Evaluating body condition in small mammals

A.I. Schulte-Hostedde, J.S. Millar, and G.J. Hickling

Abstract: Body condition (energy reserves) can have important fitness consequences. Measuring condition of live animals is typically done by regressing body mass on measures of body size and using the residuals as an index of condition. The validity of this condition index was evaluated by determining whether it reflected measured fat content of five species of small mammals (yellow-pine chipmunks (*Tamias amoenus* Allen), bushy-tailed wood rats (*Neotoma cinerea* Ord), deer mice (*Peromyscus maniculatus* Ord), red-backed voles (*Clethrionomys gapperi* Vigors), and meadow voles (*Microtus pennsylvanicus* Ord)). We also determined whether body water could predict fat content, enabling the use of hydrogen-isotope dilution for estimating condition. For all five species, condition estimates weakly predicted fat content and more accurately predicted variation in lean dry mass and water content. The relationship between body water and fat content was inconsistent among the five species, discouraging against the general use of isotope dilution in these animals. Although ecologically important, these indices are best interpreted as explaining variation in all constituents of body composition.

Résumé : La condition physique (réserves énergétiques) peut avoir une influence importante sur le fitness. La mesure de la condition physique d'animaux vivants se fait généralement par une régression de la masse du corps en fonction de mesures de la taille du corps, les résidus servant de coefficient de condition. La validité de ce coefficient de condition a été évaluée en déterminant s'il reflète bien le contenu lipidique mesuré chez cinq petits mammifères (le Tamia amène (*Tamias amoenus* Allen), le Néotoma à queue touffue (*Neotoma cinerea* Ord), la Souris à pattes blanches (*Peromyscus maniculatus* Ord), le Campagnol-à-dos-roux de Gapper (*Clethrionomys gapperi* Vigors) et le Campagnol des champs (*Microtus pennsylvanicus* Ord). Nous avons également tenté de déterminer si le contenu hydrique du corps permet de prédire le contenu lipidique, ce qui justifierait l'utilisation d'une dilution des isotopes d'hydrogène pour estimer la condition physique. Chez les cinq espèces, les indices de la condition physique se sont révélés des indicateurs médiocres du contenu lipidique; ils permettent toutefois de prédire plus exactement la masse du corps sans les graisses, la masse sèche et le contenu en eau. La relation entre le contenu hydrique et le contenu lipidique n'est pas la même chez les cinq espèces, ce qui nous empêche de recommander la méthode de dilution des isotopes chez ces animaux. Malgré leur intérêt écologique, c'est comme facteurs explicatifs de la variation de toutes les composantes du corps que ces indices semblent le plus utiles.

[Traduit par la Rédaction]

Introduction

Body condition of an animal refers to its energetic state, so an animal in good condition has higher energy reserves (usually fat) than an animal in poor condition. In mammals, the amount of fat that an individual carries can have important fitness consequences. For instance, individuals with larger fat reserves may have better fasting endurance and higher survival than individuals with smaller reserves (Millar and Hickling 1990). There are also sex-specific consequences of variation in fat reserves. In female mammals, reproductive success is correlated with body condition; reproductive traits such as litter mass, number of litters, neonatal mass, and breeding life-span increase with body condition (Atkinson and Ramsay 1995; Dobson and Michener 1995; Wauters and Dhondt 1995). Males also expend a great amount of energy during male–male competition for mates, resulting in mass loss that may be attributable to mobilization of fat reserves (Clutton-Brock et al. 1982; Anderson and Fedak 1985; Deutsch et al. 1990). Conversely, carrying fat can have fitness consequences. Locomotion, and thus predator avoidance, can be compromised by heavy fat reserves (e.g., Trombulak 1989).

Measuring energy reserves unequivocally requires destructive sampling: the animal must be killed and dried and lipids extracted using solvents to determine fat content (Dobush et al. 1985). Often, however, researchers require a measure of condition that can be applied to longitudinal studies of individuals in wild populations. Selecting an appropriate index of condition can, however, be problematic. Generally, there are two methods that have been used. A ratio between body mass and some measure of structural size (e.g., body length) has been employed by many studies. This approach assumes that body mass and size scale isometrically, and an animal that has a higher ratio is in better condition than an animal with a lower ratio. Unfortunately, there is evidence that these types of indices are not independent of body mass or size (Lidicker and Ostfeld 1991; Jakob et al. 1996; J.P. Hayes, unpublished data), which compromises the value of the index. Alternatively, body mass is regressed on a measure of

Received November 29, 2000. Accepted April 26, 2001. Published on the NRC Research Press Web site at http://cjz.nrc.ca on June 13, 2001.

A.I. Schulte-Hostedde[1] and J.S. Millar. Ecology and Evolution Group, Department of Zoology, University of Western Ontario, London, ON N6G 5B7, Canada.
G.J. Hickling. Ecology and Entomology Group, Soil, Plant and Ecological Sciences Division, Lincoln University, P.O. Box 84, Canterbury, New Zealand.

[1]Corresponding author (e-mail: aischult@julian.uwo.ca).

 DOI: 10.1139/cjz-79-6-1021

Table 1. Mass, dry mass, and fat content for five species of small mammals sampled from the Kananaskis Valley, Alberta.

	Mass (g)	Dry mass (g)	Fat content (g)
Bushy-tailed wood rat	355.9 ± 80.63	88.37 ± 22.09	12.71 ± 7.73
Yellow-pine chipmunk	51.4 ± 4.17	12.51 ± 0.96	1.46 ± 0.46
Meadow vole	33.0 ± 6.79	8.14 ± 1.54	0.57 ± 0.29
Red-backed vole	25.6 ± 3.49	6.45 ± 0.84	0.53 ± 0.18
Deer mouse	21.5 ± 2.21	5.54 ± 0.59	1.06 ± 0.50

Note: Values are given as the mean ± SD.

Table 2. Morphological measurements used in the principal components analysis for five species of small mammals sampled from the Kananaskis Valley, Alberta.

	Bushy-tailed wood rat	Yellow-pine chipmunk	Meadow vole	Red-backed vole	Deer mouse
Body length (mm)	230 ± 13.6	120.6 ± 4.03	109.1 ± 7.58	97.8 ± 6.69	86.8 ± 6.24
Skull length (mm)	57.4 ± 2.77	36.5 ± 1.00	—	—	—
Skull width (mm)	—	18.3 ± 0.84	—	—	—
Hind-foot length (mm)	43.0 ± 2.29	—	18.0 ± 0.83	18.22 ± 0.76	20.3 ± 0.74
Ear length (mm)	—	—	14.7 ± 1.47	17.60 ± 1.14	18.9 ± 1.18

Note: Values are given as the mean ± SD.

Table 3. Summary table of PC1 from principal components analysis for five species of small mammals sampled from the Kananaskis Valley, Alberta.

	Bushy-tailed wood rat	Yellow-pine chipmunk	Meadow vole	Red-backed vole	Deer mouse
Percent variance	75.1	50.0	49.3	55.0	51.0
Body length	0.883	0.799	–0.718	0.840	0.756
Skull length	0.916	0.535	—	—	—
Skull width	—	0.757	—	—	—
Hind-foot length	0.803	—	0.620	0.460	0.679
Ear length	—	—	–0.761	0.856	0.726

Note: Percent variance refers to the percent variance in the data explained by PC1.

Table 4. Results of regressions between PC1 (body size) and body mass (*M*) for five species of small mammals sampled from the Kananaskis Valley, Alberta.

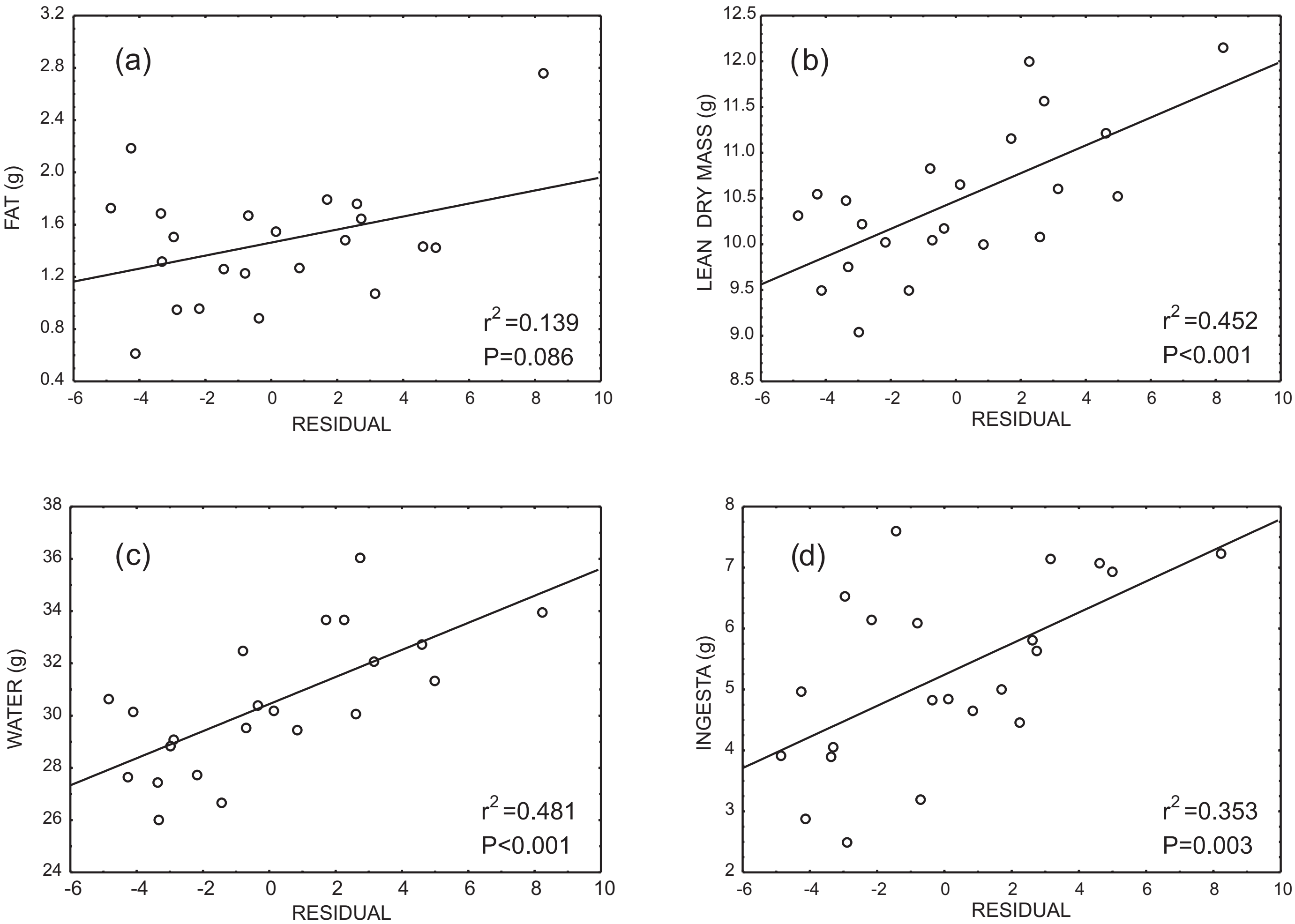
	Regression equation	r^2	*P*
Bushy-tailed wood rat	M = 355.92 + 68.15(PC1)	0.717	<0.001
Yellow-pine chipmunk	M = 51.49 + 2.31(PC1)	0.311	0.007
Meadow vole	M = –41.87 + 0.69(BL)	0.586	<0.001
Red-backed vole	M = 25.86 + 2.43(PC1)	0.487	<0.001
Deer mouse	M = 21.49 + 1.08(PC1)	0.240	< 0.001

Note: BL, body length. Body mass is measured in grams and body length is measured in millimetres.

body size and the residuals of this regression are used as an index of body condition; an individual with a positive residual is considered to be in better condition than an individual with a negative residual (e.g., Dobson 1992; Dobson and Michener 1995; Wauters and Dhondt 1995; Guinet et al. 1998). The latter "residual" approach is considered to be the most reliable index of condition because it does not vary with body size (Jakob et al. 1996; but see Kotiaho 1999). These and variations of these indices have been used for many taxa, including birds, fish, and invertebrates (e.g., Bailey 1979; Bolger and Connolly 1988; Jakob et al. 1996).

Despite widespread use of the regression approach to estimate condition, few studies have evaluated whether the resulting condition index (residuals) actually reflects fat content. Virgl and Messier (1993) evaluated this index of condition and found that it did not explain any variation in fat content in muskrats (*Ondatra zibethicus*). Krebs and Singleton (1993) used the body mass – body size regression to assess condition in house mice (*Mus domesticus*) by comparing actual mass with the mass predicted by the regression equation. This created a ratio in which an individual in average condition had a ratio of 1, an animal in poor

Fig. 1. Regressions between residuals taken from the PC1 – body mass regression and fat content (*a*), lean dry mass (*b*), water content (*c*), and ingesta (*d*) for yellow-pine chipmunks.



condition had a ratio <1, and an animal in good condition had a ratio >1. They compared these indices with measured percent fat (expressed as percent fat of whole-body mass) and found no relationship (Krebs and Singleton 1993).

Ratio indices of condition have limited utility (Jakob et al. 1996). For instance, Lidicker and Ostfeld (1991) used the ratio of body mass to body length in California voles (*Microtus californicus*) and found that this index explained 48% of the variation in fat content but concluded that this index carries little information besides body mass because the index and body mass were not independent (r^2 = 0.96).

A caveat to the interpretation of condition indices as estimates of fat content is that components of body composition include protein, ash, and water content, as well as fat content, and variation in one or more of these components can compromise interpretation of these indices. As well, variation in mass of ingesta may confound condition estimates unless ingesta is a constant proportion of body mass.

An alternative to morphometric indices of condition is the use of hydrogen-isotope dilution, which can measure total body water (Bowen and Iverson 1998; Coltman et al. 1998). Fat is hydrophobic and so water may be negatively related to the amount of fat that an animal carries, as was found by Winstanley et al. (1998).

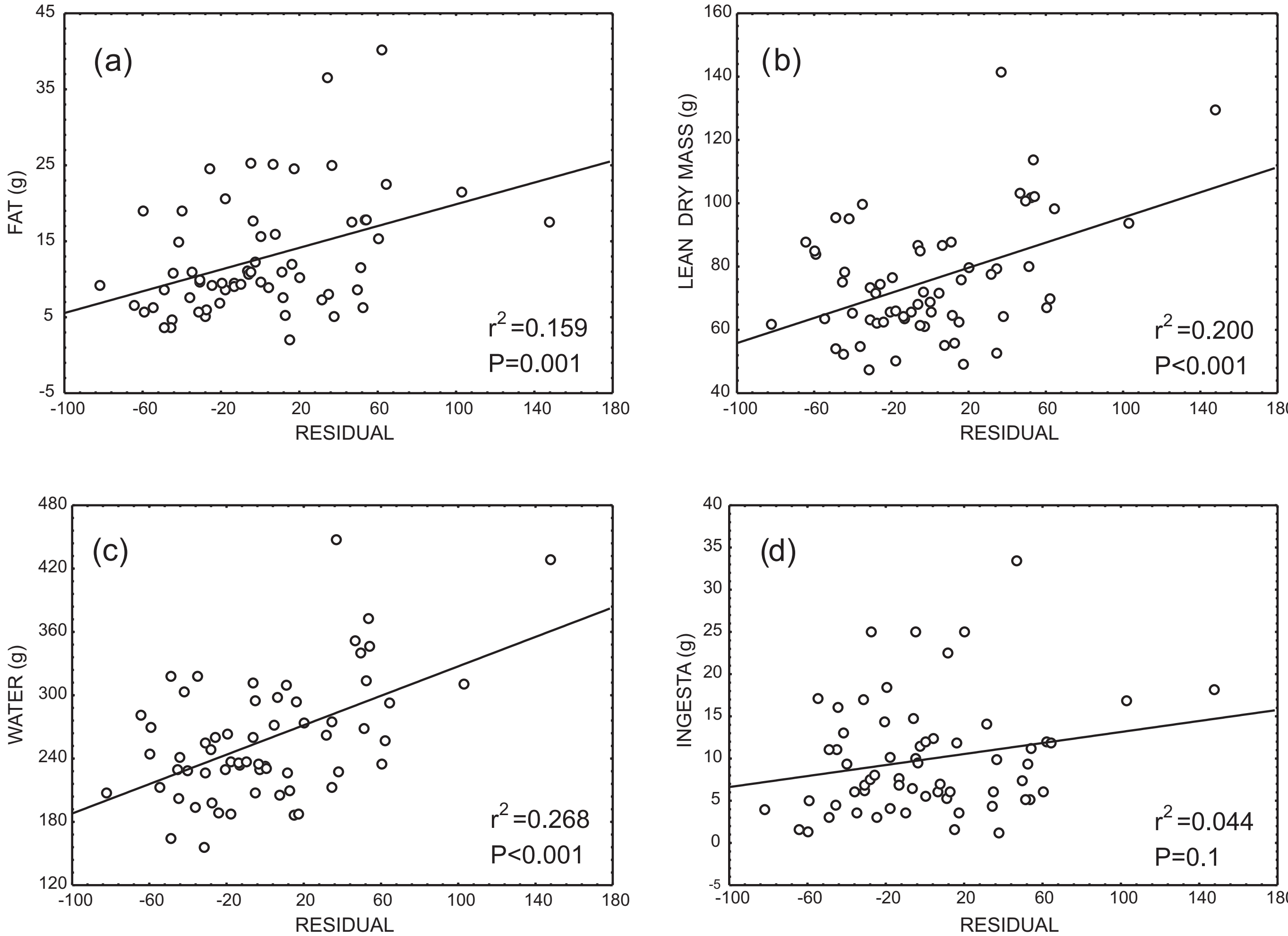
Because many studies have used residuals from the mass–size regression to estimate condition in mammals and because residuals are considered most appropriate for assessing body condition from external measurements, we used data from five species of small mammals from the Kananaskis Valley, Alberta, for which we have both structural size measurements and measures of body fat to determine (*i*) whether the index of condition based on residuals is correlated with actual measurements of fat content and (*ii*) if hydrogen-isotope dilution would be effective in estimating body fat in these animals by examining the relationship between body water and body fat.

Methods

We used data from five species of small mammals, all collected in the Kananaskis Valley, Alberta, in the Front Ranges of the Rocky Mountains (51°N, 115°W): yellow-pine chipmunks (*Tamias amoenus* Allen), bushy-tailed wood rats (*Neotoma cinereus* Ord), deer mice (*Peromyscus maniculatus* Wagner), red-backed voles (*Clethrionomys gapperi* Vigors), and meadow voles (*Microtus pennsylvanicus* Ord). All animals used in the analyses were adult males or adult females that were not pregnant or lactating.

Chipmunks (n = 23) were livetrapped from early May to late August 1998 using Longworth live traps (baited with whole oats

Fig. 2. Regressions between residuals taken from the PC1 – body mass regression and fat content (*a*), lean dry mass (*b*), water content (*c*), and ingesta (*d*) for bushy-tailed wood rats.



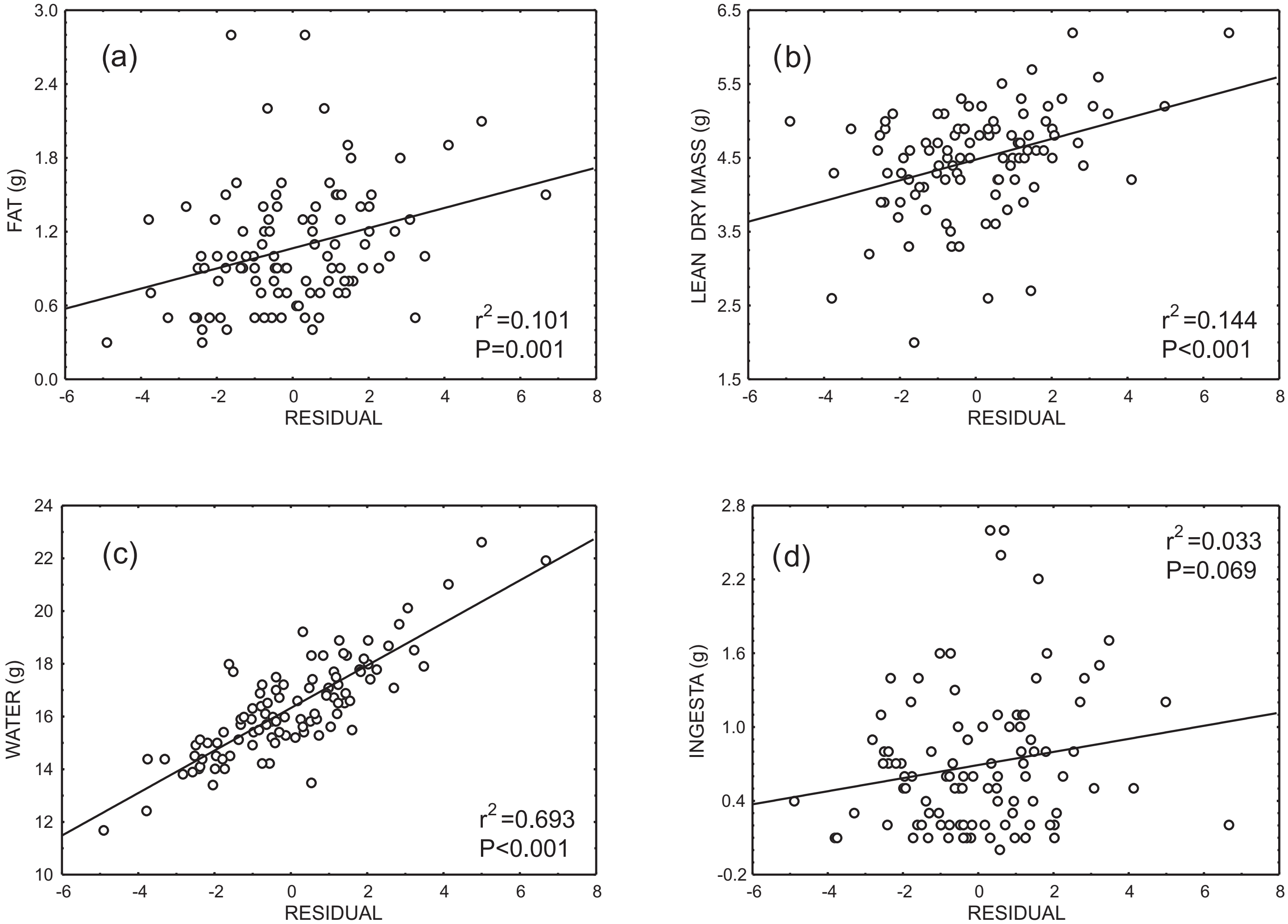
and sunflower seeds) and euthanized with an overdose of isofluorine. Body mass (±0.01 g), total body length (including tail) (±1 mm), tail length (±1 mm), skull length (±0.1 mm), and skull width (±0.1 mm) were measured and each body was frozen. Wood rats (n = 62) were collected in the summer and winter of 1984–1985 using Conibear kill traps (Hickling 1987; Hickling et al. 1991). Body mass (±0.1 g), total body length (including tail) (±1 mm), tail length (±1 mm), skull length (±0.5 mm), and hind-foot length (±0.5 mm) were measured and each body was frozen. Deer mice (n = 100), red-backed voles (n = 86), and meadow voles (n = 34) were collected from early May to late August 1987 using snap traps baited with a small string that had been soaked in aromatic oils and then tied to the treadle (Millar et al. 1990). Body mass (±0.1 g), total body length (including tail) (±1 mm), tail length (±1 mm), hind-foot length (±1 mm), and ear length (±1 mm) were measured and each body was frozen (Millar 1987; Millar et al. 1990).

Fat extractions were performed following Kerr et al. (1982) and Dobush et al. (1985). For chipmunks, deer mice, and voles, whole bodies except for stomach contents were dried, ground in a Wiley Mill or a Moulinex coffee grinder, and fat content was determined using petroleum ether in a Soxhlet fat extractor. Mass of stomach contents was measured (±0.01 g). Wood rat carcasses (excluding stomach contents (weighed separately (±0.1 g)), skull, and pelt) were ground in a meat grinder and dried. The carcass was then ground again in a Moulinex coffee grinder. Fat extraction was performed on two 4-g subsamples. We used a subsampling approach because it would be logistically difficulty to extract fat from so many relatively large animals. We assumed that these subsamples accurately represented body composition of the wood rats. Fat content of the pelt was determined by soaking the intact pelt in ether for 24 h. Total fat content was calculated as the mean of the two replicate estimates of carcass fat plus pelt fat (Hickling et al. 1991). Fat extractions for all species were performed at the Department of Zoology, University of Western Ontario. For all species, we calculated water content as the difference between fresh mass (without stomach contents) and the mass of the carcass after drying. Lean dry mass was determined by the mass of the carcass following fat removal.

To measure structural size, we conducted a principal components analysis on log-transformed body size variables for each of the five species (Iskjaer et al. 1989; Dobson 1992). The first principal component (PC1) was used as an index of structural size if all body-size variables were positively correlated with PC1 (Pimentel 1979). If this was not the case, body length was used as an index of body-size. All variables were entered into the analysis as measured except for total body length and tail length. Body length was calculated by subtracting tail length from total body length.

To calculate the estimate of body condition, we regressed mass on PC1 or body length for each species and used the residuals as

Fig. 3. Regressions between residuals taken from the PC1 – body mass regression and fat content (*a*), lean dry mass (*b*), water content (*c*), and ingesta (*d*) for deer mice.



an index of condition. To determine whether these residuals reflected fat content, we regressed the estimates of condition on absolute fat (g), lean dry mass (g), water content (g), and ingesta (g).

To determine how closely body mass was associated with body fat (i.e., is body mass a better index of condition than the residual condition index?), we regressed body fat (g) against whole-body mass (g) (including stomach contents) for each of the five rodent species.

To determine the relationship between body water and body fat, we regressed percent body fat (%) on percent body water (%) (both variables arcsine-transformed) for each of the five species.

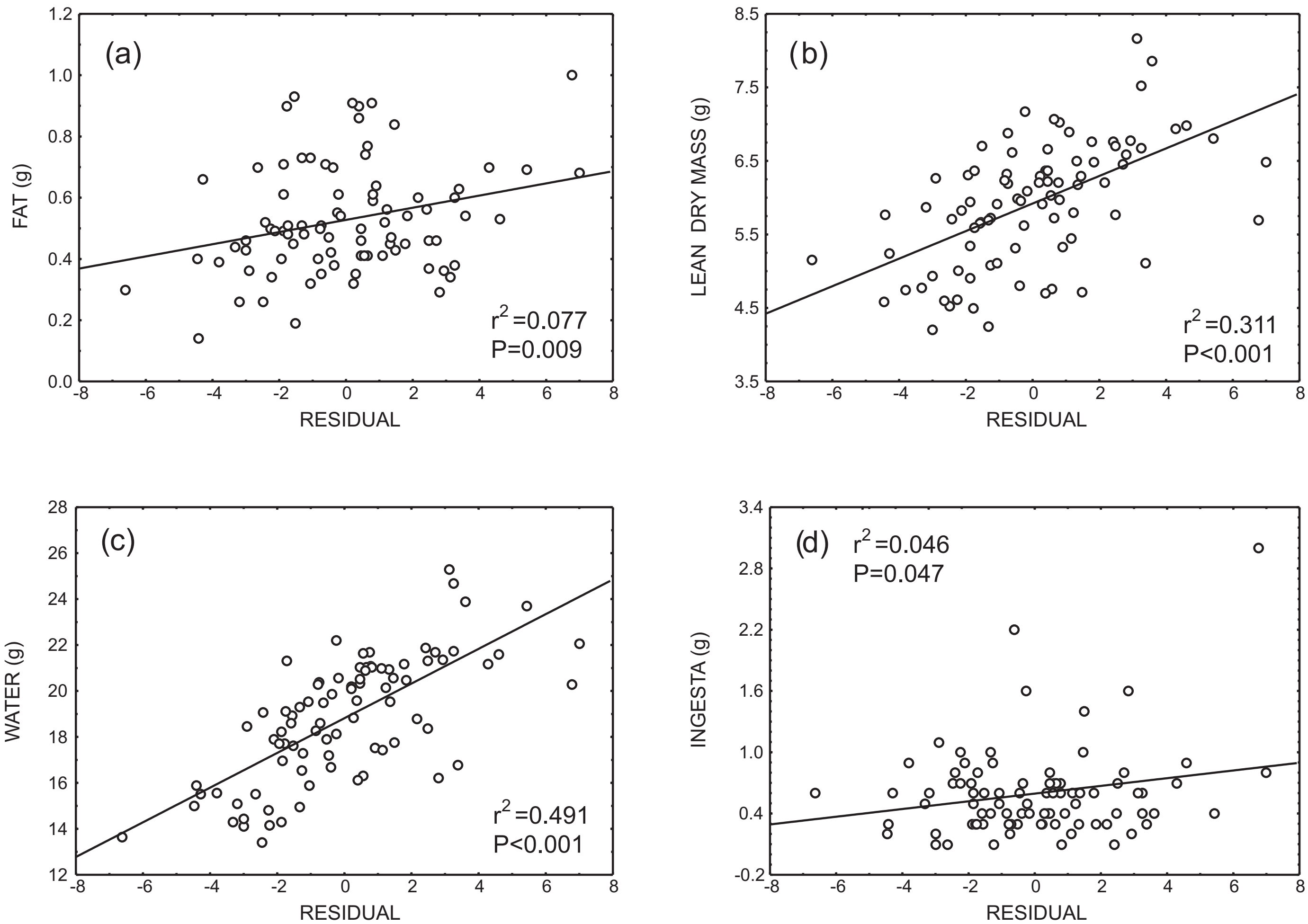
Results

On average, deer mice had the highest proportion of total body mass as fat (4.9%) compared with wood rats (3.6%), chipmunks (2.8%), red-backed voles (2.1%), and meadow voles (1.7%) (Table 1). Based on standard error, we found body length to be the most variable of the structural measurements made for all species except chipmunks (Table 2).

PC1 of morphological measurements for chipmunks, wood rats, deer mice, and red-backed voles was used to estimate body size. PC1 explained at least 50% of the overall variation in size measurements for these species (Table 3). All morphological measurements loaded positively and higher than 0.5 on PC1 except for hind-foot length of red-backed voles (0.46). Factor loadings for meadow voles were not in a consistent direction. Body length and ear length were negatively correlated with PC1, but hind-foot length was positively correlated with PC1 (Table 3). Therefore, to describe body size in meadow voles, we used body length because it was used in other studies of voles (Heske and Ostfeld 1990), and we used scores from PC1 for all other species.

For each species, we regressed body mass on body size and used the residuals as an index of condition (Table 4). All regressions were highly significant ($P < 0.001$) for all species except for chipmunks ($P = 0.03$). We removed a chipmunk that was an outlier from the regression, which improved r^2 from 0.19 to 0.31 and P from 0.03 to 0.007. We removed this chipmunk from our analyses because the residual of this individual was much lower than that of any of the other chipmunks. We therefore assumed that the outlier chipmunk was sick in some way and excluded it. Throughout the remaining analyses, we did not use this outlier chipmunk. Variance in mass explained by body size ranged from 24% in deer mice to 71.7% in wood rats (Table 4). Body mass and body size were more closely correlated in wood rats and

Fig. 4. Regressions between residuals taken from the PC1 – body mass regression and fat content (*a*), lean dry mass (*b*), water content (*c*), and ingesta (*d*) for red-backed voles.



both vole species than in deer mice and chipmunks. Residuals from these regressions weakly reflected variation in fat content for all species. Regressions between the residuals and absolute fat content were significant for wood rats, deer mice, and red-backed voles (Figs. 1–5). In all cases the variance in fat content explained by the residuals was low (r^2 < 0.2). Because residuals may reflect variation in other components of body mass, we also regressed the residuals on water content, lean dry mass, and ingesta. Residuals consistently explained more variation in lean dry mass than fat content in all species (Figs. 1–5). Regressions between residuals and ingesta were significant in chipmunks and red-backed voles, marginally significant in deer mice, and nonsignificant in wood rats and meadow voles (Figs. 1–5).

The relationship between body mass and body fat was not uniformly better than between the residual index of condition and body fat. Body mass was a better predictor of body fat than the condition index in chipmunks (r^2 = 0.193, P = 0.004) and meadow voles (r^2 = 0.148, P = 0.024) but not in wood rats (r^2 = 0.128, P = 0.004), deer mice (r^2 = 0.056, P = 0.017), or red-backed voles (r^2 = 0.036, P = 0.078).

The utility of body water to predict body fat was inconsistent. The relationship between these two variables was not significant for chipmunks, red-backed voles, and meadow voles, significantly positive for deer mice, and negative for wood rats (Table 5).

Discussion

There are two major conclusions that can be drawn from our results. First, residuals from the mass–size regression are relatively poor predictors of fat content and explain more variation in lean dry mass and water content than in fat content in all five species. Second, percent water is not consistently related to percent fat, which questions the general utility of hydrogen-isotope dilution as a predictor of fat content.

Despite the use of residuals as an index of condition in many studies (e.g., Dobson and Michener 1995; Wauters and Dhondt 1995; Guinet et al. 1998; Fisher 1999), it should not be surprising that residuals do not correlate with fat content. Both Krebs and Singleton (1993) and Virgl and Messier (1993) found no relationship between condition indices derived from the body mass – body size regression and actual measured in house mice and muskrats, respectively. This begs the question what does the index of condition actually represent? Clearly, these indices are ecologically significant, since they correlate with various aspects of mammalian life

Fig. 5. Regressions between residuals taken from the body length – body mass regression and fat content (*a*), lean dry mass (*b*), water content (*c*), and ingesta (*d*) for meadow voles.

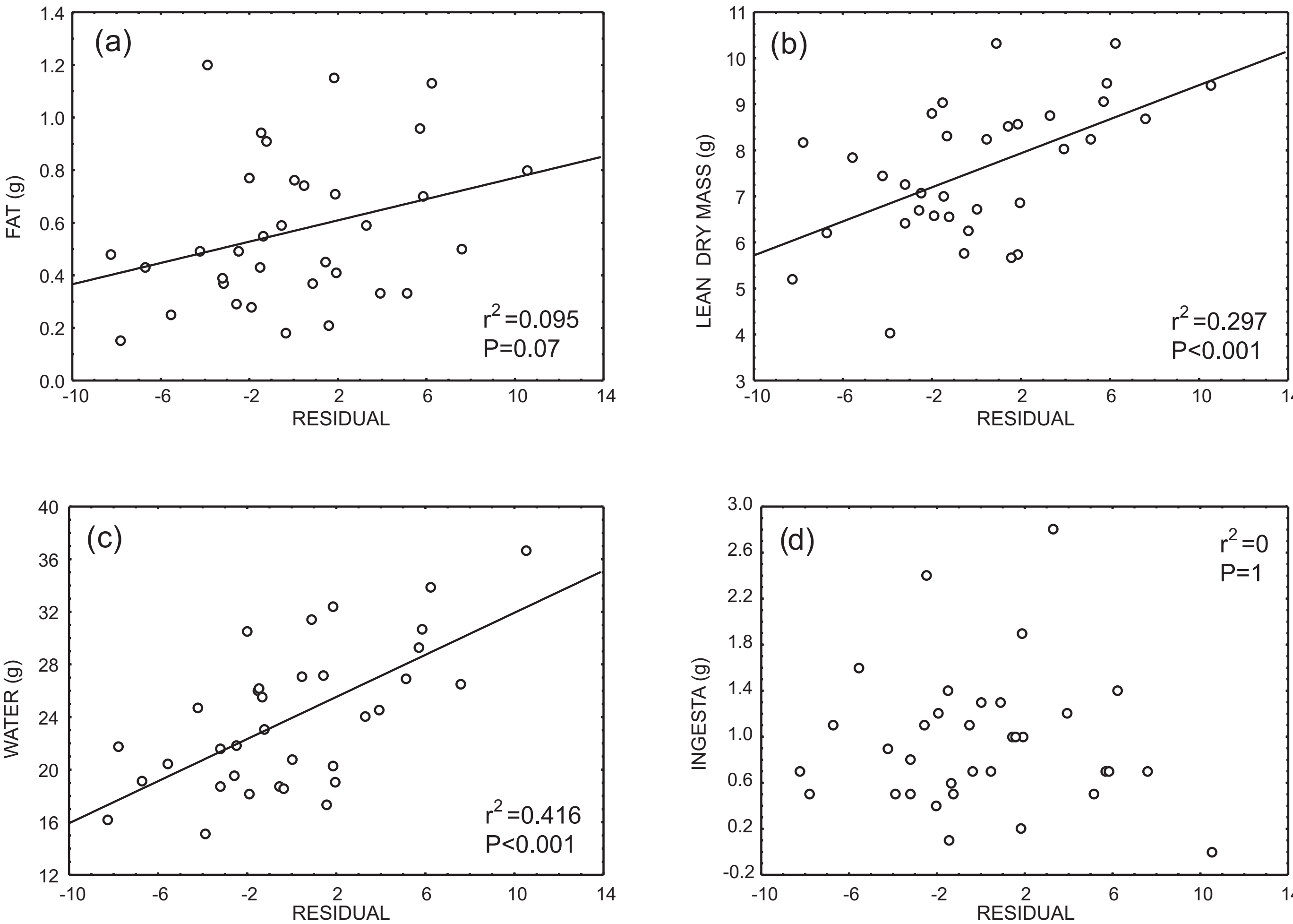


Table 5. Results of regressions between percent body water (%WATER) and percent body fat (%FAT) for five species of small mammals sampled from the Kananaskis Valley, Alberta.

	Regression equation	r^2	*P*
Bushy-tailed wood rat	%FAT = 0.372 – 0.414(%WATER)	0.315	<0.001
Yellow-pine chipmunk	%FAT = 0.086 – 0.089(%WATER)	0.117	0.119
Meadow vole	%FAT = –0.036 + 0.067(%WATER)	0.061	0.159
Red-backed vole	%FAT = 0.006 + 0.018(%WATER)	0.005	0.527
Deer mouse	%FAT = –2.08 + 0.298(%WATER)	0.629	0.001

history (e.g., Dobson 1992; Dobson and Michener 1995; Wauters and Dhondt 1995; Dobson et al. 1999; Fisher 1999), but they do not seem to reflect variation in fat content. Our results show that the body condition index reflects variation in water content, lean dry mass (composed mostly of protein), and in the case of chipmunks, ingesta. Lean body mass is therefore not constant and variation in mass is the result of variation in all body components, especially protein and water content. Because fat content is such a small proportion of body mass among our five species (1.7–4.9%), any variation in fat content is unlikely to be reflected in variation in body mass, especially if there is also variation in other components. Because condition indices correlate with aspects of mammalian life history, it is interesting to speculate whether protein is used as a source of energy in small mammals. During winter, when food resources are low, northern red-backed voles (*Clethrionomys rutilus*) and muskrats have lower protein reserves than when food resources are high (Virgl and Messier 1992; Zuercher et al. 1999). Although this may serve to minimize metabolic requirements (Zuercher et al. 1999), small mammals carry little fat as energy reserves and may catabolize protein to meet some energy requirements.

The result that residuals explain 35% of the variation in ingesta in chipmunks and explain very little variation in ingesta in the other four species has some methodological implications. Chipmunks were the only species livetrapped and then euthanized. Traps were baited with oats and sunflower seeds, which were presumably consumed by the chipmunks. Conversely, all the other species were kill-trapped, and in the case of deer mice, red-backed voles, and meadow voles, traps were specifically baited with material that could not be consumed (string soaked in aromatic oils) because stomach contents were of interest (Millar et al. 1990). Wood rat traps were baited with peanut butter (Hickling 1987). This result suggests that if condition is of primary interest and animals are being livetrapped, it may be important to (*i*) use very little to no bait or (*ii*) allow animals to process bait through their gut before weighing them. For deer mice, this can be between 2 and 15 h, depending on the water content of the seeds used as bait (Reid and Brooks 1994; also see Norrie and Millar (1990) for voles).

Alternative methods of calculating body condition exist. Many studies use a ratio between body mass and some measure of structural size. For example, Lidicker and Ostfeld (1991) used the ratio of body mass to body length in California voles to assess condition. Logically, individuals that are heavier for their size should be in better “condition”; however, they found that this index was not independent of body mass (Lidicker and Ostfeld 1991). We found the same pattern among all five of our species. The ratio of body mass to body length was highly correlated with body mass ($r^2 > 0.8$, $P < 0.001$ for all species). Ratio-type indices are often not independent of body size (J.P. Hayes, unpublished data). We also determined that variation in body fat explained by body mass alone was not substantially different from the condition indices.

The inconsistent relationship between body water and body fat indicates that hydrogen-isotope dilution should not be considered a universal method for determining fat content in small mammals. The predicted negative relationship between fat content and water content was only found in wood rats. There was no relationship between fat content and water content in chipmunks, red-backed voles, and meadow voles, but there was a positive relationship between fat content and water content in deer mice.

It is important to note that indices of condition may be appropriate for species that show more variation in fat content. Here, we have evaluated whether the residual index of condition is correlated with fat content for four non-hibernating species and one hibernating rodent (yellow-pine chipmunk), which caches food (rather than depositing fat) for winter. The poor relationship between the condition index and measured fat content may be because these animals are very lean (1–5% body fat) and variation in body fat is a very small proportion of overall body mass. In species where fat content is a higher proportion of body mass, residual indices may be more appropriate. For instance, hibernating rodents can deposit large amounts of fat, and variation in body mass may more likely be the result of variation in body fat. Under these circumstances, residual indices may be more likely to reflect variation in fat content.

If measuring variation in body fat is of primary concern, there is an alternative method that can be applied to live animals; total body electronic conductivity (TOBEC) (Walsberg 1988) has been used in studies of mammalian and avian energetics (e.g., Voltura and Wunder 1998; Bachman and Widemo 1999) and requires a species-specific calibration curve (Frawley et al. 1999). TOBEC estimates fat-free wet mass with an associated amount of error, but because fat is such a small component of body mass in many small birds and mammals, accurate estimates of fat content using this method are compromised (Zuercher et al. 1997; Frawley et al. 1999).

We conclude that in small mammals, residuals from the body mass – body size regression are more accurate indicators of variation in protein and water content than in fat content. These condition indices appear to be ecologically important, although they are best interpreted as explaining variation in all constituents of body composition rather than just in fat content.

Acknowledgements

We thank past research assistants who measured body size and analyzed body composition of the animals used in this study. Previous versions of the manuscript were improved by comments from C.D. Ankney, J.P. Hayes, M.C. Kalcounis, and P.J. Weatherhead and discussion with J. Arbour and S. Robinson. Suggestions from S. Dobson and an anonymous reviewer also improved the manuscript. We especially thank L. Brown for vigorous discussion. This study was supported by an operating grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to J.S.M. and a NSERC postgraduate scholarship to A.I.S.H.

References

Anderson, S.S., and Fedak, M.F. 1985. Grey seal males: energetic and behavioural links between size and sexual success. Anim. Behav. **33**: 829–838.

Atkinson, S.N., and Ramsay, M.A. 1995. The effects of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). Funct. Ecol. **9**: 559–567.

Bachman, G., and Widemo, F. 1999. Relationships between body composition, body size and alternative reproductive tactics in a lekking sandpiper, the Ruff (*Philomachus pugnax*). Funct. Ecol. **13**: 411–416.

Bailey, R.O. 1979. Methods of estimating total lipid content in the redhead duck (*Aythya americana)* and an evaluation of condition indices. Can. J. Zool. **57**: 1830–1833.

Bolger, T., and Connolly, P. 1988. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. **34**: 171–182.

Bowen, W.D., and Iverson, S.J. 1998. Estimation of total body water in pinnipeds using hydrogen-isotope dilution. Physiol. Zool. **71**: 329–332.

Clutton-Brock, T.H., Albon, S.D., and Guiness, F.E. 1982. Red deer: ecology and behaviour of two sexes. Chicago University Press, Chicago.

Coltman, D.W., Bowen, W.D., Iverson, S.J., and Boness, D.J. 1998. The energetics of male reproduction in an aquatically mating pinniped, the harbour seal. Physiol. Zool. **71**: 387–399.

Deutsch, C.J., Haley, M.P., and Le Boeuf, B.J. 1990. Reproductive effort of male northern elephant seals: estimates from weight loss. Can. J. Zool. **68**: 2580–2593.

Dobson, F.S. 1992. Body mass, structural size, and life-history patterns of the Columbian ground squirrel. Am. Nat. **140**: 109–125.

Dobson, F.S., and Michener, G.R. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology, **76**: 851–862.
Dobson, F.S., Risch, T.S., and Murie, J.O. 1999. Increasing returns in the life-history of Columbian ground squirrels. J. Anim. Ecol. **68**: 73–86.
Dobush, G.R., Ankney, C.D., and Krementz, D.G. 1985. The effect of apparatus, extraction time, and solvent type on lipid extraction in snow geese. Can. J. Zool. **63**: 1917–1920.
Fisher, D.O. 1999. Offspring sex-ratio variation in the bridled nailtail wallaby, *Onychogalea fraenata*. Behav. Ecol. Sociobiol. **45**: 411–419.
Frawley, B.J., Osborne, D.O., Weeks, H.P., Burger, L.W., and Dailey, T.V. 1999. Use of total body electrical conductivity to predict northern bobwhite lipid mass. J. Wildl. Manag. **63**: 695–704.
Guinet, C., Roux, J.P., Bonnet, M., and Mison, V. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. Can. J. Zool. **76**: 1418–1424.
Heske, E.J., and Ostfeld, R.S. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. J. Mammal. **71**: 510–519.
Hickling, G.J. 1987. Seasonal reproduction and group dynamics of bushy-tailed woodrats, *Neotoma cinerea*. Ph.D. thesis, University of Western Ontario, London.
Hickling, G.J., Millar, J.S., and Moses, R.A. 1991. Reproduction and nutrient reserves of bushy-tailed wood rats (*Neotoma cinerea*). Can. J. Zool. **69**: 3088–3092.
Iskjaer, C., Slade, N.A., Childs, J.E., Glass, G.E., and Korch, G.W. 1989. Body mass as a measure of body size in small mammals. J. Mammal. **70**: 662–667.
Jakob, E.M., Marshall, S.D., and Uetz, G.W. 1996. Estimating fitness: a comparison of body condition indices. Oikos, **77**: 61–67.
Kerr, D.C., Ankney, C.D., and Millar, J.S. 1982. The effect of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. Can. J. Zool. **60**: 470–472.
Kotiaho, J.S. 1999. Estimating fitness: comparison of body condition indices revisited. Oikos, **87**: 399–400.
Krebs, C.J., and Singleton, G.R. 1993. Indices of condition for small mammals. Aust. J. Zool. **41**: 317–323.
Lidicker, W.Z., and Ostfeld, R.S. 1991. Extra-large body size in California voles: causes and fitness consequences. Oikos, **61**: 108–121.
Millar, J.S. 1987. Energy reserves in breeding small rodents. Symp. Zool. Soc. Lond. No. 57. pp. 231–240.
Millar, J.S., and Hickling, G.J. 1990. Fasting endurance and the evolution of mammalian body size. Funct. Ecol. **4**: 5–12.
Millar, J.S., Xia, X., and Norrie, M.B. 1990. Relationships among reproductive status, nutritional status, and food characteristics in a natural population of *Peromyscus maniculatus*. Can. J. Zool. **69**: 555–559.
Norrie, M.B., and Millar, J.S. 1990. Food resources and reproduction in four microtine rodents. Can. J. Zool. **68**: 641–650.
Pimentel, R.A. 1979. Morphometrics: the multivariate analysis of biological data. Kendell/Hunt Publishing Co., Dubuque, Iowa.
Reid, E.D., and Brooks, R.J. 1994. Effect of water on retention time and food consumption in deer mice. Can. J. Zool. **72**: 1711–1714.
Trombulak, S.C. 1989. Running speed and body mass in Belding's ground squirrels. J. Mammal. **70**: 194–197.
Virgl, J.A., and Messier, F. 1992. Seasonal variation in body composition and morphology of adult muskrats in central Saskatchewan, Canada. J. Zool. (Lond.), **228**: 461–477.
Virgl, J.A., and Messier, F. 1993. Evaluation of body size and body condition indices in muskrats. J. Wildl. Manag. **57**: 854–860.
Voltura, M.B., and Wunder, B.A. 1998. Effects of ambient temperature, diet quality, and food restriction on body composition dynamics of the prairie vole, *Microtus ochrogaster*. Physiol. Zool. **71**: 321–328.
Walsberg, G.E. 1988. Evaluation of a non-destructive method for determining fat stores in small birds and mammals. Physiol. Zool. **61**: 153–159.
Wauters, L.A., and Dhondt, A.A. 1995. Lifetime reproductive success and its correlates in female Eurasian red squirrels. Oikos, **72**: 402–410.
Winstanley, R.K., Saunders, G., and Buttemer, W.A. 1998. Indices for predicting total body fat in red foxes in Australia. J. Wildl. Manag. **62**: 1307–1312.
Zuercher, G.L., Roby, D.D., and Rexstad, E.A. 1997. Validation of two new total body electrical conductivity (TOBEC) instruments for estimating body composition of live northern red-backed voles *Clethrionomys rutilus*. Acta Theriol. **42**: 387–397.
Zuercher, G.L., Roby, D.D., and Rexstad, E.A. 1999. Seasonal changes in body mass, composition, and organs of northern red-backed voles in interior Alaska. J. Mammal. **80**: 443–459.