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A COMPARISON OF NONINVASIVE TECHNIQUES FOR ESTIMATING TOTAL BODY FAT IN SHARP-SHINNED AND COOPER'S HAWKS

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Abstract.—We evaluated the use of three direct methods (fat scoring, condition indices, and multiple regression of external morphological variables) to estimate total body fat (TBF) in Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*). All three methods explained more than 82% of the variation in actual TBF values, and all three methods required the use of multiple equations to account for the categories of species, age, and/or sex. We also evaluated an indirect method that estimates TBF by the difference between actual mass and estimated lean mass. We estimated lean mass using a multiple regression of external morphological variables, and this technique was fairly accurate (r = 0.94). The methods evaluated here, though reasonably precise, may not be accurate enough to reliably compare estimated TBF between individual birds. Using multiple regression to directly estimate TBF from mass and tarsus length measurements is the recommended technique because (1) it provides continuous estimates of TBF; (2) it requires measuring only two external morphological characters, both of which are less subjective than fat scores; and (3) it is more explanatory than the other two methods which use external characteristics as predictors. Our results also suggest that comparing groups of birds using condition indices may yield misleading results because these indices can relate to TBF differently for species, age, and or sex classes.

COMPARACIÓN DE TÉCNICAS NO-INVASIVAS PARA ESTIMAR EL TOTAL DE GRASA CORPORAL EN *ACCIPITER STRIATUS* Y *A. COOPERII*

Sinopsis.—Evaluamos el uso de tres métodos directos (contaje de grasa, índices de condición y regresión múltiple de variables morfológicas externas) usados al estimar el total de grasa corporal (TBF) en *Accipiter striatus* y en *A. cooperii*. Cualquiera de los tres métodos explicó más del 82% de la variación en valores de TBF reales, y los tres métodos requirieron el uso de ecuaciones múltiples para explicar las categorías de especie, edad, y/o sexo. También evaluamos un método indirecto que estima el TBF a base de la diferencia entre la masa actual y la masa magra estimada. Estimamos la masa magra usando una regresión múltiple de variables morfológicas externas, y esta técnica también fué razonablemente exacta (r = 0.94). Los métodos aquí evaluados, aunque razonablemente precisos, pueden no ser lo suficientemente exactos como para comparar con confianza las TBF estimadas entre aves individuales. Se recomienda la técnica de regresiones múltiples para estimar directamente la TBF de las medidas de masa y largo del tarso porque: (1) provée estimados contínuos de la TBF, (2) requiere medir solo dos caracteres morfológicos externos, ambos de los cuales son menos subjetivos que las medidas de grasa, y (3) explica más que los otros dos métodos que usan características externas como predictores. Nuestros resultados también sugieren que comparar grupos de aves usando índices de condición pueden producir resultados incorrectos porque estos índices pueden relacionar las TBF diferentes por categorías de especie, edad o sexo.

Internally stored lipids are an important source of energy for birds (Blem 1990). Fat reserves reflect the balance of energy intake and expenditure, both of which are affected by behavior and physiology. The amount of fat stored is highly plastic, exhibiting seasonal and daily cycles

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(Blem 1990), suggesting that measuring fat reserves can provide insight into adaptive behaviors and strategies.

Despite a long history of scientific interest in how birds manage energy, the only way to accurately quantify total body fat (TBF) is by chemically extracting it using a solvent such as petroleum ether (Bligh and Dyer 1959; Blem 1990). Alternative techniques to estimate TBF that do not require sacrificing the organism under study have been developed but are less accurate (Blem 1990; Brown 1996). These alternative techniques can be divided into direct and indirect approaches (Gessaman 1999). Direct methods are those that attempt to estimate TBF directly and include fat scoring (Brown 1996), predictive multiple regression models (using external morphology as predictors; Blem 1990), condition indices (referred to as morphological indicators in Brown 1996), and cyclopropane absorption (Gessaman et al. 1998). Indirect methods are those that estimate TBF by the difference between actual mass and estimated lean mass. Indirect methods include total body electrical conductivity (TOBEC; Walsberg 1988), whole-body potassium-40 (K40) content (Hinton et al. 1998), and predictive models (using external morphology to predict lean mass; Lyons and Haig 1995). Except for cyclopropane absorption, all of the above methods require calibration by extracting fat from animal carcasses. Equations must be developed to convert the values produced by these techniques into estimates of TBF. These equations are developed using a sample population to whom the estimating techniques can be applied prior to fat extraction. Brown (1996) recommends calibrating TBF predictors for each species or population in consideration. Cyclopropane absorption, TOBEC, and K40 content are not easily used in many field settings; we do not consider these methods in this study.

Several attempts have been made to noninvasively quantify TBF in raptors, using fat scores (Clark 1985; Smith et al. 1986; Overskaug et al. 1997), condition indices (Gorney and Yom-Tov 1994; Gorney et al. 1999), and TOBEC (Harden 1993). Only two of these studies attempted to calibrate their techniques against actual values of TBF (Harden 1993; Gorney and Yom-Tov 1994). In this study we investigated various options for estimating TBF in accipiters in order to determine which technique is likely the most valuable. We calibrated and compared four field-oriented procedures: fat scoring, condition indices, and direct and indirect multiple regression models. These last two techniques use external morphometric characters as independent predictor variables (hereafter referred to as the direct external morphology and the indirect external morphology techniques, respectively). We chose to test these methods with Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) because individuals of these species are commonly observed and banded during migration at a variety of locations throughout North America, providing an obvious application for these TBF estimation techniques.

METHODS

Lab procedures.—We collected accipiter carcasses from rehabilitation facilities, state game and fish offices, private individuals, and university collections in the states of Arizona, New Mexico, and Utah. The sample contained 51 birds collected over a 2-yr period. The actual manner of death for each bird was generally unknown. Some birds had been kept in captivity for a period of time before their death. All limbs were intact and specimens had not yet begun to decompose. The body mass of most birds at the time of death was unknown.

We determined species, age (Mueller et al. 1979, 1981), and sex (Hoffman et al. 1990) for each bird. We weighed frozen birds to the nearest 0.1 g. After thawing, we measured unflattened wing chord and tail length to the nearest 1 mm with standard wing and tail rulers, and measured keel length, tarsus length, and hallux claw length to the nearest 0.1 mm with calipers. We removed and weighed all crop contents and subtracted this mass from the initial body mass to obtain an adjusted body mass. We did not remove food from the digestive tract below the crop, as this food cannot easily be detected or removed from birds captured in the field. Food below the crop undoubtedly created variability in our measurements of mass. Food in the crop, however, can be detected in the field and possibly adjusted for to achieve more accurate live mass measurements. Also, analyses can be restricted to birds with no food detectable in the crop.

Collected birds were stored frozen in sealed plastic bags until processing. Some body water may have been lost due to desiccation in the freezers, leading to slightly underestimated live masses. For some birds this error is negligible, as one 459-g bird weighed shortly after death lost only 1 g of mass after more than a year's storage in a freezer. Still, we examined lean mass water content to determine if any birds had dehydrated substantially between death and weighing. Four birds whose body water/lean mass ratio (0.49–0.59) was noticeably less than the central range of values in this sample were assigned corrected live masses. The central, continuous group of body water values ranged from 0.60 to 0.65, with a mean $\pm$ SD of 0.63 $\pm$ 0.013 (total body water (g)/lean mass (g)). The correction was made by calculating how much water, X, would have been lost if these four birds had died with 63% lean mass water content, where $X = (0.63 * \text{lean mass} - \text{total body water})/0.37$. This amount of water was added to the mass of those four birds as an adjustment. All statistical analyses used body mass adjusted for crop contents and low dehydration state.

We removed flight feathers and some body feathers after processing because defeathered birds are easier to fit into extraction thimbles. We then refroze carcasses, cleaved them several times to expose deep tissues to the air, and then freeze-dried them to constant mass. We broke up dried carcasses by hand into dime-sized or smaller pieces. We determined TBF for the whole carcass of every bird using petroleum ether extraction for approximately 24 h in a standard Soxhlet apparatus (Bligh and Dyer 1959). Blem (1990) argued that actual TBF values were superior to lipid indices (g lipid/g total body mass) for calibrating noninvasive methods. Hence we used TBF for all calibrations here. We performed a natural log-transformation of TBF prior to all analyses. The range of TBF values in the calibration sample was 0.8–18.5%.

We compared the effectiveness of the four methods (fat scoring, condition indices, direct and indirect external morphology) using (1) R^2, (2) Pearson correlation coefficient, (3) mean percent error, and (4) mean 95% prediction interval. For each bird, we calculated percent error by $(|Y_{predicted} - Y_{observed}|/Y_{observed}) * 100$ (Lyons and Haig 1995). The mean 95% prediction interval was calculated by taking the average of 1.96 * SE_{Yr} (standard error for an individual prediction; Hamilton 1992). All analyses were conducted using SYSTAT (SPSS Inc. 1997).

Fat scoring.—Fat scoring is a direct method that is quick and easily used in the field (Brown 1996). It involves capturing birds and assigning them a score based on the size and shape of subcutaneous fat deposits found at one or more locations on the body, usually in the furcular and abdominal regions. There are different scoring regimes available, with higher scores indicating larger amounts of fat. Some scoring regimes have many classes and provide a fairly precise indication of TBF (e.g., 31 classes in Kaiser's (1993) scoring regime), yet Krementz and Pendleton (1990) concluded that a scoring regime with five classes can adequately describe fat loads in birds.

The fat scoring procedure we considered uses one subcutaneous fat storage deposit in the subalar area (King and Farner 1965). We assigned all carcasses fat scores for both the left and the right subalar fat pads. This pad is located under the wing in a fold of muscle on the bird's side. The pad can be seen by pulling back the wing (dorsally) and spreading feathers to either side. The fat scoring regime used has 4 levels (0 through 3), and scores are assigned based on a visual estimation of the size of the fat pad. A score of 0 indicates no fat present at all. A score of 1 represents a streak of fat, parallel with the lengthwise body axis, that is not so deep that it reaches the level of the surrounding muscle tissue. A score of 2 represents a wider streak that is roughly at the level of the muscle, and a score of 3 represents a pad that is visibly protruding out above the level of the muscle. The length of the pad is not used in assigning scores, but the width necessarily increases with depth of the pad, as the cross-section through the fold of muscle is roughly v-shaped. This technique is the same as that which has been in use for several years at raptor migration banding sites operated by HawkWatch International, Inc. in western North America.

The fat deposit on one side of the bird is scored, based on the assumption that birds store fat in equal amounts on both sides of the body. In 1996, we collected data that would allow us to test this assumption. During spring migration in the Sandia mountains in central New Mexico, we captured migrating accipiters as part of an ongoing raptor banding program conducted by HawkWatch International, Inc. Two observers (including JPD), who periodically checked each other's scoring techniques, scored both the right and left subalar fat pads of 107 Sharp-shinned and

126 Cooper's Hawks. We then calculated the percentage of birds that received either the same or a different score for right and left sides.

Krementz and Pendleton (1990) found that fat scores taken on live birds compared very well to scores taken on dead birds after freezing and thawing, so we were not concerned that scores assigned to frozen birds would differ from scores assigned to the same birds when alive. All scores were assigned by JPD to limit inter-observer variability (Krementz and Pendleton 1990; Rogers 1991). We held birds in a consistent way while determining fat scores, as some ways of holding hawks give clearer views of the subalar pad than others (J. P. DeLong and J. A. Gessaman, pers. obs). Also, Rogers (1991) indicated that changing positions of the bird may change the appearance of the fat pad. Because of damage to the right wing of one bird that precluded a reliable scoring of the right subalar fat pad, all analyses were conducted using scores assigned to the left subalar pad.

We conducted a general linear model with fat score as an independent variable and TBF as the dependent variable. Because of the possibility that the relationship between fat scores and TBF could vary for different species, ages, and sexes, we included these three terms and all interactions among those terms in the model. We applied a backwards elimination procedure to this saturated starting model, removing nonsignificant terms ($P > 0.05$), retesting the model, and continuing to remove terms until no more terms could be removed. Nonsignificant lower order terms were retained when interactions containing those terms were significant. The number of equations needed to predict TBF from fat scores depended on the number of significant terms in the final model.

Condition indices.—Condition indices are widely used to describe body condition in birds. Body condition can be a useful indicator of TBF because it includes primarily fat reserves. However, body condition also includes carbohydrate and protein storage (Brown 1996), so any condition index will reflect more than just fat reserves. Condition indices are ratios of mass to size with variation in the ratio presumed to reflect variation in fat and lean mass (Brown 1996; but see Johnson et al. 1985). Size in these indices is often estimated by single linear measurements such as wing chord or tarsus length (Brown 1996).

We calculated twelve condition indices (Table 1) for each bird in the sample. The first index is the commonly used mass/wing chord ratio. Wing chord, however, is not likely by itself the best indicator of overall body size because size is not proportional to linear measures (Summers 1988). Rather, size is a three-dimensional character that increases to some power (three in the case of perfect cubes) as linear measures increase to the power of one. Thus, the second condition index was a ratio of mass to the cube of wing chord, which scales linearly with mass. We suspected, however, that size was even more complicated in these birds, and that morphological differences in proportions among individuals may require measuring size with more than one linear measure. For example, two individuals could have similar overall sizes, yet one may have a longer tail

TABLE 1. Equations produced by simple linear regression[a] and coefficient of determination (R^2) of twelve condition indices (body mass/measurement combination[b]) against ln(actual total body fat).

Index #	Measurement combination	Slope	Intercept	R^2
1	wc	2.139	−0.183	0.59
2	wc*wc*wc	240,754	−2.963	0.72
3	wc*tail*hall	12,279.2	−2.125	0.33
4	wc*tail*tars	57,913.7	−3.195	0.78
5	wc*tail*keel	53,214.3	−3.467	0.67
6	wc*tars*hall	6212.6	−3.970	0.62
7	wc*hall*keel	4260.4	−2.773	0.37
8	wc*tars*keel	17,251.9	−3.218	0.76
9	tail*hall*tars	4402.6	−3.205	0.49
10	tail*hall*keel	2677.2	−1.730	0.25
11	tail*keel*tars	15,058.0	−3.533	0.76
12	keel*tars*hall	1466.9	−3.809	0.53

[a] All regressions significant at $P < 0.01$.
[b] Wing chord length (wc), tail length (tail), hallux claw length (hall), tarsus length (tars), keel length (keel).

and the other a longer wing chord. Hence, the remaining ten indices were calculated with the product of three different linear measurements in the ratio's denominator. These represent all potential combinations of three different measurements that we collected (Table 1).

The strength of the relationship between each condition index and TBF was determined by simple linear regression. We then selected the condition index with the highest R^2 value and the index most commonly observed in the literature for further analysis. We constructed a saturated general linear model with the condition index as the independent variable, TBF as the dependent variable, and species, age, and sex as categorical variables. We applied a backwards elimination procedure to create a set of equations in the same manner as was done with fat scoring.

Direct external morphology.—We performed a backwards-elimination multiple regression to determine which independent variables best explained TBF in these birds. We began this procedure with mass, wing chord, tail length, tarsus length, hallux claw length, and keel length as independent variables and TBF as the dependent variable. We removed nonsignificant terms ($P > 0.05$) until all remaining terms were significant. We then constructed a general linear model starting with the remaining significant independent variables (mass and tarsus length) and added the three categorical variables species, age, and sex. We included all three-way interactions, but no four-way interactions could be included due to insufficient sample size. We then conducted a backwards elimination procedure to create a final model that accounted for the effects of species, age, and sex, in the same manner as done for fat scores and the two condition indices. We then repeated the above procedure including fat scores as an independent variable in the model.

Indirect external morphology.—Indirect methods involve estimating the fat-free (lean) mass of a bird and subtracting this estimate from the actual body mass of that bird (Gessaman 1999). Fat-free mass has been estimated by assuming that birds with fat scores of zero represent birds with no stored fat, allowing the construction of a regression between these assumed values of fat-free mass and a size parameter such as wing chord (Yong and Moore 1997). Rogers (1991), however, found that Dark-eyed Juncos (*Junco hyemalis*) with fat scores of zero had not exhausted all of their stored fat. Alternatively, fat-free mass can be estimated with a regression that relates one or more morphological measurements to known fat-free mass determined by TBF extraction (Lyons and Haig 1995; Gessaman 1999).

We calculated the actual lean body mass of each bird by subtracting the TBF (g) of the bird from the frozen (or hydration-corrected) mass (g) of the bird. We then conducted a multiple regression with each of the six external morphology measures (mass, wing chord, tail length, tarsus length, hallux claw length, and keel length), using backwards elimination to determine important predictor variables. We then added species, age, and sex terms to construct a general linear model as was done with the direct external morphology analysis. We estimated TBF by the difference between the estimates of lean mass (produced from the resulting equations) and the actual body mass of each bird.

RESULTS

Fat scoring.—Of the 233 birds scored for both right and left subalar pads in the Sandia Mountains, both Sharp-shinned Hawks (88.8%) and Cooper's Hawks (87.3%) generally had the same score for both fat pads. All birds that did not receive the same score for both pads differed by only one score level.

Fat scores were clearly related to TBF, but in a nonlinear (i.e., noninterval) manner (Fig. 1). The significant relationship between TBF and fat score for male Sharp-shinned Hawks ($R^2 = 0.41$, $P < 0.02$) is not very clear in Figure 1 because of the y-axis scale. The nonlinear problem was addressed by using the natural log-transformation of TBF as the dependent variable in the general linear model. Similar to Rogers (1991), birds with a fat score of 0 had not depleted their mobilizable fat stores (Fig. 1). Fat scores indicated different levels of TBF for different species and sex cohorts (Fig. 1). This result was also apparent in the final general linear model (Table 2). The terms in the final model ($R^2 = 0.82$, eqs. 1–4, Table 2, Fig. 2A) were fat score ($F_{1,46} = 118.88$, $P < 0.0001$), species ($F_{1,46} = 35.55$, $P < 0.0001$), sex ($F_{1,46} = 0.73$, $P = 0.398$), and sex*fat score ($F_{1,46} = 2.17$, $P < 0.005$). Because we conducted these analyses using the natural log of TBF, the predicted value from the linear equations must be converted back by taking the antilog of that predicted value.

Condition indices.—All twelve condition indices were significantly related to TBF ($P < 0.001$, $R^2 > 0.25$, Table 1). The traditional index of body mass/wing chord explained an average amount of variance ($R^2 = 0.59$).

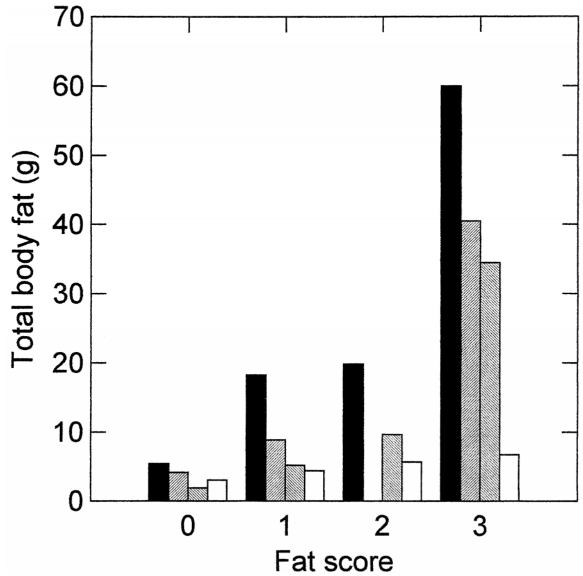

FIGURE 1. Mean TBF values for fat scores, grouped by species and sex (left to right, female Cooper's Hawks, male Cooper's Hawks, female Sharp-shinned Hawks, male Sharp-shinned Hawks). Missing bars indicate no samples for that category.

The most commonly used condition index in recent studies, which estimates size by the cube of wing chord (CI2), had higher explained variance (R^2 = 0.72), but three condition indices using combinations of three different linear measurements as size estimators had higher R^2 values (CI4, CI8, and CI11, Table 2). Of those, CI4 had the highest R^2 (0.78) and is calculated by mass (g)/[wing chord (mm) * tail length (mm) * tarsus length (mm)].

The final general linear model to predict TBF from CI2 had significant species and sex terms, thus requiring the use of four equations to account for the different relationships (R^2 = 0.76, eqs. 5–8, Table 2, Fig. 2B). The final model contained the following terms: CI2 ($F_{1,46}$ = 92.1, $P <$ 0.0001), species ($F_{1,46}$ = 4.4, P = 0.04), sex ($F_{1,46}$ = 5.5, P = 0.02), and species*CI2 ($F_{1,46}$ = 4.2, P = 0.05). The final model using CI4 as the predictor variable indicated that the relationship between this index and TBF depended only upon age (age, $F_{1,48}$ = 7.9, $P <$ 0.008; CI4, $F_{1,48}$ = 201.7, $P <$ 0.0001, R^2 = 0.81, eqs. 9 and 10, Table 2, Fig. 2C).

Direct external morphology.—From the original pool of six independent variables (mass, wing chord, tail length, hallux claw length, keel length, and tarsus length), only mass and tarsus length were significant. The model including mass and tarsus length explained a considerable amount of variation in TBF (R^2 = 0.70, $P <$ 0.0001). The backwards elimination procedure revealed that the way these two variables related to TBF depended upon species and sex. The final model included the following

TABLE 2. Technique, coefficient of determination (R^2), and corresponding equations created for using technique to predict total body fat (Y) directly or lean mass (Z). Independent variables are FS = fat score, CI2 = condition index #2 (mass/wing chord^3), CI4 = condition index #4 (mass/wing chord*tail length*tarsus length), M = mass (g), and T = tarsus length (mm).

Eq.	Model	R^2
Fat scoring model		0.82
1	$\ln(Y)_{\text{Cooper's Hawk, female}} = 1.4654 + 0.8863*FS$	
2	$\ln(Y)_{\text{Cooper's Hawk, male}} = 1.6272 + 0.5025*FS$	
3	$\ln(Y)_{\text{Sharp-shinned Hawk, female}} = 0.591 + 0.8863*FS$	
4	$\ln(Y)_{\text{Sharp-shinned Hawk, male}} = 0.7528 + 0.5025*FS$	
Condition index #2		0.76
5	$\ln(Y)_{\text{Cooper's Hawk, female}} = -1.9218 + 202183*CI2$	
6	$\ln(Y)_{\text{Cooper's Hawk, male}} = -2.3338 + 202183*CI2$	
7	$\ln(Y)_{\text{Sharp-shinned Hawk, female}} = -4.2055 + 316953*CI2$	
8	$\ln(Y)_{\text{Sharp-shinned Hawk, male}} = -4.6175 + 316953*CI2$	
Condition index #4		0.81
9	$\ln(Y)_{\text{Adult}} = -3.5778 + 60261.01*CI4$	
10	$\ln(Y)_{\text{Immature}} = -3.5778 + 60261.01*CI4$	
Direct external morphology		0.86
11	$\ln(Y)_{\text{Cooper's Hawk, female}} = 3.1380 + 0.0149*M - 0.0881*T$	
12	$\ln(Y)_{\text{Cooper's Hawk, male}} = 9.9095 + 0.0149*M - 0.1868*T$	
13	$\ln(Y)_{\text{Sharp-shinned Hawk, female}} = -0.1362 + 0.0437*M - 0.0881*T$	
14	$\ln(Y)_{\text{Sharp-shinned Hawk, male}} = 6.6353 + 0.0437*M - 0.1868*T$	
Direct external morphology		0.89
15	$\ln(Y)_{\text{Cooper's Hawk, female}} = 2.0102 + 0.01*M - 0.0505*T + 0.3006*FS$	
16	$\ln(Y)_{\text{Cooper's Hawk, male}} = 7.1548 + 0.01*M - 0.127*T + 0.3006*FS$	
17	$\ln(Y)_{\text{Sharp-shinned Hawk, female}} = -0.5727 + 0.03*M - 0.0505*T + 0.3006*FS$	
18	$\ln(Y)_{\text{Sharp-shinned Hawk, male}} = 4.5719 + 0.03*M - 0.127*T + 0.3006*FS$	
Indirect external morphology		0.99
19	$Z_{\text{Cooper's Hawk, female}} = -3.6475 + 0.7377*M + 1.0736*T$	
20	$Z_{\text{Cooper's Hawk, male}} = -12.1123 + 0.7377*M + 1.0736*T$	
21	$Z_{\text{Sharp-shinned Hawk, female}} = -27.1189 + 0.7377*M + 1.0736*T$	
22	$Z_{\text{Sharp-shinned Hawk, male}} = -35.5837 + 0.7377*M + 1.0736*T$	

terms: mass ($F_{1,44} = 148.7$, $P < 0.0001$), tarsus length ($F_{1,44} = 11.1$, $P = 0.002$), species ($F_{1,44} = 12.9$, $P = 0.0008$), sex ($F_{1,44} = 10.3$, $P < 0.003$), species*mass ($F_{1,44} = 37.2$, $P < 0.0001$), and sex*tarsus length ($F_{1,44} = 7.5$, $P < 0.009$). Adding these terms raised the R^2 to 0.86 and led to the construction of four equations to predict TBF (eqs. 11–14, Table 2, Fig. 2D). The possibility that one curvilinear model could be used to predict TBF for all groups was investigated by adding quadratic mass and tarsus length terms. These terms were not significant ($F_{1,42} < 2.25$, $P > 0.14$) and did not cause the species and sex terms to become nonsignificant, and thus curvilinear models were not appropriate and were not investigated further.

The final direct external morphology model with fat score added as a

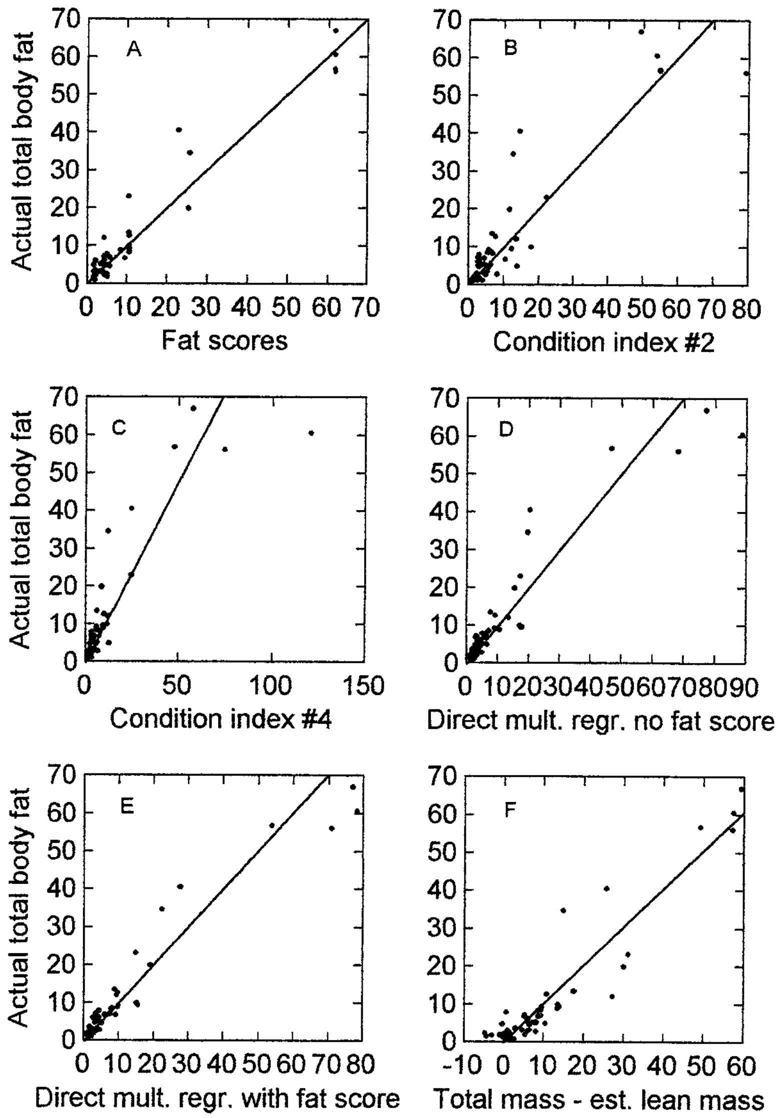

FIGURE 2. Actual values of total body fat (g) versus estimates of total body fat using (g) derived from (A) fat scores (equations 1–4), (B) condition index #2 (equations 5–8), (C) condition index #4 (equations 9 and 10), (D) direct external morphology technique (from measurements of mass and tarsus length, equations 11–14), (E) direct external morphology technique (from measurements of mass, tarsus length, and fat score, equations 15–18), and (F) indirect external morphology (body mass - estimated lean mass, equations 19–22). See Table 1 for construction of condition indices and Table 2 for equations. Lines represent perfect prediction, i.e., y = x. These plots illustrate that most methods work reasonably well but some tend to over or underestimate total body fat at high or low values. Data for 51 birds includes a mix of Sharp-shinned and Cooper's Hawks, juveniles and adults, and males and females.

TABLE 3. Pearson correlation of actual TBF against predicted values of TBF, mean error of TBF estimates[a] ± SD, mean 95% prediction interval (PI)[b] ± SD, and predicted mean TBF ± SD[c] for noninvasive techniques examined in this study.

Procedure	r	Mean error ± SD (%)	Mean 95% PI ± SD	Mean TBF ± SD (g)
Fat scoring	0.97	39.6 ± 38.5	0.30 ± 0.07	10.7 ± 16.1
Condition index #2	0.90	50.0 ± 52.8	0.23 ± 0.06	10.2 ± 15.5
Condition index #4	0.88	43.1 ± 45.0	0.23 ± 0.06	11.4 ± 21.0
DEM[d]	0.94	37.8 ± 33.4	0.32 ± 0.09	11.2 ± 18.6
DEM[e]	0.97	32.0 ± 27.0	0.30 ± 0.07	11.3 ± 18.4
IEM[f]	0.94	73.2 ± 84.6	—	11.3 ± 15.3

[a] (|Actual TBF − predicted TBF|/Actual TBF)*100.
[b] 1.96*SE_{Yi} (standard error for an individual prediction).
[c] Actual mean TBF ± SD = 11.3 ± 16.3.
[d] Direct external morphology, predicting TBF from mass and tarsus length.
[e] Direct external morphology, predicting TBF from mass, tarsus length, and fat score.
[f] Indirect external morphology, predicting lean mass from mass and tarsus length.

predictor explained slightly more variance than the model without fat scores ($P < 0.0001$, $R^2 = 0.89$, Table 2, Fig. 2E). It included the following terms: mass ($F_{1,43} = 35.4$, $P < 0.0001$), tarsus length ($F_{1,43} = 5.0$, $P = 0.03$), fat score ($F_{1,43} = 11.9$, $P < 0.002$), species ($F_{1,43} = 9.4$, $P < 0.004$), sex ($F_{1,43} = 7.0$, $P = 0.01$), species*mass ($F_{1,43} = 17.6$, $P < 0.0002$), and sex*tarsus length ($F_{1,43} = 5.4$, $P = 0.02$). There was also a more complex model that included a nonsignificant age and a significant sex*age term; however, this model would have required the construction of eight equations to predict TBF with the net gain of only 1% in explained variance. Hence we provide equations for the more parsimonious and manageable model (eqs. 15–18, Table 2).

Indirect external morphology.—The important external morphological characteristics for predicting lean mass were body mass and tarsus length (mass, $F_{1,46} = 1867.6$, $P < 0.0001$ and tarsus length, $F_{1,46} = 4.3$, $P = 0.045$). The multiple regression model using these variables to predict lean mass was very explanatory ($R^2 = 0.99$). This model contained significant categorical terms (species, $F_{1,46} = 14.2$, $P < 0.0005$ and sex, $F_{1,46} = 5.2$, $P < 0.03$), and thus required the creation of four equations to accurately predict lean mass (eqs. 19–22, Table 2). Though the method created estimates that correlated well with actual values of TBF and estimated the sample mean very closely (Table 3, Fig. 2F), many estimates of TBF were negative because the estimate of lean mass exceeded the actual body mass for that individual.

DISCUSSION

Fat scoring.—Banders at raptor migration research sites run by HawkWatch International, Inc., generally score only the right subalar fat deposit. This practice is founded on the assumption that birds store fat equally on both sides of the body, a strategy that would allow birds to maintain balance in flight. However, scoring only one pad could lead to an inaccurate assessment of fat loads. We examined this possibility for a group of birds captured during spring migration in central New Mexico and found that nearly 90% of both Sharp-shinned and Cooper's Hawks had the same fat score for both right and left subalar pads. The remaining 10% differed by only one score degree. Other subcutaneous fat storage areas (e.g., abdominal) are difficult to observe in raptors (J. P. DeLong and J. A. Gessaman, pers. obs.). Researchers hoping to achieve greater accuracy should therefore consider scoring both the left and right fad pads to eliminate error associated with individual variation in fat storing patterns. Of the 51 carcasses used in this study, however, only one had scores that differed for left and right sides. Thus it is difficult to determine the usefulness of using the mean of left and right scores with our data.

The fat scoring method (one-sided score) tested in this study explained 82% of the variance in actual TBF. This value exceeds that for five species studied by Krementz and Pendleton (1990), who considered the method to be moderately precise. The method as outlined here may allow researchers to address more precise questions in fat storage because of the greater coefficient of determination. However, there was substantial overlap in actual TBF values for fat classes. Not all individuals scored with a 3 will have higher TBF values than all birds scored with a 2, so this technique may therefore still be best suited to comparing the means of groups of birds. This conclusion is similar to those reached by other studies that have calibrated fat scores with a group of birds (e.g., Scott et al. 1995). The fat scoring model produced the second highest mean percent error and had a moderately narrow mean 95% prediction interval (Table 3). The predicted mean for the entire sample was 0.6 g lower than the actual mean (Table 3).

Unlike Krementz and Pendleton (1990), who calibrated fat scores against TBF separately for different species, we combined all 51 birds in our study into one group. Similarly, Rogers (1987) used one model to relate fat scores to TBF for several species, but sample size and range limitations precluded creating separate equations for each species. Here, using general linear models we were able to determine which categories (species, age, and sex) influenced the relationship between fat scores and TBF. We found that species was a significant variable and thus fat scores indicate different levels of TBF for Sharp-shinned and Cooper's Hawks. In addition, sex was a significant variable, and thus fat scores indicate different levels of TBF for males and females. This result is not surprising because Cooper's Hawks are larger than Sharp-shinned Hawks and females are larger than males in both species. It should be expected that a larger bird will have more grams of stored fat than a smaller bird (Fig. 1). These differences preclude the use of raw fat scores to compare groups across species and sex. The equations provided here, however, provide a means of converting fat scores into TBF values, which can then be used in comparisons of percent total body fat between groups.

Condition indices.—All of the condition indices were significantly related to TBF. We calibrated CI2 (the index most commonly in use in recent studies) and CI4 (the index with the highest R^2, Table 1) to determine the effect of species, age, and sex on the relationship between condition index and TBF. Our final model predicting TBF from CI2 revealed that species and sex influenced the relationship with TBF, hence four equations are needed when using CI2 to predict TBF (Table 2). CI4 varied in the way it related to TBF by age, requiring the use of two equations (Table 2). Both condition indices were less explanatory, produced estimates that correlated less tightly with the actual values, and had greater mean percent errors than the fat scoring technique (Tables 2 and 3). However, both condition index models had narrower mean 95% prediction intervals than the fat scoring model (Table 4). The predicted mean TBF deviated from the sample mean TBF by only 0.1 g for CI4 and by 1.1 g for CI2 (Table 4). In addition, measurements involved in calculating condition indices are less subjective than fat scores (Krementz and Pendleton 1990; J. P. DeLong and J. A. Gessaman, pers. obs.). The series of equations for use with either condition index model may thus be more reliable than fat scores when multiple observers' data are included for analysis, and the clearly continuous nature of the TBF estimates may lend themselves to simpler analytical techniques.

Direct external morphology.—The multiple regression procedure using mass and tarsus length as predictors was slightly more explanatory (86%) than both CI4 (81%), CI2 (76%), and fat scores (82%). The direct external morphology model had a lower mean percent error and a wider 95% prediction interval than either condition indices and fat scoring, and the predicted mean TBF deviated from the actual sample mean by only −0.1 g (Table 3). Though the method also requires the use of four equations to account for the effects of species and sex, it requires the input of only two independent variables (versus four in condition indices). These variables (mass and tarsus length) can be readily measured in the field and are less subjective than fat scores. Like condition indices, this method also provides a continuum of TBF estimates. If fat scores are also available and it is expected that variability (either inter- or intra-observer) in scoring technique is low, the option of using a multiple regression model with mass, tarsus length, and fat scores is available. This direct external morphology model which included fat scores as a predictor was superior to the fat scoring model in explained variance (89% versus 82%, respectively), and thus provides some benefit over using fat scores alone to predict TBF. This method also had the smallest mean percent error and a moderate width mean 95% prediction interval, and the predicted mean TBF was identical to the actual sample mean TBF (Table 3).

Indirect method.—The model predicting lean mass from body mass and tarsus length was very explanatory (R^2 = 0.99) and led to reasonably accurate prediction of TBF (Table 3, Fig. 2F). Though the correlation of estimates with actual values of TBF was high (0.94), the mean percent error was the highest of all the techniques, suggesting that this technique is the least effective at predicting TBF for individual birds (not unexpected for a group of birds with overall relatively low fat reserves; see Gessaman 1999). However, the estimated mean TBF from this method also did not deviate from the actual TBF, suggesting that this method could work quite accurately for comparing groups. Other researchers have also achieved good success with this method (e.g., Lyons and Haig 1995), where estimates correlated similarly well with actual values of fat ($r = 0.94$).

Sources of error.—Birds used in this study originated from a wide area and were not collected during a specific time of year. Thus, we expect the models presented here to be reasonably accurate at any time of year for Sharp-shinned and Cooper's Hawks from most locations in the western United States. However, equations such as these presented here are not always applicable to birds from other regions as has been shown with Sanderlings (*Calidris alba,* Castro and Myers 1990). Smith et al. (1990) found significant size differences between accipiters from Nevada and other locations in North America. Hence, the equations presented here may not be applicable to birds outside of the Rocky Mountain region.

Much of the unexplained variance in all four of these models may be due to (1) the presence of food and unejected pellets in the GI tract that were not accounted for; (2) variability in lean mass associated with the size of the GI tract itself (Piersma and Lindström 1997) and muscle development; and (3) dehydration state of carcasses that we were not able to detect or for which we could not make adjustments. It is unlikely that these complicating variables could be quantified noninvasively in the field.

Despite these uncontrollable sources of error, the noninvasive techniques we have described provide the only calibrated method of estimating TBF in these accipiters and should prove useful for studying energy management in Sharp-shinned and Cooper's Hawks. A validation of these models using an independent sample of birds would help provide additional information on their effectiveness. Nonetheless, we recommend using the direct external morphology technique to estimate TBF in these birds, as this method is the simplest, provides continuous estimates of TBF, and explained 86% of the variance in actual TBF of the calibration sample.

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