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ESTIMATION OF LEAN AND LIPID MASS IN SHOREBIRDS USING TOTAL-BODY ELECTRICAL CONDUCTIVITY

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ABSTRACT.—Total-body electrical conductivity (TOBEC) is a noninvasive technique to estimate body composition in live birds. A comparison of regression models was conducted to identify a useful equation for predicting lean and lipid mass from TOBEC and other variables in three shorebird species (*Calidris pusilla, C. alpina* and *Limnodromus griseus*). Models constructed included regressions of lean and lipid mass (independently) on body-mass and body-size variables, regressions using only TOBEC indices, and expanded models including body mass, size variables, and TOBEC indices. Linear, quadratic, and modified linear (incorporating body length) models were compared to identify the lowest-order polynomial to adequately describe variation in lean and lipid mass within and among species. Prediction intervals (95%) for all regressions were compared to evaluate accuracy of new models. New TOBEC models and TOBEC equations from the literature were used to predict body composition of individuals not included in regression analyses. Modified linear models incorporating body length showed a strong relationship between lean mass and independent variables for two of three intraspecific cases. New and existing TOBEC equations allowed accurate estimates of lean mass. Fat-mass variation was much harder to explain, whether using body-mass and body-size variables or TOBEC indices. With TOBEC it is possible to make accurate predictions of lean mass in live birds, but estimates of fat mass remain problematic. *Received 28 June 1994, accepted 6 September 1994.*

BODY COMPOSITION in free-living birds varies on daily and seasonal cycles (Helms 1968, Blem 1976), and body condition (energy stores relative to lean mass) influences the progress and culmination of many phases of the avian life cycle (Lack 1966, Walsberg 1983, Haramis et al. 1986, Blem 1990). During reproduction, migration, and winter, individuals maintaining an optimal body composition gain a selective advantage (Lack 1966, Ankney and MacInness 1978, Blem 1980, Davidson 1981). Thus, the ability to monitor changes in body composition, and to quantify lean and lipid mass, provides insight to the evolution of avian life histories.

Solvent extraction of fats from carcasses is the most accurate method for quantifying lean and lipid mass (Bligh and Dyer 1959, Dobush et al. 1985, Johnson et al. 1985), but this process is time consuming and tedious. Furthermore, destructive techniques are usually undesirable. Several noninvasive techniques to estimate body composition have been developed as alternatives to lipid extraction. Visual estimation of subcutaneous fat stores has been employed in numerous passerine studies (McCabe 1943, Helms and Drury 1961, Krementz and Pendleton 1990, Rogers 1991). Fat content also has been estimated from body mass in three ways: (1) direct linear correlation with body mass (Iverson and Vohs 1982); (2) linear correlation with a scaled body-mass measurement (Iverson and Vohs 1982, Johnson et al. 1985); and (3) multiple regression of body-mass and body-size measurements (Mascher and Marcstrom 1967, Perdeck 1985, Ringelman and Szymczak 1985, Miller 1989, Castro and Myers 1990, Sparling et al. 1992). Also, lean mass has been estimated using a correlation with body size (Mascher and Marcstrom 1967, McNeil and Cadieux 1972, Page and Middleton 1972, Iverson and Vohs 1982, and others), or by using water content and a water : lean mass ratio (Child and Marshall 1970, Campbell and Leatherland 1980). These methods have limitations and drawbacks as a result of interobserver variability and/or low explanatory power of body mass and mensural data for predicting fat and lean mass (Krementz and Pendleton 1990, Rogers 1991).

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Total-body electrical conductivity (TOBEC) is a noninvasive technique that measures body composition (Keim et al. 1988). Using a portable device, an electromagnetic field of a certain reference impedance is generated around an empty cylinder. The subject animal is placed in the cylinder, and impedance of the magnetic field is measured a second time; change in field conductance is relative to the amount of lean mass in the cylinder. Lean mass conducts electricity better than fat mass due to the electrolytic conductivity of sodium and potassium (Anonymous 1991). TOBEC values are a function of conductivity, cross-sectional area, and length of the subject (Fiorotto et al. 1987). To calibrate the device for a particular species or interspecific group, a sample of individuals must be collected and body compositions determined by solvent extraction. TOBEC values from the sample are then related to lean-mass measurements through regression analyses. TOBEC estimates of lean mass can be subtracted from body mass to estimate fat mass.

Walsberg (1988) introduced the technique to avian ecology with a calibration from a sample of 14 species. Early studies found a strong correlation between TOBEC readings and lean mass, using either a second-order polynomial equation (Walsberg 1988), or a simple linear equation (Castro et al. 1990). Roby (1991) provided the first intraspecific calibration. His results with respect to lean mass corroborated those of Walsberg (1988) and Castro et al. (1990); Roby concluded that TOBEC values provide accurate estimates of lean mass in live birds. Scott et al. (1991) used a model-testing approach to identify the most effective equation for predicting lean mass using TOBEC. They found that the relationship was linear for intraspecific studies, but that a second-order polynomial was most appropriate for interspecific studies (similar to Walsberg [1988], but contrary to Castro et al. [1990]). Morton et al. (1991) cautioned against interpretation of strong relationships between TOBEC and lean mass as evidence that lipid mass will be predicted accurately. Skagen et al. (1993) provided intra- and interspecific calibrations for two sandpiper species, and made the first attempt to determine the accuracy of lipid-mass predictions.

In this study we evaluated various models to identify the most effective model for predictions of lean mass and lipid mass both within and among three shorebird species: Semipalmated Sandpipers (*Calidris pusilla*), Dunlins (*C. alpina*), and Short-billed Dowitchers (*Limnodromus griseus*). We then used a verification set to compare our lean-mass and lipid-mass equations with those from four previous TOBEC studies.

Methods

Fifty-eight birds (20 Semipalmated Sandpipers, 18 Dunlins, and 20 Short-billed Dowitchers) were captured with mist nets on coastal mudflats at the Tom Yawkey Wildlife Center, Georgetown, South Carolina, between 29 April and 2 June 1992. Birds were weighed, measured (natural wing chord, tarsometatarsus ["tarsus"], exposed culmen, total head length [bill tip to back of skull], and body length [dorsal surface placed on flat ruler, bill tip to end of tail feathers]), and scanned within 1 h of capture in an EM-SCAN Model SA-2 Small Animal Body Composition Analyzer. Individuals were restrained using a cotton wrap with Velcro fasteners and placed on their dorsal side on a plastic tray (ca. 9 × 30 cm) provided by the manufacturer. Each bird was positioned on the tray so that when placed in the analyzer, the midsternum was centered on the long axis of the chamber. The mean of three scans was recorded as the TOBEC index for the individual.

Birds were killed using CO_2 inhalation (Custer 1988), double-bagged in plastic, and frozen (euthanasia procedures followed Clemson University Animal Welfare Protocol Number 661). In the laboratory, whole carcasses were freeze-dried for 48 h, and then weighed again to assess water content; water content was determined by subtracting freeze-dried mass from live mass. Dried carcasses were sectioned and fats were extracted from the entire carcass for 24 to 48 h using a petroleum ether solvent in a Soxhlet apparatus. At the end of each extraction, lean dry mass and fat mass (M_F) were measured to the nearest 0.1 g. Lean mass (M_L) was comprised of lean dry mass and water content.

From the 58 collected individuals, 14 (5 Semipalmated Sandpipers, 4 Dunlins, and 5 Short-billed Dowitchers) were randomly chosen as a verification set to be used in a cross-validation procedure. These individuals were used to test the accuracy of equations generated in this study and existing TOBEC equations from the literature. To preserve the lean-mass range in both the verification and calibration sets, the entire sample was sorted by lean mass within species, and a systematic random sample was chosen. To determine the percent error associated with each model, independent variables from verification individuals were placed in predictive equations and the difference between predicted values and actual values was expressed as a percentage of the actual value:

$$(|\hat{Y} - Y|/Y)\,100,$$

where $\hat{Y}$ is the predicted value and Y is the actual value. Two separate least-squares regression analyses were used to determine variation in lean mass and fat mass explained by TOBEC. Because the goal of this technique is to predict body composition of live birds, we have regressed body component (lean mass or fat mass) as the response variable on TOBEC value, mass and size (predictor variables).

Lean-mass estimates.—Four regression models were developed to relate TOBEC to lean mass. First, a stepwise regression was performed using only body-size variables to predict lean mass. Candidate predictor variables included: body mass, wing chord, total head length, body length, tarsus, and exposed culmen. Significance levels to enter and remain in the model were set at 0.15 in order to avoid omitting any predictor variables that may explain even small amounts of variation in the response variable. This stepwise regression procedure was run for each species individually and with all species combined.

Next, a first-order model using TOBEC (T) alone was generated to predict lean mass (M_L) from a simple linear regression:

$$M_L = \beta_0 + \beta_1 T, \tag{1}$$

where β_0 is the y-intercept, β_1 is the slope of the regression line, and T is the TOBEC index. A second-order equation using only TOBEC also was fit to evaluate a curvilinear model:

$$M_L = \beta_0 + \beta_1 T + \beta_2 T^2, \tag{2}$$

where T is TOBEC index.

TOBEC is a complex function of subject length, cross-sectional area, and conductivity; body length may explain additional variation in lean mass (Fiorotto et al. 1987). Therefore, a modified linear model incorporating TOBEC and body length (L) of the subject (after Fiorotto et al. 1987) was constructed:

$$M_L = \beta_0 + \beta_1 (TL)^{0.5}, \tag{3}$$

where T is TOBEC index and L is body length.

Lastly, the body-size variables resulting from the initial stepwise regression were combined with equations 1 to 3 to form "expanded" models. This allows an assessment of the additional variation in lean mass explained by TOBEC, over and above variation explained by size variables alone. These steps resulted in the creation of seven models for each species and the interspecific group: one using size variables alone, three using TOBEC indices alone, and three using size variables and TOBEC indices (expanded models).

Fat-mass estimates.—Preliminary regressions of fat mass on TOBEC revealed that, in general, TOBEC readings alone performed very poorly as estimators of fat mass. Therefore, we have restricted our analyses of fat-mass variation to three regression models instead of the seven models used in the lean-mass analyses. The first uses body-size measurements alone in a stepwise regression procedure similar to that used for lean mass. Candidate independent variables remained the same and significance levels for entry into the model and for remaining in the model were set at 0.15.

After creating the appropriate body-size regression equation for each species and for the interspecific group, these equations were expanded to include TOBEC readings in first-order and second-order models:

$$M_F = \beta_0 + \beta_1 (\ln T) + \beta_2 (X_1) \ldots \beta_n (X_n) \tag{4}$$

and

$$M_F = \beta_0 + \beta_1 (\ln T) + \beta_2 (\ln T)^2 + \beta_3 (X_1) + \ldots + \beta_n (X_n), \tag{5}$$

respectively, where T is TOBEC index and $X_1 \ldots X_n$ represents any combination of body-size measurements (wing chord, tarsus, culmen, total head length, body length) chosen in the stepwise regression. These fat-mass models are similar to those used for lean-mass predictions. Following the protocol of Morton et al. (1991), natural logarithms of TOBEC readings were used in these models. These steps allow evaluation of TOBEC terms for explaining fat-mass variation, over and above variation explained by body-size variables alone.

Model comparisons.—Regression models were evaluated by comparing: (1) mean widths of 95% prediction intervals for lean-mass and lipid-mass estimates; (2) mean square error (MSE) for each model; and (3) amount of variation (R^2) in response variable explained by predictor variable(s). For each regression of lean mass or fat mass on TOBEC, 95% prediction intervals were calculated for each data point in the regression. Mean widths of these intervals were compared to identify the model providing the narrowest intervals around estimates of lean or lipid mass.

For each body component (lean or lipid mass), the "best-fit" equation was identified based on the strength of the functional relationship between predictor variables and response variables. Best-fit equations were chosen by examining, in order of relative importance, prediction intervals, MSE, and R^2. When the best fit model was an expanded model, the amount of variation in response variable explained by TOBEC terms, given mass and size terms, was evaluated with an F-statistic (Sokal and Rohlf 1981: box 16.2). Because the strength of the functional relationship does not always indicate the predictive power of an equation with new observations, final recommendations for appropriate models were based on percent error after cross-validation. TOBEC equations from the literature were compared with new equations based on percent error of lean-mass and lipid-mass estimates in cross-validation.

TABLE 1. Characteristics ($\bar{x}$ ± SD) of birds used in calibration of EM-SCAN Model SA-2 body-composition analyzer.

Variable	Semipalmated Sandpiper	Dunlin	Short-billed Dowitcher
n	20	18	20
Body mass (g)	25.4 ± 3.3	53.5 ± 5.3	95.2 ± 25.5
Fat mass (g)	3.8 ± 2.5	4.6 ± 3.4	13.9 ± 12.6
Lean mass (g)	21.8 ± 1.3	49.3 ± 3.4	81.9 ± 13.6
Percent fat[a]	13.9 ± 7.8	8.3 ± 5.2	12.4 ± 9.4
Percent water[b]	73.8 ± 0.7	73.3 ± 0.6	73.2 ± 0.7

[a] Percentage of body mass.
[b] Percentage of lean mass.

RESULTS

Lean-mass models.—All models produced significant relationships between TOBEC and lean mass for each species (Tables 1 and 2). The relationship between TOBEC and lean mass is shown in Figure 1. For Dunlins, stepwise regression selected two variables for prediction of lean mass: body mass and tarsal length. These two variables explained 78% of variation in lean mass. TOBEC estimates of lean mass were correlated with actual lean-mass values (Fig. 2), and models using TOBEC alone (equations 1–3) explained as much variation in lean mass as body mass and tarsal length. When TOBEC and size variables were combined in a multiple regression, expanded equations were able to further reduce the MSE. The three expanded TOBEC models displayed similar functional relationships between lean mass and predictor variables. The expanded body-length model showed the smallest mean prediction interval and smallest MSE of the first-order equations; it was

TABLE 2. Predictive models for lean mass using body mass, size variables, and TOBEC (T) in Dunlins, Short-billed Dowitchers, Semipalmated Sandpipers, and all species combined.

Independent variables[a]	MSE	F	R^2
Dunlin			
Body mass, tarsus	3.07	18.98**	0.78
T	2.63	45.22**	0.79
T, body mass, tarsus	1.77	24.93**	0.88
T, T^2	2.66	22.72**	0.81
T, T^2, body mass, tarsus	1.56	21.79**	0.91
$(TL)^{0.5}$	1.92	66.19**	0.84
$(TL)^{0.5}$, body mass, tarsus	1.56	28.77**	0.90
Short-billed Dowitcher			
Body mass, wing	6.58	173.09**	0.97
T	14.45	150.16**	0.92
T, body mass, wing	7.11	106.86**	0.97
T, T^2	15.35	70.77**	0.92
T, T^2, body mass, wing	3.94	147.23**	0.98
$(TL)^{0.5}$	16.67	128.37**	0.91
$(TL)^{0.5}$, body mass, wing	7.13	106.57**	0.97
Semipalmated Sandpiper			
Body mass	0.60	25.05**	0.66
T	1.15	6.86*	0.35
T, body mass	0.35	26.95**	0.82
T, T^2	1.24	3.23[ns]	0.35
T, T^2, body mass	0.38	16.48**	0.82
$(TL)^{0.5}$	0.77	16.83**	0.56
$(TL)^{0.5}$, body mass	0.33	28.33**	0.83
Interspecific			
Body mass, wing, head length, culmen	4.28	1,648.18**	0.99
T	17.23	1,604.70**	0.97
T, body mass, wing, head length, culmen	3.82	1,477.64**	0.99
T, T^2	7.44	1,885.41**	0.99
T, T^2, body mass, wing, head length, culmen	2.77	1,698.45**	0.99
$(TL)^{0.5}$	6.47	4,343.24**	0.99
$(TL)^{0.5}$, body mass, wing, head length, culmen	3.27	1,728.43**	0.99

**, $P < 0.01$; *, $P < 0.05$; ns, $P > 0.05$.
[a] T = TOBEC index; L = body length.

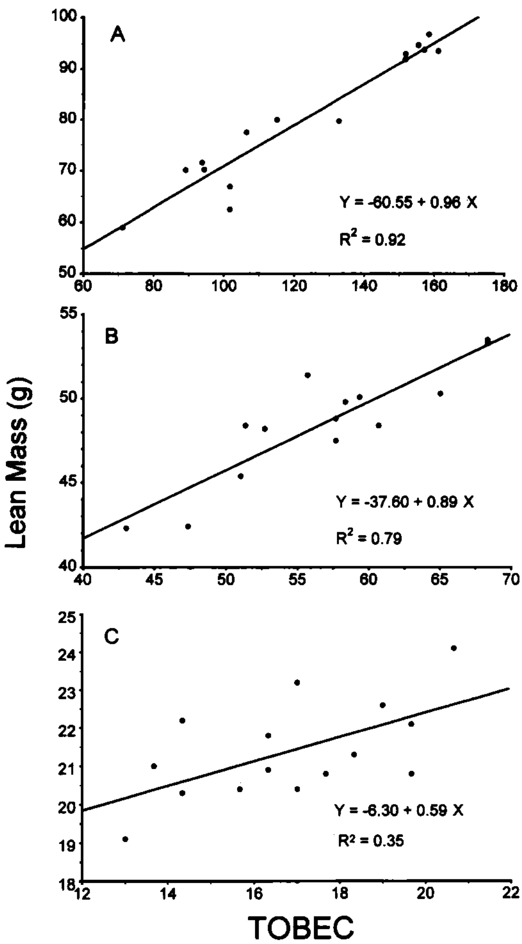

Fig. 1. Intraspecific relationships between TOBEC and lean mass as determined by solvent extraction in (A) Short-billed Dowitchers, (B) Dunlins, and (C) Semipalmated Sandpipers.

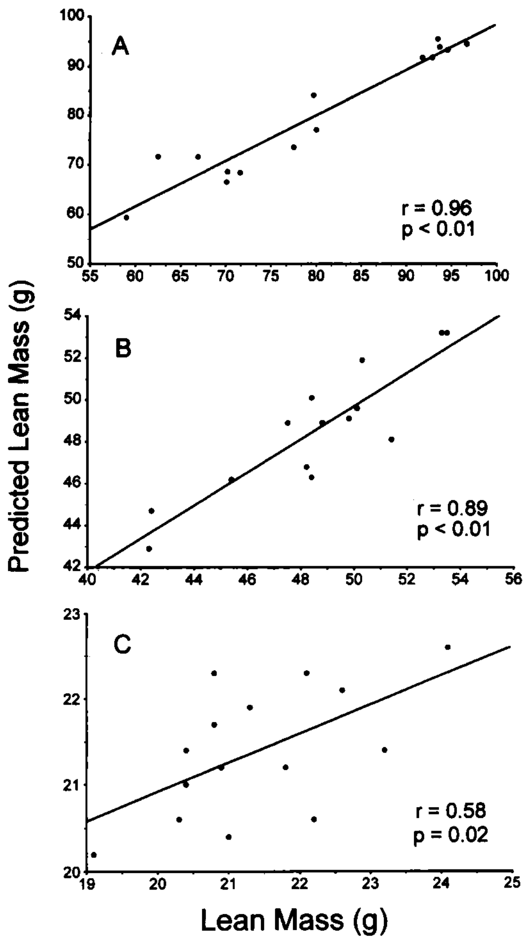

Fig. 2. Intraspecific relationships between predicted lean mass using TOBEC and actual lean mass as determined by solvent extraction in (A) Short-billed Dowitchers, (B) Dunlins, and (C) Semipalmated Sandpipers.

chosen as the best-fit model. The TOBEC term in the expanded model significantly improved the equation ($F_{1,10} = 11.65$, $P < 0.01$, $n = 14$). Estimates of lean mass for Dunlins were made using:

$$M_L = 6.93 + 0.92\,(TL)^{0.5} + 0.20\,X_1 + 0.04\,X_2, \qquad (6)$$

where T is TOBEC index, L is body length, X_1 is body mass, and X_2 is tarsal length.

For Short-billed Dowitchers, body-size variables chosen in the stepwise regression (body mass and wing chord) explained 97% of variation in lean mass (Table 2). Size variables alone explained more variation in lean mass than any model using TOBEC alone. Nevertheless, correlation between TOBEC estimates of lean mass and actual lean mass were highest in dowitchers (Fig. 2). When TOBEC readings and size variables were combined, the expanded second-order model (i.e. combined with body mass and wing chord) showed the strongest functional relationship (Table 2). This model had the smallest mean prediction interval, provided a great reduction in MSE, and the TOBEC terms in the model were significant ($F_{2,10} = 5.02$, $P < 0.05$, $n = 15$). Estimates of lean mass in Short-billed Dowitchers were made using:

$$M_L = -70.87 + 0.71\,T - 0.004\,T^2 + 0.72\,X_1 + 0.38\,X_2, \qquad (7)$$

TABLE 3. Predictive models for lipid mass using body mass, size variables, and TOBEC (T) of Dunlins, Short-billed Dowitchers, Semipalmated Sandpipers and all species combined.

Independent variables[a]	MSE	F	R^2
Dunlin			
Body mass, tarsus	2.97	23.15**	0.81
ln(T), body mass, tarsus	1.53	33.64**	0.92
ln(T), (ln[T])^2, body mass, tarsus	1.46	26.93**	0.92
Short-billed Dowitcher			
Body mass, wing	6.34	145.37**	0.96
ln(T), body mass, wing	6.21	99.22**	0.96
ln(T), (ln[T])^2, body mass, wing	4.68	99.90**	0.98
Semipalmated Sandpiper			
Body mass	0.57	167.29**	0.93
ln(T), body mass	0.34	144.44**	0.96
ln(T), (ln[T])^2, body mass	0.37	88.94**	0.96
Interspecific			
Body mass, wing, head length, culmen	4.29	159.21**	0.94
ln(T), body mass, wing, head length, culmen	2.97	188.35**	0.96
ln(T), (ln[T])^2, body mass, wing, head length, culmen	2.67	175.25**	0.97

**, $P < 0.01$.
[a] T = TOBEC index.

where T is TOBEC index, X_1 is body mass, and X_2 is wing chord.

Stepwise regression of body-size variables in Semipalmated Sandpipers included only body mass in the final equation. Body mass explained 66% of variation in lean mass. The MSE value for this model was similar to those for models using only TOBEC (Table 2). TOBEC estimates of lean mass in the Semipalmated Sandpiper showed the lowest correlation to actual lean-mass values (Fig. 2). Once again, the expanded TOBEC models (i.e. combined with body mass) explained more variation in lean mass than size measurements alone. All three expanded TOBEC models performed similarly, but the expanded body-length model resulted in the best fit; it produced the smallest mean prediction interval, the smallest MSE, and a significant TOBEC term ($F_{1,13} = 11.57$, $P < 0.01$, $n = 15$). Lean mass was estimated using TOBEC and body mass:

$$M_L = 7.09 + 0.58\,(TL)^{0.5} + 0.21\,X_1, \quad (8)$$

where T is TOBEC index, L is body length, and X_1, body mass.

When all species were combined, expanded regression equations (including TOBEC indices and size variables) provided a better fit to the data than an equation using size variables alone (Table 2). Size variables chosen by the stepwise regression procedure for the interspecific case included body mass, total head length, wing chord, and culmen length. The expanded second-order model with these size variables provided the best fit to the data ($R^2 = 0.99$, $P < 0.001$, $n = 44$), but the mean square error was similar to that for the expanded body-length model. The interspecific equation for predictions of lean mass is:

$$M_L = -27.66 + 0.32\,T - 0.001\,T^2 + 0.37\,X_1 + 0.57\,X_2 + 0.25\,X_3 - 0.63\,X_4, \quad (9)$$

where T is TOBEC index, X_1 is body mass, X_2 is total head length, X_3 is wing chord, and X_4 is culmen length.

Fat-mass models.—Coefficients of determination from regressions of fat mass on size variables ranged from 0.81 to 0.98 (Table 3). The stepwise regression equation to estimate fat mass in Short-billed Dowitcher selected body mass and wing chord (Table 3). When TOBEC was added to this equation, reductions in MSE were relatively small (MSE = 6.21 and 4.68 for expanded first- and second-order models, respectively) and TOBEC terms were not significant ($F_{2,10} = 3.12$, $P > 0.05$, $n = 15$ for second-order model). Dowitcher fat content was estimated using:

$$M_F = 20.23 + 0.50\,X_1 - 0.37\,X_2, \quad (10)$$

where X_1 is body mass and X_2 is wing chord.

The stepwise regression equation to estimate fat mass in Dunlins selected body mass and tar-

TABLE 4. Mean 95% prediction intervals (± SE) for estimates of lean mass and lipid mass using size variables and TOBEC indices with Dunlins, Short-billed Dowitchers, Semipalmated Sandpipers, and all species combined.

Model	Dunlin (n = 14)	Short-billed Dowitcher (n = 15)	Semipalmated Sandpiper (n = 15)	All species (n = 44)
Lean mass				
Mass and size	8.48 ± 0.15	12.23 ± 0.13	3.57 ± 0.03	8.82 ± 0.04
First-order TOBEC	7.55 ± 0.07	17.48 ± 0.10	4.93 ± 0.03	17.13 ± 0.03
Second-order TOBEC	7.90 ± 0.14	18.67 ± 0.28	5.31 ± 0.07	11.38 ± 0.03
(TOBEC × body length)$^{0.5}$	6.46 ± 0.06	18.77 ± 0.13	4.03 ± 0.04	10.49 ± 0.02
First-order TOBEC, mass, size	6.71 ± 0.11	13.19 ± 0.17	2.81 ± 0.03	8.43 ± 0.04
Second-order TOBEC, mass, size	6.57 ± 0.14	10.19 ± 0.16	3.04 ± 0.05	7.26 ± 0.04
(TOBEC × body length)$^{0.5}$, mass, size	6.30 ± 0.11	13.21 ± 0.18	2.75 ± 0.03	7.79 ± 0.04
Fat mass				
Mass and size	8.34 ± 0.15	12.00 ± 0.14	3.48 ± 0.02	8.85 ± 0.04
First-order TOBEC, mass, size	6.25 ± 0.11	12.33 ± 0.18	2.79 ± 0.03	7.43 ± 0.04
Second-order TOBEC, mass, size	6.34 ± 0.14	11.11 ± 0.20	3.01 ± 0.05	7.12 ± 0.04

sal length. Expanded TOBEC equations explained additional variation in fat mass beyond size variables alone (MSE = 1.53 and 1.46 for expanded first- and second-order model, respectively; Table 3). The expanded first-order model was the lowest-order polynomial to adequately describe the data and the TOBEC term was significant ($F_{1,13} = 11.32$, $P < 0.01$, $n = 14$). Fat mass of Dunlins was estimated with:

$$M_F = 25.98 - 15.41 \ln T + 0.77 X_1 - 0.01 X_2, \quad (11)$$

where T is TOBEC index, X_1 is body mass, and X_2 is tarsal length.

The stepwise regression equation to estimate fat mass in Semipalmated Sandpipers selected only body mass as a significant predictor variable (Table 3). Similar to the Dunlin sample, both expanded TOBEC equations improved the relationship between fat mass and predictor variables. The expanded first-order model again resulted in the lowest-order polynomial to adequately describe the data (MSE of 0.34 vs. 0.57 and 0.37 for size variables alone and expanded second-order model, respectively), and TOBEC significantly improved the relationship ($F_{1,12} = 9.76$, $P < 0.01$, $n = 15$). Fat content of Semipalmated Sandpipers was estimated using:

$$M_F = -5.65 - 3.53 \ln T + 0.77 X_1, \quad (12)$$

where T is TOBEC index and X_1 is body mass.

Mean widths of 95% prediction intervals were narrowest for models using body mass, size variables, and TOBEC indices (Table 4). Models using TOBEC alone generally resulted in the greatest prediction intervals, and interval widths decreased as additional variables were added to the model. Lean-mass prediction intervals for Dunlins and Semipalmated Sandpipers were reduced by 25.7 and 28.0%, respectively, using the expanded body-length model. Prediction intervals were reduced less for the Short-billed Dowitcher (16.9%), even with the best-fit model for this species, the expanded second-order model.

Reduction in prediction intervals for fat mass when using expanded TOBEC models showed a similar pattern (Table 4). The greatest reduction (23.9%), relative to intervals resulting from size alone, was found for the Dunlin, the Semipalmated Sandpiper was intermediate (19.8%), and the smallest reductions occurred with the Short-billed Dowitcher (7.4%).

Comparisons among new models.—The verification set allowed us to test new and existing models with individuals not included in the model-building procedure. Using predictive equations generated by this study, errors associated with lean-mass estimates were small (Table 5). Surprisingly, in only two of four cases (Dunlins and Semipalmated Sandpipers) did the model resulting in the best fit actually produce the smallest mean percent error. For Dunlins and Semipalmated Sandpipers, the mean percent errors of lean-mass estimates (using the expanded body-length model) was less than 4% of the actual lean mass. Models for Dunlins and

TABLE 5. Percent error ($\bar{x}$ ± SE) from predictive equations for lean and lipid mass of Dunlins, Short-billed Dowitchers, Semipalmated Sandpipers, and all species combined (interspecific).

Independent variables[a]	Lean mass	Fat mass
Dunlin (n = 4)		
Body mass, tarsus	2.19 ± 0.78	41.86 ± 17.88
T	2.96 ± 0.79	—
T, body mass, tarsus	2.60 ± 0.80	43.84 ± 17.96
T, T^2	2.69 ± 0.87	—
T, T^2, body mass, tarsus	3.73 ± 0.98	35.01 ± 9.39
$(TL)^{0.5}$	2.10 ± 0.85	—
$(TL)^{0.5}$, body mass, tarsus	2.04 ± 0.48	37.19 ± 12.35
Short-billed Dowitcher (n = 5)		
Body mass, wing	2.41 ± 0.82	29.30 ± 11.77
T	4.65 ± 0.89	—
T, body mass, wing	2.05 ± 0.6	36.90 ± 16.56
T, T^2	5.58 ± 1.19	—
T, T^2, body mass, wing	10.27 ± 5.44	14.64 ± 3.28
$(TL)^{0.5}$	3.52 ± 0.72	—
$(TL)^{0.5}$, body mass, wing	2.21 ± 0.73	51.53 ± 41.80
Semipalmated Sandpiper (n = 5)		
Body mass	3.44 ± 1.60	32.00 ± 11.96
T	4.90 ± 1.75	—
T, body mass	3.59 ± 1.21	36.81 ± 10.89
T, T^2	5.16 ± 1.85	—
T, T^2, body mass	4.27 ± 1.45	37.21 ± 11.52
$(TL)^{0.5}$	4.13 ± 1.46	—
$(TL)^{0.5}$, body mass	3.25 ± 1.16	33.94 ± 12.04
Interspecific (n = 14)		
Body mass, wing, head length, culmen	4.52 ± 1.00	73.11 ± 24.83
T	8.78 ± 1.41	—
T, body mass, wing, head length, culmen	3.77 ± 0.68	51.46 ± 12.25
T, T^2	4.53 ± 0.85	—
T, T^2, body mass, wing, head length, culmen	3.42 ± 0.59	62.17 ± 18.21
$(TL)^{0.5}$	3.46 ± 0.59	—
$(TL)^{0.5}$, body mass, wing, head length, culmen	3.07 ± 0.55	45.90 ± 19.82

[a] T = TOBEC index, L = body length.

Semipalmated Sandpipers using only body mass and size variables also resulted in small error rates (2.19 and 3.44%, respectively).

The best-fit model for Short-billed Dowitchers (expanded second-order model) resulted in the greatest mean percent error (10.27 ± SE of 5.44) of all models for this species (Table 5). This relatively large error rate was the result of one individual in the verification set. Among birds sampled, the verification set contained the largest dowitcher (maximum body-mass and wing-chord values), with the greatest fat content. This individual produced an extreme TOBEC index and, when combined with extreme body-size values in the expanded second-order model, lean mass for this individual was underestimated by more than 30%. The median percent error for the dowitcher set using the expanded second-order model was 5.11%. Nevertheless, other models produced smaller error rates (Table 5). The expanded first-order model produced the smallest mean percent error (2.05%) for dowitchers. The expanded body-length model and the mass/size model performed similarly (less than 3% error) for lean-mass estimates.

Fat mass was estimated with much less accuracy than lean mass (Table 5). The mean percent error for single-species models was generally 30 to 40% of actual fat mass, and 46 to 73% using the interspecific models. In addition to direct estimates of fat mass using multiple regression of the mass/size variables listed in Table 5, fat mass also was estimated in the two-

TABLE 6. Percent error ($\bar{x}$ ± SE) associated with selected TOBEC (T) equations from the literature. Equations are from interspecific models except where noted.

Model source	Lean mass	Fat mass
Dunlin (n = 4)		
Walsberg 1988	4.13 ± 0.75	85.47 ± 26.67
Castro et al. 1990	23.63 ± 1.48	481.25 ± 130.44
Scott et al. 1991[a]	7.24 ± 2.11	171.19 ± 98.10
Short-billed Dowitcher (n = 5)		
Walsberg 1988	6.30 ± 2.16	295.66 ± 217.92
Castro et al. 1990	24.68 ± 3.08	853.14 ± 577.43
Scott et al. 1991	6.40 ± 2.72	42.51 ± 20.98
Semipalmated Sandpiper (n = 5)		
Walsberg 1988	14.82 ± 3.39	135.79 ± 43.32
Castro et al. 1990	4.22 ± 1.81	31.02 ± 15.56
Scott et al. 1991[b]	6.96 ± 2.09	61.23 ± 19.27
Skagen et al. 1993[c]	9.04 ± 2.18	26.49 ± 7.42
Interspecific (n = 14)		
Walsberg 1988	8.72 ± 1.86	178.51 ± 78.03
Castro et al. 1990	17.07 ± 2.94	453.27 ± 217.02
Scott et al. 1991	15.97 ± 3.35	181.83 ± 49.28

[a] Intraspecific Dunlin equation; fat mass estimated indirectly.
[b] Interspecific body-length model.
[c] Lean and fat mass estimated directly using Semipalmated Sandpiper equations.

stage process described above (see Methods). In all three species, direct estimates via multiple regression using mass and size were more accurate than comparable two-stage models; mean percent errors for two-stage models were 43.83 ± 21.71% for Dunlins, 69.14 ± 58.85% for Short-billed Dowitchers, and 33.40 ± 11.55% for Semipalmated Sandpipers.

Tests of existing models.—Error associated with lean- and lipid-mass estimates for the verification set was greater using existing TOBEC models than when using new models generated by this study (Table 6). Five previously published interspecific models and four intraspecific models were tested.

Each interspecific model from previous TOBEC studies performed best with a different species. Walsberg's (1988) equation resulted in accurate estimates of lean mass for Dunlins, Short-billed Dowitchers, and the interspecific sample (mean percent errors <9%), but was less efficient for Semipalmated Sandpipers (Table 6). Errors were great (85–295% of actual fat mass) when the lean-mass estimates from this equation were subtracted from body mass to estimate fat mass.

The linear equation of Castro et al. (1990) was accurate for lean-mass estimates in Semipalmated Sandpipers (<5% error on average), but was less effective with Dunlins and Short-billed Dowitchers (Table 6). This model was relatively accurate for predictions of fat mass in Semipalmated Sandpipers as well, but errors were still more than 30% of actual fat content.

Five models of Scott et al. (1991) were tested: three interspecific models (first-order, second-order, and body-length models) and two for Dunlins (first-order and body-length models). The Dunlin-specific first-order equation showed the smallest mean percent error for lean-mass estimates (Table 6). The first- and second-order interspecific equations performed similarly and exhibited smaller errors ($\bar{x}$ = 10.56 ± 2.25 and 11.35 ± 2.05% error, respectively) than both models that incorporated body length (28.16 ± 0.94% for interspecific-length model and 37.91 ± 0.82% for Dunlin-length model). The mean percent error for fat-mass estimates in Dunlins ranged from 171.19 ± 98.10% (Dunlin first-order equation) to 786.96 ± 230.61% (Dunlin body-length equation).

The interspecific models of Scott et al. (1991) also were used to predict lean mass in Short-billed Dowitchers, Semipalmated Sandpipers, and all three species combined. For dowitchers, the second-order interspecific equation resulted in a mean percent error (6.40 ± 2.72%) similar to the first-order model (Table 6). The interspecific-length model resulted in much poorer predictions (35.66 ± 1.00%) and was least accurate of all equations tested for this species. With Semipalmated Sandpipers, however, the interspecific-length model was the most effective of all Scott et al. (1991) equations for lean-mass estimates (Table 6). For this species, first- and second-order interspecific models were poor predictors of lean mass (29.88 ± 3.85% and 82.03 ± 4.94%). The best estimates of fat mass by Scott et al. (1991) equations for Short-billed Dowitchers and Semipalmated Sandpipers were second-order interspecific and body-length interspecific, respectively (Table 6).

Two intraspecific (Semipalmated Sandpiper) equations of Skagen et al. (1993) were tested: one for predictions of lean mass and one for direct predictions of lipid mass using TOBEC, body mass, and size. Skagen et al. (1993) were the only authors to provide equations for the direct estimation of lipid mass. Interspecific equations of Skagen et al. (1991) were not tested because these equations were constructed using smaller individuals, on average, than those in the verification set.

Errors for lean-mass and fat-mass estimates of Semipalmated Sandpipers were small and similar to those exhibited by new equations of our study (Table 6). The fat-mass equation was the most accurate of all equations tested (<27% error on average). Using the interspecific lean-mass equation to produce indirect estimates of fat mass, the mean percent error increased to 82.63 ± 28.00%.

Discussion

Relationship between TOBEC and lean mass.—TOBEC shows a strong functional relationship with lean mass, and allows accurate predictions of lean mass for live birds. The nature of this relationship varies among species and interspecific samples. For two species in this investigation, results indicate that the most accurate predictions are made when body length is included in the regression equation. The expanded body-length model produced the narrowest prediction intervals and most precise estimates of lean mass in cross-validation for Dunlins and Semipalmated Sandpipers. This model may have resulted in the best functional relationship and most effective predictive equation because the TOBEC term (square root of product of TOBEC and body length) simultaneously provides a transformation to linearize the data and explains additional variation in the response variable (lean mass) via body length. For Short-billed Dowitchers, however, the strongest functional relationship between TOBEC and lean mass was provided by a model including one quadratic term (expanded second order).

These results differ from Scott et al. (1991) and allow informative comparisons. Their study was the only one to: (1) compare linear and quadratic models for intraspecific studies; and (2) test the modified linear model incorporating body length. Our results differ in two ways. First, Scott et al. (1991) conclude that intraspecific relationships between TOBEC and lean mass are linear, and that interspecific relationships are nonlinear (following Walsberg 1988). Results from our interspecific comparisons support the conclusion that these relationships are curvilinear. However, the strong functional relationship and high coefficient of determination for interspecific equations may not result in accurate predictions of body composition.

We did not find all intraspecific relationships to be linear. For dowitchers, the TOBEC model including body-size measurements and a quadratic term displayed a stronger functional relationship and explained the greatest amount of variation in lean mass (98%). When body-size measurements are not included, results corroborate Scott et al. (1991) and suggest that the linear model is more appropriate to describe the relationship between TOBEC and lean mass. This may be due to the range in size and lean mass found in our sample of dowitchers. This sample likely included individuals of both sexes of two subspecies (*L. g. griseus* and *L. g. hendersoni*) that vary in size. Body mass ranged from 63 to 137 g; fat content ranged from 1 to 27% of body mass. This range of values approaches that found in other interspecific studies and may explain why the curvilinear model was more effective with this species. These results indicate that the nature of the relationship between TOBEC and lean mass varies among species.

Scott et al. (1991) also rejected intraspecific models that included body length based on lower coefficients of determination and greater SE intercept values (resulting in greater prediction intervals). In our study, linear models using TOBEC and body-size data were similar to modified linear models incorporating body length for Dunlins and Semipalmated Sandpipers. Unlike Scott et al. (1991), however, our body-length models explained slightly more variation, showed narrower prediction intervals, and had smaller percent error for predictions of lean mass than did the simple linear model.

Skagen et al. (1993) found that improvements in 95% prediction intervals for lean-mass estimates were greater for the smaller of two species examined. We found a similar pattern; improvements were greater for Dunlins and Semipalmated Sandpipers than for Short-billed Dowitchers. The effectiveness of TOBEC for body-composition analysis with birds in this size range (20–50 g) has been questioned (Anonymous 1991, Castro et al. 1990). Results here indicate that the technique may provide greater relative benefits in this size range.

Relationship between TOBEC and fat mass.—Estimating fat mass directly from TOBEC is a departure from the original calibration of the technique. Some earlier studies used TOBEC to estimate lean mass using the regression equation, and then suggested that lipid mass could be estimated by subtracting the lean-mass estimate from body mass. In this two-step process, any absolute error associated with the lean-mass estimate ($\hat{Y} - Y$) will be reflected in the fat-mass estimate. Because fat mass is always a smaller proportion of total mass, the relative error is much greater for lipid estimates (Morton et al. 1991). Thus, the high R^2-values from the relationship of TOBEC and lean mass will overestimate the relative precision of lipid-mass estimates. As an alternative to the two-step process, Morton et al. (1991) suggested using TOBEC values in a multiple regression to estimate fat directly.

The usefulness of TOBEC in predicting fat mass is problematic; variation in fat content remains more difficult to explain than variation in lean mass. Despite high coefficients of determination (Table 3) found with regressions of fat content on TOBEC and body size, 95% prediction intervals for estimates of fat mass were large relative to average fat loads carried. Percent errors for fat estimates also were much greater than for lean mass. The new TOBEC equations in our study estimate fat directly and use TOBEC indices as an additional predictor variable to explain variation in body size, following the suggestion of Morton et al. (1991). As first reported by Morton et al. (1991) and corroborated by Skagen et al. (1993), high R^2-values from regressions of TOBEC and lean mass did not result in accurate predictions of fat mass in two stage models. However, even direct predictive equations (also generating high R^2-values) were poor predictors of fat mass. For dowitchers, the addition of TOBEC to models did not improve fat-mass estimates.

Skagen et al. (1993) provided the only previous attempt to estimate fat mass, directly or in the two-stage process. Error rates for Semipalmated Sandpiper fat-mass estimates were similar when using equations from our study and the Semipalmated Sandpiper fat equation of Skagen et al. (1993). This suggests that intraspecific calibrations for fat-mass estimates may be most effective in future TOBEC studies. However, a great deal of variation in fat mass is explained by body mass and size variables, and improvements over predictive equations using only these measurements were small.

Future TOBEC studies may gain greater insight to body-composition dynamics, and greatly improve estimates of lean mass and lipid mass if calibration curves are generated for each species of interest. If this is not feasible, investigators should choose an existing intraspecific equation. Finally, when choosing among intraspecific equations, the following should be evaluated (in order of relative importance): percent error with a verification set, 95% prediction interval widths, MSE values, and coefficients of determination.

Accuracy of existing TOBEC equations.—Predictive equations from previous TOBEC studies generally provided reasonably accurate estimates of lean mass using cross-validation; intraspecific curves provided the best estimates of lean mass. No one interspecific equation was effective for lean-mass estimates for all three species, suggesting that the mass, size, and shape of individuals used in the model-building process may influence the final predictive equation and success of its body-composition predictions with various species. Our results indicate that regression statistics (R^2, MSE) from interspecific curves overestimate the strength of the functional relationship for any one species. High R^2-values from interspecific regressions result from fitting a line through separate clouds of data points representing each species. The best-fit line for any one of those species often differs from the interspecific line. Furthermore, prediction intervals will be narrowest at the center point in the distribution of x-values in the calibration dataset; the predictive equation will be less effective with x-values from the tails of the distribution. The interspecific equation of Walsberg (1988) may have been successful for lean-mass predictions with our Dunlin sample because the median lean-mass value for birds used in construction of his predictive equation was about 60 g, roughly the mean value of Dunlins used in our study. Similarly, the Scott et al. (1991) interspecific equation, generated with birds having a median lean-mass value of about 70 g, was most successful with the Short-billed Dowitcher; dowitchers used in our study averaged 82 g.

Only one equation was useful for estimating fat content with the verification set. The Semipalmated Sandpiper equation of Skagen et al. (1993) for direct estimation of fat mass displayed an error rate similar to new equations. All other equations attempted to estimate fat using TOBEC estimates of lean mass (subtracted from body mass), and errors were so high that fat-mass estimates were of little use. These results support the conclusions of Morton et al.

(1991) regarding relative error transferred to fat-mass estimates.

In general, TOBEC improvements to body-composition estimates (beyond use of body mass and size alone) were limited. Our results indicate that intraspecific curves are most effective, particularly in the estimation of fat content. However, considerable variation in fat mass is explained by body mass. Inclusion of the TOBEC term improves the functional relationship and fat-mass estimates, albeit slightly. Decisions regarding use of TOBEC to improve body-composition estimates should be based on the specific goals of each study. Use of this technique requires additional processing time for each bird, and this cost may outweigh benefits, particularly if study objectives include processing as many birds as possible (e.g. mark/recapture studies). If research objectives include collecting several body-composition estimates from the same individuals over time (e.g. captive studies or locations with high recapture probabilities), TOBEC improvements to lean- and fat-mass estimates may be useful.

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