

## Relationships among reproductive status, nutritional status, and food characteristics in a natural population of *Peromyscus maniculatus*

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We compared digestibility of consumed food, dimensions of the alimentary tract, body fat and body size in relation to sex and reproductive status of overwintered adult *Peromyscus maniculatus* to assess the applicability of these measures of food intake and nutritional status to natural populations. Nonbreeding females were smaller than other sex and reproductive categories, but they had the largest alimentary tracts and energy reserves for their size. Lactating females were large, but they had low energy reserves and only averaged-sized alimentary tracts. Nonbreeding males ate relatively poor quality foods, had the smallest alimentary tracts for their size, and had low energy reserves. Most of these patterns were interpretable based on the known biology of this population. We conclude that these measures can provide insights into intraspecific variation in food intake and nutritional status in natural populations of *Peromyscus*.

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Nous avons comparé la digestibilité des aliments consommés, les dimensions du tractus alimentaire, les graisses corporelles et la taille du corps en fonction du sexe et du statut reproducteur chez des *Peromyscus maniculatus* adultes après l'hiver, ce qui a permis d'évaluer l'applicabilité de ces mesures à l'alimentation et au statut alimentaire de populations naturelles. Les femelles non reproductrices étaient plus petites que les animaux des autres catégories de sexe ou de statut reproducteur, mais ce sont elles qui avaient le tractus alimentaire le plus grand et les réserves énergétiques les plus abondantes pour leur taille. Les femelles nourricières étaient de bonne taille, mais avaient des réserves énergétiques plutôt basses et des tractus alimentaires de taille moyenne. Les mâles non reproducteurs consommaient des aliments relativement pauvres, avaient les tractus alimentaires les plus petits pour leur taille et leurs réserves énergétiques étaient basses. Toutes ces données peuvent s'expliquer par ce qu'on connaît de la biologie de cette population. Ces mesures donnent donc une bonne idée de la variation intraspécifique de la consommation de nourriture et du statut alimentaire chez les populations naturelles de *Peromyscus*.

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### Introduction

Reproduction in small mammals is energetically costly; females often require a twofold increase in food consumption to support their offspring (Glazier 1985; Innes and Millar 1981; Kaczmarski 1966; Lochmiller *et al.* 1982; Migula 1969; Millar 1975, 1978; Randolph *et al.* 1977). Despite the obvious deduction that the high energy demands of reproduction must be met through concomitant adjustments in foraging and digestive processes, or through negative effects on nutritional status, our understanding of these relationships in natural populations is often hampered by the difficulties in measuring these parameters. This is especially true in small rodents with nocturnal habits.

Recently, techniques have been developed that may permit an assessment of quality and quantity of ingested food as well as nutritional status, based on characteristics of individuals sampled from natural populations. These include the qualitative analysis of alimentary tract contents as an indicator of the quality of food consumed under natural conditions (MacPherson *et al.* 1985, 1988; Sadlier *et al.* 1973; Servello *et al.* 1983, 1984, 1985), the dimensions of the alimentary tract (Gross *et al.* 1985; Green and Millar 1987; Hansson and Jaarola 1989) as indicators of quantity of food consumed, and body composition, especially body fat, as an indicator of nutritional status of the individuals in the population (Evans 1973; Judd and Carpenter 1984; Judd *et al.* 1978; Millar and Schieck 1986). To date, these techniques have not been collectively applied to natural populations of small mammals, although they may prove useful in determining intrapopulation variation in nutritional status and

food characteristics. In this study, we attempted to assess the applicability of these techniques to natural populations by using them to compare nutritional status and food characteristics among mice of known reproductive status from a natural population of *Peromyscus maniculatus borealis* in southwestern Alberta. Lactating females require much more food than nonbreeding females (Millar and Innes 1983), but it is not known if these requirements are reflected in indices of food intake; a useful index of food consumption should discriminate between females of known reproductive intakes. If this holds true, the application of these methods may provide insights into the feeding ecology of other sex and reproductive status groups.

### Methods

Mice (*Peromyscus maniculatus borealis*) were collected in the Kananaskis Valley, Alberta (51°N, 115°W), during early May through August 1987. Trap lines consisted of lines of 75–150 museum special kill traps set approximately 20 m apart for three nights. Traps were set on day 1, checked during the morning on days 2 and 3, and moved to a new area on day 4. Specific areas were not trapped more than once per season. Each trap station consisted of a single trap. Each trap was unbaited, except for a small string soaked in aromatic oils that was tied tightly to the treadle (after Sadleir *et al.* 1973). This procedure prevented stomach contents from being contaminated with artificial bait. All mice were weighed (nearest 0.1 g), aged as overwintered or young of the year on the basis of size and pelage color (after Millar and Schieck 1986), and necropsied. Only overwintered mice were used in our study because young mice do not normally mature in the summer of their birth (Millar and Innes 1983; but see Lusk and Millar 1989).

Four external morphological characters (body length, tail length, ear

length, and hind-foot length) were measured for each mouse. These four measurements were used as indicators of body size, which is relevant to our energetic study as large animals require more energy for body maintenance than small animals, everything else being equal.

Digestibility of stomach contents was used as a measure of food quality. The stomach contents of each mouse were dried for 48 h at 55°C and weighed. Samples consisting of a minimum of 0.15 g dry matter were used to measure neutral detergent solubility using a method modified from Goering and Van Soest (1970). Samples were ground to a fine powder using a pestle, redried for 15 min, and weighed to the nearest 0.001 g. Samples were then mixed with 10 mL of neutral detergent solution and 0.5 g of sodium sulphite in a 100-mL Goldfish beaker and refluxed for 1 h in a goldfish apparatus. The refluxed solution was filtered under suction (using preweighed 5.5 cm Whatman No. 1 filter paper), washed two or three times with hot distilled water, and finally washed with acetone. The filter paper, with the residue, was dried at 55°C for a minimum of 2 h and weighed to the nearest 0.001 g. The weight of the remaining residue (total minus paper weight) divided by the weight of the sample represented the proportion of undigestible fibre in consumed food. The proportion, henceforth referred to as food quality, is negatively correlated with dry matter digestibility of the diet (Servello *et al.* 1983). Note that the higher the proportion, the poorer the food quality.

Quantity of food consumed was assessed from the dimensions of the digestive tract. The entire digestive tract was excised and trimmed of mesenteries and fat. The tract was straightened (but not stretched), and lengths of the small intestine (from pyloric sphincter to ileocolic sphincter) and large intestine (from caecum to anal sphincter) were measured (nearest 1.0 mm). Wet weights (nearest 0.1 g) of the small intestine, caecum, and large intestine (including contents) was recorded. Attempts to separate gut tissue and contents were abandoned because they could not be separated reliably. Therefore, all weights represent tissue mass with contents. This approach was consistent with that of Green and Millar (1987) and Schieck and Millar (1985).

Males were recorded as breeding (testes  $\geq 7$  mm) or nonbreeding (testes  $< 7$  mm); females were recorded as prebreeding (no evidence of pregnancy or lactation), pregnant (visible embryonic swellings), lactating (well-developed mammary glands and nipples), both pregnant and lactating, or postbreeding. The last two categories were later excluded from our analyses because of small sample sizes. This resulted in five sex – reproductive status (SR) categories.

Body fat was used as a measure of nutritional status. Whole animals (including skin and reproductive and alimentary tracts, but excluding stomach contents) were dried, ground in a Wiley mill, and fat content determined by ether extraction, following Kerr *et al.* (1982) and Dobush *et al.* (1985).

## Results

All overwintered males were in breeding condition when trapping started; the last male in breeding condition was captured July 15. Nonbreeding males were captured only in late breeding season and will be referred to as postbreeding males. The first pregnant female was captured May 11 and the last pregnant female was captured July 25. All of the nonbreeding females were prebreeding. Young of the year were first captured on June 15. Thus the season of births extended from approximately late May to late July. Among 66 young-of-the-year females captured, none showed any evidence of having bred.

### Body size in relation to SR categories

A measure of general body size was derived by subjecting the four external measurements (body length, tail length, ear length, and hind-foot length) to a principal component analysis using a covariance matrix to calculate principle components. The first principal component score (SIZE.PC1) accounted for 92.6% of the total variance in the four external measurements and therefore represents general body size variation. Significant differences in body size among SR categories were shown by an

TABLE 1. Analysis of variance of body size (SIZE.PC1) among sex and reproductive status (SR) categories

Source of variation	DF	SS	MS	F	p
SR	4	1 342	335	3.21	0.015
Error	138	14 404	104		
Total	142	15 745			

  

SR	N	Mean $\pm$ 1 SE
Prebreeding female	13	178.6 $\pm$ 4.1
Postbreeding male	11	190.6 $\pm$ 1.8
Breeding male	80	185.0 $\pm$ 1.2
Pregnant female	21	185.4 $\pm$ 2.2
Lactating female	18	190.3 $\pm$ 1.5

NOTE: Means  $\pm$  standard errors and sample sizes are included for reference.

TABLE 2. Analysis of covariance of food quality among sex and reproductive status (SR) categories, with Julian date and Julian date squared as covariates

Source of variation	DF	Adjusted SS	MS	F	p
Covariates	2	1045.3	522.6	3.92	0.026
SR	4	668.6	167.2	1.25	0.300
Error	54	7208.4	133.5		
Total	60	9804.0			

  

SR	N	Adjusted mean $\pm$ 1 SE
Prebreeding female	9	63.6 $\pm$ 4.7
Postbreeding male	6	78.3 $\pm$ 12.9
Breeding male	33	60.2 $\pm$ 2.6
Pregnant female	6	57.6 $\pm$ 5.1
Lactating female	7	54.8 $\pm$ 4.8

NOTE: Means  $\pm$  standard errors adjusted for covariates and sample sizes are included for reference.

analysis of variance ( $p = 0.015$ , Table 1). The mean value of body size for prebreeding females (178.63, Table 1) is the smallest among SR categories. A comparison of prebreeding females with all other SR categories showed that prebreeding females were significantly ( $p = 0.012$ , two-tailed test) smaller than other overwintered adults.

### Quality of food consumed in relation to SR categories

Many mice had too few stomach contents for neutral-detergent analysis and food quality was determined for only 61 of 143 individuals. Examination of fibre content in relation to Julian date showed that fibre content decreased (at a rate of  $0.16 \cdot \text{day}^{-1}$ ) as the summer progressed ( $r = 0.325$ ;  $p = 0.01$ ;  $N = 61$ ). For this reason, Julian date and its squared term were included as covariates in an analysis of covariance testing for differences in food quality among SR groups (Table 2). There was no strong evidence suggesting that food quality differed among SR categories ( $p = 0.300$ , Table 2), although postbreeding males appeared to eat the poorest food. The probability that postbreeding males ate food of the same quality as the rest of adults was 0.073 (two-tailed test), as calculated from a similar analysis of covariance contrasting the postbreeding males with all the other categories of mice, assuming the relationship

TABLE 3. Analysis of variance of size of the alimentary tract (GUT.PC1) among five sex and reproductive status (SR) categories

Source of variation	DF	SS	MS	F	p
SR	4	3 5756	8939	6.93	0.000
Error	142	18 3171	1290		
Total	146	21 8927			

SR	N	Means $\pm$ 1 SE
Prebreeding female	15	362.2 $\pm$ 7.8
Postbreeding male	11	324.0 $\pm$ 6.7
Breeding male	82	331.0 $\pm$ 4.2
Pregnant female	21	356.5 $\pm$ 8.4
Lactating female	18	367.5 $\pm$ 7.2

NOTE: Means  $\pm$  standard errors and sample sizes of GUT.PC1 are included for reference.

TABLE 4. Analysis of covariance of size of the alimentary tract (GUT.PC1) among size and reproductive status (SR) categories, with body size (SIZE.PC1) as a covariate

Source of variation	DF	Adjusted SS	MS	F	p
SIZE.PC1	1	13 717	13 717	11.66	0.001
SR	4	43 544	10 886	9.25	0.000
Error	137	161 212	1 177		
Total	142	215 768			

SR	N	Adjusted mean $\pm$ 1 SE
Prebreeding female	13	376.9 $\pm$ 7.4
Postbreeding male	11	319.1 $\pm$ 6.4
Breeding male	80	330.9 $\pm$ 4.1
Pregnant female	21	356.7 $\pm$ 8.2
Lactating female	18	362.8 $\pm$ 7.0

NOTE: Means  $\pm$  standard errors and sample sizes of GUT.PC1, adjusted for SIZE.PC1, are included for reference.

between food quality and season we used in the ANCOVA held throughout our sampling period.

#### Quantity of food consumed in relation to SR categories

Food quantity was assessed from the dimensions of the digestive tract, which was partially reflected by each of five morphological measurements of the digestive tract: small intestine length and weight, large intestine length and weight, and caecum weight. To derive a general measure of the size of the digestive tract, all five variables were subjected to a principal component analysis using a covariance matrix to calculate principal components. The first principal component score (GUT.PC1), which accounted for 88.3% of the total variance in the five variables, was used as a general measure of size of the digestive tract.

Differences in GUT.PC1 among five SR categories were highly significant ( $p < 0.001$ , Table 3). The differences among three SR categories of females were nonsignificant; further analysis revealed significant differences ( $p < 0.001$ ) in GUT.PC1 between the sexes, with females having larger digestive tracts than males.

Because body size and gut dimensions were correlated, body size (SIZE.PC1) was used as a covariate in an analysis of covariance testing for differences in gut dimensions among SR

TABLE 5. Analysis of covariance of fat (g) among sex and reproductive status (SR) categories, with gross weight (g) as covariate

Source of variation	DF	Adjusted SS	MS	F	p
Gross weight	1	3.6825	3.6825	17.50	0.000
SR	4	5.2537	1.3134	6.24	0.000
Error	130	27.3600	0.2105		
Total	135	36.4424			

SR	N	Adjusted mean $\pm$ 1 SE
Prebreeding female	14	1.43 $\pm$ 0.13
Postbreeding male	10	0.87 $\pm$ 0.14
Breeding male	75	1.10 $\pm$ 0.05
Pregnant female	21	1.20 $\pm$ 0.11
Lactating female	16	0.67 $\pm$ 0.12

NOTE: Adjusted means  $\pm$  standard errors and sample sizes are included for reference.

categories. Highly significant differences ( $p = 0.001$ , Table 4) were found among animals of different SR categories, with prebreeding females and postbreeding males having the largest ( $p < 0.001$  for prebreeding females against all other SR categories) and smallest ( $p = 0.042$  for postbreeding males against all other SR categories) digestive tracts for their size, respectively.

#### Fat content in relation to SR categories

Several predictions concerning fat content can be made on the basis of the previous results. First, because the prebreeding females were not burdened with the energetic costs of reproduction (little energy output) but had the largest digestive tracts for their size (large energy input), these females should be the fattest, assuming similar activity patterns among SR groups. Second, because postbreeding males appeared to eat food of relatively poorer quality than other SR groups, and had relatively small digestive tracts, they should be lean. Third, lactating females did not appear to eat significantly higher quality foods than other females and their gut dimensions were not particularly large. In view of their energy requirements being much greater than prebreeding females (Millar 1978), lactating females should have low fat reserves.

Our measurement of body fat was based on whole animals, including reproductive and alimentary tracts. Thus the greater the body mass, the more fat. To correct for body mass, we used gross body mass as a covariate in an analysis of covariance testing differences in fat among the five SR categories (Table 5). We did not use SIZE.PC1 as a covariate as it reflected only structural size and did not take the mass of embryos into account.

Nonbreeding females were the fattest among the SR categories (Table 5). Postbreeding males were lean, as expected. They were not only leaner than prebreeding females ( $p < 0.001$ ) but also leaner than breeding males ( $p = 0.040$ ). The lactating females were the leanest of all.

#### Discussion

The results of this study indicate that the qualitative assessment of stomach contents, gross measurements of the alimentary tract, and the analysis of body composition can provide insights into the relationships among food and reproductive and nutritional status in natural populations of *P. maniculatus*. All three measures showed differences than can be logically explained by

the known biology of the species in this area. For example, food quality (as indicated by decreasing fibre content of stomach contents) increased towards the end of the breeding season, as would be expected in a strongly seasonal environment where synchronized primary production results in an abundance of seeds and insects late in the summer. Similarly, females had larger digestive tracts than males, as would be expected in a population where females provide all of the energy for growth and development of offspring. Finally, lactating females had the lowest energy reserves in the form of body fat, as would be expected given the high energy demands of lactation.

Despite the general adherence of these results to what one would expect for this species in this environment, some results were not expected and may provide further insights into biology of this species in this area. Prebreeding females were characterized by a small structural size, a relatively larger index of food consumption based on size of the digestive tract, and greater energy reserves than breeding females, although the quality of foods consumed were similar to those of breeding females. Previous studies have shown that all overwintered females ultimately breed (Millar and Innes 1983; Lusk and Millar 1989). Delayed breeding appears related to microhabitat temperature in the spring (Sharpe 1987). The observation here that energy reserves are high among prebreeding females supports Sharpe's (1987) suggestion that delayed breeding may not be related to poor body condition per se. Rather, females appear to require seasonal microhabitat cues before they breed, after which they exhibit growth in structural size.

Lactating females were structurally large (Table 1) but had relatively low energy reserves (Table 5), as might be expected because the energy requirements of lactation are high (Millar and Innes 1983). However, neither the quality (as indicated by fibre content) nor the quantity of food consumed (as indicated by dimensions of the digestive tract) were significantly greater than that of other females. It is highly unlikely that females can support lactation without increasing ingestion, and the fact that the mean size of the digestive tract was largest for lactating females (Table 3) indicates that they tend to do so. However, the small range of sizes of digestive tracts among SR categories (the smallest was only 12% smaller than the largest; Table 3) indicates that other confounding factors may be involved. There are several possibilities. The size of the digestive tract is ultimately constrained by the size of the mouse. In this way, the size of the digestive tract in lactating females may be the largest possible within the constraints of body size. Alternatively, female small mammals are known to increase their foraging activities during lactation (Harland and Millar 1980; Herman 1977; Madison 1978, 1981). Perhaps the high energy demands are met through increased foraging frequency rather than increased consumption and food retention during any given foraging bout.

Postbreeding males tended to consume low quality food (not significant; Table 2) and were characterized by low energy reserves (Table 5) and low food consumption as indicated by the dimensions of the digestive tract (Table 4). There are no ready explanations for these phenomena, although it is tempting to suggest that male *P. maniculatus* in the Kananaskis may be exhibiting a tendency towards semelparity. Millar and Innes (1983) found that yearling females survived the subsequent winter better than yearling males (4 of 6 vs. 0 of 8, respectively). This survival pattern, coupled with the apparent poor nutritional status of postbreeding males, resembles that in the semelparous marsupial mouse, *Antechinus stuartii* (Tyndale-

Biscoe 1979; Lazenby-Cohen and Cockburn 1988), where males show signs of physiological senility leading to death after intense competition during their first mating season.

Finally, none of the breeding mice showed significant differences in the quality of food consumed, which may indicate that all mice are restricted to a limited range of food quality. Sadleir *et al.* (1973) also found no differences in food quality (protein/caloric ratios) among reproductive classes of deer mice. However, it must be recognized that fibre content is by no means a complete measure of food quality. Many mammals appear to select foods based on levels of digestive inhibitors as well as protein and fibre content (Batzli 1983; Bergeron and Jodoin 1987; Sinclair *et al.* 1982), and more detailed assessments of food quality may be necessary to reveal real differences in food choice among breeding mice.

In spite of these difficulties in interpreting differences in resource utilization based on these indices, the results were sufficiently consistent with expected patterns to warrant further investigation. Careful use of these indicators can provide insights into the relationships between food resources and reproductive patterns.

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