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Tools and Technology Article

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ABSTRACT Because they do not require sacrificing animals, body condition scores (BCS), thickness of rump fat (MAXFAT), and other similar predictors of body fat have advanced estimating nutritional condition of ungulates and their use has proliferated in North America in the last decade. However, initial testing of these predictors was too limited to assess their reliability among diverse habitats, ecotypes, subspecies, and populations across the continent. With data collected from mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) during initial model development and data collected subsequently from free-ranging mule deer and elk herds across much of the western United States, we evaluated reliability across a broader range of conditions than were initially available. First, to more rigorously test reliability of the MAXFAT index, we evaluated its robustness across the 3 species, using an allometric scaling function to adjust for differences in animal size. We then evaluated MAXFAT, rump body condition score (rBCS), rLIVINDEX (an arithmetic combination of MAXFAT and rBCS), and our new allometrically scaled rump-fat thickness index using data from 815 free-ranging female Roosevelt and Rocky Mountain elk (*C. e. roosevelti* and *C. e. nelsoni*) from 19 populations encompassing 4 geographic regions and 250 free-ranging female mule deer from 7 populations and 2 regions. We tested for effects of subspecies, geographic region, and captive versus free-ranging existence. Rump-fat thickness, when scaled allometrically with body mass, was related to ingesta-free body fat over a 38–522-kg range of body mass ($r^2 = 0.87$; $P < 0.001$), indicating the technique is remarkably robust among at least the 3 cervid species of our analysis. However, we found an underscoring bias with the rBCS for elk that had >12% body fat. This bias translated into a difference between subspecies, because Rocky Mountain elk tended to be fatter than Roosevelt elk in our sample. Effects of observer error with the rBCS also existed for mule deer with moderate to high levels of body fat, and deer body size significantly affected accuracy of the MAXFAT predictor. Our analyses confirm robustness of the rump-fat index for these 3 species but highlight the potential for bias due to differences in body size and to observer error with BCS scoring. We present alternative LIVINDEX equations where potential bias from rBCS and bias due to body size are eliminated or reduced. These modifications improve the accuracy of estimating body fat for projects intended to monitor nutritional status of herds or to evaluate nutrition's influence on population demographics.

KEY WORDS *Alces alces*, body condition score, *Cervus elaphus*, elk, moose, mule deer, nutritional condition, *Odocoileus hemionus*, rump fat, ultrasonography.

Nutritional condition is the integrator of nutritional intake and expenditure, can substantially affect survival and reproduction and, thus, is a key measure of habitat quality (Parker et al. 2009). Practical techniques to measure nutritional condition of live, free-ranging ungulates have been unavailable, but new approaches were tested and are receiving substantial use across North America. These new approaches principally include 2 methods: a rump body condition score (rBCS) and maximum thickness of the rump-fat layer (MAXFAT) measured using ultrasonography.

Body condition scoring is used for a wide range of management and research purposes in the livestock industry (Jeffries 1961, Wildman et al. 1982, Edmonson et al. 1989) and has been developed for predicting body fat of caribou (*Rangifer tarandus*; Gerhart et al. 1996, 1997), elk (*Cervus elaphus*; Cook et al. 2001*a*, *b*), and mule deer (*Odocoileus hemionus*; Cook et al. 2007). Use of MAXFAT measured using ultrasonography to predict total body fat was developed and tested for moose (*Alces alces*; Stephenson et al. 1998), elk (Cook et al. 2001*a*, *b*), and mule deer (Stephenson et al. 2002, Cook et al. 2007) and has been used in field settings for moose (Keech et al. 1998, 2000), caribou (Parker et al. 2005, Gustine et al. 2007), bighorn sheep (*Ovis canadensis*; T. R. Stephenson, California Department of Fish and Game, unpublished data), and white-tailed deer (*Odocoileus virginianus*; G. D. DelGiudice, Minnesota Department of Natural Resources, unpublished data; W. J. McShea, Conservation and Research Center, unpublished data). Others arithmetically combined the rump portion of the BCS (rBCS) and MAXFAT into one

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index (rLIVINDEX) for elk and mule deer (Cook et al. 2001*a*, *b*, 2007). This index also has received widespread use (e.g., Evans et al. 2006, Schoenecker et al. 2006, Bishop 2007, Conner et al. 2007, and Tollefson 2007).

The rBCS and MAXFAT indices, separately or in combination, offer important advantages and a variety of potential applications that are incompatible with older techniques such as bone-marrow and kidney fat (Stephenson et al. 1998; Cook et al. 2001*a*, *b*). Rump fat measured at its maximum point of thickness is linearly correlated across a broad range of total body fat compared to most indices derived from a single depot of fat (Stephenson et al. 1998; Cook et al. 2001*a*, *b*; Takahashi et al. 2004). Moreover, BCS usually integrates across both muscle and fat over some or all of the body, and rBCS combined with MAXFAT in the rLIVINDEX covers the entire range of body fat likely to be encountered in cervids of North America (Cook et al. 2001*a*, 2007). Therefore, the combined technique provides better predictions of total body fat than do older indices of single fat depots, in part because sequence of mobilization and depletion of different depots are not synchronous (Robbins 1983, Cederlund et al. 1989, Harder and Kirkpatrick 1994). Similarly, indices of a single fat depot may be too limited to adequately span important thresholds between body fat and survival and reproduction and, thus, may not be well related to these measures of animal performance (e.g., Cook et al. 2001*b*, 2007).

Because total body fat is related to key aspects of animal performance such as pregnancy probability (e.g., Cameron 1994, Heard et al. 1997, Cook et al. 2004*a*, Gustine et al. 2007), fetal sex allocation (Kohlmann 1999), size and vigor of neonates (Keech et al. 2000), and probability of overwinter survival (Hobbs 1989, Cook et al. 2004*a*) and because fat levels can be a valuable indicator of the adequacy of the nutritional and bioenergetic environment (Crête and Huot 1993, Cook et al. 2004*a*, Parker et al. 2009), there is considerable need for identifying explicit relationships between 1) fat indices and body fat, 2) habitat quality and body fat, and 3) body fat and performance. Explicit quantitative relationships linking these have largely been unavailable for biologists, yet could have inordinate value for research and management. Key for development of this potential, however, are robust indices of condition, practical for field applications, that can be used to accurately estimate nutritional condition among observers, animal populations, and environmental conditions.

Despite stringent testing under controlled conditions, additional evaluations are needed before rBCS, MAXFAT, and rLIVINDEX are applied to ungulates among diverse habitats or among subspecies or ecotypes. Also, the original tests of these indices used at least some animals held in captivity, raising questions of robustness of predictor equations when used with wild stock.

We evaluated reliability of rBCS and MAXFAT for estimating ingesta-free body fat (IFBF) across species and subspecies, within subspecies across broad geographic areas, and between captive and free-ranging animals. We used 2 data sets collected from elk, moose, and mule deer. The first data set was derived from animals that were sacrificed and homogenized to obtain measures of body composition (hereafter, the homogenization data; Cook et al. 2001*a*, Stephenson et al. 2002, Cook et al. 2007), including IFBF, which we used as a standard for evaluating these condition variables. The second data set was collected from 1998 to 2007 from 19 free-ranging elk and 7 free-ranging mule deer herds from various locations in the western United States and included rBCS scores, MAXFAT measurements, and either girth circumference for estimating body mass or directly measured body mass (Cook et al. 2003). No direct measure of IFBF determined via sacrifice and homogenization was collected for these free-ranging herds.

We conducted 3 general sets of analyses. First, using an allometric scaling function, we evaluated the extent to which the relationship between percent IFBF and MAXFAT remained constant across species of cervids using data from the homogenization data set. Second, using data from the wild deer and elk herds, we evaluated 1) the extent to which the relationship between the original rBCS index and the original MAXFAT index differed among subspecies, populations, and captive versus free-ranging animals, and 2) the magnitude of bias in IFBF estimates that might arise from variations in the relationship between MAXFAT and rBCS among herds. Third, we used these data sets to test a priori hypotheses regarding possible biases arising from influences of variation in body size (e.g., 1-cm thickness of rump fat might indicate a higher % body fat in small vs. large deer) and observer bias associated with repeatability of body condition scores (Cook et al. 2007). We evaluated new indices and predictor equations with potential to dampen effects of these possible biases.

STUDY AREA

Data were collected from 19 elk herds located in the northwestern United States and the Rocky Mountain region (Fig. 1). We partitioned our data into 4 regions: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (Roosevelt elk); 2) the hills and mountains east of Interstate 5 and west of the crest of the Cascades Mountains in western Oregon and Washington (Rocky Mountain elk); 3) the inland Northwest from the crest of the Cascades east across Washington and Oregon (Rocky Mountain elk); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (Rocky Mountain elk). Mule deer data were collected from 7 herds, including 5 in central and eastern Washington and 2 in California (Fig. 1). For analysis purposes, we stratified deer data into 2 regions, Washington and California.

METHODS

Animal Capture and Measures of Nutritional Condition

Methods associated with data collection, euthanasia, and carcass-processing in the earlier homogenization studies were described by Stephenson et al. (1998, 2002) and Cook et al. (2001*a*, *b*, 2007).

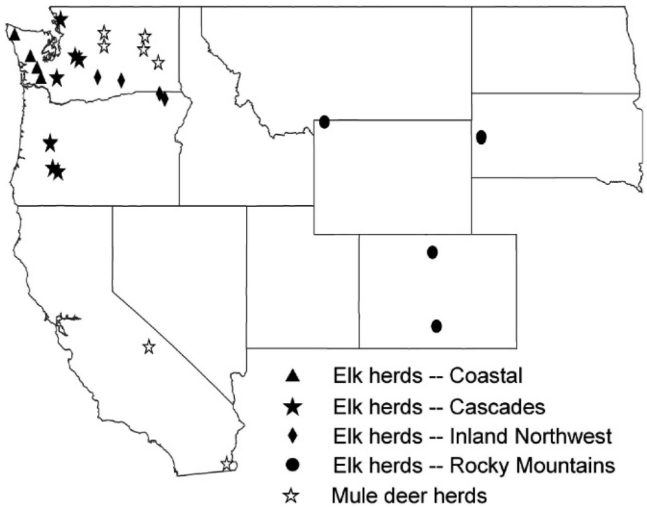

Figure 1. Study areas of 7 mule deer and 19 elk herds in Washington, Oregon, Montana, Colorado, and South Dakota, USA, during 1998 through 2007.

Data from our second data set were collected for a variety of objectives using different methods by various agencies. Briefly, animals were captured using 1 of 4 techniques: 1) helicopter pursuit and chemical immobilization using projectile syringes, 2) helicopter pursuit and net-gunning without chemical constraint (the only capture method for deer), 3) drive capture operations using helicopters, and 4) chemical immobilization with projectile syringes delivered from the ground. For chemical immobilization of elk, we used a cocktail of carfentanil citrate (3.6 mg) and xylazine hydrochloride (100 mg) and reversed anesthesia with naltrexone hydrochloride (360 mg) and either tolazoline hydrochloride (1,000 mg) or yohimbine hydrochloride (25 mg). Generally, we captured animals twice per year, usually in March to early April and November to early December. We fitted each female with telemetry collars at first capture and recaptured collared females subsequently over ≥ 2 years, in a repeated-measures design. However, for 5 of the elk herds, we captured individuals only once. After capture, we obtained mass by weighing via a hanging spring scale or a platform load-cell scale for deer (Detectomatic 11S scale; Detecto Scales, Brooklyn, NY) or by estimating mass using measurements of chest–girth circumference for elk (Cook et al. 2003).

We collected rBCS scores as described for elk by Cook et al. (2001*a*) and mule deer as described by Cook et al. (2007). Two experienced investigators collected rBCS for elk (J. G. Cook and R. C. Cook), whereas multiple individuals with variable training collected rBCS for deer. We collected MAXFAT measurements as described by Stephenson et al. (1998, 2002) and Cook et al. (2001*a*, *b*, 2007) via ultrasonography using either a Sonovet 600, Sonovet 2000 (Universal Medical Systems, Bedford Hills, NY), or an Aloka 210 (Aloka, Wallingford, CT), each equipped with a 5.0-MHz, 7.0-cm probe. We emphasize that methods we used to collect these data from free-ranging animals were identical to those used to collect data from animals used in the original homogenization studies. We then used values of rBCS and MAXFAT to estimate IFBF using regression equations presented by Stephenson et al. (2002) and Cook et al. (2001*a*, 2007) from the homogenization studies. We conducted this research in accordance with approved animal welfare protocol (Starkey Experimental Forest and Range Animal Care and Use Committee Protocol no. 92-F004; Wisdom et al. 1993).

Statistical Analysis

Reanalysis of multispecies homogenization data.—Our primary purpose for combining and reanalyzing nutritional condition data from the earlier studies was to explore the extent to which MAXFAT was robust as an IFBF index across cervid species. We assumed that if the explicit relationship between MAXFAT and IFBF was consistent among cervid species of markedly different body size with appropriate adjustments for size, this relationship should be consistent within cervid species across subspecies and populations and should be consistent between captive and free-ranging animals. Also, if the relation was invariant among species, we argue that MAXFAT adjusted for body size should be a reliable surrogate of IFBF for within-species evaluations of our nutritional condition data sets collected from free-ranging herds.

The first step of our reanalysis of the homogenization data involved scaling MAXFAT measurements to reflect differences in body size. To our knowledge, an allometric scaling equation is unavailable for subcutaneous fat. Based on our observations during processing approximately 100 elk, deer, and moose, deposition of subcutaneous fat spreads from the rump across the upper ribs to the withers and ventrally over the ribs and across the brisket as IFBF increases. Thus, we reasoned that rump fat would scale approximately proportional to surface area (SA), rather than isometrically to body mass ($BM^{1.0}$) or proportionally to metabolic mass (e.g., $BM^{0.75}$; Hudson and White 1986). We found multiple sources for allometric scaling in the literature. Parker (1983) presented an allometric scaling equation for mule deer and elk combined of $SA = 0.139 \times BM^{0.628}$, although the animals primarily included juveniles and subadults. McMahon (1973) presented a general allometric scaling exponent for SA of $BM^{0.625}$ (also see Hudson and White 1985). Additionally, 2 SA (m^2) equations using BM (kg) were presented for large ungulates:

$$SA = 0.142 \times BM^{0.635}, \text{ and} \quad (1)$$

$$SA = 0.150 \times BM^{0.560}. \quad (2)$$

Equation 1 was presented by Moen (1973) and equation 2 was presented by Brody (1964). The scaling exponent of 0.560 was considered more appropriate for large ungulates such as moose and the larger exponent was more appropriate for small ungulates such as deer (Moen 1980).

We compared inter-specific relations between IFBF and MAXFAT formulated 5 ways: 1) MAXFAT unscaled, 2) MAXFAT scaled isometrically with BM (i.e., MAXFAT/$BM^{1.0}$), 3) MAXFAT scaled allometrically with a metabolic rate exponent (i.e., MAXFAT/BM$^{0.75}$), 4) MAXFAT scaled allometrically with an averaged, or overall, SA exponent (e.g., MAXFAT/[0.146 $\times$ BM$^{0.598}$]), and 5) MAXFAT scaled allometrically with SA exponents of 0.560 for moose and elk and the average of the 2 higher values identified above (0.635 and 0.625) for deer. Using the homogenization data for moose, mule deer, and elk (excluding data from all M in the data sets; Stephenson et al. 1998, 2002; Cook et al. 2001*a*, 2007), we tested homogeneity of slopes and intercepts (dependent variable = IFBF; independent variables = MAXFAT, species, MAXFAT $\times$ species) of regression lines among the 3 species using analysis of covariance (ANCOVA) with PROC GLM (SAS Institute 1988). In a second step, we selected the best scaling approach (i.e., the one that provided homogenous slopes and intercepts among species) and recalculated with linear regression new equations that related IFBF to scaled rump-fat thickness (scaledMAXFAT).

Creating ratios of variables, such as dividing MAXFAT by body mass, for nutrition and physiological studies for the purpose of removing effects of body size has been the focus of considerable criticism because such ratios may introduce statistical problems when used as the dependent variable (Packard and Boardman 1988, Raubenheimer 1995, McCoy et al. 2006). We did not use ratios as a dependent variable. However, a second concern is that use of ratios to remove the effect of body size on a physiological trait (e.g., rump-fat thickness) may fail to completely remove the effect if the relation between the physiological trait and body size is allometric. As a check, we conducted a residuals analysis where we regressed scaledMAXFAT (the independent variable) with IFBF (dependent variable), generated residuals to produce IFBF values with the effect of BM^x removed (where x = the scaling coeff. for our best-scaled MAXFAT index), and regressed these IFBF residuals with BM (independent variable). Such an approach would indicate if BM still influenced the relationship between MAXFAT and BM after removing the effect of BM^x. A remaining significant effect of BM, would suggest that our scaled-MAXFAT index was inadequate for our purposes.

Finally, we compared predictions of scaledMAXFAT equations for elk with those from the unscaled MAXFAT approach across substantially different body sizes. The original elk homogenization data set contained many young, small elk (yearlings and 2-yr-olds) such that BM ranged 145–250 kg ($\bar{x}$ = 188 kg). We selected 15 elk from the smallest third of this data range and recalculated 2 equations using this subset, one using the original MAXFAT and the other using our best scaling approach identified as described above (scaledMAXFAT). We then predicted IFBF for all elk, subtracted these predictions from actual IFBF, and evaluated both data sets via regression to identify potential for bias from equations developed with small animals and applied to larger animals within the same species. An appropriately scaled MAXFAT equation should be less prone to bias than the original MAXFAT approach under these circumstances.

Free-ranging elk and deer data.—Without direct measures of IFBF, we evaluated the validity of MAXFAT and rBCS by comparing consistency of the relation between the 2 indices across subspecies and locations (herds) and captive versus free-ranging animals. For this analysis, we could use only data from wild deer and elk with measurable rump fat ($\geq$0.3 cm for elk, $\geq$0.2 cm for deer; Cook et al. 2001*a*, Cook et al. 2007). We then identified the magnitude of bias that might be expected in situations where the relationship between MAXFAT and rBCS showed evidence of inconsistency.

We used a repeated-measures general linear mixed-effects model (PROC MIXED; SAS Institute 1993) to evaluate differences in the relationship between MAXFAT and rBCS among locations (herds) for both deer and elk. The response variable was rBCS and explanatory variables included MAXFAT, location (herd), and third-order polynomials of time. We subtracted from all dates the midpoint of capture dates to reduce co-linearity in polynomial effects for time. We used Akaike's Information Criterion corrected for small sample size (AIC$_c$) to select the best fitting error structure from those deemed biologically appropriate (see Verbeke and Molenberghs 2000). The error structures we considered were simple or variance component, compound symmetry, spatial power, spatial Gaussian, and spatial exponential. We considered spatial covariance structures instead of autoregressive structures (e.g., AR(1) and Toplitz) due to the unequally spaced temporal data (i.e., time between subsequent observations was not equal). We performed model selection by backward stepwise elimination with forward looks. We set the statistical significance required for a variable to enter (alpha-to-enter) and leave (alpha-to-exit) the model to 0.05. To start backwards stepwise selection, we established an initial model that contained MAXFAT, location (herd), third-order polynomials of time, and any interactions with time that we deemed potentially significant (e.g., time $\times$ location). We used multiple comparisons based on a priori hypotheses to identify differences in the relationship between rBCS and MAXFAT among regions (Coastal, Cascades, Inland, Rocky Mountains), subspecies (Roosevelt, Rocky Mountain), and free-ranging versus captive existence given significant overall test results for location (herd).

Estimated BM of adult females varied in our samples (180–280 kg for elk, 40–97 kg for deer), introducing the possibility that variation in the relationship between MAXFAT and rBCS among herds might arise from differences in animal size rather than from differences among populations, subspecies, or captive versus free-ranging existence per se. To test for that possibility, we selected the most appropriate scaling function derived from the multispecies scaling analysis described above (scaled-MAXFAT), scaled all our wild and captive elk and deer data, and reconducted the mixed-models analysis. If scaling MAXFAT accounted for variation among populations, then we expected fewer significant differences in the mixed-models analysis.

Development of new IFBF prediction equations.—The original rLIVINDEX from Cook et al. (2001*a*, *b*, 2007) was an arithmetic combination of rBCS and MAXFAT that was considered superior to either of the 2 indices for elk and deer. The rLIVINDEX = MAXFAT − 0.3 + rBCS when MAXFAT $\geq$0.3 cm (0.2 cm for deer) and rLIVINDEX = rBCS when MAXFAT <0.3 cm (0.2 cm for deer; where 0.3 cm [0.2 cm for deer] represents the point at which rump fat is depleted and measurements reflect fascia thickness). Using the homogenization data (i.e., from Cook et al. 2001*a*, 2007; Stephenson et al. 2002), we created 2 alternate versions of the rLIVINDEX for elk and deer using techniques similar to those used to develop the original rLIVINDEX (we developed no additional moose eqs because no validated BCS scoring system exists for moose). We derived the first alternate version to reduce observer bias of the rBCS (newLIVINDEX). We derived the second alternate version to reduce observer bias of the rBCS and account for bias that might arise due to differences in animal size (scaledLIVINDEX).

Our strategy for reducing observer bias in rBCS was to build a new index (newLIVINDEX) in 3 segments that 1) used only rBCS when no rump fat was present (MAXFAT <0.3 cm for elk and <0.2 cm for deer), 2) combined rBCS and MAXFAT when MAXFAT ranged from $\geq$0.3 cm to <0.4 cm for elk ($\geq$0.2 cm to <0.3 cm for deer), and 3) used only MAXFAT when rump fat $\geq$0.4 cm for elk and $\geq$0.3 cm for deer (Fig. 2). For elk, we used the MAXFAT equation (IFBF = 3.550 × [MAXFAT] + 5.63) from Cook et al. (2001*a*) when MAXFAT $\geq$0.4 cm; we used the rBCS equation (IFBF = 4.478 × [rBCS] − 4.62) from Cook et al. (2001*a*) when MAXFAT <0.3 cm; and we used the average of both Cook et al. (2001*a*) predictions of IFBF when 0.3 cm $\leq$ MAXFAT < 0.4 cm (Appendix A). We used the average when 0.3 cm $\leq$ MAXFAT < 0.4 cm simply because measurement error with ultrasound is more likely to occur when the MAXFAT measurement is at or near 0.3 cm (i.e., when actual rump fat is depleted or nearly so).

We used a similar approach for deer but with 2 differences. First, the thresholds for deer were at 0.2 cm and 0.3 cm (vs. 0.3 cm and 0.4 cm for elk). Second, we recalculated rBCS and MAXFAT equations using data from Cook et al. (2007), excluding the 4 castrated males, and including data from Stephenson et al. (2002). The rBCS equation we used here sans castrates was as follows: IFBF = 3.869 × (rBCS) − 2.71 (r^2 = 0.81, $S_{y \cdot x}$ = 2.133, n = 21, P < 0.001); the MAXFAT equation was as follows: IFBF = 5.596 × (MAXFAT) + 5.98 (r^2 = 0.82, $S_{y \cdot x}$ = 1.568, n = 21, P < 0.001; Appendix A).

This approach provided new index values, in units of IFBF, in 3 segments over the total range of IFBF in our sample. We regressed these new index values with observed IFBF to integrate into one seamless equation across these 3 segments, thereby providing a new model of IFBF for newLIVINDEX (Appendix A).

We derived a second new index (scaledLIVINDEX) to reduce potential for observer bias and to account for bias that might arise due to differences in animal size. We calculated the scaledLIVINDEX in the same manner as the newLIVINDEX except that we used scaledMAXFAT in place of MAXFAT. (In an initial analysis, we were unable to find any evidence that allometric scaling of rBCS improved its relation with IFBF for either species, and we thus limited scaling to MAXFAT in our new versions of LIVINDEX). The variable scaledLIVINDEX also provided new index values in units of percent IFBF in 3 segments, and we again developed an integrated IFBF model by regressing these index values on observed body fat using the homogenization data sets for deer and elk (Appendix A).

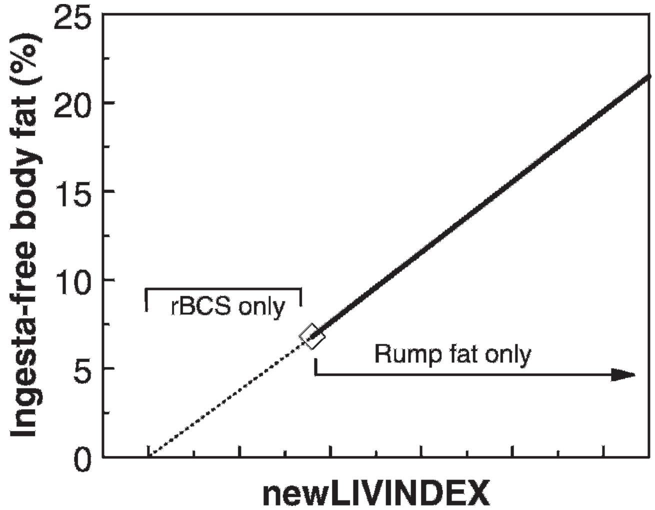

Figure 2. General structure of a new body-fat index for mule deer and elk that reflects 1) only a rump body condition score (rBCS) at levels of condition where no rump fat is present, 2) a combination of rBCS and rump-fat thickness (MAXFAT) when 0.3 $\leq$ MAXFAT < 0.4 (0.2 $\leq$ MAXFAT < 0.3 for deer), and 3) only MAXFAT, when MAXFAT >0.4 (>0.3 for deer). The diamond symbol indicates the point of transition from rBCS- to a MAXFAT-based index across the spectrum of body fat expected for either species. This formulation provides an alternative to the original rLIVINDEX (Cook et al. 2001*a*, 2007) that blended rBCS and MAXFAT indices across the entire range of body fat.

Development of equations to predict BM from girth.—Because scaledMAXFAT and the scaledLIVINDEX requires estimates of BM, which often are unavailable for large ungulates, we generated equations to estimate BM from girth circumference for both mule deer and elk for scaledLIVINDEX. For elk, girth equations presented by Cook et al. (2003) are poorly suited for our purposes because 1) girth equations that required estimates of IFBF to estimate BM introduces a circular argument (i.e., must estimate IFBF for the eq to estimate BM, but here we need to estimate BM to estimate IFBF), and 2) some of the equations were for pregnant elk in spring; mass of the products of conception confounds allometric scaling and, thus, pregnancy-free BM–girth equations would be preferable. We developed a new girth equation for elk from a reanalysis of data from Cook et al. (2003) using yearlings and adults, either nonpregnant or pregnant during their first trimester, with BM ranging 135–267 kg:

$$\begin{aligned} \text{BM} = -193.4 + 2.777 \times (\text{girth circumference [cm]}); \\ (r^2 = 0.77,\ S_{y \cdot x} = 14.193,\ n = 118) \end{aligned} \quad (3)$$

We derived a similar equation (nonpregnant or first trimester pregnant including yearlings, with total range in

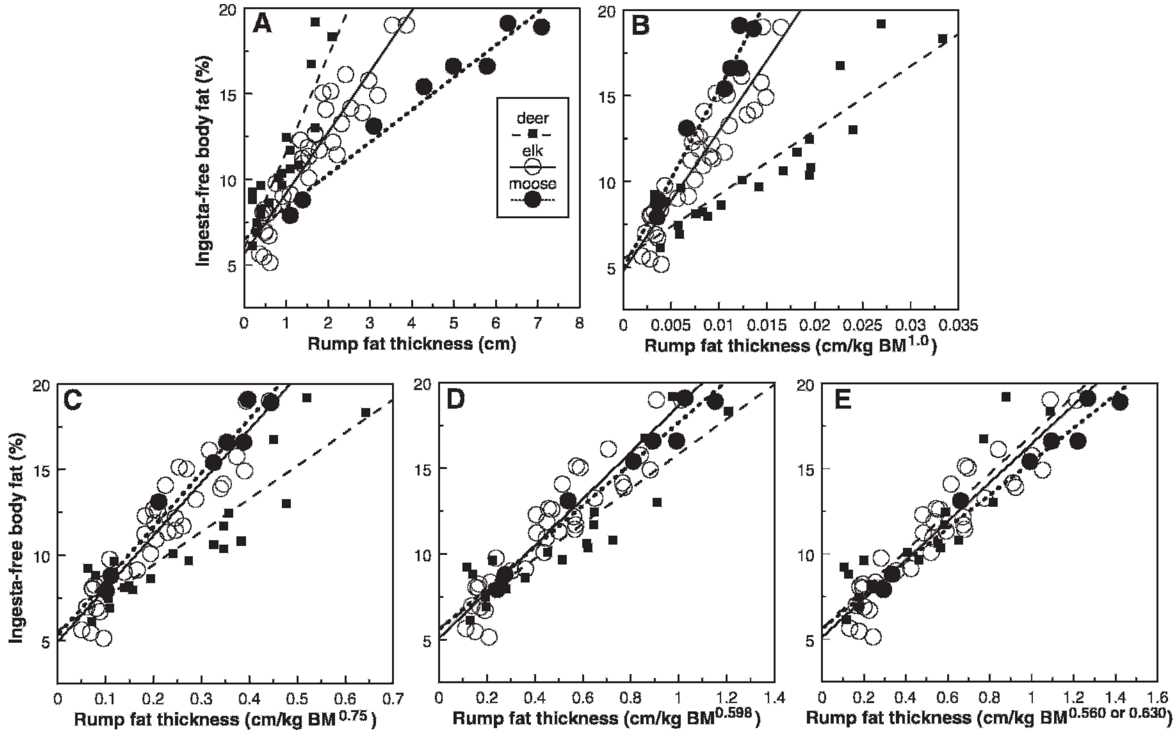

Figure 3. Relations of ingesta-free body fat and rump-fat thickness (MAXFAT) illustrating a progression of scaling to account for differences in body size from (A) original unscaled data, (B) isometric scaling with rump-fat thickness (MAXFAT) divided by body mass (BM), (C) allometric scaling using a classic energy-scaling exponent (i.e., $BM^{0.75}$), (D) allometric scaling using an averaged surface-area scaling function across large and small cervids ($0.146BM^{0.598}$), and (E) an allometric scaling using separate surface-area scaling functions for large ($0.150BM^{0.560}$) and small ($0.142BM^{0.630}$) cervids. Equations and associated statistics for relations in graph E are presented in Table 1. We used homogenization data for elk, collected 1998–1999 from captive females in Oregon, USA (Cook et al. 2001*a*), mule deer, collected 1996–1997 and 2002–2004 from females in Washington, Oregon, and California, USA (Stephenson et al. 2002, Cook et al. 2007), and moose, collected 1993–1995 from captive females in Alaska, USA (Stephenson et al. 1998).

BM = 29–97 kg) for mule deer from the Washington data described above and Cook et al. (2007):

$$BM = -60.8 + 1.292 \times (\text{girth circumference [cm]}); \quad (r^2 = 0.74,\ S_{y \cdot x} = 6.257,\ n = 199) \tag{4}$$

Magnitude of potential bias.—We conducted 2 sets of analyses to evaluate the magnitude of potential bias in the relationship between MAXFAT and rBCS among populations. For the first analysis, we evaluated population-level differences in IFBF estimated using our different models. For each population, we calculated mean estimates of IFBF using 5 indices: 1) original MAXFAT, 2) original rBCS, 3) original rLIVINDEX, 4) scaledMAXFAT, 5) newLIVINDEX, and 6) scaledLIVINDEX. In addition, we subtracted estimates of IFBF derived from each of the approaches from estimates of IFBF from scaledMAXFAT (assuming that the scaledMAXFAT eq is potentially the best predictor of IFBF), estimated means and 95% confidence intervals of IFBF differences among indices, and plotted these for each of the free-ranging herds of the study to identify the magnitude of differences among indices across herds.

To illustrate causes of differences in the relationship between MAXFAT and rBCS, and how our new indices might address these potential biases, we evaluated the change in differences across the range of IFBF represented in our free-ranging animal data (6–19% for elk; 6–21% for deer). For each percentage point of IFBF in the data, we calculated mean estimates of IFBF for all individuals having that level of IFBF using 5 indices: 1) original MAXFAT, 2) original rBCS, 3) original rLIVINDEX, 4) scaledMAXFAT, 5) newLIVINDEX, and 6) scaledLIVINDEX and subtracted them from estimates of IFBF derived from the scaledMAXFAT equation. We plotted means and 95% confidence intervals of IFBF differences among indices by percentage point to illustrate the magnitude of differences among techniques for any given level of condition. We segregated elk data by subspecies (Rocky Mountain vs. Roosevelt) and deer data by region (WA vs. CA). We treated data from animals from the homogenization studies (Cook et al. 2001*a*, 2007) the same and plotted them separately.

RESULTS

Reanalysis of multispecies homogenization data.—Slopes of regression lines between IFBF and MAXFAT diverged markedly among species ($P < 0.001$); the larger the species, the lower IFBF for any given level of MAXFAT (Fig. 3A). The point at which rump fat was depleted corresponded to IFBF of about 6% for each species (i.e., no difference in intercepts, $P = 0.87$).

Scaling rump fat isometrically by dividing MAXFAT by BM only slightly reduced the divergence in slopes among species, and our analysis indicated different slopes ($P < 0.001$) but no difference in intercepts ($P = 0.59$; Fig. 3B).

Table 1. Regression equations of ingesta-free body fat (IFBF [%]) and allometrically scaled rump-fat thickness (scaledMAXFAT in cm) for mule deer, elk, and moose and for all 3 species combined. For elk and moose, scaledMAXFAT = MAXFAT/0.150BM$^{0.560}$; for mule deer, scaledMAXFAT = MAXFAT/ 0.142 BM$^{0.630}$, where MAXFAT is maximum rump-fat thickness (cm) and BM is body mass (kg). We used homogenization data for elk collected 1998–1999 from captive females in Oregon, USA (Cook et al. 2001*a*); for mule deer collected 1996–1997 and 2002–2004 from females in Washington, Oregon, and California, USA (Stephenson et al. 2002, Cook et al. 2007); and for moose collected 1993–1995 from captive females in Alaska, USA (Stephenson et al. 1998).

Application	Eq	r^2	$S_{y\cdot x}$	*n*	*P*
Combined eq[a]	IFBF = 5.61 + 10.54 × (scaledMAXFAT)	0.87	1.38	64	<0.001
Mule deer[b]	IFBF = 5.63 + 11.35 × (scaledMAXFAT)	0.82	1.58	21	<0.001
Elk	IFBF = 5.10 + 11.35 × (scaledMAXFAT)	0.87	1.31	35	<0.001
Moose[c]	IFBF = 5.63 + 9.78 × (scaledMAXFAT)	0.97	0.81	8	<0.001

[a] Eq developed using data values for elk, deer, and moose.
[b] We excluded from these deer eqs data from 4 castrated M originally included by Cook et al. (2007).
[c] No body mass estimates were available for 2 moose originally used in this data set and we removed the remaining M sample; thus, our $n = 8$ vs. $n = 11$ presented by Stephenson et al. (1998) for the original data.

Scaling rump fat allometrically by dividing rump fat by metabolic mass (BM$^{0.75}$) resulted in close alignment between moose and elk but not deer (Fig. 3C). Slopes remained heterogeneous ($P < 0.001$) and intercepts remained similar ($P = 0.65$) among species. Scaling rump fat using SA exponents largely eliminated differences among species (Fig. 3D, E), although the averaged SA scaling equation still resulted in heterogeneous slopes ($P = 0.041$; but similar intercepts, $P = 0.69$).

However, using different scaling functions for small and large cervids as suggested by Moen (1980) effectively converged the slope coefficients (Fig. 3E). With this approach, we found no evidence that intercepts ($P = 0.75$) or slopes ($P = 0.51$) differed among the 3 species. We considered this scaling approach using the 2 different scaling functions (Fig. 3E) to be the best overall index of IFBF for subsequent analyses, and we used this as our scaledMAXFAT index (Table 1). For this best index, we found no relation between IFBF residuals and BM ($P = 0.12$), indicating that this scaling approach effectively removed effects of BM on the relation between IFBF and MAXFAT.

With an unscaled MAXFAT and scaled MAXFAT pair of linear equations developed for the smallest 15 elk in the homogenization sample, the unscaled MAXFAT equation significantly overestimated IFBF of the larger animals up to 4 percentage points, whereas there was no evidence that the scaled MAXFAT equation was biased (Fig. 4A, B). Because the sample of captive elk from Cook et al. (2001*a*) included many young and small animals, our analysis suggests that some bias might result from applying the original MAXFAT equations where wild elk are substantially larger.

Free-ranging deer and elk data.—From 1998 to 2006, we captured 2,665 free-ranging female elk. Of these, 49% had no measurable rump fat, and MAXFAT or rBCS measurements were missing for a few, leaving 1,306 samples available for our analyses (815 unique individuals). From 2001 to 2007, we captured 907 free-ranging female mule deer. Of these, 51.5% had no measurable rump fat, and MAXFAT or rBCS measurements were missing for a few, leaving 438 samples available for our analysis (250 unique individuals).

The final repeated-measures mixed-effects model selected for both deer and elk included the variables MAXFAT, time, location, location × MAXFAT, and time × location. For elk, a MAXFAT × location interaction ($P < 0.001$) indicated that the relationship between MAXFAT and rBCS changed among locations (herds). Rerunning this analysis using scaledMAXFAT in place of the original MAXFAT produced similar results ($P < 0.001$), indicating that scaling MAXFAT failed to eliminate differences among elk herds. Location (herds) was not significant for deer using either the original MAXFAT data ($P = 0.354$) or the scaledMAXFAT data ($P = 0.054$).

Given the global insignificant result of the general linear mixed-effects model, we did not test contrasts for deer. In elk, we found no difference in wild versus captive animals ($P = 0.301$) but within wild elk, we found an overall regional effect ($P = 0.013$). We found no differences among any of the regions populated by the Rocky Mountain subspecies (Cascades vs. Inland, Cascades vs. Rocky Mountains, Rocky Mountains vs. Inland; $P \geq 0.249$). However, the relationship between MAXFAT and rBCS differed between Roosevelt elk in the coastal region of our study and Rocky Mountain elk overall ($P = 0.001$) and between Roosevelt elk and each region of our study populated with the Rocky Mountain subspecies (Coastal vs. Cascades, Coastal vs. Inland, Coastal vs. Rocky Mountains; $P \leq 0.031$). Scaling MAXFAT did not change these general results. However, slope coefficients of the relationship between scaledMAXFAT and rBCS were up to 60% steeper on average for herds with thin elk versus those with fat elk, indicating an important bias associated with estimating rBCS (Fig. 5; assuming scaledMAXFAT provides unbiased estimates of IFBF).

Development of new IFBF equations.—For both elk and deer, the newLIVINDEX equation, unscaled with respect to BM but adjusted for rBCS bias, resulted in slightly higher coefficients of determination (2–4%) and lower standard errors compared to the original rLIVINDEX equations (Fig. 6), but our point for creating the new variables was to make them more robust among observers and field conditions. For elk, the new equation seemed slightly less curvilinear at low levels of condition than was the original rLIVINDEX. For deer, the new equation seemed to reduce deviations from the regression line of 2 or 3 of the fattest deer in the sample. Our scaledLIVINDEX provided

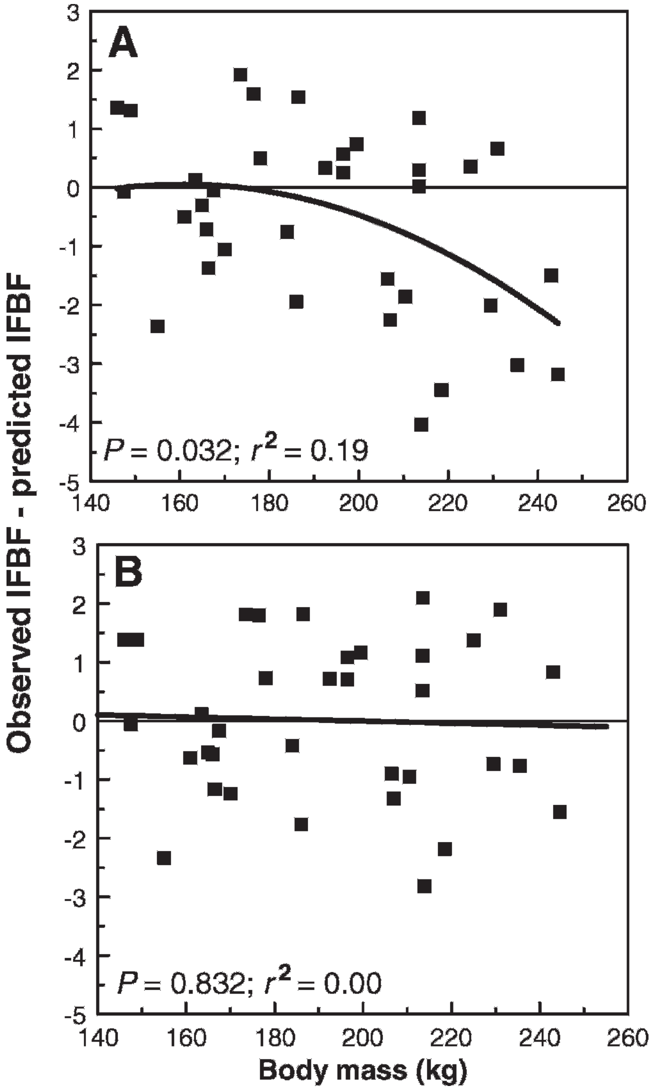

Figure 4. Differences between observed (actual) ingesta-free body fat (IFBF) and predicted IFBF using 2 prediction equations. The equations were built with rump-fat thickness data (MAXFAT) collected only from the smallest 33% of elk (range in body mass= 143–185 kg) to predict IFBF of all elk using either 1) the original unscaled MAXFAT data (IFBF = 4.45 + 4.74 × [MAXFAT]) in graph A, and 2) the new allometrically scaled MAXFAT data (IFBF = 4.36 + 12.680 × [scaledMAXFAT]) in graph B, where scaledMAXFAT = MAXFAT/0.150(body mass)$^{0.560}$. Data were collected by Cook et al. (2001*a*) 1998–1999 from captive females in Oregon, USA. These analyses indicate that the equation unscaled with respect to body mass increasingly overestimated IFBF as body mass increased whereas the scaled equation exhibited no tendency for this bias.

coefficients of determination and standard errors that were virtually identical to the unscaled newLIVINDEX equations (Fig. 6).

Magnitude of potential bias.—Using the scaledMAXFAT equation (Table 1) as a surrogate to true IFBF for elk at the population level, we found the greatest error among indices for estimating IFBF (i.e., scaledMAXFAT vs. rBCS, MAXFAT, rLIVINDEX, newLIVINDEX, and scaledLIVINDEX) generally was due to rBCS (Fig. 7A). Maximum extent of error for any single herd using rBCS was 1.7 percentage points of IFBF compared to 0.8, 1.0, 0.8, and 0.2 for MAXFAT, rLIVINDEX, newLIVINDEX, and scaledLIVINDEX, respectively (Fig. 7B). Typically, all indices except scaledLIVINDEX overestimated IFBF relative to scaledMAXFAT.

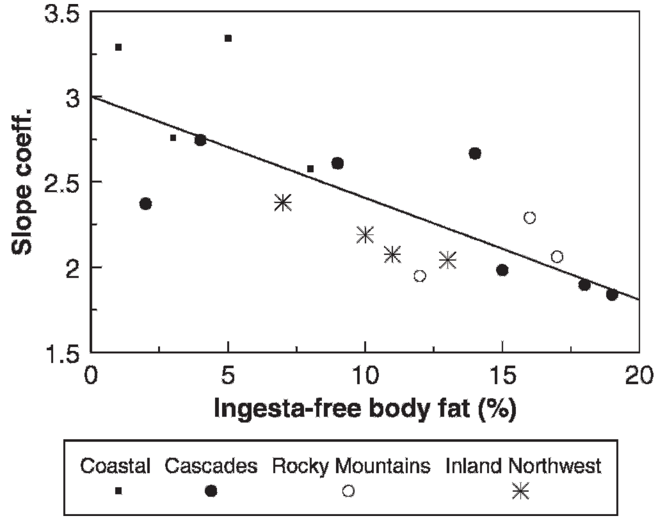

Figure 5. Within-herd slope coefficients for the relationship between the allometrically scaled rump-fat thickness (scaledMAXFAT) and rump body condition score (rBCS) plotted with mean (herd-level) ingesta-free body fat in female elk. Slope coefficients were from 19 wild populations, sampled 1998 to 2006, in Washington, Oregon, Colorado, Wyoming, and South Dakota, USA, which we grouped into 4 geographic regions for analysis.

For deer, at the population level, maximum error associated with using rBCS was substantially greater than the other indices (3.2, 1.0, 1.0, 1.0, and 0.2 percentage points of IFBF for rBCS, MAXFAT, rLIVINDEX, newLIVINDEX, and scaledLIVINDEX, respectively; Fig. 7A, B). Typically, all indices except the new scaledLIVINDEX overestimated IFBF relative to scaledMAXFAT for Washington mule deer, which was probably a result of both rBCS scoring error and the tendency for Washington deer to be heavier and physically larger than the other deer in our sample. For California mule deer, rBCS or those indices that incorporated rBCS (rLIVINDEX) tended to overestimate IFBF; those indices using unscaled rump-fat measurements (MAXFAT, newLIVINDEX) tended to underestimate IFBF because these females were lighter and smaller than other deer in our sample.

There was a slight overestimation bias of IFBF using rBCS at low levels of condition for deer, and, in elk, rBCS consistently underestimated IFBF at high levels of condition (by up to 5 percentage points of IFBF; Fig. 8A). For fatter deer, bias tended to be substantially more erratic as condition increased (Fig. 8B), suggesting increasing observer error especially in those animals with >10% IFBF. For both species, the magnitude of error for the original MAXFAT and rLIVINDEX indices across virtually all levels of nutritional condition was low, and a consistent trend in bias was weak or nonexistent (Fig. 8C, D, E, F). Patterns of error with the newLIVINDEX mirror that of the original MAXFAT (compare Fig. 8D, H), whereas the scaledLIVINDEX eliminated virtually all apparent bias (Fig. 8I, J).

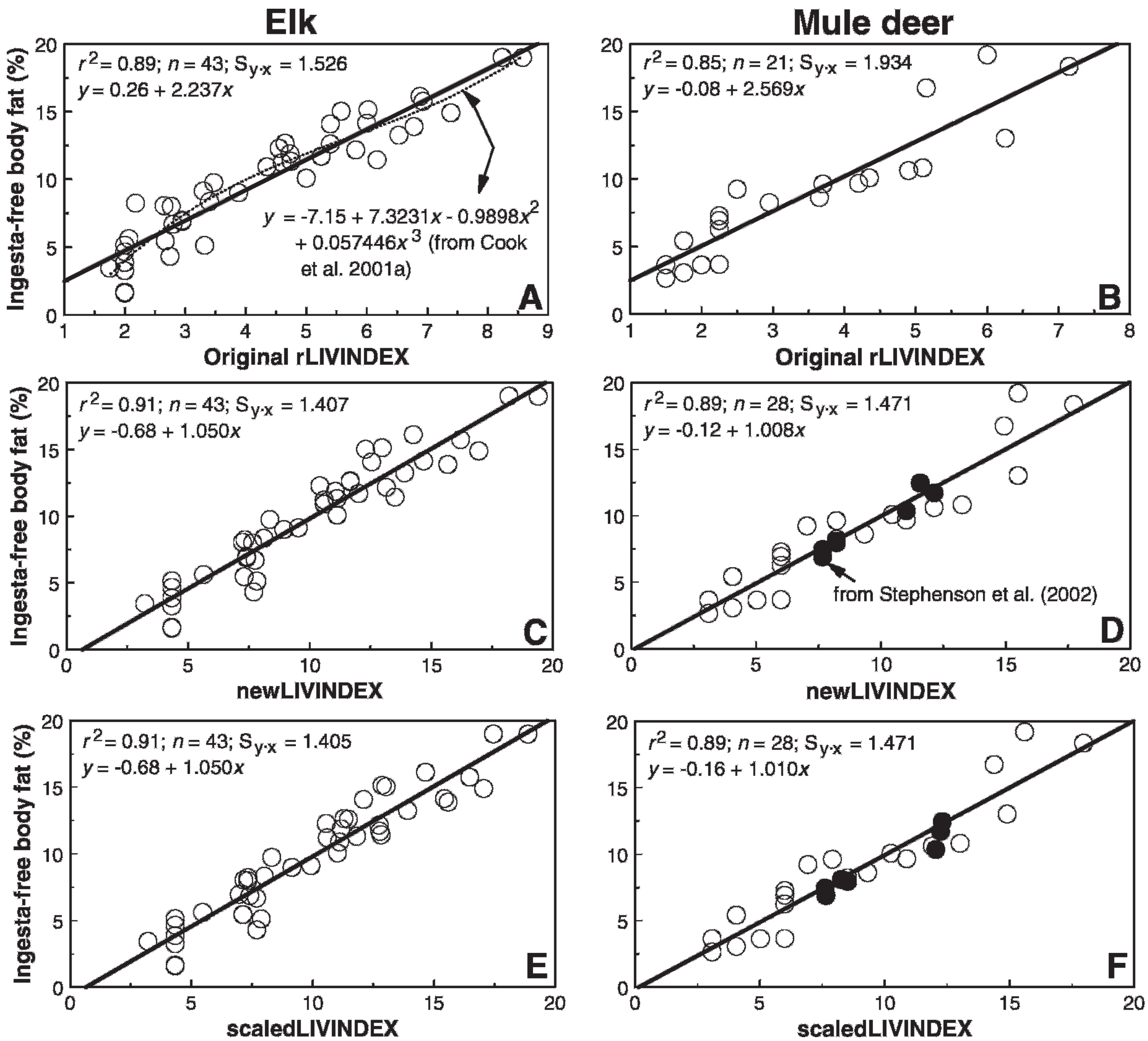

Figure 6. Relationships of indices of nutritional condition and ingesta-free body fat for female elk and mule deer. We used homogenization data for elk collected 1998–1999 from captive females in Oregon, USA (Cook et al. 2001*a*) and mule deer collected 1996–1997 and 2002–2004 in Washington, Oregon, and California, USA (Stephenson et al. 2002, Cook et al. 2007). Graphs A and B present relations originally described by Cook et al. (2001*a*, 2007). Graphs C and D present relations for an alternative index (newLIVINDEX) where 1) only rump body condition (rBCS) is used to predict condition when rump-fat thickness (MAXFAT) is depleted, 2) combines the 2 indices at low levels of MAXFAT, and 3) uses only MAXFAT at moderate and high levels of rump fat. Graphs E and F present relations for a second alternative index (scaledLIVINDEX) constructed as described for graphs C and D, except that MAXFAT is scaled allometrically to body mass using equations presented in Table 1. Data depicted by dark circles are from Stephenson et al. (2002) and were unused for development of equations previously by Cook et al. (2007).

DISCUSSION

Direct measurements of IFBF obtained via homogenization would provide the best standard to evaluate how accuracy and bias differ among indices of nutritional condition across subspecies, populations, between wild versus captive animals, and across varying environmental conditions. Such data would have been prohibitively difficult and expensive to obtain for our study, and therefore, we required a reliable alternative measure of IFBF. Our allometrically scaled MAXFAT index was robust from the smallest deer (38 kg) across all sizes of elk (139–253 kg) to the largest moose (522 kg) in our sample. Given its ability to predict IFBF among individuals across species (r^2 = 0.87), this index should predict at least as well among individuals within species.

However, creating ratios to remove effects of body size from an anatomical variable such as MAXFAT sometimes is not effective (Packard and Boardman 1988, Raubenheimer 1995, McCoy et al. 2006), although our residuals analysis indicated that it was effective in this particular case. Convergence of slopes among the 3 ungulate species indicated the scaling exponents for SA were effective surrogates for scaling rump-fat thickness. Based on subcutaneous fat deposition we observed in processing the 25 deer, 49 elk, and 10 moose carcasses in the original homogenization studies, subcutaneous fat normally occurs only near the top of the rump and the brisket in moderately thin animals. As total body fat and MAXFAT increase, subcutaneous fat spreads forward from the rump toward the withers, ventrally across the rump and ribs, and from the brisket caudally across the abdomen. Thus, our analyses

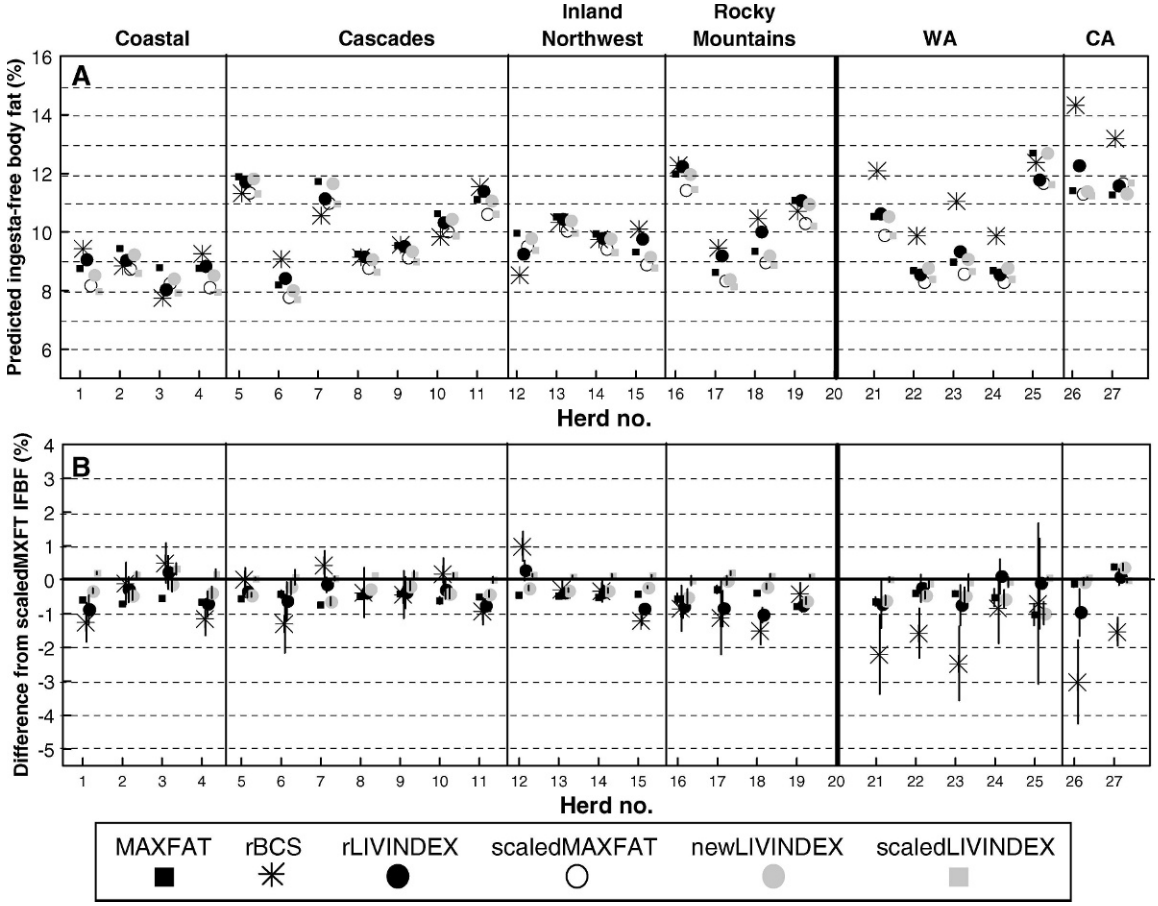

Figure 7. (A) Ingesta-free body fat (IFBF) values generated from 6 indices: original rump-fat thickness (MAXFAT); rump body condition scores (rBCS); original rLIVINDEX; allometrically scaled rump-fat thickness (scaledMAXFAT); unscaled newLIVINDEX; and scaledLIVINDEX. (B) Difference plus 95% confidence intervals in predicting ingesta-free body fat of MAXFAT, rump BCS, rLIVINDEX, newLIVINDEX, and scaledLIVINDEX from values obtained using scaledMAXFAT. Negative values indicate an overestimation of IFBF; positive values indicate an underestimation of IFBF. For both graphs, points are herd averages and separated by region and by species. Data for herds 1–19 were from 19 elk populations in Washington, Oregon, Colorado, Wyoming, and South Dakota, USA, 1998–2006, and data for herds 21–27 were from 7 mule deer populations in California and Washington, USA, 2001–2007.

support our observation that as MAXFAT increases, amount of subcutaneous fat correspondingly increases in proportion to SA of the animal. As an informal exercise, we iteratively stepped up and stepped down at 0.01 intervals the allometric exponents (i.e., from 0.63 for deer and 0.56 for elk and moose) and reran the ANCOVA each time. No combination of allometric scaling coefficients improved the relation to any substantive degree, and most worsened the relation markedly. All-in-all, we considered that scaled-MAXFAT provided a suitable alternative to directly measured IFBF for evaluating robustness of live animal indices across regions, populations, and subspecies.

We identified a herd (location) effect for elk on the relationship between MAXFAT and rBCS. This herd effect ostensibly was a function of some unidentified anatomical difference(s) between Roosevelt and Rocky Mountain elk that, at first glance, suggests that either the MAXFAT or rBCS or both varied in ability to predict body condition accurately between the 2 subspecies. Substituting scaled-MAXFAT did not change the mixed-models results as we postulated it may, suggesting that the location effect was unrelated to body size differences across subspecies. Thus, either the specific relationship between MAXFAT and rBCS changes due to variation in some fundamental difference in animals among herds, or at least between subspecies, or there were errors in application of rBCS.

Significant differences between elk subspecies evident in the repeated-measures mixed-effects model contrasts arose primarily from underestimation bias of rBCS on elk >12% IFBF (Fig. 8A). This trend produced different relationships between MAXFAT and rBCS among herds with higher IFBF versus those with lower IFBF. The more animals in high condition within a herd, the shallower the slope of the relationship between MAXFAT and rBCS (Fig. 5). Few fat elk existed in our Roosevelt herds (i.e., virtually none had >13% IFBF) compared to most herds of the Rocky Mountain subspecies. At least some of the rBCS bias was related to an upper limit of rBCS at high levels of condition (i.e., an elk with 2 cm of rump fat often would receive the same rBCS score as an elk with 4 cm of rump fat).

For deer, the repeated-measures ANOVA showed no location (herd) effect. The deer rBCS was originally

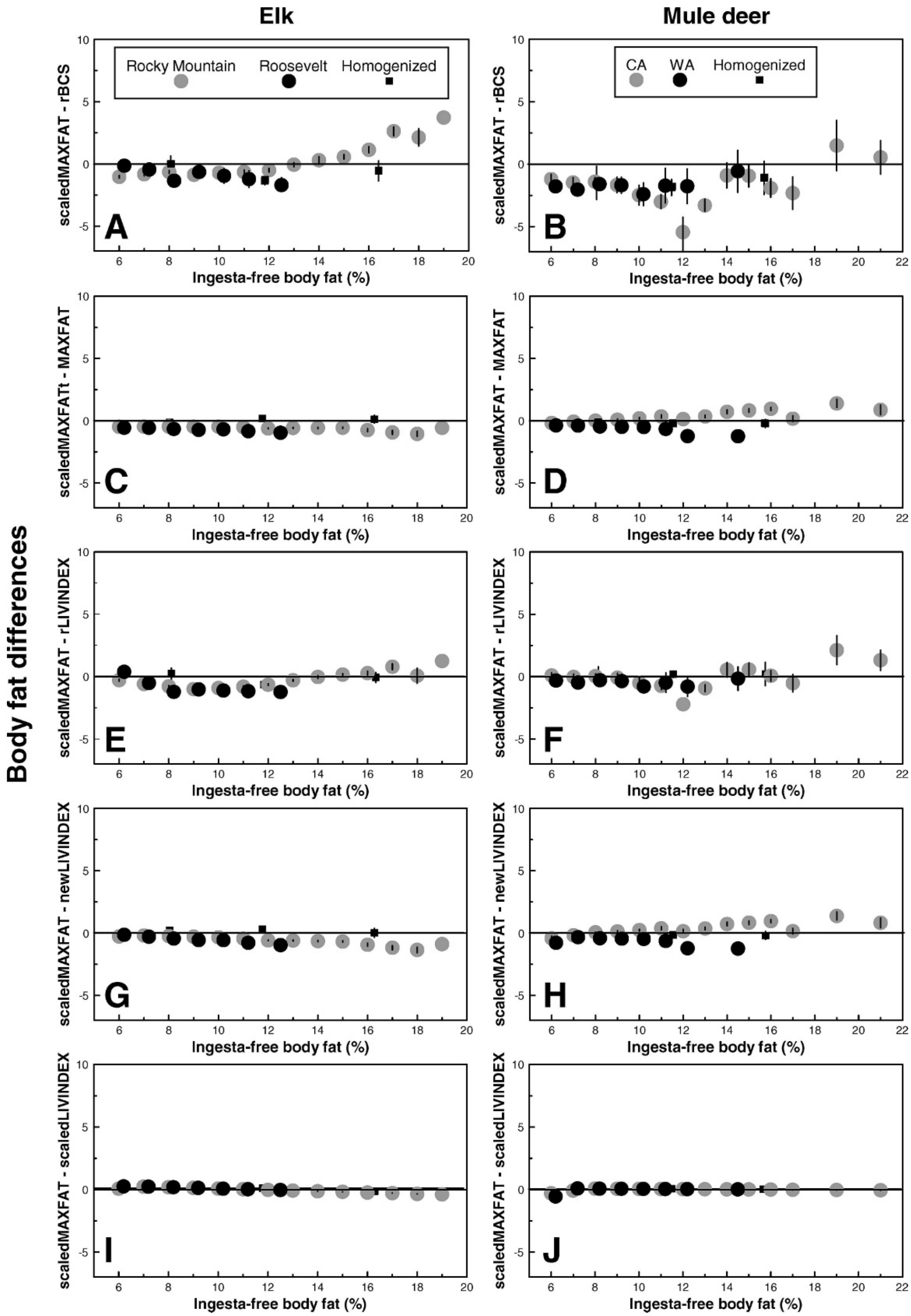

Figure 8. Difference in estimated ingesta-free body fat (IFBF) derived from the allometrically scaled rump-fat thickness index (scaledMAXFAT) and estimated ingesta-free body fat derived from 5 other indices (rBCS [graphs A, B], unscaled MAXFAT [graphs C, D], original rLIVINDEX [graphs E, F], newLIVINDEX [graphs G, H], and scaledLIVINDEX [graphs I, J]) across different levels of IFBF, on the *x*-axes, derived using the scaledMAXFAT index. We used elk data, grouped by Roosevelt and Rocky Mountain subspecies, from 19 populations in Washington, Oregon, Colorado, Wyoming, and South Dakota, USA, 1998–2006, and data from 7 mule deer populations, grouped by region (WA and OR, USA), 2001–2007. For both species, data from homogenization studies (Cook et al. [2001*a*] 1998–1999 and Cook et al. [2007] 1996–1997 and 2002–2004) are included separately. Vertical bars are 95% confidence intervals. These data illustrate that the magnitude of bias for several of the indices tends to vary across different levels of IFBF.

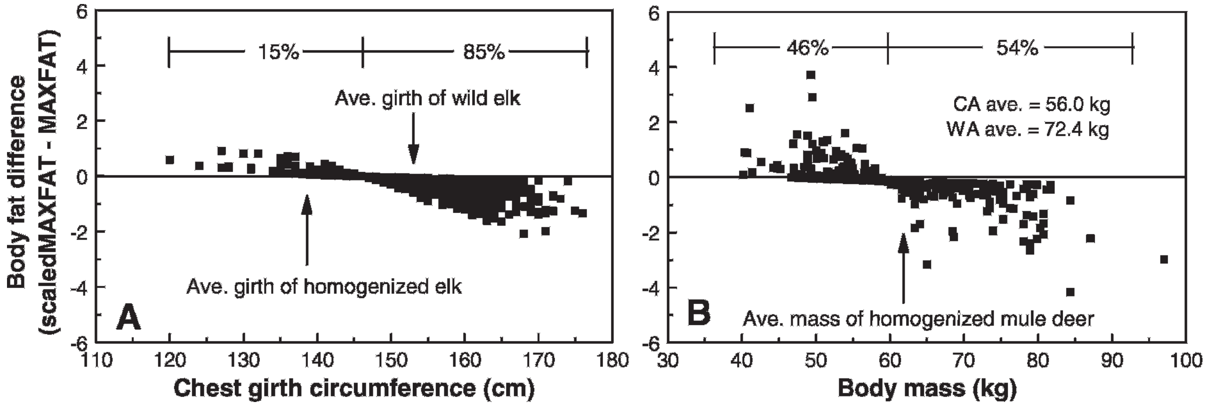

Figure 9. Differences in estimated ingesta-free body fat using unscaled rump-fat thickness (MAXFAT) versus allometrically scaled rump-fat thickness (scaledMAXFAT) across a range of body size in elk (A) and mule deer (B). We used data collected from adult females in 19 elk populations in Washington, Oregon, Colorado, Wyoming, and South Dakota, USA, 1998–2006, and 7 mule deer populations in California and Washington, 1998–2007. These graphs provide a visual representation of the value of scaling the original MAXFAT measurement. Above or below approximately 146-cm girth circumference (about 212 kg), bias in predicting ingesta-free body fat in elk occurs due to differences in body size. Above or below approximately 60 kg in deer, bias in predicting ingesta-free body fat occurs.

developed with a broader scale (0–6 vs. 1–5) to reduce underscoring of well-conditioned animals (Cook et al. 2007). Although this broader scale probably helped keep the relationship of MAXFAT with rBCS more consistent in deer than in elk (i.e., little evidence of strong overestimation of IFBF at high levels of condition [Fig. 8B]), we caution against concluding that the rBCS worked better for deer than elk. Finding an insignificant result from the mixed-models analysis may have resulted from substantially lower sample sizes and, probably more importantly, erratic rBCS scoring in the deer data, particularly above about 9% IFBF (Figs. 7B, 8B). The latter would increase variation in the relationship between MAXFAT and rBCS and reduce chances of finding a significant difference. Only 2 observers collected rBCS data from elk, and each developed the original score and had many years of experience. In contrast, the deer data originated from multiple scorers with little to extensive experience.

The potential for observer bias to reduce the value of the rBCS and accuracy of the original rLIVINDEX, particularly as a function of inadequate training, has been noted previously by Cook et al. (2001*a*, 2007). The homogenization studies on elk and deer show that rBCS can be an accurate predictor of IFBF if collected by experienced observers. However, our experience has shown that rarely do biologists get adequate training and handle enough animals to become precise with scoring techniques. Our results here underscore this concern; thus, it might be tempting to drop rBCS entirely as a condition index. However, our data from large samples of wild deer and elk indicate the MAXFAT index is sufficient for only about half the elk and mule deer that biologists encounter in the wild (most animals encountered during late winter and early spring possess little to no subcutaneous fat). This deficiency of the MAXFAT index presents a greater challenge to measuring IFBF accurately in free-ranging deer and elk than does the scoring error associated with rBCS taken by experienced observers at low to moderate levels of IFBF. Thus, we opted to develop a new LIVINDEX that only uses rBCS to provide data in the range where MAXFAT does not apply (Fig. 2). Results of stringent tests (Cook et al. 2001*a*, *b*, 2007) illustrated that rBCS is more accurate and sensitive at low levels of IFBF because skeletal features, a key criteria used for rBCS, are more detectable. Hence, the use of rBCS remains justified for animals with little or no subcutaneous fat.

Although the newLIVINDEX resolves much of the error and bias associated with rBCS, it does not address effects of body size on estimates of IFBF. It stands to reason that if scaling MAXFAT makes it a robust index across species of cervids varying in body size, it should also reduce bias across the extremes of BM within species. For wild elk, the original MAXFAT equation tended to overestimate IFBF due to larger BM of the wild elk than those in the original homogenization study (Fig. 8C). In fact, 85% of elk in the wild elk data set were large enough that some overestimation of IFBF would be expected (Fig. 9A), largely because the original MAXFAT equation was developed using a high proportion of young and, thus, relatively small elk (Cook et al. 2001*a*).

For deer, addressing bias associated with body size may be more important because the effect of allometric scaling is greater in smaller animals. For example, failure to scale results in over- or underestimation up to 4 percentage points of IFBF in deer (Fig. 9B), about double that of elk (Fig. 9A), a magnitude of bias with potentially substantial biological significance. For instance, female deer in California evidently were smaller than deer in Washington (Fig. 9B), and so the original MAXFAT index tended to underestimate IFBF in California deer and overestimate IFBF in Washington deer (Fig. 8D).

We also considered and rejected scaling rBCS. Our exploratory attempts to scale rBCS using both deer and elk homogenization data, much as we did for MAXFAT, worsened the relationship between rBCS and IFBF. Body condition scoring is a palpation technique that tends to adjust for differences in animal size (e.g., rBCS of a small animal with 1 cm of MAXFAT will exceed the rBCS for a large animal with 1 cm of MAXFAT). This higher rBCS = a higher IFBF estimate, thereby automatically adjusting for body size.

We caution that although the scaledLIVINDEX improves IFBF estimates, either BM or girth circumference must be measured to use this variable. The potential gain in accuracy or robustness offered by the scaledLIVINDEX equation may be offset with losses via this new source of measurement error. Errors of estimates of BM may result from changes in gut fill, changes due to pregnancy, or errors of measurement. Measurement errors (e.g., inadequately tightening the measuring tape [Cook et al. 2003]) or effects of pregnancy are more relevant to variation in estimates of BM than errors resulting from gut fill change. For example, increasing (or decreasing) daily food intake 50% will change BM by about 3% (e.g., increasing BM of a 225-kg F elk to 232 kg [Cook et al. 1998]), which would result in a difference in estimated IFBF using the scaledMAXFAT equation of only 0.06%. In contrast, mass of products of conception as early as mid-February is about 10 kg in elk ($n = 4$; J. Cook and R. Cook, National Council for Air and Stream Improvement, unpublished data) and increases rapidly thereafter. Also, a 10-cm error in measuring girth circumference (a level of error that, in our experience, does occur, usually because the tape measure is held too loosely) = 28 kg error in BM.

Variation in the amount of error and bias among techniques brings up 2 issues: 1) validity of previously published results using the original indices (rLIVINDEX, MAXFAT, and rBCS), and 2) selection of the most accurate methods for use in the future. Our analyses suggest that conclusions are probably robust from previous elk studies using rLIVINDEX or MAXFAT where rBCS and MAXFAT were estimated by experienced biologists (Cook et al. 2004*a*, *b*; Bender et al. 2006; Evans et al. 2006) because estimates at the population or individual level should be within ±1 percentage point (Fig. 7). This was also true for rLIVINDEX estimates at the population level in deer, despite the erratic rBCS scoring (Fig. 7). However, our results for deer suggest effects of erratic scoring or body size bias may have greater implications for studies involving sequential measurements taken on individual animals (e.g., the original MAXFAT index resulted in error up to ±4 percentage points of IFBF; Fig 9B). To our knowledge, no such individual animal analyses have yet been published in peer-reviewed outlets for deer.

For future work, biologists should consider the amount of error or bias we found for the different indices before selecting among them (see Fig. 7 and Fig. 9). Based on these figures, we recommend that biologists avoid using the original rBCS as the sole index. Also, we see no reason to continue using the original rLIVINDEX. In elk, the decision to use newLIVINDEX or scaledLIVINDEX depends on the cost and logistics of collecting accurate BM data. If estimates of BM are unavailable or unreliable, newLIVINDEX will resolve rBCS bias in fatter animals. If accurate estimates of BM are available, we recommend the scaledLIVINDEX over newLIVINDEX to account for wide ranges in animal size, although in most herds a small overestimation bias of <1 percentage point of IFBF should be expected. If all animals have measurable rump fat, then the equation for MAXFAT (Appendices B, C) or scaledMAXFAT (Appendices B, C) in place of newLIVINDEX and scaledLIVINDEX would be appropriate. Potential for biasing estimates of IFBF, due to variation in BM, is greater for deer than elk (Fig. 9B). Thus, we strongly recommend using scaledLIVINDEX or scaledMAXFAT for deer. We present steps for calculating the newLIVINDEX and scaledLIVINDEX for deer and elk, with alternative versions that accept girth-based estimates of BM (Appendix A), as well as equations for predicting IFBF (Appendices B, C).

Finally, our evaluation of the rBCS and rump-fat techniques revealed bias previously unreported, and we provide new equations that help ameliorate this concern. Past concerns particularly regarding adequate training still persist, however, and, although not a focus herein, we reemphasize that ultrasound measurements of MAXFAT are just as prone to error as rBCS. Despite the new equations presented here, the LIVINDEX approach is not user-friendly, and its use by untrained workers can and does produce large errors that are misleading and can confound scientific advances in nutritional ecology (see Cook et al. 2007). Biologists contemplating using these techniques should not underestimate the crucial need for adequate training and experience.

MANAGEMENT IMPLICATIONS

Managers of ungulate populations typically are challenged with maintaining viable populations and providing a harvestable surplus to support hunter recreation. Thus, understanding how nutrition contributes to population demographics and habitat contributes to healthy, well-nourished populations is important at both local and regional levels. Declines in large ungulate populations include bighorn sheep (Wakelyn 1987), woodland caribou (Thomas and Gray 2002), mule deer (Carpenter 1998), and elk (Johnson et al. 2004). The economic ramifications and controversy instigated by the declines highlight the need for clarifying nutrition's contributions to herbivore populations.

Estimates of nutritional condition provide key insights of nutrition's influences on populations and habitat's influences on nutrition, but how best to obtain accurate and reliable measures of nutritional condition for routine management is poorly defined. Testing described here and previous tests of the rBCS and rump-fat indices (e.g., Stephenson et al. 1998, 2002; Cook et al. 2001*a*, 2007) help improve new tools superior to those previously available. The techniques help open the door to a variety of sampling designs useful for evaluating influences of habitat on populations and feedbacks between herbivores and vegetation. Perhaps foremost among these is an initial screening to evaluate the need for detailed nutritional evaluations or for monitoring long-term trends. Live-animal indices may be particularly useful for monitoring wherever hunting restrictions preclude access to dead animals. Live-animal indices lend themselves to repeated measures or before-and-after studies to directly assess effects of treatments and contribute understanding of top-down versus bottom-up influences, predisposition to predation and starvation, and influences of seasons, weather, and a variety of habitat conditions.

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Appendix A. Calculating unscaled and scaled new LIVINDEXs for elk and deer.

Acronym Definitions

BM = body mass (kg)

PM = mass of the products of conception (kg): ignore if in first trimester through early second trimester (i.e., through about mid-Jan). For elk, assume equal to 9.7 kg during mid-second trimester (9.7 kg was mean PM of 4 pregnant wild F elk sacrificed in mid-Feb as described by Cook et al. [2001*a*]). We have no empirical data of PM for elk after early March nor any PM data for mule deer. (Note: if using the girth eq provided here, the eqs are set up to exclude PM and, thus, the PM term is excluded from calculating the indices; see below).

MAXFAT = thickness of the rump-fat layer (cm; Stephenson et al. 1998, Cook et al. 2001*a*)

rBCS = rump body condition score (Cook 2001; Cook et al. 2001*a*, 2007)

scaledMAXFAT = MAXFAT scaled allometrically based on surface-area scaling functionsgirth = girth circumference (cm) measured as described by Cook et al. (2003).

Elk

1. newLIVINDEX (unscaled)
   - Step 1. If MAXFAT <0.3, then newLIVINDEX = $4.478 \times (\text{rBCS}) - 4.62$.
   - Step 2. If MAXFAT ≥ 0.4, then newLIVINDEX = $3.550 \times (\text{MAXFAT}) + 5.63$.
   - Step 3. If $0.3 \leq$ MAXFAT <0.4, then newLIVINDEX = $\{[4.478 \times (\text{rBCS}) - 4.62] + [3.550 \times (\text{MAXFAT}) + 5.63]\}/2$.
   - Step 4. Calculate ingesta-free body fat (IFBF) = $-0.68 + 1.050 \times (\text{newLIVINDEX})$
2. scaledLIVINDEX (scaled, where BM is estimated by weighing)
   - Step 1. Calculate scaledMAXFAT = $\text{MAXFAT}/\{0.150 \times [(\text{BM} - \text{PM})^{0.560}]\}$.
   - Step 2. If MAXFAT <0.3, then scaledLIVINDEX = $4.478 \times (\text{rBCS}) - 4.62$.
   - Step 3. If MAXFAT ≥ 0.4, then scaledLIVINDEX = $11.350 \times (\text{scaledMAXFAT}) + 5.10$.
   - Step 4. If $0.3 \leq$ MAXFAT <0.4, then newLIVINDEX = $\{[4.478 \times (\text{rBCS}) - 4.62] + [11.350 \times (\text{scaledMAXFAT}) + 5.10]\}/2$.
   - Step 5. Calculate IFBF = $-0.68 + 1.050 \times (\text{scaledLIVINDEX})$
3. scaledLIVINDEX (scaled, where BM is estimated using girth circumference)
   - Step 1. Calculate BM = $2.777 \times (\text{girth}) - 193.41$ (i.e., eq 3 above).
   - Step 2. Calculate scaledMAXFAT = $\text{MAXFAT}/[0.150 \times (\text{BM}^{0.560})]$
   - Step 3. If MAXFAT <0.3, then scaledLIVINDEX = $4.478 \times (\text{rBCS}) - 4.62$.
   - Step 4. If MAXFAT ≥ 0.4, then scaledLIVINDEX = $11.350 \times (\text{scaledMAXFAT}) + 5.10$.
   - Step 5. If $0.3 \leq$ MAXFAT <0.4, then scaledLIVINDEX = $\{[4.478 \times (\text{rBCS}) - 4.62] + [11.35 \times (\text{scaledMAXFAT}) + 5.10]\}/2$.
   - Step 6. Calculate IFBF = $-0.68 + 1.050 \times (\text{scaledLIVINDEX})$

Final Step: double-check calculations with known values:
- Example 1: If MAXFAT <0.3 cm, rBCS = 2.0, girth = 145 cm (BM = 209 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 3.9\%$, $\text{IFBF}_{\text{scaledLIVINDEX}} = 3.9\%$
- Example 2: If MAXFAT = 0.4 cm, rBCS = 3.0, girth = 150 cm (BM = 223 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 6.7\%$ and $\text{IFBF}_{\text{scaledLIVINDEX}} = 6.2\%$
- Example 3: If MAXFAT = 0.3 cm, rBCS = 2.75, girth = 150 cm (BM = 223 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 6.9\%$ and $\text{IFBF}_{\text{scaledLIVINDEX}} = 6.6\%$
- Example 4: If MAXFAT = 1.0 cm, rBCS = 3.5, girth = 155 cm (BM = 237 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 8.9\%$ and $\text{IFBF}_{\text{scaledLIVINDEX}} = 8.4\%$

Mule Deer

1. newLIVINDEX (unscaled)
   - Step 1. If MAXFAT <0.2, then newLIVINDEX = $3.869 \times (\text{rBCS}) - 2.71$.
   - Step 2. If MAXFAT ≥ 0.3, then newLIVINDEX = $5.596 \times (\text{MAXFAT}) + 5.98$.
   - Step 3. If $0.2 \leq$ MAXFAT <0.3, then newLIVINDEX = $\{[3.869 \times (\text{rBCS}) - 2.71] + [5.596 \times (\text{MAXFAT}) + 5.98]\}/2$.
   - Step 4. Calculate IFBF = $-0.12 + 1.008 \times (\text{newLIVINDEX})$
2. scaledLIVINDEX (scaled, where BM is estimated by weighing)
   - Step 1. Calculate scaledMAXFAT = $\text{MAXFAT}/[0.142 \times (\text{BM} - \text{PM})^{0.630}]$
   - Step 2. If MAXFAT <0.2, then scaledLIVINDEX = $3.869 \times (\text{rBCS}) - 2.71$.
   - Step 3. If MAXFAT ≥ 0.3, then scaledLIVINDEX = $11.35 \times (\text{scaledMAXFAT}) + 5.63$.
   - Step 4. If $0.2 \leq$ MAXFAT <0.3, then scaledLIVINDEX = $\{[3.869 \times (\text{rBCS}) - 2.71] + [11.35 \times (\text{scaledMAXFAT}) + 5.63]\}/2$.
   - Step 5. Calculate IFBF = $-0.16 + 1.010 \times (\text{scaledLIVINDEX})$
3. scaledLIVINDEX (scaled, where BM is estimated using girth circumference)
   - Step 1. Calculate BM = $1.2925 \times (\text{girth}) - 60.80$ (i.e., eq 4 above)
   - Step 2. Calculate scaledMAXFAT = $\text{MAXFAT}/[0.142 \times (\text{BM}^{0.630})]$.
   - Step 3. If MAXFAT <0.2, then scaledLIVINDEX = $3.869 \times (\text{rBCS}) - 2.71$.
   - Step 3. If MAXFAT ≥ 0.3, then scaledLIVINDEX = $11.350 \times (\text{scaledMAXFAT}) + 5.63$.
   - Step 4. If $0.2 \leq$ MAXFAT <0.3, then scaledLIVINDEX = $\{[3.869 \times (\text{rBCS}) - 2.71] + [11.35 \times (\text{scaledMAXFAT}) + 5.63]\}/2$.
   - Step 5. Calculate IFBF = $-0.16 + 1.010 \times (\text{scaledLIVINDEX})$

Final Step: double-heck calculations with known values:
- Example 1: If MAXFAT <0.2 cm, rBCS = 2.0, girth = 100 cm (BM = 68 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 4.9\%$ and $\text{IFBF}_{\text{scaledLIVINDEX}} = 4.9\%$
- Example 2: If MAXFAT = 0.3 cm, rBCS = 3.0, girth = 105 cm (BM = 75 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 7.6\%$ and $\text{IFBF}_{\text{scaledLIVINDEX}} = 7.1\%$
- Example 3: If MAXFAT = 0.2 cm, rBCS = 2.75, girth = 105 cm (BM = 75 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 7.5\%$, and $\text{IFBF}_{\text{scaledLIVINDEX}} = 7.2\%$
- Example 4: If MAXFAT = 1.0 cm, rBCS = 3.5, girth = 110 cm (BM = 81 kg), then $\text{IFBF}_{\text{newLIVINDEX}} = 11.5\%$ and $\text{IFBF}_{\text{scaledLIVINDEX}} = 10.6\%$

Appendix B. Live-animal indices of ingesta-free body fat (IFBF) for elk, abbreviation used in the text, measurements needed to use the indices, and the equation to estimate IFBF. Body mass = BM. All equations were developed using homogenization data collected 1998–1999 from captive females in Oregon, USA (Cook et al. 2001*a*).

Elk body-fat index	Abbreviation	Measurements needed	IFBF eq
Rump body condition[a]	rBCS	rump BCS	$4.478x - 4.62$[a]
Rump-fat thickness (cm)[a,b]	MAXFAT	rump-fat thickness (cm)	$3.550x + 5.63$[a,b]
rLIVINDEX[a]	rLIVINDEX	rump BCS, rump-fat thickness (cm)	$-7.15 + 7.323x + 0.989x^2 + 0.058x^3$[a]
Rump-fat thickness; scaled for BM[b,c]	scaledMAXFAT	rump-fat thickness, BM (kg; or girth circumference [cm])	$11.350x + 5.10$[b,c]
New LIVINDEX; unscaled for BM[c]	newLIVINDEX	rump BCS, rump-fat thickness (cm)	$1.050x - 0.68$[c]
ScaledLIVINDEX; scaled for BM[c]	scaledLIVINDEX	rump BCS, rump-fat thickness (cm) BM (kg; or girth circumference [cm])	$1.050x - 0.68$[c]

[a] Presented in Cook et al. (2001*a*).
[b] Can only be used on animals having ≥0.3 cm rump-fat thickness.
[c] New indices designed to remove the bias of body size (scaledMAXFAT), observer bias associated with rBCS (newLIVINDEX), or both size and rBCS bias (scaledLIVINDEX).

Appendix C. Live-animal indices of ingesta-free body fat (IFBF) for deer, abbreviation used in the text, measurements needed to use the indices, and the equation to estimate IFBF. Body mass = BM. All equations were developed using homogenization data for mule deer collected 1996–1997 and 2002–2004 from females in Washington, Oregon, and California, USA (Stephenson et al. 2002, Cook et al. 2007).

Mule deer body-fat index	Abbreviation	Measurements needed	IFBF eq
Rump body condition[a]	rBCS	rump BCS	$3.869x - 2.71$[a,b]
Rump-fat thickness (cm)[a,c]	MAXFAT	rump-fat thickness (cm)	$5.596x + 5.98$[a,b,c]
rLIVINDEX[a]	rLIVINDEX	rump BCS, rump-fat thickness (cm)	$2.569x - 0.08$[a,b]
Rump-fat thickness; scaled for BM[c,d]	scaledMAXFAT	rump-fat thickness (cm), BM (kg; or girth circumference [cm])	$11.350x + 5.6$[c,d]
New LIVINDEX; unscaled for BM[d]	newLIVINDEX	rump BCS, rump-fat thickness (cm)	$1.006x - 0.12$[d]
ScaledLIVINDEX; scaled for BM[d]	scaledLIVINDEX	rump BCS, rump-fat thickness (cm), BM (kg; or girth circumference [cm])	$1.010x - 0.16$[d]

[a] Presented in Cook et al. (2007).
[b] New indices designed to remove the bias of body size (scaledMAXFAT), observer bias associated with rBCS (newLIVINDEX), or both size and rBCS bias (scaledLIVINDEX).
[c] Can only be used on animals having ≥0.2 cm rump-fat thickness.
[d] Reflects new eq developed without 4 castrate animals originally included in Cook et al. (2007).