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An evaluation of condition indices and predictive models for noninvasive estimates of lipid mass of migrating Common Yellowthroats, Ovenbirds, and Swainson's Thrushes

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ABSTRACT. Noninvasive methods of measuring lipid mass in birds are widely used, but not frequently evaluated. I evaluated the ability of three noninvasive indicators of fat content (fat scores, body mass, body mass/wing chord) and regression models to predict lipid mass in two migratory songbirds previously unexamined in this context—Common Yellowthroat (*Geothlypis trichas*) and Ovenbird (*Seiurus aurocapillus*). I also examined the accuracy of these methods for Swainson's Thrushes (*Catharus ustulatus*) for comparison to a previous study. Fat score, body mass, and body mass/wing chord were highly correlated with chemically extracted lipid mass in each species. In all three species, birds with no visible subcutaneous fat possessed considerable quantities of fat, ranging from 9.8 to 19.7% of total dry body mass. Forward-selected regression models explained 69−87% of lipid mass variation, with prediction errors of 14.6−27.5%. An existing predictive model for the Swainson's Thrush overestimated lipid mass by an average of 92%. Fat score, body mass, and the regression models generated here are reliable predictors of lipid mass in two of the three migrating species examined. The accuracy of the methods, in addition to their low cost and simplicity, justifies their continued use in field studies of birds.

SINOPSIS. **Evaluación de índices de condición y modelos de predicción para métodos no invasivos de estimados de grasa corporal en migratorios como *Geothlypis trichas* y *Seiurus aurocapillus* y *Catharus ustulatus***

Los métodos no invasivos, son de amplio uso para determinar la cantidad de grasa en aves. Sin embargo, raras veces estos han sido evaluados. Evalue la confiabilidad de tres métodos no invasivos para determinar la cantidad de grasa (marcador de grasa, masa corporal, masa corporal/cuerda del ala) y de modelos de regresión para predecir la masa de lípidos en dos especies de aves canoras migratorias (*Geothlypis trichas* y *Seiurus aurocapillus*) que previamente no habían sido examinadas en este contexto. También examine la exactitud de estos métodos en el zorzal (*Catharus ustulatus*) como comparación de un estudio previo hecho en esta especie. El marcador de grasa, la masa corporal y la masa corporal/cuerda del ala, se correlacionaron muy bien con la cantidad de lípidos extraidos químicamente en cada especie. Individuos de las tres especies, sin marcas visibles de grasa subcutanea, en promedio, arrojaron cantidades considerables de grasa entre 9.8–19.7% de la masa corporal total. Una selección de modelos de regresión explicaron entre el 69–87% de la variación en grasa corporal, con una predicción de error entre 14.6–27.5%. El modelo de predicción existente para el zorzal arrojó un sobreestimado de grasa corporal de 92%. Los tres métodos no invasivos para determinar la cantidad de grasa y los modelos de regresión generados para estos, son predictores confiables para dos de las tres especies examinadas. La exactitud de los métodos, en unión a su bajo costo y simplicidad, justifican su uso para estudios de aves.

Key words: body composition, *Catharus ustulatus*, fat scores, *Geothlypis trichas*, lipid indices, lipid mass, *Seiurus aurocapillus*

Fat is the primary source of fuel for the energy-demanding flights of migrating birds (Blem 1990). Because the ability of birds to store fat throughout migration is a chief determinant of their overall migration success (Moore et al. 1995), measurement of fat is central to the study of avian migration ecology. In addition, the quantity of fat in breeding and wintering birds is often of interest because lipid storage can affect reproduction and survival during these life-history stages (Lima 1986, Rogers 1987, Rowe et al. 1994). Body condition attained during one season can also affect fitness and survival

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during subsequent seasons (Smith and Moore 2003, Studds and Marra 2005).

Lipid mass can be measured via solvent extraction of dead specimens. This method offers accurate direct measurements, but is time consuming, costly, and requires sacrificing birds or acquiring birds that have already died from other causes. Noninvasive alternative methods are less accurate than chemical extraction, but are advantageous because they allow repeated measurements on the same individuals and can be used on species of conservation concern that cannot be sacrificed. In addition, many noninvasive methods are inexpensive and can be used quickly and easily in the field (Krementz and Pendleton 1990, Roby 1991, Rogers 1991, Burger 1997).

Modern noninvasive techniques of measuring fat content, such as magnetic resonance imaging (MRI), dual-energy x-ray absorptiometry (DXA), and heavy water dilution (Karasov and Pinshow 1998, Piersma and Klaassen 1999, Korine et al. 2004) are accurate, but remain largely cost-prohibitive. Popular inexpensive, noninvasive methods include visible subcutaneous fat scores (Moore and Kerlinger 1987, Dunn 2003), body mass (Jones et al. 2002), body mass corrected for structural size variation (Johnson et al. 1985, Winker 1995, Benson and Winker 2005), and predictive regression models based on data from live birds with no visible subcutaneous fat (Strong and Sherry 2001). Some studies have validated the ability of these latter methods to predict true fat content in passerines (Rogers 1991, Conway et al. 1994, Spengler et al. 1995). Method performance, however, may vary among species, and species-specific models are needed for accurate estimates of lipid mass (Skagen et al. 1993, Spengler et al. 1995).

Although Common Yellowthroats (*Geothlypis trichas*) and Ovenbirds (*Seiurus aurocapillus*) are well-studied migratory songbirds, I am unaware of any prior validations of lipid indices and predictive models for these species. I examined relationships between three routinely used indicators of fat content and actual lipid mass in Common Yellowthroats and Ovenbirds to construct predictive equations and determine the techniques that best estimate fat content. I also examined the accuracy of the techniques for Swainson's Thrushes (*Catharus ustulatus*) for comparison to a previous study (Spengler et al. 1995).

METHODS

Study specimens. The birds used in my study were killed by collisions with buildings during spring and autumn migration through New York, New York and Toronto, Ontario, during 2005–2006. Specimens were salvaged by the Fatal Light Awareness Program (FLAP) and New York City Audubon Society (NYCAS) to document the hazards of illuminated skyscrapers and reflective windows to migrants (Knoepfli and Krajnc 2005, Gelb and Delacretaz 2006). Due to the manner of specimen collection, the time interval between death and collection was unknown, but was estimated to be no longer than 6 h (FLAP, NYCAS, pers. comm.). Birds were bagged and stored frozen at –20°C for up to 6 mo before processing.

Laboratory procedures. Specimens were thawed at room temperature until flexible. Unflattened wing chord was measured to the nearest 1 mm. Visible subcutaneous fat in the furcular hollow was ranked on a 6-point scale (Moore and Kerlinger 1987), with the carcass positioned as a living bird would be during fat scoring. The appearance of the fat was not noticeably different from that of living birds and I assumed scoring performance was unaffected by the birds' state (i.e., dead vs. alive; Krementz and Pendleton 1990). All fat scores were assigned by the same individual to avoid potential interobserver variation. Birds were then weighed to the nearest 0.001 g (Denver Instrument, Denver, Colorado). A ventral midline incision was made to expose the thoracic and abdominal cavities and expedite desiccation. Birds were then oven-dried to a constant mass at 75°C. Dry carcasses were re-weighed and homogenized (including feathers) with a household electric blender. Soluble fat was extracted from duplicate 1 g ($\pm$0.1 g) samples of the homogenate using petroleum ether in a Soxtec apparatus (FOSS, Inc., Laurel, Maryland). Following extraction, samples were oven-dried overnight and weighed the following day. Mass losses of duplicate samples were converted to percentages of original dry sample masses and averaged (CV of all duplicates $<$15%). The average value (hereafter lipid%) was multiplied by total dry body mass to yield total body lipid mass (hereafter lipid mass).

Statistical analyses. Pearson's product-moment correlations were used to measure the relationships between chemically determined lipid mass and total wet body mass, wing chord, size-corrected mass (wet mass/wing chord), fat score, and percent water content (wet mass – dry mass/wet mass). Multiple regression was used to generate partial correlation coefficients and re-examine the associations of lipid mass with total wet body mass, wing chord, and fat score individually while controlling the effects of the other variables (Spengler et al. 1995, Zar 1999). The initial Pearson's correlation tests revealed that percent water content and size-corrected mass were highly correlated with the other predictor variables in most cases and were thus omitted from this regression analysis to reduce potential error from multicollinearity (Zar 1999).

I used stepwise multiple regression with forward selection ($\alpha = 0.1$) to determine what combination of variables best explained variation in extracted lipid mass in each species. Equations incorporating every variable and equations including only variables chosen by forward selection are presented. Following Conway et al. (1994) and Spengler et al. (1995), I evaluated the predictive ability of each equation with cross-validation tests (INFLUENCE option, SAS). Coefficients of determination were calculated as total sum of squares minus predicted residual sum of squares divided by total sum of squares. Predicted residuals from multiple regression were then used to calculate the absolute error (mean of the absolute value of predicted residuals) and percent error (absolute error/true lipid mass) of each model (Conway et al. 1994).

Statistical tests were performed with SYSTAT (version 10.0; SPSS 2000) and SAS (version 9.0; SAS Institute 2002) software. Results were considered significant at $\alpha \leq 0.05$.

RESULTS

Lipid%, mean fat score, and percentage water content were similar across species (Table 1). For all three species, birds with no visible subcutaneous fat (i.e., zero fat score), on average, possessed considerable quantities of fat, ranging from 9.8% to 19.7% of total dry body mass (Fig. 1).

Body mass, body mass/wing chord, fat score, and percentage water content were significantly correlated with lipid mass in all species (Table 2). Wing chord was not significantly correlated with lipid mass in any species, and was only significantly correlated with lean body mass for Common Yellowthroats ($r = 0.45$, $P = 0.01$). Only for Common Yellowthroats was there a stronger correlation of lipid mass with size-corrected body mass than with body mass alone. Lipid mass was correlated with percentage water content in each species more than any other variable (Table 2). After controlling for the effects of the other indices, body mass and fat score remained significantly correlated with lipid mass in all three species, and wing chord became significantly correlated with lipid mass in the Common Yellowthroat (Table 3).

Models that included every predictor variable accounted for 74%–88% of the observed variation in lipid mass (Table 4). Forward-selected models explained 69–87% of lipid mass variation. For each model, the coefficients of determination calculated from cross-validation tests were lower than those originally produced by multiple regression. Percent errors were lowest for Ovenbird and Swainson's Thrush models (14.6% and 18.7%, respectively). Percent error was highest in the all-inclusive model for Common Yellowthroats (30.1%). Variables included

Table 1. Mean (±SD) values of wet mass, lean mass, lean dry mass, lipid mass, lipid percentage (subsample lipid mass/dry mass), wing chord, fat score, and water percentage of three species of passerine killed by building collisions during spring and autumn migration in New York, New York and Toronto, Ontario, 2005–2006.

Species	*N*	Wet mass (g)	Lean mass (g)	Lean dry mass (g)	Lipid mass (g)	Lipid %	Wing (mm)	Fat score	Water %
Common Yellowthroat	30	9.99 ± 1.15	7.05 ± 0.88	2.83 ± 0.23	1.23 ± 0.60	28.64 ± 10.57	53.93 ± 3.42	2.63 ± 1.22	59.6 ± 3.5
Ovenbird	19	19.12 ± 1.52	12.91 ± 1.30	5.10 ± 0.25	2.52 ± 1.14	31.84 ± 9.78	73.95 ± 1.99	2.90 ±1.49	60.2 ± 2.9
Swainson's Thrush	22	31.62 ± 2.48	22.00 ± 2.23	8.27 ± 0.47	3.77 ± 1.69	29.88 ± 10.32	96.68 ± 3.29	2.36 ± 1.65	62.1 ± 3.8

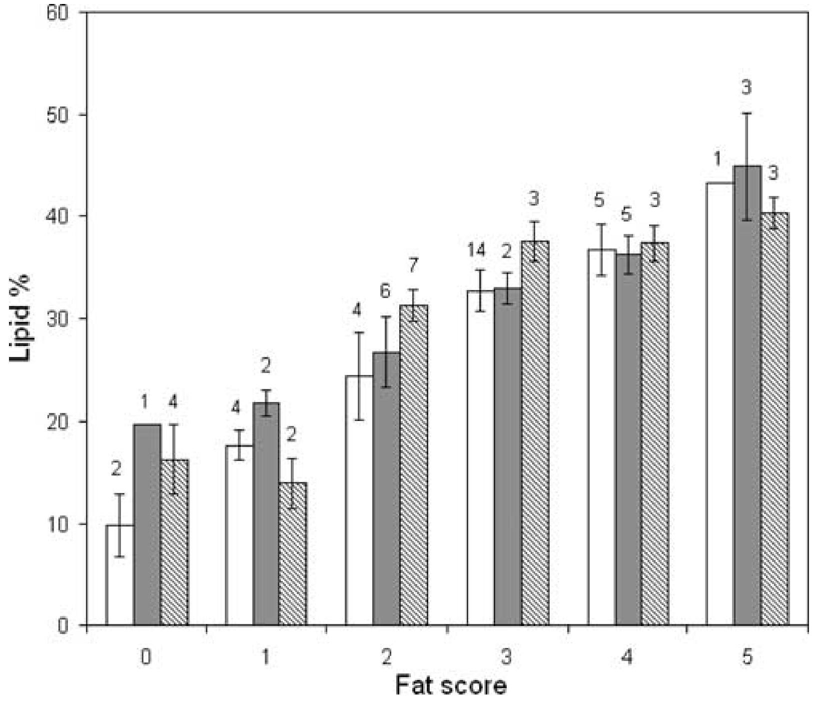

Fig. 1. Corresponding mean (±SE) percent lipid (subsample lipid mass/dry mass) for different fat scores (left to right: Common Yellowthroat, Ovenbird, and Swainson's Thrush). Sample sizes above bars.

by forward selection were the same for Ovenbirds and Swainson's Thrushes (fat score and body mass). Fat score was selected for inclusion in all three species (Table 4). The regression model for Swainson's Thrushes presented by Spengler et al. (1995; Lipid mass $= -15.184 + 0.636 \times$ body mass $+ 0.679 \times$ fat score) overestimated lipid mass of the specimens in my study by an average of 92%.

DISCUSSION

Three simple, inexpensive indices and models were identified for accurately estimating lipid mass in Common Yellowthroats, Ovenbirds, and Swainson's Thrushes. Fat score and body mass were highly correlated with total body fat in each species. Selection procedures included fat score in the predictive models for all species, and body mass was included in two of the three species. Only for Common Yellowthroats was size-corrected body mass selected over body mass. Using wing chord to correct body mass for structural body size variation does not appear to considerably improve the ability of body mass to predict lipid content in either Ovenbirds or Swainson's Thrushes. The nonsignificant correlations between wing chord and lean body mass may be due to variation in lean tissue mass among birds of equal structural size because

Table 2. Pearson's correlation coefficients of lipid mass with predictor variables.

Species	N	Body mass	Wing chord	Mass/ wing chord	Fat score	Water %
Common Yellowthroat	30	0.68^{**}	-0.01	0.73^{**}	0.75^{**}	-0.81^{**}
Ovenbird	19	0.81^{**}	-0.15	0.81^{**}	0.75^{*}	-0.92^{**}
Swainson's Thrush	22	0.78^{**}	0.29	0.71^{*}	0.85^{**}	-0.92^{**}

$^{*}P \leq 0.001$, $^{**}P \leq 0.0001$.

Table 3. Partial correlation coefficients of lipid mass with body mass, wing chord, and fat score obtained from multiple regressions.

Species	Body mass	Wing chord	Fat score
Common Yellowthroat	0.54**	−0.39*	0.60***
Ovenbird	0.67**	−0.31	0.59**
Swainson's Thrush	0.70***	0.01	0.82***

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$.

fat is not the only tissue to change in mass during migration (Piersma 1990, Scott et al. 1994, Karasov and Pinshow 1998). In addition, wing chord may be an unreliable indicator of structural size for these species (see Rising and Somers 1989). Other measurements (e.g., tarsus length) may be more appropriate for adjusting body mass for body size for Ovenbirds and Swainson's Thrushes, but were not examined in my study.

The sizable fat loads of birds with no visible fat indicate that fat scoring provides conservative measures of energy stores. Birds scored as zero are likely to have intraperitoneal or other unseen metabolically available fat deposits (see also Rogers 1991). In turn, using the body masses of zero fat class birds to estimate lean body mass for a species (Dunn 2001, Mulvihill et al. 2004), and subsequently quantify the lipid content of conspecifics as the difference of that lean body mass and total body mass, will probably underestimate true lipid mass. The poor resolution at the lower end of the scale may also make fat scoring insufficient for studies of bird populations with limited energy stores (Rogers 1991).

Regression equation performance is better gauged by the extent of prediction error as determined by cross-validation tests than by coefficients of determination (Conway et al. 1994). Judging models here by their error showed that each model performed better than suggested by their coefficients of determination. Estimating lipid mass in the Common Yellowthroat, the smallest species, was least accurate, as the error represented a greater proportion of its average fat mass (27.5%) than the other larger species examined. The forward-selected model for the Common Yellowthroat may be too weak to detect all but gross differences in lipid mass among study groups. Conversely, the models produced for Swainson's Thrushes and Ovenbirds had low prediction errors and appear sufficient for estimating lipid mass of living birds with acceptable accuracy. Contexts in which these models could

Table 4. Coefficients of determination (R^2, R^{2b}), absolute error (g), and percent error of regression models for predicting lipid mass (LM).

Equation[a]	R^2	R^{2b}	Absolute error[b]	Percent error[b]
Common Yellowthroat				
A: LM = 34.090 − 0.665 W + 3.397 BM + 0.263 FS − 170.641 MW	0.74	0.59	0.25 ± 0.06	30.1 ± 17.0
B: LM = −1.82 + 0.243 FS + 13.027 MW	0.69	0.62	0.25 ± 0.08	27.5 ± 10.6
Ovenbird				
A: LM = −177.323 + 2.304 W − 8.555 BM + 0.326 FS + 665.053 MW	0.88	0.77	0.33 ± 0.09	15.1 ± 5.0
B: LM = −6.506 + 0.425 BM + 0.312 FS	0.76	0.63	0.44 ± 0.14	18.7 ± 5.1
Swainson's Thrush				
A: LM = 15.297 − 0.235 W + 1.067 BM + 0.615 FS − 73.361 MW	0.87	0.82	0.44 ± 0.17	17.3 ± 11.6
B: LM = −7.458 + 0.620 FS + 0.309 BM	0.87	0.84	0.41 ± 0.15	14.6 ± 7.4

[a]Regression equations include all of the condition indices (A), and indices selected by forward selection (B). BM = body mass, W = wing chord, FS = fat score, MW = mass/wing chord.

[b]Coefficients of determination and lipid mass prediction errors from cross-validation tests. Error values are means ± 95% CI.

be of use include comparisons of lipid mass across years and study sites. The models are likely inadequate, however, for revealing subtle differences in lipid mass, such as those of individual birds during the day.

The forward-selected model for Swainson's Thrushes presented by Spengler et al. (1995) included the same variables as in my study (fat score and body mass), but had greater prediction error (27.3%). Further, the model overestimated the lipid content of the Swainson's Thrushes I examined by an average of 92%. This large error may be due to inter-observer differences in fat scoring (Krementz and Pendleton 1990) or differences in the body composition of the birds used in each study. The average lipid content (12.4%) and lean dry body mass (7.7 g) of the birds examined by Spengler et al. (1995) were lower than those I examined (Table 1), perhaps because Spengler et al. (1995) examined birds that had just completed nonstop flights across the Gulf of Mexico. Regardless of the source of the error, it renders the validity of using models built from one set of birds to predict lipid mass in entirely different study groups questionable. Season and geographic location are likely to significantly affect regression model performance (Spengler et al. 1995) and should always be considered when estimating lipid mass in this manner. To obtain sufficient sample sizes when generating the models presented here, I combined spring and autumn migrants, as well as individuals of different sexes and ages. Such combinations likely weaken model accuracy, and developing models that account for potential variation within these variables is recommended.

Fat scoring was the best single indicator of lipid mass in two of the three species examined. Fat score was significantly correlated with lipid mass and was included in forward-selected models in each species. Body mass was also found to be a strong index of lipid mass, and in two of the three species, explained more variance in fat content than when corrected by a morphological measurement. Modern noninvasive techniques for assessing body composition, such as MRI and DXA, require costly equipment and skills that make them unavailable to many researchers. Traditional simple and inexpensive approaches to assessing lipid content, such as those examined here, are, therefore, likely to remain commonplace and useful in field studies of birds.

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