetooth Reservoir, Larimer County, Colorado. For studies of nonshivering thermogenesis (NST) the voles were trapped overnight. Measures of basal metabolism (BMR) were made the day of capture as in Wunder et al. (1977). NST was measured the next day (as in Wunder, 1984) in animals which had maintained body mass overnight (indicating they were eating and drinking). These same animals were then sacrificed for studies of gut morphology in the January 1984 and May 1984 samples. Thus, they had been eating rodent lab chow in the lab for one day. Gut measurements were made as in Gross et al. (1985). *M. ochrogaster* under in the studies of the effects of lactation on gut size were all born and raised in the lab. They were held at 12°C (because it is reported that they breed best in the lab at that T_A), given a mix of horse chow and rat chow pellets and water *ad libitum*. They had cotton for nests. Experimental animals had litter sizes adjusted to three young at birth and were allowed to continue lactation to day 14. Controls went through pregnancy but babies were removed at birth. Virgins had never bred. Since *M. ochrogaster* has a post partum estrus some of the controls and experimentals were also pregnant. However, there did not appear to be any effect of pregnancy on gut measurements.

RESULTS AND DISCUSSION

As indicated in figure 1, when a small, nonhibernating mammal is faced with a cold environment it must modify that thermal environment to reduce the cold exposure (microenvironment or insulation) or increase its thermogenesis to maintain body temperature (T_B). One way to increase thermogenesis is to increase basal metabolism (BMR) but that is expensive because energy expenditure is increased continuously even if the animal are in thermoneutrality. Another means of increased thermogenesis is nonshivering thermogenesis (NST). With this mode of thermogensis the animal expends extra energy only when cold exposed and then in a most efficient manner.

Below I discuss several morphophysiological parameters which can be used to define the energy stress state of a small, herbivorous mammal. These are: 1) BMR, 2) NST, 3) state of brown fat, 4) gut size parameters. At present it is difficult to quantify the relation of each of these to an energy state. However, with specific data for a particular species this may become possible.

Basal Metabolic Rate

It is well known that BMR of small mammals increases following cold acclimation (Webster, 1974; Wunder, 1979). Earlier literature indicated or implied that this is a consistent response to cold exposure (Webster, 1974). However, we (Wunder, Gettinger and Seidel, un-
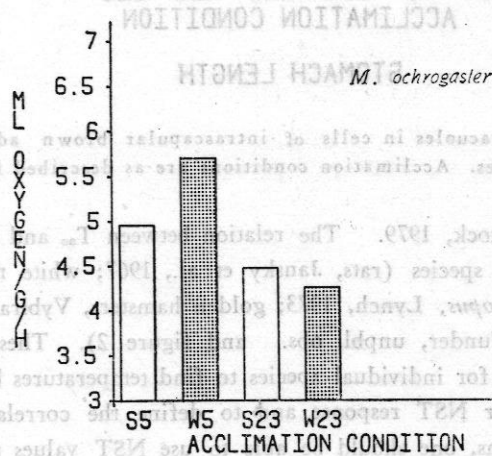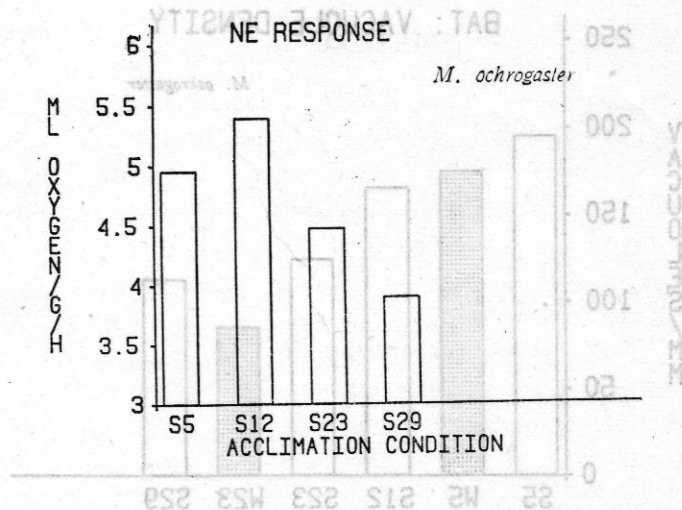
NE RESPONSE

M. ochrogaster

M L O X Y G E N / G / H

6
5.5
5
4.5
4
3.5
3

S5   S12   S23   S29
ACCLIMATION CONDITION

M. ochrogaster

M L O X Y G E N / G / H

7
6.5
6
5.5
5
4.5
4
3.5
3

S5   W5   S23   W23
ACCLIMATION CONDITION

Fig. 2 A + B Metabolic response to injection of norepinephrine by prairie voles.
Under acclimation condition, the letter refers to animals caught in summer (S)
or winter(W) and the number to the temperature to which they were acclimated(°C).

pbl. obs.) have recently found that BMR does not always increase in all species of small forms following cold acclimation. At first we thought this correlated to whether they ate energy dense (carnivore, omnivore) or energy dilute (herbivore) food. But that relation is not clear. Wunder et al., (1977) demonstrated that BMR of *M. ochrogaster* increased following cold exposure and may increase in winter. However, this varies from year to year and seems to correlate to weather conditions (Wunder, 1978b). In any case, it seems safe to conclude that if BMR is increased, the small mammal has been cold exposed. Although cold exposure does not always cause an increase in BMR. Other factors can influence BMR (Wunder 1979), so one must be somewhat cautious in using this parameter to indicate cold exposure.

Nonshivering Thermogenesis and Brown Fat

It is fairly well established that as acclimation temperature (T_{ac}) decreases the NST capacity of small mammals increases (Jansky, 1973). Thus, it seems reasonable to conclude that animals with increased NST over their "control" levels have been cold exposed. However, there are some complications with a recently described phenomenon called diet induced ther-
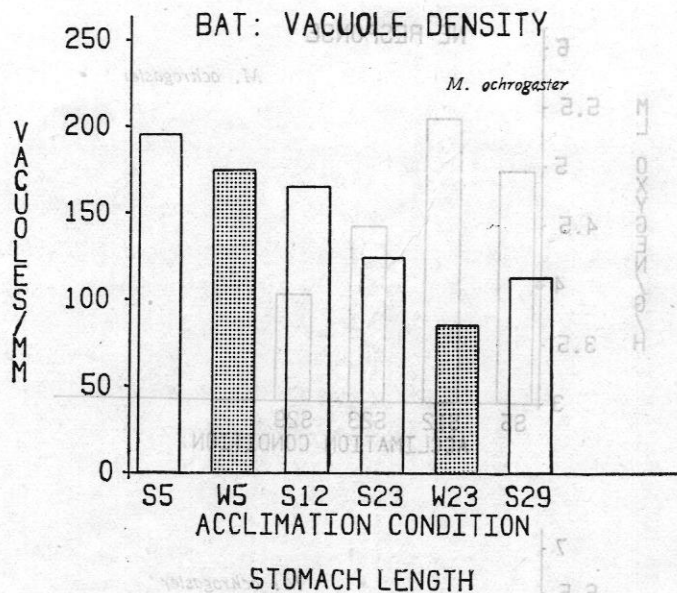
BAT: VACUOLE DENSITY

Fig. 3 Density of fat vacuoles in cells of intrascapular brown adipose tissue taken from prairie voles. Acclimation conditions are as described for figure 2.

mogenesis——Rothwell and Stock, 1979. The relation between T_{ac} and NST has only been quantitatively shown in a few species (rats, Jansky et al., 1967; white mice, Mejsnar and Jansky, 1971; *Peromyscus leucopus*, Lynch, 1973; golden hamsters, Vybiral et al., 1975; *Microtus ochrogaster, Simon and* Wunder, unpbl. obs. and figure 2). These studies show that one must calibrate the relation for individual species to find temperatures below which further cold exposure elicits no greater NST response and to define the correlation relationships. However, given such calibrations, one should be able to use NST values to estimate T_{ac} and vice versa. For field biologists the measurement of NST in freshly caught animals could be used as a gauge to their field exposure temperature. Since brown adipose tissue (BAT) is the major site of NST (Foster and Frydman, 1978), one might predict that some aspect of BAT might also be used as an indictor of thermal challenge in small mammals. Several components of BAT change following cold acclimation. The amount of BAT may be increased, its histology may change from a unilocular state to a multilocular state (Tarkkonen, 1970) and its biochemistry may change (Cannon et al., 1981; Nichols and Locke, 1984). Thus one could use BAT as an indicator of thermal challenge. The BAT state may be a bit more complex than NST as we known that mass changes do not always correlate with NST capacity (Heldmaier et al., 1982; personal obs.). However, in prairie voles we find that BAT vacuole density correlates fairly well with T_{ac} and is not affected by season; although there is a tendency to fewer vacuoles in animals tested in winter compared to summer (Simon and Wunder, unpbl. obs.-fig. 3).

Various factors other than temperature may affect the BAT and NST capacity of small herbivores. For example photoperiod, norepinephrine or thyroxine injections and diet may cause increases in NST in addition to T_{ac} (see Wunder, 1979 and 1985). Thus one should be cautious to sort these effects out.

Since we know that the presence of BAT and increased levels of NST indicate low tem-

perature exposure in small mammals and their absence or reduced values indicate little or no thermal stress, what do we find in field caught animals? Relatively few such data exist. Didow and Hayward (1969) reported that BAT mass was highest during winter in field caught meadow voles (*M. pennsylvanicus*). And Aleksiuk (1971) reported similar results for red squirrels (*Tamiasciurus hudsonicus*). Lynch (1973) reported that in white-footed mice (*Peromyscus leucopus*) NST increased in fall and remained reasonably high in winter decreasing again in spring-summer. This correlated reasonably well with the effects found following cold T_{ac} in the lab. Feist and Rosenmann (1976) compared NST values for red-backed voles (*Clethrionomys rutilus*) caught in summer and winter with lab acclimated animals. They found that NST was highest in winter compared to summer and the field-caught animals had values equal to or higher than those acclimated to 5°C in the lab (Table 1). Thus one can conclude that Alaskan red-backed voles are, indeed, cold exposed in winter. Merritt (1986) also reports that NST in short-tailed shrews (*Blarina brevicauda*) captured in Pennsylvania is higher in winter than in summer. But he does not report lab acclimation data. We can now add data for prairie voles and pika (*Ochotona princeps*). We have studied NST in pra-

Table 1   Metabolic Response of Small Mammals to Norepinephrine Following Temperature Acclimation or Seasonal Acclimatization

Species	NE Response[1] Acclimation		Acclimatization	
	Warm	Cold	Summer	Winter
Clethrionomys rutilus[3]	7.4(20)[2]	11.5(5)	6.8	18.7
Peromyscus leucopus[4]	4 (26)	8 (5)	4	8
Phodopus sungorus[5]	6.5(23)	11.5(10)		13.3
Microtus ochrogaster[6]	4.1(23)	5.8(5)	2.6	3.5

1. Values given are ml O_2 $(g \cdot h)^{-1}$.
2. Number in parentheses is acclimation temperatures(°C).
3. Feist and Rosenmann (1976).
4. Lynch (1973). Values from a graph.
5. Heldmaier et al. (1982). Winter animals were held in cages outside.
6. Wunder (unpbl. obs.).

irie voles both in the lab and in the field for several years and find what we originally thought was a photoperiod effect (Wunder, 1984) and now realize is an endogenous rhythm (Wunder, 1985). In any case what we find in the lab is the following. NST values are low in fall, increase to peak in winter and decrease in spring (fig. 4). When we collect *M. ochrogaster* from the field, measure BMR the day of capture and NST one day later as in Wunder (1984), we find results as in figure 4 (Wunder, Ralph, Arnold, unpbl. obs.). One striking conclusion can be drawn. The NST response of field-caught animals in mid-winter is lower than that of animals acclimated to 23°C in the lab. This could be due to any of many reasons but the most likely are: 1) Voles may be stressed in the lab and never adjust to it. Thus they secrete high levels of NE and stimulate BAT and NST. 2) The animals develop more BAT when given a good diet in the lab, showing what nutritionists call diet-induced thermogenesis (Rothwell and Stock, 1979). 3) The voles are not exposed to low temperature during the winter in the field. I would argue against # 1 since we have now studied several species and have looked at the allometry of their NST response. The allometry correlation is quite good. If much of the NST response were due to "stress" I would expect much variation between species since there should be some variation in the response of animals to the lab. And
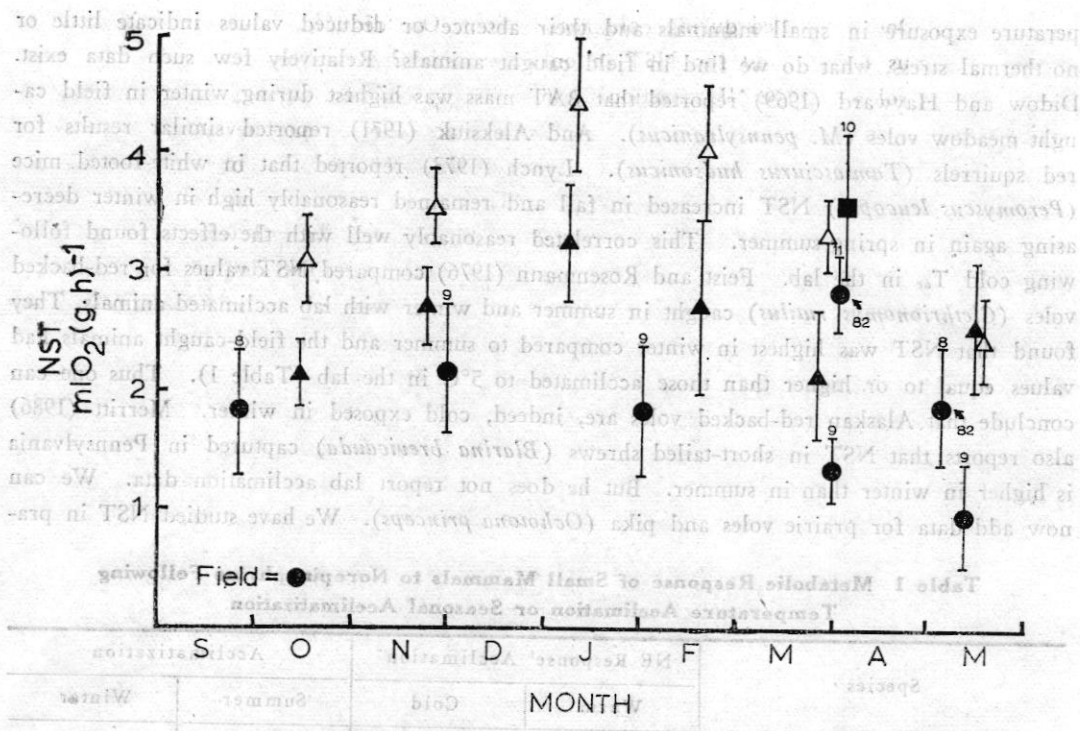
Fig. 4 Nonshivering thermogenic response (response to NE-BMR) of prairie voles held in the lab at 23°C (shaded triangles) or held in cages outside (unshaded triangles) as in Wunder (1984). Shaded circles indicate values for voles captured in the field at different times of yeay (letters indicate months of the year). Numbers (81 or 82) refer to the year of measurement.

lab animals (rats, mice and hamsters) fit the allometry quite well. They should be adjusted to laboratory circumstances. Number two is possible but unknown; and if a factor, then it must add to the T_A effect producing a higher thermogenesis than T_A would alone (see the plateau effect in figure 2 with animals on chow and low T_{ac} in the lab). The last factor seems the most plausible and is yet counter to our intuitive feel of what these animals should be experiencing in winter. Measurements of metabolism in the field in winter and summer should be made using radioisotopes.

Pika (O. princeps) also live in cold macroenvironments in Colorado. One population is reasonably easy to reach in summer and winter. These pika live at about 12,000 feet elevation near Loveland Pass, Clear Creek County, Colorado. We have shot animals in winter to sample for BAT. Four animals collected in January 1981 showed no BAT upon dissection. Two animals collected by shotgun in March 1981 also had no BAT. At those times the animals had lots of snow cover and only came out on to rocks or the snow surface for short periods each day and then only in low numbers. Following those dissections I had concluded that pika may not develop BAT since we had found none in midwinter. However, it was puzzling that this tissue can be found in other Lagomorpha but not in these primitive forms. Thus in September 1982 I collected four live pika from this same site. Upon return to the lab I measured BMR and injected the animals with norepinephrine (0.4 mg/Kg, a dose taken from our allometric relationship eliciting highest metabolism in small mammals). There was no metabolic response to norepinephrine. I then cold (5°C) acclimated the pika for 14 days. They are hard to keep alive in the lab and one died before we started cold

acclimation. One more died during cold acclimation. One died during the second BMR determination, thus I could test for NST in only one animal. Nonetheless it showed a strong NST response following the NE injection (2.46 ml O_2(g h)$^{-1}$ for a 151 g pika). It and the animal which died during acclimation were dissected and showed high levels of BAT. I collected one more pika from the field in December 1982. It showed lots of BAT. That year we had no good snow cover at Loveland Pass by December. Thus it appears that pika can, indeed, form and use BAT but only do so when cold exposed. In fall when it is cold they may use the tissue but once snow arrives and insulates their habitat and dens they lose the BAT as they are living in an effectively warm envitronment. However, they are well insulated and have increased BMR even after living in the lab (MacArthur and Wang, 1973).

Energy Acquisition and Gut Morphology

It has long been known that gut morphology of small mammals can be related to food habits (Davis and Golley, 1963; Vorontsov, 1967). Even more recently Schieck and Millar (1985) drew conclusions about the relationship between gut morphology and food habits of small mammals showing that herbivores tend to have longer hind guts and larger caeca. Hansson (1985) found that Clethrionomys glareolus from northern Sweden eat a more energy dilute diet than those in the south and have correspondingly larger guts. Most of these studies assume that gut size is relatively fixed or do not consider how gut size might change seasonally. Although Hansson (1985) did look at potential changes and the effects of genetic background on those changes.

Animal scientists and some ecologists have long known that gut morphology may Change in relation to need and/or fiber content in the diet (Sibly, 1981). More recently we documented how these stressors affect gut size in prairie voles (Gross et al., 1985). We modified the animals need for energy by placing them in the cold; and we modified their ability to get energy from food (energy dilution) by modifying the fiber content of the food. From that study we demonstrated that not only does the size of the gut (measured as length and/or dry mass of tissue) change in response to those stressor but different protions of the gut change in response to different stressors. Generally, when stressed with decreased T_A (intestine increases (site of chemical digestion andcreased energy need) the size of the small in absorption). When stressed with fiber (energy dilution of the diet), the caecum (site of biological fermentation) increases in size. Thus, provided one has some baseline or comparison points'one ought to be able to daw couclusions about the relative energy needs of animals from different sets of conditions (e.g. winter vs. summer; high vs. low food availability) by looking at relative gut size, especially the length and mass of the small intestine. Likewise by assaying the length and mass of the caecum one cught to be able to draw conclusions about "quality" of the diet from small herbivores. More recently we have also found that lactation, another form of increased energy need, drives an increase in gut size (Wunder, Peterson, and Hammond, unpbl. obs.). Intehestingly, in addition to the large small intestine found with a temperture effect, we also found that lactating females increase stomach size over contactating females and nonbreeding animals (fig. 5).

It is not clear why lactation should affect this change in stomach size when increased need due to thermoregulatory needs did not. However, Madison (1981) has shown that activity of lactating female M. pennsylvanicus tends to become reduced and centralized relative to nonlactating animals. Thus it may be that lactating females take fewer, larger meals and spend more time in the nest brooding young.

LACTATING MICROTUS

□=Control
▥=Virgin
▨=Experimental

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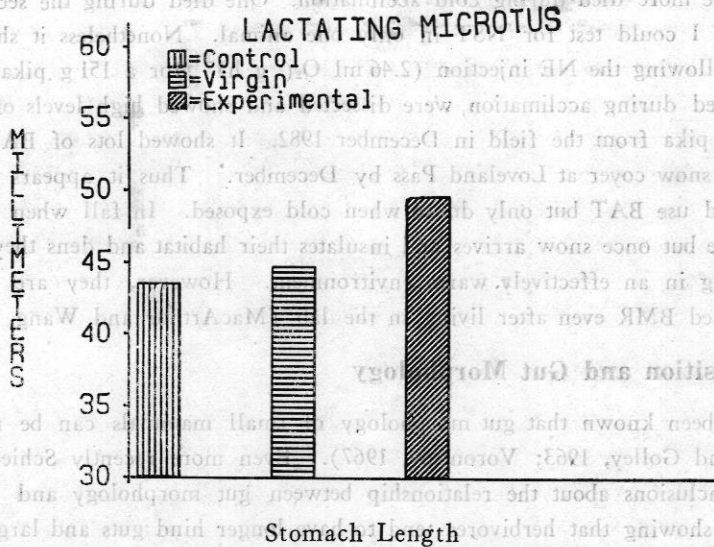55
50
45
40
35
30

MILLIMETERS

Stomach Length

Fig. 5 Stomach size in prairie voles. Controls had gone through pregnancy, virgins had never bred and experimentals had gone through 14 days of lactation with a litter size of three.

Given the discussion above I suggest that changes in gut morphology could be used to indicate the level of energy stress for small herbivores from the field. Within a species of herbivore, a long small intestine would indicate increased energy needs (e.g. temperature, lactation, activity). If coupled with a large stomach it should indicate lactation. An increased caecum size should indicate a change in food habits to foods of higher fiber content. However, it should be kept in mind that these comparisons can probably only be made within a species and then only in a comparative sense.

We have used the logic above to predict that voles should have longer small intestines in winter because it should be cold and they should have higher thermoregulatory needs. And we predicted that the caecum should be larger in winter because plant material used as food should be dead with a higher fiber content than in summer. There have been few studies designed to look at gut parameters of small herbivores on a seasonal basis. We have some preliminary drata which I will presen here and we have initiated a longer term study. Only Gebczynska and Gebczynski (1971) have presented data on the effects of reproduction on certain parameters of the gut, studying *Microtus oeconomus* in a Polish forest. The length measures they made are the most valuable to this discussion. Unfortunately they did not measure dry mass of the tissue, only fresh wet mass. Gross et al. (1985) pointed out the problems with using we mass for good comparisons. Geczynska and Gebczynski (1971) noted that total intestinal length was greatest in summer, lowest in spring and intermediate in winter. They also noted that "length of the intestines is always greatest in nursing females". These results for field caught animals are similar to our lab findings reported above.

Interestingly our field data (ten animals captured in January 1984 and ten in May 1984) for *M. ochrogaster* show that our predictions given above do not hold. Gut sizes of voles captured at these times are similar. The only significant differences were that the stomach, caecum and total gut length and dry mass of the small intestine were larger in May animals (Table 2). This poses some interesting speculation. The gut data suggest that voles are processing more energy in May than in January. Although we did not include animals which

Table 2 Gut Measurements of *Microtus ochrogaster* Captured in the Field

Measurement	Season	
	January	May
Stomach Length[1]	39.9±2.4*	46.8±3.0*
Stomach Dry Mass[2]	0.115±0.037	0.102±0.008
Small Intestine Length	305±13	319±16
Small Intestine Dry Mass	0.1006±0.008*	0.1221±0.020*
Total Length	734±32*	789±25*
Body Mass	36.7±4.1	41.5±4.9

1. Length given in mm. All sample sizes are ten. Values given are means±2SEM.
2. Mass given in grams.
* indicates significant ($P < 0.05$) difference between samples.

were obviously pregnant or lactating in the May sample, it appears as though reproductive activity in spring effects a greater energy need than thermoregulation in the winter. It may be that because of the potential for increased energy need due to cold and decreased food availability due to high fiber in winter, voles could not make enough profit to breed. Thus they simply leave their nests for short periods to forage and then spend most of their time in well-insulated nests. For that reason they have low energy need because of reduced activity and reduced exposure to cold. This conclusion is supported by our findings on NST capacity discussed above. During spring (May) they breed and males use much energy to stay active and find females and females would be processing extra energy for lactation. Although we have no data on the time necessary for gut size change in voles to occur, we do know that guts increase in size for rats within days (Fell et al., 1963) and once females have had a litter, it can take 30 days for the gut to return to the smaller, nonbreeding size (Fell et al., 1963). Thus even though we eliminated females which were obviously breeding from our field sample analysis, some voles may have had enlarged guts due to prior lactation. An analysis comparing males and females, however, showed no differences due to sex but samples of each were, obviously, small. It would be valuable to compare NST and gut sizes of voles from population cycle phases when there are many voles and they are breeding in winter. I would predict a much different picture of gut size and NST capacity.

SUMMARY

I have presented arguements indicating that BMR, NST, and BAT can be used to indicate that small mammals are being stressed by cold and have increased their capacity for thermogenesis. Data from prairie voles and pika captured in the field indicate they may not be highly cold stressed in winter.

Gut morphology patterns allow us some insight into detecting increased need for energy by small herbivores or changes in diet quality. Field data are scarce but some indicate that breeding females increase gut size and that energy processing for reproduction in spring and/or summer may be greater than that necessary for thermoregulation during winter in prairie voles.

ACKNOWLEDGEMENTS

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应用形态-生理学的测定来指示草食性小哺乳动物的能量状态

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摘 要

本文探讨了草食性小哺乳动物如何调节它们的能量积累和分配，以满足它们在不同环境压力下的能量需要和达到能量平衡的途径。

作者认为通过草食性小哺乳动物的能流是呈阶级式（cascade）的，并按顺序将能量分配到不同的生命过程中去，所获得的能量首先保证体温调节，然后才满足其他的需要。

确定草食性小哺乳动物的能量状态的四个主要参数是，(1)基础代谢（BMR）；（2）非颤抖性产热（NST）；（3）棕色脂肪组织（BAT）；（4）消化道(胃、小肠、盲肠、大肠)的大小(长度、湿重和干重)。

草食性小哺乳动物的 BMR 随冷驯化而增加，这是它们对冷暴露的一种反应，但并非所有的小哺乳动物都呈现这一规律，因为食物的质量和其他因素也会影响 BMR。当草食性小哺乳动物的驯化温度下降至某一限度时，则它们的非颤抖性产热能力增加。在野外条件下，小哺乳动物的 NST 在秋季增加，冬季最高，春季和夏季下降。除环境温度外，影响小哺乳动物非颤抖性产热(NST)能力还有光周期，注射去甲肾上腺素和甲状腺素，以及食物条件等。小哺乳动物的非颤抖性产热(NST)能力往往和动物的棕色脂肪组织(BAT)有密切关系。因此，人们用 BAT 来作为草食性小哺乳动物在冷压下对能量需要的一个指示物。随着冷压的增加，动物 BAT 的一些成分发生变化，BAT 组织会从一个单腔室(unilocular)变为多腔室(multilocular)状态，脂肪组织密度有增加的趋势，BAT 的重量也可能增加。草食性小哺乳动物消化道的大小不是像人们所假定的那样，保持稳定不变。通过将动物保持在 5℃ 冷环境下驯化，或者人为地改变它们食物中的能量密度(如在食物中加入纤维素等)，则它们的消化道大小发生变化。通常，随着环境温度下降，动物处于冷压下，对能量的需要增加，它们的小肠大小(化学消化和吸收的部位)增加，当食物中纤维素含量增加时，盲肠(氨基酸发酵的部位)大小增加。

人们根据上述四个指标，即可对草食性小哺乳动物的能量状态作出判断。