The Nutritional Ecology of Meadow Voles (*Microtus pennsylvanicus*) under Differing Environmental Conditions

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Thesis presented to the Faculty of Virginia
Polytechnic Institute and State University
in partial fulfillment of the requirements

Master of Science
in
Biology

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July 20, 2000
Blacksburg, Virginia

Keywords: nutrition, gastrointestinal morphology, fiber, voles

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(ABSTRACT)

The simultaneous effects of dietary fiber, temperature, and daylength on the gastrointestinal morphology and physiology in meadow voles (*Microtus pennsylvanicus*) were investigated. Voles were randomly divided (10 in each group) and placed in 15-day treatment regimes [cold (5° C) and warm (21° C), daylengths long (18L:6D) and short (6L:18D), and diets of high fiber (50% neutral detergent fiber [NDF]) and low fiber (5% NDF) content] followed by a 5-day digestibility trial to determine diet digestibility in relation to food intake. Total mass of individuals, length, wet mass and dry mass of the stomach, small intestine, caecum, large intestine, adrenal glands, liver, and kidneys was evaluated. Data was analyzed by ANOVA using the SAS system.

Meadow voles increased food intake but decreased turnover time and digestive efficiency under low ambient temperature condition, short daylength, and/or high dietary fiber. Increased energy demand had a minimal effect on the gastrointestinal tissue mass but resulted in slightly increased length of all tissues except the small intestine. The increased food intake and small changes to gastrointestinal morphology during times of increased energy demands suggest that meadow voles are able to meet their energy needs primarily through increased food intake, and therefore more energetically expensive gastrointestinal changes are minimized.

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Introduction

Meadow voles (*Microtus pennsylvanicus*) are small herbivores that consume foods of very low nutritional quality in winter (Batzli and Cole 1979, Cole and Batzli 1978, Goldberg *et al* 1980, Batzli 1985). They have the widest geographic distribution of any species of *Microtus* (Reich 1981) and remain active throughout the year even though their energy needs are elevated under cold ambient air temperatures and low-quality diets (Wunder 1978, 1985). Other small- to moderate-sized herbivores and gramnivores living in cold climates either hibernate or are capable of short bouts of torpor. Yet meadow voles do not have a physiological capacity for torpor or hibernation. In winter, the vegetative parts of plants undergo seasonal senescence, becoming much lower in quality (i.e. energy content as the relative fiber content increases (Van Soest 1982). As a consequence of their small body size and high mass-specific metabolic rates, meadow voles are particularly susceptible to these changes in nutrient and energy availability (Batzli 1985).

Increased food intake can partially or fully compensate for low-quality, high-fiber food (low digestibility or low-nutrient content) such that the energy and nutrient requirements of these mammals may still be met (Innes and Millar 1981, Derting and Bogue 1993). However, this compensation is not always sufficient to maintain energy balance, and there are indications that the quality of available forage may be correlated with seasonal differences in vole population densities (Batzli 1985). Because their reproductive season is temporally linked to the availability of higher-quality food, seasonal changes in density (population increases during the reproductive season and declines during the non-breeding season) may also be a function of dietary quality and overall nutritional status (Batzli and Pitelka 1969, 1970, Cole and Batzli 1978, Batzli 1985). Therefore, voles must use adaptations which increase the amount of energy and nutrients obtained from their low-quality diet if population numbers are to remain relatively stable (Hammond and Wunder 1991).

Voles have three options for maintaining the digestibility of their low-quality diet during times of high-energy need. They may change the composition of their diet, they

may increase food intake, or modify their gastrointestinal morphology or physiology to meet their increased energy needs. These options need not be mutually exclusive; and they may use a combination of these strategies to compensate for declining diet quality and nutrient availability (Hammond and Wunder 1991, Derting and Bogue 1993). For example, under moderate energy demands (40-50% increase in BMR), meadow voles (*M. pennsylvanicus*) increased food intake and increased mucosal mass of the small intestine and caecum, but gastrointestinal tissue length was not affected (Derting and Bogue 1993). Under extreme environmental conditions (high dietary fiber and low temperature) however, prairie voles (*M. ochrogaster*) exhibited increased gastrointestinal tissue mass and length (Hammond and Wunder 1991).

Reports of many mammals from boreal regions, having lower body masses in winter than in summer are common (Schwarz 1964, Sealander 1966, Fuller *et al* 1969, Brown 1973). In field studies with marked individuals it has been shown that meadow voles lose mass and/or decrease growth rates in winter (Barbehenn 1955, Brown 1973, Iverson and Turner 1974). Iverson and Turner (1974) found that male meadow voles lost 29 percent and females 46 percent of their body mass between August and February. Barbehenn (1955) found that meadow voles lost 15-20 percent of their body mass over a similar winter period. Meadow voles born in middle to late summer stop growing in the fall, maintain their weight and linear dimensions through the winter, and then resume growth in the spring (Brown 1973). Several proximate factors during winter could be important in causing or cueing such changes. Two factors that negatively affect growth (and hence the energy costs of it) are decreased food quality and an increased proportion of energy intake necessary for thermoregulation (Wunder 1985). Photoperiod may also directly affect growth. Pinter (1968) showed that photoperiod affected growth of montane voles (*M. montanus*) and Petterborg (1978) showed that photoperiod affects differential growth (and hence maturation) in different seasonal cohorts of this species. Pistole and Cranford (1982) found that photoperiod has an effect on growth in meadow voles and the affect differs by cohort age. In these studies, young animals on long-day photoperiods grew faster than animals on short-days and adult animals on long days maintained a higher body mass than those on short days. Furthermore, adults on short

days lost body mass, whereas those on long days resumed growth, or maintained high body mass. When animals in any treatment (long-to-short, short-to-long photoperiod) were switched to the alternate photic conditions their body mass dynamics were reversed to reflect their new photic environment. The energetic consequences of such changes are that animals on short days maintain lower body masses or have lower growth rates and require a lower energetic commitment to growth (Pinter 1968, Petterborg 1978, Pistole and Cranford 1982).

Several investigators have investigated the relationships between dietary fiber ingestion, photoperiod changes, and ambient temperature changes in relation to changes in body size and gut morphology (Schwarz 1964, Sealander 1966, Pinter 1968, Fuller *et al* 1969, Brown 1973, Iverson and Turner 1974, Petterborg 1978, Pistole and Cranford 1982, Hammond and Wunder 1991). However, none have examined the combined effects of these factors and relationships between them on the nutritional ecology of meadow voles.

This study investigated the simultaneous effects of dietary fiber level, ambient air temperature, and photoperiod on the food intake and gastrointestinal morphology in meadow voles. The specific hypotheses of this investigation were

Hypothesis 1: Increases in food intake rate are sufficient to overcome low to intermediate levels of energy demand (low diet quality, short photoperiod, *or* low temperature). The greatest increases should be in response to high dietary fiber levels rather than to the other variables.

Hypothesis 2: In situations where energy demand is high (high dietary fiber, short daylength, *and* low ambient temperature) increases in intake rate will be insufficient to meet energy requirements and changes in gastrointestinal morphology will be necessary. Changes in morphology of the gastrointestinal tract may be subtle and could well involve changes in physical length and/or mass and also changes in physiological function.

The results should demonstrate the potential for behavioral, morphological, and physiological changes that meadow voles may undertake to survive the conditions they are exposed to in a natural environment.

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Materials & Methods

The experimental animals were herbivorous meadow voles (*M. pennsylvanicus*) which eat primarily the vegetative parts of plants (Batzli 1985). Meadow voles were captured from old fields on the Observatory area (off Prices' Fork Road) of the campus of Virginia Polytechnic Institute and State University (Virginia Tech). Sherman live traps were placed in vole runways and traps were covered with grass and loose material to reduce exposure to ambient air temperatures. Traps were checked every 4-6 hours to minimize the amount of time animals were confined in traps. Upon capture, animals were weighed (Pesola 50 g balance, ±0.1 g) and ear-tagged for permanent identification, aged, sexed, and breeding condition was determined. Field-captured animals were housed in the lab for a minimum of 60 days prior to being used in experimental trials. Only adult (>25 g) males and females that were not pregnant or lactating for six weeks prior to an experimental trial were used. Subadults and lactating females were not used in this study because their gastrointestinal tracts may differ due to their increased energy needs for growth or lactation (Gebczynska and Gebczynski 1971).

Experimental Design

The experiment was a completely randomized design with three treatments (temperature, daylength, dietary fiber level) arranged in a factorial layout. One hundred twelve meadow voles were randomly assigned to one of two groups of 56 animals each corresponding to two levels of diet quality. Fiber content was used as the low-quality component variable in the diets: high fiber (50% crude fiber) and low fiber (5% fiber). Each of the diet treatments was then subdivided into two levels of ambient air temperature exposure: warm (21±1° C) or cold (5±1° C). These subgroups were further subdivided into two levels of daylight exposure: long daylength (16L:8D) and short daylength (8L:16D). This resulted in the assignment of 14 animals to each combination of dietary fiber, ambient temperature, and daylength, across a total of 8 experimental trials (Table 1).

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Table 1. Experimental design with 8 trials consisting of all combinations of high (50%) and low (5%) dietary fiber, high (21°C) and low (5°C) ambient temperature, and long (16L:8D) and short (8L:16D) daylength.

Trial	Fiber level (%)	Temperature (°C)	Daylength (hours)
1	50	21	16
2	50	5	16
3	50	21	8
4	50	5	8
5	5	21	16
6	5	5	16
7	5	21	8
8	5	5	8

Diets were prepared from purchased ingredients of known quality (Table 2) in consultation with an animal nutritionist, Dr. K. E. Webb (Virginia Tech). Diets were similar in composition (percent by mass, Ainsworth MX400 ±0.01 g) except for the crude fiber/sucrose ratio (Table 2). Diets were in powdered form to decrease the potential for sorting of high-quality and low-quality components (Peterson and Wunder 1997). Food was available *ad lib* and placed in truncated cone-shaped feeding jars to decrease spillage and soiling of food by animal feces and urine.

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Table 2. Components and composition (percent by mass) of the two experimental diets utilized in the diet trials for meadow voles.

	Diet Type	
	5% Fiber	50% Fiber
Sodium Caseinate (US Biochemical #12865)	20	20
Corn Starch (CPC Foodservice)	15	15
Corn Oil (CF Sauer Foodservice)	5	5
Mineral Mix (Teklad AIN-76)	4	4
Vitamin Mix (Teklad AIN-76A)	1	1
Cellulose (Teklad #160390)	5	50
Granulated Sugar (Dixie Crystals)	50	5
Total	100	100

The crude fiber levels (5% and 50%) were chosen as extreme, but biologically reasonable levels, with the expectation they could induce a measurable change in gut morphology. Batzli and Cole (1979) showed that, under ambient temperatures of 21-27° C and 12L:12D daylength, dietary fiber content must be above 50% before voles were unable to compensate for low-quality diets by increasing food intake. An ambient temperature of 5°C constitutes a thermoregulatory stress (metabolic costs are more than double those in thermoneutrality) for prairie voles (*M. ochrogaster*) (Wunder *et al* 1977) and field voles (*M. agrestis*) (McDevitt and Speakman 1994) under laboratory conditions. Long (16L:8D) and short (8L:16D) daylength were chosen to simulate summer and winter photoperiodicity respectively. One trial (n=8) was conducted under laboratory animal maintenance condition (23°C, 14L:10D) using ground rodent chow to establish a baseline conditions for the animals in the trials (See appendix 1).

Animals were housed in mesh-bottomed cages without nesting material and maintained on their respective treatments for a 24-day period consisting of a four-day period to acclimate to the experimental diet followed by a 20-day diet trial. During the four-day acclimation period voles were given ground rodent chow for two days and a

50:50 mix of ground rodent chow and experimental diet for two days, then switched to the experimental diet for the 20-day diet trial. Food intake rate was measured and feces were collected during the last five days of the diet trial following the 15-day adjustment period. The adjustment period length was chosen because prairie voles have been reported to make significant adjustments in their gastrointestinal morphology due to increased energy need or decreased energy availability (Gross *et al* 1985). Since meadow voles require 12-15 days to wean their young (Reich 1991), they would have to make gastrointestinal adaptations to meet those increased energy demands of lactation within that period of time. Lactating prairie voles (*M. ochrogaster*) have significantly longer small and large intestines than those of either pregnant or non-pregnant, non-lactating animals (Wunder 1992).

Animals were weighed daily using an Ainsworth MX400 balance (±0.01g). Because digestive efficiency calculations assume animal maintain a constant body mass over a discrete interval, any animals with mass losses in excess of 15% from their initial body mass during any part of the study were removed from the trial. Animals were sacrificed by cervical dislocation at the end of each trial. All groups were sacrificed at the same time of day (two hours after lights on) to control for differences in gastrointestinal fill associated with cyclic feeding patterns (Johnson 1982).

Digestibility calculations

To determine the extent by which food intake and diet digestibility changed to accommodate for increased energy demands, measurements to assess gross rates of energy utilization were made (following methods of Derting and Bogue 1993). Food ingestion measurements (food removed from feeder minus spilled food) using standard gravimetric techniques (Drozdz 1975) were made using an Ainsworth MX400 balance (±0.01g). Feces were collected daily during the last five study days. Spilled food was analyzed by bomb calorimetry (Parr Model 1271) and its energy content was compared to that of the starting experimental diets to determine if the animals were able to sort the food into high- and low-quality components and thereby alter the intake composition

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(Peterson and Wunder 1997). Energy intake was calculated as the dry mass of food ingested (grams/day) multiplied by the energy equivalent of the food (kJ/g) as indicated by calorimetry. The apparent digestive coefficient (ADC) was calculated using dry masses as:

$$\frac{\text{Mass of food ingested} - \text{Mass of feces produced}}{\text{Mass of food ingested}} \times 100$$

Digested energy (kJ/day) was then calculated as the product of energy intake and apparent digestive coefficient. Dietary turnover time was estimated as the total mass of gastrointestinal tract contents (g) divided by the rate of food ingestion (Hammond and Wunder 1991). This calculation provided an estimate of the amount of time that food is retained in the gut and, thus, the processing time for one complete gut volume of food (Derting and Bogue 1993).

Measurements of Morphological Changes

The following measurements were made on each experimental animal: total body mass, gastrointestinal tract (GIT) wet mass with and without digesta, GIT length, and GIT dry mass. The components of the gastrointestinal tract measured were the stomach, small intestine (from the pyloric sphincter of the stomach to the ileocecal valve), cecum (from the ileocecal valve to the spiral valve), and large intestine (distal cecum to anus) (Hammond and Wunder 1991). Wet and dry mass of the adrenal glands, liver, and kidneys were also measured. The wet mass with and without contents for each section of the gastrointestinal tract was determined using a Mettler Analytical Balance AE260 (±0.0001 g). Wet mass was obtained immediately upon dissection after the tissue was blotted dry. To determine the mass without contents, each gastrointestinal section was opened lengthwise, and the contents removed by saline flushing. The tissue was then blotted dry and weighed again. Content mass was calculated as the difference between gastrointestinal section mass with contents and its mass without contents. The intact length of gastrointestinal tract sections without contents was determined to the nearest

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mm by gently straightening (without stretching) and lying flat each section of tissue along a metric ruler. The method used for measuring the length of gastrointestinal tract sections was the same as used by several researchers (Leopold 1953, Gross *et al* 1985, Hammond and Wunder 1991, Derting and Bogue 1993). The dry mass of organs and tissues was obtained after placing the emptied organs in an oven at 60 C for at least 48 hours (Derting and Bogue 1993). The mass of the liver and kidneys were measured to determine if these organs changed in response to increased energy demands (Konarzewski and Diamond 1994, Hammond and Wunder 1995).

Statistical Analysis

The effects of experimental variables was analyzed across all treatment groups separately for animals acclimated to high temperature and low temperature by comparing all pairs using Tukey-Kramer Honestly Significant Difference ($p<0.05$). These results are reported in Tables 2-9 with means ± SEM. Data was also analyzed for effects of independent variables and for multivariate interactions between variables using ANOVA ($p<0.05$). All statistics were analyzed using a PC version of JMP Statistics (SAS Institute 1996).

Results

Changes in diet digestibility and in gastrointestinal system and accessory organ morphology of meadow voles were measured and compared by univariate and multivariate analysis across all treatments as listed below.

Univariate comparisons across all treatments

<u>Body mass, energy utilization, and food processing</u>

Meadow voles in high ambient temperature showed no significant difference in body mass during the experiment regardless of dietary fiber level or daylength (Table 2a). Food intake and fecal production were measured during the digestive trial phase of the experiment and both variables were scaled to final body mass to permit direct comparisons. Food intake ($F_{1,42}$=70.83, p<0.0001) and fecal production ($F_{1,42}$=530.93, p<0.0001) were both significantly higher in meadow voles fed the high fiber diet (Table 2a, Figure 1). Turnover time did not differ by dietary fiber or daylength, however, the apparent digestive coefficient (ADC) for voles fed a low fiber diet was approximately double (low fiber, 87.95±1.36 %; high fiber, 44.50±1.36 %) that of those fed a high fiber diet ($F_{1,42}$=513.54, p<0.0001) (Table 2a, Figure 2).

Table 2a. Means (± 1 SE) from differing dietary fiber level and daylength on body mass, energy utilization, and food processing in meadow voles (*M. pennsylvanicus*) under high ambient temperature (23 °C). Within a category, means followed by different letters are significantly different (Tukey-Kramer HSD, p<0.05)

	5% fiber		50% fiber	
	16L:8D (n=9)	8L:16D (n=12)	16L:8D (n=10)	8L:16D (n=11)
Initial body mass (g)	30.76 ± 2.20	28.93 ± 0.52	31.52 ± 1.35	33.83 ± 1.32
Final body mass (g)	31.04 ± 1.04	28.56 ± 0.57	30.83 ± 0.98	32.07 ± 1.47
Body mass change (g)	0.29 ± 1.13[A]	-0.37 ± 0.98[A]	-0.69 ± 1.07[A]	-1.75 ± 1.02[A]
Feces (g/day)*	0.0873 ± 0.03[A]	0.0920 ± 0.03[A]	0.6611 ±0.03[B]	0.6831 ± 0.03[B]
Food intake (g/day)*	0.7582 ± 0.06[A]	0.7594 ± 0.05[A]	1.1634 ± 0.06[B]	1.1912 ± 0.06[B]
Turnover time (hrs)	15.78 ± 1.27[A]	13.56 ± 1.10[A]	11.67 ± 1.21[A]	10.08 ± 1.15[A]
Digestive efficiency	88.10 ± 1.81[A]	87.85 ± 1.57[A]	44.04 ± 1.72[B]	44.91 ± 1.64[B]

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Meadow voles in low ambient temperature exhibited no significant changes in body mass when compared to all other groups regardless of dietary fiber or daylength (Table 2b). Voles on short daylength gained mass ($F_{1,42}=10.22$, p=0.003) and those on long daylength lost mass ($F_{1,42}=5.98$, p=0.02) on the high fiber diet compared to animals in all other treatments (Table 2b). Food intake was higher ($F_{1,42}=36.33$, p<0.0001) on high fiber regardless of daylength (Table 2b, Figure 1). Fecal production differed among all four treatments ($F_{3,42}=358.04$, p<0.0001) with production lowest on low fiber and long daylength and highest on high fiber and long daylength (Table 2b, Figure 1).

Dietary turnover time did not differ regardless of diet or daylength (Table 2b, Figure 2). Apparent digestive coefficients differed with daylength among those fed the low fiber diet ($F_{1,19}=34.81$, p<0.0001), with the efficiency on short daylength being lower (short daylength, 73.90±0.75 %; long daylength, 85.69±1.45 %). Apparent digestive coefficients were almost four times lower for voles on the high fiber diet ($F_{1,42}=1057.41$, p<0.0001) (low fiber, 81.35±1.64 %; high fiber, 22.01±0.94 %) (Table 2b, Figure 2).

Table 2b. Means (± 1 SE) from differing dietary fiber level and daylength on body mass, energy utilization, and food processing in meadow voles (*M. pennsylvanicus*) under low ambient temperature (5 °C). Within a category, means followed by different letters are significantly different (Tukey-Kramer HSD, p<0.05).

	5% fiber		50% fiber	
	16L:8D (n=12)	8L:16D (n=7)	16L:8D (n=10)	8L:16D (n=12)
Initial body mass (g)	39.91 ± 1.79	36.03 ± 4.03	38.75 ± 1.38	38.15 ± 1.60
Final body mass (g)	39.58 ± 1.40	36.40 ± 3.20	36.29 ± 1.32	41.74 ± 1.19
Body mass change (g)	-0.33 ± 0.98[ABC]	0.37 ± 1.28[ABC]	-2.46 ± 1.07[AB]	3.59 ± 0.98[AC]
Feces (g/day)*	0.1480 ± 0.03[A]	0.2991 ± 0.04[B]	1.5067 ± 0.03[C]	1.2398 ± 0.03[D]
Food intake (g/day)*	1.07 ± 0.05[A]	1.17 ± 0.07[A]	1.84 ± 0.06[B]	1.73 ± 0.05[B]
Turnover time (hrs)	11.23 ± 1.10[A]	10.83 ± 1.45[A]	9.48 ± 1.21[A]	11.41 ± 1.10[A]
Digestive efficiency	85.69 ± 1.57[A]	73.90 ± 2.06[B]	23.20 ± 1.72[C]	21.01 ± 1.57[C]

*Values are expressed per gram final body mass

Figure 1. Amounts of food eaten and feces produced by meadow voles on treatments of high (21 C) or low (5 C) ambient temperature, high (50%) or low (5%) dietary fiber level, and long (16L:8D) or short (8L:16D) photoperiod. Error bars = 1 SEM.

	5- 5- 8	5- 5-16	5-50- 8	5-50-16	21- 5- 8	21- 5-16	21-50- 8	21-50-16
■ Eaten	1.17	1.07	1.73	1.84	0.76	0.76	1.19	1.16
▨ Feces	0.30	0.15	1.24	1.51	0.09	0.09	0.68	0.66
N =	7	12	12	10	12	9	11	10
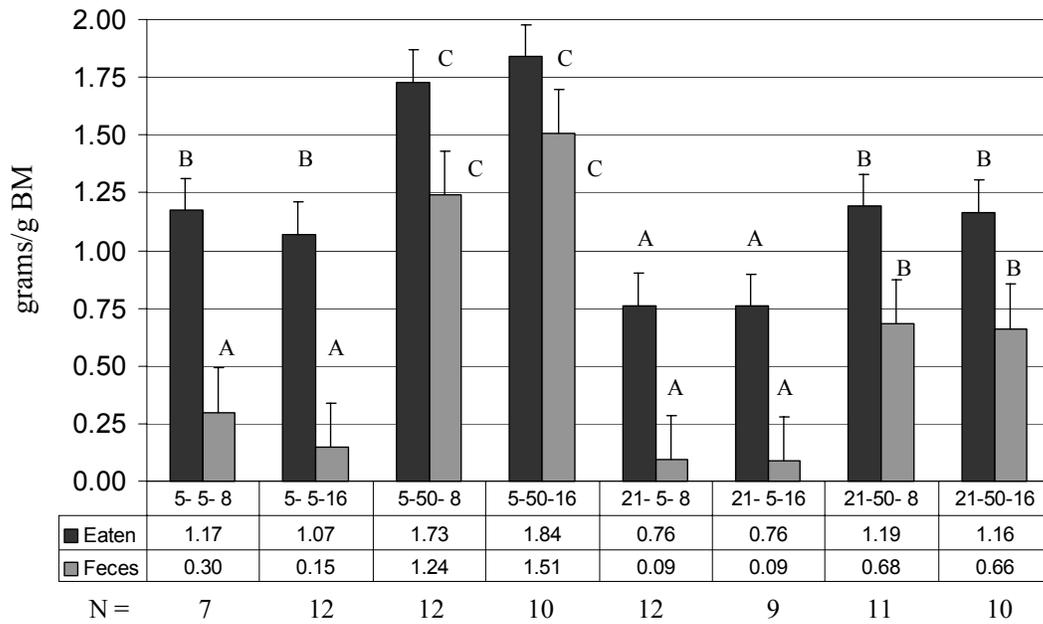
Figure 2. Turnover time and digestive efficiency of meadow voles on treatments of high (21 C) or low (5 C) ambient temperature, high (50%) or low (5%) dietary fiber level, and long (16L:8D) or short (8L:16D) photoperiod. Error bars = 1 SEM.

	5- 5- 8	5- 5-16	5-50- 8	5-50-16	21- 5- 8	21- 5-16	21-50- 8	21-50-16
■ TO time	10.83	11.24	11.41	9.48	13.56	15.78	10.08	11.67
▨ Dig Eff %	73.90	85.69	21.01	23.20	87.85	88.10	44.91	44.04
N =	7	12	12	10	12	9	11	10

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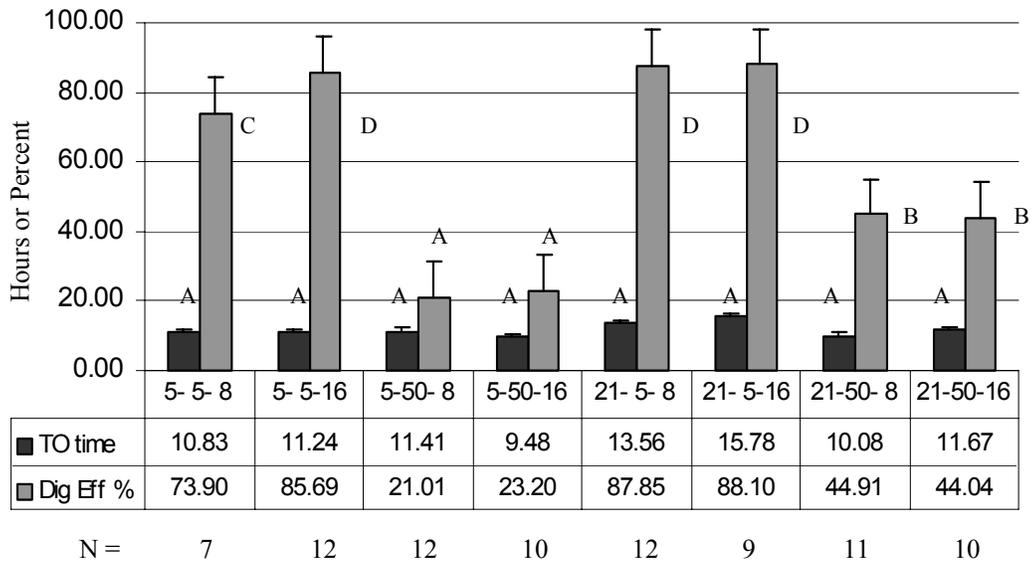
Mass of gastrointestinal tissue

Stomach wet or dry masses did not differ on high temperature regimes regardless of dietary fiber level or daylength (Table 3a, Figures 3 and 4). Small intestine wet mass was lowest on low fiber and long daylength ($F_{1,42}$=35.23, p<0.0001). The small intestine dry mass of each group did not differ significantly from that of the voles fed the high fiber diet and acclimated to long DL. Small intestine dry mass on long daylength was similar, but lower than that of then short daylength condition ($F_{1,42}$=9.99, p=0.003). Small intestine dry mass was lower on low fiber and long daylength ($F_{3,42}$=12.61, p=0.001) (Table 3a, Figure 4). Caecal wet or dry mass did not differ regardless of dietary fiber level or daylength (Table 3a, Figures 3 and 4). There was no effect of dietary fiber level or daylength on large intestine wet mass, although dry mass was significantly higher on short daylength and high fiber ($F_{3,42}$=6.68, p=0.001) (Table 3a, Figures 3 and 4).

Table 3a. Means (± 1 SE) from dietary fiber level and daylength on wet and dry mass of the gastrointestinal system of meadow voles (*M. pennsylvanicus*) under high ambient temperature (23 °C). Within a category, means followed by different letters are significantly different (Tukey-Kramer HSD, p<0.05). All values are expressed per gram final body mass.

	5% fiber		50% fiber	
	16L:8D (n=9)	8L:16D (n=12)	16L:8D (n=10)	8L:16D (n=11)
Wet Mass				
Stomach	0.0115 ± 0.0007[A]	0.0106 ± 0.0006[A]	0.0110 ± 0.0006[A]	0.0093 ± 0.0006[A]
Small Int.	0.0188 ± 0.001[A]	0.0301 ± 0.001[B]	0.0293 ± 0.001[B]	0.0290 ± 0.001[B]
Caecum	0.0222 ± 0.002[A]	0.0164 ± 0.002[A]	0.0178 ± 0.002[A]	0.0202 ± 0.002[A]
Large Int.	0.0113 ± 0.001[A]	0.0097 ± 0.001[A]	0.0101 ± 0.001[A]	0.0137 ± 0.001[A]
Dry Mass				
Stomach	0.0024 ± 0.0001[A]	0.0022 ± 0.0001[A]	0.0024 ± 0.0001[A]	0.0021 ± 0.0001[A]
Small Int.	0.0040 ± 0.0003[AC]	0.0058 ± 0.0003[BC]	0.0049 ± 0.0003[ABC]	0.0051 ± 0.0003[BC]
Caecum	0.0040 ± 0.0004[A]	0.0028 ± 0.0003[A]	0.0033 ± 0.0003[A]	0.0036 ± 0.0003[A]
Large Int.	0.0019 ± 0.0002[A]	0.0018 ± 0.0002[A]	0.0019 ± 0.0002[A]	0.0026 ± 0.0002[B]

Stomach wet ($F_{1,42}$=9.07, p=0.005) and dry mass ($F_{1,42}$=15.14, p=0.0004) on low temperature was higher on high fiber and short daylength (Table 3b. Figures 3 and 4). Small intestine wet mass was lower on high fiber and short daylength ($F_{3,42}$=44.75, p<0.0001) as was dry mass ($F_{1,42}$=17.85, p<0.0001). Small intestine dry mass did not significantly differ, regardless of diet, on long daylength but was significantly higher than the high fiber and short daylength group ($F_{1,42}$=27.28, p<0.0001). Caecal wet mass ($F_{3,42}$=8.89, p=0.0001), and dry mass ($F_{3,42}$=11.39, p<0.0001), and large intestine wet mass ($F_{3,42}$=183.19, p<0.0001), and dry mass ($F_{3,42}$=113.44, p<0.0001) all were significantly higher on high fiber and short daylength (Table 3b, Figures 3 and 4).

Table 3b. Means (± 1 SE) from dietary fiber level and daylength on wet and dry mass of the gastrointestinal system of meadow voles (*M. pennsylvanicus*) under low ambient temperature (5 °C). Within a category, means followed by different letters are significantly different (Tukey-Kramer HSD, p<0.05). All values are expressed per gram final body mass.

	5% fiber		50% Fiber	
	16L:8D (n=12)	8L:16D (n=7)	16L:8D (n=10)	8L:16D (n=12)
Wet mass				
Stomach	0.0098 ± 0.0006^{AC}	0.0117 ± 0.0008^{AC}	0.0108 ± 0.0006^{AC}	0.0123 ± 0.0006^{BC}
Small Int.	0.0220 ± 0.001^{A}	0.0208 ± 0.001^{A}	0.0234 ± 0.001^{A}	0.0141 ± 0.002^{B}
Caecum	0.0172 ± 0.002^{A}	0.0182 ± 0.002^{A}	0.0179 ± 0.002^{A}	0.0252 ± 0.002^{B}
Large Int.	0.0093 ± 0.001^{A}	0.0114 ± 0.001^{A}	0.0101 ± 0.001^{A}	0.0296 ± 0.001^{B}
Dry mass				
Stomach	0.0025 ± 0.0001^{ABC}	0.0023 ± 0.0002^{AB}	0.0022 ± 0.0001^{AB}	0.0030 ± 0.0001^{AC}
Small Int.	0.0055 ± 0.0003^{AC}	0.0044 ± 0.0004^{BC}	0.0047 ± 0.0003^{ABC}	0.0031 ± 0.0003^{D}
Caecum	0.0036 ± 0.0003^{A}	0.0033 ± 0.0004^{A}	0.0033 ± 0.0003^{A}	0.0051 ± 0.0003^{B}
Large Int.	0.0023 ± 0.0002^{A}	0.0022 ± 0.0002^{A}	0.0021 ± 0.0002^{A}	0.0065 ± 0.0002^{B}

Figure 3. Wet mass of emptied GI tissues of meadow voles on treatments of high (21 C) or low (5 C) ambient temperature, high (50%) or low (5%) dietary fiber level, and long (16L:8D) or short (8L:16D) photoperiod. Error bars = 1 SEM.

|	5- 5- 8	5- 5-16	5-50- 8	5-50-16	21- 5- 8	21- 5-16	21-50- 8	21-50-16
Large Int.	0.0114	0.0093	0.0296	0.0101	0.0097	0.0113	0.0137	0.0101
Caecum	0.0182	0.0172	0.0252	0.0179	0.0164	0.0222	0.0202	0.0178
Small Int.	0.0208	0.0220	0.0141	0.0234	0.0301	0.0188	0.0290	0.0293
Stomach	0.0117	0.0098	0.0123	0.0108	0.0106	0.0115	0.0093	0.0110
N =	7	12	12	10	12	9	11	10
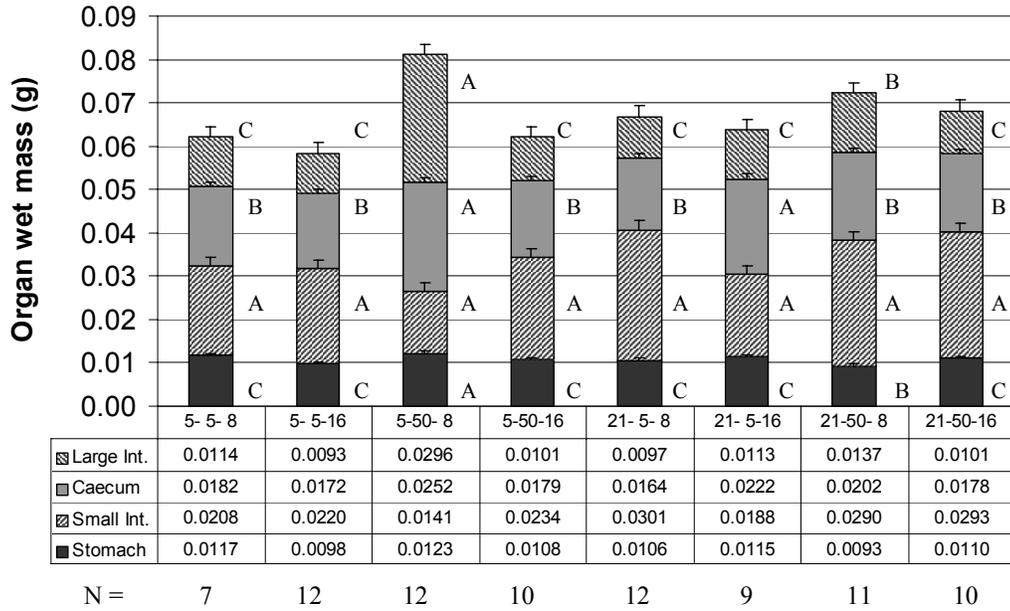
Figure 4. Dry mass of emptied GI tissues of meadow voles on treatments of high (21 C) or low (5 C) ambient temperature, high (50%) or low (5%) dietary fiber level, and long (16L:8D) or short (8L:16D) photoperiod. Error bars = 1 SEM.

	5- 5- 8	5- 5-16	5-50- 8	5-50-16	21- 5- 8	21- 5-16	21-50- 8	21-50-16
Large Int.	0.0022	0.0023	0.0065	0.0021	0.0017	0.0019	0.0026	0.0019
Caecum	0.0032	0.0036	0.0051	0.0033	0.0028	0.0040	0.0036	0.0033
Small Int.	0.0044	0.0055	0.0031	0.0047	0.0058	0.0039	0.0051	0.0049
Stomach	0.0023	0.0025	0.0029	0.0022	0.0022	0.0024	0.0021	0.0024
N =	7	12	12	10	12	9	11	10
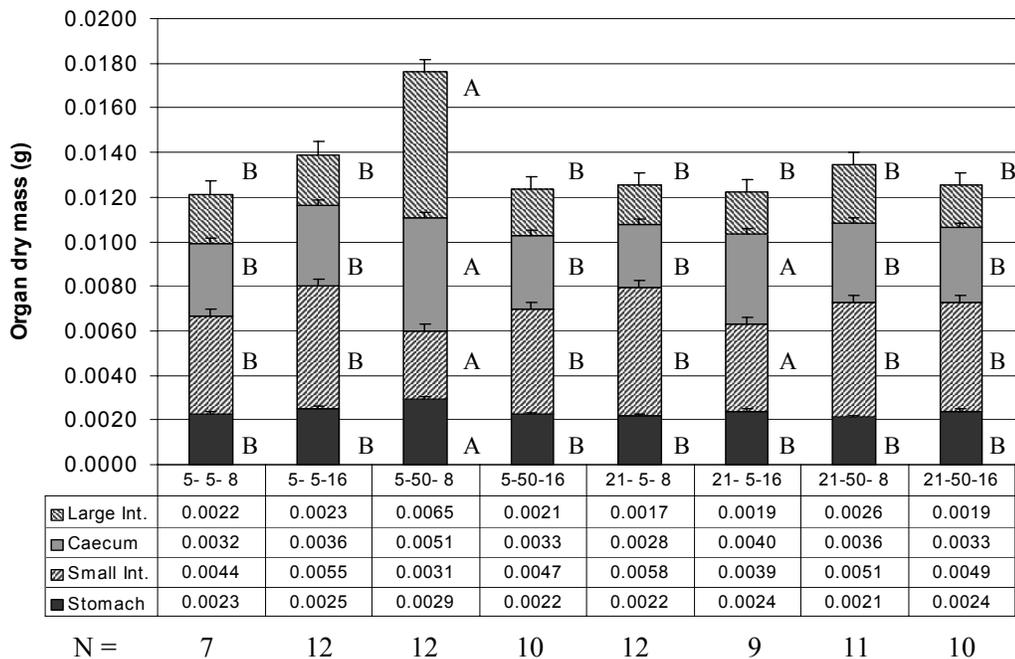
<u>Mass of gastrointestinal contents</u>

Stomach content mass on high temperature was greatest ($F_{1,42}$=30.93, p<0.0001) on high fiber regardless of daylength. Stomach content mass was greatest on high fiber and long daylength ($F_{3,42}$=12.37, p<0.0001) (Table 4a, Figure 5). Small intestine or caecal content mass did not differ regardless of diet or daylength (Table 4a, Figure 5). Large intestine content mass in short daylength was highest on the high fiber diet ($F_{1,42}$=5.56, p=0.02) and lowest on low fiber ($F_{1,42}$=6.09, p=0.02) (Table 4a, Figure 5).

Table 4a. Means (± 1 SE) from dietary fiber level and daylength on mass of contents and length of the gastrointestinal system of meadow voles (*M. pennsylvanicus*) under high ambient temperature (23 °C). Within a category, means followed by different letters are significantly different (Tukey-Kramer HSD, p<0.05). Mass of contents is expressed per gram final body mass.

|	5% fiber		50% fiber	
	16L:8D (n=9)	8L:16D (n=12)	16L:8D (n=10)	8L:16D (n=11)
Contents (g)				
Stomach	0.0119 ± 0.002^{AB}	0.0074 ± 0.002^{AB}	0.0204 ± 0.002^{C}	0.0181 ± 0.002^{AC}
Small Int.	0.0179 ± 0.002^{A}	0.0166 ± 0.002^{A}	0.0222 ± 0.002^{A}	0.0202 ± 0.002^{A}
Caecum	0.0595 ± 0.009^{A}	0.0558 ± 0.007^{A}	0.0665 ± 0.008^{A}	0.0544 ± 0.008^{A}
Large Int.	0.0079 ± 0.002^{ABC}	0.0039 ± 0.001^{AB}	0.0050 ± 0.002^{ABC}	0.0087 ± 0.001^{BC}
Length (mm)				
Stomach	22.89 ± 0.83^{A}	22.58 ± 0.73^{A}	22.90 ± 0.80^{A}	23.73 ± 0.76^{A}
Small Int.	269.89 ± 10.78^{AC}	318.75 ± 9.34^{BC}	312.50 ± 10.23^{ABC}	313.09 ± 9.75^{ABC}
Caecum	198.44 ± 10.04^{AB}	191.00 ± 8.70^{A}	221.60 ± 9.53^{AB}	228.82 ± 9.08^{B}
Large Int.	184.67 ± 9.43^{AB}	193.08 ± 8.17^{AB}	222.80 ± 8.95^{ABC}	238.09 ± 8.53^{BC}

Stomach content mass on low temperature was highest on the high fiber diet and short daylength ($F_{1,42}$=13.01, p=0.001) (Table 4b, Figure 5). Small intestine content mass was similar on low fiber regardless of daylength, while on high fiber, long daylength was greater than on short daylength ($F_{1,42}$=25.88, p<0.0001) (Table 4b, Figure 5). Caecal content mass did not significantly differ by diet or daylength (Table 4b, Figure 5). Large intestine content mass was lower on low fiber regardless of daylength ($F_{1,42}$=36.81,

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p<0.0001). Large intestine content mass was highest on high fiber and short daylength
($F_{1,42}$=144.82, p<0.0001).

Table 4b. Means (± 1 SE) from dietary fiber level and daylength on mass of contents and
length of the gastrointestinal system of meadow voles (*M. pennsylvanicus*) under low
ambient temperature (5 °C). Within a category, means followed by different letters are
significantly different (Tukey-Kramer HSD, p<0.05). Mass of contents is expressed per
gram final body mass.

	5% fiber		50% Fiber	
	16L:8D (n=12)	8L:16D (n=7)	16L:8D (n=10)	8L:16D (n=12)
Contents (g)				
Stomach	0.0166 ± 0.002^{AB}	0.0109 ± 0.002^{AB}	0.0197 ± 0.002^{ABC}	0.0257 ± 0.002^{BC}
Small Int.	0.0219 ± 0.002^{A}	0.0236 ± 0.002^{AC}	0.0389 ± 0.002^{BC}	0.0089 ± 0.002^{C}
Caecum	0.0572 ± 0.007^{A}	0.0593 ± 0.010^{A}	0.0782 ± 0.008^{A}	0.0757 ± 0.007^{A}
Large Int.	0.0063 ± 0.001^{AB}	0.0087 ± 0.002^{ABC}	0.0142 ± 0.002^{BC}	0.0361 ± 0.001^{D}
Length (mm)				
Stomach	24.42 ± 0.73^{A}	25.57 ± 0.95^{A}	24.70 ± 0.80^{A}	25.67 ± 0.73^{A}
Small Int.	316.50 ± 9.34^{ABC}	293.57 ± 12.22^{AC}	334.50 ± 10.23^{AB}	274.33 ± 9.34^{C}
Caecum	234.58 ± 8.70^{ACD}	204.86 ± 11.38^{AD}	254.70 ± 9.53^{ABC}	268.50 ± 8.70^{BC}
Large Int.	226.75 ± 8.17^{A}	218.29 ± 10.70^{AC}	253.60 ± 8.95^{AB}	339.17 ± 8.17^{BC}

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Figure 5. Content mass of GI tissues of meadow voles on treatments of high (21 C) or low (5 C) ambient temperature, high (50%) or low (5%) dietary fiber level, and long (16L:8D) or short (8L:16D) photoperiod. Error bars = 1 SEM.

|	5- 5- 8	5- 5-16	5-50- 8	5-50-16	21- 5- 8	21- 5-16	21-50- 8	21-50-16
Large Int.	0.009	0.006	0.036	0.014	0.004	0.008	0.009	0.005
Caecum	0.059	0.057	0.076	0.078	0.056	0.059	0.054	0.067
Small Int.	0.024	0.022	0.009	0.039	0.017	0.018	0.020	0.022
Stomach	0.011	0.017	0.026	0.020	0.007	0.012	0.018	0.020
N =	7	12	12	10	12	9	11	10
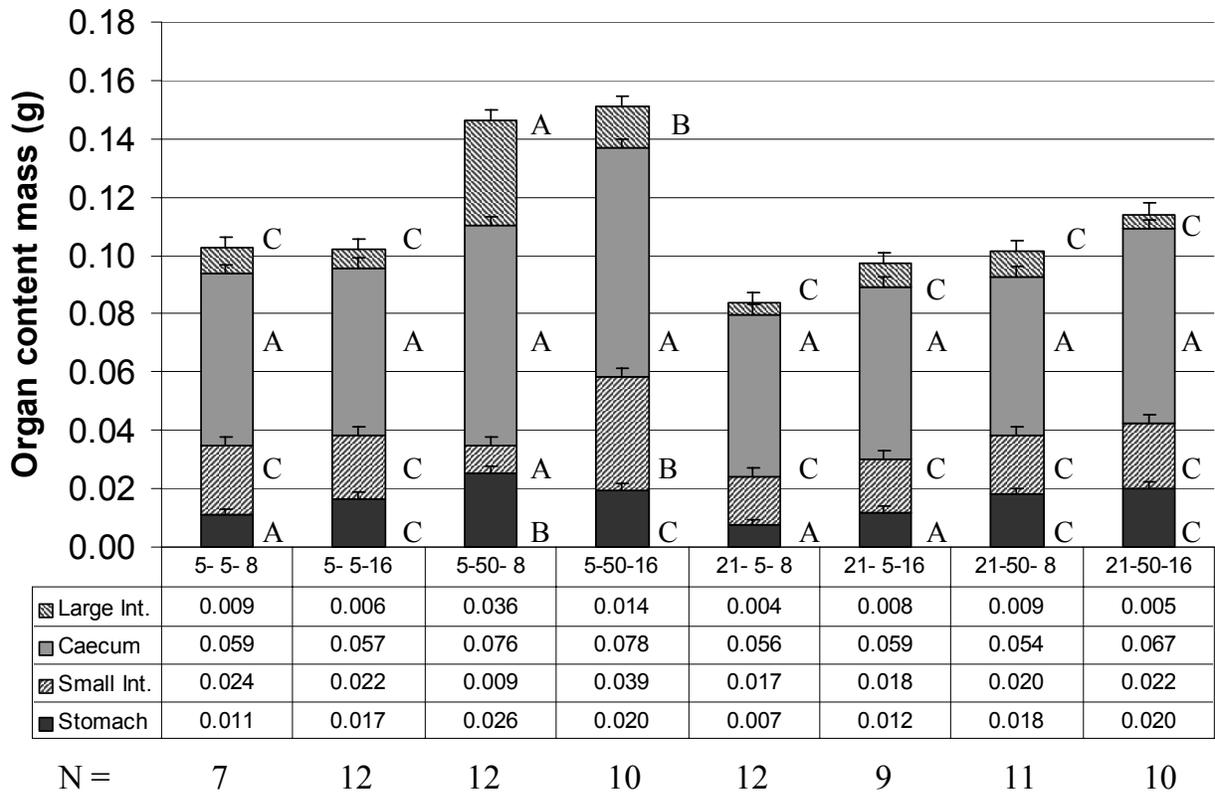
Length of gastrointestinal tissues

Voles acclimated to high temperature did not differ in stomach length regardless of diet or daylength (Table 4a, Figure 6). Small intestine length was shortest on low fiber and long daylength ($F_{1,42}=10.59$, p=0.002) (Table 4a, Figure 6). Caecal length was shortest on low fiber and short daylength ($F_{1,42}=4.78$, p=0.03) and longest on high fiber ($F_{1,42}=5.31$, p=0.03)and short daylength (Table 4a, Figure 6). Large intestine length on high fiber was significantly longer than on low fiber ($F_{1,42}=17.62$, p=0.0001). Large intestine length was longest on high fiber and short daylength ($F_{1,42}=9.90$, p=0.003) (Table 4a, Figure 6).

Stomach length under low temperature conditions was similar regardless of diet

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or daylength (Table 4b, Figure 6). Small intestines were longer on high fiber and long daylength ($F_{1,42}$=13.10, p=0.0008), and shorter on high fiber and short daylength ($F_{1,42}$=19.39, p<0.0001). Voles acclimated to long daylength had significantly longer small intestine tissue regardless of diet ($F_{1,42}$=26.74, p<0.0001) (Table 4b, Figure 6). Caecal length was longer on high fiber regardless of daylength ($F_{1,42}$=17.86, p=0.0001), but longest on short daylength and high fiber ($F_{1,42}$=10.04, p=0.003) (Table 4b, Figure 6). Longer large intestines were present in animals fed the high fiber diet ($F_{1,42}$=38.18, p<0.0001) or acclimated to short daylength ($F_{1,42}$=13.78, p=0.0006) (Table 4b, Figure 6).

Figure 6. Length (in mm) of emptied GI tissues of meadow voles on treatments of high (21 C) or low (5 C) ambient temperature, high (50%) or low (5%) dietary fiber level, and long (16L:8D) or short (8L:16D) photoperiod. Error bars = 1 SEM.

	5- 5- 8	5- 5-16	5-50- 8	5-50-16	23- 5- 8	23- 5-16	23-50- 8	23-50-16
Large Int.	218.29	226.75	339.17	253.60	193.08	184.67	238.09	222.80
Caecum	204.86	234.58	268.50	254.70	191.00	198.44	228.82	221.60
Small Int	293.57	316.50	274.33	334.50	318.75	269.89	313.09	312.50
Stomach	25.57	24.42	25.67	24.70	22.58	22.89	23.73	22.90
N =	7	12	12	10	12	9	11	10

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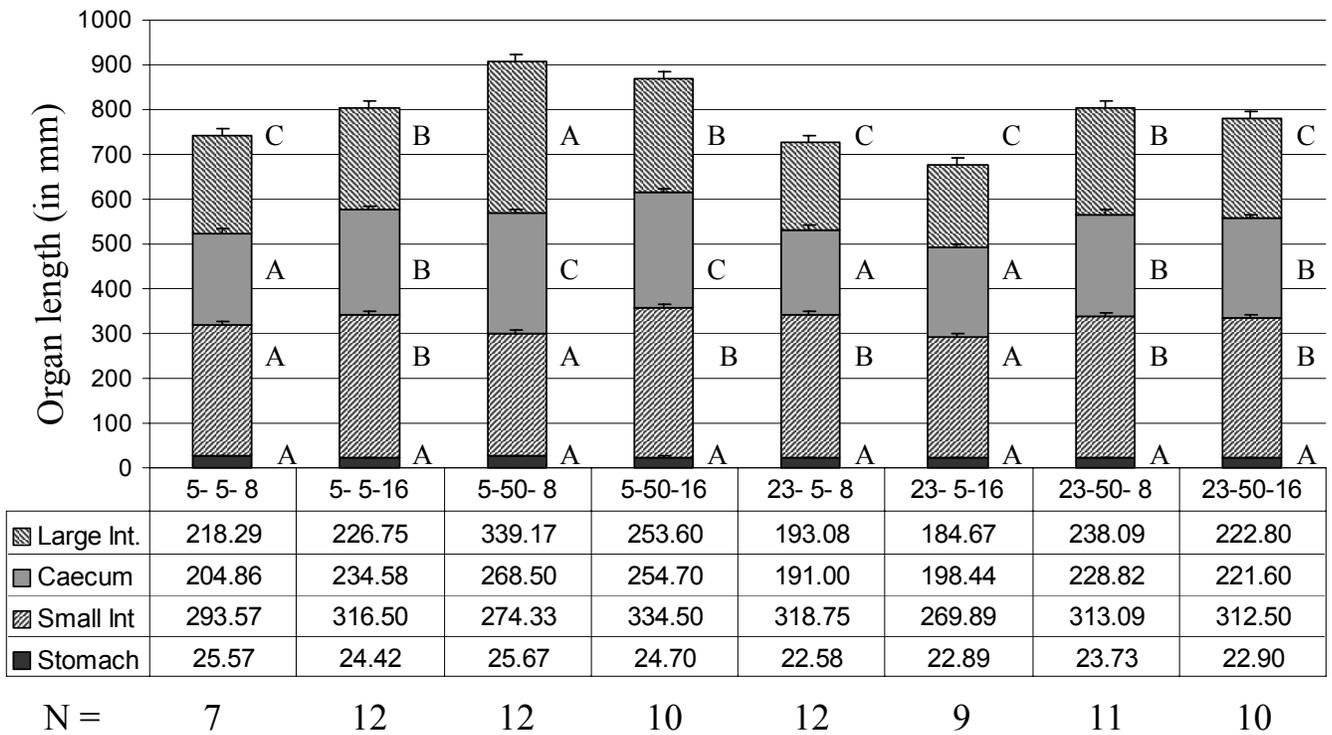
Mass of accessory organs

Liver wet ($F_{1,42}$=25.71, p<0.0001) and dry mass ($F_{1,42}$=28.19, p<0.0001) on high temperature was highest in animals fed the low fiber diet and acclimated to long daylength (Table 5a). Kidney wet mass was highest on low fiber and long daylength ($F_{1,42}$=13.29, p=0.0008). Kidney dry mass was highest on low fiber diet and long daylength ($F_{1,42}$=8.88, p=0.005), and lowest on high fiber and short daylength ($F_{1,42}$=7.11, p=0.01) (Table 5a). Adrenal gland wet mass did not differ regardless of diet or daylength. Adrenal gland dry mass was lower in voles fed the high fiber diet and acclimated to short daylength ($F_{1,42}$=8.40, p=0.006) (Table 5a).

Table 5a. Means (± 1 SE) from dietary fiber level and daylength on accessory organs of meadow voles (*M. pennsylvanicus*) under high ambient temperature (23 °C). Within a category, means followed by different letters are significantly different (Tukey-Kramer HSD, p<0.05). All values are expressed per gram final body mass.

	5% fiber		50% Fiber	
	16L:8D (n=9)	8L:16D (n=12)	16L:8D (n=10)	8L:16D (n=11)
Liver				
wet mass	0.0583 ± 0.003^{A}	0.0428 ± 0.002^{B}	0.0426 ± 0.002^{B}	0.0401 ± 0.002^{B}
dry mass	0.0178 ± 0.0008^{A}	0.0135 ± 0.0007^{B}	0.0137 ± 0.0007^{B}	0.0122 ± 0.0007^{B}
Kidney				
wet mass	0.0139 ± 0.0006^{AC}	0.0111 ± 0.0005^{BC}	0.0115 ± 0.0006^{ABC}	0.0113 ± 0.0006^{BC}
dry mass	0.0037 ± 0.0002^{AB}	0.0032 ± 0.0002^{ABC}	0.0033 ± 0.0002^{ABC}	0.0030 ± 0.0002^{AC}
Adrenal				
wet mass	0.0006 ± 0.0001^{A}	0.0007 ± 0.0001^{A}	0.0004 ± 0.0001^{A}	0.0004 ± 0.0001^{A}
dry mass	0.0002 ± 0.00003^{AB}	0.0002 ± 0.00003^{AB}	0.0002 ± 0.00003^{AB}	0.0001 ± 0.00003^{A}

Liver wet mass under low temperature conditions was highest on low fiber diet and short daylength ($F_{1,42}$=6.28, p=0.017) and lowest on high fiber diet and long daylength ($F_{1,42}$=19.20, p<0.0001) (Table 5b). Kidney wet mass was lowest on low fiber and long daylength ($F_{1,42}$=6.48, p=0.02) and highest on low fiber and short daylength ($F_{1,42}$=9.90, p=0.003). Kidney dry mass did not differ by diet or daylength (Table 5b). Adrenal gland wet mass was higher on short daylength regardless of diet ($F_{1,42}$=25.17, p<0.0001), but dry mass was higher on high fiber and short daylength ($F_{1,42}$=21.05, p<0.0001).

Table 5b. Means (± 1 SE) from dietary fiber level and daylength on accessory organs of meadow voles (*M. pennsylvanicus*) under high ambient temperature (5 °C). Within a category, means followed by different letters are significantly different (Tukey-Kramer HSD, p<0.05). All values are expressed per gram final body mass.

	5% fiber		50% Fiber	
	16L:8D (n=12)	8L:16D (n=7)	16L:8D (n=10)	8L:16D (n=12)
Liver				
wet mass	0.0518 ± 0.002[ABC]	0.0599 ± 0.003[AB]	0.0506 ± 0.002[AC]	0.0559 ± 0.002[ABC]
dry mass	0.0168 ± 0.0007[A]	0.0177 ± 0.0009[A]	0.0138 ± 0.0007[B]	0.0175 ± 0.0007[A]
Kidney				
wet mass	0.0117 ± 0.0005[AC]	0.0147 ± 0.0007[BC]	0.0136 ± 0.0006[ABC]	0.0130 ± 0.0005[ABC]
dry mass	0.0034 ± 0.0002[A]	0.0039 ± 0.0002[A]	0.0034 ± 0.0002[A]	0.0038 ± 0.0002[A]
Adrenal				
wet mass	0.0003 ± 0.00001[A]	0.0006 ± 0.00002[B]	0.0004 ± 0.0001[A]	0.0005 ± 0.0001[B]
dry mass	0.0002 ± 0.00003[A]	0.0002 ± 0.00003[A]	0.0001 ± 0.00003[A]	0.0004 ± 0.00003[B]

Multivariate comparisons

Body mass, energy utilization, and food processing

Meadow voles gained mass on short daylength and lost mass on long daylength ($F_{1,83}$=4.26, p=0.04). Body mass changes were also significantly affected by the interaction of temperature and daylength ($F_{1,83}$=8.55, p=0.005). Body mass changes on high temperature were similar regardless of daylength (short daylength, -1.06±0.72; long

daylength, -0.20±0.80), but under low temperature, meadow voles gained mass on short daylength (short daylength, 3.67±1.53 g; long daylength -1.40±0.74 g).

Both food intake and fecal production were higher on high fiber (intake, $F_{1,83}$=5.37, p=0.02; feces, $F_{1,83}$=173.19, p<0.0001) and long daylength (intake, $F_{1,83}$=17.40, p<0.0001; feces, $F_{1,83}$=5.37, p=0.02) and food intake was higher on low temperature ($F_{1,83}$=23.24, p<0.0001). Food intake was affected by the interaction of temperature and fiber ($F_{1,83}$=6.39, p=0.01) and temperature and daylength ($F_{1,83}$=6.47, p=0.01). There was a greater difference in the food intake of meadow voles under the two temperatures on the high fiber diet (low temperature, 1.68±0.04 g; high temperature, 1.18±0.05 g) than on the low fiber diet (low temperature, 0.90±0.11 g; high temperature, 0.76±0.05 g). Food intake under high temperature was unchanged regardless of daylength (short daylength, 0.98±0.05 g; long daylength, 0.96±0.05 g), but on low temperature, food intake was increased under long daylength (short daylength, 1.13±0.10 g; long daylength, 1.45±0.05 g). Fecal production was affected by the interactions of temperature and fiber ($F_{1,83}$=25.44, p<0.0001) and temperature and daylength ($F_{1,83}$=19.15, p<0.0001). Fecal production on high temperature was higher on the low fiber diet (low temperature, 0.05±0.02 g; high temperature, 0.09±0.02 g), but lower on the high fiber diet (low temperature, 1.20±0.05 g; high temperature, 0.67±0.05 g). Fecal production under high temperature was unchanged regardless of daylength (short daylength, 0.39±0.05 g; long daylength, 0.37±0.06 g), but under low temperature, production was higher on long daylength (short daylength, 0.21±0.11 g; long daylength, 0.83±0.05 g).

Dietary turnover time was shorter on the high fiber diet ($F_{1,83}$=5.30, p=0.02). Apparent digestive coefficients were higher on the low fiber diet ($F_{1,83}$=161.93, p<0.0001) and short daylength. ($F_{1,83}$=4.36, p=0.04) and were slightly affected by the interaction of temperature and fiber ($F_{1,83}$=4.49, p=0.037). Digestive efficiency under low temperature was higher on the low fiber diet (low temperature, 93.78±6.47 %; high temperature, 87.97±3.05 %), but lower on the high fiber diet (low temperature, 31.85±2.71 %; high temperature, 44.47±3.03 %).

Mass of gastrointestinal tissue

Stomach dry mass was higher under low temperature ($F_{1,83}$=6.84, p=0.01) and both wet and dry mass were significantly affected by the interaction of temperature and daylength (wet, $F_{1,83}$=6.09, p=0.02; dry, $F_{1,83}$=7.89, p=0.006). Stomach wet mass on low temperature was higher on short daylength (low temperature 0.0119±0.0009 g; high temperature, 0.0100±0.0004 g), but lower on long daylength (low temperature, 0.0103±0.0004 g; high temperature, 0.0112±0.0005 g). Stomach dry mass was similar under long daylength regardless of temperature (low temperature, 0.0024±0.0001 g; high temperature, 0.0024±0.0001 g), but under short daylength, dry mass was higher under low temperature (0.0029±0.0002 g) and lower under high temperature (0.0022±0.00009 g).

Small intestine wet mass was lower on low temperature ($F_{1,83}$=12.33, p=0.0008), whereas dry mass was lower in meadow voles fed the high fiber diet ($F_{1,83}$=5.62, p=0.02). Small intestine wet and dry mass were both significantly affected by interactions of all three variables; fiber and daylength (wet, $F_{1,83}$=16.64, p=0.0001; dry, $F_{1,83}$=6.91, p=0.01), temperature and fiber (wet, $F_{1,83}$=10.07, p=0.002; dry, $F_{1,83}$=8.26, p=0.005), and temperature and daylength (wet, $F_{1,83}$=6.12, p=0.02; dry, $F_{1,83}$=6.24, p=0.015). Small intestine wet mass was similar on low fiber regardless of temperature (low temperature, 0.024±0.002 g; high temperature, 0.024±0.001g), but on high fiber, wet mass was greatest under high temperature (0.029±0.001 g) and lowest under low temperature (0.020±0.0009 g). Small intestine wet mass was similar under long daylength regardless of temperature (low temperature, 0.023±0.001 g; high temperature, 0.024±0.001 g), but under short daylength, wet mass was higher under high temperature (0.030±0.0009 g) and unchanged on low temperature (0.023±0.001 g). Small intestine wet mass on the low fiber diet was higher under short daylength (low fiber, 0.028±0.002 g; high fiber, 0.023±0.0009 g), but lower under long daylength (low fiber, 0.020±0.001 g; high fiber, 0.026±0.001 g). Small intestine dry mass under low temperature was lower on high fiber (low fiber, 0.0057±0.0005 g; high fiber, 0.0048±0.0002 g), but unchanged under high temperature regardless of diet (low fiber, 0.0048±0.0002 g; high fiber, 0.0050±0.0002 g).

Small intestine dry mass on high temperature was lowest on long daylength (short daylength, 0.0055±0.0002 g; long daylength, 0.0044±0.0002 g), but was similar under low temperature regimes regardless of daylength (short daylength, 0.0047±0.0004 g; long daylength, 0.0051±0.0002 g). Small intestine dry mass was similar under long daylength regardless of diet (low fiber, 0.0047±0.0002 g; high fiber, 0.0048±0.0002 g), but under short daylength, dry mass was higher on low fiber (0.0058±0.0005 g) and lower on high fiber (0.0043±0.0002 g).

Caecal wet and dry mass were both affected by the interaction between fiber and daylength (wet, $F_{1,83}=5.29$, p=0.02; dry, $F_{1,83}=4.21$, p=0.044). Caecal wet mass under long daylength was similar regardless of diet (low fiber, 0.020±0.001 g; high fiber, 0.018±0.001 g), but under short daylength, wet mass was lower on the low fiber diet (0.015±0.003 g), but unchanged on the high fiber diet (0.021±0.001 g). Caecal dry mass on the low fiber diet was lower under short daylength (low fiber, 0.0030±0.0005 g; dry mass, 0.0040±0.0002 g), but higher under long daylength (low fiber, 0.0038±0.0002 g; high fiber, 0.0033±0.0003 g).

Large intestine wet and dry mass were both higher under low temperature (wet, $F_{1,83}=5.37$, p=0.02; dry, $F_{1,83}=5.37$, p=0.02) and short daylength (wet, $F_{1,83}=12.44$, p=0.0007; dry, $F_{1,83}=14.97$, p=0.0002) and both were affected by the interaction of temperature and daylength (wet, $F_{1,83}=8.52$, p=0.0052; dry, $F_{1,83}=10.11$, p=0.002). Large intestine wet mass under long daylength was similar regardless of temperature (low temperature, 0.010±0.001 g; high temperature, 0.011±0.001 g), but under short daylength, wet mass was higher under low temperature (0.020±0.002 g) and unchanged under high temperature (0.012±0.001 g). Large intestine dry mass under long daylength was similar regardless of temperature (low temperature, 0.0022±0.0003 g; high temperature, 0.0020±0.0003 g), but under short daylength, dry mass was higher under low temperature (0.0047±0.0005 g) and unchanged under high temperature (0.0020±0.0003 g).

Mass of gastrointestinal contents

Stomach content mass was significantly affected only by dietary fiber level and was higher in voles fed the high fiber diet ($F_{1,83}$=10.05, p=0.002). Small intestine content mass was higher on the high fiber diet ($F_{1,83}$=30.34, p<0.0001) and under long daylength ($F_{1,83}$=49.11, p<0.0001) and was affected by interactions between temperature and daylength ($F_{1,83}$=37.77, p<0.0001) and temperature and fiber ($F_{1,83}$=10.48, p=0.002). Small intestine content mass under low temperature was lower on the low fiber diet (low temperature, 0.010±0.003 g; high temperature, 0.017±0.001 g) and higher on the high fiber diet (low temperature, 0.027±0.001 g; high temperature, 0.021±0.001 g). Small intestine content mass under low temperature was higher under long daylength (short daylength, 0.006±0.003 g; long daylength, 0.030±0.001 g) and under high temperature was unchanged regardless of daylength (short daylength, 0.018±0.001 g; long daylength, 0.020±0.001 g).

The mass of caecal contents was unaffected by any of the independent variables or interactions between variables. Large intestine content mass was higher under low temperature ($F_{1,83}$=10.73, p=0.002) and high fiber ($F_{1,83}$=6.78, p=0.01) and was affected by the interaction between temperature and fiber ($F_{1,83}$=4.44, p=0.038). Large intestine content mass on the low fiber diet was similar regardless of diet (low temperature, 0.0083±0.004 g; high temperature, 0.0059±0.002 g), but on the high fiber diet, content mass was higher under low temperature (0.0201±0.002 g) and unchanged under high temperature (0.0069±0.002 g).

Length of gastrointestinal tissues

Stomach tissue was longer under low temperature than under high temperature ($F_{1,83}$=5.58, p=0.02). Small intestine length was affected by the interactions between temperature and daylength ($F_{1,83}$=7.96, p=0.006) and fiber and daylength ($F_{1,83}$=5.74, p=0.02). Small intestine length under low temperature was longer under long daylength (short daylength, 296.56±14.32 mm; long daylength, 325.50±6.95 mm); and under high temperature, small intestine tissue was longer under short daylength (short daylength,

315.92±6.77 mm; long daylength, 291.19±7.46 mm). Small intestine length on the high fiber diet was shorter under short daylength (low fiber, 315.22±15.15 mm; high fiber, 297.26±6.15 mm) and longer under long daylength (low fiber, 293.19±7.16 mm; high fiber, 323.50±7.26 mm). Caecal length was longer under low temperature ($F_{1,83}$=7.18, p=0.01) and high fiber ($F_{1,83}$=8.30, p=0.005). Large intestine length was longer under low temperature ($F_{1,83}$=17.55, p<0.0001), high fiber ($F_{1,83}$=8.80, p=0.004), and short daylength ($F_{1,83}$=4.30, p=0.042).

Mass of accessory organs

Both liver wet mass and dry mass were higher under low temperature (wet mass, $F_{1,83}$=5.75, p=0.02; dry mass, $F_{1,83}$=11.00, p=0.001) and dry mass was higher on the low fiber diet ($F_{1,83}$=9.83, p=0.002). Liver wet mass was affected by the interactions of temperature and fiber ($F_{1,83}$=8.85, p=0.004) and fiber and daylength ($F_{1,83}$=7.38, p=0.008). Liver wet mass on the low fiber diet was lower under short daylength (low fiber, 0.044±0.004 g; high fiber, 0.049±0.001 g) and higher under long daylength (low fiber, 0.055±0.002 g; high fiber, 0.047±0.002 g). Liver wet mass on the low fiber diet was similar regardless of temperature (low temperature, 0.049±0.004 g; high temperature, 0.050±0.002 g), but on the high fiber diet, wet mass was lower under high temperature (0.041±0.002 g) and higher under low temperature (0.054±0.002 g). Liver dry mass under long daylength was similar regardless of temperature (low temperature, 0.015±0.0005 g; high temperature, 0.016±0.0005 g), but under short daylength, wet mass was higher under low temperature (0.018±0.001 g) and lower under high temperature (0.013±0.0005 g). Liver dry mass under short daylength was similar regardless of diet (low fiber, 0.016±0.001 g; high fiber, 0.015±0.0004 g), but under long daylength, dry mass was higher on the low fiber diet (0.017±0.0005 g) and unchanged on the high fiber diet (0.014±0.0005 g).

Kidney wet mass was higher under long daylength ($F_{1,83}$=6.28, p=0.01) and was affected by the interaction between fiber and temperature ($F_{1,83}$=13.49, p=0.0004) and fiber and daylength ($F_{1,83}$=4.82, p=0.03). Kidney wet mass was similar under long

daylength regardless of diet (low fiber, 0.013±0.0004 g; high fiber, 0.013±0.0004 g), but under short daylength, wet mass was lower on the low fiber diet (0.010±0.0009 g) and was unchanged on the high fiber diet (0.012±0.0004 g). Kidney wet mass under low temperature was lower on the low fiber diet (low temperature, 0.010±0.0009 g; high temperature, 0.012±0.0004 g) and higher on the high fiber diet (low temperature, 0.014±0.0004 g; high temperature, 0.011±0.0004 g). Kidney dry mass was similar under long daylength regardless of temperature (low temperature, 0.0034±0.0001 g; high temperature, 0.0035±0.0001 g), but under short daylength, dry mass was higher under low temperature (0.038±0.0002 g) and lower under high temperature (0.0031±0.0001 g).

Adrenal gland wet mass was not significantly affected by any of the variables or interactions between them. Adrenal gland dry mass was higher under low temperature ($F_{1,83}$=17.47, $p<0.0001$), short daylength ($F_{1,83}$=14.41, $p=0.0003$), and low fiber ($F_{1,83}$=9.24, $p=0.003$), and was affected by the interaction between temperature and daylength ($F_{1,83}$=19.13, $p<0.0001$). Adrenal gland dry mass under long daylength was similar regardless of temperature (low temperature, 0.00016±0.00002 g; high temperature, 0.00017±0.00003 g), but under short daylength, dry mass was higher under low temperature (0.00043±0.00005 g) and unchanged under high temperature (0.00015±0.00002 g).

Discussion

The variables manipulated in this experiment: dietary fiber level, ambient temperature, and daylength had significant impacts on the feeding behavior and gastrointestinal morphology of meadow voles (*Microtus pennsylvanicus*). Increases in energy demand from exposure to high dietary fiber, low ambient temperature, and short daylength led to changes in the rate of food intake and food processing in meadow voles. The voles maintained body mass under short daylength, but lost mass under long daylength conditions. Initial mass of voles used in this study (34.79±0.73 g) was slightly lower than that of typical adults (44 g; Reich 1981). The lower than average mean body mass of voles in this present study helps explain why they did not lose mass on short daylength. Pistole and Cranford (1982) demonstrated that subadult meadow voles increased in body mass regardless of daylength until low adult mass was reached, and only then, did they begin to lose mass on short daylength. Since, based on their body mass, the voles used in this present study were probably of a subadult mass/age class, their low body mass may have precluded the expected mass losses brought about by short daylength.

The increased use of nesting material in cold temperatures can help to lower energy requirements (Glaser and Lustick 1975, Vogt and Lynch 1982). However, in this present study, voles were not given nesting material, and therefore could not take advantage of this energy-saving behavior. In addition to being exposed to these low temperature conditions, some voles were also under the burden of high dietary fiber, which has been shown to increase food intake, shorten turnover times, and lower digestive efficiency (Hammond and Wunder 1991, Derting and Bogue 1993, Castle and Wunder 1995). Food intake increased on the high fiber diet in this present study. The 52% increase in food ingested on the high fiber diet in this study corresponds to the 66%-188% intake increase found in similar studies using lactating voles (Innes and Millar 1981, Gittleman and Thompson 1988). Consequently, dietary turnover time was shorter on the high fiber diet. The shorter turnover time in voles fed the high fiber diet was similar to results from other studies (Hammond and Wunder 1991, Derting and Bogue 1993), which have shown that food intake increases under increased energy demand.

Although the apparent digestive coefficient for animals under low ambient temperature conditions was 400% lower for voles fed the high-fiber diet than for those fed the low-fiber diet, food intake rates only increased 160% and dietary turnover times remained constant. Voles fed the high-fiber diets were unable to sufficiently increase their intake in order to overcome the low digestibility of their high-fiber diet and consequently lost body mass during the trials.

The tissues of the gastrointestinal tract have been identified as most responsive to changes in energy demands, either due to increased thermoregulatory costs (Gross *et al* 1985), low quality diet (Hammond and Wunder 1991) or high reproductive expenditure (Fell *et al* 1963, Barnett 1973, Hammond and Diamond 1992). In this present study, changes in gastrointestinal tissues were minimal in meadow voles under the harshest conditions (high dietary fiber, low ambient temperature, and short daylength). This relates to the observation that meadow voles were able to increase food intake and shorten dietary turnover time to meet energy needs.

Wet and dry mass of the stomach increased under short daylength and low temperature conditions. Golley (1960) noted that stomachs of meadow voles were large relative to the rest of the gastrointestinal tract, and he suggested that this permitted them to eat large volumes of favorable food supplies before retiring to shelter where digestion takes place. Meadow voles under the simulated winter conditions in this present study were able to increase their stomach mass at the onset of winter to allow for this extra storage capacity. An interaction between low temperature and high dietary fiber caused small intestine wet and dry mass decreases, but overall tissue length was not significantly affected. This suggests that there may be a decrease in uptake capacity in the face of increased food intake under low temperature conditions (Hammond and Wunder 1991) and that the voles were likely 'stripping' easy to digest nutrients from the low quality food as it passed quickly through their small intestine. Voles exhibited no change in caecal wet or dry mass in response to low ambient temperature or short daylength. Large intestine wet and dry mass was significantly higher under the combination of short daylength and low ambient temperature in both species.

Increases in gastrointestinal tissue wet mass are often accompanied by increases in dry mass (Gross *et al* 1985, Hammond and Wunder 1991). If changes in tissue wet

mass are not accompanied by changes in dry mass, it is assumed that there is no change in the total amount of tissue (Hammond and Wunder 1995). However, changes in gastrointestinal tissue wet mass are correlated with changes in uptake capacity of nutrients, without the accompanying changes in dry mass (Hammond and Diamond 1994, Konarzewski and Diamond 1994). Changes in wet and dry tissue mass were correlated in this present study, and tissues of the hindgut (caecum and large intestine) were more significantly affected by low ambient temperature and short daylength, and less affected by high dietary fiber, than those in the foregut (stomach and small intestine). These results are consistent with the absorptive function of these tissues. More nutrient absorption occurs in the foregut than in the hindgut and therefore, the changes in tissue mass observed in this present study probably reflects changes in the absorptive capacity of the gastrointestinal tract, especially when dietary turnover time is increased.

As energy requirements increase seasonally due to lower ambient temperature in winter, voles that are able to process food at a faster rate and increase energy assimilation would potentially have higher survivorship. These changes have opposite effects, however, as it has been established that with short turnover times there is a corresponding decrease in diet digestibility (Tyrell and Moe 1975, Moe 1981, Van Soest *et al* 1983). Without an adjustment of gastrointestinal volume, digesta must be transported faster with increased intake, because the space it can occupy is limited (Gross *et al* 1985). Therefore, gastrointestinal capacity is critical in determining how much of the digestible nutrients in food can be assimilated and how much will be passed as feces (Demment and Van Soest 1985). In this study, mass of digesta in all sections of the tract, especially the caecum, was higher on the high fiber diet. The increase in stomach content mass was expected for meadow voles based on their increased food intake rates under higher energy demands. This occurred, with the stomach content mass of meadow voles on the high-fiber diet being 40% greater than that of those fed the low-fiber diet. The mass of digesta in the caecum was also expected to increase significantly in voles fed the high fiber diet since most of the microbial digestion of cellulose takes place in the caecum, and increased tissue volume would be necessary in the face of increased food intake, if dietary turnover times were to remain constant.

MacPherson *et al* (1988) explored seasonal and habitat variation in the diet of pine voles (*M. pinetorum*) in four apple orchards. They reported that stomach content mass declined in winter and suggested that this was related to the winter decrease in food availability and they further suggested that if the mass of stomach contents had increased, it would reflect an increase in the availability of winter forage and, therefore, an increase in food intake. However, Hammond (1993) suggested that higher stomach content mass due to increased food intake actually reflects a decrease in forage quality. This latter explanation may be more likely because in this present study and other studies on voles, food intake and mass of gastrointestinal contents increase when animals were fed a low-quality diet (this study, Keys and Van Soest 1970, Hammond and Wunder 1991).

Increases in content mass are sometimes accompanied by increases in length in some gastrointestinal tissues under conditions of high energy demand (Fell *et al* 1963, Gebczynska and Gebczynski 1971, Cripps and Williams 1975, Hammond and Diamond 1992). When a moderate increase in energy demand (30-40% above control levels) was imposed on meadow voles through administration of exogenous thyroxine, significant increases in the masses of gastrointestinal tissues occurred without a significant increase in tissue length (Derting and Bogue 1993). The results of Derting and Bogue (1993) showed an increase in both gastrointestinal mass and length, suggesting that voles in their study were under more stress than in this present study. However, increases in food intake in both this present study and that of Derting and Bogue (1993) were similar to that of lactating voles (Innes and Millar 1981, Gittleman and Thompson 1988). During reproduction in a number of small-mammal species, changes in gastrointestinal tissue length occurred only during the energetically expensive period of lactation but not during the less intense period of gestation (Fell *et al* 1963, Gebczynska and Gebczynski 1971, Cripps and Williams 1975, Hammond and Diamond 1992).

In this present study, the gastrointestinal length (except the small intestine) increased in meadow voles acclimated to low temperature and in those on the high fiber diet. However, length measurements, as opposed to mass measurements, are less reliable as estimates of changes in nutrient absorption because they are a function of tissue thickness and elasticity (Freehling and Moore 1987, Hammond and Diamond 1994). Thicker, heavier tissue is more elastic; therefore, gastrointestinal tract length is correlated

with its mass. Changes in length are more likely a reflection of the ability of the tract to elongate and simply hold more digesta volume (Freehling and Moore 1987). Changes in mass of the tract, however, reflect changes in uptake rate of nutrients and volume (Karazov and Diamond 1983, Toloza *et al* 1991, Hammond and Diamond 1992) as well as changes in gastrointestinal tract volume (Hammond and Wunder 1991, Derting and Bogue 1993). Changes in tissue length are considered the response of last resort for meeting increased energy demands because they require the synthesis and elaboration of new tissue.

Accessory organs such as the liver and kidneys are reported to increase mass under conditions of increased energy demand. In this present study, increased liver, kidney, and adrenal gland mass occurred under cold ambient temperatures. Since voles increased food intake in response to low ambient temperatures, presumably, they were partially using these nutrients obtained from increases in food intake to fuel increases in accessory organ mass, thus allowing them to conserve their bodily reserves. Increased liver mass may also be an indication of higher metabolic rate. An increased metabolic rate would advantageous under cold ambient temperature conditions because it would lead to more internal heat production that may help the voles meet their thermoregulatory needs. This could be especially important when diet quality is reduced and the voles may not be able to get sufficient nutrients from their diet, even with increased food intake rates. In cold-acclimated rats, liver, heart and kidney mass have been shown to increase while subcutaneous fat, muscle, and pelage mass decreased (Heroux and Campbell 1959). Heroux and Campbell (1959) suggested that, since intake rate was not affected, the animals were drawing on their bodily reserves to satisfy thermoregulatory requirements. McDevitt and Speakman (1994) described a similar result in their laboratory study of field voles (*M. agrestis*) acclimated to 10 °C. They found that liver and kidney mass both increased under low temperature conditions, but these were accompanied by a substantial (106%) increase in food intake. They also found that subcutaneous fat, muscle, and pelage mass were unaffected by low temperature. These results showing an increase in adrenal gland mass were in contrast to a field study by Seabloom *et al* (1978) that showed adrenal gland mass in meadow voles did not change significantly from winter to summer, although differences involving age and reproductive condition did exist. These organs:

the liver, kidneys, and adrenal glands, though they have been seldom examined, have profound roles in energy utilization and the increases in metabolic activity necessary to survive the stressful environments to which voles experience during winter.

It has been proposed that there are stages of compensatory changes in the gastrointestinal system as energy demand increases (Derting 1989, Derting and Bogue 1993). The initial response to an increase in energy demand is increased food intake. Increases in food intake may be equivalent to energy demand increase, in which case the animal shows no change in body mass (Derting and Bogue 1993), or may exceed the energy demand resulting in accelerated growth or gain in body mass (Derting 1989). With increased food intake, voles will have shorter dietary turnover times unless a change in gastrointestinal volume occurs through increases in tissue mass and/or length. My original hypothesis that voles with increased energy needs will have a larger gastrointestinal capacity is supported by the responses of meadow voles in this present study. With reduced energy availability (high dietary fiber) or increased energy needs (low temperature), gastrointestinal tissue wet mass, content mass, and length increased. Tissue dry mass, however, was lower with reduced energy availability but was higher with increased energy demand. With shorter turnover times, less metabolic machinery would be necessary allowing for lower tissue masses (Karasov and Diamond 1983, Toloza *et al* 1991, Hammond and Diamond 1992).

If increases in food intake are insufficient to allow increased energy demands to be met, compensatory changes in the gut that increase the mass and absorptive area of existing small intestine or caecum tissue occur (Gebczynska and Gebczynski 1971, Toloza *et al* 1991, Derting and Bogue 1993). Finally, as energy demand increases further, modifications of gastrointestinal tissue may become insufficient to meet energy needs, and the actual size of tissues, particularly the small intestine and caecum, increases through the production of additional organ length (Gross *et al* 1985, Green and Millar 1987, Bozinovic *et al* 1990, Hammond and Wunder 1991, Hammond and Diamond 1992). These changes in tissue mass did not occur, however, further supporting the fact that the meadow voles were able to meet their increased energy demands by simply increasing intake and modifying turnover time.

The results of this study are important because they detail previously undescribed differences in the ways that meadow voles respond to low ambient temperature, short daylength, and high dietary fiber. Meadow voles were able to meet the increased energy demands brought on by these harsh environmental conditions by simply increasing their food intake, and therefore modifying dietary turnover time. Although numerous digestibility studies have been conducted using this species, none have looked at all three environmental variables simultaneously and analyzed the interactions between them. This study yields valuable information that will help future researchers understand the strategies employed by these animals under harsh environmental conditions.

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APPENDIX

The results of experiments conducted to establish the baseline condition of meadow voles (*M. pennsylvanicus*) entering digestive trials. One trial (n=8) was conducted under maintenance conditions (23°C, 14L:10D). Ground rodent chow and water were available *ad lib*. All other experimental conditions and techniques were as listed in the Materials and Methods section. Means of body mass, energy utilization, and food processing for both species under maintenance conditions are listed in Table 10. Means of gastrointestinal tissue wet and dry mass, content mass, and length under maintenance conditions are listed in Table 11. Means of accessory organ wet and dry mass for both species under maintenance conditions are listed in Table 12.

Table 10. Means ($\pm$ 1 SE) of body mass, energy utilization, and food processing in meadow voles (*M. pennsylvanicus*) under maintenance conditions (21 °C, rodent chow, and 14L:10D).

	Meadow voles (n = 8)
Body mass change (g)	-1.21 $\pm$ 1.14
Fecal production (g/day)*	0.29 $\pm$ 0.02
Food intake (g/day)*	0.85 $\pm$ 0.07
Turnover time (hrs)	13.00 $\pm$ 1.38
Digestive efficiency	64.27 $\pm$ 3.42

*Values are expressed per gram final body mass

Table 11. Means (± 1 SE) of gastrointestinal tissue wet and dry mass, mass of contents and tissue length of meadow voles (*Microtus pennsylvanicus*) under maintenance conditions (21 °C, rodent chow, and 14L:10D). All mass values are expressed per gram final body mass. Length values are expressed in mm.

	Meadow voles (n = 8)
Wet Mass	
Stomach	0.0104 ± 0.0007
Small Int.	0.0243 ± 0.0020
Caecum	0.0198 ± 0.0024
Large Int.	0.0133 ± 0.0007
Dry Mass	
Stomach	0.0046 ± 0.0004
Small Int.	0.0092 ± 0.0008
Caecum	0.0053 ± 0.0005
Large Int.	0.0048 ± 0.0005
Contents	
Stomach	0.0120 ± 0.0037
Small Int.	0.0236 ± 0.0031
Caecum	0.0446 ± 0.0050
Large Int.	0.0084 ± 0.0034
Length	
Stomach	21.38 ± 1.25
Small Int.	347.13 ± 13.00
Caecum	223.63 ± 10.76
Large Int.	235.00 ± 11.97

Table 12. Means (± 1 SE) of accessory organ mass of meadow voles (*M. pennsylvanicus*) under maintenance conditions (21 °C, rodent chow, and 14L:10D). All values are expressed as gram of tissue per gram final body mass.

	Meadow voles (n = 8)
Liver	
Wet mass	0.0445 ± 0.0032
Dry mass	0.0141 ± 0.0008
Kidneys	
Wet mass	0.0119 ± 0.0005
Dry mass	0.0032 ± 0.00008
Adrenal Glands	
Wet mass	0.0004 ± 0.00007
Dry mass	0.0001 ± 0.00004

VITA

Jeffrey Scott Buchanan was born in Huntington, West Virginia on October 23, 1968. He attended Milton High School in Milton, West Virginia, graduating in 1986. He then joined the United States Navy in which he served for six years attaining the rate of Machinist Mate Second Class. He married Melinda Ann Crockett in 1990. Jeffrey began his studies at Virginia Tech in1992 and received a Bachelor of Science in Biology in 1997. He has two children, Carey Elizabeth (born in 1992) and Sarah Grace (born in 1996).