

SEASONAL ENERGY BUDGETS OF A FOSSORIAL RODENT
GEOMYS PINETIS

By

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Ecology can be defined as the relationship of an animal to its environment. To describe this relationship we can describe the flow of energy and nutrients through individuals or populations. Energy and nutrient availability and quality should influence the survival and growth of individuals and the numbers and distribution of populations. Therefore, we should expect that natural selection will act to optimize physiological mechanisms which affect the acquisition, conservation and use of energy and nutrients.

To test these contentions, energy budgets at various seasons of the year have been calculated for a population of the fossorial rodent, *Geomys pinetis* (the Florida pocket gopher). Field budgets have been estimated from data acquired in the laboratory on feeding efficiency, activity, and thermoregulatory energy expenditures. Data on microclimate, food availability and quality, population fluctuations, demographic parameters and parasite loads have been collected from the field.

The results show that this population of *Geomys* fluctuates in numbers seasonally with an increase through the spring and summer and

a decline through late fall and winter. Measurements of resting rate of metabolism (M_b) and conductance (C) and body temperature (T_b) show that *Geomys* changes its pattern of thermoregulation in the warmer months to avoid overheating in a microclimate (a closed burrow system) offering limited opportunity for heat loss. The energy budgets show that each individual must acquire more energy in the cooler months of the year to support increased thermoregulatory costs. Life table data suggest that newly recruited individuals have the highest mortality during the seasons of population decline.

This mortality may be associated with an inability of these individuals who usually have a small suboptimum territory, to meet the high energy demands of the fall and winter. A large increase in energy spent in reproduction is evident in the spring which is associated with increased survivorship of young born early in the year. This increase occurs at a time when the micro-environmental demands are severe; nitrogen, energy and water content of the food are minimal; and parasite loads are high.

A picture emerges of an animal which has modified its reproductive behavior to deal with a changing energy and nitrogen supply. Its micro-habitat protects it from large fluctuations in temperature but impose constraints on thermoregulatory parameters of M_b and C. The intensely territorial nature and the seasonal changes in thermoregulatory physiology of pocket gophers are probably mechanisms for ensuring population survival under these limits.

INTRODUCTION

Ecology can be broadly defined as the relationship of organisms to their environment. One means of describing this relationship is to measure the flow of energy through and between individuals and populations. Organisms need a constant input of energy for maintenance. The sources of this energy, its quality or concentration, its available quantity, and the uses to which it is put should all exert an influence on the persistence and growth of individuals and the numbers and distribution of populations. The presence or absence of other necessary nutrients, such as fixed nitrogen, phosphorus, various salts and water may exert an influence on the ability of an organism to use energy. Therefore, the persistence of individuals and populations depends on the presence of energy and essential materials. We would expect that natural selection would optimize physiological mechanisms to ensure maximum fitness with respect to the acquisition, conservation and use of energy and various necessary substances.

Much of the energy intake of endotherms is expended to maintain body temperature (T_b) independent of ambient temperature (T_a). Endotherms employ numerous adaptations to retain body heat, although when T_a is high the retention of heat often becomes a problem. Therefore it might be expected that the manipulation of thermoregulatory parameters is an important way in which animals balance energy demand against supply to ensure a sufficient increment of energy for survival.

I will evaluate the effects of energy use and nutrient supply on population fluctuations in *Geomys pinetis* (Rafinesque), the Florida pocket gopher. I will show that seasonal variations in the physiological parameters of *G. pinetis* can be understood as ways of enhancing survival in response to variations in energy availability and requirements.

Pocket gophers are particularly suitable for a study of this sort. They are locally abundant in Florida and easy to obtain. They are a convenient size (100-300 g) for maintaining and manipulating experimentally. *Geomys pinetis* is found in areas with deep sand soils that have a natural flora of long leaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*) with a sparse understory of wire grass *Aristida stricta* and other herbs (Laessle, 1942). Gophers feed on roots, stems and tubers which they pull into the burrow from below without exposing themselves above ground (Barrington, 1940). Gophers are common where the natural flora has been destroyed for pasture and crop lands and along roadsides.

Geomys pinetis lives almost entirely within its sealed burrows. Exits to a burrow are concealed beneath mounds of earth ejected from the burrow. One animal lives in each burrow which is a single tube, greatly twisted about with several spherical chambers. Burrows may be up to 100 m long and traverse an area of up to 0.5 ha that is defended from other gophers (Brown and Hickman, 1973). The restriction of a single gopher to one burrow facilitates the estimation of population numbers by counting groups of mounds (Ingles *et al.*, 1949; Ried *et al.*, 1966).

Conditions within the burrow are considerably different from conditions at the surface (Kennerly, 1964; McNab, 1966; Darden, 1972) which has led to some physiological adaptations by gophers (Darden, 1972; Chapman and Bennett, 1975) and provides a uniquely convenient microhabitat in which to estimate thermoregulation and energy expenditure. Within the burrow, oxygen is less abundant and carbon dioxide more abundant than at the surface. This has led to adaptations in blood buffering capacity and sensitivity to CO_2 that enable gophers to live under these conditions. Temperature fluctuations within the burrow are buffered from rapid changes above the ground and the relative humidity within the burrow is always very high. Some authors have interpreted the low rate of basal metabolism and high conductance of gophers and other fossorial mammals as an adaptation to an environment in which heat loss is difficult (McNab, 1966; Bradley *et al.*, 1974), although others have challenged this idea (Gettinger, 1975). To evaluate the importance of thermoregulation and its contribution to energy expenditure accurate measurements of the microenvironmental temperature are necessary. The stability of the burrow microclimate allows a much more accurate evaluation of temperature than is possible at the surface where constantly changing solar input, convection, evaporation and radiative heat loss make the thermal environment very complex (Gates, 1963).

MATERIALS AND METHODS

Field

I studied population fluctuations of pocket gophers and made micro-environmental measurements on 17 hectares of the University of Florida Sandhill Research Farm near Biven's Arm Lake, Alachua County, Florida. This area is cattle pasture dominated by planted Bahia grass *Paspalum notatum* with an extensive complement of other herbs and forbes. This study area is surrounded on two sides by similar pasture and on a third by Biven's Arm Lake. On the fourth side the area is bounded by approximately 30 ha of seminatural long leaf pine-turkey oak association, which is the normal floral type for deep, well-drained sandy soils in this area. Pocket gophers used for laboratory physiological studies were obtained from the Sandhill study area and from roadsides elsewhere in Alachua County. Surveys of other pocket gopher populations were obtained from Morningside Park east of Gainesville, San Felasco Hammock north of Gainesville, and from the Lochloosa Wildlife Management Area, all in Alachua County, Florida. Aerial photographs of the sandhill site and Morningside Park were overlaid with a grid of 25 m intervals to permit accurate location of gopher territories and allow estimation of area.

Climatic data for Gainesville, Florida, were extracted from climatological data collected by the Department of Agronomy, University of Florida, at a weather station 1 km from the sandhill site. Additional

data were taken from Dohrenwend and Harris (1975) and Butson and Prine (1968). These data were augmented by occasional measurements of air temperature and precipitation taken at the study site.

Soil temperatures were monitored with copper constantan thermocouples (Thermoelectric P.24.T) permanently buried in the soil in the northwest corner of the sandhill site. Soil temperature profiles were obtained monthly, reading directly from a Thermoelectric minimate millivolt meter. To establish that these temperatures were representative of the entire study area, spot checks of soil temperature were made by inserting the probe of a YSI telethermometer into a hole in the ground made with a 1/4" diameter steel rod to a measured depth. Temperatures were measured in pocket gopher burrows and in the soil at the same depth near to them by the same method.

The population density of pocket gophers was estimated by directly counting the number of gopher territories in a known number of 25 m x 25 m quadrats. For the purpose of this study, territory is defined as the portion of the home range that is defended from other gophers. This is identical with the occupied burrow system. The location of the mounds of soil that gophers eject from their burrows reflects the burrow system beneath (Ried *et al.*, 1966). It is usually possible to clearly differentiate groups of mounds that constitute a single gopher burrow; the area that these mounds occupy I have termed a territory. In a few cases where it was not possible to clearly differentiate between two gopher burrow systems they were counted as one. Freshly ejected soil is clearly differentiated from older mounds so that recent gopher activity and hence recent occupancy of the burrow can be established.

To provide more information on the persistence of individual *Geomys* in the population, I noted the position of gopher territories and recorded the gopher's presence or absence every month. *Geomys* were live trapped by locating open burrows with a steel rod and placing a Sherman pocket gopher trap (Sherman, 1941) into the burrow. *Geomys* enter the trap during their efforts to repair the damage to the burrow.

Captured *Geomys* were taken to the laboratory where the following data were recorded: body mass (weight), length of the right hind foot from talus to base of the claw of the largest toe, sex, and reproductive status if this was discernible (*e.g.* descended testes, enlarged nipples, plugged vagina). Each animal was assigned a number and marked by tattooing small spots of dark pigment on the naked toes of the hind foot in a coded pattern (Ross, 1976). The tattooing was done with a 23 g needle using a commercial tattooing ink. The animals were then released where they had been captured.

To evaluate various parameters of the food resources available to pocket gophers, core samples of the pasture at the sandhill site were taken throughout the year. An iron ring 21.9 cm diameter was thrown randomly from the center of a randomly assigned quadrat and all vegetation enclosed by the ring to a depth of 20 cm was removed with a shovel and stored in a plastic bag. This sampling technique provides a sample like that which a gopher would normally encounter when feeding. These samples were taken to the laboratory where all dead and inorganic matter were removed. The sample was then divided into an above ground and a below ground portion. Above ground plant parts were defined as those having obvious visible green coloration and all

the remaining plant parts were defined as below ground. Thus, all of the underground stems and rhizomes fell in the below ground sample.

Each portion was weighed, dried at 90°C for 48 hr, and reweighed. The change in weight was recorded as water content. The dry samples were then ground to a fine powder in a Waring blender and stored in plastic bags for later analysis. Total nitrogen content of each sample was determined using a micro Keldahl apparatus following the technique described in Harrow *et al.* (1944).

Sample values were divided by $\pi\left(\frac{d}{r}\right)^2$, where $d = 0.219$ m to obtain an estimate of the potential nutrients available/m². Mean values are shown followed by 2 standard errors of the mean throughout this thesis unless otherwise indicated.

Laboratory

Captive animals were housed in 28 cm x 18 cm x 12 cm plastic mouse cages with 2 cm of sawdust, and fed raw sweet potato, peanuts, and fresh grass. Animals survived better if the relative humidity was kept high by placing a solid lid on the cage and dampening the sawdust slightly (Hanley, 1944).

Gophers were weighed to 0.1 g on an Ohaus triple beam balance, and the length of the hind foot was measured from the talus (heel) to the base of the longest toes' claw with vernier calipers.

The rate of metabolism was calculated using an equation of Depocas and Hart (1957) from values of oxygen consumption obtained in an open flow system employing a Beckman G2 paramagnetic oxygen analyzer with a 2% O₂ range.

The animal was placed in a plexiglass chamber 22 cm in diameter and 16 cm high, with a volume of 6 L. Room air was drawn through the chamber at a rate of 300-800 cc/min. The air was then drawn through a column of soda lime to remove CO_2 and a column of Drierite (CaSO_4) to remove water. The volume of the air flow was measured with a Brooks Rotameter R15A calibrated against a Brooks precision volumeter with a stop watch. A portion of the air flow was then pumped through the oxygen analyzer. The system is arranged (Fig. 1) so that a negative pressure is maintained in the chamber and the absorbent train. Thus any leakage must be into the system. Such leakage dilutes the sample with room air but also must register as increased air flow, so that the effect of leakage is negligible. Similarly leakage past the pumps must be out of the system which does not change the pO_2 of the sample and thus has no effect. Only leakage in the pump itself and between pump and flow meter can affect the reading and great care was taken to eliminate air leaks from this part of the train. The maximum inaccuracy in the estimate of rate of metabolism was computed to be 14% of the estimate.

The efficiency of the absorbing train was tested by bubbling air from the train through 0.1 M KOH and titrating this against 0.1 M HCl. The test showed that no measurable quantity of CO_2 passes the soda lime in an 8 hr run. Similarly, by weighing a tube of Drierite through which sample air was passed from the train, it was established that no measurable amount of water passes through the train in an 8 hr run.

The oxygen consumption of single pocket gophers was measured over a range of temperatures (5°C - 37°C) in this apparatus. Animals captured

at various times of the year were tested within 3 weeks of capture. The animals were maintained as described above in a dark room with an ambient temperature of $24^{\circ}\text{C} \pm 1^{\circ}\text{C}$ (range) and relative humidity of $48\% \pm 3.6\%$ between runs. Body temperatures were measured before and after each determination with a Schultheis quick reading thermometer or with a YSI small animal probe on YSI multichannel telethermometer calibrated against a precision thermometer. The thermistor or probe was inserted between 1 and 3 cm into the rectum to give a measurement of core temperature.

Test runs established that the system reached equilibrium oxygen concentration after 45 min and that there was no appreciable difference in the lowest oxygen consumption reading taken through a 24 hr run. Therefore a standard format was adopted in which each animal was placed in the chamber at a given temperature and allowed to equilibrate for one hour. After one hour the first stable low point in oxygen consumption maintained for 10 min was used as resting rate of metabolism. A typical run is shown in Fig. 2. In general several animals were run at a given temperature on any one day so that any transient effect of changing temperature on metabolic rate was avoided.

To measure oxygen consumption during activity, animals were first equilibrated at a given temperature for one hour, then placed in the plexiglass chamber that was $2/3$ full of slightly damp sand. Under these conditions most pocket gophers dig energetically and construct short spiral burrows around the walls of the chamber. After a period to allow oxygen concentration to equilibrate digging could be restimulated by shaking the chamber and collapsing the burrow. It was possible to

measure oxygen consumption of a gopher at rest in its artificial burrow and then throughout a sustained period of digging. The stable maximal value of oxygen consumption was used. In one instance incomplete sealing of the chamber allowed it to partially fill with water and the oxygen consumption of a gopher during a period of sustained swimming was measured.

Food and water intake and excretion were measured in gophers maintained singly in metabolism cages. The cages were located in a dark room where $T_a = 24^\circ\text{C} \pm 1^\circ\text{C}$, $\text{RH} = 48\% \pm 3.6\%$ (2 SE). Each day any food remaining was weighed and fresh food was weighed and put in the cage. The difference (wt. food in-wt. food out) estimates the food eaten and, if the water content of the food is known, water intake. However, the estimate of water intake is confounded because the food loses water to the air. This was partially corrected by weighing control portions of food daily and subtracting the weight loss of control portions from the weight of "food in." The maximal and minimal estimates of water intake can be established. In one case I assumed that as soon as the food was put in the cage the gopher ate its daily ration and then the food lost water to the air for 24 hrs. In the other case I assumed that the food lost water to the air for 24 hrs then the gopher ate its entire ration immediately before I weighed "food out." These methods give maximum and minimal estimates of water intake respectively, and as gophers presumably space their eating over a period of 24 hrs the true values lie somewhere between.

Funnels beneath the metabolism cages separated urine and feces, which were collected under mineral oil. Urine volumes were measured and

a sample frozen for analysis. Feces were weighed, then dried at 105°C for 24 hr and weighed again to determine water content. Dry feces were preserved for analysis. The collecting funnels were shown to collect 90% of the urine and 100% of feces by dripping or dropping known volumes and weights of urine or feces through the metabolism cage.

Activity cycles of pocket gophers were measured by placing animals in glass aquaria balanced on blocks of foam rubber so that the cage wobbled whenever the animal moved. A contact switch connected to an Angus Esterline event recorder recorded wobbles of the cage as strokes on the record. The proportion of each hour in which activity was recorded was estimated visually to give the distribution of activity through 24 hr and these hourly estimates were summed to give the total activity period. Two sets of experiments were conducted with the activity cages. Animals captured in the summer were placed in the cages in a constant temperature room at 28°C. The lighting was dim but daily fluctuations of light level corresponding to normal working hours (8 am to 11 pm) were discernible within the room. The animals were fed daily at 4 pm (1600 hrs) and otherwise not disturbed. After 10-12 days at 28°C the temperature was changed over a 24 hr period to 20°C and activity recorded for another 10 days. This experiment was repeated in the winter with animals captured in the winter that were first exposed to 20°C in the chambers and then to 28°C for 10 days each.

Figure 1. Metabolism chamber and absorbent train used to measure rates of metabolism of *Geomys pinetis*.

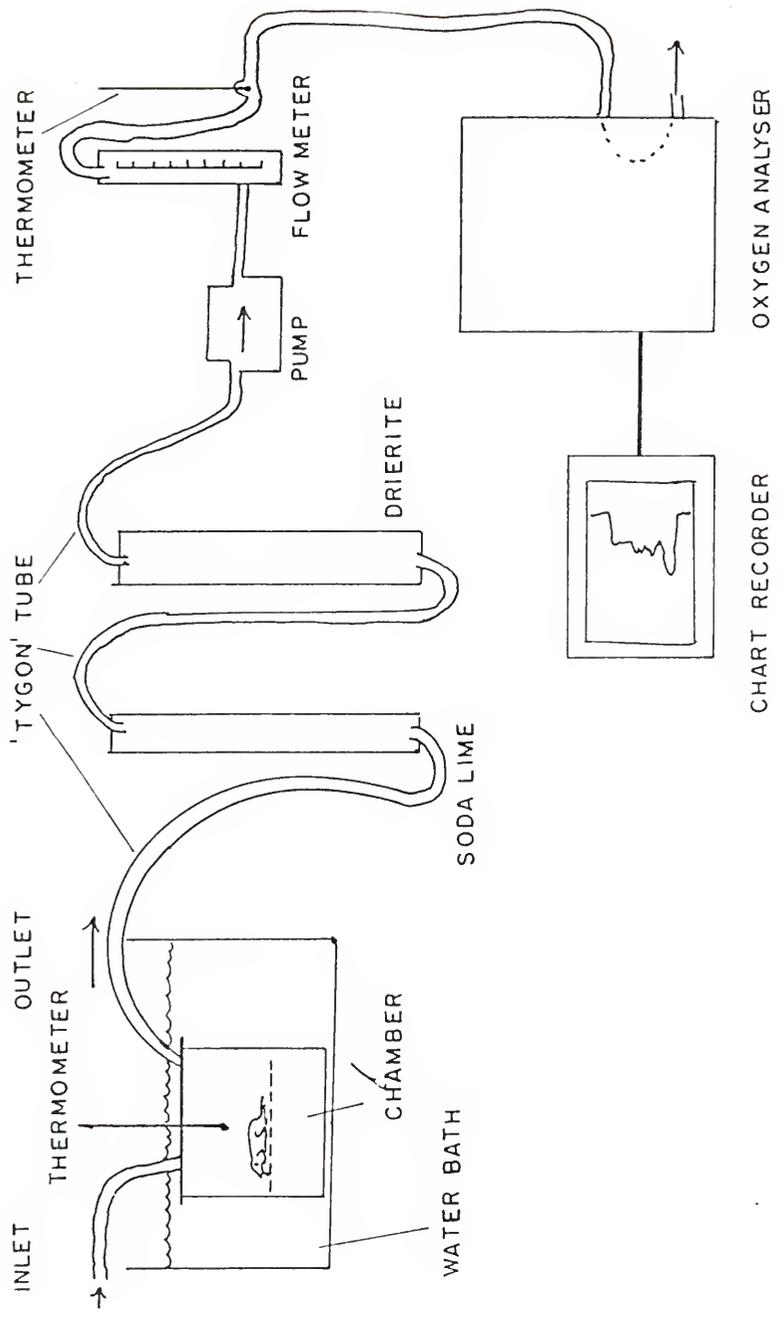
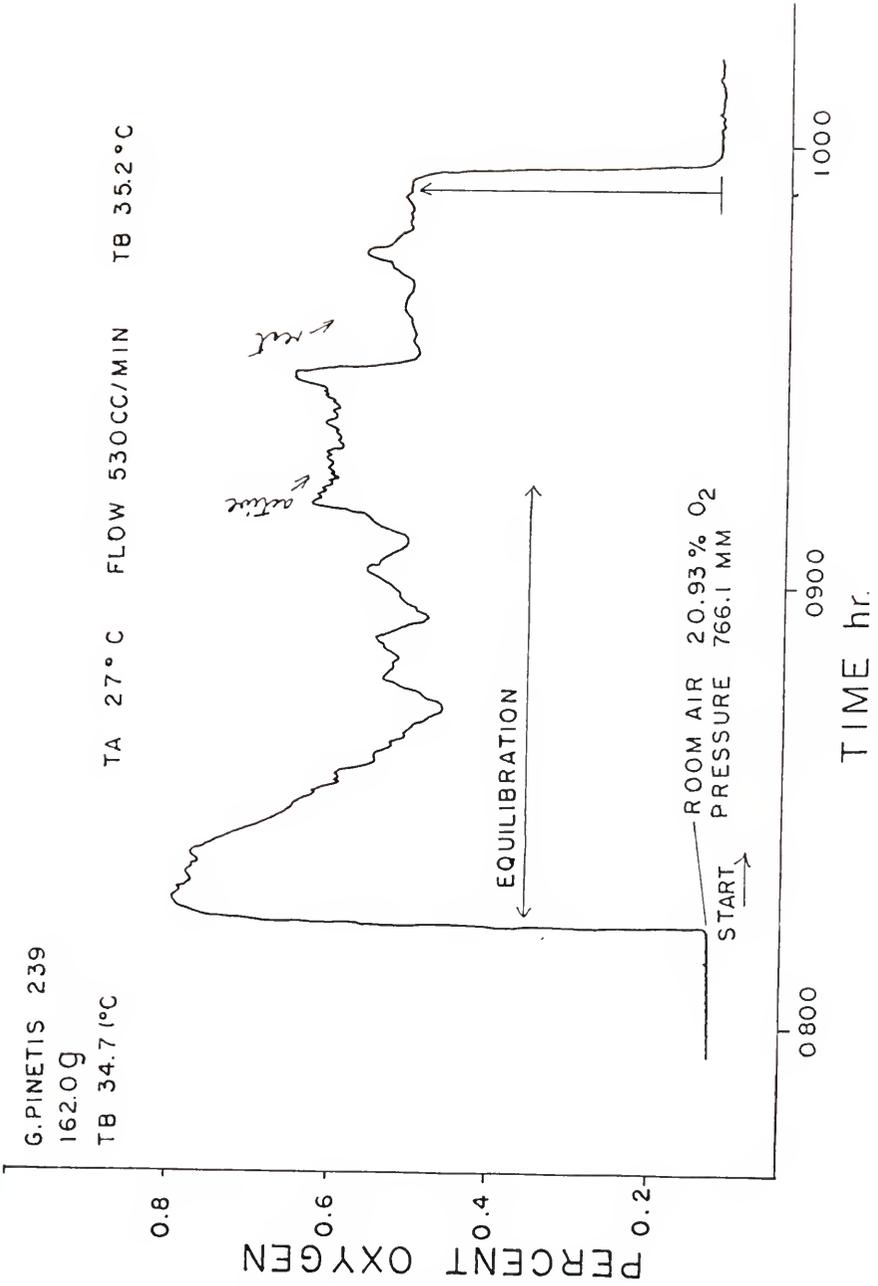


Figure 2. A typical run of oxygen consumption of *Geomys pinetis*.



CLIMATE

Macroclimate

Gainesville's climate belongs to the warm temperate, humid, moist forest life zone of Holdridge (1967). Mean annual precipitation is 1371 mm (54") with a maximal monthly mean of 220 mm falling in July and August and a dryer period with monthly mean rainfall of between 50 mm and 100 mm from October to May.

Mean annual temperature is about 20°C with a maximal mean monthly temperature of 32°C in June, July and August and a minimal mean monthly temperature of 8°C in December and January. There are usually about 12 days with frost between November and February and the frost-free period is in excess of 300 days a year.

Comparing monthly temperature and rainfall values for the years 1973-1975 with the 70-year average values, several deviations from the mean values can be seen. Both maximal and minimal temperatures (Fig. 3) follow the long term average except during the winter and spring (January through May). In this period variations above and below the average are more pronounced. Thus 1973 is seen to be a more or less average year, whereas both 1974 and 1975 had warmer winter and spring temperatures.

Rainfall is more variable than temperature (Fig. 4). 1973 had a wetter spring (February, March, April) than usual, but was drier in October and November, the beginning of a dry spell that continued, with a brief break in December, 1973, until May 1974. Unusually high

Figure 3. Air temperature. Agronomy Weather Station, Gainesville, Florida,
1 km from the Sandhill Research Farm site.

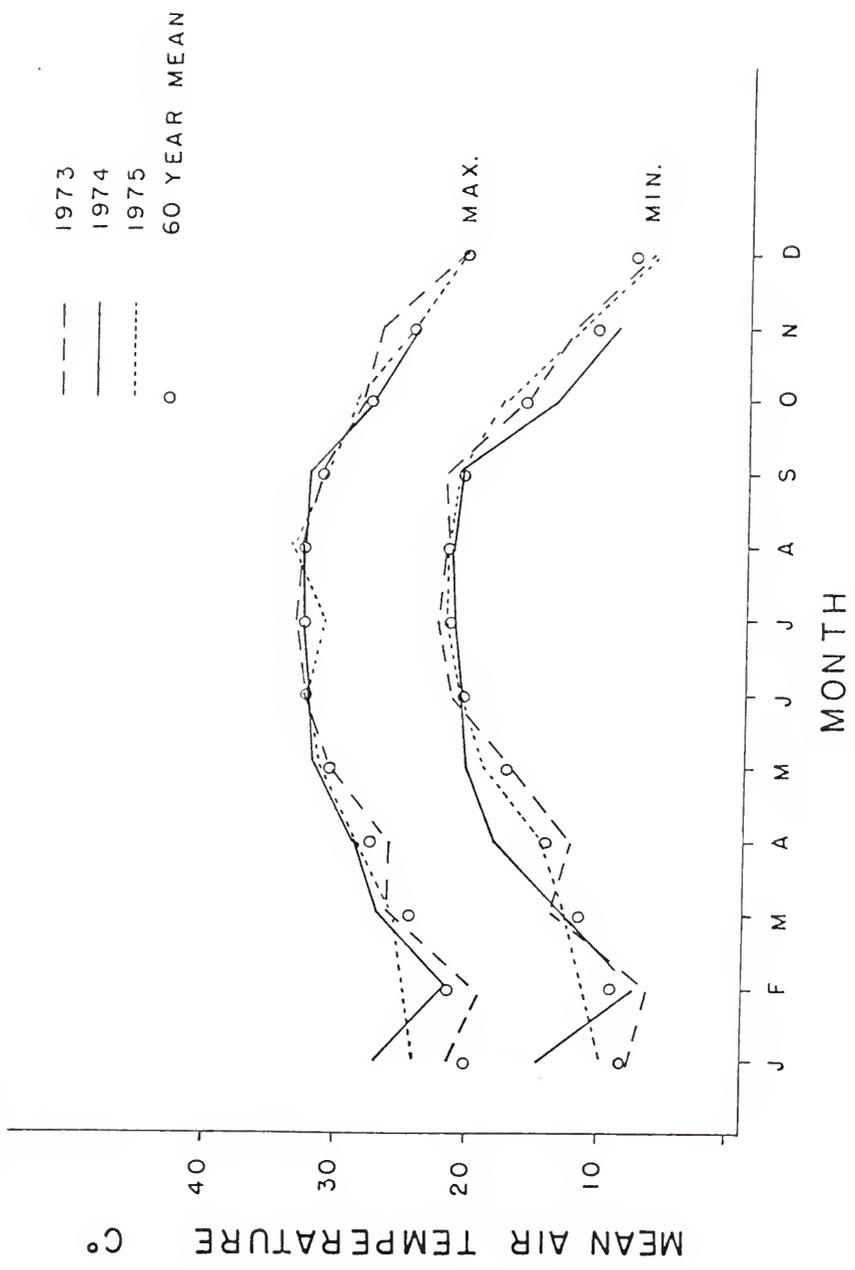
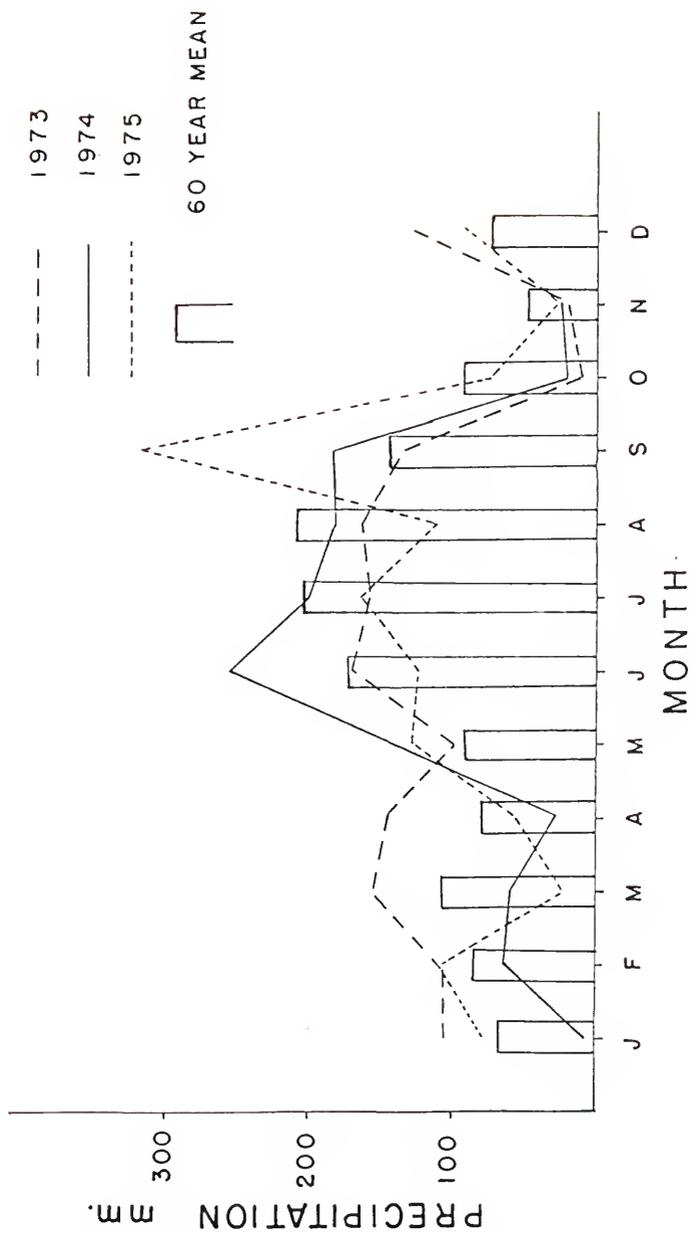


Figure 4. Precipitation. Agronomy Weather Station, Gainesville, Florida,
1 km from the Sandhill Research Farm site.



rainfall in May and June partially made up for the winter drought, but dry months in October and November led to a net deficit in annual rainfall of about 200 mm for 1974. 1975 had a slight deficit in summer rain coupled with an unusually wet September to give an average annual rainfall.

The variations from the 70-year mean seen in 1973-1975 are consistent with variations observed over the last 30 years. Butson and Prine (1968) compute the probability of excessively wet and dry weeks and show that in April and May and again in October and November the expectation of no rain rises to greater than 0.25 in Gainesville. Conversely the expectation of zero rain is less than 0.05 during June, July, August and most of September.

The Gainesville climate, therefore, is characterized by a predictable wet-warm season in June through September, with a drier fall and spring that may be unpredictably very dry. The winter is mild and cool with a minimum of freezing weather. The effect of these climatic variations on pocket gopher microenvironment, food availability and food quality will be considered.

Microclimate

The temperature found within the burrows (T_{bw}) is similar to that found in the adjacent soil (T_{soil}): Regression of T_{bw} against T_{soil} yields the relationship:

$$T_{bw} = 1.14 T_{soil} - 2.71^{\circ}\text{C} \quad (r = 0.88)$$

Therefore, measurement of soil temperatures gives a reasonable estimate of temperature conditions faced by pocket gophers.

Temperature profiles for various seasons and times of the day are shown in Fig. 5. It can be seen that the temperature of the top 30 cm of soil varies widely through the day in response to changing solar input and air temperature, but that below 30 cm all the temperature profiles converge on a common deep soil temperature. It is interesting that daily variation in temperature seems to penetrate deeper during the colder months. Heat flow through soil is described by the parameter K diffusivity ($\text{mm}\cdot\text{sec}^{-1}$) where $K = \frac{k}{\rho c}$ (Gates, 1962; Monteith, 1973) and k is thermal conductivity of the soil ($\text{watts m}^{-1}\text{C}^{-1}$), ρ is soil density ($\text{g}\cdot\text{cc}^{-1}$) and c soil specific heat ($\text{J}\cdot\text{g}\cdot\text{C}^{-1}$). If the temperature at the surface of the soil varies as a sinusoidal wave then

$$T(z,t) = \bar{T} + A(z) \sin(\omega t - zD), \text{ Monteith (1973) (eq. 1)}$$

where $T(z,t)$ = temperature at time t and depth z

\bar{T} = mean temperature at the surface

$A(z)$ = amplitude of oscillation of T at depth z

$\omega = (2\pi/24)\text{hr}^{-1}$ (daily cycle) or $(2\pi/365)\text{day}^{-1}$
annual cycle

$$D = \left(\frac{2K}{\omega}\right)^{1/2}$$

Equation (1) can be solved to give the depth of maximal penetration of the daily or annual heat wave ($= \sqrt{2} D$), and the depth at which the temperature is exactly out of phase with the surface ($= \pi D$). I have estimated K and c to be 0.0013 and 0.3 respectively and specific gravity of sandy soils is 1.4 (Gates, 1962). I therefore, predict the maximal penetration of the daily temperature variation to be 22 cm and the temperature to be 180° out of phase with the surface at 48 cm depth. This agrees rather well with the profiles for the warmer months. Vari-

ations in soil moisture content, and variations from a simple sine wave in the temperature variations at the surface are responsible for slight variations from these idealized predictions at other times of the year.

In an attempt to evaluate seasonal temperature fluctuations, temperatures were recorded from below 30 cm depth for each month of the year (Fig. 6). A more complete picture of the thermal environment of pocket gophers is attained by showing 1) soil temperature isotherms as a function of depth and season, and 2) the distribution of burrow depths (Fig. 7).

Several clear points emerge. The majority of gopher burrows occur between 30 cm and 90 cm depth with a mean depth of $52 \text{ cm} \pm 3 \text{ cm}$. No attempt was made to establish seasonal changes in the depth of burrows, as casual observations indicate that gophers distribute tunnels throughout the soil column at all times of the year (Brown and Hickman, 1973). Thus any choice of temperature within the soil column was achieved by the gopher moving in its burrow rather than by changes in the burrow itself.

The diel and annual temperature fluctuations in gopher burrows are greatly reduced from variations of temperature in the air or at the surface soil. Figure 7 can be used to evaluate the absolute limits of temperature faced by gophers. For 3 months in the winter (December, January, February) the gophers are exposed to temperatures of 15°C to 20°C . During March, April and May; and September, October and November the gophers can remain in temperatures between 20 and 25°C , although in May warm temperatures of 30°C or more penetrate to 30 cm. In June, July

and August the gophers cannot reach temperatures below about 25°C and may be exposed to considerably higher temperatures near the surface.

In summary, for 3 months in the summer gophers cannot get to temperatures below 25°C by moving vertically in the soil. For 3 months in the winter they cannot move to temperatures above 20°C except by coming very close to the surface during the day. For the remainder of the year gophers can choose temperatures between 20°C and 30°C by moving vertically in the soil. The effect of this thermal regime on behavior will be discussed under Feeding Strategy and Activity below.

Figure 5. Soil temperature profiles as a function of season and time at Sandhill Research Farm site showing the convergence of temperature profiles below 30 cm. Open circles represent burrow temperatures.

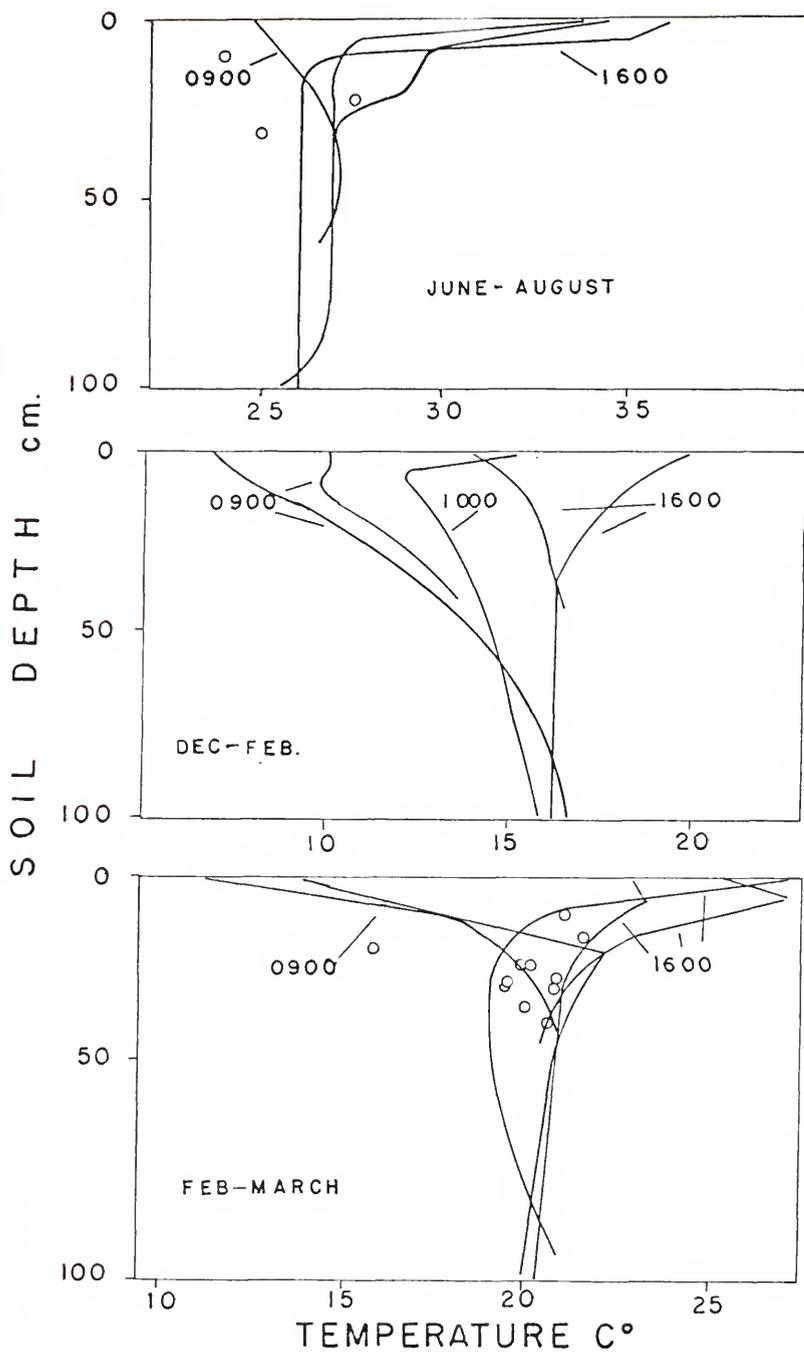


Figure 6. Soil temperature below 30 cm. Sandhill Research Farm site. Each circle represents the mean of soil temperature measurements taken on a given day. Lines encompass the range of values.

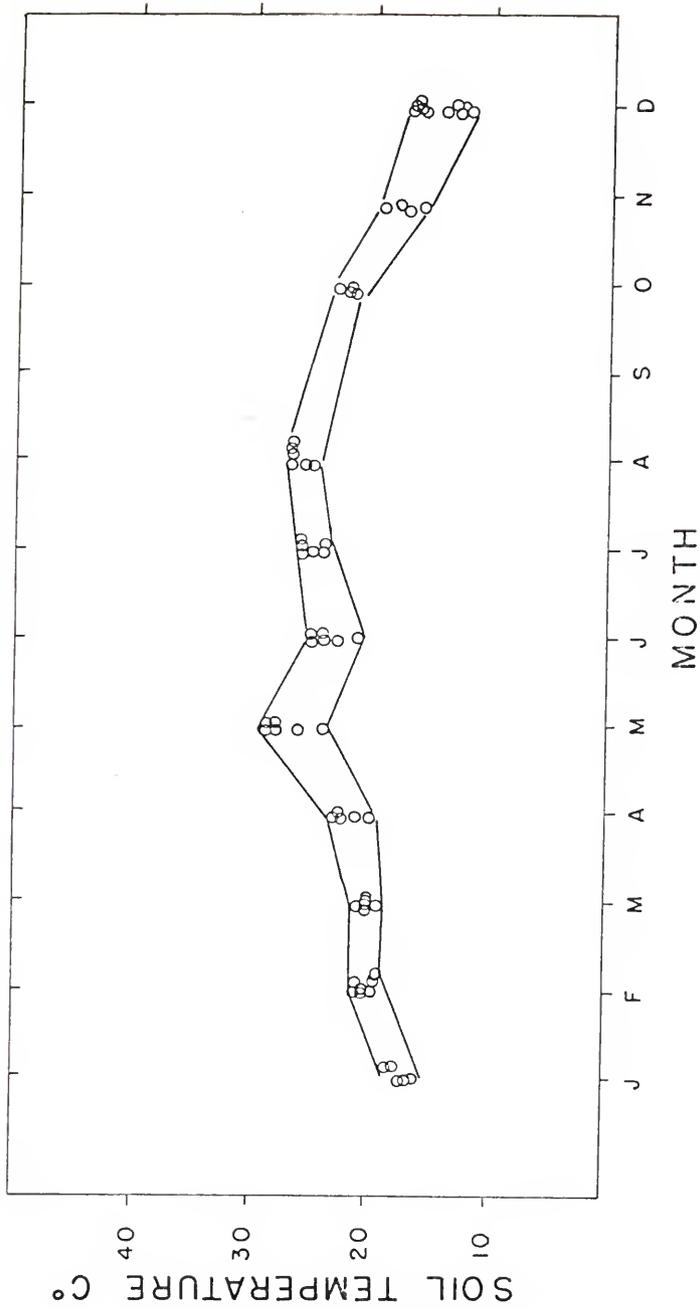
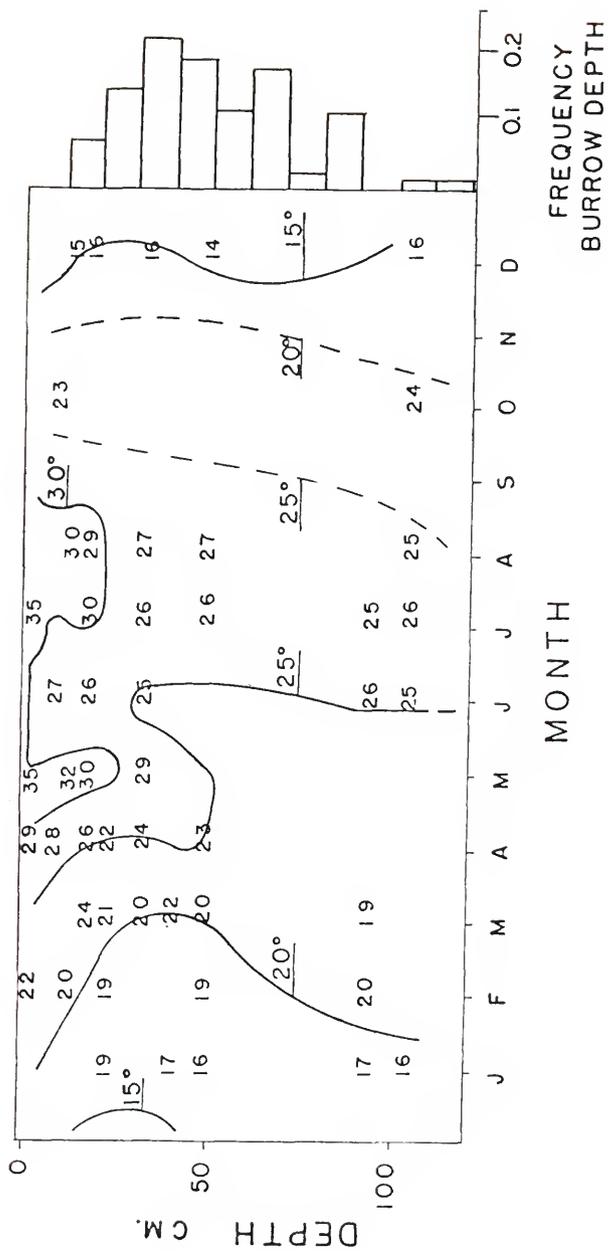


Figure 7. Seasonal soil temperature profiles and depth of *Geomys pinetis* burrows at the Sandhill Research Farm site showing temperature isotherms.



FEEDING

Methods

The plants on the study site were identified and an estimate was made of the relative abundance of each species. Collections of gophers' food caches were made during trapping operations. Discarded plant material in the burrow was also collected and identified.

In the laboratory food and water assimilation and loss were estimated by several means. Gophers in standard metabolism cages were fed sweet potato to approximate their natural diet of roots and tubers. After they were accustomed to this diet and their weight had stabilized, the food eaten by five gophers was estimated by subtracting food not eaten from food given over a 24 hr period.

Water intake and loss was calculated in the following way. First I measured weight loss of pieces of sweet potato in an empty cage adjacent to the cages containing gophers. By carefully measuring the time period between weighings (10-40 hrs), I calculated percent weight loss/24 hrs. This experiment also showed that most weight loss occurred within 24 hrs and was independent of initial weight of the piece of sweet potato (14-40 g). The calculated weight loss/24 hrs was an excellent estimate of actual weight loss over a carefully measured 24 hrs. Mean weight loss over 24 hrs was 23.5 ± 0.99 percent, *i.e.* approximately 25 percent.

I dried samples of sweet potato from several different batches over the course of the feeding experiment. Samples were dried at 60°C

for 72 hrs and dried under vacuum at 52°C for 24 hrs or lyophilized in freeze drier apparatus. There were no differences in the estimates of total water content of sweet potato. The mean water content of sweet potato is 74.49 ± 0.9 percent, *i.e.* approximately 75 percent water.

If it is assumed that the gopher eats the food after all water loss has occurred and just before the uneaten food is reweighed then:

$$F_i = E + R + W$$

where F_i = weight of food given

W = weight of water lost in 24 hrs

E = weight of food eaten

R = weight of remaining uneaten food

By rearranging

$$E = F_i - R - W$$

but $W = 0.25 F_i$

therefore

$$\begin{aligned} E &= (F_i - R) - 0.25 F_i \\ &= 0.75 F_i - R. \end{aligned}$$

The proportion of water minus its water loss in E (W_e) must equal the weight of water in the food given divided by the total weight of F_i minus its water loss.

$$W_e = \frac{0.75 F_i - 0.25 F_i}{F_i - 0.25 F_i}$$

$$W_e = 0.66$$

Multiplying the weight of food eaten (E) by its water content (W_e) gives water intake (W_i)

$$\begin{aligned} W_i &= W_e \cdot E \\ &= 0.66 (0.75 F_i - R). \end{aligned} \tag{eq. 2}$$

This is the minimum water intake possible when F_i and R are known.

Alternately, let us assume that the gopher consumes its ration immediately; then the uneaten food (R) loses water for 24 hrs.

$$F_i = E + R + W$$

therefore, $E = F_i - R - W$

but, $W = 0.25 (F_i - E)$

therefore, $E = F_i - R - 0.25 F_i$

i.e., $0.75 E = 0.75 F_i - R$

or $E = \frac{0.75 F_i - R}{0.75}$

The weight of water in the food eaten is $E \times 0.75$. Therefore water intake

$$W_i = 0.75 (F_i - R). \quad (\text{eq. 3})$$

The weight of uneaten food was subtracted from the food given each gopher, and maximal and minimal water intake were calculated for each day. The values reported here are the maximal estimates. In this experiment gophers had a mean dry matter intake (DMI) of $2.8 \pm 0.625 \text{ g} \cdot 100 \text{ g}^{-1} \text{ day}^{-1}$ and a mean maximal water intake of $8.1 \pm 1.7 \text{ g} \cdot 100 \text{ g}^{-1} \text{ day}^{-1}$.

When urine and feces were collected, another dimension was added to the water balance calculation. Food and water inputs were calculated as before. The measured urine volume corrected for the efficiency of the collector was added to fecal weight \times average fecal water content. The weight change of the animal must be equal to the sum of inputs and outputs.

Change in weight = total in - total out

$$\Delta W = (\text{dry food} + \text{water}) - (\text{feces} + \text{urine} + \text{evaporation} + \text{metabolism}) \quad (\text{eq. 4})$$

Metabolism includes the oxidation of body tissue and food to CO_2 , hair loss, and other minor avenues of tissue loss. This term can be estimated

from the metabolic rate and will be ignored in the present calculation but considered later. All these parameters were measured except evaporative water loss. The total urine and fecal production, food intake, and weight changes were summed for the experimental period (7-12 days) and divided by days to give average daily inputs and outputs for each animal.

Evaporative water losses were calculated by rearranging equation 4.

$$\text{Evaporative water} = (\text{dry food} + \text{water}) - (\text{feces} + \text{urine}) + \Delta W$$

These values were all divided by initial body weight to give water and material exchange in $\text{g} \cdot 100 \text{ g}^{-1} \text{ day}^{-1}$. The metabolic rate of a resting gopher at 24°C is about $1.3 \text{ ccO}_2 \text{ g}^{-1} \text{ hr}^{-1}$ (Figs. 14 to 19), which is equivalent to $3120 \text{ ccO}_2 \cdot 100 \text{ g}^{-1} \text{ day}^{-1}$. Assuming an RQ of 1 and dividing by the density of CO_2 at STP (3.09 g/L), we get $1.01 \text{ g CO}_2 \text{ g}^{-1} \text{ day}^{-1}$ of weight loss due to metabolism. An active gopher has about twice the metabolic rate of a resting gopher, so the amount of weight loss due to metabolism is between 1 and $2 \text{ g} \cdot 100 \text{ g}^{-1} \text{ day}^{-1}$. This amount should be subtracted from both evaporative loss and from total water loss.

Results and Discussion

Pocket gophers are well known to feed on roots and tubers although some species consume large amounts of above ground plant parts (Wade, 1972; Myers and Vaughan, 1964; Vaughan, 1967). *Geomys pinetis* depends completely on underground plant parts, and has appropriate behavioral modifications.

Only 4 species of plants were consistently found in food caches, *Paspalum notatum* (Bahia grass), *Eupatorium* spp. (dogfennel), *Chenopodium*

spp. (Lambs quarters), and *Alysicarpus vaginalis* (legume). Usually only one of these was present in any food cache. Gut contents of newly captured gophers that died contained only Bahia grass and in no cases was there any soil in the stomachs. The plants found at the sandhill study site are shown in Table 1, with estimates of their deduced importance in *Geomys*' diet and their relative abundance. Bahia rhizomes formed an overwhelming proportion of all dietary samples on the study area.

The absence of soil in gopher stomachs and the common presence of fresh leafy plant material in burrows beneath fresh mounds led me to observe the actual feeding behavior of pocket gophers in the lab. From observations made on caged gophers given natural foods I can reconstruct the probable feeding behavior.

Geomys pinetis has two foraging techniques. Firstly gophers expel mounds of sand onto the surface of the soil. Field observations lead me to suggest that the mounds function as protection for the gopher when it removes some of the plant material that has been covered by sand. The gopher then takes the plants down into the burrow, where in safety it fastidiously removes all soil, small roots, and leaves, using its incisors and forepaws with amazing dexterity. It cuts the stem and rhizome into 2-3 cm sections, which are then transported to spherical food cache chambers. Some of the discarded material is macerated and used as nesting material in spherical nest chambers. Secondly, gophers also gnaw on roots and rhizomes which impinge on their burrows. The long tubers of *Eupatorium* spp. (dogfennel) and *Cnidioscolus stimulosus* (tread softly) were excavated with evidence of such feeding activity. These observations agree with those of Barrington (1940) and Vaughan (1966).

The quality and quantity of the gopher food is shown in Table 2 where biomass, water content, and nitrogen content of core samples of below ground plant parts are shown. It was not possible to separate out the very fine roots and some dead material from the samples as a gopher would do, and so the true quality of the food is underestimated. However the seasonal trends should still be evident. Both biomass and water content are extremely variable, and the differences in the means of samples from different seasons are not significantly different.

The large standard error of the plant biomass estimates indicates that this resource is very unevenly distributed. The sampling core diameter (21.9 cm) was deliberately chosen to represent a sample that a gopher might take in the course of its feeding activity beneath a mound. Therefore I would expect that a gopher is exposed to a similar level of variability as it samples the available resource.

The water and nitrogen content of plants is seasonally variable. Thus, while the maximal water content is similar from season to season, the lower limit is considerably less in February and April. This corresponds to the driest period of the year and a period of extended drought in 1974 when these samples were collected. The nitrogen content approaches a significant difference in different seasons ($F = 2.51$, $p = 0.1$). The below ground plant parts are low in nitrogen in April and June and higher in fall and winter. Therefore it seems that the patchy and variable nature of the food and water resources coupled with the gophers' method of foraging may result in uncertainty in the gain to the gopher from any foraging episode. As the gopher's cost when extending the burrow is high, the uncertainty of food quality may

exert considerable effect on the ability of a gopher to persist in a given area.

Having established what *Geomys pinetis* eats and what its food contains it is necessary to ask what *Geomys* requires from its food. Due to the highly porous nature of the soil they inhabit, gophers are rarely exposed to free water. In the laboratory they do not readily drink from bowls although under certain conditions they can be taught to drink from bottles. In addition to nutrient and energy requirements gophers get all their water from their food. The results of the feeding experiments give estimates of the water and food requirements of pocket gophers.

In one set of experiments the average weight change was very small or positive; these gophers are shown as normal in Table 3. The mean total water loss for the normal gophers is $24.74 \pm 2.02 \text{ g} \cdot 100 \text{ g}^{-1} \cdot \text{day}^{-1}$. Of this, $5.73 \pm 1.5 \text{ g} \cdot 100^{-1} \cdot \text{day}^{-1}$ is urine, $0.5 \pm 0.4 \text{ g} \cdot 100 \text{ g}^{-1} \cdot \text{day}^{-1}$ is water lost in feces, and the remainder $18.51 \pm 2.7 \text{ g} \cdot 100 \text{ g}^{-1} \cdot \text{day}^{-1}$ is insensible or evaporative water loss. The average metabolic rate of gophers under the conditions of this experiment is $1.3 \text{ cc } O_2 \cdot \text{g}^{-1} \text{ hr}^{-1}$ which is equivalent to $3120 \text{ cc } O_2 \cdot 100 \text{ g}^{-1} \text{ day}^{-1}$. The stoichiometry of the reduction of O_2 to H_2O as a final electron acceptor in cellular metabolism is such that 1 mole of O_2 forms 2 moles of H_2O , and each mole of H_2O weighs 18 g; therefore, the average production of metabolic water by a resting gopher is equal to:

$$\frac{3.120}{22.4} \times 2 \times 18 = 5.01 \text{ g } H_2O \cdot 100 \text{ g}^{-1} \text{ day}^{-1}$$

This is a minimum estimate. If this amount is added to the measured free water intake ($17.34 \text{ g } 100 \text{ g}^{-1} \cdot \text{day}^{-1}$), then the total $22.35 \text{ g } 100 \text{ g}^{-1} \cdot \text{day}^{-1}$ approaches the mean total water loss of $24.74 \text{ g } 100 \text{ g}^{-1} \cdot \text{day}^{-1}$. That is, these gophers are approximately in water balance which is in agreement with the small net weight change.

The estimate of evaporative water loss calculated by subtraction can be checked by calculating the expected evaporative water loss due to respiration. The alveolar PO_2 of mammals is relatively constant at 13% (Guyton, 1976). Therefore, the volume of air ventilated can be calculated from the volume of O_2 respired. If the temperatures and relative humidities of this volume of inspired and expired are known, the amount of water vapor in these volumes can be calculated and the difference between the amount of water inspired, and the amount expired is the net water loss. The nasal temperature of expired air of pocket gophers at 24°C is 25°C . Therefore, it seems certain that gophers have efficient nasal counter-current heat exchangers as has been described for many desert animals (Jackson and Schmidt-Nielsen, 1964; Schmidt-Nielsen *et al.*, 1970) and recently for other mesic animals (Getz, 1968). Assuming that the expired air is 100% saturated, the calculated water loss at 24°C (54% RH) is $43.5 \text{ g } 100 \text{ g}^{-1} \cdot \text{day}^{-1}$. This figure could be reduced if the gopher breathes air that has been humidified and warmed, but will be increased during activity. Gophers in the metabolism cages assumed a characteristic posture sitting upright on the tail with the head bowed down between the protruding hips and covered with the forepaws, a position that may humidify and warm the air they breath.

One source of error in the collecting technique was the tendency of fecal pellets to adhere to the collecting funnel and lose water before collection. The effect of this is to underestimate the fecal component of water loss, but it does not change the net water balance calculated. The increment of water loss in feces is incorrectly judged to be evaporative water loss. Evaporative water losses other than by respiration (sweating) are included in the experimental estimate but not the calculated one. These various influences appear to balance out as the experimental and theoretical estimates are quite close.

In summary, pocket gophers in water balance have a net water loss of about 25% of their body weight/day. Of this, 75% is insensible, 23% urinary, and 2% water lost in feces.

These estimates are comparable to those made by Judd and Reichman (1972) on *Pappogeomys* and *Thomomys* (15% - 30% body weight per day water intake) but are greater than the expected water intake calculated by Hudson's (1962) equation

$$\text{water intake} = 0.24 W^{-0.12}$$

This expected water intake is between 12 and 14 g 100 g⁻¹·day⁻¹ for pocket gophers between 100 g and 200 g body weight. The estimated evaporative water loss (EWL) is very much higher than the evaporative water loss reported for several desert species, but is comparable to that reported for *Citellus leucurus* (Hudson, 1962), *Neotoma lepida* (McMillen and Lee, 1967), and numerous bat species (Studier, 1970). Chew (1961) gives an equation predicting EWL for mammals. His equation

$$\log \text{EWL} = \log 0.087 + 0.883 \log W$$

predicts EWL between 5 and 10 mg/g/hr for average size pocket gophers which compares favorably with the observed rate of 7.7 mg/g/hr.

In another set of experiments the gophers showed an average weight loss of $2 \text{ g} \cdot 100 \text{ g}^{-1} \cdot \text{day}^{-1}$ indicating a net water loss. These gophers were dehydrated by the end of the experimental period. The reason for their weight loss is immediately apparent in their reduced water intake, $9.32 \pm 0.89 \text{ g} \cdot 100 \text{ g}^{-1} \cdot \text{day}^{-1}$, or 53% of the intake of normal gophers. Mean urinary output was slightly reduced to $3.7 \pm 2.0 \text{ g} \cdot 100 \text{ g}^{-1} \cdot \text{day}^{-1}$, but this is not significantly different from the urinary output of normal gophers ($t = 1.64$ 9 d.f. N.S.). The fecal component of water loss was reduced largely because the dehydrating gophers defecated very little, not because their feces were drier. The evaporative water loss of dehydrating gophers was $10.43 \pm 3.2 \text{ g} \cdot 100 \text{ g}^{-1} \cdot \text{day}^{-1}$ which is significantly different from that of the normal gophers ($t = 4.10$ 9 d.f. $P < 0.1$). How this reduction is accomplished is not known, but postural changes that humidify incurrent air and a reduction in activity and hence volume of air respired would both reduce evaporative water loss.

The pocket gopher seems to have relatively ineffective renal control of water loss. The mean urine osmolarity of two normal pocket gophers was 494 ± 90 (2SE) mOsm/l, while the osmolarity of two gophers dehydrated to 75% of their body weight was only 1760 ± 400 (2SE) mOsm/l. This represents a very modest renal concentrating ability comparable to man and the white rat, two notoriously poor renal concentrators (Schmidt-Nielsen, 1964).

The water intake of dehydrated gophers was close to that observed in the previous feeding experiment, suggesting that these gophers were also in negative water balance. Only the maximum estimates of water

intake are compatible with the independently derived water loss measurements. This suggests that the assumptions inherent in the maximum estimate are essentially correct; *i.e.*, gophers rapidly eat their ration of fresh (moist) food and then ignore the drying remainder. This behavior suggests that selection has imparted a degree of specificity, with respect to water content, on a gopher's choice of food to make up for the poor control of water loss.

Pocket gophers have a large caecum which seems to provide a suitable habitat for microorganisms that digest cellulose. Riggs and Studier (1966) describe cellulose digesting bacteria from the gut of *Thomomys bottae* and Wilks (1962) describes the reingestion of feces in *G. busarius* and *T. monticola*. I have observed *G. pinetis* eating feces directly from the anus. The significance of this ruminant like mode of digestion to the nutritional status of *G. pinetis* is uncertain. True ruminants obtain fixed nitrogen and vitamins from their symbionts but the function of "hind gut" ruminants is not well understood (Moir, 1965). The presence of a caecum leads to a long retention time for food in the gut (approximately 3 days), making the estimation of assimilation efficiency difficult (Drodz, 1975). A rough estimate, obtained by dividing fecal dry weight by dry matter intake, was 83% assimilation efficiency which compares favorably with estimates of 77.5%-88.9% for herbivorous rodents (Drodz, 1975).

Table 1. Common plants at Sandhill Reserach Farm. Listed in approximate order of abundance. Use by pocket gophers: √√√-known extensive use, √√-occasional use, √-suspected use or used in laboratory.

% Cover	Species	Common	Gopher Use
50	<i>Paspalum notatum</i> var. <i>saurmae</i>	bahia grass	√√√
50	<i>Cynodon dactylon</i>	Bermuda grass	√√
10	<i>Paspalum ciliatifolium</i>	hairy bahia grass	
10	<i>Sporobolus poiretii</i>	smut grass	
10	<i>Panicum maximum</i>	panic grass	
10	<i>Ricardia scabra</i>	succulent	√
1	<i>Cyperus</i>	sedge	
1	unidentified	sedge	
1	<i>Sida rhombifolia</i>	tea weed	√
1	<i>Chenopodium</i>	Lambs quarters	√√
1	<i>Cnidioscolus stimulosus</i>	Tread softly	√√
1	<i>Eupatorium compositifolium</i>	Dog fennel	√√
1	<i>Eupatorium capillifolium</i>	Dog fennel	√√
1	<i>Bidens pilosa</i>	Spanish needles	
1	<i>Ambrosia artemisiifolia</i>	Ragweed	
< 1	<i>Orontium aquaticum</i>	Golden club	
< 1	<i>Erechtites hieracifolia</i>	fireweed	
< 1	<i>Aster dumosus</i>	daisy	
< 1	<i>Tragia wrens</i>	--	√
< 1	<i>Cenchrus echinatus</i>	sandspur	
< 1	<i>Pyrrhopappus carolinianus</i>	False dandelion	√
< 1	<i>Gaura argustifolia</i>	--	
< 1	<i>Indigofera hirsuta</i>	legume	
< 1	<i>Alysicarpus vaginalis</i>	legume	√
< 1	<i>Rubus trivialis</i>	blackberry	
< 1	<i>Asimina longifolia</i>	paw paw	
< 1	<i>Phyllanthus</i>	spp.	
< 1	<i>Chloris petraea</i>	fingergrass	

Table 2. Seasonal changes in food and water resources of *Geomys pinetis*.

	Feb	April	June	Aug
Biomass				
Mean dry wt g m ⁻²	515.9	593.6	511.9	523.9
+ 2SE	170	213	209	122
Water content				
g H ₂ O 100 g dry sample ⁻¹	49.5	51.5	56.0	60.1
Range	27-63	44-56	53-60	57-65
Nitrogen				
mg N g dry sample ⁻¹	8.58	5.95	5.77	8.66
+ 2SE	2.26	1.19	1.80	2.10

Table 3. Water and dry food output and input of *Geomys pinetis* during feeding trials in the laboratory.

Animal	Output				Input			
	Urine	Feces	Evaporation	Total	Dry Feces	Water	Dry Food	Total
Normal								
#220	7.4	1.0	16.8	25.2		17.4	8.2	25.6
#221	6.3	0.7	15.9	22.9		15.9	7.1	23.0
#281	3.9	0.2	19.3	23.4		16.3	6.2	22.5
#282	5.3	0.1	21.9	27.3		19.8	6.8	26.6
Mean	5.73 23%	0.5 2%	18.51 75%	24.74		17.34	7.0	24.34
2SE	1.5	0.4	2.7	2.02		1.8	0.8	
Dehydrated								
#220	1.7	0.02	16.0	17.72		10.9	5.0	15.9
#221	1.3	0.0	11.8	13.1		8.6	3.8	12.4
#281	6.3	0.01	8.8	15.11		9.3	3.2	12.5
#282	3.7	0.2	10.8	14.70		9.2	3.8	12.0
#228	5.9	0.1	7.5	13.5		10.1	3.5	13.6
#230	3.5	0.1	7.7	11.30		7.8	2.8	10.6
Mean	3.73 26%	0.07 1%	10.43 73%	14.23		9.3	3.68	12.98
2SE	2.0	0.08	3.2	1.80		0.9	0.75	

POPULATION DYNAMICS

Methods

The total number of gophers present on the study area was determined by direct counts of active mounds made by pocket gophers. In an attempt to verify that counting active mounds is a reasonable estimate of population numbers, population estimates in subsections of the study area were made. Then all burrow systems active or inactive were extensively trapped and the actual number of pocket gophers present determined. Even if gophers were not captured, evidence of their presence in the form of buried or filled traps and burrows was obtained.

By monitoring individual territories over a period of time it was possible to identify which territories were apparently inactive in a given month but active in subsequent months. It can then be assumed that the apparent inactivity was not due to the absence of the gopher. The presence and absence data were arranged in the calendar format of Petruszewicz and Andrzejewski (1962). In this way it was possible to correct the presence or absence counts backwards in time and so estimate how well the mound building activity reflects actual population numbers.

Standing crop (N) estimates do not reveal the total number of individual animals that have contributed to production, growth, respiration, etc., over a time period. A useful analogy is that of a

tank of water with fixed volume (equivalent to standing crop N) with a variable inflow and outflow. Inflow and outflow can both be large relative to volume in the tank, but as long as they are equal the volume will not change. It is necessary to calculate the average time that any individual spends in the population \bar{t}' (Grodzinski *et al.*, 1975)

$$l = t$$

$$\bar{t}' = \frac{l}{V} = \frac{\sum_i t_i}{V}$$

where $V(nu)$ is the number of discrete individuals in the population during a given period.

\bar{t}' can be calculated for the subset of the total population that was scored monthly for presence or absence; it is equal to 3.33 ± 0.68 months. Then, turnover rate (θ) can be calculated (Grodzinski *et al.*, 1975)

$$\theta = \frac{T}{\bar{t}'}$$

where T is any given time period. The values of θ and \bar{t}' should be the same in the general population and so V for the total population can be calculated from the equation (Grodzinski *et al.*, 1975)

$$V = \bar{N} \theta$$

using \bar{N} = mean standing crop for period T .

Brown (1971) provides the seasonal age and sex structure for a population of *G. pinetis* in Hillsborough County, Florida, in 1968. His estimates are similar to those obtained by Wing (1960) for a population of *Geomys* in Alachua County, Florida. By assuming that the age and sex structure and proportion of pregnant females was similar in my popu-

lation, I can apportion discrete numbers of individuals into sex and age classes. The turnover rate, mean residence time \bar{t} , standing crop \bar{N} , and numbers of individuals apportioned into adult males, adult females, pregnant or lactating females, and juvenile classes are shown for 3-month time period from fall 1973 to spring 1975 in Table 4. These figures will be used in the calculation of an energy budget. The recapture of marked gophers allowed estimates of growth rate, longevity and movements in the field to be made.

To evaluate the suitability of different habitats for pocket gophers, total counts were made in a series of habitats with different histories of disturbance. Disturbance histories were deduced from local records, conversation with local residents, management records and from floral clues. The presence of wire grass and large long leaf pines indicates undisturbed sand hill habitat; slash pine is only present when the area has not been burned for some years. Because wire grass does not recolonize once it is removed its absence in otherwise apparently undisturbed areas is indicative of previous disturbance, usually by agriculture. In this way a 7 ha rectangular plot in Morningside Park is recognizable as an old farm site although at the present time it carries a mature flatwood pine community. The pines are large slash pine about 30 years old and wire grass is absent. Careful examination of the ground surface revealed old plough furrows still visible after 30 years.

Results and Discussion

The results of five experiments establishing the effectiveness of the census are shown in Table 5. Although the difference between

observed and estimated numbers of gophers is not greater than would be expected by chance (χ^2 test), it appears that counting active mounds often overestimates the actual number present. The major criticism of direct count of mounds as a population density estimator is that it would underestimate the actual number by failing to score animals present but not actively making mounds. This seems not to be the case.

A total of 100 pocket gophers was captured between 1973 and 1976, of which 58 came from the Sandhill Research Farm study site. Of these 58, 29 were marked and released at their point of capture and seven were subsequently recaptured. The dates of capture and recapture and the changes in weight of these animals are shown in Table 6.

Most of the gophers were recaptured in the same territory in which they were released within 2 to 4 months. Only one gopher had moved a long enough distance to be recorded in a 25 m square quadrat different from the quadrat in which it was first captured. One gopher (#203) was recaptured after 17 months in the same quadrat as that in which it was released.

In addition, two pocket gophers were recaptured but their tattoos had faded or eroded so that their identification was not certain. It was possible to make tentative identification from tattoo traces and scars on the feet, which had the appearance of old tattoo marks. If these are accepted then one of these gophers (female #234) was recaptured 100 m from her original capture point after 20 months. This animal had lost most of its tail and appeared to be old when recaptured. The other (#210) was recaptured after 20 months after moving a minimum of 250 m from its original point of capture. This animal (#210) was first

captured as a juvenile (71 g) and seemed to be a mature adult female when recaptured.

Wing (1960), Ewel (1970) and Brown (1971) have studied the reproductive biology of *G. pinetis*. They breed throughout the year except in November, but there are two main concentrations of reproductive activity, in February and March, and again in June to October. Females are reported to have 1.52 ± 0.11 (Wing, 1960) or 1.74 ± 0.51 (Brown, 1971) young at a time and evidence from scars in the uterus suggests that many females breed twice a year. Figure 8 shows the percentage of females with active corpora lutea reported by Brown (1971). In contrast, other geomyids have larger numbers of offspring (2.5-10) and most only breed once a year (Asdell, 1946).

The number of active pocket gopher territories counted each month on the 17 ha study site at the Sandhill Research Farm in the period November, 1973 through July, 1975 is shown in Fig. 9. The number of territories that appear to have active gophers in residence is highest during the fall (October-December) and lowest in the spring (March-July). The highest number is 75 in 1973 and 104 in 1974. The lowest number is 25 in 1974 and 34 in 1975. The corrected counts obtained from the calendar method of a subset of the total population mirror the seasonal fluctuation of the total counts. Similar seasonal fluctuations in population number are shown by Miller (1948), Howard (1961), and Wilks (1963).

Examination of the calendar records show that there are two periods of recruitment of new individuals into the population, which correspond to the appearance of young gophers that have left the maternal burrows. These recruitment pulses follow the peaks of reproductive activity in

February-March and June-October by about three months (Brown, 1971); see Fig. 8.

The calendar records of presence or absence were grouped into 3-month intervals and used to calculate life tables, assuming that gophers appearing in the population are newly recruited juveniles of 3 months of age. The age-specific survival (P_x) was calculated and is shown in Fig. 10 for the two recruitment pulses separately and for the grouped data for the whole period. It is clear that lowest survival of newly recruited gophers is in the first few months of independence. The value of P_x rises to a constant level of about 0.6 per 3-month interval after 9 months in the population. The lowest survival period for the spring cohort is in the second 3-month interval while the survival of the fall cohort is lowest in the first 3-month interval after recruitment. That is, both cohorts show lowest survival in the first winter period to which they are exposed.

The probability of survival during this critical period is higher for the spring cohort than for the fall cohort. This may be a reflection of their greater size and experience which enable them to resist the rigors of winter. The significance of this fact to the annual reproductive output of *Geomys pinetis* will be discussed later.

Table 4 shows a 3-month average of the change in standing crop (ΔN) from each month to the next, which is a better indicator of the time of mortality than the standing crop (N) itself. It is clear that the period November-April is the time of population decline and the survivorship values show that it is the death of newly recruited juveniles that make the greatest contribution to this decline.

The mean body weight of pocket gophers at their time of capture is shown in Fig. 11. The mean weight of males is $175.8 \text{ g} \pm 14.4$, but this estimate includes a pulse of smaller individuals measured in the fall. Mean weight of adult male gophers is closer to 230 g. Mean weight of female gophers is 145.6 ± 6.4 . Individuals weighing less than 99 g were considered to be newly recruited females and are shown as individual points on Fig. 11. The presence of smaller gophers seems to follow the known peaks in breeding activity by about 3 months, reinforcing the conclusion that the periodic appearance of new individuals in the population is a result of the preceding breeding peak. Small sample sizes and large differences in weight of gophers from any particular month obscured any statistical significance of seasonal changes. The mean standing crop (\bar{N}) multiplied by the mean weight in that month yields the estimate of biomass shown in Table 4.

The changes in weights of recaptured gophers after a known period of time can be used to estimate growth rate. Figure 11 shows that adult animals maintain a relatively constant weight or may show a decline in weight during the winter months.

The mean daily rate of weight increase of seven animals for which data are available is $0.46 \text{ g/day} \pm 0.18$ (1SE), which can be taken as a first approximation of growth rate. However, growth rates in animals usually follow sigmoidal patterns, with young animals growing faster. Ricklefs (1967) gives methods for evaluating the growth constant K , given data on age and size. My data represent fragments of such data but can be transformed to fit Rickleff's treatment by calling the day of first capture (and weight) day 0. Then, the transformed weight changes should approximate a straight line whose slope equals K .

The Gompertz transformation gives the best fit to a straight line and is compatible with other estimates of growth in pocket gophers:

$$W = e^{-bk^{-Kt}}$$

The growth constant $K = 0.005 \pm 0.001$, which is equivalent to a maximum rate of growth of 0.56 g day^{-1} for a 300 g gopher during its fastest growth period.

Table 7 shows the results of the counts made on different successional stages of the sandhill community. The undisturbed sites have lower gopher densities than the disturbed sites. The slightly higher count on the site burned one month before the census is probably a result of the greater ground visibility on the newly burned site.

The number of nematode parasites *Protospirura ascaroidea* recovered from *G. pinetis* stomachs is shown in Fig. 12. These parasites are 10-35 mm [?] long and weigh $0.28 \pm 0.02 \text{ g}$ each ($N = 30$). Figure 12 shows the marked seasonal variation in parasite load. There are almost no parasites in the summer but the numbers build up alarmingly in the fall and winter. Some gophers carry between 5 and 10% of their body weight in stomach parasites. These parasites have four effects on *Geomys*. They absorb some of the energy which the gopher assimilates. They probably live on gut tissue rather than on the gopher's vegetable diet directly, causing physical damage to the stomach and reducing the absorptive surface. Small black ulcerous sores were observed on many gophers with high parasite loads. The parasites can occupy a considerable part of the gopher's stomach volume reducing the available volume for food. Parasites are rarely the direct cause of death in wild populations but build up to high

concentrations in animals that have their resistance lowered by other stresses (Michel, 1969). However, in at least one population of rabbits (*Oryctolagus cuniculus*) the presence of high parasite loads has been implicated in the reduction of population density (Dunsmore, 1971).

Table 4. Seasonal changes in population estimates of *Geomys pinetis* on Sandhill Research Farm, Alachua County, Florida.

Month	N	$\Delta\bar{N}$	B	\bar{N}	ϕ	V = N ϕ	Total	σ^*	\bar{V} /ha	\bar{f}	\bar{f}_p	Juv
Nov 75	65	--	669									
Dec 75	75		763									
Jan 74	71	- 6.6	718	70.3	1.33	94	5.5	1.8	1.8	3.7	1.0	0
Feb 74	65	- 15.3	656									
Mar 74	55	- 13.3	975									
Apr 74	25	- 10.0	271	35.0	1.25	44	2.6	0.8	0.8	1.4	0.4	0.4
May 74	25	+ 16.6	270									
Jun 74	25	+ 21.6	269									
Jul 74	25	+ 23.3	226	43	1.76	76	4.5	2.0	2.0	2.1	0.9	0.4
Sep 74	85	+ 6.6	920									
Oct 74	86	+ 6.3	825	90	1.58	143	8.4	3.8	3.8	3.9	0.7	0.7
Nov 74	100	- 2.0	1029									
Dec 74	104	- 15.0	1058									
Jan 75	80	23.3	809	80	2.14	170	10.0	3.4	3.4	6.6	1.8	0
Feb 75	55	- 15.3	555									
Mar 75	34	- 1.6	369									
Apr 75	34	+ 9.6	369	39	1.15	45	2.6	0.8	0.8	1.4	0.6	0.4
May 75	50	+ 7.0	540									
Jun 75	63	--	--									
Jul 75	55	--	--									

N - Standing crop, monthly estimate of 17 ha study area.

$\Delta\bar{N}$ - Change in standing crop, running average of three months.

B - Biomass = mean weight x N.

\bar{N} - Mean standing crop for three month interval.

ϕ - Turnover rate for three month interval.

V/ha - Mean number of discrete individuals present on one hectare during three month interval.

\bar{V} - Mean number of discrete individuals present during three-month interval per ha.

σ^* - Discrete males per ha; \bar{f} -Total discrete females per ha; \bar{f}_p -discrete females pregnant per ha, or lactating; Juv - juveniles per ha.

Table 5. Comparison between estimated numbers of *Geomys pinetis* (as a proportion of the active to inactive territories) and the actual number, verified by trapping, in the same area.

Date	Estimated	χ^2	Actual	Location
Feb 76	6	0.17	5	Morningside Park
Jun 75	8	0.50	6	Sandhill Research Farm
Mar 75	6	0.0	6	Sandhill Research Farm
Jul 74	11	0.36	9	Sandhill Research Farm
Apr 73	3	0.0	3	Sandhill Research Farm

Table 6. Changes in weight and time between weighings of *Geomys pinetis* in the field.

#	Captured	Recaptured	Period	ΔW	Initial W
002	3/9/72	30/10/72	2 mos	+ 5.2 g	138.6
003	4/9/72	30/10/72	2 mos	- 0.8 g	171.6
201	8/9/72	1/11/72	2 mos	+ 48.8 g	60.25
221	13/6/73	31/8/73	3 mos	+ 1.5 g	138.5
260	7/4/75	18/7/75	3 mos	+ 8.0 g	76.4
236	11/6/74	3/11/74	4 mos	+ 25.9 g	104.5
203	1/2/72	18/4/74	17 mos	- 9.8 g	252

Table 7. Density of *Geomys pinetis* at sites with different histories showing greater density at sites with earlier successional stages (Samples February, 1976).

Area	Pocket Gophers/Ha	
Morningside Park Undisturbed	2.13	
Burned 1 month before	2.84	climax succession
Farm Site (20-40 yr)	1.96	
Burned 12 months before	4.79	
Sandhill Site	3.20-4.20	early succession

Figure 8. Percent of female *Geomys pinetis* with active corpora lutea in each month showing the bimodal reproductive activity.

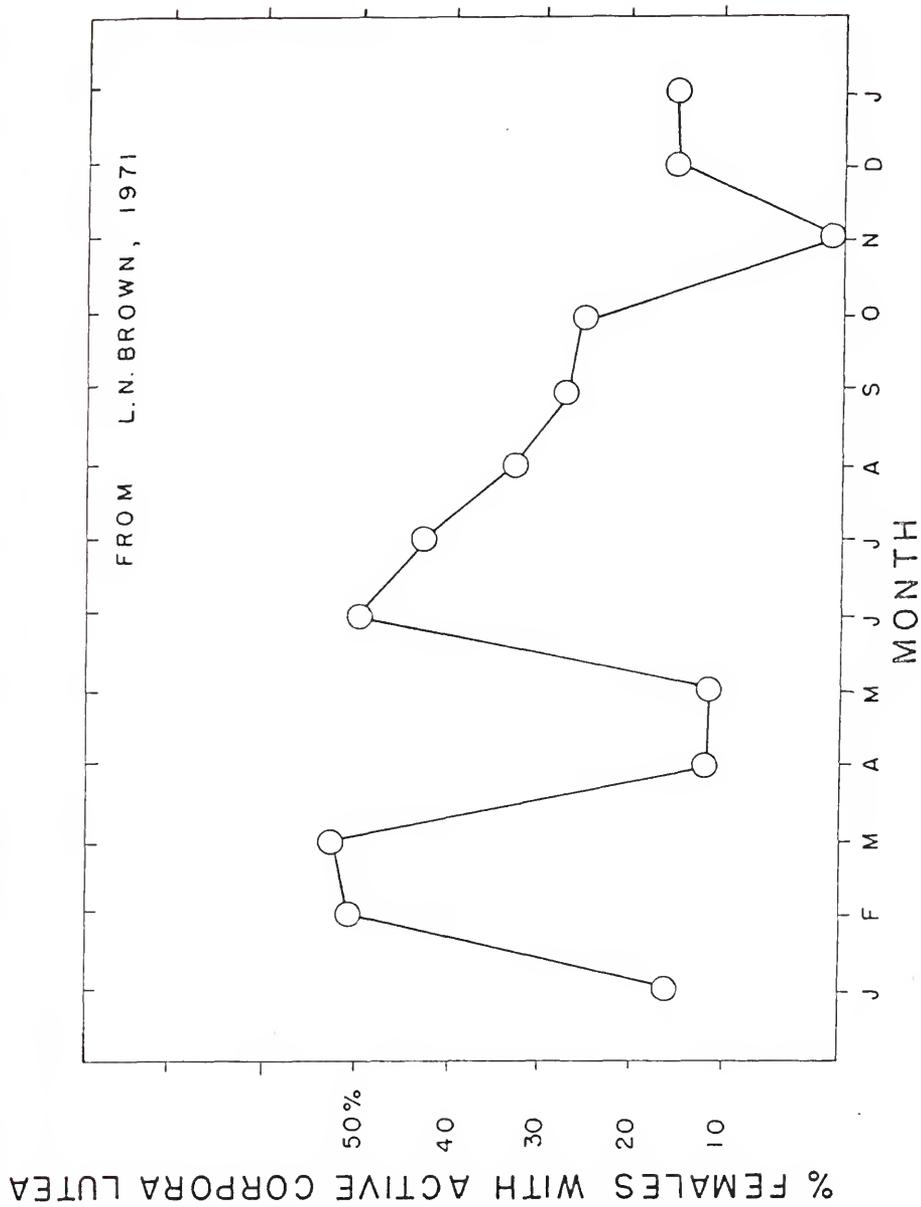


Figure 9. Number of *Geomys pinetis* on 17 ha Sandhill Research Farm site.

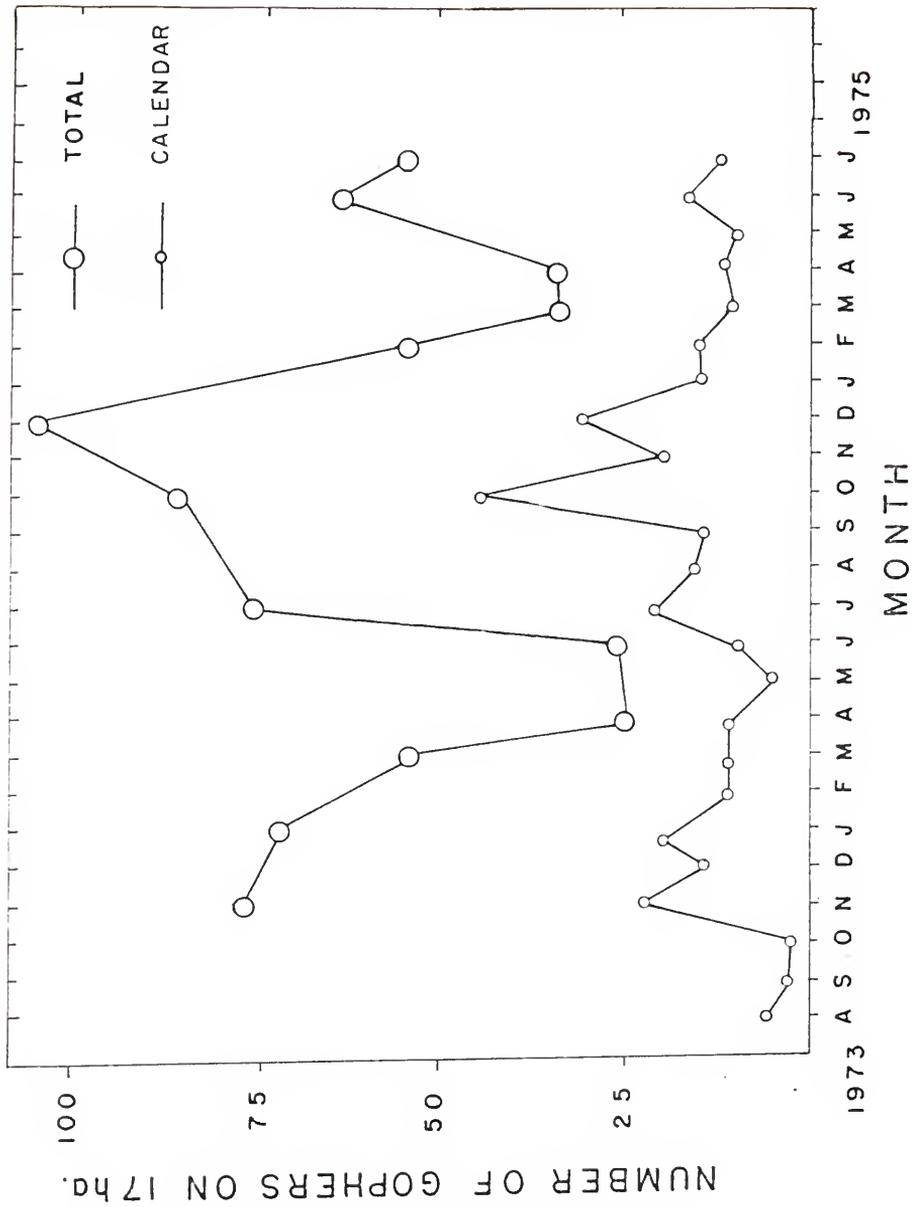


Figure 10. Age specific survival of *Geomys pinetis* after appearance in the adult population at approximately 6 months age.

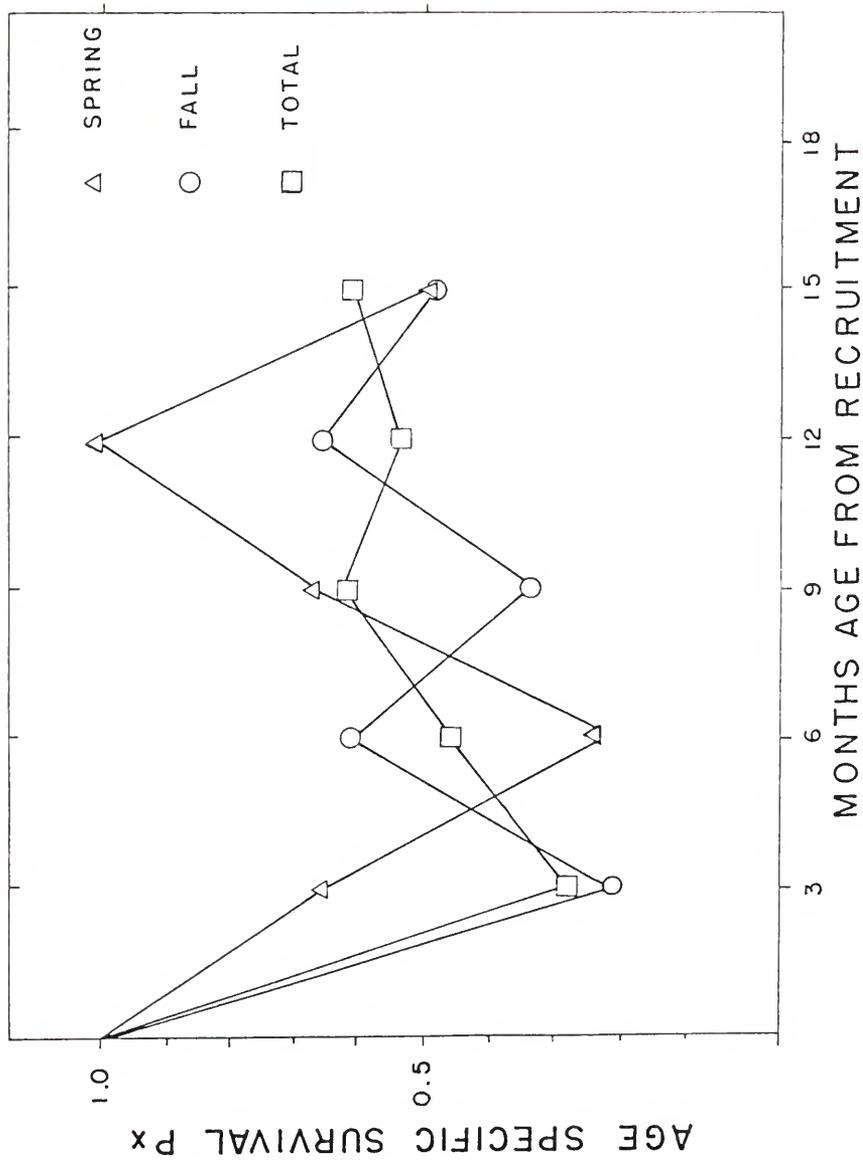


Figure 11. Seasonal changes in mean body mass of *Geomys pinetis* males and females.

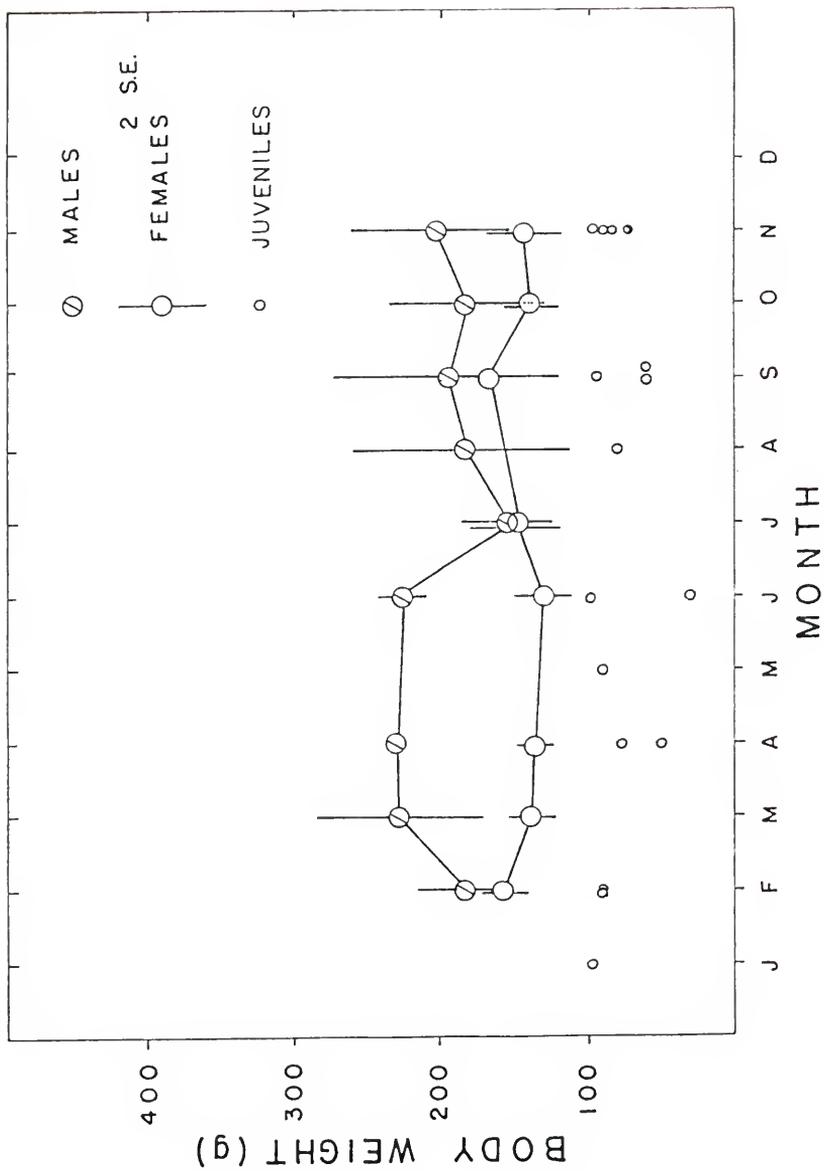
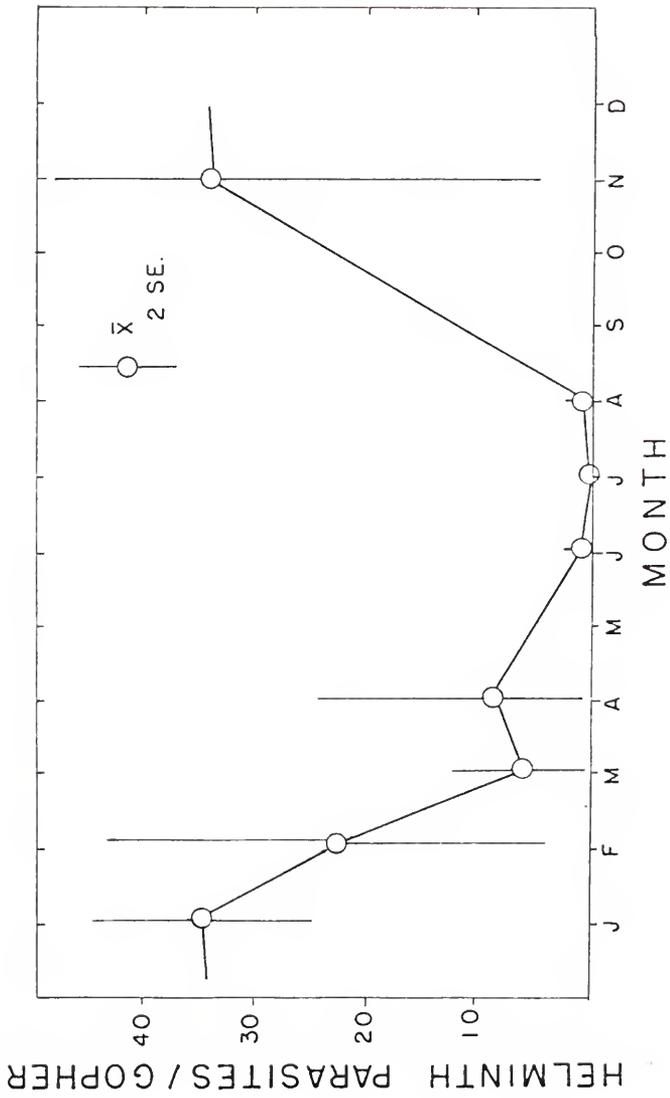


Figure 12. Seasonal changes in number of nematode parasites per individual *Geomys pinetis* stomach.



ACTIVITY AND ITS COST

Daily activity cycles of pocket gophers were continuously measured in activity cages (see Methods). The activity period was estimated at 20°C and 28°C in March and again in July, 1975. Three animals captured in March and run at 20°C were active for an average of 5.6 hr/day (\pm 1.6 hr). At 28°C they were active for a mean of 3.7 hr/day (\pm 0.8 hr). These mean values are significantly different ($t = 27.3$), indicating that pocket gophers reduce their activity when ambient temperatures are warm. This reinforced an observation that in the summer months gophers seem to do less active mound building and are harder to trap than at cooler times of the year.

The experiment was repeated with three animals captured in June and run first at 28°C and then at 20°C. At 28°C the June animals were active for 3.46 hr/day (\pm 0.7 SE), which is not significantly different from the activity at 28°C of the March animals. At 20°C there was a reduction in activity to a mean of 2.2 hr/day (\pm 1.1 hr) and the animals stopped eating. This experiment was terminated after three days as the gophers were rapidly dehydrating. The value for June animals at 20°C just fails to be significantly different from the value at 28°C but is significantly different from both the values for March ($t = 2.25$ and 2.07 , respectively). However, the small number of determinations (9 animal days) and the obvious decline in condition of these gophers makes the interpretation of this result uncertain. I conclude that summer acclimated

animals are in a physiological condition that does not allow them to thermoregulate at low temperatures for a long period. This is in good agreement with the data obtained on thermoregulation.

Pocket gophers do not show a bimodal diurnal activity pattern. Instead gophers are alternately active and at rest throughout the day and night with a cycle period of about 40 min. This observation is in agreement with the observed patterns of metabolic activity. Pocket gophers enter traps in the field at any time of the day or night although field observations indicate that most mound building activity occurs at dusk and dawn. No evidence of a crepuscular activity cycle was seen in the lab. This pattern of activity is similar to that described for *Geomys bursarius* by Vaughan and Hansen (1961). Other reports on the activity patterns of fossorial rodents suggest that this is a common pattern (Eisenberg and Maliniak, 1973; Jarvis, 1973).

Several lines of evidence suggest that the measured length of the activity period is a low estimate. It is possible to estimate activity from 24 hr metabolic rate determinations and several such determinations give values of 4 hr/day to 9 hr/day. Also one pocket gopher was fitted with a small radio transmitter which changed the amplitude of its output as the orientation of a small broadcasting antenna changed with respect to a fixed receiving antenna. By transforming the received signal through a Honeywell chart recorder a continuous record of activity was obtained for 24 hrs of a gopher in the laboratory. The record obtained showed 9.0 hr/day of activity. The radio tracing technique was not successful in the field and this experiment was not repeated. It is possible that gophers under laboratory conditions, either in metabolism chambers or

with radios, are stimulated to extra activity. Given the uncertainties of the various estimates of activity period it is probably reasonable to suggest that gophers are active for 6 hrs/day at cool temperatures (20°C) and that this figure is reduced to 4 hrs/day at warmer temperatures (28°C). This reduction is consistent with the observations of DeCoursey (1960) and Rawson (1960) that several other rodents reduce the period of activity at higher temperatures although the pattern of activity is unchanged.

During activity, pocket gophers maintained T_b 's of 35-37°C over a wide range of ambient temperatures (mean 36.4 ± 0.5) (Fig. 13). In contrast, when at rest, the level of T_b is lower and there is considerable lability at high and low T_a 's. The resting T_b 's at T_a greater than about 32°C are elevated to approximately the same level as T_b during activity and this T_b (about 37°C) probably represents a maximum tolerable T_b above which serious and perhaps irreversible thermal stress is experienced.

The cost of activity can be estimated from the metabolic rates of gophers digging in a sand-filled metabolism chamber. The results of these determinations at various temperatures are shown in Fig. 13. On several occasions pocket gophers refused to dig in the experimental chamber and the resting metabolism obtained fits well on the generalized resting metabolism line obtained independently.

The mean regression line in Fig. 13 permits an estimate of the energy expenditure of a pocket gopher during activity at various environmental temperatures to be made. The maximal rate of metabolism during activity increases at lower ambient temperatures. In the thermoneutral zone the maximal rate of metabolism during activity is three times M_b .

At the lowest temperatures tested, active M_b is five times M_b but less than twice as great as the metabolic rate of a gopher resting at that temperature. This suggests that heat produced by activity substitutes for nonactive heat production at lower temperatures which agrees with classical theory (Hart, 1971), but conflicts with results obtained from other rodents. Although several exceptions are found in the literature, Hart (1971) reports that in rodents equal levels of activity increase oxygen consumption an equal amount independently of temperature.

Figure 13. Rate of metabolism of active *Geomys pinetis*.

THERMOREGULATION

Methods

Samples of 5 to 12 gophers were brought to the laboratory and their oxygen consumption measured in August, 1973, January, 1974, April, 1974, July, 1974, October, 1974, and March, 1975. Oxygen consumption was measured at ambient temperatures between 5°C and 35°C during the day (0800-1800 hrs) within three weeks of capture.

The oxygen consumption [$\text{ccO}_2(\text{g}\cdot\text{hr})^{-1}$] of gophers in each sample was plotted against ambient temperature (Figs. 14-19). The thermoneutral zone (TNZ), lower limit of thermoneutrality (T_l), standard metabolism (M_b) and conductance (C) were calculated.

Figures 14-19 all clearly show a region of ambient temperature (T_a), called TNZ, where there is no change in oxygen consumption, and a region where oxygen consumption increases with decreasing T_a . The points which are unambiguously within the TNZ, excluding points for which body temperature (T_b) is elevated above the mean body temperature, were averaged to give mean resting metabolism within the thermoneutral zone, hereafter called basal metabolism (M_b).

Conductance (C) was calculated by drawing a line from each value of the oxygen consumption measured below the thermoneutral zone to a T_a equal to body temperature of the pocket gopher measured at the end of the determination of that value (see Methods). The slope of these lines are all independent estimates of the conductance of the gopher, and were

averaged to give the mean conductance for pocket gophers from each seasonal group.

M_b and C in different seasons have been analyzed statistically with analysis of the variance to test the null hypothesis that there is no difference in these parameters between seasons. However, the statistical treatment is of only limited aid in understanding the changes in M_b and C . This is in part due to the variability between different individuals and the accumulated variety inherent in making measurements at different times. In addition it is likely that the wide variance in all the measured parameters is due to variation in the ways in which different individuals respond to an environmental challenge. For example, one animal may respond to a high temperature by reducing heat production (M_b), another by increasing heat loss ($C\Delta T$), while a third may make small adjustments in both. Adequate temperature regulation could be achieved by any of these responses. However, M_b and C may also respond to other factors such as water loss or energy expenditure. Therefore a mixture of responses is the most likely solution and such a mixture is likely to obscure significant differences between any pair of measurements.

A solution to this dilemma is provided by the treatment of endotherm thermoregulation developed by McNab (1970, 1973, and 1974). In these papers McNab has developed and refined the use of an equation which describes heat loss, temperature, and heat production of an endotherm based on Newton's law of cooling. Considerable debate has resulted concerning the correctness of this treatment, its real name, and its usefulness (see Calder and King, 1972; Gettinger, 1975). Careful read-

ing of the original paper shows that McNab (1970) anticipated these criticisms and showed them to have negligible effects on the predictions from his calculations. In the absence of an effective criticism supported by properly analyzed data we will consider the treatment a useful one.

Newton's law of cooling states that the fall in temperature of a cooling body is proportional to the temperature differential between the body and its environment. If the temperature of the body remains constant then heat output (M_b) must be equal to heat loss (dQ/dt) and so metabolism can be set equal to the differential ($T_b - T_a$) times a heat transfer coefficient (conductance).

$$M = C(T_b - T_a) \quad (\text{eq. 5})$$

Equation 5 can be applied to living homoiotherms if M is basal rate of metabolism (M_b) and T_a is the lower limit of thermoneutrality (T_ℓ). Both M_b and C are largely determined by an animal's mass. Generalized equations have been derived for "standard" mammals by Kleiber (1960) $M_b = 3.4W^{-0.25}$ and by Herreid and Kessel (1967) $C = 1.0W^{-0.51}$ and so the observed M_b and C can be described as some function f of the expected M_b and C , such that $M_b \text{ observed} = fm_b \text{ expected}$ and $C \text{ observed} = fc \text{ expected}$. One can then examine the combined effect of changes in M_b and C from expected by computing

$$F = \frac{fm}{fc} \quad (\text{eq. 6})$$

By substituting the standard equations into equation 6 (McNab, 1974) it can be shown that:

$$F = \frac{M_b \text{ observed}}{C \text{ observed}} \times \frac{1}{3.4W^{0.25}} = \frac{(T_b - T_\ell) \text{ observed}}{(T_b - T_\ell) \text{ expected}}$$

F then is seen to be an expression of the ability of a mammal to keep its body temperature different from ambient temperature at the lower limit of thermoneutrality, compared to that of a "standard" mammal. F responds to changes in both M_b and C and shows the effect of such changes on the independence of a mammal's T_b from T_a . Because the standard equations are computed as a function of body mass (W), F factors out the effect of body size. When F has a value greater than 1.0, it indicates that an animal can maintain a high well-regulated body temperature over a wide range of T_a . Conversely when F is less than 1.0, the ability to regulate T_b in the face of fluctuating T_a is lower.

F has been calculated for each seasonal sample. The mean body mass of the gophers in the sample was used to calculate $3.4W^{0.25}$ and this was divided into the observed ratio of M_b/C .

Results and Discussion

When all the data on oxygen consumption for gophers from different seasons are pooled together, the mean M_b is $0.852 \text{ ccO}_2 \text{ g}^{-1} \text{ hr}^{-1}$, which is 87% of the M_b expected from the mean weight of pocket gophers in the sample used (146.0 g). The mean conductance is $0.114 \text{ ccO}_2 \text{ g}^{-1} \text{ C}^\circ^{-1}$ which is 144% of the expected value. This confirms McNab's (1970) values for *Geomys pinetis* and justifies his statement that *Geomys* has low basal rates and high conductances compared with expectations based on weight (Table 8).

The mean weight of gophers from different seasonal samples varied significantly (Table 9) (F test $P < 0.001$). A regression of mean basal metabolism on mean body weight, however has a correlation coefficient

of only 0.098. I conclude that over the narrow range of body weights involved (100-300 g) weight has little effect on oxygen consumption.

To establish the effect of acclimation (Chaffee and Roberts, 1971) during captivity over the period of measurement (always less than four weeks) I made determinations of basal metabolism immediately after capture and during the course of the captivity of gophers in two samples, one in summer (August, 1973) and one in winter (October, 1974). There is no significant difference in the estimate of basal metabolism over the period of three weeks (Fig. 20).

Continuous measurements of oxygen consumption of gophers over 24 hours at temperatures within the TNZ revealed that there were no diurnal changes in oxygen consumption. Instead gophers tend to show intermittent periods of high O_2 consumption (activity) and low O_2 consumption (rest) throughout the day and night.

The differences in M_b measured in samples captured at different seasons are obscured by the large variance of the estimates (Fig. 21). An analysis of the variance reveals that the differences in the means are greater than would be expected by chance ($F = 3.27$, $P < 0.5$); however it is not possible to discern significant differences between pairs of values because of the large variance and the sigmoid nature of the change in M_b from season to season. Nevertheless a clear pattern is visible in Fig. 21 with low M_b in the warmer months and high M_b in the cooler months. Values of M_b for the same season in different years are very similar, *e.g.* January, 1974; March, 1975, indicating that the pattern of change in M_b is a reproducible phenomenon.

The differences between seasonal estimates of conductance are more variable than the measurements of M_b . An analysis of variance

reveals significant differences between some of the values, but again a paired comparison did not reveal any meaningful differences except between the extreme values. Figure 22 shows a trend toward low C in the cooler months and high C in the warmer months. Regressions of C against burrow temperature and minimal monthly temperature have regression coefficients of 0.61 and 0.62 respectively (Fig. 23) ($P = 0.20$). While this value is below conventional levels of significance, levels of regression accounting for approximately 40% of the variance in values cannot be ignored. Reference to Fig. 7 showing soil temperature profiles makes it clear why conductance should depend on the minimal temperature. In the warmer months of the year gophers can avoid the extremes of temperature in the surface soil by burrowing deeper. However, below about 30 cm the soil temperature does not change appreciably and a critical problem for the gopher is the maximal temperature in the coolest soil level. Figure 7 shows that this is about 25°C. A higher C in hotter months facilitates the flow of heat from the animal to the soil. In the winter months temperatures in the soil are uniformly cool, except for surface fluctuations. Increases in conductance serve to reduce the energy expenditure for thermoregulation during the winter.

It is not possible to reject the null hypothesis of no difference in M_b and C at different seasons although there are some strong indications that both M_b and C change in ways that are adaptive in the pocket gopher's environment.

The values of F are shown in Fig. 24. Inspection of these values resolves much of the ambiguity concerning seasonal adjustments in M_b and C . It is quite clear that F has lower values in the warmer months and

higher values in the cooler months. The regression of F against mean monthly maximum temperature has a coefficient of -0.67 (45% of the variance). Thus, in the warmer months the decrease in M_b and increase in C suggested by the statistical analysis are sufficient to reduce the temperature differential ($T_b - T_a$) to half of that of a "standard" animal. Conversely in the cooler months pocket gophers increase their ability to maintain T_b independent from T_a at lower temperatures. I interpret this to mean that in the warmer months M_b can be reduced and C increased because the higher T_a reduces the need for active thermoregulation. In the cooler months pocket gophers must increase their ability to keep T_b independent from T_a to minimize the energetic cost of keeping warm.

I have already suggested that the changes in M_b and C in the summer can be interpreted as responses to the danger of overheating in a closed burrow as suggested by Kennerly (1964), and McNab (1966). Body temperature is determined by heat production (M_b) and loss ($C\Delta T$) and so the effect of changes in M_b and C , revealed by changes in F , should have an effect on T_b . I have analyzed changes in the body temperature of gophers after exposure to different ambient temperatures during the measurement of their rate of metabolism. The mean T_b measured before each measurement for the different samples is shown in Table 9 and indicates that under standard laboratory conditions ($24^\circ\text{C} \pm 1^\circ\text{C}$ range) inactive gophers maintain a constant body temperature of about 35°C . The differences among seasons are not significant ($F = 7.7$, d.f. $\frac{4}{126}$).

The T_b measured after each measurement of rate of metabolism shows the response of the gopher to a thermal challenge. These T_b 's

are shown with the rate of metabolism in Figs. 14-19. There is considerable variation of T_b in response to T_a at different seasons. To examine the effect of T_a on T_b in more detail I have calculated the difference between the T_b measured before the determination of rate of metabolism (T_{in}) and T_b measured at the end of the determination (T_{out}). Regression coefficients of this relationship plotted against T_a are greater than 0.60 for the samples shown in Fig. 25. In the remaining samples the variation was such as to obscure any relation. It can be seen in Fig. 25 that at T_a 's between 18.8 and 26.8 the difference $T_{b\ in} - T_{b\ out}$ becomes positive. The gopher begins to store heat above these T_a 's forcing T_b to rise. It is surprising that this effect occurs at an ambient temperature as low as 18.8°C. That is, pocket gophers store heat at all environmental temperatures to which they are exposed in the summer. It is of even greater significance to note that gophers store heat ($T_{b\ in} - T_{b\ out} > 0.0$) at all environmental temperatures above 5°C when they are active.

Clearly, heat storage is a potential hazard for gophers at all times during warm seasons and during activity even during cold periods. This potential difficulty exists even after the marked adjustments in M_b , C , and consequently in F have been made, which attests to the difficulty of heat dissipation in a closed burrow saturated with water vapor.

Table 8. Basal rate of metabolism (M_b) and conductance (C) as a percentage of that expected from body mass (W).

	M_b	C
Aug 73	88%	148%
Jan 74	90%	127%
Apr 74	75%	141%
Jul 74	71%	134%
Oct 74	104%	159%
Mar 75	94%	153%

Table 9. Basal rate of metabolism (M_b), conductance (C), body temperature (T_b), mean body mass (W), and F for *Geomys pinetis* in various seasons.

	$M_b \pm 2SE$	C \pm 2SE	$T_b \pm 2SE$	W \pm 2SE	F
Aug 73	0.895 0.08	0.126 0.010	36.06 0.35	125.5 9.6	0.62
Jan 74	0.853 0.10	0.095 0.004	36.05 0.35	162.3 10.9	0.74
Apr 74	0.740 --	0.112 0.006	35.92 0.28	143.9 8.8	0.56
Jul 74	0.686 0.20	0.104 0.008	35.41 0.19	150.4 7.1	0.55
Oct 74	1.031 0.08	0.130 0.010	35.04 0.20	136.4 7.8	0.68
Mar 75	0.908 0.10	0.116 0.012	34.50 0.40	156.7 17.0	0.65

M_b - $ccO_2 \cdot g^{-1} \cdot hr^{-1}$

C - $ccO_2 \cdot g^{-1} \cdot hr^{-1} \cdot C^{\circ-1}$

T_b - body temperature before measurement of M_b , C

W - g of the sample

Figure 14. Rate of metabolism of resting *Geomys pinetis*, sample collected in August, 1973.

BODY TEMP, °C

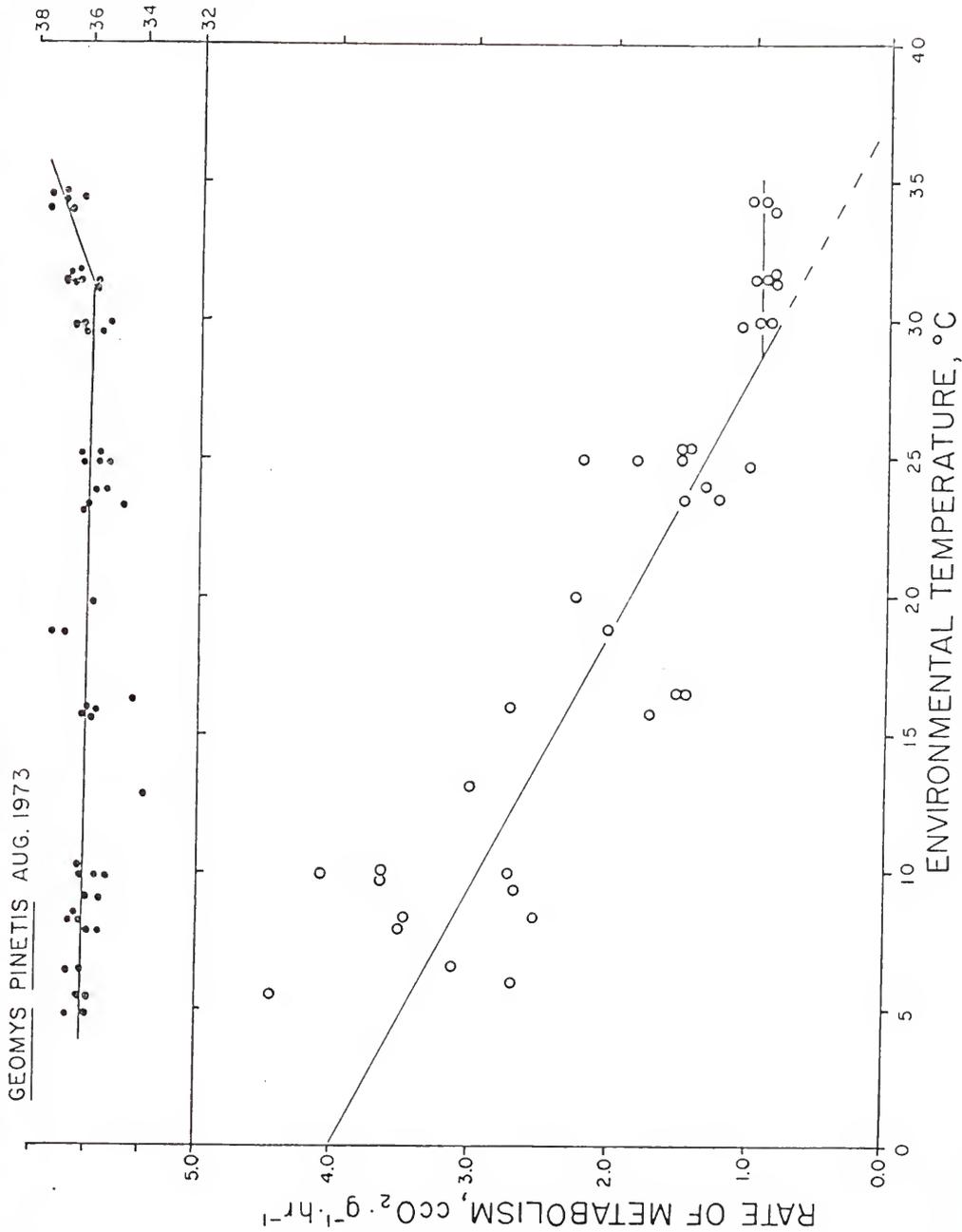


Figure 15. Rate of metabolism of resting *Geomys pinetis*, sample collected on January, 1974.

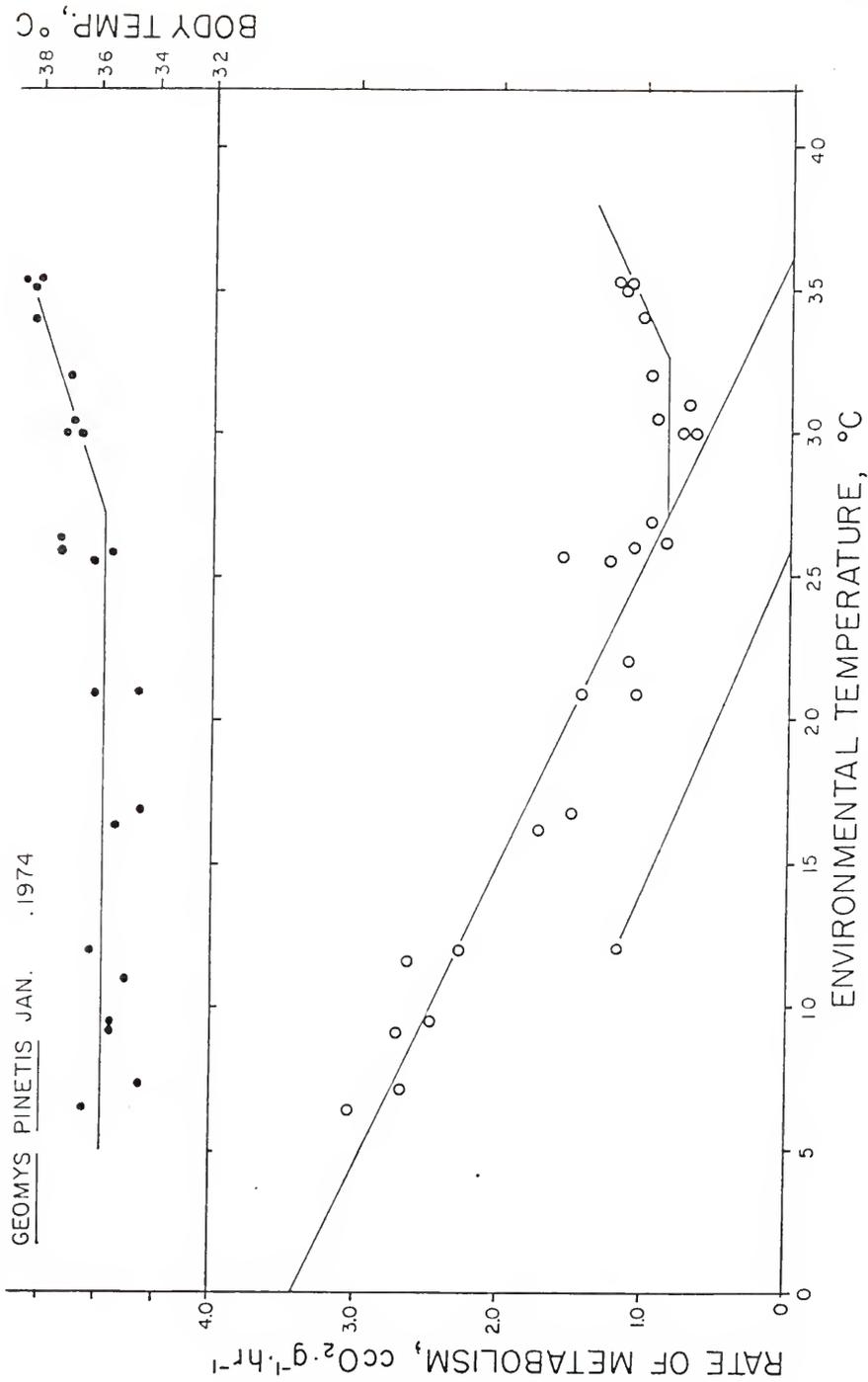


Figure 16. Rate of metabolism of resting *Geomys pennsylvanicus*, sample collected in April, 1974.

GEOMYS PINETIS APRIL 1974

BODY TEMP., °C

RATE OF METABOLISM, $\text{cc O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$

ENVIRONMENTAL TEMPERATURE, °C

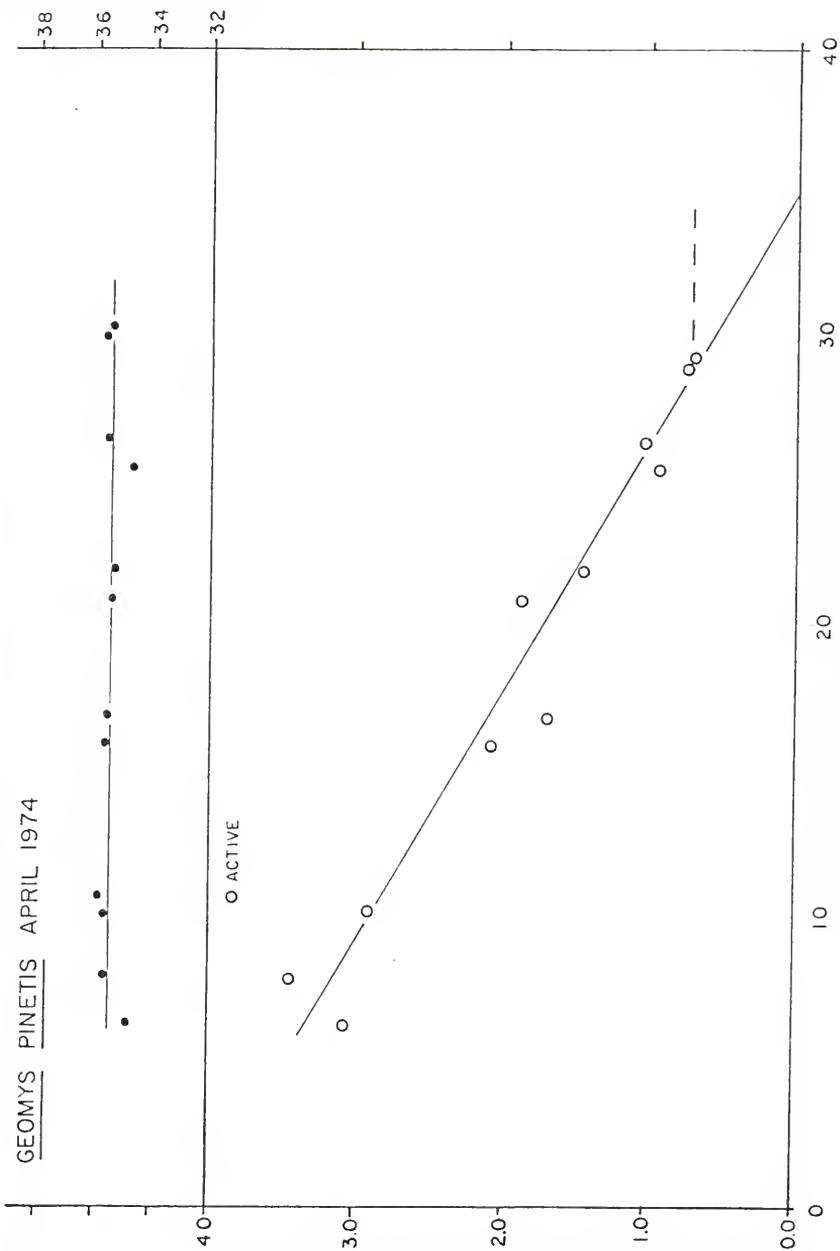


Figure 17. Rate of metabolism of resting *Geomys p. pinetis*, sample collected in July, 1974. Solid circles are values determined on another Beckman oxygen analyzer.

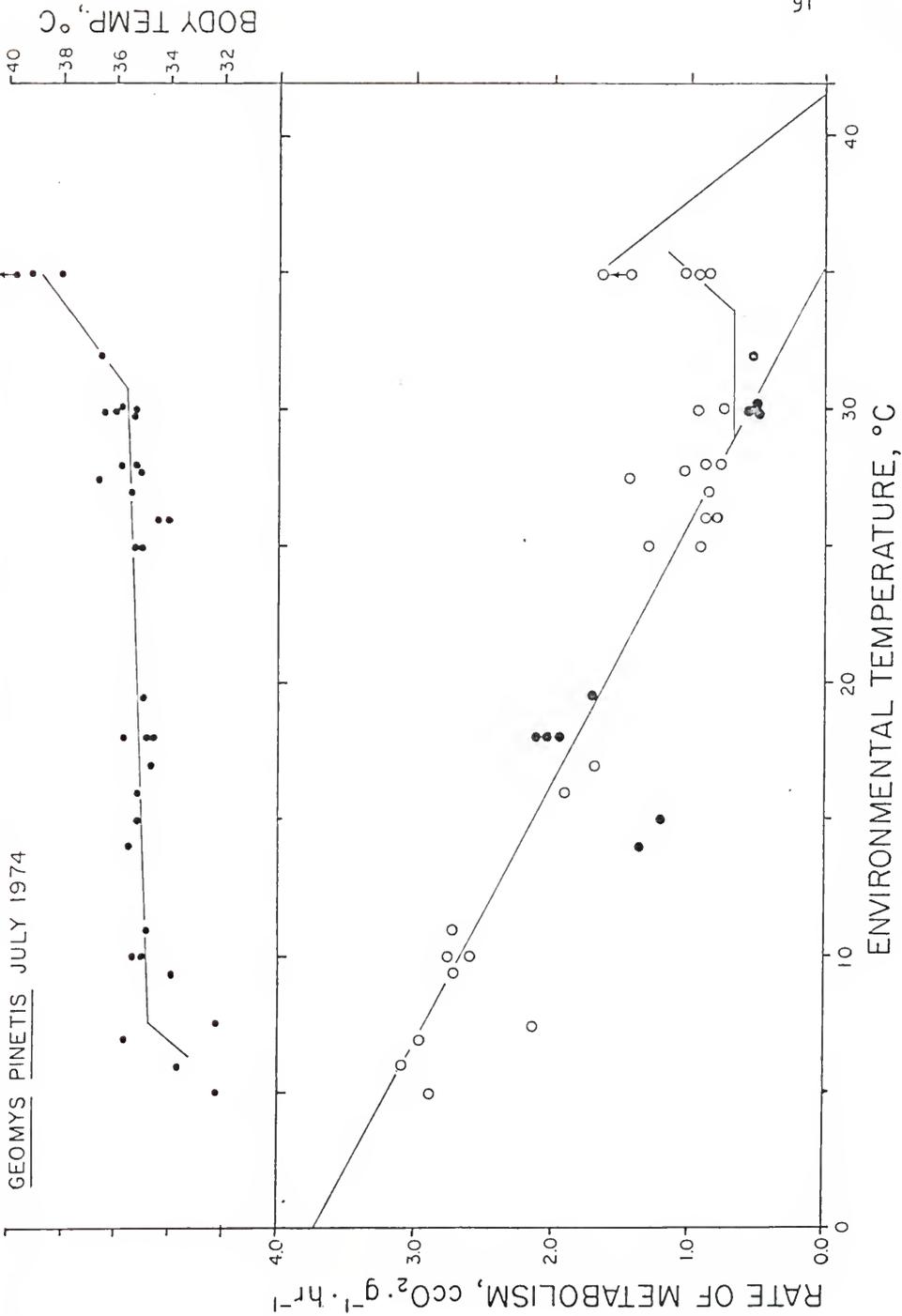


Figure 18. Rate of metabolism of resting *Geomys pinetis*, sample collected in October, 1974.

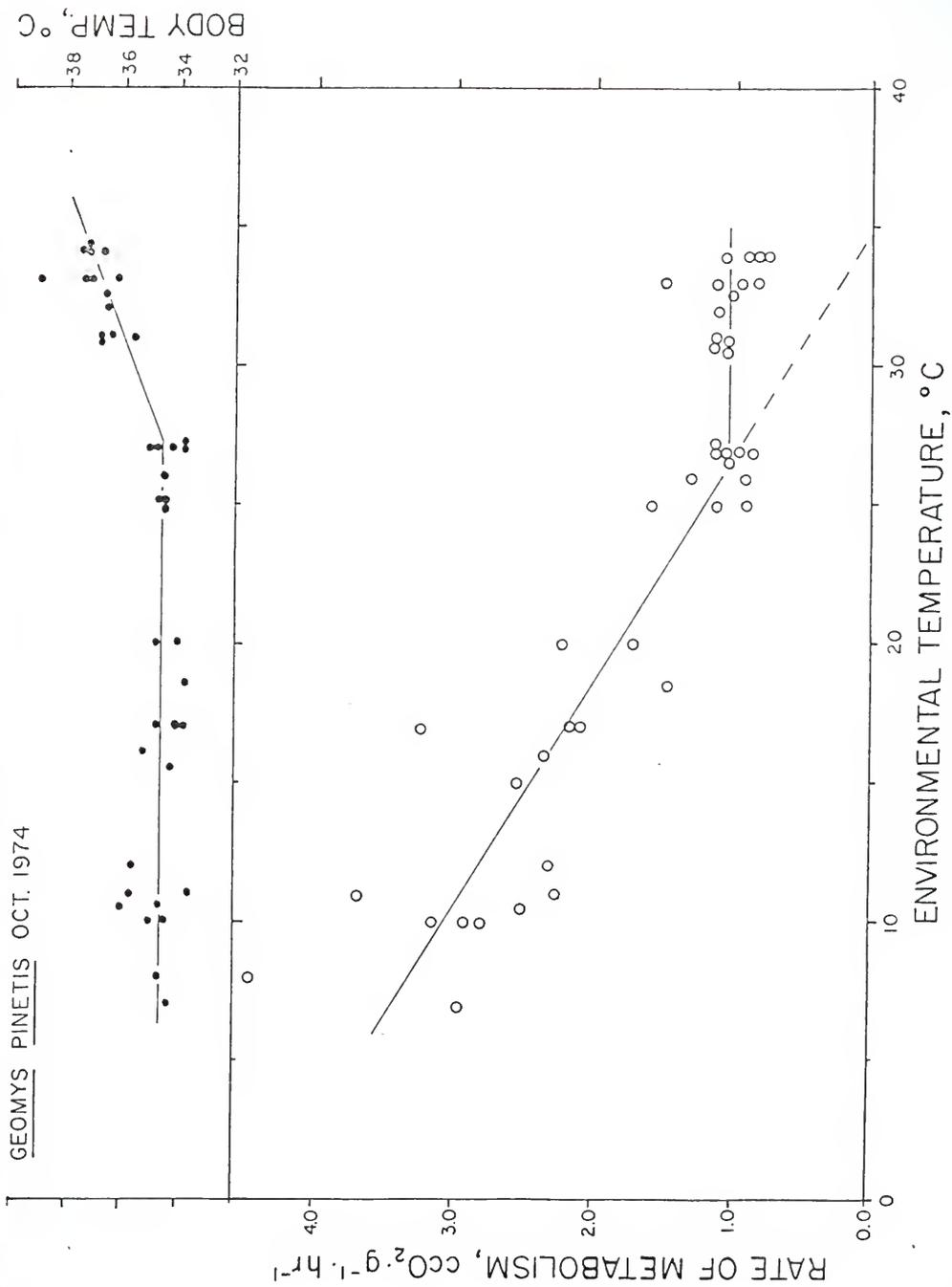


Figure 19. Rate of metabolism of resting *Geomys pinetis*, sample collected in March, 1975.

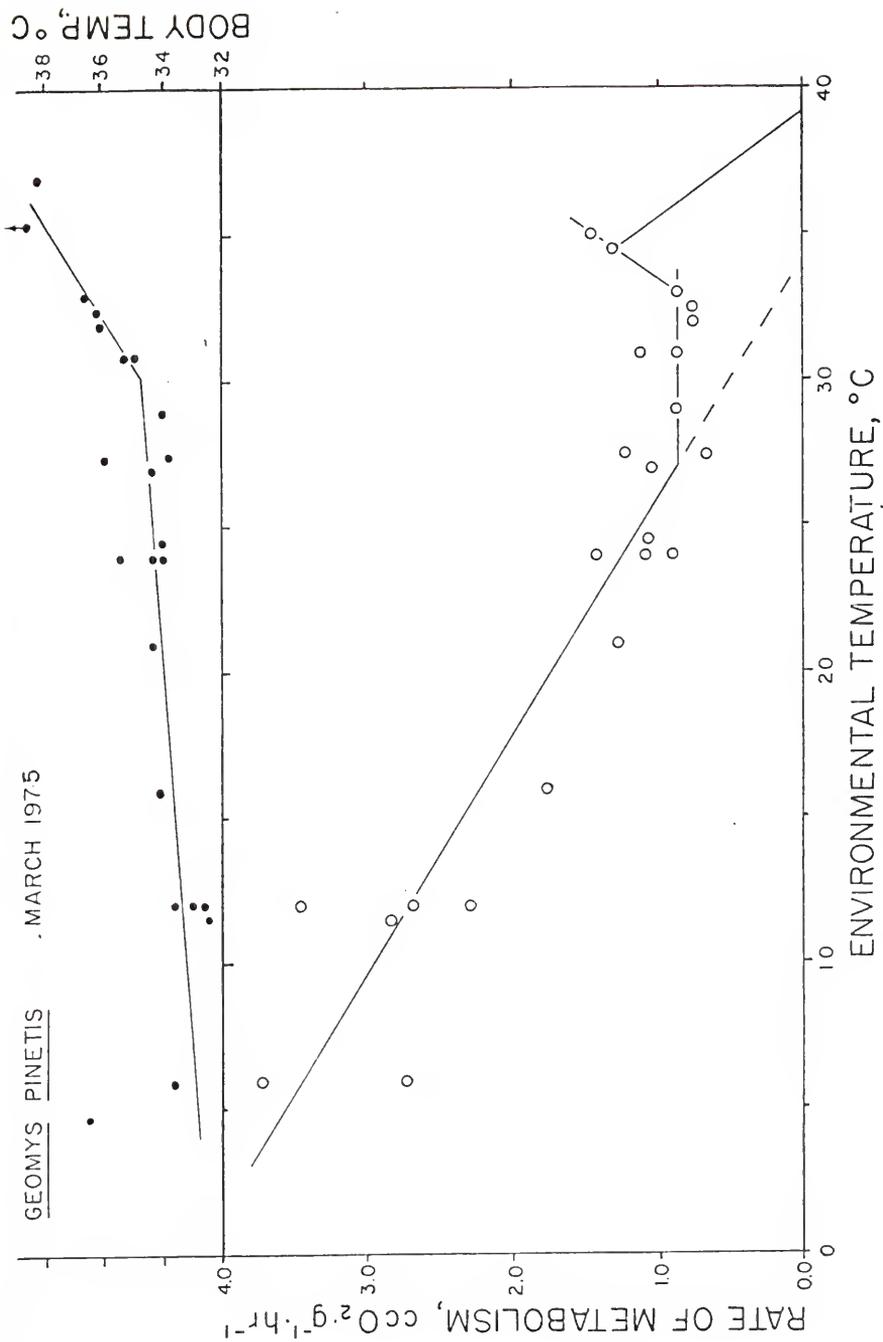


Figure 20. Basal rate of metabolism of resting *Geomys pinetis*, samples collected in August, 1973, and October, 1974, showing the absence of any change in basal rate of metabolism over the three week sampling period.

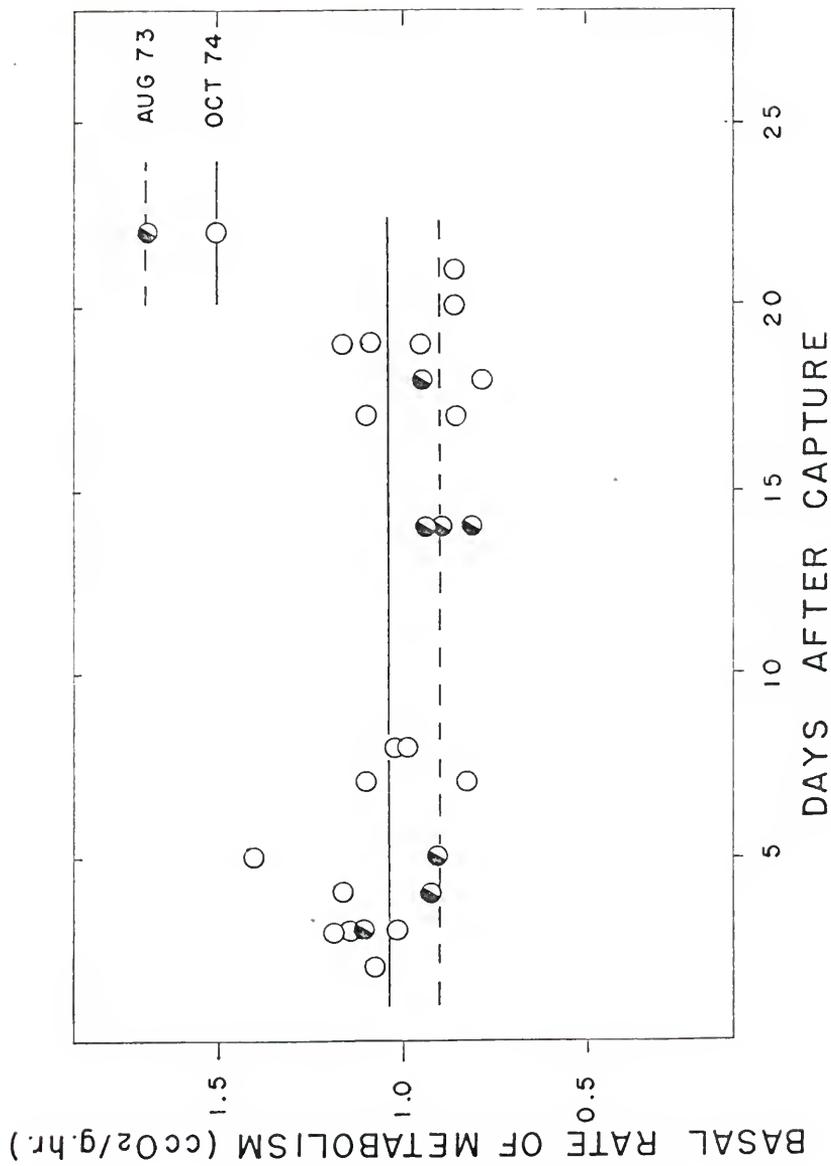


Figure 21. Mean basal rate of metabolism of *Geomys pinetis*, samples from different seasons.

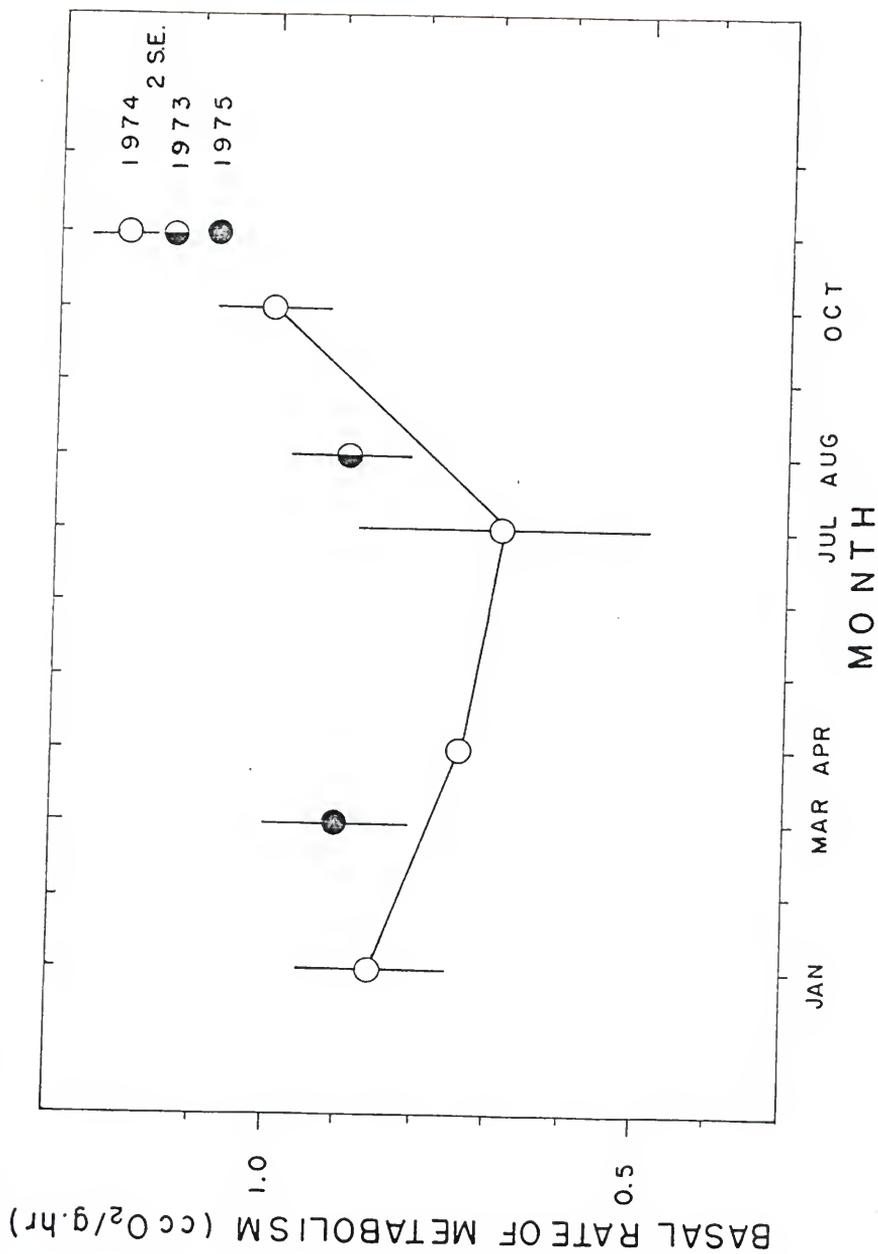


Figure 22. Mean conductance of resting *Geomys pinnatus*, samples from different seasons.

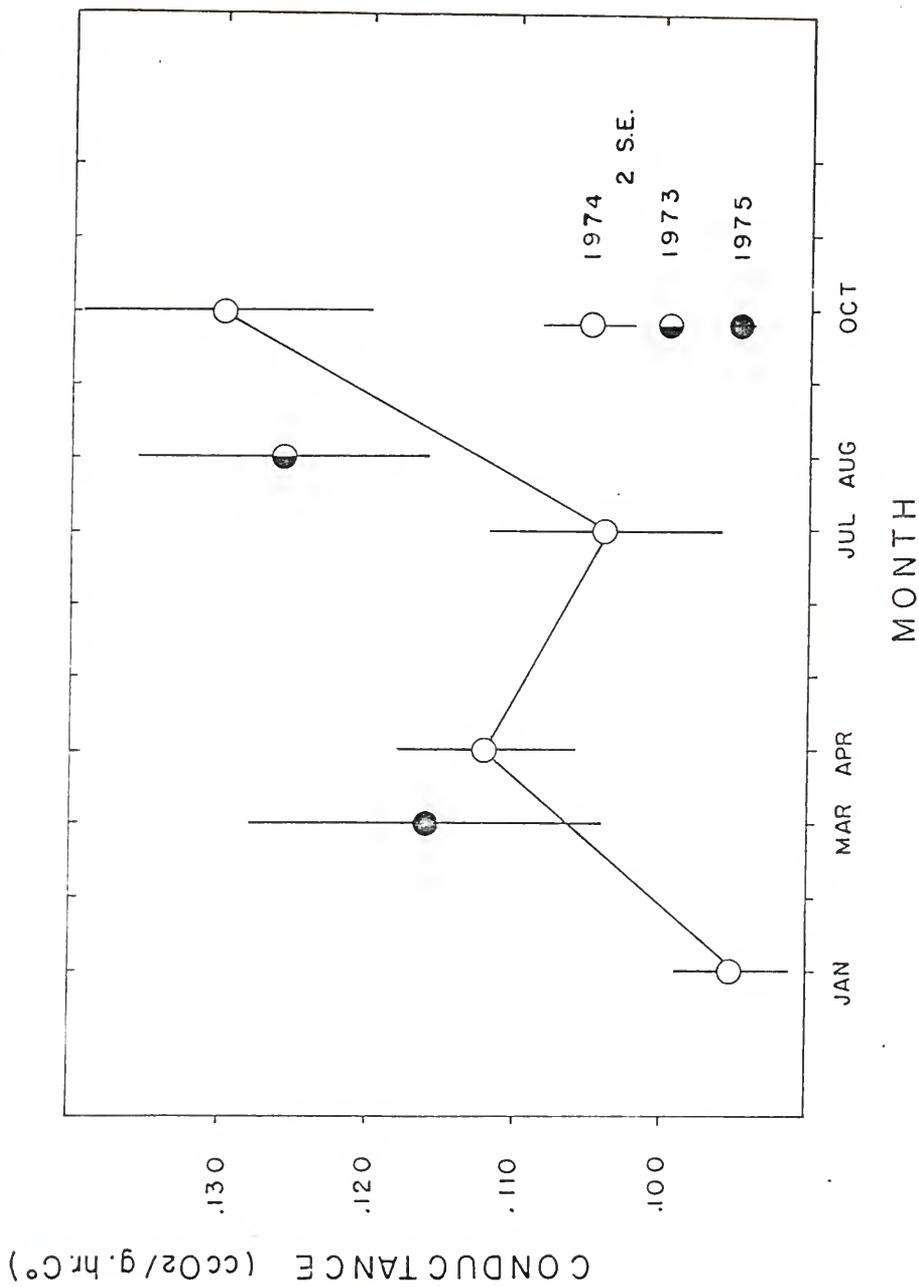


Figure 23. Regression of mean conductance at different seasons against ambient temperatures in each season.

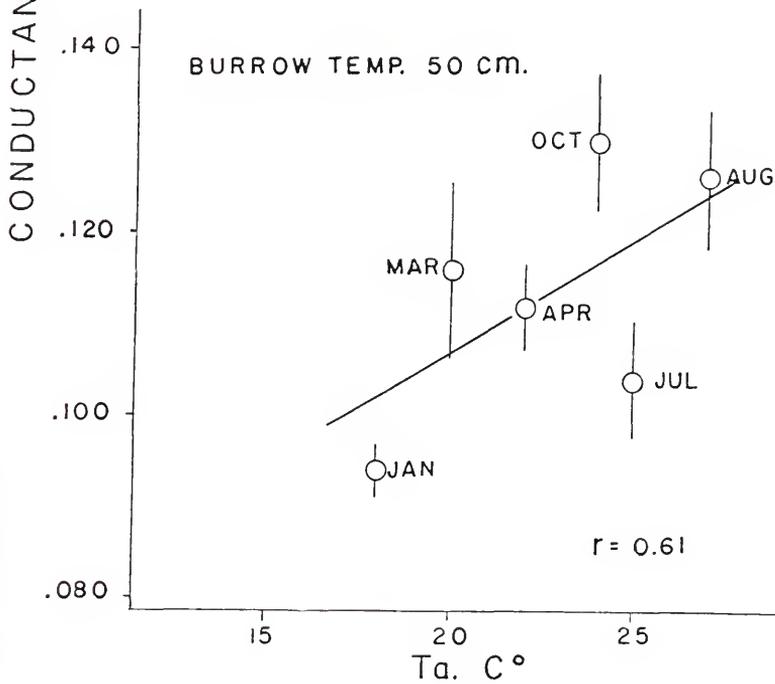
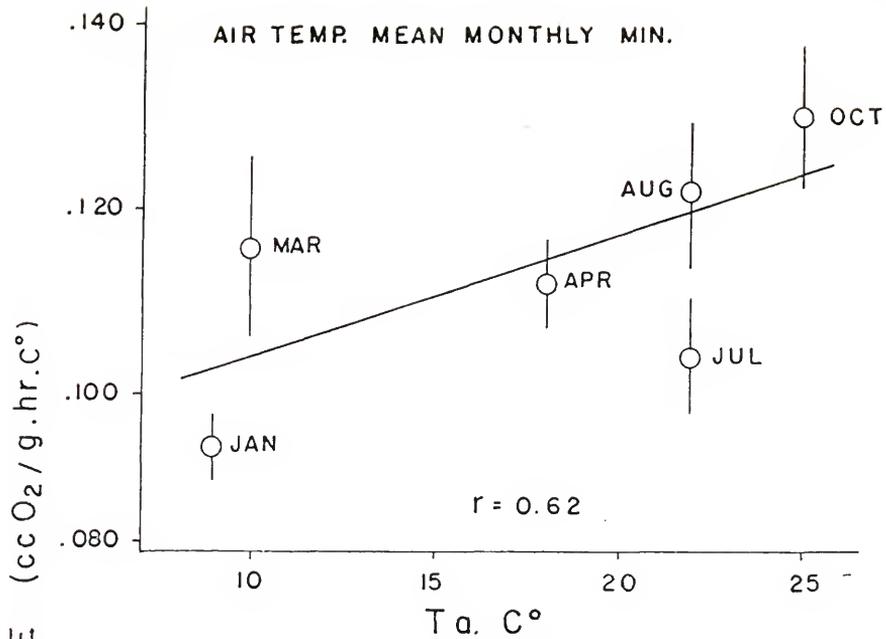


Figure 24. F (the ratio of the observed basal rate of metabolism divided by observed conductance to expected basal rate of metabolism divided by expected conductance), samples from different seasons.

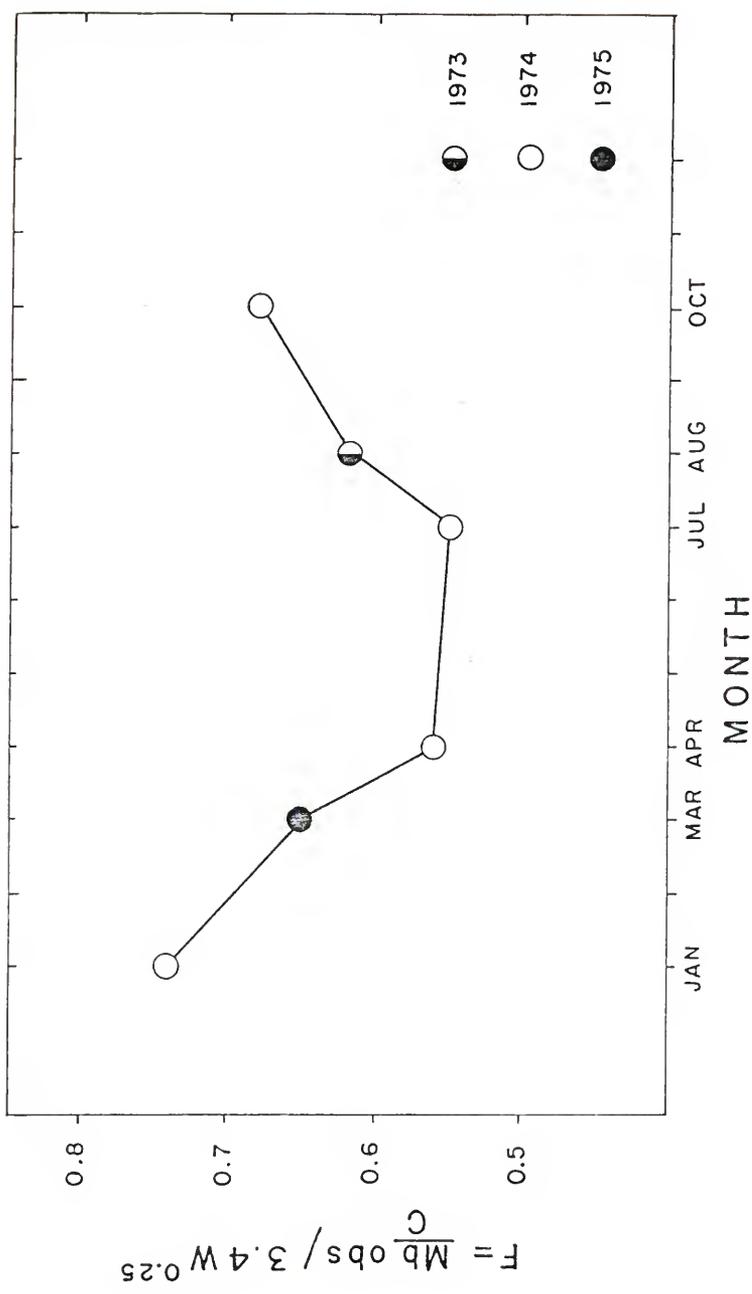
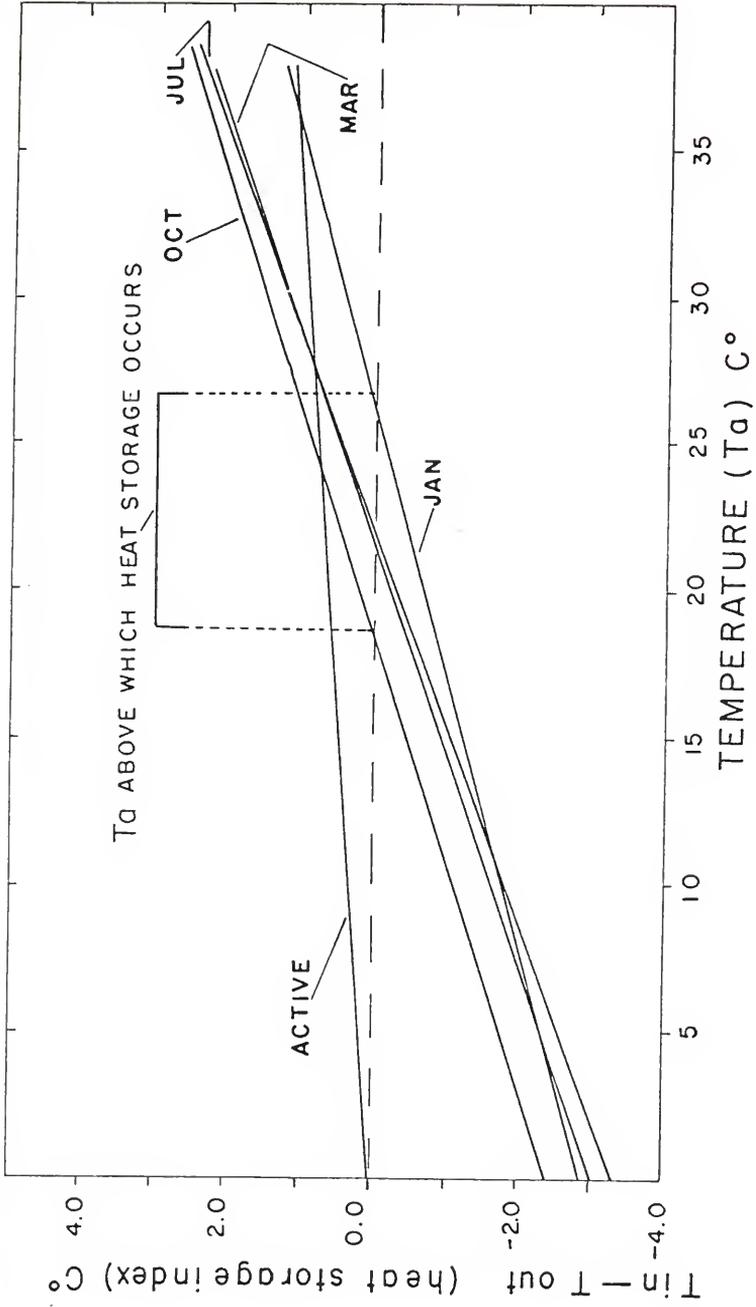


Figure 25. Change in body temperature of *Geomys pinetis* after exposure to different ambient temperatures, showing heat loss and heat storage.



THE ENERGY BUDGET

Methods

The results in the preceding chapters provide a body of data from which energy budgets for pocket gophers can be calculated. The theoretical basis for calculating such budgets is described by Wiegert (1968), Petruszewicz and Macfadyen (1970), and Grodzinski *et al.* (1975). Briefly stated

$$E = P + R + U + W \quad (\text{eq. 7})$$

that is, energy consumed (E) is equal to the sum of energy stored as biomass (P), energy lost in feces and urine (F + U), energy respired (R) and work done (W). The work done by a biological system on its environment and by the environment on the system is usually ignored or supposed to be negligible by Wiegert (1968) and Grodzinski *et al.* (1975). In view of the importance of biological systems in maintaining nutrient cycles and atmospheric components, this may be an incorrect supposition. I will return to this point in the discussion when I discuss the possible effect of pocket gophers on nutrient distribution and soil aeration.

For the purposes of this thesis, I will rearrange equation 7 and introduce the concept that production is made up of growth (Pg) and reproduction (Pr); thus,

$$E - (F + U) = R + Pg + Pr + W$$

That is, the energy assimilated is distributed between respiration, growth, and reproduction. The data presented on nutrient and caloric

intake of pocket gophers (and the nutrient and energy content of their food) will be used to examine the seasonal variations in the left-hand side of equation. The data on rate of metabolism, the effects of temperature, growth rates, and reproductive data from the literature will be used to examine the responses of the right-hand side of equation to seasonal changes in the left-hand side.

Energy budgets can be calculated for a pocket gopher on one day representative of the seasonal conditions at that time of year. If these budgets are multiplied by the number of pocket gophers known to be present in an area, then an estimate of the energy flow through the population on that day can be gained. If the number of such days during a period and the number of gophers present during this period are known, then an estimate of energy flow during this period can be made. Lastly, these estimates can be summed to give the total energetic impact of the total population for a whole year. These four estimations become progressively less accurate as assumptions are piled one atop another. Nevertheless, each tier of the energy budget reveals aspects of the gophers' responses to changing environmental conditions.

In the calculation of energy budgets, I will follow the terminology and methods outlined in Petruszewicz and Macfayden (1970) and Grodzinski *et al.* (1975) as adopted by the International Biological Program.

The respiration portion of the energy budget was calculated in the following way. For a given month, the deep soil temperature was estimated from Figs. 6 and 7 and this was assumed to be the temperature which the gopher was exposed to at rest. The resting rate of metabolism at that temperature in that month was calculated from Figs. 14-19.

The time at rest was taken from page 68. The rate of metabolism was converted to calories assuming $1 \text{ cc } O_2 = 4.8 \text{ cal}$ and the daily energy expenditure at rest calculated in $\text{cals g}^{-1} \text{ day}^{-1}$. The temperature at 10 cm was assumed to be the temperature to which an active pocket gopher was exposed. This was obtained from Fig. 7 and the rate of active metabolism at that temperature taken from Fig. 13. The period of activity was taken from page 68 and the daily energy expenditure during activity was calculated.

The energy expenditure at rest and the energy expenditure while active were summed to give total respiration per gram day. This represents the cost per gram day of being a pocket gopher, and is equivalent to average daily metabolic rate (ADMR) of Grodzinski and Wunder (1975) (Fig. 26).

By subtracting the resting rate of metabolism from the active rate of metabolism at the 10 cm temperature, the increment of energy expenditure actually involved in activity was calculated and is expressed as a percentage of the total daily energy expenditure. These calculations were repeated for April, July, and October, 1974 (Table 10).

The total daily energy expenditure per gram was multiplied by the mean weight of male gophers and the standing crop of male pocket gophers ($0.5 N$) in that month to give the total energy flow for a day in that month through 1 hectare ($\text{cal ha}^{-1} \text{ day}^{-1}$) due to males. This was also calculated using the mean weight of females and their standing crop to give the female contribution to energy flow. Numbers and weights were taken from Figs. 9 and 11 assuming that the sex ratio is 1:1. Males and

females were treated separately because of the weight differences between males and females. The summed respiratory expenditure is shown in Fig. 27.

The daily energy expenditures per hectare are in the nature of "snapshots" of the energy flow picture taken at single points in time for which data are known. These estimates do not account for the turnover of animals in a period, neither do they evaluate increments of energy expenditure due to growth or reproduction.

In Table 4, the biomass turnover rate and the number of discrete individuals in 3-month intervals were calculated. The discrete number of individuals in the three-month period was pro-rated among age and sex classes of individuals using Brown's 1971 data for seasonal age and sex distributions, averaged over 3-month intervals (Table 4). The intervals are arranged so that the central month is one for which the daily expenditure has been calculated above.

The mean number of discrete individuals in each sex and age class was multiplied by the mean weight of those individuals (Fig. 11), the daily energy expenditure (Fig. 26), and the number of days in the period to give the total energy flow through the individuals in that period. The group of pregnant females had their daily energy expenditure multiplied by 1.85 following the measurements of Kaczmarek (1966) and Migula (1969), who suggest that the cost of pregnancy and lactation integrated over the period of pregnancy and lactation causes an increase in the daily energy budget of 85%. The energy expenditure by respiration including the cost of reproduction is shown for six 3-month periods for which adequate data exist in Fig. 28 and Table 12.

The number of calories diverted into new individuals is given by the number of newborn gophers multiplied by their mean weight and mean energy content. Newborn pocket gophers from Alachua County are reported to weigh 5.1 g (mean of three individuals) by Barrington (1940). Brown (1971) reports the weight of two newborn from another population at 5.8 g each. I have taken 5 g to be a conservative estimate of the weight of newborn pocket gophers.

The energy content of 22 species of rodents reported in Grodzinski *et al.* (1975) and Fleharty *et al.* (1973) varies from 1.37-2.25 kcal/g live weight with a mean value of 1.67 ± 0.11 (2SE) kcal/g live weight. The energy content of newborn rodents is about the same as that of adults when computed on a dry weight basis. However, newborn rodents have more water and less fat than adults (Gorecki, 1965; Fleharty *et al.*, 1973; Sawicka-Kapusta, 1974). Therefore, they have a lower energy content per gram live weight. The mean energy content of neonate rodents of six different species is 0.94 ± 0.14 kcal/g live weight (Sawicka-Kapusta, 1974; Gorecki, 1965; Gelbczynski, 1975; Fleharty *et al.*, 1973; Fleharty and Choate, 1973). I have assumed that neonate gophers have an energy content of 1.00 kcal/g live weight.

The discrete number of newborn individuals (V_r) can be estimated from the number of pregnant females using equation (Petrusewicz and Macfadyen, 1970):

$$V_r = \frac{\bar{N} (f \cdot S) T \cdot L}{tp} \quad (\text{eqn. 8})$$

where

\bar{N} = mean standing crop in period T

T = days in period under consideration
(approximately 90)

t_p = length of the gestation period

L = litter size

f = proportion of females pregnant

S = proportion of females in population

In addition to the calories appearing as new individuals in the population, the respiratory cost to the females of supporting these individuals to weaning should be considered part of the cost of reproduction. This is calculated as the increment of respiration of pregnant and lactating pocket gophers above their normal maintenance cost which is 0.85/1.85 of the respiration of reproducing females from Table 12.

The energy flow due to growth could be calculated if the biomass turnover rate were known or if an accurate growth curve were available. As these data are not available, the simplest estimate of production due to growth (P_g) is given by the equation: (Petrusewicz and Macfadyen, 1970):

$$P_g = V \bar{N} T$$

where V = mean growth rate in kcal day^{-1} ; \bar{N} is standing crop; and T is time period. I have substituted N_u (discrete individuals) for \bar{N} as a better estimate of the discrete individuals present in the period. The mean growth rate of seven individuals calculated from their change of weight between captures from the field is $0.46 \pm 0.18 \text{ g day}^{-1}$. This estimate includes growth rates from immature as well as adult animals of both sexes. Growth at this rate would allow the attainment of size to independence in 180 days, the attainment of mean adult female weight in 330 days and the attainment of mean adult male weight in 500 days. These estimates seem compatible with the observed recruitment of juveniles

following breeding, but overestimates the time to reach mean adult size. The calculated growth rate is in good agreement with the growth rates of adult *Sigmodon hispidus* reported by Fleharty and Choate (1973), but these authors show that growth rate is variable between different age classes and between seasons. Fragmentary data from the recapture of adult gophers suggests that growth may be small or negative during the winter months, but not enough data exist to allow the calculation of this effect.

In addition to the P_g of adult animals in the population, it is possible to calculate the energetic value of the growth of new individuals that are the result of reproduction. I have already calculated the discrete number of juveniles in each 3-month period. Gophers appear to leave the maternal burrow and appear as independent animals between 80-90 g weight. If I assume that their rate of growth is 0.5 g day^{-1} (a little higher than adult animals), then I would predict that they would achieve this weight during their second 3-month period after birth. This prediction is compatible with the observed period between the known breeding peaks and the observed appearance of young individuals in the population. I have assumed that there is no mortality between birth and recruitment and that gophers of this age have an energy content intermediate between that of neonates and adults of 1.3 kcal g^{-1} live weight. I have calculated for each 3-month period the P_g of animals born in that period growing from 5 g-45 g and the P_g for animals born in the previous period that are growing from 45 g-90 g.

Results and Discussion

The calculated values for energy flow ($\text{kcal}\cdot\text{ha}^{-1}$) due to respiration, growth, and reproduction are shown in Table 13. The values for the four seasons of 1974 have been summed to estimate annual energy flow.

The results of these calculations can be seen in Tables 10-14 and Figs. 26-28. The average daily metabolic rate (ADMR) varies from season to season. It is highest in the winter when the exposure to low temperatures, particularly during activity, causes a large increase in the energy expenditure. ADMR is lowest in the summer. Fall ADMR exceeds that of spring because even though the resting component is lower in fall, the temperature during activity is also low and so this component of the ADMR is increased. ADMR may be thought of as the response of pocket gophers to the changing seasonal conditions.

The component of ADMR that can be attributed to activity over and above the thermoregulatory expenditure during activity ranges from 21-27% (mean 23.5%). Reports on the activity costs for other rodents (McNab, 1963; Gebzynski *et al.*, 1972) gives values of 8% to 43% (mean value 22.0 ± 7.59). There appears to be a size-related increase in percentage of respired energy used in activity. A regression of these data with body weight has a correlation coefficient of + 0.55 where activity percentage = 0.1146 body weight + 15.97. The wide variation in results due to differing conditions of temperature and season and an intrinsic variability between animals leads to the low coefficient, nevertheless larger rodents appear to spend a greater proportion of their daily respiration on activity than smaller rodents.

Most workers have ignored the work done by the animal on its ecosystem because they consider it difficult to measure. However, the energy expenditure due to activity multiplied by some efficiency factor must be at least a first approximation of work done on the system by gophers. From the laboratory estimates of rate of metabolism in digging pocket gophers I can estimate the approximate mass of the sand moved from tunnels dug in the metabolism chamber ($1861 \text{ g} \pm 200 \text{ g}$) and the time taken to dig them ($26 \pm 8 \text{ min}$). Assuming that the only work done is to move the mass of sand vertically against gravity for the mean depth of the tunnel (7.5 cm) I can calculate the work done on the sand which is $8.3 \times 10^{-4} \text{ Joules} \cdot \text{sec}^{-1}$. The total rate of metabolism of actively digging gophers is about $2.0 \text{ ccO}_2 \text{ g}^{-1} \text{ hr}^{-1}$ which is equivalent to $16,700 \times 10^{-4} \text{ J} \cdot \text{sec}^{-1}$. The efficiency of work done by an active gopher on the sand is then 0.05%.

I can multiply the estimated rate of metabolism of active gophers in the field from Table 10 by the biomass of males and females and sum these daily estimates over the period of a year to give the total calories respired by active pocket gophers per ha per yr. Multiplying this total by the estimated work efficiency of 0.05% I arrive at an estimate of annual work done by digging pocket gophers of $9.34 \text{ kcal ha}^{-1} \text{ yr}^{-1}$ which is 0.011% of the total assimilated energy.

The proportion of the total energy assimilated appearing as work done on the system is so small that it can be safely ignored in the calculation of energy budgets. However, the absolute amount of work done is equivalent to moving about 4 metric tons of sand 1 m on every hectare of the study area each year. This would seem to be a significant

redistribution of material which may function to move soil nutrients from deeper soil layers back to the leached surface layers. This figure compares favorably with estimates of soil displacement of other gophers (1.25 metric tons ha^{-1} range 0.1-17.2) given by Miller (1957) estimated from the volume of gopher mounds on the surface.

The ADMR, which is weight-specific ($\text{cal g}^{-1} \text{day}^{-1}$), has been multiplied by weight and number of animals present to give a first estimate of daily energy flow through the population. This is seen to be greatest and not appreciably different in the fall and winter when a large biomass and lower temperatures ensure a large energy flow. In spring, the energy respired is smallest due to the small number of animals present. In summer, the decrease ADMR is offset by a large standing crop to give an intermediate energy flow. Energy flow through the population represents the demand made by pocket gophers on their energy supply in response to the changing seasonal conditions affecting them.

A better estimate of total energy flow is given in Fig. 28 and Table 12, where total turnover of pocket gopher individuals, sex and size distributions, and the effects of pregnancy and lactation have been considered. The pattern is very similar except that the larger number of discrete individuals in the fall months causes the estimate for fall to be increased above that in winter. Finally in Table 13, the estimates of growth and reproductive energy flow are integrated to give a total assimilated energy budget. The gross annual energy assimilation of this population of pocket gophers, $88,421.8 \text{ kcal ha}^{-1} \text{ yr}^{-1}$, compares favorably with estimates accurately determined for other small rodents, e.g., *Sigmodon hispidus* $133,956 \text{ kcal ha}^{-1} \text{ yr}^{-1}$ (Fleharty and Choate,

1973); *Peromyscus polionotus* 167,000 and 256,000 kcal ha⁻¹ yr⁻¹ (Odum ^S*et al.*, 1962); *Dipodomys merriami* plus *Lepus californicus* 81,090 kcal ha⁻¹ yr⁻¹ (Chew and Chew, 1970). Also the percentage of the annual energy expenditure appearing as productivity (3.1%) is within the range of values of 1% to 5% reported by many other authors (Fleaharty and Choate, 1973; Drodz *et al.*, 1972; Chew and Chew, 1970; Johnson and Groepper, 1970; McNeill and Lawton, 1970).

From these similarities it can be argued that the annual estimates of energy flow and hence the component seasonal energy budgets are as accurate as the present state of the art permits. Of the total energy flow, a large percentage, 96.9%, follows the respiration pathway and this estimate is based on direct counts of individuals and accurate measurements of metabolic rate.

The above values for P_g and P_r are a measure of the quantitative impact on the various physiological and demographic properties of the population on its own persistence. In this way it can be seen that the amount of new biomass produced by reproduction is least in the spring (8.5 kcal ha⁻¹) and about equal during the other seasons (15.2-17.3 kcal ha⁻¹). There is some loss of resolution due to the arbitrary division of a continuous process into discrete periods. For instance, the winter-spring division separates two portions of one continuous early breeding pulse in February-March. Nevertheless, the fact that seasonal variations are still visible argues forcibly that they are fundamental properties of the population. Total productivity mirrors the pattern of respiration and total assimilation. This is largely because all these estimates respond to biomass measurements in the period.

It is significant that the percentage of total assimilation appearing as productivity is greatest during spring (5.7%) and least in fall (2.7%) and winter (2.1%). The cost of reproduction is constant in winter, spring, and summer at about 10%, but is less in fall, 5.2%, perhaps a reflection of a large biomass of nonreproductive individuals present in the fall.

To summarize the salient features of the energy flow pattern in this population: the maintenance cost (ADMR in $\text{cal g}^{-1} \text{day}^{-1}$) is determined largely by ambient temperature and, as it varies by a factor of almost 2 through the year, must constitute a significant factor in the persistence of individuals. The energy flow through the population is largely through respiratory pathways and is a result of changes in biomass. The channeling of energy into growth and reproduction is seasonally variable. The production of new individuals is least in the spring, but constitutes a significantly higher proportion of the available assimilated energy than at other seasons. This apparent paradox between the small absolute result and the large relative investment in reproduction in the spring constitutes a focus for the understanding of the reproductive and physiological strategy of *Geomys pinetis* which will be examined in the general discussion and conclusions.

Table 10. Calculation of average daily metabolic rates of individual *Geomys pinetis*.

	Winter Jan	Spring April	Summer July	Fall Oct	
T burrow 30 cm	17	22	26	23	C°
M _b rest. at T burrow	1.84	1.45	1.00	1.46	ccO ₂ g ⁻¹ ·hr ⁻¹
T rest	18	20	20	18	hr·day ⁻¹
R rest	159.0	139.2	96.0	126.0	cal·g ⁻¹ ·day ⁻¹
T burrow 10 cm	20	28	28	24	C°
M active at T burrow	3.5	3.0	3.0	3.2	ccO ₂ g ⁻¹ ·hr ⁻¹
Time active	6.0	4.0	4.0	6.0	hr·day ⁻¹
Total R during activity	100.8	57.6	57.6	92.2	cal·g ⁻¹ ·day ⁻¹
ADMR	259.8	196.8	153.6	218.2	cal·g ⁻¹ ·day ⁻¹
M active at T burrow	2.0				
Cost activity	57.6	41.5	41.5	51.8	cal·g ⁻¹ ·day ⁻¹
%ADMR	22%	21%	27%	24%	

Table 11. Calculation of population energy flow on one day in different seasons *Geomys pinetis*.

	Winter-Jan	Spring-April	Summer-July	Fall-Oct	
ADMR	259.8	196.8	153.6	218.2	cal g ⁻¹ ·day ⁻¹
Males					
\bar{W}	187	232	232	187	g·# ⁻¹
N	2.059	0.735	2.206	2.490	# ha ⁻¹
R	100,132	33,558	78,611	101,600	C cal·ha ⁻¹ ·day ⁻¹
Females					
\bar{W}	156	137	150	139	g·# ⁻¹
N	2.059	0.735	2.206	2.490	# ha ⁻¹
R	83,449	19,816	50,826	75,521	cal·ha ⁻¹ ·day ⁻¹
Total E	183,481	53,374	129,437	177,121	cal·ha ⁻¹ ·day ⁻¹

Table 12. Energy flow due to respiration (R) for three month intervals of a population of *Geomys pinetis*. Apportioned between males (♂) or lactating pregnant females (♀ preg), non-pregnant females (♀ non-preg), and juveniles (Juv) showing the relative contribution of pregnant (or lactating) females to the total energy flow (% preg).

	Total	preg	not preg	total	% preg	Juv
Winter 74	29,358	3,494	6,450	9,414	15,864	22
Spring 74	8,264	3,364	1,837	2,483	4,320	22
Summer 74	12,738	6,602	3,303	2,380	5,683	26
Fall 74	35,355	19,977	4,110	10,157	14,267	12
Winter 75	47,316	19,731	11,299	16,286	27,585	24
Spring 75	9,102	3,364	2,998	2,160	35,158	33
Total for calendar year 1974	85,717	15,700				18

All figures kcal·ha⁻¹·3-month period⁻¹

Table 13. Productivity of reproduction (Pr), productivity of growth (Pg), cost of reproduction (Pr + R preg), respiration (R) and total assimilated energy (P + R) for a population of *Geomys pinetis* at different seasons.

	Pr	Pg	0-90 g	Pg 90 g+	P total	Pr + R Preg	R total	P + R
Winter 74	17.3	203		380	600.3	2,980.3	29,358.8	29,959.1
Spring 74	8.5	304		184	496.5	852.5	8,264.4	8,760.9
Summer 74	16.3	296		318	630.3	1,533.3	12,738.9	13,369.2
Fall 74	15.2	375		587	977.2	1,903.2	35,355.4	36,332.6
Winter 75	19.7	411		691	1,121.7	5,210.7	47,316.0	48,437.7
Spring 75	9.4	344		184	537.4	1,386.4	9,102.4	9,639.8
Total for calendar year 1974	57.3		2,647		2,704.3	7,269	85,717.5	88,421.8

Pr - Productivity appearing as kcal of new individuals

Pg - Productivity due to growth between 0 g and 90 g

Pg 90 g+ - Productivity due to growth above 90 g

Pr + R preg - Total cost of reproduction

R preg - The increment of respiration energy of pregnant (or lactating) females above their normal ADMR

R total - Total respiration from Table

P total - Gross productivity due to growth and reproduction

P total + R total - Total assimilated energy

Table 14. Respiration, cost of reproduction, and productivity as a percentage of total assimilation for different seasons

	$\frac{\text{Respiration}}{\text{Total Assimilation}}$	$\frac{\text{Cost of Reproduction}}{\text{Total Assimilation}}$	$\frac{\text{Production}}{\text{Total Assimilation}}$
Winter 74	97.9%	9.9%	2.1%
Spring 74	94.3%	9.7%	5.7%
Summer 74	95.3%	11.5%	4.7%
Fall 74	97.3%	5.2%	2.7%
Total for calendar year 1974	96.9%	8.2%	3.1%
Winter 75	97.7%	10.8%	2.3%
Spring 75	94.4%	14.4%	5.6%

Figure 26. Average daily metabolic rate of *Geomys pinetis* at different seasons of the year.

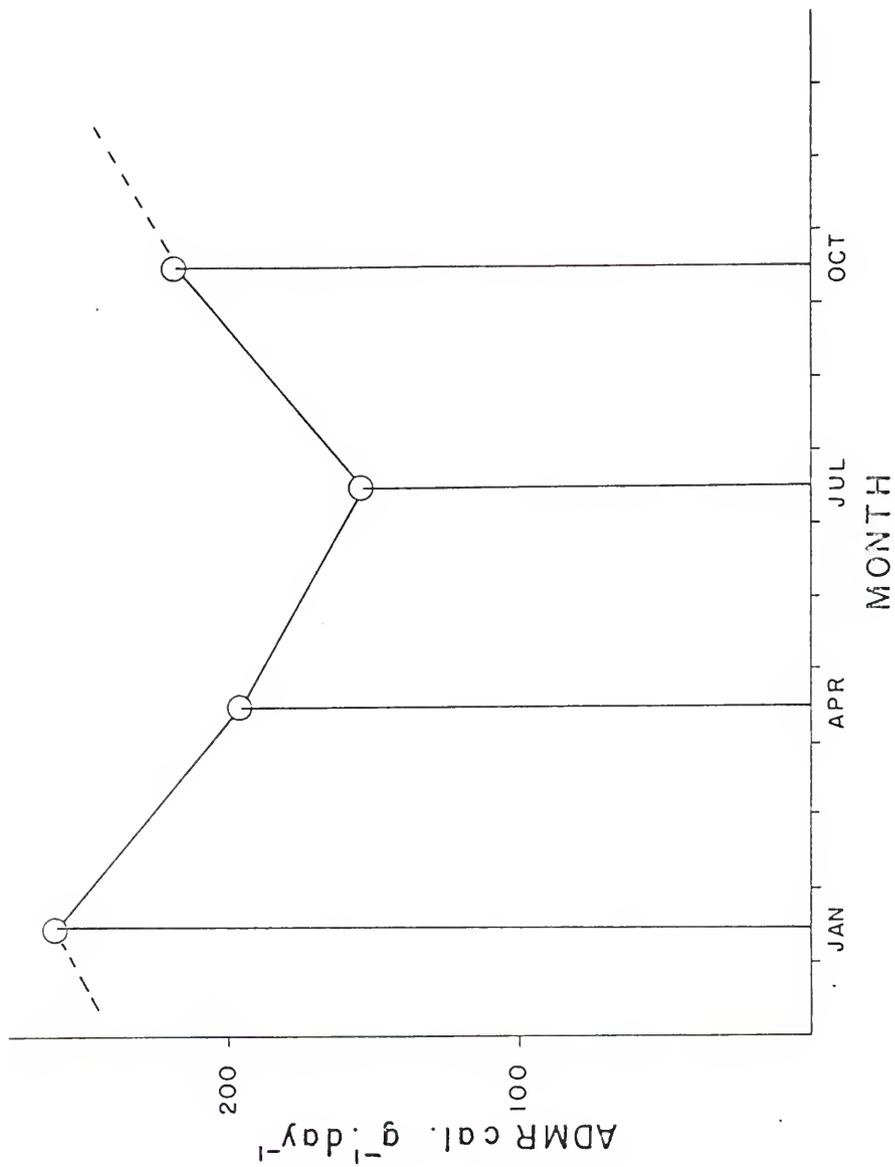


Figure 27. Total daily energy flow by respiration through a population of *Geomys pinetis*.

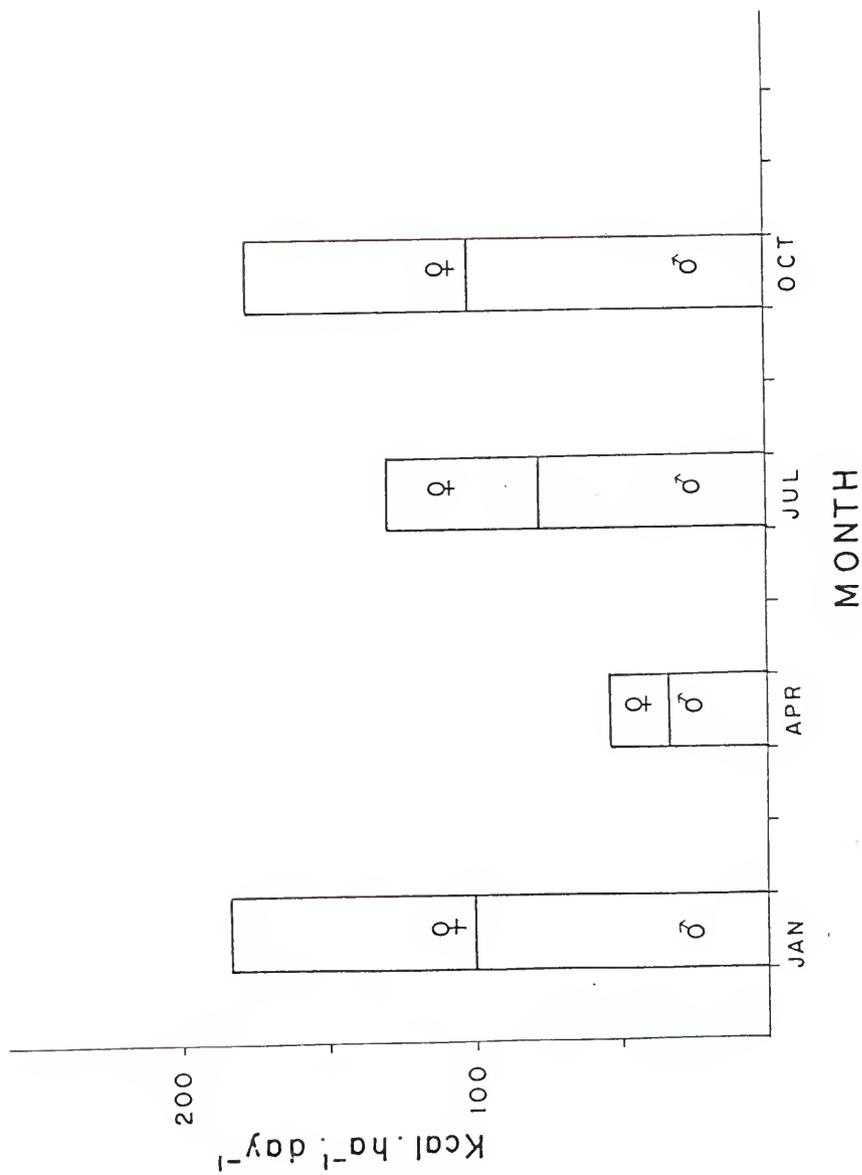


Figure 28. Total energy flow for three-month periods through a population of *Geomys pinetis*.

GENERAL DISCUSSION

From the preceding chapters a number of conclusions have been made concerning this population of *Geomys pinetis*.

1. The environment to which pocket gophers are exposed possesses a distinct seasonality, particularly in the temperature of the soil and in the water content and quality of gopher forage.
2. The population numbers of *G. pinetis* fluctuate regularly from season to season.
3. Mortality is greatest in the late fall and winter.
4. This mortality falls predominantly on newly established individuals and is associated with low temperatures, declining nutrient and water availability, and increased nematode parasite loads.
5. Most breeding takes place in two periods each year, February-March and June-October.
6. Basal rate of metabolism (M_b) and Conductance (C) vary seasonally in a way that reduces the danger of overheating in the summer and allows adequate thermoregulation in the winter.
7. Body temperature (T_b) rises during activity at all ambient temperatures (T_a) to which gophers are exposed. This constitutes a limit on the period of activity particularly at higher T_a 's and so activity is reduced at higher T_a .
8. The water requirements of gophers are relatively high and water concentration mechanisms are poor. All water intake is obtained from water in the food.

9. The energetic cost of maintaining a pocket gopher is greatest in the fall and winter and least in the spring and summer.
10. The energetic impact of the population on its habitat is largely determined by the population numbers and is greatest in the fall and winter.
11. The total number of calories appearing as secondary productivity is greatest in the fall; however, the cost of producing this is the smallest proportion of the total assimilated energy of any season. Conversely, while the total calories appearing as secondary productivity is least in the spring, this represents the highest proportion of total energy assimilated of any season. That is, while the results of the spring production are small in an absolute sense, they represent a disproportionately higher investment of the available energy.

There is increasing awareness among ecologists that biological systems are made up of intricate mutually interacting subsystems. In any system with feedback loops it becomes impossible to identify causes and effects. Feedback loops are an integral part of biological systems. One way to resolve this dilemma of tautology is to describe the operation of the system empirically without regard to what is cause and what is effect. A description of the operation of the system can then be generalized to give predictions about other systems. To this end I will discuss three sets of operations which interact to define population number in *Geomys pinetis*: feeding strategy, thermoregulatory strategy, and reproductive strategy. The common denominator which focuses their action on population number is their effect on energy flow through the population.

There is no clear agreement in the literature on the effect of changing food supply on rodent populations. Some workers have calculated the energy demands of populations in ways similar to those I have used, and then compared these demands to the available food supply. It is recognized that some foods are not actually available or are not used, and that the food supply may only exert its effect at a critical time of the year. Nevertheless these workers all find that food supply exceeds the maximum possible demand by a considerable amount and so conclude that food supply cannot limit populations (Gorecki and Gebczynska, 1962; Odum *et al.*, 1962; Grodzinski, 1963; Pearson, 1964; Drodz, 1966; Chew and Chew, 1970). However, several experiments involving the addition of suitable foods to natural populations have shown that with extra food the population density can be maintained at a higher level and that this effect is often due to improved survival of juveniles (Bendel, 1959; Hansson, 1971; Flowerdew, 1972). Other workers (Krebs and Deland, 1965; Chitty *et al.*, 1968; and Fordham, 1971) found that the addition of suitable food did not noticeably affect population density or juvenile survival. Therefore there must be variability in the responses of different populations. This situation is resolved by Hubbell (1973) who uses a simple analog model to consider the effect of changing food supply on population oscillations. He shows that the response of population numbers depends on the interaction between intrinsic rate of increase, the feeding rate, and a factor expressing the availability of food. He goes on to say that the population abundance depends only on the rate of food supply and the feeding rate.

In my population of *Geomys pinetis* individuals show evidence of malnutrition in the winter and spring even though the population levels

are low and the standing crop of food remains constant. However, in this period the water content and nitrogen content of the food decline. I have shown that the water requirements of gophers are about $0.2 \text{ g} \cdot \text{g}^{-1} \text{ day}^{-1}$. This requirement is likely to be a maximum estimate and can be satisfied by eating about $0.27 \text{ g} \cdot \text{g}^{-1} \text{ day}^{-1}$ of food with a water content of 75% in the laboratory.

In the field, when the food has a water content of 65% a gopher has to eat $0.31 \text{ g} \cdot \text{g}^{-1} \text{ day}^{-1}$ to meet its water requirement. If the food has the lowest water content which I measured in the field (30%), a gopher must eat $0.66 \text{ g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ or 2/3 of its body weight daily. This is clearly impossible, because the average stomach volume of *G. pinetis* is $12.4 \pm 5.9 \text{ ml}$ and the estimated passage time through the gut is 3 days. What this means is that during the drier portions of the year many of the patches of food that a gopher samples will have too little water for the gopher to eat.

This situation provides an explanation for some of the behavioral and morphological adaptations which gophers possess. It is clearly beneficial to live in a territory that has a high density of food patches of suitable water content and it may be beneficial to defend that territory from other gophers. Also, once a suitable food patch is found it is advantageous to transport and store high water content food. This is perhaps why pocket gophers have pockets (extended external cheek pouches)! In this context it is interesting to note that many other rodents with pockets, e.g. kangaroo rats (*Dipodomys* spp.), pocket mice (*Perognathus* spp.), and hamsters (*Mesocricetus auratus*), are largely fossorial and live in dry habitats.

McNab (1966) first suggested that the low M_b and high C of all fossorial rodents, including *G. pinetis*, was an adaptation which avoided excessive heat storage. He showed that while diffusion of O_2 and CO_2 was unlikely to be limiting under normal burrow conditions, this factor may restrict *G. pinetis* to soils with a low water holding capacity, effectively forcing them into a microenvironmental desert. McNab (1966) notes that the low M_b of heteromyid rodents and desert dwelling *Peromyscus* may be a water conserving mechanism, but discounts this for *G. pinetis*. In the light of the data on water requirements and poor renal function of *Geomys*, the low M_b may well function to reduce water loss.

McNab (1966) argues convincingly that the major factor influencing the low M_b and high C (best shown by the factor F) is T_a . However, many authors point out that T_a in a closed burrow is greatly buffered from ambient extremes (Kennerly, 1964; McNab, 1966; Studier and Proctor, 1971). This study shows that significant heat loading can occur at the moderate T_a measured in gopher burrows. The significance of the reduction of F , which minimizes this effect, has been demonstrated. In a series of comparisons across broad taxonomic categories McNab (1966) found that the reduction in F in fossorial rodents is correlated with maximal burrow temperature. Bradley *et al.* (1974) compared two species of *Thomomys* from habitats with different thermal regimes and found the same correlation, lower F with higher T_a . Daily and seasonal fluctuations in T_a may span the same range as differences between locations. If the major determinant of F is T_a , then a seasonal adjustment of F would be predicted. I have shown that this does occur with F being least during the months of high

T_a . A similar result may be inferred from the ranges of T_b of *B. busarius* for summer and winter given by Kennerly (1964).

The dynamics of soil temperature changes seem to reduce the behavioral options open to *G. pinetis*. Wilks (1963) and Howard and Childs (1959) observed deeper tunnels in *Geomys* and *Thomomys* during the summer and suggested that these served as refuges from high T_a . The soil temperature profiles during the summer months in Gainesville show this to be of limited use to *G. pinetis*, which perhaps explains why no increase in summer burrow depth is observed in this species.

The numbers in the population vary seasonally, increasing from May to November and decreasing from December to April. The decrease in population numbers is largely due to the disappearance of recently established animals, and these are presumed to be mostly newly recruited juveniles from the spring and summer breeding. The age distributions reported by Brown (1971), the size distribution, the presence of small animals in the population, and the estimated growth rates are all compatible with this presumption. Juveniles are shown to have lower survivorship than adult animals and the period of greatest mortality falls in the first winter period (November-January) to which they are exposed. Animals which first appear in the summer are thought to be the product of the early spring breeding pulse by the survivors of the previous winter. Only a few adults take part in this breeding pulse, and the absolute amount of energy expended by the populations in the spring breeding is low. However the proportion of the total assimilated energy spent on breeding is higher in the spring than at any other time of the year. The greater survivorship of the products of the spring breeding

pulse during their first winter, compared to juveniles born in the summer and fall, provides strong selection for some breeding in the spring even though it is expensive.

The cause of mortality during the winter is unknown; however, no observations or data exist to suggest that either emigration or predation is involved. A 2 ha section at the edge of the study area was completely cleared of pocket gophers. In the following 18 months only one pocket gopher invaded this cleared area, suggesting that there is little emigration away from the study area. A superficial examination of owl pellets and raccoon scats on the study area failed to reveal any evidence of predation on *Geomys*.

The information on the physiology of *G. pinetis* suggests a physiological explanation for the observed mortality. The resources available to an individual gopher are limited to those within its territory. In the fall and early winter the population density is high so the area available per gopher is reduced. Hansen and Remmenga (1961) report that mean territory area is reduced at high population density in *Thomomys* and this is also true for *Geomys pinetis*. One noticeable feature of the study area was a number of territories that were continually occupied throughout the year, presumably by the same gopher. Such gophers were invariably large adults. The population in the fall is largely composed of juveniles and young adults and I think many of these animals establish small territories in suboptimum areas or between the territories of established animals. In the early fall such territories are adequate to support a gopher. As the winter progresses the temperature in the soil falls and the water content of some of the available food is reduced.

The lowered temperature requires an increased energy expenditure for thermoregulation, increasing ADMR, which is translated into a high demand by the total population for resources. At the same time much of the food is no longer available because its water content is too low to meet a gopher's water requirements. This leads to progressive starvation and dehydration by those gophers whose territories are too small, or poorly located with respect to the distribution of suitable patches of food. These are the juveniles and young adults who, I have shown, constitute the bulk of the winter mortality.

Barrington (1940) observed that in the laboratory, fights between gophers always ended with the death of the smaller animal. It is possible that significant mortality occurs due to large animals killing small ones as they defend good territories. As the physiological condition of the animals declines their resistance to parasites is lowered and their parasite loads build up. In addition to the physical damage and nutrient diversion that a large parasite load causes, the bulk of parasites occupies volume in the stomach, further reducing the ability of a gopher to meet its energy and water requirements. The result is a cyclic decline in condition leading to death in all the gophers except those whose large or particularly favorable territories encompass a greater proportion of the food with higher water content. In support of this explanation I have often observed that animals captured in late winter and spring die within a day or two of capture. This is insufficient time for a gopher in normal nutritional and water balance to starve to death, suggesting that such deaths are due to a pre-existing debilitation exacerbated by the stress of capture.

Considering the energy-related mortality of pocket gophers, it is of interest to consider how sufficient energy is directed into reproduction to insure the subsequent success of individuals or the population. This was recognized by Darwin (1896) and is perhaps most succinctly stated by Fisher (1958, p. 47):

It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction.

I will now examine the circumstances of life history and environment that lead to the observed apportionment of energy in pocket gophers. Lack (1954) showed that the clutch size in birds seems to be set such as to maximize the survival of offspring in any given breeding episode, and Cole (1954) demonstrated the interaction of clutch size and frequency with demographic parameters of a population. Fisher (1958) coined the term reproductive value to describe the contribution of an individual to the ancestry of future generations, taking into account the past and future survivorship of the individual and the remaining potential fecundity. Williams (1966) extended Fisher's concept, and concluded that the criteria for determining the selective value of spending energy on a given reproductive episode must include the cost to the parent organism compared to remaining (or residual) reproductive value. The relationship of reproductive effort to demographic life history parameters on one hand and a cost to risk calculation on the other has been the central paradigm on which a multitude of theoretical studies have been

based. These are reviewed in Stearns (1976) and several broad generalizations have emerged.

It has been shown by Charnov and Shaffer (1973) that the quantitative conclusions of Cole (1954) and Gadgil and Bossert (1970) are an artifact of unnatural assumptions about mortality. In particular, Gadgil and Bossert's (1970) contention that reproductive effort must increase with age is now known to be a special one. Charnov and Shaffer (1973) conclude that the value of a particular life history strategy depends on the relative survival of juvenile and adult organisms. Shaffer (1974a) and Bell (1976) come to similar conclusions. In general, increased mortality of juveniles compared to adults leads to a reduction in clutch size and an increase in the number of breeding episodes. Murphy (1968) showed that the risk of complete failure of a reproductive episode is an important determinant of reproductive tactics. He showed that in environments imposing variable and unpredictable mortality on juveniles, clutch size will decrease.

Lack's (1954) ideas on the optimum clutch size have been extended by the recognition that more is involved in success of a brood than the number of fledged young. There are complex interactions between adult survival, available resources, survival of juveniles, the uncertainty of the environment and the probability of extinction all of which determine optimum clutch size (Stearns, 1976).

Two schools of thought have developed concerning the optimum strategies for reproduction. These schools differ on the basis of their concept of fitness. Stearns (1976) points out that "fitness is something everybody understands but no one can define precisely." He goes

on to recognize the familiar r and K concept of fitness proposed by Dobzhansky (1950) and developed by MacArthur and Wilson (1967), Lewontin (1965), and others, as one school, and what he calls "bet hedging" as the other. The bet hedging concept of fitness may be thought of as an attempt to minimize the probability of extinction (Shaffer, 1974a). While the difference between these two concepts may not be obvious the conclusions arrived at when they are used as the basis for mathematical models are very different. The proponents of r and K type fitness suggest that in fluctuating unpredictable environments populations with rapid development, early maturity, large clutch sizes, short life and a tendency to breed only once will be favored (MacArthur and Wilson, 1967; Pianka, 1970; Levins, 1968; Lewontin, 1965). In contrast Shaffer (1974), Bell (1976), Williams (1966), and Murphy (1968) predict, based on a bet hedging tactic, that in fluctuating environments populations will favor a strategy of slower development, late maturity, small clutch sizes, repeated breeding attempts and long life. The data I have collected on *Geomys pinetis* provide a ready test of these alternatives.

I have already argued that the environment experienced by pocket gophers is variable and unpredictable because of their restricted food habits. The severity of the winter cool drought, coupled with an unpredictable spring drought, is sufficient to cause large changes in population density and to result in the evolution of an energetic strategy that apparently serves to ensure some juvenile survival through the unfavorable time of the year. Similarly the problems imposed by heat dissipation in the summer are severe enough to require considerable

metabolic, morphological, and behavioral adaptation to offset their effects. Thus, the pocket gopher's environment is clearly variable from a gopher's viewpoint.

Geomys pinetis has the smallest clutch size of any geomyid and is one of the few gophers to show more than one breeding peak a year. Several other species are described as polyestrus, but have a strict breeding peak imposed upon them by the severe environments in which they live (e.g. *Thomomys bottae*, Howard and Childs, 1959).

Based on my observed growth rates *G. pinetis* takes between 4 and 6 months to grow to the minimum size for reproduction. This is an uncommonly long period compared with many cricetid rodents, although good data on this point are not available for other gophers. Gophers that survive the juvenile mortality period seem to be fairly long-lived. From my recapture data and longevity records in the laboratory I would estimate that some gophers survive for two full years after their first winter. My estimates of the cost of reproduction--5.2%-14.4% (annual mean 8.2%)--are perhaps the most correct available, as many authors only calculate the calories appearing as young and ignore the increased respiration of the mother. The calculated reproductive effort and the observed tactics of energy partitioning of *G. pinetis* seem to support the predictions of Shaffer (1974) and Murphy (1968), and to oppose those of Pianka (1970), Levins (1968), and MacArthur and Wilson (1967).

Stearns (1976) shows the relationship between the ratio of juvenile to adult mortality and the number of breeding seasons per female. While these data are rather variable and may be variously compromised by the methods used, they suggest that when the mortality of juveniles is twice

that of adults, between 2 and 6 breeding seasons per female are expected. The survival curves given in Fig. 10 indicate a maximum mortality of about 0.6 for young individuals and a minimum of about 0.3 for older animals. Depending on whether they breed in their first year of life or not, gophers have between 4 and 6 reproductive episodes per female, surprisingly close agreement.

The predictions of the r and K selection model have been verified by several studies (*e.g.* Gadgil and Solbrig, 1972) of organisms with an effective means of dispersal. Thus the predictions of strategy for fluctuating environments are predicated on the possibility that propagules can leave one habitat and find another. Pocket gophers have very poor dispersal ability and perhaps this is the reason that their strategy is based on persisting in a marginal habitat until a favorable season allows a brief increase in population density.

This leads me to ask what conditions have led to the adoption of this strategy in *G. pinetis*. Mertz (1971) has suggested that a life history strategy like the one described for *G. pinetis* has the important effect of prolonging the time to extinction in the face of an unfavorable environment. The typical habitat for *G. pinetis* in Florida is the turkey oak, long leaf pine, sandhill community. This community is notoriously poor in nutrients, and parasite problems are such that only with modern veterinary and fertilizing techniques has it been possible to farm on this soil. Historically this community was periodically burned (Laessle, 1942), increasing the ground cover vegetation and releasing nutrients. From my study of the food and water requirements of *G. pinetis* I predicted that gophers would only reach high densities on the early successional

patches of this habitat. Other authors have made similar observations (Starner, 1956). Table 7 shows pocket gopher density related to burning history for several plots in Morningside Park, Alachua County, Florida and several other climax sandhill communities. It is apparent that the density of gophers is lowest in the climax and highest in the artificial early seral stage of pasture land.

I conclude from this that *G. pinetis* has evolved its observed life history strategy to persist in suboptimum climax communities and periodically to take advantage of the patches rejuvenated by burning. This has preadapted *G. pinetis* to take advantage of the patches artificially rejuvenated by man, which are its preferred habitat at the present time.

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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.



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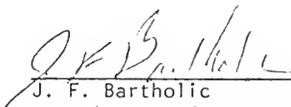
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