RESTITUTION OF MASS–SIZE RESIDUALS: VALIDATING BODY CONDITION INDICES

Albrecht I. Schulte-Hostedde,[1,5] Bertram Zinner,[2] John S. Millar,[3] and Graham J. Hickling[4]

[1]*Department of Biology, Laurentian University, Sudbury, Ontario P3E 2C6 Canada*
[2]*Department of Mathematics and Statistics, Auburn University, Auburn, Alabama 36849 USA*
[3]*Department of Biology, University of Western Ontario, London, Ontario N6A 5B7 Canada*
[4]*Department of Fisheries and Wildlife, Michigan State University, Lansing, Michigan 48824 USA*

Abstract. Body condition can have important fitness consequences, but measuring body condition of live animals from wild populations has been the subject of much recent debate. Using the residuals from a regression of body mass on a linear measure of body size is one of the most common methods of measuring condition and has been used in many vertebrate taxa. Recently, the use of this method has been criticized because assumptions are likely violated. We tested several assumptions regarding the use of this method with body composition and morphometric data from five species of small mammals and with statistical simulations. We tested the assumptions that the relationship between body mass and body size is linear, and that the proportion of mass associated with energy reserves is independent of body size. In addition, we tested whether the residuals from reduced major axis (RMA) regression or major axis (MA) regression performed better than the residuals from ordinary least squares (OLS) regression as indices of body condition. We found no evidence of nonlinear relationships between body mass and body size. Relative energy reserves (fat and lean dry mass) were generally independent or weakly dependent on body size. Residuals from MA and RMA regression consistently explained less variation in body composition than OLS regression. Using statistical simulations, we compared the effects of violations of the assumption that true condition and residual indices are independent of body size on the OLS, MA, and RMA procedures and found that OLS performed better than the RMA and MA procedures. Despite recent criticisms of residuals from mass–size OLS regressions, these indices of body condition appear to satisfy critical assumptions. Although some caution is warranted when using residuals, especially when both inter-individual variation in body size and measurement error are high, we found no reason to reject OLS residuals as legitimate indices of body condition.

Key words: body condition; body mass; body size; Clethrionomys gapperi; *fat;* Microtus pennsylvanicus; Neotoma cinerea; Peromyscus maniculatus; *reduced major axis; regression analysis; residuals;* Tamias amoenus.

INTRODUCTION

The body condition of an animal refers to its energetic state. An animal in good condition is assumed to have more energy reserves than an animal in poor condition. For instance, individuals with larger energy reserves may have better fasting endurance and higher survival than individuals with smaller reserves (Millar and Hickling 1990). Other fitness parameters related to reproduction and survival have been found to correlate with body condition among many taxa (e.g., Dobson 1992, Dobson and Michener 1995, Wauters and Dhondt 1995, Bachman and Widemo 1999, Shine et al. 2001).

Measuring the body condition of live animals has been the subject of much recent debate (Jakob et al. 1996, Kotiaho 1999, Green 2001, Hayes and Shonk-wiler 2001, Schulte-Hostedde et al. 2001, Speakman 2001). However, the common objective has been to determine the mass of an individual relative to its body size. An animal can be heavy because it is structurally large or because it is carrying metabolizable tissue such as fat and protein (Dobson 1992). Indices of body condition attempt to determine the mass of the individual associated with energy reserves after correcting for structural body size. One of the most common methods used to measure condition involves regressing body mass on some linear index of body size, and using the residuals from this regression (typically ordinary least squares [OLS] regression) 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 (Jakob et al. 1996, Schulte-Hostedde et al. 2001).

Recently, Green (2001) reviewed the use of residual indices of condition in ecological studies and identified six key assumptions underlying this methodology that are likely to be violated in some or all studies. These assumptions fall into three categories. The first two are related to the initial regression between body mass and

PLATE 1. Yellow-pine chipmunk (*Tamais amoenus*). Photo credit: J. S. Millar.

body size. These assumptions are (1) that mass increases linearly with body size (or the body size indicator [BSI]), and (2) that the residual index of condition and true condition (the proportion of mass associated with energy reserves) of an animal are independent of body size (or BSI). Assumptions 3 and 4 are related to the index of body size: (3) that the index of body size (BSI) is an accurate measure of overall structural size, and (4) that there is no correlation between the BSI relative to other structural components and the parameter against which the residual index of condition is analyzed. The final assumptions are related to the use of OLS regression in determining residual indices of condition. Ordinary least squares (OLS) regression assumes (5) that X is strictly independent of Y (i.e., that X and Y are not mutually interdependent), and (6) that there is no ''error'' in X (i.e., the scatter in points around a slope is due to variation in Y, not X). Green (2001) concluded that many of these assumptions are likely violated in some or all studies, and suggested that alternative regression models such as model II regression or nonparametric methods should be used to calculate residual indices of condition.

Because of the extensive use of residuals as indices of condition (e.g., mammals: Dobson et al. 1999, Fisher 1999; birds: Schluter and Gustafsson 1993, Weatherhead et al. 1999, Merilä et al. 2001; amphibians: Judge and Brooks 2001; reptiles: Weatherhead et al. 1995, Shine et al. 2001), it is critical that assumptions and criticisms of this statistical technique be empirically tested with appropriate data. Recently, we attempted to determine whether the residual index of condition (as calculated from OLS regression between body mass and body size) was correlated with actual measurements of body fat in five species of small mammals (Schulte-Hostedde et al. 2001). Residual indices were weakly correlated with fat, and more closely correlated with lean dry mass (composed mostly of muscle protein) and water. Here, we reexamine these data to determine whether Green's (2001) concerns regarding the

use of residuals from ordinary least squares regression are valid, and whether the assumptions which Green (2001) outlined are likely to be violated in field studies.

For each of five species of small mammals, we first assessed linearity between body mass and body size. We then determined whether the portion of body mass composed of energy reserves (body fat and lean dry mass, which is predominantly composed of protein) was independent of body size. Our major goal was to determine which regression model produced residuals that best predicted energy reserves. We used residuals from OLS regression between a multivariate index of body size (derived from a principal-components analysis) and body mass. It has been suggested that using multiple regression to determine the direct relationship between condition and an independent variable is a preferred alternative to the use of residuals (Hayes and Shonkwiler 2001). Thus we conducted a multiple regression between body size and body mass, and components of body mass (fat, lean dry mass, and water). We interpreted the partial correlation coefficients between body mass and body components as measures of the relationship between ''condition'' and body composition. Green (2001) suggested that alternative (Model II) regression models such as reduced major axis (RMA) regression and major axis (MA) regression should be preferred over OLS regression, because they assume that error occurs in X as well as Y (where X corresponds to the measure of body size). Ordinary least squares (OLS) regression assumes that there is no error in X, because X is set by the researcher (McArdle 1988). We assessed the relationship between residuals obtained from both MA and RMA regression and body composition, and compared this relationship to that found between residuals from OLS regression and body composition. Finally, we used numerical simulations to compare the effects of a violation of the assumption that the residual index of condition and true condition (the proportion of mass associated with energy reserves) of an animal are independent of body size (or BSI; Green 2001) on the different regression procedures (OLS, MA, RMA).

METHODS

We used data from five species of small mammal collected in the Kananaskis Valley, Alberta, Canada, in the Front Ranges of the Rocky Mountains (51° N, 115° W): yellow-pine chipmunks (*Tamias amoenus* Allen; see Plate 1), bushy-tailed woodrats (*Neotoma cinerea* Ord; see Appendix), deer mice (*Peromyscus maniculatus* Wagner), red-backed voles (*Clethrionomys gapperi* Vigors), and meadow voles (*Microtus pennsylvanicus* Ord). All animals used in the analyses were either adult males or adult females, which were not pregnant or lactating.

Chipmunks ($n = 22$) were live trapped from early May to late August 1998 using Longworth live traps (baited with whole oats and sunflower seeds) and eu-

thanized with an overdose of isoflourine. 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. Woodrats ($n = 62$) were collected in summer and winter of 1984–1985 using Conibear kill-traps (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 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, tail length, hind foot length, and ear length (all ± 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 (excluding 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). Woodrat 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. 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 in the Department of Biology, 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 both water and fat removal.

To measure overall structural size, we conducted a principal-components analysis of log-transformed body size variables for each of the five species (Iskjaer et al. 1989, Dobson 1992). The first principal component (PC1) was only used as an index of structural size if all body size variables were positively correlated with PC1 (Pimentel 1979). 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. We log-transformed and standardized (mean of 0, standard deviation of 1) body mass and body size (PC1 scores) in all analyses to remove the heteroscedastic nature of the data and standardize all variables measured with different units (i.e., mass, PC scores). Residuals obtained using untransformed body mass tended to increase with body size (PC1).

Assessing linearity

We assessed whether the relationship between body mass and body size (PC1 and body length) was linear by inspecting plots of the residuals and the independent variable (body size). If the residuals were evenly distributed across the range of body sizes, we assumed that the relationship was linear. In addition, we conducted quadratic regressions to determine whether the addition of a second order term would improve the proportion of variation in body mass explained by body size. Colinearity between X and X^2 may occur in polynomial regressions, and it is appropriate to standardize X to a mean of 0 under these circumstances (Legendre and Legendre 1998). In four of five species, we used a principal-component score which had a mean of 0 as X. For meadow voles, we standardized body length (mean of 0, standard deviation of 1) for all individuals for the polynomial regressions.

Testing for independence of energy reserves from body size

To test for the independence of energy reserves from body size, we conducted a multiple regression between the mass of energy reserves (body fat and lean dry mass) and both body size (PC1 or log body length) and body mass. The partial correlation coefficient for body size was used to determine whether energy reserves were related to body size.

Comparing residuals

Slope and intercepts for OLS regression between body mass and body size (PC1 or body length in the case of meadow voles), and MA and RMA regressions between body mass and body size (PC1 and body length) were calculated for all five species. To calculate RMA and MA slopes and intercepts, we used the program ''Model II regression'' (Legendre 2001). Several methods have been suggested for calculating residuals as indices of condition. We used residuals (y-axis deviations) from OLS, RMA, and MA regressions as indices of condition, and regressed them independently on absolute fat (g), lean dry mass (g), and water (g). We also used the partial correlation coefficient of mass from a multiple regression of body components (fat, lean dry mass, and water) on body size (PC1 or body length) and body mass to describe the relationship between condition and body composition (Hayes and Shonkwiler 2001). Finally, unlike OLS regression, RMA and MA regression do not minimize the sum of squared y-axis deviations, and therefore we used the ''true'' residual from these alternative regression models as indices of condition. Reduced major axis (RMA) regression minimizes the sum of the areas of the triangles defined by each data point, the point on the regression line corresponding to the X value, and the point corresponding to the Y value (McArdle 1988). Major axis (MA) regression minimizes the sum of

squared distances perpendicular to the regression line. Thus, the true residuals for these regression models are the signed area of the triangle defined by each data point and the points on the regression line corresponding to the **X** and **Y** variables (RMA, where a triangle above the slope is positive and a triangle below the slope is negative), and the perpendicular distance between the data point and the regression line (MA).

Statistical simulations

We assumed an allometric relationship between the body mass and the body size of an animal from a given population. This relationship is an allometric equation:

$$\text{median}\{\text{body mass} \mid \text{body size}\} = a(\text{body size})^b$$

for some constants a and b. This equation can be transformed into a linear equation by log transforming both sides. After adding a random term to account for deviations from the allometric relationship, one obtains

$$\log(\text{body mass}) = \beta_0 + \beta_1 \log(\text{body size}) + \delta$$

where β_0 and β_1 are constants and δ is a random variable with median 0. The index of body condition (predicted energy reserves) is δ. To examine the effect of a violation of Assumption 2 (that the residual index of condition and true condition [the proportion of mass associated with energy reserves] of an animal are independent of body size [or BSI; Green 2001]), we produced data where there was no relationship between energy reserves (Z) and body size (X). More specifically, we created random samples of **X**, **Y** (body mass), and Z, where the random vector (**X**, **Y**) was independent from the random variable Z. Then the residuals of the regression of **Y** on **X**, calculated by OLS, MA, and RMA regression are independent of Z. We randomly introduced errors into the measurements of **X**, **Y**, Z, and thereby obtained the measurements X', Y', and Z'. We then calculated the residuals of Y' with respect to X' using OLS, MA, and RMA regression, and report the number of times that the residuals and Z' are found to be significantly correlated. Because any detected correlation is due to an error caused by a violation of the assumption that body condition and size are independent, the method in which the detection rate is significantly lower than the others is judged to be the better method.

For four of the five data sets (yellow-pine chipmunk, bushy-tailed woodrat, deer mouse, and red-backed vole; because the index of size for the meadow vole was univariate, this species was excluded), we randomly created 10 000 new data sets, each with variables standardized with a mean of 0 and a standard deviation of 1. These new data sets "look like" the collected data set except that there is no relationship between the body size and true condition (mass associated with energy reserves). To do this, we added a random amount to each observed value of **X**. This random amount is normally distributed with mean 0 and stan-

dard deviation 0.05 which corresponds roughly to 5% error in the measurements. Instead of the measured response Z, we used a random selection from all the measured responses of Z. The random selection is denoted Z_R. Then (X', **Y**) is independent of Z_R and in particular there is no correlation between the residuals of **Y** regressed on X' and the defined body condition Z_R.

To create a violation of the assumption that energy reserves are independent of body size, we estimated the parameters β_0 and β_1 in the linear model $Z = \beta_0 + \beta_1 X + \varepsilon$ using the OLS procedure and calculated 90% confidence intervals for the intercept and slope (I and S, respectively). These intervals were fixed for all simulated data sets. We randomly chose $\beta_0 \in I$ and $\beta_1 \in S$ using the uniform distribution and let $Z' = Z_R + \beta_0 + \beta_1 X$.

The simulation study was performed using the statistical software R, Version 1.7.1, for Microsoft Windows (*available online*).[6] The programs used are available from the authors upon request.

RESULTS

The descriptive statistics for body size components, body mass, and body composition are provided in Schulte-Hostedde et al. (2001). The first principal component (PC1) of morphological measurements for woodrats, chipmunks, red-backed voles, and deer mice was used to estimate body size. PC1 explained at least 50% of the overall variation in size measurements for these species (Table 1). All morphological measurements loaded positively and higher than 0.5 on PC1 except for hind foot length of red-backed voles (0.460). Factor loadings for meadow voles were not in a consistent direction (Table 1). Therefore, to describe body size in meadow voles we only used log-transformed body length (as in other studies of voles; e.g., Heske and Ostfeld 1990). We used PC1 scores appropriately standardized for all other species.

Assessing linearity

Visual inspection of residuals suggested that log-transformation adequately linearized the data for all species. The addition of a quadratic term to the regression equations increased r^2 negligibly (<0.02), and the quadratic term was nonsignificant ($P > 0.26$) in all cases.

Testing for independence of energy reserves from body size

We found several cases in which energy reserves were not independent of body size. In both deer mice and red-backed voles, large individuals had less fat than small individuals after controlling for body mass. In bushy-tailed woodrats, deer mice, and red-backed voles, large individuals had more lean dry mass than

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[6] ⟨http://www.r-project.org/⟩

TABLE 1.   Factor loadings of morphological traits on PC1 from principal-components analysis for five species of small mammals sampled from the Kananaskis Valley, Alberta, Canada.

Trait	Woodrat	Chipmunk	Meadow vole	Red-backed vole	Deer mouse
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	NA	NA	NA
Skull width	NA	0.757	NA	NA	NA
Hind foot	0.803	NA	0.620	0.460	0.679
Ear length	NA	NA	−0.761	0.856	0.726

Notes. Variance refers to the percentage of the variation in the data explained by PC1 (see Schulte-Hostedde et al. 2001). ''NA'' denotes not applicable.

small individuals after controlling for body mass (Table 2).

Comparing residuals from alternative regression models to body composition

As expected, standardization of the body mass and size (PC1 scores or body length) resulted in OLS slope estimates equal to the correlation coefficient (r), and intercepts equal to 0 for all five species (Table 3). In addition, slope and intercept estimates for both RMA and MA regression were 1 and 0, respectively, for all five species. All regression models (OLS, RMA, MA) pass through the mean of the **X** and **Y** variable, and with standardized data the means of both **X** and **Y** are 0. It follows from the equations for the slope for MA and RMA regression (see formulae 10.11, 10.12 in Legendre and Legendre [1998]), that the slope is 1 when the variance in both **X** and **Y** are equal, as occurs when both variables are standardized.

Generally, residuals obtained by OLS regression were more closely correlated with body components (fat, lean dry mass, water) than residuals (both *y*-axis residuals and ''true'' residuals) obtained from MA and RMA regression (Tables 4 and 5). *Y*-axis residuals and ''true'' residuals from MA and RMA were similarly correlated with body components (Tables 4 and 5). When the relationship between body mass (corrected for body size) and fat, lean dry mass, and water was assessed directly via multiple regression (Table 2), the partial correlation coefficients between mass and body

components were generally higher than those derived from OLS residuals and body components, especially with respect to lean dry mass and water.

Statistical simulations

The results of the statistical simulations revealed that the proportion of simulations in which the null hypothesis (that actual energy reserves are independent of body size) was falsely rejected was substantially higher with RMA and MA regression when compared with OLS regression (Table 6). Residuals from OLS regression tended to be falsely related to energy reserves 4–5% of the time, whereas residuals from RMA and MA regression tended to be falsely related to energy reserves 10–30% of the time.

DISCUSSION

''Condition'' is a nebulous term and authors often do not explicitly define its use. A major, though often unstated, assumption is that condition refers to the energetic state of an animal. An animal in ''good'' condition is thought to be in positive energy balance, whereas an animal in ''poor'' condition is in negative energy balance (Jakob et al. 1996, Speakman 2001). While many authors assume that animals that are heavier than predicted by their body size have more metabolizable tissue than individuals that are lighter than predicted by body size (e.g., Dobson 1992), it is unlikely that this extra mass is composed strictly of fat. Unless animals are depositing energy (fat) for a specific

TABLE 2.   Partial correlation coefficients from multiple regression of body size (PC1 for all species except meadow voles) and body mass on body components (fat, lean dry mass, water) for five species of small mammals.

Component	Woodrat	Chipmunk	Meadow vole	Red-backed vole	Deer mouse
PC1					
Fat	−0.221	−0.023	−0.090	−0.234*	−0.293*
Lean dry mass	0.337*	0.175	0.137	0.256*	0.266*
Mass					
Fat	0.426*	0.362	0.300	0.326*	0.360*
Lean dry mass	0.831*	0.796*	0.840*	0.777*	0.394*
Water	0.969*	0.820*	0.980*	0.971*	0.887*

Note: Body length was used as an index of body size for meadow voles because body size components did not load in consistent directions in a principal-components analysis.

 * $P < 0.05$.

TABLE 3. Intercepts and slopes obtained from ordinary least squares (OLS) regression between standardized body mass (log-transformed) and body size (PC1 and log-transformed, or standardized body length for meadow voles) for five species of small mammals.

Species	Intercept	Slope ($= r$)	95% CI	P
Woodrat	0	0.847	±0.137	<0.001
Chipmunk	0	0.563	±0.385	0.006
Meadow vole	0	0.773	±0.228	<0.001
Red-backed vole	0	0.700	±0.155	<0.001
Deer mouse	0	0.495	±0.174	<0.001

Notes: Body length was used as an index of body size for meadow voles because body size components did not load in consistent directions in a principal-components analysis. The 95% confidence intervals for the slope, which must be equal to the correlation coefficient (r), and corresponding P values are also included.

purpose (e.g., migration or hibernation), it seems likely that variation in condition reflects variation in all constituents of body composition including fat, protein, water, and skeletal tissue. For example, residual indices of condition reflect variation in all of these constituents in small mammals (Schulte-Hostedde et al. 2001). Therefore, our definition of condition does not restrict variation in size-corrected mass to variation in fat alone, but to all components of body composition. The fact that condition reflects variation in all of fat, lean dry mass, and water may explain why, in many cases, residuals explain a moderate amount of variation in body composition of small mammals.

Data from the five species of small mammals examined here generally fit the most critical assumptions regarding the measurement of condition using residuals from mass–size regressions (Green 2001). First, the relationship between body mass and body size appeared to be reasonably linear for all species. Nonlinear relationships may be more likely when intraspecific variation in body size (**X**) is larger than that found in small mammals. For instance, allometric (nonlinear) relationships between body mass and body size may be more likely in taxa with indeterminate growth, such as reptiles and amphibians, than in taxa with determinate growth, such as mammals and birds. Hayes and Shonkwiler (2001) examined bivariate plots of mass and body

size in six species: chuckwalla (*Sauromalus obesus*), desert tortoise (*Gopherus agassizii*), trout (*Oncorhynchus clarki*), mason bee (*Osmia* sp.), orange-crowned warbler (*Vermivora celata*), and white-ankled mouse (*Peromyscus pectoralis*). Relationships appeared to be nonlinear when the range of body sizes was large (>100%), and linear when the range of body sizes was small (<25%).

Second, there was evidence of size dependence of energy reserves among three of the five examined species. The general pattern appears to be that larger individuals carry less fat and/or more lean dry mass than smaller individuals. Nonetheless, the amount of variation in energy reserves explained by body size was low (5.5–11.3%). The assumption that energy reserves are independent of body size may occasionally be violated in natural populations, if larger individuals have greater access to food resources.

The statistical simulations provide evidence that ordinary least squares (OLS) regression is preferred over major axis (MA) and reduced major axis (RMA) regressions. Residuals derived from both MA and RMA regression of body mass (log-transformed) on body size were far more likely to be falsely related to energy reserves than residuals derived from OLS regression. This result, coupled with the fact that RMA and MA residuals consistently predicted less variation in body

TABLE 4. Correlation coefficients (r) between y-axis residuals and absolute fat, lean dry mass, and water for five species of small mammals.

Regression and component	Woodrat	Chipmunk	Meadow vole	Red-backed vole	Deer mouse
OLS					
Fat (g)	0.409***	0.353†	0.287†	0.326*	0.357***
Lean dry mass (g)	0.421***	0.660***	0.554***	0.547***	0.352***
Water (g)	0.518***	0.690***	0.631***	0.701***	0.832***
RMA/MA					
Fat (g)	0.315*	0.207	0.184	0.303*	0.371***
Lean dry mass (g)	0.166	0.323	0.268	0.229*	0.078
Water (g)	0.264*	0.357†	0.336†	0.378***	0.545***

Notes: Residuals were obtained from the regression between body mass and body size (PC1 or body length for meadow voles) using ordinary least squares (OLS) regression, reduced major axis (RMA) regression, and major axis (MA) regression. Body length was used as an index of body size for meadow voles because body size components did not load in consistent directions in a principal-components analysis.

† $P < 0.10$; * $P < 0.05$; *** $P < 0.001$.

TABLE 5. Correlation coefficients (*r*) between ''true'' residuals and absolute fat, lean dry mass, and water for five species of small mammals.

Regression and component	Woodrat	Chipmunk	Meadow vole	Red-backed vole	Deer mouse
RMA					
Fat (g)	0.340*	0.221	0.229	0.332*	0.405***
Lean dry mass (g)	0.192	0.332	0.297†	0.170†	0.019
Water (g)	0.269*	0.355†	0.387*	0.318*	0.529***
MA					
Fat (g)	0.315*	0.207	0.184	0.303*	0.371***
Lean dry mass (g)	0.167	0.323	0.268	0.228*	0.078
Water (g)	0.264*	0.357†	0.336†	0.378***	0.545***

Notes: Residuals were obtained from the regression between body mass and body size (PC1 or body length) using reduced major axis (RMA) regression, and major axis (MA) regression. Body length was used as an index of body size for meadow voles because body size components did not load in consistent directions in a principal-components analysis.

† $P < 0.10$; * $P < 0.05$; *** $P < 0.001$.

composition, suggests that RMA and MA regressions do not offer many benefits when compared to OLS regression.

Although recently called into question (Kotiaho 1999, Green 2001, Hayes and Shonkwiler 2001), residuals from the body mass–body size OLS regressions consistently explained significant amounts of variation in fat, water, and lean dry mass. Residuals from RMA/MA regression were often significantly correlated with body components; however, the coefficient of determination was consistently lower in the RMA/MA analysis than in the OLS analysis. Therefore, qualitatively, OLS residuals appeared to be somewhat superior to RMA/MA residuals with respect to predicting body composition.

RMA (or Model II) regression has been advocated as a more appropriate approach for describing the functional relationship between two variables measured with error (LaBarbera 1989, Ebert and Russell 1994, Herrera 1992, Fairbairn 1997). Most uses of regression in ecology and evolution involve variables that are both measured; thus there is error in both dependent and independent variables. The use of OLS regression (which assumes that **X** values are measured without error and set by the researcher) therefore seems inappropriate. There is abundant evidence that RMA slope estimates accurately depict functional relationships between variables measured with error (McArdle 1988,

TABLE 6. Proportion of false rejections of the null hypothesis that energy reserves are independent of body size, in simulations for four species of small mammals.

Species	OLS	MA	RMA
Chipmunk	0.0404	0.1251	0.1275
Deer mouse	0.0476	0.1746	0.1815
Red-backed vole	0.0465	0.0934	0.0949
Woodrat	0.0408	0.2902	0.2966

Notes: Proportions are based on 10 000 simulations for each regression model. Key to abbreviations: OLS, ordinary least squares regression; MA, major axis regression; RMA, reduced major axis regression.

LaBarbera 1989, Legendre and Legendre 1998). However, if the purpose of regression is prediction, as is done with residual indices of condition, OLS regression is most appropriate (Legendre and Legendre 1998). Calculating residuals as an index of condition requires the comparison of observed mass to predicted mass. In other words, residuals are used to determine why an animal is heaver/lighter than predicted based on body size. Because OLS regression minimizes error in **Y** (mass), residuals from OLS regression should predict body mass more precisely than RMA regression. Typically, measurement error is a major source of variation in measures of body size (Yezerinac et al. 1992); therefore using the average of repeated measurements may be one method of minimizing error in **X** (e.g., Schulte-Hostedde and Millar 2000). Despite this approach, correcting for measurement error, particularly in the context of RMA and MA regression, requires the modeling of error in both **X** and **Y** variables, something that is rarely done (Carroll and Ruppert 1996). The arguments contrasting OLS and RMA/MA residuals, however, become trivial when *r* approaches 1 because the RMA slope is equal to the OLS slope divided by the correlation coefficient (Legendre and Legendre 1998).

An important issue in the evaluation of body condition indices derived from mass–size regressions is the high correlation between residuals and mass (**Y**). In OLS regression, residuals and **X** (size) are independent of each other, whereas residuals and **Y** (mass) are positively related. In RMA regression, the correlations between residuals and mass (**Y**) and size (**X**) are of equal magnitude (Green 2001). This has the potential to be a serious weakness of the use of OLS residuals because, when validating residual indices of condition against components of body mass (i.e., fat, lean dry mass, water), these relationships may become biased (i.e., relationships between residuals and fat, for example, may tend to be significant because fat is a component of mass). One reason for this bias is the correlated error structure which occurs between the mea-

surement of total mass and its components (A. J. Green, *personal communication*). Any error in measuring mass automatically affects the value of absolute fat, lean dry mass, or water. Because modeling measurement error was not done, it is impossible to assess the affects of measurement error of mass on the error structure of the data. Nonetheless, an alternative approach to validating condition indices might be to examine these indices against a mass-independent physiological measure of condition such as levels of liver glycogen or blood glucose.

Regardless of which condition index is used, it is important that it correlate with constituents of body composition. If condition is assumed to reflect variation in fat, it is important to validate this assumption. As seen here, condition does not necessarily reflect fat. Body condition indices were more closely correlated with lean dry mass and water in five species of small mammals, perhaps because the proportion of body mass composed of fat is often small (Schulte-Hostedde et al. 2001). Low protein reserves during periods of low food resources indicate that small mammals may catabolize protein to meet some energy requirements (Virgl and Messier 1992, Zuercher et al. 1999). Determining the degree to which condition indices correlate with energy reserves requires the independent evaluation of body composition.

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APPENDIX

Images of bushy-tailed woodrats are available in ESA's Electronic Data Archive: *Ecological Archives* E086-010-A1.