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CHALLENGES IN CREATING AN AMERICAN KESTREL BODY CONDITION INDEX BASED ON SIZE-ADJUSTED MASS

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ABSTRACT.—Size-adjusted mass is a common body condition index (BCI) used to indicate nonstructural energy reserves (fat and protein). BCIs are calculated from ratios of mass divided by a morphometric(s) or residuals of a regression between mass and a morphometric(s). The morphometrics used in BCIs must accurately represent structural size to reliably index energy reserves and, ideally, BCIs should be validated with comparisons to true fat and protein reserves. Many studies of American Kestrels (*Falco sparverius*) have included BCIs in ecological analyses; unfortunately, few studies have reported how well morphometrics represented structural size or provided validation of BCIs relative to independent measures of energy reserves. We evaluated relationships between several morphometrics and mass to better understand which morphometrics may best represent structural size for two kestrel populations: captive birds at McGill University in Montreal, Canada, and free-living kestrels in southwestern Idaho, U.S.A. We also compared BCIs based on different morphometrics with subjective (visual) fat scores. Our data showed few strong ($r >$ 0.5) correlations between morphometrics and few strong correlations between each morphometric and mass. Moreover, correlations between morphometrics and mass depended on sex and location. Similarly, not all BCIs had statistically significant, positive correlations with subjective fat scores and correlations varied between sexes, suggesting that the reliability of each BCI differed between males and females. The morphometrics that best represent structural size most likely differ between males and females, and information from both sexes should not be combined to create one size measure for kestrels. Unless BCIs for specific American Kestrel subpopulations are validated, mass and additional qualitative information, such as fat scores, may be the most appropriate indicators of fat and protein stores.

KEY WORDS: *American Kestrel*; Falco sparverius; *body condition index*; *energy*; *fat*; *mass*; *morphometrics*.

DESAFÍOS PARA CREAR UN ÍNDICE DE CONDICIÓN CORPORAL PARA *FALCO SPARVERIUS* BASADO EN LA MASA AJUSTADA POR TAMAÑO

RESUMEN.—La masa ajustada por tamaño es un índice de condición corporal (ICC) usado comúnmente para indicar reservas de energía no estructurales (grasa y proteínas). Los ICCs son calculados a partir del cociente entre masa y una (o varias) medida/s morfométrica/s o los residuos de una regresión entre masa y una (o varias) medida/s morfométrica/s. Las medidas morfométricas usadas en ICC deben representar con precisión el tamaño estructural para indexar de modo fiable las reservas de energía e, idealmente, los ICCs deberían ser validados mediante comparaciones con reservas verdaderas de grasa y proteínas. Muchos estudios de *Falco sparverius* han incluido ICCs en los análisis ecológicos; desafortunadamente, pocos estudios han informado que tan bien las medidas morfométricas representaron el tamaño estructural y han brindado validación de los ICCs con relación a medidas independientes de reservas energéticas. Evaluamos las relaciones entre varias medidas morfométricas y la masa para entender mejor cuáles medidas morfométricas representan mejor el tamaño estructural en dos poblaciones de *F. sparverius*: aves cautivas en McGill University en Montreal, Canadá, y aves libres en el sudoeste de Idaho, U.S.A. También comparamos los ICCs basados en diferentes medidas morfométricas con puntuaciones subjetivas (visual) de grasa. Nuestros datos mostraron pocas correlaciones fuertes ($r > 0.5$) entre las medidas morfométricas y pocas correlaciones fuertes entre cada medida morfométrica y la masa. Más aún, las correlaciones entre medidas morfométricas y masa dependieron del sexo y el lugar. De modo similar, no todos los ICCs presentaron

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correlaciones positivas estadísticamente significativas con las puntuaciones subjetivas de grasa y las correlaciones variaron entre los sexos, sugiriendo que la fiabilidad de cada ICC varió entre machos y hembras. Las medidas morfométricas que mejor representaron el tamaño estructural variaron con mayor probabilidad entre machos y hembras, por lo que la información de ambos sexos no debe ser combinada para crear una medida de tamaño para *F. sparverius*. A menos que los ICCs sean validados para subpoblaciones de *F. sparverius*, la masa y la información adicional cualitativa, como las puntuaciones de grasa, pueden ser los indicadores más apropiados de reservas de grasa y proteínas.

[Traducción del equipo editorial]

The term ''body condition'' is commonly used to describe the relative proportion of nonstructural energy reserves (fat and protein) to mass (Green 2001). Body condition may reflect individual and habitat quality or predict survival and reproductive outcomes (Jakob et al. 1996). For predators such as raptors, body condition may be of interest because many hypotheses about raptor ecology focus on food availability and foraging proficiency, which can be difficult and expensive to measure.

Direct measures of energy reserves or structural size (e.g., skeletal volume, Moser and Rusch 1988) require destructive sampling. In addition to the undesirable act of sacrificing birds, destructive sampling limits investigations because there are no subsequent data on behavior or physiology. Mass and morphometrics (measures of a physical characteristic) that represent structural size may be collected from live birds and a body condition index (BCI) may be created by estimating size-adjusted mass, or the proportion of mass not related to structural size (Iko 1991, Piersma and Davidson 1991). BCIs are based on ratios between total mass and a structural-size measure or residuals generated from a regression between a structural size measure and mass (Green 2001). Positive residuals reflect greater-than-predicted mass for a given size, representing the contribution of fat or protein reserves to mass. Consequently, individuals with positive residuals are considered to be in relatively better body condition than other individuals in the sample, whereas negative residuals reflect lower-than-predicted mass (i.e., fewer energy reserves) and individuals in relatively poorer body condition (Jakob et al. 1996). The validity of BCIs ideally should be verified by quantifying the relationship between the BCI and a direct measure of fat and protein reserves (Schamber et al. 2009).

The use of ratios and regression residuals to create a BCI requires a number of assumptions, including that the structural-size measure accurately represents overall structural size (Green 2001, Schulte-Hostedde et al. 2005). Univariate morphometrics may be used to indicate structural size, or multiple morphometric variables may be used to generate a principal component (PC) score that represents variation in size (Rising and Somers 1989, Dawson and Bortolotti 1997b). When the structural-size measure is biased relative to true structural size, the effect of size will not be adequately represented in the BCI and the subsequent analyses involving a BCI will have a confounding size component, making relationships difficult to interpret. For example, a positive relationship between a BCI and brood size could indicate that birds in better condition have more offspring or, if the effect of size has not been appropriately accounted for, that larger birds have more offspring.

Structural-size measures based on multiple morphometrics, such as a PC score, may be a more reliable indicator of structural size than univariate measures (Freeman and Jackson 1990). The objective of principal component analysis (PCA) is to combine multiple, correlated variables and create multiple, uncorrelated PCs (Manly 1994, O'Rourke et al. 2005). Ideally, each of the morphometrics used in a PCA to indicate structural size would be positively correlated with true structural size. Unfortunately, these relationships are rarely validated (Schamber et al. 2009). Using multiple positively correlated morphometrics in a PCA to generate a structural-size measure may be the next best choice because positive correlations between morphometrics most likely reflect a common positive relationship with size. In this case, the PCA would result in unidirectional and high loadings (>0.5) on all eigenvectors, a high eigenvalue (% of variation explained), and PC 1 would most likely significantly correlate with mass (Rising and Somers 1989, Reynolds 1996). If the morphometrics used in the PCA are not positively correlated, then eigenvectors may have low, positive or negative loadings and PC 1 may be related to variation in shape, in which case it should not be used as a measure of size. The number of observations in a PCA should be at least five times greater than the number of variables (Karr

and Martin 1981, O'Rourke et al. 2005); therefore, reliable PC structural-size measures will most likely be generated from large samples with positively correlated morphometrics (Iskjaer et al. 1989).

Raptor morphology has been shaped by many natural and sexual selection processes so that the morphometrics that best represent structural size may vary among sex and age classes (Ellegren 1992, DeLong and Gessaman 2001) or across geographic areas (Castro and Myers 1990). Some morphometrics, such as culmen or tail length, may be affected by wear or seasonal growth, resulting in biased or imprecise size measures. Other traits, such as appendage shape, may not correspond to a linear change in structural size. In samples consisting mostly of lean birds, a morphometric's (or PC score) ability to represent structural size should be reflected by a relatively high correlation coefficient (r) with mass (Green 2001). Green (2001) suggested that correlations between measure of size and mass with r values <0.5 will result in large and influential biases in BCIs and r values >0.7 may generate a more reliable BCI. However, most studies are typically made up of birds with mixed body conditions. When variation in energy stores is high, correlations between mass and structural-size measures may be low, and the best size measure may correlate with mass well below a fixed cut-off as high as $r = 0.7$ (Piersma and Davidson 1991). Thus, the interpretation of r values for correlations between a size measure and mass as an indicator for how well a given size measure represents true structural size depends on the properties of a sample.

American Kestrels (*Falco sparverius*) are a popular research subject because of their small size, wide-ranging distribution, and their proclivity for nesting in boxes and breeding in captivity (Smallwood and Bird 2002, Bardo and Bird 2009). They have been used as model species in a variety of research areas, including raptor biology, toxicology, and predator ecology (Bardo and Bird 2009). Kestrels are routinely captured at hawk migration sites and in human-constructed nest boxes where they are banded, weighed, and measured (with measurements frequently contributing to the construction of BCIs). Our objectives were to: (1) review techniques used to create kestrel BCIs; (2) examine correlations among several morphometrics to select variables that would create a PC score that reliably represents size; (3) assess correlations between several univariate morphometrics, PC scores, and mass; and (4) evaluate whether BCIs based on mass and univariate

morphometric ratios, residuals from a regression of a PC score and mass, or mass alone best correlated with fat scores from live birds. For objectives 2–4 we hypothesized that quantitative relationships would depend on sex.

METHODS

Literature Review. We searched peer-reviewed journals published between 1985–2009 with ISI Web of Science using the terms American Kestrel* ('*' is a wildcard that allows for any character to follow) or *Falco sparverius* combined with one of the following: body, condition, development*, growth, mass, nutrition*, size, and status. We then identified articles that indexed the amount of energy reserves (fat and protein) and classified articles depending on subject age (adult versus nestling and juvenile American Kestrels). We excluded studies in which condition was inferred from blood parameters or immune system response.

American Kestrel Morphometrics. We studied captive, after-hatch-year American Kestrels in Canada and free-living, incubating American Kestrels in Idaho, U.S.A. Although including kestrels from two populations introduces several sources of variation (location, captivity, season) between study groups, within study groups these factors did not vary and we analyzed each study group separately (see below). We (EHS and LB) measured nine morphometrics and mass of kestrels housed in aviaries at McGill University's Avian Science and Conservation Centre in Montreal, Quebec, Canada, in January 2009. The original birds that contributed to the colony, and new additions to the captive population, came from the region surrounding Montreal. From April–June 2008 and 2009, we (EHS) measured seven morphometrics, scored subcutaneous fat stores (described below), and measured mass of incubating kestrels captured after clutch completion in nest boxes in southwestern Idaho.

We selected five morphometrics commonly measured on raptors: exposed culmen length (hereafter "CULMEN"), tail length (TAIL), unflattened wing chord (WING), tarsometatarsus length (TARSUS), and hallux length (HALLUX). We also used four morphometrics more commonly measured on passerines and shorebirds: keel length (KEEL), bill depth (BILL DEP), bill width (BILL WID), and head-bill length (HEADBILL). To measure CULMEN, we placed calipers at the base of the bill where it meets the cere and measured to the tip of the upper mandible (Bortolotti 1984, Pyle 2008). We measured TAIL using a

ruler placed between the central rectrices from the point where skin meets feather shaft to distal feather tip (Pyle 2008). We measured WING from the wrist (bend of wing) to the distal end of the ninth primary using a ruler with a perpendicular stop at zero (Pyle 2008). We placed calipers at the notch at the end of the lateral condyle of the tibiotarsus to the distal end of the tarsometatarsus in the underside of the foot to measure TARSUS (modified from Pyle 2008). We used calipers to measure HALLUX as the distance between the distal end of the talon to the talon cuticle (Bortolotti 1984). To determine KEEL of captive birds, we ran a string from the tracheal pit to the posterior keel edge and then measured the length of the string. This procedure required two people and proved difficult in the field; therefore, we used a notched steel ruler for KEEL measurements in the field (Bryant and Jones 1995). We did not evaluate the difference between the two types of KEEL measurements but KEEL measurement error should not have contributed to our ability to detect relationships between morphometrics because data from captive and free-living birds were analyzed separately. We used calipers to measure HEADBILL as the distance from the maximum protrusion of the beak to the occipital bone (Pyle 2008). We measured BILL DEP with calipers at a right angle to the cutting edges of the bill (tomia) at the base of the bill (Bortolotti 1984) and BILL WID with calipers held perpendicular to the bill anterior to the cere (Senar and Pascual 1997, Pyle 2008). For BILL DEP and BILL WID, we exerted caliper pressure until we met resistance.

We measured TAIL, WING, TARSUS, and HALLUX on the right side, except for when heavy feather wear or deformities were present. In the case of feather wear, we measured the left side if possible or excluded the bird from analysis. We recorded caliper measurements to the nearest 0.01 mm and ruler measurements to the nearest 0.1 mm. We determined mass to the nearest 0.1 g using a digital scale. We scored crop content as full (1), partially full (0.5), or empty (0). We scored the size and shape of visible subcutaneous fat under the right subalar region as: no visible fat (0), a trace of fat (1), a thin layer of fat across the pit (2), and a fat bulge that visibly protruded above the level of the muscle (3), as in De-Long and Gessaman (2001).

Data Analysis. We removed birds with partial or full crops or heavy feather wear on both sides from analyses (Canada males $n = 2$, Idaho males $n = 7$, Idaho females $n = 15$). All variables except fat scores had a normal distribution (Shapiro-Wilk test, Proc Univariate, SAS 9.1, Cary, North Carolina U.S.A.), so we used parametric techniques unless otherwise stated. We examined relationships between morphological traits using Pearson's correlation and separated our results between males and females and between kestrels measured in Canada and Idaho. We did not evaluate relationships between morphometrics and mass solely based on correlation P-values because P-values indicate whether results are likely given the null hypothesis of $r = 0$ and P-values are influenced by sample sizes (Johnson 1999). Instead, we evaluated relationships between morphometrics and mass with correlation coefficients that indicate the strength of association between two linear measures to be consistent with Green's (2001) recommendations (i.e., although a high r usually corresponds with a low P-value, a low P-value does not always correspond with a high r).

We selected three morphometrics measured on kestrels captured in Idaho that had positive correlations with each other (and with mass) and entered them into a male-only and female-only PCA (Proc Princomp, SAS 9.1, Cary, North Carolina, U.S.A.) to generate a sex-specific, PC-1 (size) score for each individual. We used three variables to stay within the variable-to-observation ratio recommended by Karr and Martin (1981) and O'Rourke et al. (2005). We created sex-specific linear regressions with PC-1 scores as the independent variable and body mass as the dependent variable. We then calculated the residual for each individual to use in BCI comparisons.

We calculated several BCIs based on ratios of mass and single morphometrics that we predicted may be good indicators of size (i.e., WING, TARSUS, KEEL, and TAIL) and a BCI based on a ratio of mass and wing-cubed (cubing a linear morphometric is a technique used to measure volume, DeLong and Gessaman 2001). We calculated Spearman correlations (Proc Corr, SAS 9.1, Cary, North Carolina U.S.A.) between fat scores and BCIs or mass and examined Spearman correlation coefficients (r_s) and P-values (a test of the null hypothesis that $r_s = 0$) to examine which BCI might best indicate energy stores.

We calculated residuals from a sex-specific regression between mass (dependent variable) and WING (independent variable) and residuals from a linear regression based on all birds pooled together to examine the effect of pooling across sexes. We selected wing as a size measure because WING is a mor-

Table 1. Pearson's product-moment correlation coefficients (r) and sample sizes for paired morphometric comparisons based on data collected from captive American Kestrels at McGill University, Montreal, Canada. Females are above and to the right of the diagonal, males are below and to the left on the diagonal, samples sizes are in parentheses.

	CULMEN[a]	BILL DEP	BILL WID	KEEL	WING	TAIL	TARSUS	HALLUX
Culmen		*0.33*[b] (30)	−0.08 (30)	0.15 (31)	−0.16 (31)	0.14 (25)	0.07 (31)	**0.38**[c] (30)
Bill dep	0.21 (24)		0.19 (29)	−0.11 (30)	0.13 (30)	−0.07 (25)	0.02 (30)	0.21 (29)
Bill wid	0.18 (24)	−0.24 (24)		−0.20 (30)	0.27 (30)	**−0.72** (24)	0.17 (30)	0.01 (29)
Keel	0.21 (24)	−0.13 (24)	0.32 (24)		0.06 (31)	0.24 (25)	*0.33* (31)	0.09 (30)
Wing	−0.23 (24)	−0.14 (24)	−0.02 (24)	*0.38* (24)		−0.12 (25)	0.23 (31)	0.03 (30)
Tail	−0.13 (22)	−0.12 (22)	**−0.54** (22)	0.25 (22)	0.44 (22)		**−0.41** (25)	−0.30 (25)
Tarsus	0.37 (24)	−0.02 (24)	0.20 (24)	0.32 (24)	−0.17 (24)	−0.01 (22)		0.26 (30)
Hallux	−0.28 (24)	−0.10 (24)	−0.19 (24)	−0.17 (24)	*0.37* (24)	0.43 (22)	−0.16 (24)	

[a] Exposed culmen length (CULMEN), bill depth (BILL DEP), bill width (BILL WID), keel length (KEEL), unflattened wing chord (WING), tail length (TAIL), tarsometatarsus length (TARSUS), and hallux length (HALLUX).
[b] Italic indicates $P < 0.1$.
[c] Bold indicates $P < 0.05$.

phometric commonly used in BCIs. We compared the residuals from sex-specific or pooled regressions by taking the difference between the two residuals and testing the null hypothesis that the mean of the difference was zero using a one-sample t-test (analogous to a paired t-test approach, Proc ttest, SAS 9.1, Cary, NC U.S.A.).

RESULTS

Literature Review. We found 81 unique articles addressing kestrel condition indices. Of these 81 articles, 30 indexed kestrel energy reserves (Appendix). Most of the 30 articles ($n = 25$) included a size-adjusted mass BCI, either a ratio or a residual from a regression of PC scores (independent variable) and mass (dependent variable). Some authors (27%, $n = 8$) provided evidence about how well PC scores correlated with or predicted mass in the form of a correlation coefficient or P-value. In some cases r values were <0.5 and P-values were not significant (3 of 8). Four studies (of the 30 that estimated kestrel energy reserves) used the same condition index for adult males and females (Wiebe and Bortolotti 1993, Murza et al. 2000, Ardia 2002, Hinnebusch et al. 2010). One study (Yamamoto and Santolo 2000) used total-body electrical conductivity to estimate fat and lean body mass. Articles that included information on juvenile and nestling condition reported mass, a ratio of mass and a morphometric, and residuals from a regression of mass on predicted size (or age, Appendix). In one case (Butler and Dufty 2007), the authors did not develop a BCI because the P-value of the regression of mass and tarsus (size mea-

sure) was not statistically significant. More than half (53%) of the papers on young kestrels used the same condition index for male and female nestlings.

Kestrel Morphometrics. Relationships between morphological traits differed between American Kestrels from Canada (Table 1) and kestrels in Idaho (Table 2). The strongest positive correlation for female kestrels housed at McGill was between HALLUX and CULMEN ($r = 0.38$, $n = 30$). Female kestrels captured in Idaho exhibited positive correlations between BILL DEP and CULMEN ($r = 0.46$, $n = 27$) and also between WING and TAIL ($r = 0.65$, $n = 28$). Male kestrels housed at McGill had no statistically significant, positive correlations between any morphometrics. Male kestrels captured in Idaho had positive correlations between BILL DEP and CULMEN ($r = 0.52$, $n = 21$), BILL DEP and KEEL ($r = 0.52$, $n = 21$), BILL DEP and WING ($r = 0.55$, $n = 21$), and WING and TAIL ($r = 0.57$, $n = 41$, Table 3).

A PC score based on WING, TAIL, and BILL DEP explained 54% of the total morphological variation among female kestrels captured in Idaho. Female kestrel mass was positively correlated with PC-1 scores ($r = 0.42$, $n = 25$, $P = 0.03$). The first PC based on WING, CULMEN, and BILL DEP explained 63% of the total variation among morphometrics of male kestrels captured in Idaho. Male PC-1 scores increased with mass ($r = 0.64$, $n = 21$, $P = 0.01$). Few of the univariate morphometrics of captive and free-living American Kestrels had strong ($r > 0.5$) positive correlations with mass (Table 3). HEADBILL ($r = 0.44$, $n = 31$), CULMEN ($r = 0.52$, $n = 31$), WING ($r = 0.38$, $n = 31$), and HALLUX ($r = 0.45$, $n =$

Table 2. Pearson's product-moment correlation coefficients (r) and sample sizes for paired morphometric comparisons based on data collected from free-living American Kestrels nesting in southwestern Idaho, U.S.A. Females are above and to the right of the diagonal, males are below and to the left on the diagonal, samples sizes are in parentheses.

	CULMEN[a]	BILL DEP	KEEL	WING	TAIL	TARSUS	HALLUX
Culmen		**0.46**[b] (27)	0.26 (27)	0.21 (43)	−0.11 (28)	0.02 (27)	0.16 (44)
Bill dep	**0.52** (21)		0.06 (27)	0.12 (26)	0.24 (17)	−0.20 (27)	0.17 (27)
Keel	0.09 (21)	**0.52** (21)		0.22 (26)	0.16 (17)	−0.23 (27)	−0.07 (27)
Wing	0.11 (41)	**0.55** (21)	0.29 (21)		**0.65 (28)**	0.19 (26)	*0.29*[c] (43)
Tail	−0.09 (41)	0.29 (21)	0.34 (21)	**0.57 (41)**		0.17 (17)	0.10 (28)
Tarsus	0.33 (21)	0.14 (21)	−0.14 (21)	*0.37* (21)	0.12 (21)		0.09 (27)
Hallux	−0.06 (41)	*0.40* (21)	0.27 (21)	0.20 (41)	0.16 (41)	0.19 (21)	

[a] See Table 1 for definitions.
[b] Bold indicates $P < 0.05$.
[c] Italic indicates $P < 0.1$.

30) had statistically significant correlations with mass of captive females. WING was weakly ($r < 0.5$) correlated with mass ($r = 0.30$, $n = 43$, Table 3) of free-living female kestrels. TARSUS was correlated with mass of captive males ($r = 0.70$, $n = 23$) and BILL DEP was positively correlated with mass of free-living males ($r = 0.60$, $n = 21$, Table 3). The mass of female kestrels captured in Idaho ranged from 102–158 g (mean = 133 g, CV = 8.7%) and 113–162 g (mean = 136 g, CV = 8.2%) for McGill kestrels. The mass of male kestrels captured in Idaho ranged from 92–130 g (mean = 108 g, CV = 6.5%) and 107–134 g (mean = 122 g, CV = 6.1%) for McGill kestrels.

Mass was strongly correlated with subjective fat scores of female kestrels in Idaho ($r_s = 0.40$, $P = 0.008$, Table 4). Mass divided by WING ($r_s = 0.39$, $P = 0.009$), mass divided by WING-cubed ($r_s = 0.34$, $P = 0.03$) and mass divided by TAIL ($r_s = 0.36$, $P = 0.02$) also were correlated with female fat scores (Table 4). Only the ratio of mass divided by WING

($r_s = 0.34$, $P = 0.03$) and mass divided by WING-cubed ($r_s = 0.42$, $P = 0.006$) were correlated with fat scores from male kestrels. All other BCIs and mass had no statistically significant correlations with male fat scores (Table 4).

The regression between female mass and WING (female mass = 22.6 + 0.57*WING, Fig. 1) had a different intercept and slope than the regression for male mass and WING (male mass = 43.9 + 0.33*WING, Fig. 1). Results from the sex-specific regressions were also different from the sex-combined (all data pooled) regression between mass and WING (mass = −194.9 + 1.63*WING, Fig. 1). Residuals for females from the sex-combined regression were higher than the residuals from the female-only model (mean of difference = 6.4, SD = 0.67, $t = 9.4$, $P < 0.001$, Fig. 1). Residuals for male birds from the sex-combined regression were lower than the residuals from the male-only model (mean of difference = −10.2, SD = 1.09, $t = −9.4$, $P < 0.001$, Fig. 1).

Table 3. Pearson's product-moment correlation coefficients (r) of nine morphometrics with body mass of female and male American Kestrels in captivity at McGill University (CAN) or captured in southwestern Idaho (ID); samples sizes are in parentheses.

LOCATION/ SEX	MORPHOMETRICS								
	HEADBILL[a]	CULMEN	BILL DEP	BILL WID	KEEL	WING	TAIL	TARSUS	HALLUX
CAN female	**0.44**[b] (31)	**0.52 (31)**	*0.32*[c] (30)	0.09 (30)	0.15 (31)	**0.38 (31)**	−0.12 (25)	*0.35* (31)	**0.45 (30)**
ID female		0.20 (44)	0.26 (26)		0.11 (27)	*0.29* (43)	0.28 (28)	0.12 (27)	0.19 (44)
CAN male	0.21 (22)	0.29 (23)	−0.12 (23)	*0.38* (23)	0.24 (23)	−0.15 (23)	−0.28 (21)	**0.70 (23)**	−0.31 (23)
ID male		0.25 (41)	**0.60 (21)**		0.20 (21)	*0.28* (41)	0.14 (41)	0.23 (21)	0.15 (41)

[a] Head to distal tip of bill length (HEADBILL), for other definitions please see Table 1.
[b] Bold indicates $P < 0.05$.
[c] Italic indicates $P < 0.1$.

Table 4. Spearman's correlation coefficient (r_s) and sample sizes (in parentheses) between body fat scores and body condition indices for female and male American Kestrels captured in southwestern Idaho, U.S.A.

	BODY CONDITION INDEX						
	MASS/WING	MASS/WING³	MASS/TARSUS	MASS/KEEL	MASS/TAIL	RESIDUAL FROM REGRESSION OF MASS AND PC SCORES	MASS
Female	**0.39**[a] (43)	**0.34** (43)	0.31 (27)	0.34 (27)	**0.36** (41)	0.36 (25)	**0.40** (44)
Male	**0.34** (41)	**0.42** (41)	−0.01 (21)	−0.07 (21)	0.28 (41)	−0.19 (21)	0.23 (41)

[a] Bold indicates $P < 0.05$.

DISCUSSION

Many approaches have been used to create an American Kestrel BCI based on size-adjusted mass. Both the type and number of morphometrics that have been used to represent size have varied among studies. The morphometrics that best represent structural size may be determined (and should be validated) by examining relationships among external, linear morphometrics and a direct estimate of structural size, such as skeletal volume (Piersma and Davidson 1991). In the absence of such information, the explanatory power of size measures based on morphometrics from free-living birds may be evaluated by examining correlations between size morphometrics and mass. However, in many studies of kestrel body condition we reviewed, the relationship between the size measure and mass was not reported or correlation coefficients were low. Low correlation coefficients may indicate that most morphometrics do not adequately represent structural size, and therefore do not adequately remove size effects, or that energy reserves were highly variable within study populations. High variation in energy reserves may be particularly important during periods of fat deposition, such as the premigratory period when fat constitutes as much as 7–8% total body mass for females and 5–6% total body mass for males (Gessaman 1979, Hardin 1993). However,
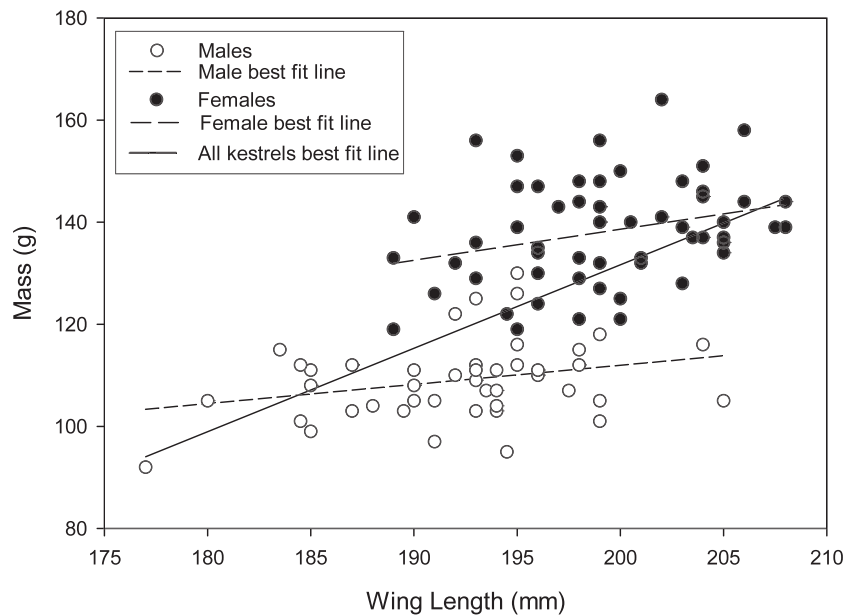

Figure 1. The relationships between wing length and body mass for male and female after-hatch-year American Kestrels captured in southwestern Idaho, U.S.A. Body condition indices created from residuals of sex-specific regressions between wing length and mass were significantly different from body condition indices created from a combined-sex regression.

kestrels do not show nearly the increase (or variation) in fat stores as some other groups of birds such as passerines (e.g., 14–50%, Blem 1990) or shorebirds (e.g., 27–73%, Gudmundsson et al. 1991), so the effect of fat stores on correlations between morphometric measurements and mass may be lower for kestrels compared with other birds.

We found few strong positive correlations between morphometrics for all groups (males and females, Idaho and Canada) of kestrels. When morphometrics do not positively correlate with each other, techniques such as PCA (which depend on common variance) may not result in reliable size measures, and PC-1 may represent variation in shape rather than size. Similarly, residuals from regressions of mass and PC-1 scores did not have a statistically significant correlation with subjective fat scores. With our data it seemed that the use of multiple morphometrics in a PCA did not notably improve our ability to measure size compared to the use of univariate morphometrics, underscoring the importance of examining the relationship between external and skeletal measurements to better understand which morphometrics are truly representative of kestrel size.

We documented variation in correlations between univariate size measures and mass across sex and location. For example, BCIs based on residuals from sex-specific regressions of mass and WING were statistically significantly different from BCIs based on a regression created from sex-pooled data. Like most raptors, kestrels exhibit reverse sexual size dimorphism; thus, combining structural-size measures across sexes will most likely result in males being scored in ''poorer'' condition and females in ''better'' condition because confounding size effects have not been adequately removed. This example illustrates the importance of creating a kestrel BCI for each sex. This same problem likely exists for nestling kestrels where males and females grow at different rates (J. Heath unpubl. data). Similarly, correlations between morphometrics varied between locations. This may not be surprising, because raptors have many selective pressures that may cause morphometrics to co-vary with shape (Sustaita 2008). Given the geographic and sex-based variation we observed, the discovery of a standard set of external morphometrics that best represents kestrel size at all locations or for both sexes seems unlikely. Our results suggested that size-adjusted BCIs for kestrels should be constructed separately for each sex, location, and age group. However, even after controlling for each of these factors that affect the correlation between size and mass, size-adjusted BCIs for kestrels may still have low explanatory power until it is better understood which morphometrics best represent size for each sex.

To our knowledge, none of the BCIs that have been reported for kestrels have been validated relative to direct fat and protein measures. Ideally, carcasses could be obtained to estimate directly fat and lean body mass, and these measures could be compared to multiple BCIs (Schamber et al. 2009). Such an approach could also provide an opportunity to validate the use of external morphometrics as indicators of skeletal volume. Given the considerations above, validation of BCIs relative to either subjective fat scores or direct measures of energy reserves should be done separately for each population, sex, or age class. However, this requires destructive sampling, which may not be feasible, especially in areas where kestrel populations are declining. If destructive sampling is not possible, researchers may choose to compare their BCIs with subcutaneous fat scores, as an indirect form of validation. Subjective fat scores may have high interobserver error (Krementz and Pendleton 1990) and still require validation with direct fat measures (Kaiser 1993, DeLong and Gessaman 2001). We attempted to reduce inter-observer error by having one person (EHS) score fat and we considered fat scores to be informative because they have been useful in predicting total body fat for other raptors (i.e., DeLong and Gessaman 2001). Unfortunately, most of our BCIs correlated weakly with subjective fat scores, likely because our various size measures were biased or imprecise. The weak correlations between BCIs and fat scores illustrated the problems associated with using indices that have not been validated. Subsequent analyses of body condition effects on kestrel life history characteristics and fitness will have low statistical power when condition is poorly estimated or, when statistically significant patterns are found, size effects may be misinterpreted as body-condition effects.

Some authors have suggested that in the absence of dependable BCIs, mass may be the best indicator of energy stores (Schamber et al. 2009). We think that this conclusion may be applicable for kestrels given the generally weak correlations that we observed between kestrel BCIs and fat scores, particularly because a strong correlation between any BCI for kestrels and true energy reserves has yet to be demonstrated through independent validation. However, because mass represents variation in energy reserves and structural size, apparent relationships between mass and life-history parameters should be

interpreted with caution and inferences about condition should be supported by other evidence such as qualitative fat scores. Future research that focuses on understanding correlations among kestrel morphometrics and size would greatly advance the ability to calculate size-adjusted mass, index nonstructural energy reserves, and make informed decisions regarding how to approach creating new location-, sex-, and age-specific BCIs for kestrels.

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Appendix. Technique, measure of fit, and sex specificity of body condition indices (BCI) for adult and juvenile American Kestrels complied from a review of 30 published articles.

TECHNIQUE FOR ESTIMATING CONDITION	AGE	PROVIDED MEASURE OF FIT	SAME INDEX FOR SEXES	CITATION
Lean body mass, fat mass from total-body electrical conductivity (TOBEC)	Adult	Cited Harden 1993	Males only	Yamamoto and Santolo 2000
Mass divided by PC score based on unflattened wing chord, central rectrix, outer rectrix, tenth primary, exposed culmen, tarsus width	Adult	No	No	Bortolotti and Iko 1992; Wiebe and Bortolotti 1992, 1994, 1995a; Dawson and Bortolotti 1997a
Mass divided by unflattened wing chord	Adult	No	Yes	Murza et al. 2000
Residuals from a regression of mass and PC scores based on longest primary and central tail rectrix	Adult	No	Yes	Ardia 2002
Residuals from a regression of mass and PC scores based on unflattened wing chord, central rectrix, outer rectrix, tenth primary, exposed culmen, tarsus width	Adult	Male: $P = 0.06$, female: $P = 0.01$	No	Dawson and Bortolotti 2006, 2008
Residuals from a regression of mass and PC score based on unflattened wing chord, central rectrix, outer rectrix, tenth primary, exposed culmen, tarsus width	Adult	Male: $r = 0.31$, female: $r = 0.17$	No	Dawson et al. 2001; Bortolotti et al. 2002
Residuals from a regression of mass and PC score based on unflattened wing chord, central rectrix, outer rectrix, tenth primary, exposed culmen, tarsus width	Adult	No	No	Dawson and Bortolotti 1997b, 2000
Size covariate (PC score based on unflattened wing chord, central rectrix, outer rectrix, tenth primary, exposed culmen, width of tarsus) in regressions of mass and various response variables	Adult	No	Yes	Wiebe and Bortolotti 1993
Residuals from a regression of mass and PC scores based on unflattened wing chord, tarsus length	Adult	No	Males only	Love et al. 2003c
Cube root of mass divided by wing chord	Adult	No	Yes	Hinnebusch et al. 2010
Mass	Juvenile	No	Females only	Heath and Dufty 1998
Mass	Nestling	No	Yes	Love et al. 2003a
Mass	Nestling	No	Yes	Wiebe and Bortolotti 1995b
Mass, tenth primary length at 12 and 20 d	Nestling	No	No	Dawson and Bortolotti 2008
Mass, tenth primary length at 24 d	Nestling	No	No	Dawson and Bortolotti 2002, 2003
Mass divided by tarsus length	Nestling	No	Unclear	Love et al. 2003b
Residuals from a regression of mass and cubed primary length	Nestling	$r = 0.44$	Yes	Bortolotti et al. 2000, Tella et al. 2000a, Tella et al. 2000b
Residuals from a regression of mass and tarsus length	Nestling	No	Yes	Ardia 2006
Residuals from a regression of mass and tarsus length	Nestling	$P = 0.21$, rejected index	Yes	Butler and Dufty 2007
Residuals of a regression of mass and age	Nestling	No	Yes	Sockman and Schwabl 2001