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Received 11 March 1996, accepted 6 June 1996.
Associate Editor: T. E. Martin

The Auk 114(4):762–769, 1997

Estimating Lipid and Lean Masses in a Wintering Passerine: An Evaluation of TOBEC

MICHAEL F. BURGER[1]
School of Natural Resources and Environment, University of Michigan, 430 East University, Ann Arbor, Michigan 48109, USA

Body composition is an important aspect of the energetic and ecological relationships between birds and their environments. Although lipid extraction with a solvent is widely regarded as the most accurate method of quantifying body fat (e.g. Johnson et al. 1985), it is time consuming and cannot be used for repeated measures on the same individual. Total body electrical conductivity, or TOBEC (Walsberg 1988), measured using the commercially available EM-SCAN Small Animal Body Composition Analyzer, is a recent tool that provides an alternative to solvent extraction. TOBEC is used as a variable in a regression model with or without body mass and morphometric variables to estimate either lean or lipid mass (Walsberg 1988, Castro et al. 1990, Morton et al. 1991, Roby 1991, Scott et al. 1991, Skagen et al. 1993, Conway et al. 1994, Asch and Roby 1995, Lyons and Haig 1995).

Use of TOBEC in these models has varied. In some models TOBEC has been used as the dependent variable, after which the equation is solved for lean mass (an independent variable). The resulting estimate of lean mass is then subtracted from body mass to yield an estimate of lipid mass (Walsberg 1988, Roby 1991, Skagen et al. 1993, Asch and Roby 1995). Morton et al. (1991) pointed out that this two-stage method produces the same absolute error (in grams) for estimates of lean mass and lipid mass, but because lipid mass makes up a smaller proportion of body mass than does lean mass, the relative error for the lipid mass estimate is higher. They further suggested estimating lipid mass directly by fitting a regression model with lipid mass as the dependent variable and body mass and TOBEC as independent variables. Skagen et al. (1993) verified that this direct approach provides a more accurate estimate of lipid mass than the original two-stage method. Conway et al. (1994) and Lyons and Haig (1995), using a different approach, estimated both lean mass and lipid mass directly (as dependent variables) from body mass and TOBEC. Additionally, Lyons and Haig (1995) used a two-stage approach of estimating lipid mass by subtracting direct (rather than inverse) estimates of lean mass from body mass to compare with direct estimates of lipid mass.

The equipment for and application of this technology continue to evolve, and validation of the technique for individual species is recommended (Asch and Roby 1995). This report has two purposes. The first is to propose predictive equations from which lean mass and lipid mass can be estimated for Northern Cardinals (*Cardinalis cardinalis*). The data set used to construct this model includes cardinals from widely separated parts of the species' distribution, captured at different times of day, so as to maximize the ranges in body size and body fat included in the data set. In this manner I reduce the possibility that future uses of this equation will result in an extrapolation beyond the range of the model-building data

[1] E-mail: mburger@umich.edu

set (see Castro and Myers 1990). Second, I discuss differences among the estimating approaches incorporating TOBEC and demonstrate that direct estimates of lean mass and lipid mass (as dependent variables) are associated with the same absolute error, and that only one variable need be estimated.

Field and laboratory measurements.—Ninety-eight male Northern Cardinals were captured in mist nets at six locations during January and February 1994. These locations included rural and agricultural areas near Ann Arbor, Michigan; Paynetown State Recreation Area, Monroe Reservoir property, and Indiana University properties near Bloomington, Indiana; Eufaula National Wildlife Refuge near Eufaula, Alabama; Ledges State Park and U. S. Army Corps of Engineers Saylorville Lake property near Boone, Iowa; Fountain Grove Wildlife Area near Chilicothe, Missouri; and U. S. Army Corps of Engineers Wallace Lake Reservoir property and Bodcau Wildlife Area near Shreveport, Louisiana. Roughly half of the collected birds at each location were obtained within the first two hours after sunrise and the rest were obtained within two hours before sunset.

Within 40 min of capture, birds were weighed and scanned in an EM-SCAN SA-3000 (Model 3057 chamber; 57 mm diameter) Small Animal Body Composition Analyzer. This chamber size was the smallest into which the largest individuals would fit. A 12-volt car battery was used as the power source, and scanning was done inside the field vehicle. Birds were restrained during scanning by putting them in the toe of a nylon stocking and securing them dorsal side down with two rubber bands on the half-cylinder plastic tray supplied by the manufacturer. This restraining method usually held them sufficiently still for scanning; however, scans were omitted if a bird was seen moving during scanning. Manufacturer's scanning instructions were followed (EM-SCAN Inc. 1993); birds were removed from the chamber after one scan and then were reinserted for the next scan and positioned in the chamber so the TOBEC display values were maximal. Seven scans were made of each bird; the high and low values were discarded, and the mean of the remaining five scans was recorded as the TOBEC value for that bird. Birds were sacrificed using thoracic compression, after which natural wing chord ($\pm$ 1 mm) and body length ($\pm$ 1 mm; dorsal surface placed flat on ruler, measured from bill tip to tail tip) were measured. Birds were then placed in two plastic bags and frozen.

Birds were thawed and dissected in the laboratory. Ingesta were removed from the entire length of the digestive tract. The remaining carcass (including feathers) was wrapped in filter paper, freeze-dried, and weighed daily until the change in mass from one day to the next was 0.05 g or less. Total freeze-drying time usually was four or five days. This mass comprised the dry mass of the bird. Dry carcasses (in filter papers) were broken up and placed into a cellulose thimble, and petroleum ether was used to extract the non-polar lipids for 24 h in a Soxhlet apparatus. After extraction, the thimble and its contents were air-dried in a fume hood for 1 h, oven-dried at 90°C for 40 min, cooled in a desiccator at room temperature for 20 min, and weighed. Oven-drying, cooling, and weighing were repeated until the mass of the entire thimble and its contents changed by only 0.05 g or less. Filter papers and cellulose thimbles had been stored in desiccators, and the dry masses of these determined in advance. Subtracting the sum of the dry masses of the filter papers and thimble from the dry mass of the thimble and its contents after extraction gives the lean dry mass of the bird. Subtracting lean dry mass from dry mass yields lipid mass, and subtracting lipid mass from body mass (determined in the field) yields lean (i.e. fat-free) mass.

Body-composition estimation.—Body components (lean and lipid masses) were estimated both with and without TOBEC. The complete data set (n = 98) was randomly split into two sets of 49 birds each, a model-building set and a validation set. To best preserve the full ranges of lean masses and lipid masses, both data sets were made up of nearly the same number of birds from each location and from each sampling time within each location.

The general procedure was to find the best model for predicting lean mass and lipid mass with and without TOBEC included in the model. Models for predicting lean mass and lipid mass were identical in their ability to predict one another, and only the lean mass models are shown (see Discussion). The model-building data set was used to construct all possible regression models, to narrow them down to a subset of "good" models, and to arrive at a "best" model using cross-validation. Next, the validation data set was used to evaluate the good models, to choose the best prediction equation from among them, and to validate that equation.

The procedures used for selecting the best model followed Neter et al. (1990), including using coefficients of determination (R^2), mean squared errors (MSE), and the C-statistic to arrive at a subset of good models, and using the prediction sum of squares (PRESS statistic; the sum of the squares of the residuals for each case after fitting the equation with the remaining $n - 1$ cases) for each of the good models to arrive at the best model.

The constant and regression coefficients from each model in the subset of good models then were used to estimate lean mass for each of the birds in the validation data set (n = 49). The absolute error of these estimates was calculated as:

$$ae = |\hat{Y} - Y|, \quad (1)$$

where ae is the absolute error, $\hat{Y}$ is the estimate of lean mass, and Y is the true value of lean mass measured in the laboratory. Relative absolute error was calculated as:

$$Rae = (ae / Y) \times 100, \tag{2}$$

where *Rae* is the relative absolute error, Y is the measured value of lean mass, and *ae* is from equation 1. Absolute error and relative absolute error of the lean mass estimates were compared for all of the good models, and the model with the lowest mean absolute error and mean relative absolute error for all birds in the validation data set was selected as the best prediction model. This model was validated according to Neter et al. (1990) by: (1) comparing the regression constant and coefficients of the model fitted with the model-building data set with those of the model fitted with the validation data set, (2) comparing the coefficients of determination for the models fitted with both data sets, and (3) comparing the MSE from the model fitted with the model-building data set with the mean squared prediction error (MSPR; Neter et al. 1990) from the validation data set. Finally, the entire data set ($n = 98$) was used to estimate the regression coefficients of the chosen models and to calculate prediction intervals for mean and maximum values of all independent variables.

For estimation of body components without TOBEC, all possible least-squares regression models were fitted using the model-building data set with lean mass as the dependent variable and body mass, wing chord, and body length as independent variables. When estimating lean mass with TOBEC in the model, a modified list of all possible regression models (see below) was fitted with lean mass as the dependent variable and a pool of potential independent variables including TOBEC value, TOBEC squared, natural logarithm of TOBEC, and natural logarithm of TOBEC squared, in addition to those used without TOBEC. Although visual inspection of the raw data did not suggest a nonlinear relationship between TOBEC and lean mass, first- and second-order terms of both log-transformed TOBEC values and untransformed values were included in the pool of potential independent variables because they have been found to describe the relationship in other data sets (see Morton et al. 1991, Skagen et al. 1993, Asch and Roby 1995, Lyons and Haig 1995). Models were included only if they: (1) included body mass as one of the independent variables (body mass explains most of the variation in lean mass and lipid mass), and (2) TOBEC was incorporated in biologically relevant forms (e.g. second-order terms were not included without first-order terms). To avoid merely fitting the data, no more than two TOBEC terms were included except for the "complete" model that was required to calculate the C-statistic (Neter et al. 1990). Models incorporating only TOBEC terms as independent variables also were run to evaluate how well lean mass might be estimated by TOBEC alone.

Finally, three different approaches of estimating lipid mass were compared. First, for the chosen model that included TOBEC, an estimate of lipid mass was made by subtracting the estimate of lean mass (equation generated with the model-building data set, but estimated with the validation data set) from body mass for each bird (the two-stage approach). Second, a direct estimate of lipid mass was made by fitting an equivalent model using the model-building data set (but with lipid mass as the dependent variable) and then using that equation to estimate lipid mass for the birds in the validation data set (the direct approach). Third, inverse regression was used with a comparable model to estimate lean mass, which was then subtracted from body mass to estimate lipid mass (inverse, two-stage approach). The mean absolute and mean relative absolute errors associated with the lipid-mass estimates were used to compare these three approaches.

I used SYSTAT 5.2 for all statistical calculations. All variables incorporated in the models, and the residuals of the models presented, met assumptions of normality and equal variances.

Univariate statistics.—For the 98 male Northern Cardinals in the total sample, body mass averaged 47.6 $\pm$ SE of 0.43 g (range 38 to 57 g), lean mass averaged 44.04 $\pm$ 0.33 g (range 36.25 to 51.99 g), natural wing chord averaged 93.0 $\pm$ 0.26 mm (range 87 to 99 mm), body length averaged 197.8 $\pm$ 0.81 mm (range 176 to 212 mm), TOBEC index averaged 195.6 $\pm$ 3.11 (range 113.6 to 279.2), and lipid mass averaged 3.55 $\pm$ 0.15 g (range 0.84 to 8.23 g). In the model-building data set ($n = 49$), body mass averaged 47.8 $\pm$ 0.63 g (range 39 to 56 g), lean mass averaged 44.25 $\pm$ 0.49 g (range 37.59 to 51.99 g), natural wing chord averaged 93.2 $\pm$ 0.39 mm (range 87 to 98 mm), body length averaged 198.9 $\pm$ 1.15 mm (range 183 to 210 mm), TOBEC index averaged 197.0 $\pm$ 4.56 (range 113.6 to 279.2), and lipid mass averaged 3.59 $\pm$ 0.21 g (range 0.84 to 6.66 g). In the validation data set ($n = 49$), body mass averaged 47.3 $\pm$ 0.60 g (range 38 to 57 g), lean mass averaged 43.83 $\pm$ 0.45 g (range 36.25 to 50.76 g), natural wing chord averaged 92.9 $\pm$ 0.36 mm (range 87 to 99 mm), body length averaged 196.7 $\pm$ 1.12 mm (range 176 to 212 mm), TOBEC index averaged 194.2 $\pm$ 4.27 (range 144.4 to 278.4), and lipid mass averaged 3.51 $\pm$ 0.22 g (range 1.08 to 8.23 g).

Several variables were significantly correlated with lean mass (Table 1). Correlation was strongest with body mass, followed in ranked order by wing chord, TOBEC, and body length. Only two variables were significantly correlated with lipid mass.

Models excluding TOBEC.—Of the models that were fitted with lean mass as the dependent variable, two satisfied the selection criteria better than the others (Table 2). Cross-validation revealed that model 1 had a lower PRESS statistic than model 2, making it the model best fitting the model-building data set. Model 1 predicted lean mass of the birds in the validation data set with a mean absolute error of 0.75 $\pm$ 0.078 g and a mean relative absolute error of 1.7 $\pm$ 0.17% of the measured lean mass (Table 3). Model 2 predicted lean mass with a mean absolute error of 0.74 $\pm$ 0.077 g and a mean relative absolute error of 1.7 $\pm$ 0.17%. Although the dif-

TABLE 1. Correlation matrix between body mass, natural wing chord, total body length, TOBEC index, lean mass, and lipid mass for 98 wintering male Northern Cardinals.

	Body mass	Wing chord	Body length	TOBEC	Lean mass
Wing chord	0.519**				
Body length	0.389**	0.481**			
TOBEC	0.379**	0.118	0.222*		
Lean mass	0.958**	0.569**	0.436**	0.453**	
Lipid mass	0.777**	0.244*	0.164	0.098	0.564**

*, $P < 0.05$; **, $P < 0.01$.

ferences were small, model 2 was chosen as the best model to estimate lean mass of wintering cardinals without the inclusion of TOBEC index and was successfully validated. Predictions of lipid mass, produced by subtracting the lean-mass estimates produced by model 2 from body mass, differed from actual lipid mass of the birds in the validation data set by an average of 0.74 ± 0.077 g, with mean relative absolute error in fat estimation being 25.8 ± 3.62%.

Models including TOBEC.—Of the models fitted with lean mass as the dependent variable and including at least one TOBEC term, seven were included in the subset of good models (Table 2). No model containing only TOBEC terms as independent variables was included in the subset. TOBEC alone explained only 21.8%, and TOBEC squared only 28.4%, of the variation in lean mass. Cross-validation revealed that model 4T (body mass, wing chord, and TOBEC included as independent variables) best fit the model-building data set (Table 2). Three of the models were equal in their ability to predict lean mass for each bird in the validation data set, with a mean absolute error of 0.68 ± 0.071 g for model 4T, 0.68 ± 0.067 g for 8T, and 0.68 ± 0.068 g for 9T (Table 3). The simplest model (4T) was chosen and successfully validated. Predictions of lipid mass for birds in the validation data set, produced by subtracting lean-mass estimates of model 4T from body mass, differed from measured lipid mass by an average of 0.68 ± 0.071 g, which translates into an average relative absolute error of 23.5 ± 3.37%.

The selected prediction model with TOBEC included decreased the mean absolute error of lean-mass estimates by only 0.06 g, and the mean relative absolute error by only 0.1%, relative to the selected prediction model that did not include TOBEC (Table 3). This difference was equal to a 2.3% decrease in the mean relative absolute error of lipid-mass estimates. Equations for both models when fitted with the complete data set (n = 98), coefficients of determination, MSEs, and 95% confidence and prediction intervals for mean and maximum values of independent variables are presented in Table 4. Equations for direct prediction of lipid mass fitted with the complete data set, coefficients of determination, MSEs, and 95% confidence and prediction intervals for lipid mass also are presented (Table 4).

Comparison of methods.—Three different methods of estimating lipid mass of wintering Northern Cardinals were compared. Estimating lipid mass directly (as the dependent variable) produced the same absolute error (0.68 ± 0.071 g) and relative absolute error (23.5 ± 3.37%) as predicting lean mass (as the dependent variable) and subtracting that estimate from body mass (Table 5). In contrast, employing inverse regression to estimate lean mass, and then subtracting that estimate from body mass, produced estimates of lipid mass with

TABLE 2. Selection criteria used to evaluate how well "good" models (i.e. with lean mass as the dependent variable) fit the model-building data set (n = 49), including coefficient of determination (R^2), mean squared error, C-statistic, and prediction sum of squares (PRESS).

Model no.[a]	Variables in model[b]	No. terms in model	R^2	MSE	C	PRESS
1[c]	M, W	3	0.934	0.801	2.38	42.17
2	M, W, L	4	0.935	0.812	3.99	43.18
3T	M, T	3	0.931	0.837	10.78	43.73
4T[c]	M, W, T	4	0.942	0.715	3.91	38.76
5T	$M, W, \mathrm{Ln}T$	4	0.942	0.723	4.43	39.04
6T	M, W, T, T^2	5	0.944	0.717	5.04	40.35
7T	$M, W, T, \mathrm{Ln}T$	5	0.943	0.724	5.51	41.16
8T	M, W, L, T, T^2	6	0.944	0.729	6.80	41.22
9T	$M, W, L, T, \mathrm{Ln}T$	6	0.943	0.739	7.38	42.39

[a] T indicates inclusion of TOBEC in model.
[b] M = body mass, W = wing chord, L = body length, T = TOBEC, LnT = natural log of TOBEC.
[c] Model best fitting the model-building data set in cross-validation.

TABLE 3. Absolute error and relative absolute error ($\bar{x} \pm$ SE) of lean-mass predictions for birds in a validation data set ($n = 49$) when estimated from models in the subsets of "good" models fitted with a model-building data set ($n = 49$).

Model no.[a]	Model equation[b]	Absolute error (g)	Relative error (%)
1	$LeM = -0.7044 + 0.7077(M) + 0.1191(W)$	0.75 ± 0.078	1.7 ± 0.17
2[c]	$LeM = -1.5407 + 0.7017(M) + 0.1050(W) + 0.0122(L)$	0.74 ± 0.077	1.7 ± 0.17
3T	$LeM = 8.2825 + 0.7218(M) + 0.0073(T)$	0.74 ± 0.070	1.7 ± 0.16
4T[d]	$LeM = -4.6246 + 0.6594(M) + 0.1619(W) + 0.0114(T)$	0.68 ± 0.071	1.6 ± 0.16
5T	$LeM = -12.8349 + 0.6657(M) + 0.1570(W) + 2.0135(\mathrm{Ln}T)$	0.69 ± 0.071	1.6 ± 0.16
6T	$LeM = -1.7735 + 0.6479(M) + 0.1696(W) - 0.0210(T) + 0.0000845(T^2)$	0.69 ± 0.068	1.6 ± 0.15
7T	$LeM = 11.9310 + 0.6516(M) + 0.1675(W) + 0.0327(T) - 3.9672(\mathrm{Ln}T)$	0.69 ± 0.069	1.6 ± 0.16
8T	$LeM = -1.7939 + 0.6431(M) + 0.1581(W) + 0.0097(L) - 0.0270(T) + 0.0000989(T^2)$	0.68 ± 0.067	1.6 ± 0.15
9T	$LeM = 14.3885 + 0.6482(M) + 0.1589(W) + 0.072(L) + 0.0360(T) - 4.6467(\mathrm{Ln}T)$	0.68 ± 0.068	1.6 ± 0.15

[a] T indicates inclusion of TOBEC in model.
[b] LeM = lean mass, M = body mass, W = wing chord, L = body length, T = TOBEC, LnT = natural log of TOBEC.
[c] Best model without a TOBEC term.
[d] Best model including a TOBEC term.

much greater absolute error (1.89 ± 0.233 g) and relative absolute error (65.6 ± 10.89%) than the other two methods (Table 5). Furthermore, although the maximum relative absolute error in lipid-mass prediction using the first two methods was a considerable 132.3% of the actual lipid mass, the maximum relative absolute error produced by the inverse, two-stage method was 458.3% of the actual lipid mass.

Discussion.—Both selected models accurately predicted lean mass of a validation data set. Model 2 (containing only body mass and morphometric variables) predicted lean mass with an average error of 0.74 g, whereas model 4T (containing TOBEC index in addition to body mass and a morphometric variable) predicted lean mass with an average error of 0.68 g. These values translated into mean errors of 1.7% and 1.6% relative to lean mass, respectively.

For the model without TOBEC, mean and maximum 95% confidence intervals indicated that the predicted mean lean mass of a new sample of wintering cardinals would fall within 0.18 to 0.51 g of the true lean mass, an interval equal to only 2.3 to 6.5% of the range of lean masses (15.74 g) in the sample. Prediction of lean mass for a single new case would lie within 1.80 to 1.86 g of the measured value with 95% probability, an interval covering 22.9 to 23.6% of the observed range of lean masses. In most applications, however, the prediction interval of interest probably would lie somewhere between these two extremes. For example, one might be interested in comparing the mean lean mass of cardinals captured in one location with that of cardinals from another location, sampling 10 birds from each location to make the comparison. In this case, the mean predicted lean mass for 10 new cases would be expected to fall within 0.59 to 0.76 g of the actual mean lean mass of the group (Table 4). Actual differences in mean

TABLE 4. Equations of selected models to predict lean and lipid masses of wintering Northern Cardinals fitted with the complete data set ($n = 98$). Estimates (g) are ± 95% confidence intervals (with 95% prediction intervals for the mean of 10 new cases [PI-10], 95% prediction intervals for a single new case [PI] in parentheses) for mean (mean X) and maximum (maximum X) values of independent variables.

Model equation[a]	R^2	MSE	Estimates (PI-10, PI): Mean X	Estimates (PI-10, PI): Maximum X
$LeM = -1.795 + 0.683(M) + 0.101(W) + 0.0197(L)$	0.926	0.811	44.0 ± 0.18 (0.59, 1.80)	51.4 ± 0.51 (0.76, 1.86)
$LeM = -2.385 + 0.652(M) + 0.140(W) + 0.012(T)$	0.936	0.706	44.0 ± 0.17 (0.55, 1.68)	52.0 ± 0.59 (0.79, 1.77)
$LiM = 1.795 + 0.317(M) - 0.101(W) - 0.020(L)$	0.647	0.811	3.6 ± 0.18 (0.59, 1.80)	5.7 ± 0.51 (0.76, 1.86)
$LiM = 2.385 + 0.348(M) - 0.140(W) - 0.012(T)$	0.693	0.706	3.6 ± 0.17 (0.55, 1.68)	5.0 ± 0.59 (0.79, 1.77)

[a] LeM = lean mass, M = body mass, W = wing chord, L = body length, T = TOBEC, LiM = lipid mass.

TABLE 5. Absolute error and relative absolute error ($\bar{x} \pm$ SE) of lipid-mass predictions for birds in a validation data set ($n = 49$) when estimated from comparable models employing two-stage, direct, and inverse two-stage methods of estimation.

Equation[a]	Absolute error (g)	Relative error (%)
Two-stage		
$LiM = M - LeM$, where	0.68 ± 0.071	23.5 ± 3.37
$LeM = -4.625 + 0.659(M) + 0.162(W) + 0.011(T)$		
Direct		
$LiM = 4.625 + 0.341(M) - 0.162(W) - 0.011(T)$	0.68 ± 0.071	23.5 ± 3.37
Inverse two-stage		
$LiM = M - LeM$, where	1.89 ± 0.233	65.6 ± 10.89
$LeM = -31.495 + 0.328(M) + 0.455(W) + 0.089(T)$; from		
$T = 352.467 - 3.676(M) - 5.094(W) + 11.191\ (LeM)$		

[a] LeM = lean mass, M = body mass, W = wing chord, T = TOBEC, LiM = lipid mass.

lean mass between certain geographic locations can exceed 4 or 5 g in this species (Burger unpubl. data). Therefore, for the purposes of determining whether the average lean mass of cardinals differs between locations, sampling 10 birds from each location and using the model to predict lean mass would be sufficient to avoid Type II errors. Confidence and prediction intervals for the model including TOBEC were comparable (Table 4), and the conclusions were the same.

The models fared less well, however, when predicting lipid mass. Although the absolute errors of the lipid-mass predictions are of the same magnitude as those of the lean-mass predictions, they translate into greater average relative absolute errors of lipid-mass estimates of 25.8 and 23.5%, respectively (see Morton et al. 1991, Skagen et al. 1993). Again, for the model not including TOBEC, the 95% confidence interval around the mean fat estimate of a new sample had the same width as that for lean mass, ranging from 0.18 to 0.51 g for mean and maximum values of the independent variables, respectively. Because the range in lipid mass (7.39 g) was smaller than that for lean mass, the intervals covered a greater percentage of the range in lipid mass, 4.9 to 13.8%, respectively. As for lean mass, predicting lipid mass for a single new case is less useful. The 95% prediction intervals for mean and maximum values of independent variables, 1.80 to 1.86 g, covered 48.7 to 50.3% of the observed range of lipid masses. For a realistic application like the geographic comparison of lean mass above, however, the models would provide adequate power. For a sample of 10 birds, prediction of the mean lipid mass would be expected to fall within 0.59 to 0.76 g of the actual mean value (Table 4), which is less than the difference in mean lipid mass of cardinals between some locations, and even between morning and evening values within certain locations (Burger unpubl. data). Intervals and conclusions were similar for the model containing TOBEC index (Table 4).

These errors and intervals are similar in magnitude to those obtained for Wood Thrushes (*Hylocichla mustelina*; Conway et al. 1994), and much smaller than the errors obtained for House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*; Asch and Roby 1995). Although the confidence and prediction intervals obtained in this study are somewhat smaller than those obtained for Semipalmated Sandpipers (*Calidris pusilla*) and White-rumped Sandpipers (*C. fuscicollis*; Skagen et al. 1993), sandpipers have greater lipid mass relative to lean mass, which would make their equations even more useful for detecting differences among groups of birds (interval width compared with observed range of body component) than those from this study.

The inclusion of TOBEC as an independent variable in the prediction model had a minimal effect on the accuracy of estimates of lean mass and lipid mass for wintering cardinals. The best model including a TOBEC variable reduced the mean error of predicted lean mass and lipid mass in a validation data set by only 0.06 g compared with the best model not including TOBEC, which translates into a difference of 0.1% in relative error for lean mass and 2.3% in relative error for lipid mass.

Considerable debate continues about which variable (e.g. lean mass, lipid mass, or TOBEC) should be the dependent variable in a regression model used to estimate a value (e.g. lean mass or lipid mass) that can be measured by way of slow, inconvenient, but accurate means (e.g. solvent extraction) versus a measure that is relatively faster, more convenient, and usually less accurate (e.g. TOBEC; see Skagen et al. 1993, Asch and Roby 1995). Two approaches to this problem are used. The "classical approach" would be to fit the model with TOBEC as the dependent variable, and then solve (invert) for one of the independent variables (e.g. lean mass; Osborne 1991), which then could be subtracted from body mass in a two-stage estimation of lipid mass. Nearly three decades ago, however, Krutchkoff (1967) introduced what became known as the "inverse approach," or the method of fitting the data with, for example, lean mass as the dependent variable to estimate it directly (Osborne 1991). The various methods perform differently. The direct method (Krutchkoff's inverse approach) usually is superior when the values estimated are close to the values used to construct the estimation model, i.e. when the application is not an extrapolation beyond the model-building data set (Osborne 1991; also see Kubokawa and Robert 1994). In avian body-composition estimations, lipid mass (and lean mass) has been predicted more accurately using the direct approach (as the dependent variable; Morton et al. 1991, Skagen et al. 1993, Asch and Roby 1995), perhaps because these intraspecific applications fall within the criteria for which the direct method outperforms the classical method.

Several researchers have fitted models with lipid mass as the dependent variable and body mass, TOBEC, and body morphometrics as independent variables (Morton et al. 1991, Skagen et al. 1993, Conway et al. 1994, Asch and Roby 1995, Lyons and Haig 1995), and some have fitted models with lean mass as the dependent variable (e.g. Scott et al. 1991, Conway et al. 1994, Lyons and Haig 1995). What has not been clear is that a model with lean mass as the dependent variable and body mass as an independent variable predicts lean mass with the same error as a model with lipid mass as the dependent variable predicts lipid mass, as long as the models include the same independent variables (Table 4). Because the sum of lipid mass and lean mass equals body mass, a model fitted with lean mass as the dependent variable (and that includes body mass) will fail to fit the same amount of variation in lean mass as a model fitted with lipid mass as the dependent variable will fail to fit in lipid mass. In other words, body mass can explain the same amount (absolute, not relative) of variation in lean mass as it can explain in lipid mass.

For example, the equation that represents the relationship between body mass, lean mass, and lipid mass is, by definition:

$$LiM = M - LeM, \tag{3}$$

where LiM is lipid mass, M is body mass, and LeM is lean mass. Because the relationship is exact, there is no error associated with this "model." From regression, an equation is determined that relates lean mass to body mass, other independent variables, and the error, or portion of lean mass that is not explained, such as:

$$LeM = \beta_0 + \beta_1(M) + \beta_2(W) + \beta_3(T) + e, \tag{4}$$

where the βs represent the constant and coefficients from the regression model, W is wing chord, T is TOBEC index, and e is the unexplained error. Substituting equation 4 for lean mass in equation 3 yields:

$$LiM = M - [\beta_0 + \beta_1(M) + \beta_2(W) + \beta_3(T) + e], \tag{5}$$

which can be rewritten as:

$$LiM = -\beta_0 + (1 - \beta_1)(M) - \beta_2(W) - \beta_3(T) - e \tag{6}$$

(see Tables 4 and 5).

What is particularly important for the question of comparing prediction errors of the two approaches, however, is that the unexplained error in lipid mass from equation 6 is equal to the unexplained error in lean mass from equation 4 multiplied by -1 (Table 5). In fact, when fitting the complete data set with lean mass as the dependent variable and body mass, wing chord, and TOBEC as the independent variables, saving the residuals e_1, and then fitting the set with lipid mass as the dependent variable and saving the residuals e_2, an examination of the residuals indicates that for each case, $e_1 = -(e_2)$, and that $|e_1| = |e_2|$. Thus, for each case, the absolute difference (in g) between the predicted value and the actual value is the same when lean mass is the dependent variable as when lipid mass is the dependent variable. This holds for all models with the same independent variables, as long as body mass is included, and enables the model-selection procedure in this study to focus only on models predicting lean mass. If only models predicting lipid mass had been analyzed, the same model forms would have been selected as best.

This relationship was not obvious in the two papers (Conway et al. 1994, Lyons and Haig 1995) in which both lean mass and lipid mass were estimated directly as dependent variables, because not all variables were the same between the two suites of models. Conway et al. (1994) included fat score as an independent variable when predicting lipid mass, but not when predicting lean mass, and Lyons and Haig (1995) used log-transformed TOBEC when predicting lipid mass, but not when predicting lean mass. In both studies, the direct estimates of lipid mass were associated with smaller mean absolute errors than the estimates of lean mass, which implies that lean-mass estimates could have been better. That is, inclusion of fat score in Conway et al.'s (1994) models to predict lean mass probably would have reduced the absolute error associated with the estimates, and likewise for the inclusion of log-transformed TOBEC by Lyons and Haig (1995).

In summary, my results suggest that the predictive equations for estimating body composition of wintering Northern Cardinals are accurate enough to be useful. Because TOBEC technology did not enhance the accuracy of the estimates significantly, there is no apparent reason to purchase the expensive TOBEC equipment. Moreover, researchers should fit their data with either lean mass or lipid mass as the dependent variable, and estimate the other variable by subtracting the estimate from body mass. Either approach will yield the same error, and often will result in smaller prediction intervals than the inverse, two-stage method while preserving the fundamental, definitive relationship between lipid mass, lean mass, and body mass (equation 3).

Acknowledgments.—I am indebted to Terry Root for providing the EM-SCAN unit used in this study and to Jason Weckstein for his tireless assistance in the field. Thanks to R. and T. Robinson, T. Dietsch, S. and J. Hinshaw, University of Michigan, and personnel of Ledges State Park, Indiana University, Fountain Grove Wildlife Area, Eufaula NWR, and the U. S. Army Corps of Engineers for providing access to field sites. T. Root, K. Hall, R. Burke, B. Fahey, and J. Parody made helpful comments on earlier drafts, and G. Fowler provided statistical advice. This research was performed under appointment to the U. S. Department of Energy, Graduate Fellowships for Global Change Program, administered by the Oak Ridge Institute for Science and Education. Additional funding was provided by the U. S. Fish and Wildlife Service.

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Received 28 June 1996, accepted 14 March 1997.
Associate Editor: M. E. Murphy

The Auk 114(4):769–773, 1997

Nest Predation in Black-capped Chickadees: How Safe are Cavity Nests?

BETH J. CHRISTMAN[1,3] AND ANDRÉ A. DHONDT[2]
[1] *Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, New York 14853, USA; and*
[2] *Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850, USA*

Cavity nests traditionally have been thought to offer birds a greater degree of protection against nest predation than open-cup nests (Lack 1954, Nice 1957, Ricklefs 1969, Martin and Li 1992; but see Nilsson 1986). However, early work on the relative safety of cavity nests primarily was conducted on nests built in boxes, which often exhibit lower predation rates than nests in natural cavities (Nilsson 1984). Recent attention has focused on nest predation in natural situations. Because nest predation is important in shaping life-history evolution (Martin and Clobert 1996), it is important to con-

[3] E-mail: bjc14@cornell.edu