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LABORATORY FATTENING AND DIETARY-FAT EFFECTS ON MEADOW VOLES (*MICROTUS PENNSYLVANICUS*)

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ABSTRACT.—When removed from the field and maintained under laboratory conditions, meadow voles exhibited significant change in body composition. Voles increased body mass due primarily to large gains in lipid mass combined with small losses in fat-free mass. Lipid deposition amounts increased as dietary fat was increased, and animals demonstrated a leveling of body mass instead of continuous unregulated obesity. When dietary fat content was changed, lipid deposition or utilization responded directly. Thus, meadow voles regulate overall body mass and body composition (lipid and fat-free mass) at levels that correspond to dietary quality (fat) and abundance in the laboratory, and they deposit considerably more lipid than do animals in the field. Our experiments demonstrate that food quality has a substantial effect on the body composition of wild-caught animals maintained in the laboratory.

Key words: meadow voles, body composition, fat, dietary fat, EM-SCAN.

In the wild, relative body fat levels of many small mammals are quite low, often ranging from 3% to 8% of total body mass (Fleharty et al. 1973, Iverson and Turner 1974, Schreiber and Johnson 1975, Morton and Lewis 1980, Voltura 1997), with seasonal variation in body fat reported in some species. However, seasonal change in lipid is often the result of decreases in lean mass, not increases in lipid mass, resulting in an overall increase in relative fat content in winter. The above-mentioned studies suggest that potential causes for such leanness in the wild may be due to high metabolic demands, low diet quality and/or availability, active lifestyle, or some combination of these.

Whether field-caught (Hayward 1965, Batzli and Esseks 1992, Voltura 1997) or lab-reared (Sawicka-Kapusta 1970, 1974, Ferns and Adams 1974, Holleman and Dieterich 1978, Donald et al. 1980, Batzli and Esseks 1992, Voltura and Wunder 1998), small mammals held under laboratory conditions often increase body fat within weeks to levels exceeding those observed in the field. In these studies body fat often exceeded 10% of body mass within 30 days. Suggested causes include confinement that reduces activity; unnatural, highly digestible diets; stable environmental conditions; or any combination thereof. In these studies animals were maintained on either laboratory rodent chow or alfalfa, with changes in body composition reported incidental to other research focus areas. Thus, a study to document the rate of change in body composition in wild-caught rodents maintained in the laboratory was warranted.

Hence, we sought to document the degree and rate of lipid deposition using noninvasive and repeatable measures with individual animals over time, in wild-caught meadow voles kept under laboratory conditions. In addition, we investigated the effect of dietary fat on already fattened animals to more fully understand body composition dynamics in voles.

METHODS

Experiment 1: Laboratory Condition Effects

Meadow voles were trapped using Sherman live-traps (28 × 18 × 13 cm) from local populations in 3 mixed-grass riparian fields at the U.S. Air Force Academy, El Paso County, Colorado. Trapping was conducted in January (winter), April (spring), and June (summer) 1997 to represent different seasons. For each trapping session we collected 12 adult voles (>30 g) of equal sex ratios. Because pregnant small rodents maintain extremely low fat levels (Gyug and Millar 1980, Lochmiller et al. 1983, Voltura 1997), we omitted all pregnant females (determined by observation and/or abdominal

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palpation). Due to low trapping success and the difficulty in aging voles, 5 animals <29 g were used in the January group. For all trapping sessions, traps were set approximately 1 hour before dusk and checked within 1 hour of sunrise. During January and April, trapping also occurred during daylight hours, with traps checked every 2 hours.

Upon capture, voles were given an apple slice and piece of lab rodent chow (Lab Diet 5001, PMI Feeds) to assist in rehydration and provide gut-fill. Voles were held in capture traps and transported to a laboratory at the U.S. Air Force Academy to noninvasively estimate body composition using an EM-SCAN® device (Voltura and Wunder 1998, Unangst and Wunder 2001). Unangst and Wunder (2001) demonstrated the estimation accuracy of lipid mass to be 1.44 ± 0.26 g in meadow voles. All body composition estimates were completed within 2 to 3 hours of capture. Voles were then individually housed (28 × 18 × 13-cm cage) in an environmental chamber at 23°C with natural photoperiod and fed lab chow (approximately 100 g; Lab Diet 5001, PMI Feeds) and water weekly. Although each group began with 12 voles (6 male, 6 female), animals that did not survive the entire 6-week experimental period were omitted from analyses. Thus, an unequal number of voles completed each session. Total body mass (Ohaus E400D, 0.01 g), body composition (fat-free mass and lipid mass), and food intake were measured weekly. After removing orts (uneaten food), we replaced food weekly. Intake was determined by subtracting orts from the food offered. Individual intake values were then summed by group and divided by 7 for daily intake.

Experiment 2: Dietary-fat Effects

In this experiment we used lab-fattened voles from the June group (experiment 1) combined with an additional 12-vole group captured in September 1997. As previously described in experiment 1, we fed the June voles lab chow for 6 weeks. After 6 weeks the diet was changed to high fat for 3 more weeks. In contrast, we fed the September group a high-fat diet for the initial 6 weeks instead of lab chow. Then the diet was switched to lab chow (cakes of ground lab chow) for 3 more weeks. The high-fat diet consisted of lab chow with added fat (vegetable oil), resulting in a calculated dietary fat of 5–25%. Lab chow was mixed with distilled water and vegetable oil (4:2 by volume) to form a paste and then pressed into cakes with a quarter-pound hamburger press. To evaporate water and minimize fat volatilization, we then baked the cakes at a low temperature (80°C) for 4 hours and dried them for an additional 24 hours at 50°C. Vegetable oil was selected to maximize available polyunsaturated fats, the most prevalent lipid form in natural vegetation (National Research Council 1964, VanSoest 1994). To ensure that nutrient dilution on the high-fat diet did not occur, a proximate analysis (Nahm 1992) of the high-fat diet was completed by the Soil, Water, and Forage Analysis Laboratory, Colorado State University, Fort Collins, Colorado. We compared body composition patterns between the June and September groups to determine whether body composition response would be affected by dietary fat and the order of food presented.

Statistics

For both experiments a repeated-measures ANOVA (SAS proc mixed; SAS Institute, Inc. 1989) with time (week) as the fixed effect and subject as a random effect was performed for each body composition parameter: total body mass, lipid mass, fat-free mass, relative lipid mass, and relative fat-free mass (component/total body mass). To test the similarity in body composition response between groups in experiment 1, we used a repeated-measures ANOVA (SAS proc mixed) with time (week) and seasonal group as fixed effects and subject nested within group as the random effect. In experiment 2 we made comparisons between groups for all body composition parameters with repeated-measures ANOVA (SAS proc mixed) using time (week) and group (environmental condition, food type) as fixed effects and subject nested within group as a random effect. For all experiments, a repeated-measures ANOVA was also completed for food intake and intake per gram body mass. In addition, a change value for each body composition parameter was calculated to better illustrate the magnitude of change over time. Change values included the change from experiment start to week 2, start to week 4, start to week 6, and week 6 to week 9 (when appropriate). Change values were calculated by subtracting the initial value at the start of the

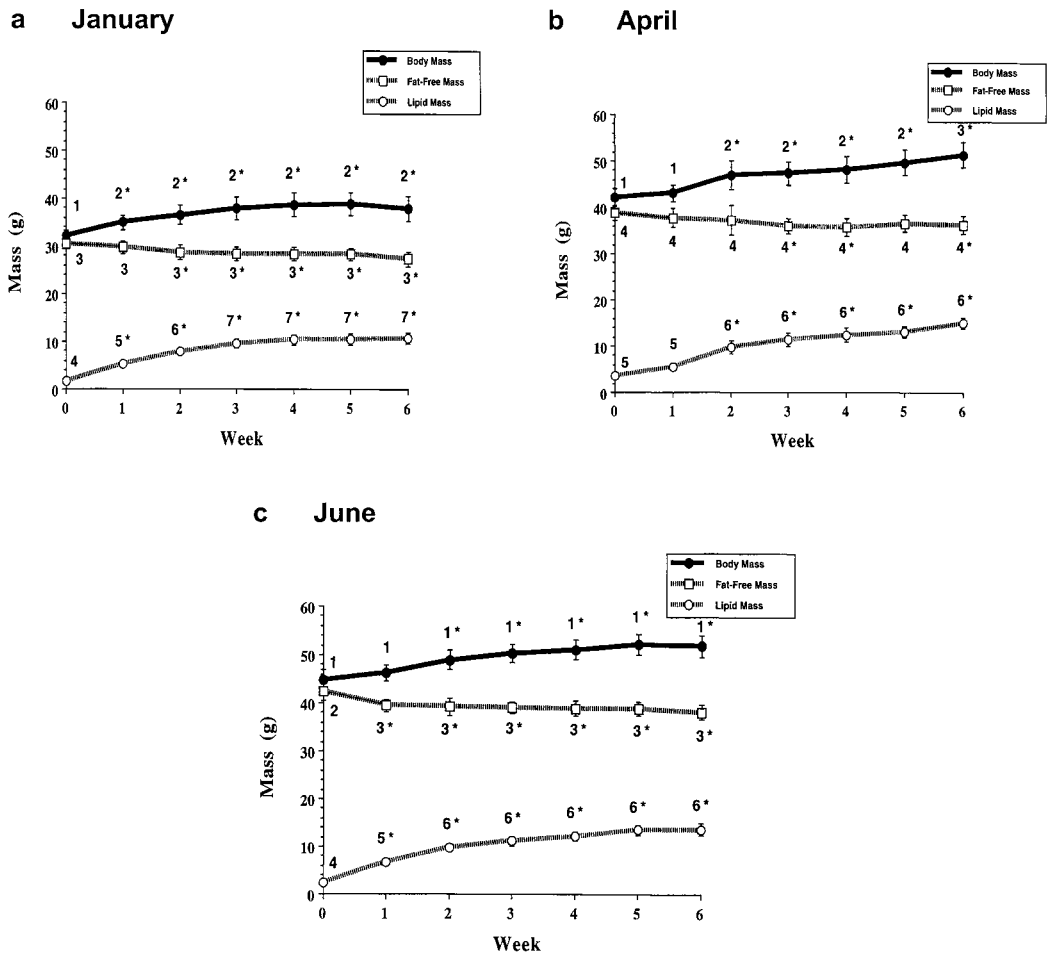

Fig. 1. Comparison of body composition dynamics of voles captured in January, April, and June and fed laboratory rodent chow (Lab Diet 5001, PMI Feeds) and water ad lib for 6 weeks. Values represented are mean plus/minus 1 standard error (error bars). Different numbers indicate a significant difference between consecutive weeks ($P < 0.05$). * indicates a significant difference by week from the parameter value at the start of the experiment.

experiment from week 2, week 4, or week 6 value, respectively, and week 6 from week 9. For all comparisons, statistical significance was set at $P < 0.05$.

RESULTS

Experiment 1: Laboratory Condition Effects

Gains in total body mass in all groups were mainly due to large increases in lipid mass coupled with small losses in fat-free mass (Fig. 1). In each group all body composition parameters demonstrated significant change over time ($P < 0.01$), with a leveling in lipid mass and body mass reached within 3 weeks. In the January group a gain in total body mass of 6.18 ± 2.18 g was due mainly to an increase in lipid mass (8.84 ± 1.21 g), combined with a loss of fat-free mass (2.95 ± 1.30 g; Table 1). The April capture group gained 8.90 ± 1.79 g in total body mass, with increases in lipid mass of 10.29 ± 1.12 g and losses of fat-free mass of 2.50 ± 1.17 g (Table 1). Similar change was shown in the June group, with an increase in total body mass (7.08 ± 2.97 g) due to lipid mass gains of 10.40 ± 1.85 g and fat-free mass losses of 4.29 ± 2.27 g (Table 1).

Because the January group had lower total body mass and fat-free mass when beginning the manipulation than the April and June groups ($P < 0.05$), we compared the groups

TABLE 1. Comparison of body composition parameters for seasonal groups fed laboratory rodent chow (Lab Chow 5001, PMI Feeds) and water ad lib. Values are mean plus 1 standard error in parentheses. ANOVA *F* value indicates degree of similarity or difference for 3 groups for each body composition parameter from the start of experiment to each successive 2-week period. No significant differences were found for any body composition parameter between groups at any time period ($P < 0.05$).

Time Condition	*F* value (ANOVA)	January 97 ($n = 12$)	April 97 ($n = 9$)	June 97 ($n = 10$)
Start to week 2				
Mass change (g)	0.9736	4.30 (1.31)	4.70 (2.38)	4.16 (1.24)
Lipid mass change (g)	0.4617	5.90 (0.58)	6.22 (1.48)	7.40 (0.60)
Fat-free mass change (g)	0.5743	–1.85 (1.13)	–1.52 (1.39)	–3.20 (0.94)
% mass change	0.8851	12.97 (3.84)	11.04 (5.90)	10.06 (3.48)
% lipid mass change	0.5401	410.55 (86.73)	315.03 (112.61)	476.14 (96.98)
% fat-free mass change	0.8311	–6.23 (3.54)	–4.29 (4.03)	–7.32 (2.38)
Start to week 4				
Mass change (g)	0.9806	6.40 (1.96)	5.84 (2.17)	6.28 (2.09)
Lipid mass change (g)	0.6936	8.41 (1.19)	8.81 (1.46)	9.86 (1.10)
Fat-free mass change (g)	0.5277	–2.27 (1.09)	–4.22 (1.07)	–3.54 (1.51)
% mass change	0.7658	19.46 (6.01)	13.73 (5.10)	15.56 (5.64)
% lipid mass change	0.5752	592.63 (135.49)	434.12 (139.38)	661.27 (167.38)
% fat-free mass change	0.6808	–7.40 (3.57)	–11.36 (2.93)	–7.50 (3.66)
Start to week 6				
Mass change (g)	0.7245	6.18 (2.18)	8.90 (1.79)	7.08 (2.97)
Lipid mass change (g)	0.6841	8.84 (1.21)	10.29 (1.12)	10.40 (1.85)
Fat-free mass change (g)	0.7400	–2.95 (1.30)	–2.50 (1.17)	–4.29 (2.27)
% mass change	0.9575	19.31 (6.65)	21.03 (4.26)	18.18 (8.05)
% lipid mass change	0.4651	625.80 (136.18)	414.49 (108.92)	696.02 (211.24)
% fat-free mass change	0.8985	–9.44 (4.05)	–6.49 (3.14)	–8.48 (5.81)

TABLE 2. Summary of the effects of food quality on body composition. For 6 weeks group A was fed laboratory rodent chow (Lab Diet 5001, PMI Feeds), and group B was fed a high-fat diet. After 6 weeks diet was switched for an additional 3 weeks. All values are mean plus 1 standard error (in parentheses).

Time Condition	Group A	Group B
Start to week 6 (A = lab chow, B = high fat)		
Mass change (g)	7.08 (2.97)*	5.74 (2.08)*
Lipid mass change (g)	10.40 (1.85)*	13.18 (0.94)*
Fat-free mass change (g)	–4.29 (2.27)*	–7.44 (1.53)*
Week 6 to week 9 (diet change: A = high fat, B = lab chow)		
Mass change (g)	5.86 (0.81)**	–8.69 (1.22)**
Lipid mass change (g)	2.99 (0.55)**	–6.41 (1.81)**
Fat-free mass change (g)	2.88 (0.57)**	–3.52 (1.02)**

* indicates significant difference from body composition parameter at start of experiment.
** indicates significant difference from body composition parameter at week 6 following change in diet ($P < 0.05$).

for relative lipid mass and relative fat-free mass (proportion of total body mass). No significant time-by-group interaction ($F_{10,166} = 1.15$; $P = 0.33$) nor group effect ($F_{2,30} = 0.52$; $P = 0.60$) was found for either relative lipid mass or relative fat-free mass, suggesting no seasonal effect on body composition change.

Thus, when meadow voles are removed from the wild and held in the lab with lab chow under stable experimental conditions, they increase total body mass and lipid mass and decrease lean mass regardless of season of capture.

Experiment 2: Dietary-fat Effects

As reported above, voles eating lab chow over 6 weeks increased total body mass, with gains in lipid mass and losses of fat-free mass. When the diet was switched after 6 weeks to a high-fat diet for an additional 3 weeks, voles gained an added 5.86 ± 0.81 g of total body mass, with increases in both lipid mass (2.99 ± 0.55 g) and fat-free mass (2.88 ± 0.57 g; Fig. 2, Table 2). In the September group voles directly

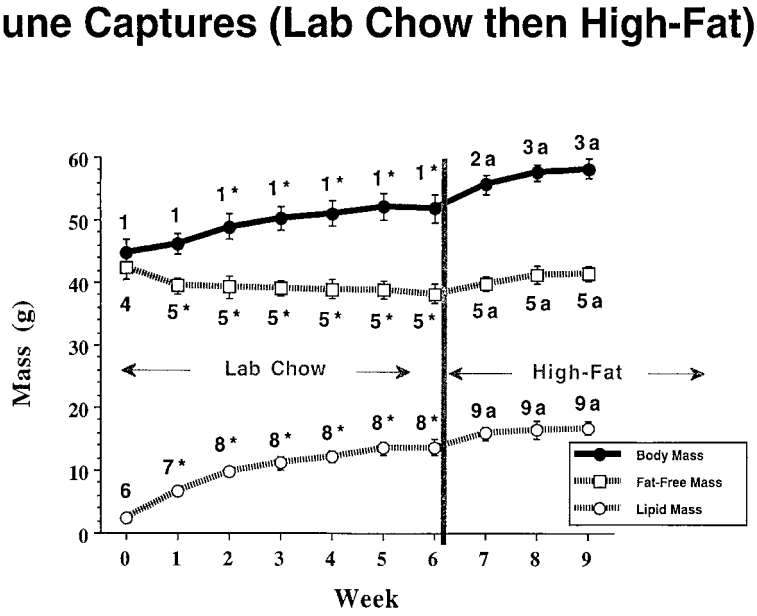

Fig. 2. Body composition change for June voles fed laboratory rodent chow for 6 weeks, then a high-fat diet for an additional 3 weeks. Values represented are mean plus/minus 1 standard error (error bars). Different numbers indicate a significant difference between consecutive weeks ($P < 0.05$). * indicates a significant difference from parameter value at the start of the experiment ($P < 0.05$). "a" indicates a significant difference from parameter value at week 6 to the following 3 weeks ($P < 0.05$).

from the field were given the high-fat diet rather than lab chow for 6 weeks. After 6 weeks on the high-fat diet, they had gained 13.18 ± 0.94 g of lipid mass (26.58 ± 1.18 % relative body fat). Over the same time period, total body mass increased 5.74 ± 2.08 g, with losses in fat-free mass of 7.44 ± 1.53 g (Fig. 3, Table 2). When diet was changed to lab chow for 3 additional weeks, voles lost 8.69 ± 1.22 g in total body mass from the body mass at week 6, including 6.41 ± 1.81 g of lipid mass and 3.52 ± 1.02 g of fat-free mass.

Overall, voles gained more lipid mass and lost more fat-free mass when eating a high-fat diet (Table 2) than those on a lab-chow diet. Because the June group ate more lab chow (approximately 1.5 g per day) than the September group ate high-fat chow (Table 3), the smaller losses in fat-free mass estimates may be due to gut-fill effects (Voltura and Wunder 1998).

The September group showed small, but nonsignificant, increases (<0.5 g) in intake when their high-fat food was switched to lab chow (Table 3). In the June group voles eating lab chow showed slight decreases in food intake over the initial 6-week period, with continued decreases when provided the high-fat diet, potentially reflecting the higher caloric value per gram of food due to increased fat in the high-fat diet.

DISCUSSION

In these experiments we demonstrated that significant change in body composition results when meadow voles are removed from the natural environment and held under stable laboratory conditions with ad lib food. Regardless of season, the body composition pattern was consistent. In all experiments increases in body mass were due to large gains in lipid mass, combined with small losses in fat-free mass. Changes in body fat in our study are similar to those reported by Ferns and Adams (1974), Sawicka-Kapusta (1974), and Batzli and Esseks (1992) for microtine rodents removed from the field and captive-reared, but none of these authors reported changes in fat-free mass. Ferns and Adams (1974) showed that after 3 weeks in the lab, *M. agrestis* increased body fat 4- to 5-fold the amounts seen in wild voles.

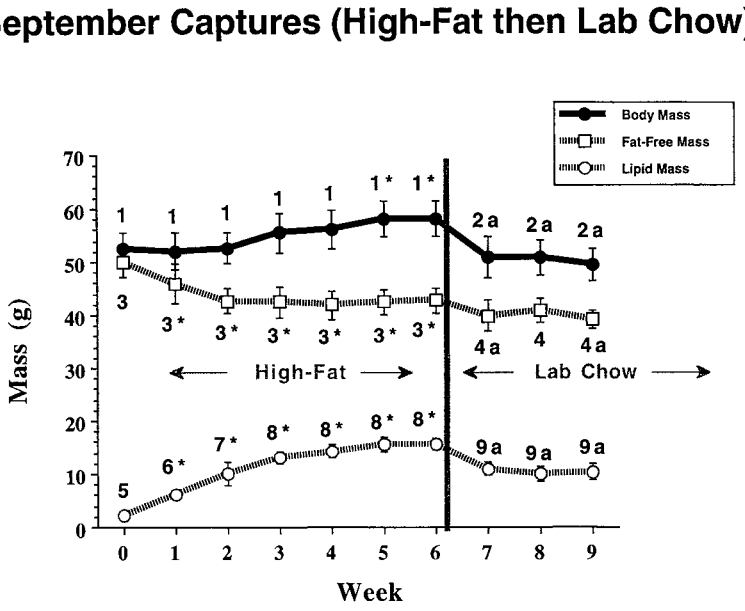

Fig. 3. Body composition change for September voles fed a high-fat diet for 6 weeks, then laboratory rodent chow for an additional 3 weeks. Values represented are mean plus/minus 1 standard error (error bars). Different numbers indicate a significant difference between consecutive weeks ($P < 0.05$). * indicates a significant difference from parameter value at the start of the experiment ($P < 0.05$). "a" indicates a significant difference from parameter value at week 6 to the following 3 weeks ($P < 0.05$).

Sawicka-Kapusta (1970, 1974) demonstrated that the body-fat content of laboratory *M. arvalis* was >10% after 20 days of age and that wild-caught *Clethrionomys glareolus* reached levels >10% body fat by 30 days of age when kept in laboratory cages. When brown lemmings (*Lemmus sibiricus*) were removed from the field and held in the laboratory, Batzli and Esseks (1992) found that animals increased body fat from field levels of 3–5% up to 9–13% when fed natural vegetation. When fed unnatural, highly digestible food (rabbit chow), brown lemmings further increased body fat to over 30%. Hollemann and Dieterich (1978) also reported that brown lemming body fat exceeded 10% after 3 weeks of age, with values as high as 44% in a laboratory colony fed lab chow.

Such increases in fat are uncommon in microtine rodents in the wild. Although decreases in total body mass and increases in relative body fat have been reported as an overwinter survival strategy (Fuller et al. 1969, Iverson and Turner 1974, Zuercher et al. 1999), the mass decrease is due primarily to reductions in lean tissue. Presumably, these reductions lessen overall energy requirements in response to thermoregulatory or nutritional constraints. However, when these constraints are removed, as in our study, voles deposit fat at levels not observed in the field. Based on the plateau in body composition, our study animals not only increased overall size (mass) but also seemed to regulate this change possibly to retain some "acceptable or ideal" size relative to perceived environmental constraints.

Batzli and Esseks (1992) reported that food intake is positively correlated with body fat. In contrast, we found that food intake decreases over time as voles became fatter. Because fat tissue is less metabolically active than lean tissue, increased body fat should not require increased metabolic energy once fat is deposited. In addition, because voles were simultaneously losing fat-free mass, overall metabolic demands may have been reduced even though voles were becoming heavier. Thus, to ingest identical calories, voles could eat less high-fat diet than lab chow or reduce food intake as body composition changed.

When voles were fed lab chow (5% fat), they increased relative body fat from <5% to approximately 25% within 6 weeks. By further

TABLE 3. Summary of food intake rates for groups fed different diets. For 6 weeks group A was fed laboratory rodent chow (Lab Diet 5001, PMI Feeds), and group B was fed a high-fat diet. After 6 weeks diet was switched for an additional 3 weeks. Values are mean plus 1 standard error (in parentheses).

Week	Group A	Group B
Week 1 (A = lab chow, B = high fat)		
Intake/d (g)	8.04 (0.48)	6.30 (0.64)
Intake/g body mass (g/g^{-1})	0.18 (0.01)	0.12 (0.01)
Week 2		
Intake/d (g)	8.57 (0.37)	6.30 (0.64)
Intake/g body mass (g/g^{-1})	0.18 (0.01)	0.12 (0.01)
Week 3		
Intake/d (g)	7.02 (0.38)*	5.77 (0.38)
Intake/g body mass (g/g^{-1})	0.14 (0.01)	0.10 (0.00)
Week 4		
Intake/d (g)	6.48 (0.30)	4.82 (0.23)
Intake/g body mass (g/g^{-1})	0.13 (0.01)	0.09 (0.00)
Week 5		
Intake/d (g)	6.67 (0.34)	4.96 (0.27)
Intake/g body mass (g/g^{-1})	0.13 (0.01)	0.09 (0.00)
Week 6		
Intake/d (g)	6.13 (0.30)	5.22 (0.35)
Intake/g body mass (g/g^{-1})	0.12 (0.01)	0.09 (0.01)
Week 7 (diet change: A = high fat, B = lab chow)		
Intake/d (g)	5.55 (0.31)	5.63 (0.38)
Intake/g body mass (g/g^{-1})	0.10 (0.01)	0.11 (0.01)
Week 8		
Intake/d (g)	4.50 (0.21)	5.71 (0.23)
Intake/g body mass (g/g^{-1})	0.08 (0.00)	0.12 (0.00)
Week 9		
Intake/d (g)	4.54 (0.14)	5.71 (0.23)
Intake/g body mass (g/g^{-1})	0.08 (0.00)	0.12 (0.00)

* indicates significant differences between consecutive weeks within a group ($P < 0.05$).

increasing dietary fat to 25% (high-fat diet), voles gained additional body fat to levels exceeding 30%. However, regardless of diet, voles did not continue to increase body mass. Rather, they showed a leveling (reduction in change) in body mass with each diet. In all cases rapid lipid deposition occurred within 1 to 2 weeks in the lab, followed by a leveling (less change) in all body composition parameters for the remaining time. When fat content of the diet was changed, body composition responded in a similar direction. We suggest that body composition changes relate to diet, where voles regulate body mass and body composition at levels respondent to dietary quality and abundance. Unlike laboratory rats, which continue to deposit added body fat without limit when given ad lib food (Donald et al. 1980), animals in our study reached certain body composition levels relative to diet quality. Because we did not observe progressive diet-induced obesity, we feel that voles may endogenously regulate body composition cued by diet by differentially varying lipid and fat-free mass in relation to diet.

There are many possible explanations for higher body fat levels observed when animals are held in the laboratory (Hayward 1965, Batzli and Esseks 1992). Paramount among these are the following: (1) an unnatural highly digestible food, (2) a reduction in activity lessening overall energy demands, (3) stable environmental conditions reducing energy demands for thermoregulation, or (4) some interaction of these. Although we cannot comment on activity or environment from this study, our results indicate that food quality has a strong effect on body composition when animals are removed from their natural environment and acclimated to laboratory conditions.

As initially identified by Hayward (1965) in *Peromyscus* sp., the fundamental change in

body composition with removal from the field may likely influence many physiological parameters measured. Acknowledging that this dramatic change in body fat can occur within a few weeks is necessary to ensure that laboratory results gathered from wild-caught animals maintained in the laboratory are not biased by such body composition dynamics.

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