Oikos

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Appendix 1.

Similarities between the Thorpe–Lleonart equation and residuals from OLS regression

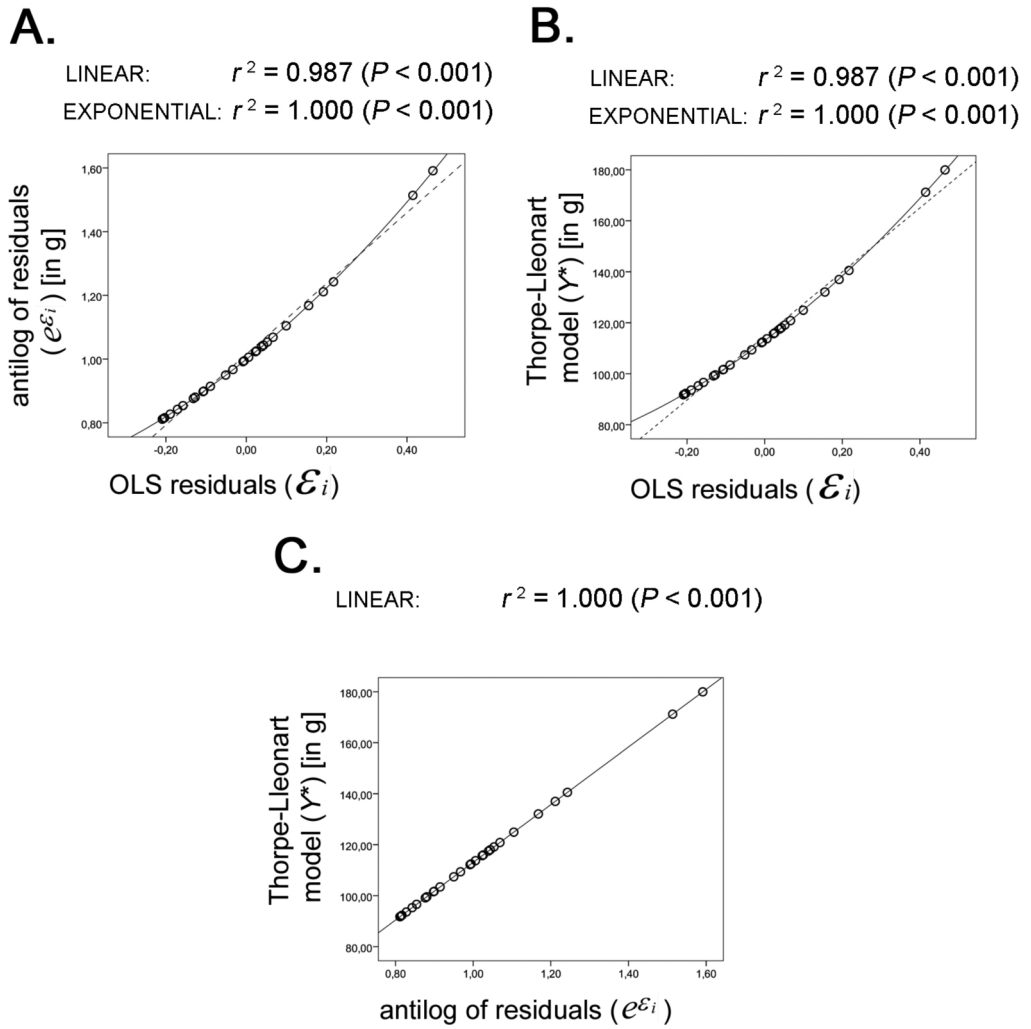

Figure 1–1. Example in water snakes of the linear and exponential functions relating values computed by the Thorpe–Lleonart model, OLS residuals from OLS regression on ln-transformed variables, or back-transformed (antilog) residuals. See Table 1–1 for the corresponding data for several individual snakes.

The scaled mass index is based on two main statistical principals: the mathematical basis of the Thorpe–Lleonart (TL) model (itself reliant on OLS regression), combined with the use of standardised major axis regression as the method of line-fitting. The starting point of the Thorpe–Lleonart model is a modified power equation which predicts the whole body mass when X equals a specific arbitrary value (X_0) via the stochastic allometric equation $Y = aX^b e^{\varepsilon}$, which contains a multiplicative error term ($e^{\varepsilon i}$). In this case ε_i are roughly equivalent to the residual errors from the linear OLS regression equation $\ln Y = \ln a + b \ln X + \varepsilon$ (but see Hayes and Shonkwiler 2006).

From the allometric equation $Y = aX^b e^{\varepsilon}$, if $\hat{y}$ denotes the predicted value for Y (i.e. $\hat{y} = a x^b$), then the observed y values become $y_i = \hat{y}_i e^{\varepsilon i}$. Similarly, the linear regression equation can be expressed as $\ln y_i = \ln \hat{y}_i + \varepsilon_i$, which after backtransformation (i.e. taking antilogs) leads also to $y_i = \hat{y}_i e^{\varepsilon i}$. This explains why a $e^{\varepsilon i} - \varepsilon_i$ plot produces a perfect exponential fit (Fig. 1-1A). An identical fit is provided when plotting the predicted Y* scores from the TL model against the OLS residuals (Fig. 1-1B). Likewise, the Y* scores are perfectly correlated with the antilogs of the OLS residuals from regression of ln Y against ln X (Fig. 1-1C).

Despite this close statistical relationship between the TL model and the OLS residual index, they are not mathematically or biologically equivalent (Table 1-1). The error terms from the simple linear equation on raw Y–X variables $Y = a + b X + \varepsilon$ (for convenience indicated from hereon as ε_{raw}), on log variables $\ln Y = \ln a + b \ln X + \varepsilon$ (indicated from hereon as as ε_{log}), and from the stochastic power equation $Y = \alpha X^{\beta} e^{\varepsilon i}$ (indicated from hereon as $e^{\varepsilon-power}$) are not identical to each other (i.e. $\varepsilon_{raw} \neq \varepsilon_{log} \neq e^{\varepsilon-power}$) nor to the Y* scores from the TL model of Eq. 1.

The use of R_{i-raw} values (additive error, where R indicates residuals) gives CI scores the same units as the independent Y variable (body mass in g), but relies on ad hoc models without incorporating the scaling principle between mass and length. In contrast, the use of R_{i-log} values invokes an underlying allometric model with multiplicative error $Y = \alpha X^{\beta} e^{\varepsilon i}$ (Packard 2009), but CI scores are no longer in readily comprehensible units. This is because R_{i-log} values are additive errors in the logged model with the same units as the Y' (= ln Y) variable. Residuals may seem attractive in a condition context because they provide positive and negative scores which imply 'good' and 'bad' condition respectively (Table 1-1). However, R_{i-log} scores can not be interpreted in a more quantitative way unless they are mathematically modified. For instance, according to these scores, individual no. 4 from Table 1-1 was relatively 'heavier' than individual no. 3 (0.46 vs 0.04, in 'ln g' units). However, further consideration may be confusing, since direct comparison of the scores might imply that the condition of snake no. 4 is approximately 12.1 times (= 0.464 / 0.038) greater than that of no. 3 (i.e. that no. 4 is 12.1 times 'relatively heavier or fatter'). This would be very misleading from a biological perspective, given the scale and units of measurement. Furthermore, such comparisons (ratios between individual scores) are even more non-sensical when there are negative values in the denominator (e.g. when comparing the R_{i-log} score for snakes no. 3 and no. 1 in Table 1-1).

An attempt can be made to recover the original scale by the back-transformation of R_{i-log} values by taking anti-logs (i.e. $e^{R_{i-log}}$, the fourth column in Table 1-1). Such back-transformed results may then suggest that snake no. 4 is in 1.53 times (= 1.59 / 1.04) better condition than no. 3, which is biologically more reasonable. However, such back- transformation is rarely used in the literature and requires an additional calculation compared to the TL model. Note also that justifying an allometric fit by such backtransformation is not tenable because the multiplicative error term of the stochastic power equation is necessarily adimensional (i.e. while $e^{R_{i-log}}$ would have units, the error term is unitless: $e^{\varepsilon} = Y/a X^b = Y/\hat{Y}$, then [g] / [g] = [∅]). Furthermore, these back-transformed $e^{R_{i-log}}$ and TL scores are different (compare columns 4 and 6 in Table 1-1), and only the TL model computes the whole body mass for a given body length.

Estimating the whole body mass in the original scale from R_{i-log} values requires adding the arithmetic mean of the dependent variable, i.e. $\overline{\ln Y} + R_{i-log}$ (or $\overline{Y'} + R_{i-log}$), and then backtransforming the sum via antilogs. Such a process provides the predicted body mass for the geometric mean of body length. Following with our example from Table 1-1, the predicted body mass for snakes no. 3 and no. 4 at body length of 56.25 cm (= antilog of $\overline{\ln X}$ or $\overline{X'}$) would be $\hat{Y}_3 = 110.41$g and $\hat{Y}_4 = 169.09$g respectively (i.e. no. 4 is 1.53 times 'heavier' than no. 3). Note that the ratio (1.53) remains the same as for $e^{R_{i-log}}$.

However, the 'antilogs of $[\overline{Y'} + R_{i-log}]$' are still not equivalent to the results of the TL model (compare columns 5 and 6 in Table 1-1) because the former results are based around the geometric mean of body mass, not the arithmetic mean.. Thus, according to the results of the TL model, snake no. 4 was again 1.53 times heavier than snake no. 3 when both were standardized to a length of 57.43 cm (Table 1-1). However, this value is in fact slightly different (1.531424 for antilogs, 1.531430 for Y*) owing to the subtle differences in the way these different values are computed, as explained above.

Y* scores produced by the TL model are directly developed from the allometric power equation, a nonlinear model likely to provide better fit to the true M–L relationship. Unlike OLS residuals, the CI provided by the TL model avoids the need for tiresome further calculations to provide results in the original scale, and single Y* values are easier to grasp from a condition perspective, since they predict the whole body mass for a given body length. Our scaled mass index provides different results to the TL model because it relies on line-fitting by SMA regression. For example, according to the scaled mass index, snake no. 4 was 1.67 times heavier than snake no. 3 when both were standardized to a length of 57.43 cm (Table 1-1).

Table 1-1. Examples in water snakes (total n = 28) of individual scores which could be potentially used as condition indices. R_{i-raw}, residuals from an OLS regression of body mass (M) against snout_vent length (L); R_{i-log}, residuals from an OLS regression of ln M against ln L; $e^{R_{i-log}}$, antilogs of R_{i-log}; Antilog of $[\overline{\ln Y} + R_{i-log}]$, antilogarithms of the sum of R_{i-log} and the arithmetic mean value of ln M; Y*, values computed by the Thorpe–Lleonart model following equation 1; $\hat{M}_i$, values computed by the scaled mass index following Eq. 2 (L_0 = 57.43 cm).

No. individual snake	R_{i-raw}	R_{i-log}	$e^{R_{i-log}}$	Antilog of $[\overline{\ln Y} + R_{i-log}]$	Y*	$\hat{M}_i$
	(g)	($\log_e$ g)	(g)	(g)	(g)	(g)
1	–73.93	–0.19	0.83	87.93	93.59	90.18
2	–15.03	0.10	1.10	117.37	124.92	123.90
3	5.54	0.04	1.04	110.41	117.52	112.43
4	78.63	0.46	1.59	169.09	179.97	188.30
5	6.11	0.02	1.02	108.73	115.73	117.66
6	–17.30	–0.20	0.82	86.72	92.30	93.47

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Appendix 2

On the consequences of measurement errors in body mass (M) and body length (L) for condition indices dependent on OLS methods

The OLS method assumes that there is no natural variability or measurement error (which also includes the sampling error) in the X (or L) variable (Warton et al. 2006). Apart from the dubious assumption about the inexistence of natural variability in body length, the OLS assumption is clearly violated since length measures of vertebrates are also subject to considerable measurement error (Yezerinac et al. 1992). We did not have access to datasets with repeated measurements of mass or length from the same animal, but here we consider the importance of the potential effects of measurement error. The Thorpe–Lleonart (TL) model based on OLS regression produces standardized mass values that are strongly correlated with OLS residuals from the simple linear regression performed on ln-transformed variables (Appendix 1). Thus, we used the TL model (see Eq. 1 in the main text) to assess the consequences of measurement error for body mass (M) and length measurements (e.g. body length or tarsus length) for the reliability of OLS methods.

For example, the Thorpe–Lleonart equations for meadow voles, starlings and water snakes calculated for data from Schulte-Hostedde et al. (2001), Ardia (2005) and Weatherhead and Brown (1996) respectively can be written as:

meadow voles: $M_i^* = M_i\ (109.147 / \text{body length}_i)^{(2.291)}$

starlings: $M_i^* = M_i\ (44.338 / \text{head\_bill length}_i)^{(1.927)}$

water snakes: $M_i^* = M_i\ (57.436 / \text{snout\_vent length}_i)^{(2.989)}$

For example, X_0 in equation 1 from the main text for voles is taken as the arithmetic mean for body length = 109.147 mm.

These formulas produce values that are very strongly correlated with the OLS residuals from ln-body mass against ln-body length for meadow voles, ln-head_bill length for starlings or ln-snout_vent length for snakes. The coefficient of variation (CV) is independent of the measurement scale and we assumed an arbritrary measurement error of CV = 5% when taking biometric measurements of a random meadow vole whose true values are body mass M = 36.20g and body length L = 109.00mm. Assuming a normal distribution for both variables, a 5% measurement error in body mass would imply a standard deviation of SD_M = 1.81, and consequently 95 % confidence intervals for measured mass of [32.65, 39.75] (in g). If the confidence interval extremes were two repeated measures of body mass, the two pairs of M–L measurements for the vole would be 32.65 g – 109 mm (A) and 39.75 g – 109 mm (B). According to the above equation, the mass predicted by the TL model would be: M_i^* =32.75g (A) and M_i^* = 39.87g (B); i.e. a CV_{M^*} = 9.80% (respect to the true value of body mass).

Repeating this exercise for a 5% measurement error in body length would give an SD_L = 5.45mm with 95 % confidence intervals of [98.32, 119.68] (in mm). If the confidence interval extremes were two repeated measures of body length, the two pairs of repeated M–L observations for the vole would be 36.20 g – 98.32 mm (C) and 36.20 g – 119.68 mm (D). According to the above equation, the predicted mass would now be M_i^* = 45.99 g (C) and M_i^* = 29.31 g (D); i.e. CV_{M^*} = 23.04%.

Similarly, in a random starling whose true values are body mass M = 78.30 g and head_bill length L= 45.02 mm, a 5% measurement error in body mass would cause CV_{M^*} = 9.52%, and 5% measurement error in head_bill length would cause CV_{M^*} = 18.68%. Finally, for a water snake whose body mass is M = 154 g and snout_vent length L= 61.60 cm, the error in body mass would imply a CV_{M^*} = 15.63% and in snout_vent length a CV_{M^*} = 48.27%. These results are summarized in Table 2-1 of this Appendix:

Table 2-1. Coefficient of variation in predicted body mass (Thorpe–Lleonart model based on OLS methods) in three different species caused by an equal proportion of measurement error when measuring mass or length.

	Meadow vole	Starlings	Water snake
5% measurement error in:			
Body mass (M or Y)	9.80%	9.52%	15.63%
Length measurement (L or X)	23.04%	18.68%	48.27%

Clearly, a given measurement error in L has much greater consequences for condition indices dependent on OLS methods than the same error in M.

This simulation is consistent with empirical results obtained by Krebs and Singleton (1993) in small mammals, which showed the important effect of measurement error in length measures compared with body mass measures. Linear body measures are often taken with calipers or rulers, and the final value depends on the technical skill of the investigator. In contrast, body mass is usually measured with spring scales or analytical balances without direct intervention of the observer, with accuracy being more dependent on the calibration of the tool. Thus, measurement error in L may be substantially higher than that in M, and a 5% measurement error is not unlikely when measuring lengths. In fact, Yezerinac et al. (1992) found that as much as 10–30% of the total variance in length in fifteen skeletal characters in passerines was due to the inability to make precise measurements, and concluded that, the smaller the morphological trait being measured, the greater the effect of measurement error. Thus, the measurement error in both variables should not be neglected when selecting the method (model I [OLS] or model II [SMA] regression) for fitting a line to the M–L dataset.

In conclusion, measurement error exists for linear measures of body size (traditionally used as the X value for the calculation of OLS residuals) and should not be ignored. OLS methods produce condition indices that are especially sensitive to measurement error in L. SMA methods are more appropriate because they recognize the existence of measurement error and natural variability in L (Green 2001, Warton et al.·2006).

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Appendix 3

Drawbacks to the use of PCA as a body size indicator when producing condition indices

The usage of PC1 from a PCA of different morphometric measurements has often been advocated as the best size indicator for use in constructing non-destructive indices of condition (Green 2001, Schulte-Hostedde et al. 2001, Blackwell 2002). However, this should not be taken as a rule of thumb (LaBarbera 1989), and there are several reasons why the use of a single linear measure (e.g. body length) can be preferable:

1) individual measures can better reflect structural size than PC1, and often correlate better with body mass or body components. This is the case for starlings (Ardia 2005) and also for red-backed voles (data reanalyzed from Schulte-Hostedde et al. [2001], r = 0.705 for ln-body length against ln-body mass; r = 0.477 for ln-PC1 [from a PCA on body length, foot length and ear length] against ln-body mass). Similarly, in the wood mouse *Apodemus sylvaticus*, the Algerian mouse *Mus spretus* and the greater white-toothed shrew *Crocidura russula*, body length is correlated more strongly with body mass than PC1 from a PCA of four linear measurements (Peig unpubl.). One reason for this is that some measurements are harder to take and more subject to measurement error than others (e.g. it is almost inevitable that the length of a small structure such as an ear or foot is measured less accurately than body length; Yezerinac et al. 1992). Another reason is that some measures (e.g. tail length) may reflect plastic characters that have a poor relationship with overall structural size (Yezerinac et al. 1992, Badyaev and Martin 2000). However, a PCA weights all variables equally so that combining poor indicators of structural size with good ones through a PCA can provide relatively poor information.

2) conducting a PCA involves the inherent loss of information due to the reduction of the dimensional space (Shea 1985), and even PC1 rarely explains more than 55% of the variation in linear measures (Schulte-Hostedde et al. 2001). Furthermore, it has sometimes been suggested that, in a PCA of linear measures, PC1 can be taken to represent size while PC2 represents shape (Shea 1985, Blackwell 2002). This is because the loading factors of different linear measurements on PC1 are often consistently positive. For example, Schulte-Hostedde et al. (2001) considered PC1 to represent structural size only if all linear measures have positive signs, and for that reason they rejected PC1 as a valid size measure for meadow voles. Principal components may indeed represent integrated information about size. However, they also encompass information about animal shape (Shea 1985, Lleonart et al. 2000), even when the computed loading factors with linear measures are all positive. This is because different absolute values of the loading factors indicate different rates of increase of the original variables. For example, in *Crocidura russula*, PC2 from a PCA of four linear measures was correlated more strongly with body mass than PC1, and hence is probably a better indicator of structural size (Peig unpubl.). This is despite the fact that only PC1 has positive factor loadings for all four measures.

3) another disadvantage of using PCA is that it can complicate the interpretation of scaling relationships between body mass and linear size measures. A PCA involves dimensional reduction by linear combination of variables, and creates a new dimension (e.g. PC1) which does not represent either a linear measure of physical size, nor any other known physical dimension such as volume or mass. Thus, when body mass is regressed against such variables, the computed values of the scaling exponent β are totally unpredictable and can not be compared with the value of 3 that would be expected under isometry. For example, the OLS slope between mass and PC1 was as low as 0.69 for meadow voles and as high as 68.15 for wood rats (Schulte-Hostedde et al. 2001).

4) smilarly, using PCA as L in equation 2 complicates the interpretation of the values of the saled mass index. If, for example, L is body length (mm), and L_0 is taken as the arithmetic mean of length for all individuals studied, the saled mass index represents individual mass standardized for the mean length L_0 (mm). These values are easier to understand and to compare between studies than values based on PC1 (a parameter which can not be measured in mm).

5) i order to compute reliable principal components that can then be applied to analyses based on OLS methods, it is important that the linear measures used for a PCA have a normal distribution (Sokal andhlf 1995). However, this is often not the case. For example, Schulte-Hostedde et al. (2001) calculated OLS residual indices of condition for deer mice and red-backed voles using PC1 from a PCA including body length, foot length and ear length. However, foot length and ear length were discontinuous variables (rounded to the nearest mm) and did not have a normal probability distribution, even after log transformation (our own re-analysis, Kolmogorov-Smirnov *Z* test: $p < 0.05$). In addition, extracting principal components from length measurements can greatly distort their original relationship with body mass due to transformations of variables. For instance, Schulte-Hostedde et al. (2005) conducted a PCA on log transformed length measurements, and the resulting PC1 was again log transformed to remove heteroscedasticity in the final regression model with log body mass as an independent variable. Such transformations on transformed data complicate the interpretation of the results.

In conclusion, although any index of condition can be calculated using a principal component from a PCA, we consider the use of the single linear measure that is best correlated with body mass (after log transformation) to be the rule of thumb most likely to produce useful results that can be readily interpreted. Finally, it is worth emphasizing that the scaled mass index does not rely on a single size measurement chosen by subjective criteria, but on two size indicators (mass and length) strongly correlated as reliable estimates of true structural size.

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Appendix 4

An example applying the scaled mass index to the effect of a change in habitat quality on body condition

We used data taken from Cade et al. (2008) on the body mass and body length of a piscivorous fish (the walleye *Stizostedion vitreum*, n = 6857) before (years 1980–1988) and after (1989–2004) the introduction of a primary prey species (the alewife *Alosa pseudoharengus*) in a lake in the USA.

M is the observed body mass and L is the observed body length of walleye. For walleye studied prior to the introduction of alewife (1980–88) (n = 4789), the characteristics of the scaled mass index $\hat{M}$ (Eq. 2) are as follows:

b_{SMA} = 3.304, 95% CI [3.289, 3.319], L_0 = 359.32 mm (arithmetic mean of L). Mean $\hat{M}$ = 421.02g, 95% CI [419.65, 422.39].

For walleye studied after the introduction of alewife (1989–2004) (n = 2067), b_{SMA} = 3.328 [3.312, 3.345]. There was no significant difference in the value of b_{SMA} for the two time periods ($t_{.05[6854]}$ = 1.895, p > 0.05). Thus, the values for the initial study without alewife (b_{SMA} = 3.304, L_0 = 359.32 mm) can be applied in Eq. 2 to calculate the scaled mass index of walleye after alewife introduction. This gives mean $\hat{M}$ = 434.64g [432.64, 436.63]. The Scaled mass index values are significantly higher after alewife introduction than before ($t_{.05[6854]}$ = –12.960, p < 0.001), showing that body condition increased in response to availability of the new prey (Fig. 4-1).

Exactly the same result would be obtained if we took the specific slope value for the 1989–2004 period (b_{SMA} = 3.328) and L_0 provided for the 1980–1988 study period (L_0 = 359.32 mm). This would now give values of $\hat{M}$ = 433.03 g [431.02, 435.03] for 1989–2004, which is also significantly higher than for the 1980–1988 period ($t_{.05[6854]}$ = –11.660, p < 0.001). Another way to obtain the same result would be to use both the b_{SMA} and L_0 calculated for the whole dataset (b_{SMA} = 3.335 [3.324, 3.346], L_0 = 381.90 mm). This value for b_{SMA} might represent a reliable 'historical' slope for this particular fish species. This would now give values of $\hat{M}$ = 513.18 g [511.49, 514.87] for 1980–88 and $\hat{M}$ = 530.12 g [527.65, 532.58] for 1989–2004 ($t_{.05[6854]}$ = –10.932, p < 0.001). Finally, the same conclusion would be obtained by using the same historical slope (b_{SMA} = 3.335 [3.324, 3.346]) and any other arbitrary L_0 value favoured by biologists for walleyes (e.g. L_0 = 370 mm, the median body length for the whole dataset). This would now give values of $\hat{M}$ = 461.76 g [460.24, 463.28] for 1980–1988 and $\hat{M}$ = 477.00g [474.79, 479.22] for 1989–2004 ($t_{.05[6854]}$ = –10.932, p < 0.001). Note that different means and confidence intervals between assays are due to the different body length (L_0 values) for which the scaled mass index is calculated.

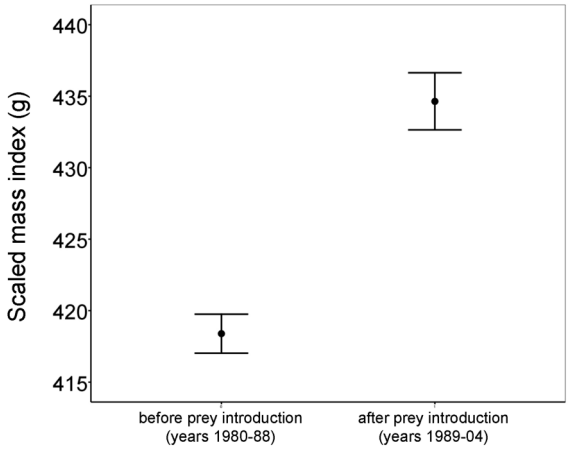

Figure 4-1. Change in body condition (scaled mass index) of walleye in response to introduction of a prey species. The data shown represent walleye body mass standardized to a length of 359.32 mm (the mean length for the 1980–1988 period).

Cade et al. (2008) used a different method (quantile regression) to study the changes in condition, and also concluded the walleye's body condition improved following the introduction of the prey species. Like quantile regression and the scaled mass index, OLS residuals computed on the whole dataset suggest a change in condition after alewife introduction ($t_{.05[6854]}$ = –91.491, p < 0.001), but the residual values themselves are not as easily interpreted as the above scaled mass indices. Furthermore, the use of OLS residuals for inter-study comparisons is fraught with difficulties. For instance, if residuals are calculated separately for the periods with and without alewife, the mean residuals are necessarily zero for each period, making comparisons impossible. Furthermore, the OLS slopes of log M against log L are significantly different for the two study periods (1980–1988 b_{OLS} = 3.260 [3.245, 3.275], 1989–2004 b_{OLS} = 3.307 [3.291, 3.3.25], $t_{.05[6854]}$ = 3.649, p < 0.001), meaning that the slope value for one particular study cannot be applied to the other one to compare condition scores. For example, if the regression line estimated from the previous dataset (i.e.using the b_{OLS} value and intercept for 1980–1988) is used to recalculate OLS residuals for the 1989–2004 period, these residuals correlate with body length (n = 2067, r = 0.27, p < 0.001). Because the OLS residual method is an enclosed analysis, residuals are always likely to correlate significantly with body length when calculated using parameters estimated from previous datasets, even when there is relative homogeneity of slopes between studies. This indicates that OLS methods are inappropriate for these analyses, since they rely on the key assumption that the condition index (OLS residuals) is independent of X (L).

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Appendix 5

The relationship between the OLS residual and scaled mass indices of condition

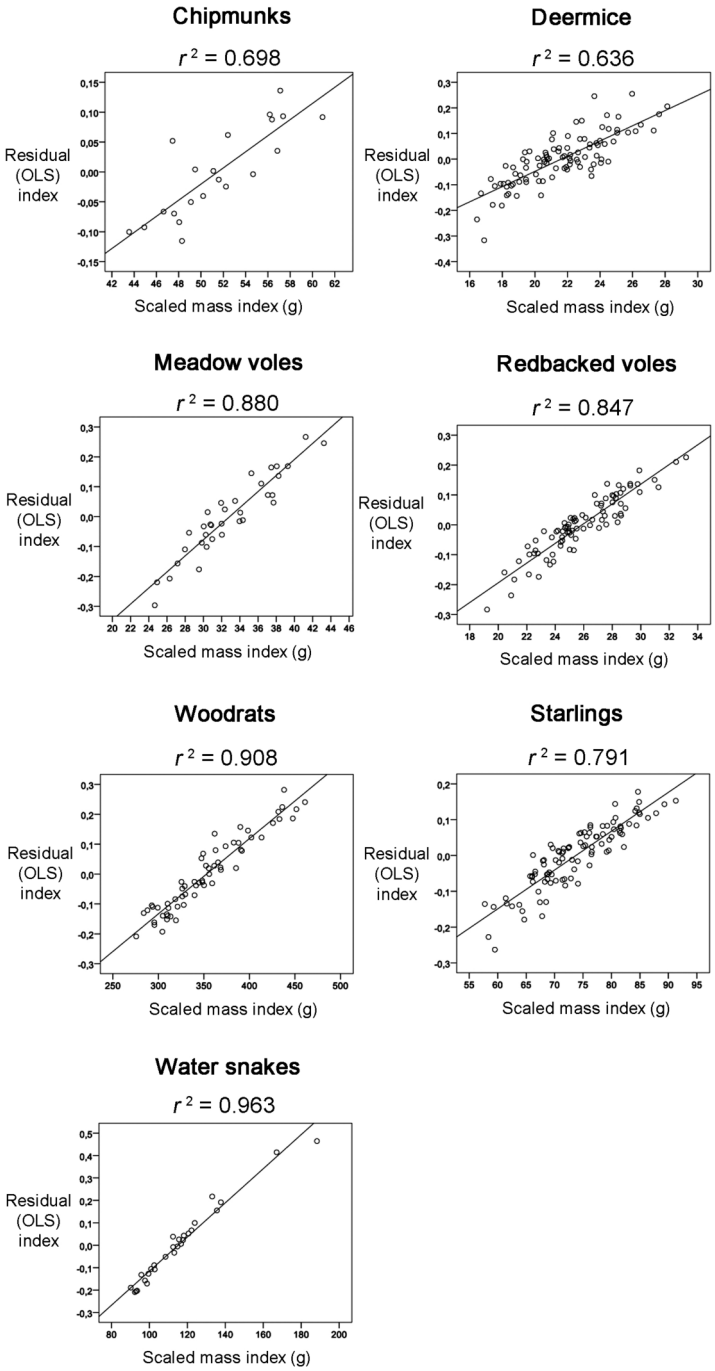

Figure 5-1. The variation (r^2) explained by the linear relationship between the Residual index (from an OLS regression of lnM on lnL) and the scaled mass index of body condition for seven animal species. Both indices used the same linear body measurement (i.e. L, body length for small mammals, head-bill length for starlings, and snout-vent length for water snakes).

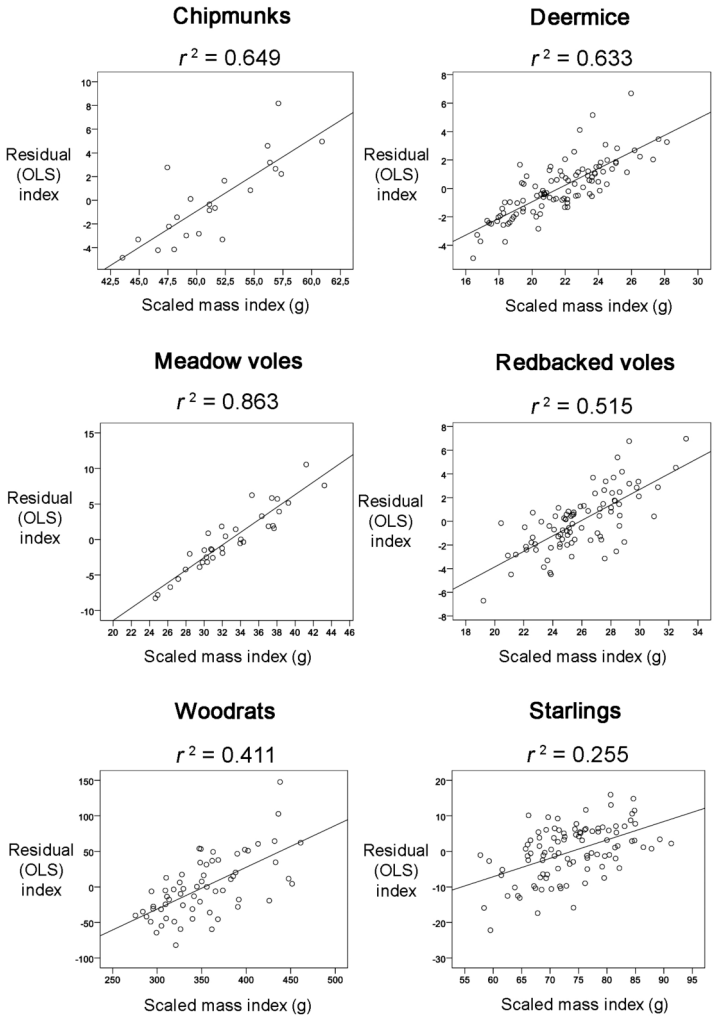

Figure 5-2. The variation (r^2) explained by the linear relationship between the original OLS residual index proposed by Shulte-Hostedde et al. (2001, 2005) and Ardia (2005) as a reliable estimate of true condition, and those we computed by the scaled mass index (Table 3). The residual index used by the above-cited authors was calculated by OLS regression of body mass against single linear body measurements or those combined by principal component analyses (X), as follows: In chipmunks, the first principal component (PC1) of a PCA performed on log-body length, log-skull width and log-skull length; in deermice, meadow voles and redbacked voles, the PC1 of a PCA on log-body length, log-foot length and log-ear length; in woodrats, the PC1 of a PCA on log-body length, log-skull length and log-ear length; and in starlings, tarsus length. The scaled mass index was computed using body length for small mammals and head-bill length for starlings.

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