Interpretation of body condition index should be informed by natural history

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Abstract

1. Estimates of body condition are regularly made in wildlife studies, particularly those focused on individual and/or population performance; however, many studies assume that it is always beneficial to be heavier or have a higher body condition index (BCI), without accounting for the physiological significance of variation in the composition of tissues that differ in their function such as fat and lean mass.
2. We hypothesized that the relationship between BCI and masses of physiologically important tissues (fat and lean) would be conditional on the annual patterns of energy acquisition and expenditure of individuals under study, and tested relationships in three

species with contrasting ecologies in their respective natural ranges: an obligate hibernator (Columbian ground squirrel, *Urocitellus columbianus*), a facultative hibernator (black-tailed prairie dog, *Cynomys ludovicianus*), and a food-caching non-hibernator (North American red squirrel, *Tamiasciurus hudsonicus*).

3. We measured fat and lean mass in adult males and females of these three species using quantitative magnetic resonance (QMR). We measured body mass, two measures of skeletal structure (zygomatic width and right hind foot length) to develop sex- and species-specific BCIs, and tested the utility of BCI to predict body composition in each species.
4. Body condition indices were more consistently and more strongly correlated with lean mass than fat mass. The indices were most positively correlated with fat when fat was expected to be very high (pre-hibernation prairie dogs). However, in all cases, fat and lean mass were better predicted by overall body mass rather than BCI.
5. These results support our hypothesis that the utility of BCI in estimating fat is conditional on the natural history and annual energetic patterns of the species with regards to expected energy balances at the time of sampling, but measuring body mass alone is likely capturing sufficient variation in fat and lean masses in most cases.

Key words: energetics, fat, food-caching, hibernation, lean, phenology

Introduction

Body mass is among the most frequently measured physical traits of organisms, because it often accounts for much of the observed variation in other traits of interest as well as ecological processes (Woodward et al., 2005). However, the mechanisms underlying these associations may depend on the different components comprising body mass, rather than mass itself. For processes in which energy stores or reserves (see (Lindström & Piersoma, 1993) for distinction) are the currency of interest, the non-structural components of body mass that represent metabolizable tissues (fat and lean mass; (Krebs & Singleton, 1993a) are likely more relevant than size alone. For example, relatively high fat stores facilitate successful migration (Bairlein, 2002) and hibernation (Humphries et al., 2003), while a higher proportion of lean mass can enhance athletic performance (e.g., takeoff velocity in domestic cats *(Harris & Steudel, 2002)*. Understanding relationships with the components of body mass may provide greater insight into the mechanisms linking body mass to performance.

A given body mass may be distributed across structural elements of different sizes. Body condition indices (BCIs) attempt to control for this by considering total body mass relative to structural size (e.g., a linear skeletal measurement such as body length, tarsus length, foot length, or a combination thereof; (Green, 2001; Jakob et al., 1996; Schulte-Hostedde et al., 2001)) to give some indication of an individual's energetic 'condition'. Typically, individuals with relatively higher body mass:skeletal size ratios are considered to be in 'better' condition than individuals with lower ratios, as the former are assumed to have more energetic stores than individuals of similar structural size, but with a lower metabolizable fraction (Schulte-Hostedde et al., 2001). Accurate measures of 'condition' in this energetic sense are widely applicable to scenarios such as livestock breeding programs (e.g., maximizing meat or offspring production), conservation biology (e.g., measuring responses to habitat degradation; (Stevenson & Woods, 2006; Wikelski & Cooke, 2006), and in exploring evolutionary and ecological patterns (e.g., condition-dependent dispersal; (Bonte & De La Peña, 2009) and migration (Andersen et al., 2000)). To better understand mechanisms underlying these relationships requires a closer consideration of what physiological component of ‘condition’ BCIs are describing (e.g., lean versus fat mass; (Schulte-Hostedde et al., 2001).

The dynamic nature of body condition across time (Krebs and Singleton 1993) demands that its correlates and consequences be considered within the context of a species’ natural history (Molnár et al., 2009). The composition of a body in ‘good condition’ in an adaptive sense (i.e., that which is associated with increased survival and/or fitness, *sensu* (Wilson & Nussey, 2010), should therefore be expected to vary over time depending on circannual energetics. Fat reserves are an important source of metabolizable energy (~39.6 kJ/g for dry fat, in contrast to 17.8 kJ/g for dry lean mass, (Jenni & Jenni-Eiermann, 1998)) that fuel organisms through energetically-expensive behaviours or during periods of energetic shortfall. For example, individuals with higher fat fractions entering hibernation are more likely to survive over winter and breed successfully the following spring (Boyer & Barnes, 1999). Fatter is not always better though: during the active season, carrying more body mass can decrease running speed (Trombulak, 1989) and alter circulating hormones (Taylor et al., 1982). Arboreal species may trade off fat stores for locomotion (Dittus, 2013), and for species that primarily store energy off-body as external food caches, fat reserves may not confer the same advantages during resource-scarce seasons as they may for species that store energy exclusively on-body. Furthermore, a higher lean fraction may be associated with increased activity, as shown in captive rats (*Rattus norvegicus*; (Swallow et al., 2010). The body composition associated with better performance is therefore likely to be highly dependent on natural history, as well as on the various activities an animal undertakes throughout the year (Wells et al., 2019).

Because body mass and structural size can be measured from live animals, BCIs are less invasive than chemical composition analyses that require lethal sampling (Reynolds & Kunz, 2001). In many species, BCIs correlate well with chemical quantification of fat mass in vertebrates including birds (Chang & Wiebe, 2016) and reptiles (Weatherhead & Brown, 1996), and invertebrates including arthropods (Jakob et al., 1996; Kelly et al., 2014; Moya-Laraño et al., 2008). However, BCIs are not without drawbacks. Acquiring the structural size component(s) of the index can be challenging. Krebs and Singleton (Krebs & Singleton, 1993b) warned of low repeatability attributable to measurement bias across different observers (although this can be significantly reduced by taking replicate measurements; (Blackwell et al., 2006), and estimating lengths of long bones yield the most accurate estimates when measured from museum specimens (e.g., (Dobson, 1992)), but can be challenging to measure on live, unanesthetized animals in field conditions (Green, 2001). Because skeletal morphology often reflects natural history, as selection favours certain shapes for certain lifestyles (e.g., arboreal vs. fossorial), the body component of interest may not be accurately reflected by BCI. For example, BCI can correlate more strongly with lean mass rather than fat mass (Schulte-Hostedde et al., 2001). Furthermore, the efficacy of BCI in predicting the masses of body components may be no more effective than prediction through body mass alone (e.g., body mass predicts fat stores in bats just as well as BCI; (McGuire et al., 2018). Finally, since BCI estimates the non-skeletal component of body composition in a general sense, its interpretation and therefore significance may differ depending on the energetic aspects of the natural history of the focal species (e.g., for a fat-storing hibernator versus a food-caching non-hibernator). We thus expect the correlation between BCIs and body composition (i.e., fat and lean mass) to with both species and timing in annual cycles, reflecting the dynamic nature of energy budgets in seasonally dependent activities.

We studied natural populations of three different mammal species to evaluate concordance between BCIs and the energetic components of interest to many biologists (fat and lean mass), and determined whether these relationships differ according to species' primary energy storage mode (e.g., on-body fat storage vs. off-body food caching). We hypothesized that the relationship between BCI and body composition depends on both the extent to which the species relies on on-body energy stores (i.e., fat) for overwinter survival, and with the expected energetic balance within a stage of the annual cycle (i.e., season).

We selected three species in the family Sciuridae which differ in patterns of energy storage and metabolic demands: North American red squirrels (*Tamiasciurus hudsonicus*, hereafter, red squirrels), black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter prairie dogs), and Columbian ground squirrels (*Urocitellus columbianus*, hereafter ground squirrels). We also compare ground squirrels before and after hibernation to characterize within-species shifts in energy stores. Red squirrels are arboreal mammals that store cached conifer cones in a central larder ('midden'; (Smith, 1968) from late summer through autumn (Fletcher et al., 2010). Red squirrels are relatively sexually monomorphic, weighing ~230-250 g on average as adults (Boutin & Larsen, 1993), but males typically maintain larger cache sizes than females (Archibald et al., 2013; Fisher et al., 2019; Haines et al., 2022). Red squirrels remain euthermic throughout winter without using torpor (Brigham & Geiser, 2012), and are not known to gain significant amounts of fat prior to winter, during which they rely on cached resources for energy.

Prairie dogs are semi-fossorial and can weigh up to 1710 g, but show high within- and between-individual variation in body mass (Kusch et al., 2021). They are sexually dimorphic in body mass (Hoogland, 1995, 2003); however, the extent of this dimorphism varies seasonally (Hoogland, 1995, 2003; Kusch et al., 2021). Throughout most of their range, prairie dogs are active throughout the winter; however, in southwestern Saskatchewan, where our study population is located (the northern edge of the species distribution), they are known to hibernate for ~4 months during winter (Gummer, 2005; Lehmer et al., 2006). Prairie dogs of both sexes increase overall body mass, and fat mass specifically, leading up to winter (Kusch et al., 2021; Lehmer & Van Horne, 2001). In hibernators, the greatest energy savings are achieved during steady state torpor, when body temperature approximates ambient temperature, while most energy is spent during interbout arousals to euthermy (Geiser & Ruf, 1995; Karpovich et al., 2009). Prairie dogs in this population use torpor during winter, but are not considered efficient hibernators, because they have a high minimum body temperatures during hibernation (16.9 °C for males; Hawkshaw, 2022) and do not maintain steady state torpor (mean torpor bout duration ~126 hours for males, ~90 hours for females (Hawkshaw, 2022).

Ground squirrels are also semi-fossorial. Body mass varies substantially across their active season (~400 g at emergence from hibernation in spring, to up to ~700 g prior to immergence in late summer; (Dobson et al., 1992). These obligate hibernators are notable for their short active season (~4 months) and extended time spent metabolically depressed in hibernation (~8 months) each year (Dobson et al., 1992). Ground squirrels reach lower minimum body temperatures (0 °C) and have longer torpor bout durations (~390 hours for males; Young, 1990) than prairie dogs. Ground squirrels exhibit male-biased sexual dimorphism, and individuals experience significant body mass changes across time (Boag & Murie, 1981). Forage quality and availability is low upon emergence in the spring (Lane et al., 2012; Young, 1990). Consequently, body fat stores that remain after hibernation are presumed important for supporting reproduction (Broussard et al., 2005).

We 1) characterized morphology and body composition of these three species, 2) evaluated the correlation of BCI with body composition variables (lean and fat mass), and 3) determined whether the correlation between BCI and body composition variables was higher than between body mass and body composition variables. We expected hibernators (ground squirrels and prairie dogs) to have the highest fat fraction within the pre-winter season given the importance of on-body energetic reserves to sustain hibernation, compared to non-hibernating red squirrels which rely on hoarded food, and compared to post-emergence ground squirrels in spring who have metabolized fat stores overwinter. Because fat stores are expected to represent the bulk of the pre-hibernation weight gain in the lead up to winter, we also expected high concordance between BCI and fat mass in pre-winter hibernators. Conversely, we expected the lowest concordance between BCI and fat mass to be in red squirrels, as lean mass is likely to be more important to sustained caching activity (Fletcher et al., 2015). Finally, we test the null hypothesis that BCI and body mass perform equally well in predicting lean and fat mass.

Materials and Methods

Study sites and population monitoring

We sampled free-ranging non-breeding adults from populations within the northern regions of their respective ranges in Canada: red squirrels in the southwest Yukon (61° N, 138° W, ~ 850 m a.s.l.), prairie dogs in Grasslands National Park, Saskatchewan (49°N, 107°W, ~770 m a.s.l.), and ground squirrels in Sheep River Provincial Park, Alberta (50°N, 114°W, ~ 1500 m a.s.l.). For all populations, we collected data through live-trapping. All populations were monitored for at least one year prior to data collection for the present study. For detailed descriptions of population and reproductive monitoring, see (Dantzer et al., 2020; McAdam et al., 2007)) for red squirrels, (Kusch et al., 2020)) for prairie dogs, and (Lane et al., 2019) for ground squirrels. Briefly, all individuals received permanent uniquely marked ear tags (National Band and Tag Company, Newport, KY) upon first trapping. We included only adults (individuals one year of age or older) to minimize effects of skeletal growth dynamics. For ground squirrels and prairie dogs, we knew ages for all individuals captured at first emergence following birth. For red squirrels and some older ground squirrels and prairie dogs, exact ages were not known, but we could confidently remove young-of-the-year based on size and breeding/nipple status on first trapping (red squirrels excluded if under 150 g with small pink nipples at first trapping, ground squirrels excluded if under 400 g, prairie dogs excluded if under 800 g a with small pink nipples at first trapping). We excluded all pregnant (assessed by abdominal palpations) and lactating (assessed by milk expression) females to remove variance related to maternal investment in offspring.

Morphometric measurements

We measured body mass and size for all live-trapped individuals (Table 1). We weighed each prairie dog to the nearest 5 g using a Pesola spring scale (Pesola AG, Baar, Switzerland), and weighed red squirrels and ground squirrels to the nearest 1 g on an electronic balance. We measured zygomatic arch width ('ZW') to the nearest millimeter using calipers (analogue for red squirrels and prairie dogs; digital for ground squirrels). We measured right hind foot ('RHF') length from heel to longest toe (excluding claw) to the nearest millimeter using a ruler fit with a heelstop at 0 mm. We measured both ZW and RHF three times per handling, and used the mean value for analyses.

We took these measurements during the same handling occurrence as body composition analyses for all red squirrels, all prairie dogs except one, and most ground squirrels. For the remaining prairie dog and ground squirrels, we used skeletal measurements taken on the nearest date to when composition analyses were completed. The prairie dog was an adult and unlikely to be growing, so we used measurements taken 81 days prior. The median interval between skeletal measurements and composition scans for ground squirrels was 0 days (range: 0-120). We excluded data from ground squirrels that were younger than 3 years of age if their skeletal measurements were taken more than two weeks before or after the date of body composition and mass measurements, as younger squirrels may still be growing structurally (Dobson, 1992). A single yearling (female) remained in the spring dataset, so we removed all yearling ground squirrels.

Body composition

We measured pre-winter body composition of red squirrels between late-September and mid-October in 2018 and 2019, prairie dogs in late October 2018 (due to variable torpor patterns in prairie dogs, immergence date into hibernation was not known), and ground squirrels between late-July and late-August 2019 within a week of immergence for most individuals (median = 3.5 days; range = 0-15). We measured spring body composition of ground squirrels for which we were confident were captured within a few days of emergence from hibernation (median = 1 day; range = 0-3) between mid-April and early May 2019. Most individual ground squirrels were measured in one season only, but 21 individuals were measured in both seasons. As we do not expect ground squirrels to change skeletal size substantially after they have reached maturity, we recorded morphometric data once per individual.

We used a quantitative magnetic resonance (QMR) body composition analyzer (EchoMRI-1600, Echo Medical Systems, Houston, TX) to measure absolute lean and fat mass (g). This technology provides a relatively non-invasive method of estimating body composition precisely, and accurately (Tinsley et al., 2004). The remaining components not captured as fat and lean mass are free water and skeletal mass (McGuire & Guglielmo, 2010). Quantities measured using QMR correlate well with carcass-derived quantities for numerous species across multiple taxa, most relevant here being rodents, including laboratory rats *Rattus norvegicus domestica* (Johnson et al., 2009) and house mice *Mus musculus domesticus* (Jones et al., 2009). The QMR approach allows for repeated measures of live animals, both awake and sedated (McGuire & Guglielmo, 2010; Tinsley et al., 2004; Zanghi et al., 2013b, 2013a).

We housed our QMR system in a custom-designed trailer to enable transportation to each study site. The trailer was climate-controlled to stabilize the temperature, as the magnet within the QMR system is temperature-sensitive. We targeted an ambient temperature of 21 °C as per manufacturer recommendations, although field conditions widened the range of stabilized temperature to ± 7 °C. We calibrated the system daily to a 943 g canola oil standard at the stabilized temperature, which was held for at least five hours prior to scanning animals (Guglielmo et al., 2011). Our QMR system was outfitted with an additional antenna to measure animals from 100 g up to 1600 g to accommodate the range of body masses of the three species. Details of similar systems are described elsewhere (McGuire & Guglielmo, 2010), and we followed similar protocols here. We live-trapped squirrels in the field and transported them to the trailer. We placed each squirrel in a clear plexiglass holding tube with perforations to allow ample airflow to the animal, then inserted the tube into the QMR chamber. We recorded body composition through a minimum of two scans, reporting the average values for each individual. In 2019, we administered a mild sedative via intramuscular injection to red squirrels prior to scanning and collecting morphometric data (100 μg/kg of dexmedetomidine, reversed by 1 mg/kg atipamezole) to minimize stress and movement during scans. Sedation was not necessary for the semi-fossorial prairie dogs or ground squirrels, who remained still and even fell asleep in the chamber.

Calculating body condition indices (BCIs)

We retained individuals in the dataset for which we had measurements for all of the following: ZW, RHF, body mass, and body composition. Within each species, we calculated coefficients of variation for all variables, and analyzed relationships among variables. While principal components analysis has been used previously as a general measure of structural size to derive BCI (Schulte-Hostedde et al., 2005), we determined that it was not appropriate for our dataset because correlation coefficients between ZW and RHF were not always positive (Supplementary Fig. S1). Instead, we selected the single skeletal measure that had the greatest coefficient of variation (CV) to generate a residual index (Jakob et al., 1996). Red squirrels showed a negative but non-significant relationship between RHF and ZW (Table 1) so we chose to use ZW to generate the BCI for this species ('ZW index'). The relationships between RHF and ZW appeared to differ in direction between male and female prairie dogs; however, neither correlation was significant, so we generated a ZW index for this species. In ground squirrels, only data for females pre-winter showed a significant (positive) relationship. Females in spring and males in both seasons showed no significant relationship between RHF and ZW. We therefore used RHF to generate the single-metric BCI ('RHF index') for ground squirrels.

To calculate each BCI, we regressed either RHF (log transformed and standardized to mean zero, unit variance) alone on body mass (log transformed and standardized to mean zero, unit variance; generating the RHF index), or ZW (log transformed and scaled) alone on body mass (log transformed and standardized to mean zero, unit variance; generating the ZW index).

Residual plots are shown in Supplementary Fig. S2. We calculated BCIs within season (pre-winter/spring) and within sex for each species using separate regressions. Because some CV values within species/seasons were similar for RHF and ZW, we also ran models using the BCI derived from the alternate skeletal measurement (Supplementary Online Material). We indicate in the results when results differed from the primary BCI model.

Statistical analyses

We performed all analyses in R (v.4.0.3, (R Core Team, 2020). We compared morphological measures between the sexes within each species using a two-sample t-test. To assess the efficacy of the selected BCI for each species in predicting body composition variables, we modeled, separately for each species (and for ground squirrels, separately for each season), linear models for fat mass (g) and lean mass (g), each predicted by the selected BCI interacting with sex. We also modeled fat and lean mass predicted by body mass interacting with sex. We compared the fit of the BCI model and body mass model for each component for each species using Akaike's information criterion adjusted for small sample size (Burnham & Anderson, 2002), confirming no missing data. To compare the utility of BCI to predict fat and lean mass across species, we fit a linear model for data from all three species (including both seasons for ground squirrels) together. For fat and lean mass separately, we defined an interaction term between species-specific BCI and species as the independent variable. We fit a similar model set with body mass (scaled within species) instead of BCI.

Results

Morphological measurements

Males were significantly heavier than females in all three species: males were 3.3% heavier in red squirrels, 9.6% heavier in prairie dogs, 27.9% heavier in pre-winter ground squirrels, and 26.6% heavier in spring ground squirrels (Table 1). Right hind foot length was different between sexes only for ground squirrels in spring, with male RHF 1.6 mm longer than in females. Zygomatic width was significantly larger in male prairie dogs and ground squirrels than females, but similar between red squirrel males and females.

Body composition

In autumn, red squirrels showed the lowest percent body fat, with 2.4% in males and 2.9% in females (Table 1) while prairie dogs had the highest percent body fat, with 30.9% and 35.4% in males and females, respectively. Ground squirrels were the only species to have significant sex differences in fat (in both seasons). They showed their highest body fat levels pre-winter before entering hibernation (25.0% for males, 20.8% for females), and lowest in spring (12.4% fat for males, 7.7% fat for females).

Relationship between BCI, body mass, and body composition

The relationship between BCI/body mass and fat/lean mass was positive in almost all cases (Figures 1-4; the exception being for male prairie dog lean mass, Figure 2b). Both BCI and body mass were significant predictors of fat and lean mass in their respective models for all species, while sex and the BCI × sex interaction largely were not significant (Tables 2-5). For red squirrels, the BCI and body mass models performed similarly in predicting fat but both had weak correlations (Table 2, Figure 1). Red squirrel lean mass was better predicted by both BCI and mass models than fat mass, with the body mass model providing a better fit. Sex was not significant in the main ZW BCI model, but was in the alternate RHF BCI model (Supplementary Table S3). For prairie dogs, both ZW BCI and body mass predicted fat well, but the body mass model was a better fit for both fat and lean mass (Table 3, Figure 2). The BCI × sex interaction was not significant in the main ZW BCI model, but was in the alternate RHF BCI model (Supplementary Table S4). For pre-winter ground squirrels, the two models for fat were indistinguishable based on AICc and had similar correlation strengths (Table 4, Figure 3). The body mass model was a better fit for lean mass. This pattern held for spring, with BCI and body mass models being similar for fat, and the body mass model providing a better fit for lean mass (Table 5, Figure 4). Patterns did not change using ZW BCI instead (Supplementary Tables S5-6).

In the models including data from all species (and for ground squirrels, both seasons), the effects of BCI, species, and the BCI × species interaction were significant for fat (Table 6, Figure 5A). In the model for lean mass, BCI and species, but not their interaction, were significant (Figure 5B). Patterns for models fitted with body mass instead of BCI differed slightly, with body mass being significant in the fat model only in interaction terms except for spring ground squirrels. In the lean model, all interaction terms were significant except for body mass × spring ground squirrels. The strength of the correlations in both BCI and body mass model sets were strong (adjusted $R^2 > 0.9$ for all) and similar within each component.

Discussion

We demonstrate that the utility of condition indices in predicting energetic components, specifically fat, is conditional on expected energetic state given ecological considerations. If BCI is a reliable indicator of 'condition' as it relates to on-body energy stores, it should be strongly correlated with fat mass. However, when individuals were expected to be in a leaner state (e.g., food-caching red squirrels, spring ground squirrels), correlations between BCI and fat were low to moderate. When individuals were expected to have higher fat stores (e.g., pre-hibernation prairie dogs and ground squirrels), BCI models predicted fat well. Furthermore, the relationship between BCI and fat depended on species (and season, for ground squirrels). This contingency suggests that the assumption that high BCI is necessarily indicative of high fat stores should be tempered depending on the species and/or time of year. In nearly all cases, BCI was positively correlated with lean mass. Because fat and lean mass have significantly different energetic values (Jenni & Jenni-Eiermann, 1998), interpretations of BCI as they relate to metabolizable energy should take into account species-specific natural history and annual energetic patterns. For example, some red squirrels that would have ranked as lower condition based on BCI had nearly twice as much fat as some individuals who had higher BCI values. Furthermore, models fit with body mass were almost always more highly correlated with fat and lean mass than models with BCI.

The selection of these three species, and the time of year at which they were studied, provides insight into how body composition manifests in BCI when individuals are in a peak positive energy balance after accumulating surplus energy to sustain them through upcoming energetic shortfalls, and when they are expected to have depleted much of that accumulated energy. By investigating these relationships at the ends of the continuum of energetic states that organisms may experience throughout the year, we demonstrate that interpretation of ‘condition’ indices should be sensitive to seasonal energetic demands. For example, red squirrels primarily store energy as cached food so were expected to carry little fat. In comparison, we expected prairie dogs to have high fat stores to sustain them through inefficient hibernation (Gummer, 2005; Hawkshaw, 2022), and indeed they had the highest percent body fat of all three species.

These results illustrate that the relative importance of fat and lean mass is likely to vary with seasonal activities interacting with natural history.

Almost every relationship between either predictor variable (BCI or body mass) and body component (fat or lean mass) was positive, save for male prairie dog lean mass. Echoing Schulte-Hostedde et al. (2001), BCIs are capturing variation in both components. There are, however, fine scale, but important, differences worth discussing. We found that in general, lean mass had less variation around the line of best fit than fat mass, reflective of previous studies on small-non hibernating mammals that also found that BCIs tend to be more effective in predicting lean dry mass and water compared with predicting fat mass (Schulte-Hostedde et al., 2001; Tidhar & Speakman, 2007). Given the dynamic nature of body composition in hibernating species, estimating fat levels can be particularly difficult since many studies using residual-derived BCIs to assess fat assume that lean mass scales with body size, while fat mass is assumed to vary with condition (McGuire et al., 2018).

We have shown that the utility of body mass and/or BCI to describe energy-relevant components is conditional on natural history and annual energetic cycles. Quantitative magnetic resonance provides fine-scale measurements that may be important for specific energetics questions, but general relationships between body mass and fat/lean quantities are positive. Ultimately, this study strengthens the case for using body mass as a covariate to capture general variation in soft tissue in most scenarios, as we have demonstrated that BCIs do not confer an advantage in predicting fat and lean mass in these three species. Further research into mass and composition dynamics across seasons and in different energetic contexts will help determine the extent to which such relationships hold outside seasons of expected extremes of energy budgets.

Ethics. All procedures were approved by the University of Saskatchewan Animal Research Ethics Board. Fieldwork was completed under permits issued by Yukon Territorial Government (red squirrels); Grasslands National Park and the Saskatchewan Ministry of the Environment (prairie dogs); and Alberta Parks (ground squirrels).

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Conflict of Interest. We have no competing interests.

Author Contributions. AEW designed the study, collected data, performed data and statistical analysis, and drafted the manuscript. JEL participated in the design. All authors contributed to data collection, provided valuable discussion and contributions to the writing of the manuscript, and gave final approval for publication.

Data availability: Data are archived on FigShare and will be made public with an associated DOI upon acceptance.

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Tables & Figures

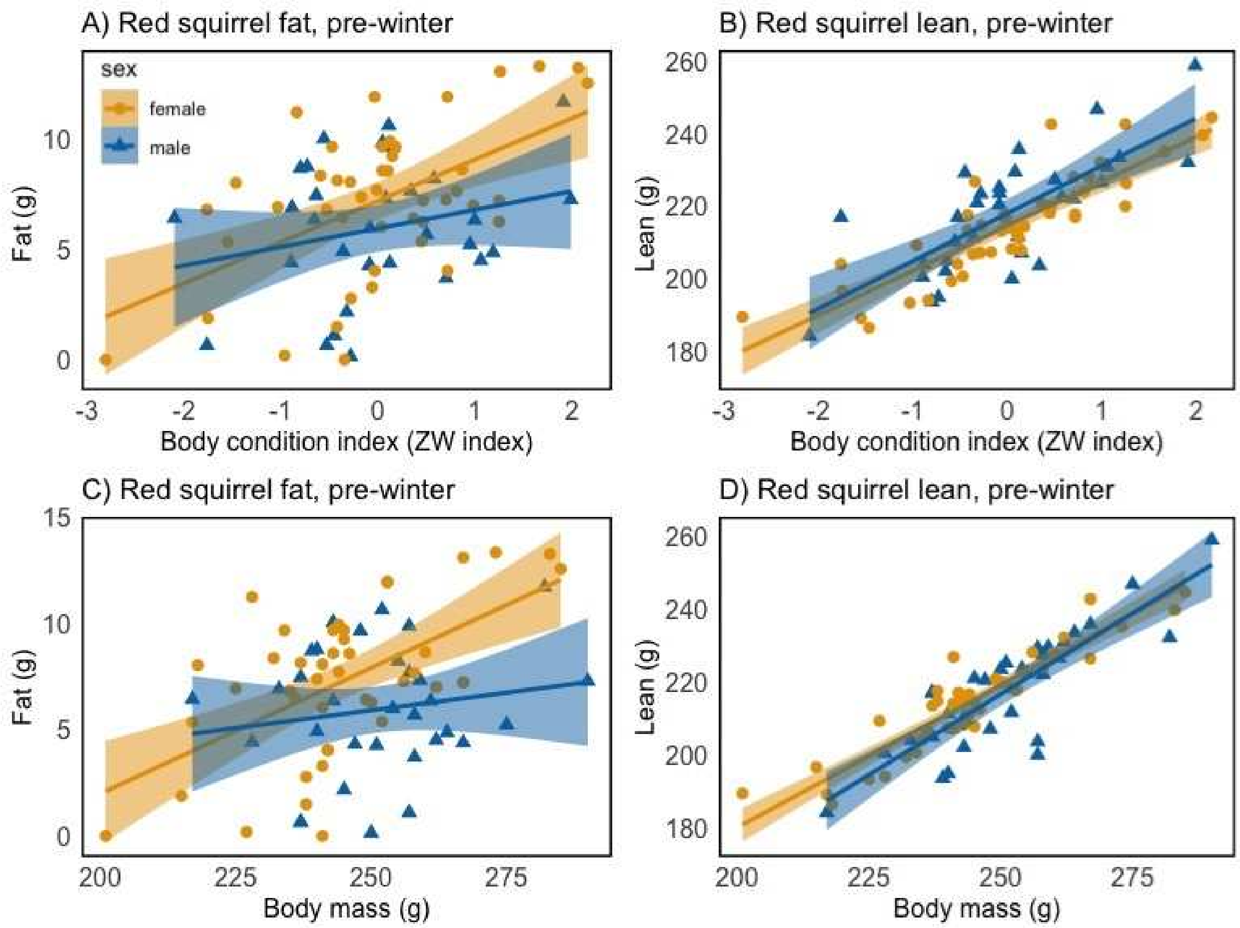

Figure 1. Body composition (fat [A,C] and lean [B,D] in grams) as a function of zygomatic-derived body condition index (ZW index, A-B) and body mass (C-D) for male (blue triangles) and female (orange circles) North American red squirrels pre-winter.

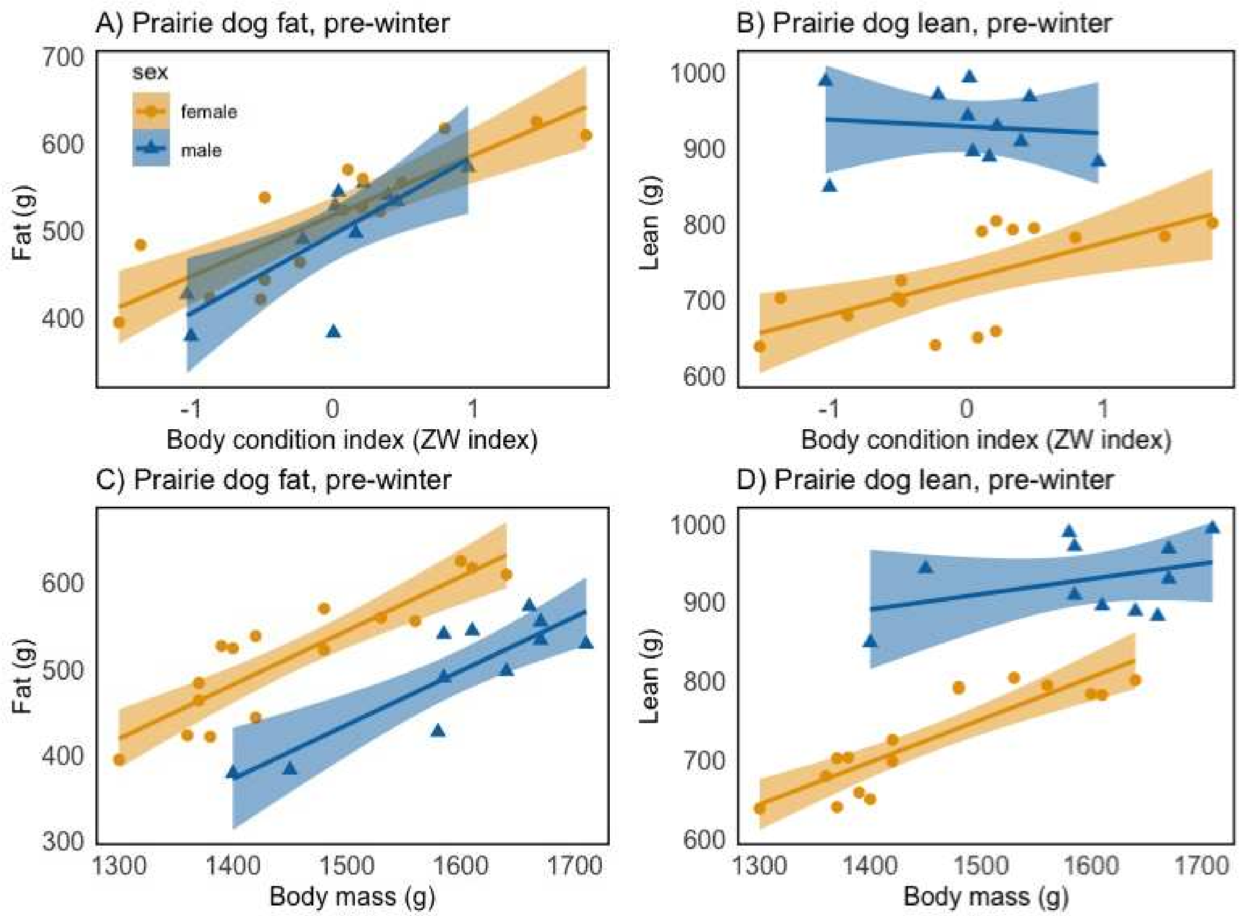

Figure 2. Body composition (fat [A,C] and lean [B,D] in grams) as a function of zygomatic-derived body condition index (ZW index, A-B) and body mass (C-D) for male (blue triangles) and female (orange circles) adult non-breeding black-tailed prairie dogs pre-winter.

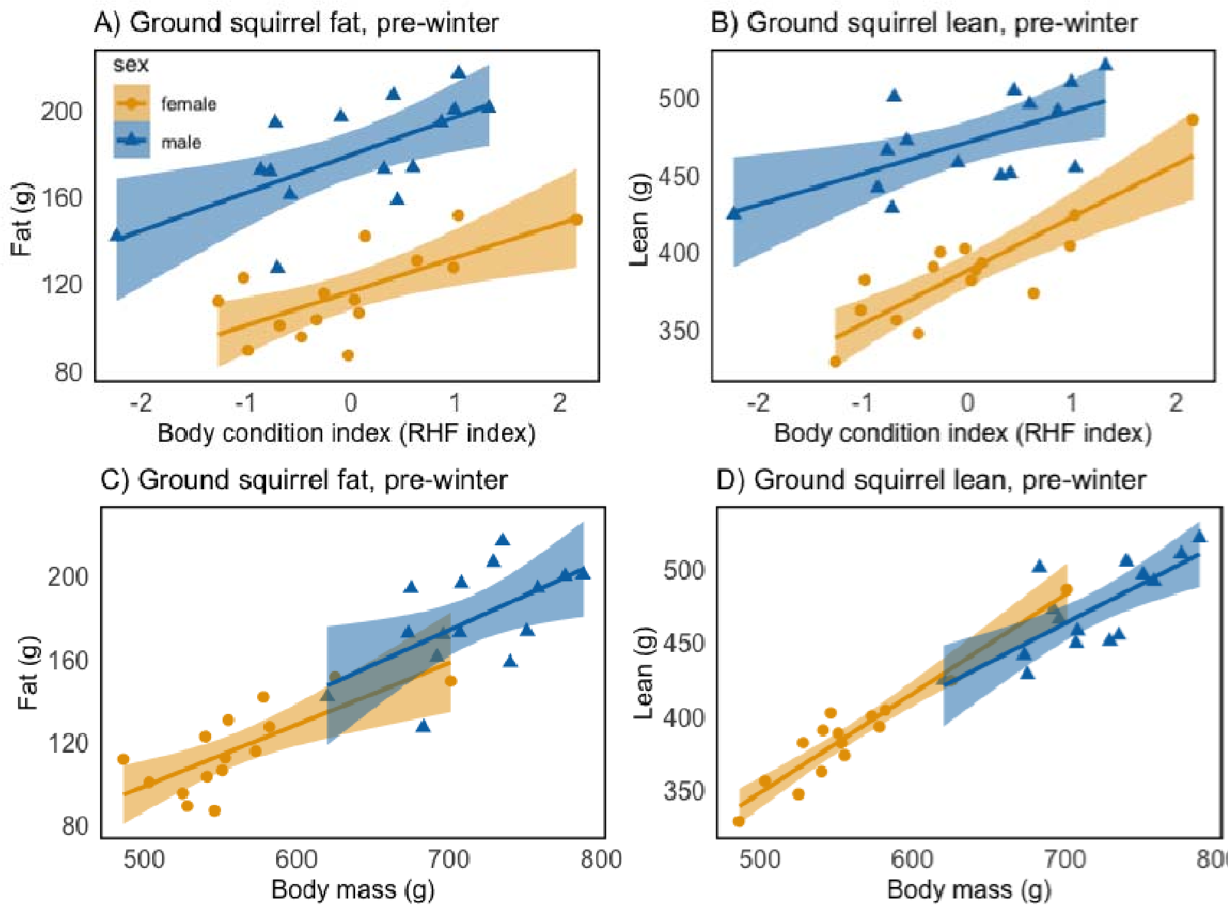

Figure 3. Body composition (fat [A,C] and lean [B,D] in grams) as a function of right hind foot-derived body condition index (RHF index, A-B) and body mass (C-D) for male (blue triangles) and female (orange circles) adult non-breeding Columbian ground squirrels pre-winter.

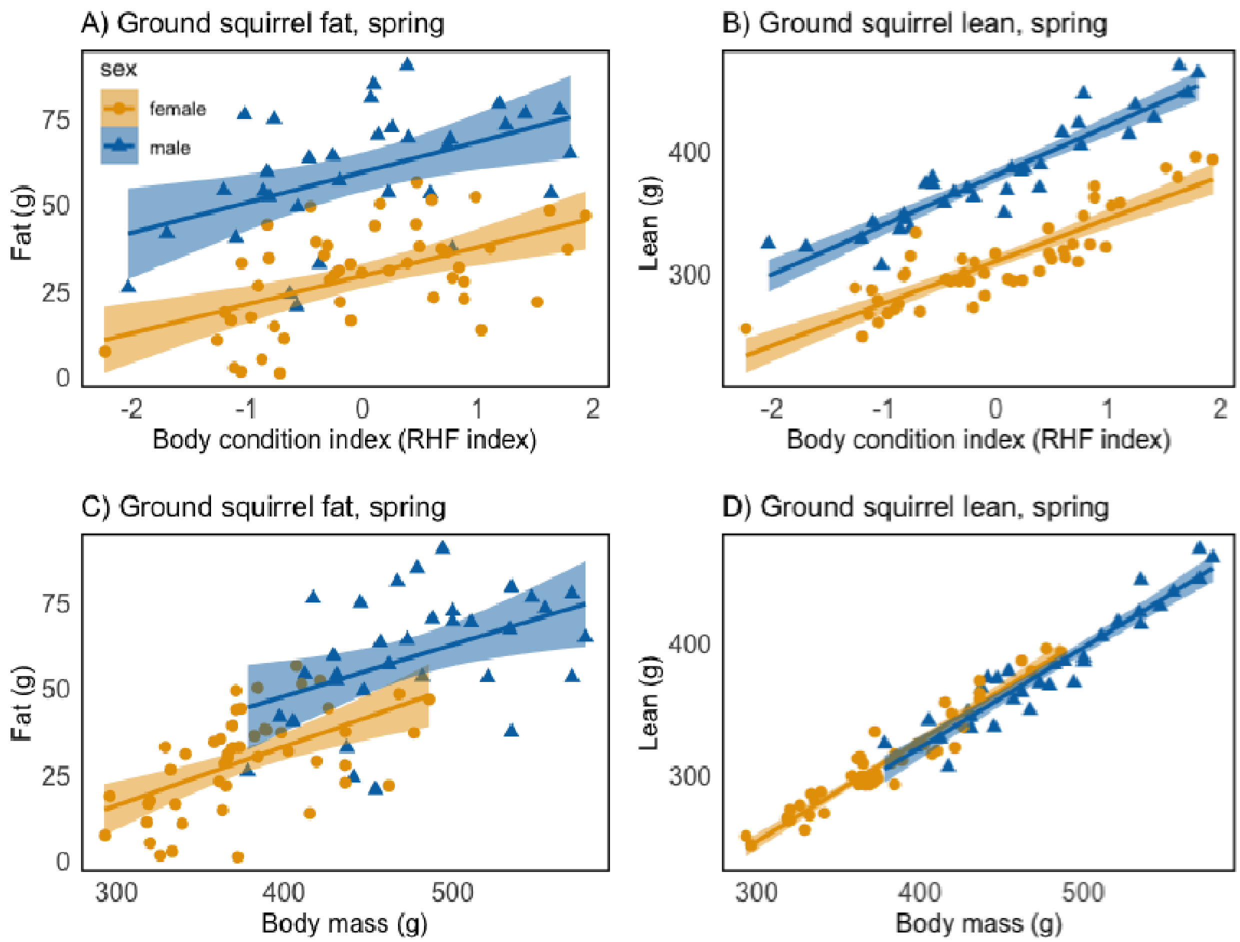

Figure 4. Body composition (fat [A,C] and lean [B,D] in grams) as a function of right hind foot-derived body condition index (RHF index, A-B) and body mass (C-D) for male (blue triangles) and female (orange circles) adult non-breeding Columbian ground squirrels in spring.

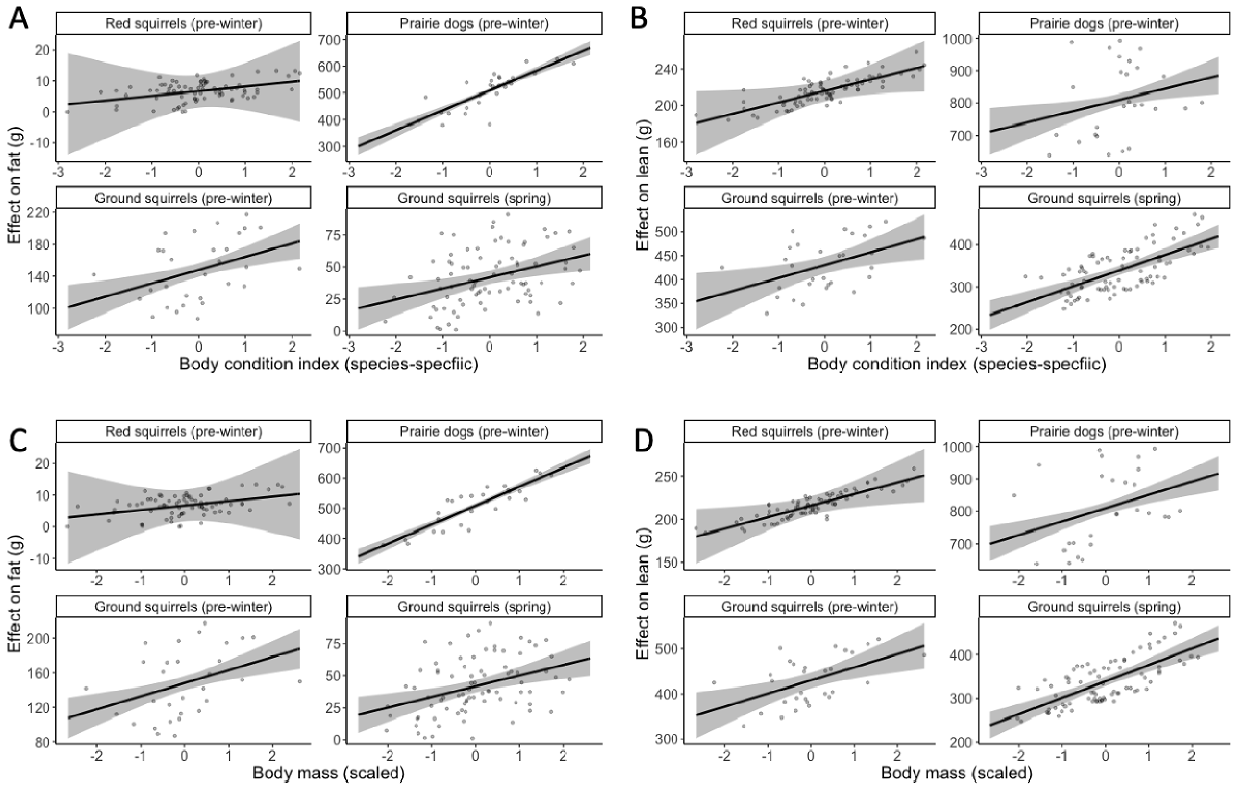

Figure 5. Partial plots showing the relationship between (A, B) species-specific body condition indices and (C, D) body mass on (A, C) fat and (B, D) lean mass in two linear models for adult non-breeding North American red squirrels (pre-winter), black-tailed prairie dogs (pre-winter), and Columbian ground squirrels (pre-winter and spring).

Table 1. Summary of morphometric data (body mass, right hind foot length, and zygomatic width) and body composition (fat mass, lean mass) for adult non-breeding male and female North American red squirrels (pre-winter), black-tailed prairie dogs (pre-winter), and Columbian ground squirrels (pre-winter and spring). Values reported as mean ± SEM. Sample sizes for each sex (♂ = males,♀ = females) are indicated in the species column.

Species		Body mass (g)	Right hind foot length (mm)	Zygomatic width (mm)	Fat (g)	Lean (g)
North American red squirrels						
	Male (*n* = 31)	251.8 ± 2.7 *	45.8 ± 0.3	28.9 ± 0.2	6.1 ± 0.5 (2.4%)	217.8 ± 2.9 (86.5%)
	Female (*n* = 40)	243.8 ± 2.8 *	45.6 ± 0.2	28.3 ± 0.1	7.2 ± 0.6 (2.9%)	214.0 ± 2.3 (87.8%)
Black-tailed prairie dogs						
	Male (*n* = 11)	1596.4 ± 28.7*	56.9 ± 0.4	49.8 ± 0.4*	495.6 ± 20.8 (30.9%)	928.8 ± 14.4* (58.3%)
	Female (*n* = 16)	1456.9 ± 25.8*	56.2 ± 0.2	47.9 ± 0.3*	517.5 ± 18.2 (35.4%)	727.5 ± 15.9* (49.9%)
Columbian ground squirrels						
Pre-winter	Males (*n* =15)	715.4 ± 11.5 *	46.4 ± 0.5	35.0 ± 0.4 *	179.3± 6.5* (25.0%)	471.7 ± 8.0* (66.0%)
	Female (*n* = 15)	559.1 ± 13.3 *	45.3 ± 0.4	33.3 ± 0.3 *	116.4 ± 5.3* (20.8%)	388.4 ± 9.4* (69.5%)
Spring	Males (*n* =33)	478.3± 89.5 *	46.7 ± 0.4 *	35.4 ± 0.2 *	59.7 ± 3.2 * (12.4%)	380.5 ± 7.5 * (79.6%)
	Female (*n* = 48)	377.7 ± 6.7 *	45.1 ± 0.2 *	33.3 ± 0.2 *	29.5 ± 2.1 * (7.7%)	310.1 ± 5.3 * (82.2%)

**denotes significant differences between males and females; Welch two-sample t-test with α = 0.05*

Table 2. Model coefficients for linear models testing whether a body condition index (BCI) derived from zygomatic width (ZW index) explains observed variation in fat and lean mass in North American red squirrels pre-winter. Reference group for sex: female.

Component	Model	Independent terms	Estimate	*t*	*p*	AICc	Adjusted R^2
Fat	~ BCI*sex	Intercept	7.22 ± 0.44	16.54	< 0.001 *	390.7	0.215
		BCI	1.87 ± 0.44	4.26	< 0.001 *		
		Sex	-1.25 ± 0.68	-1.85	0.069		

		BCI*sex	-1.03 ± 0.73	-1.42	0.161		
	~mass*sex	Intercept	-21.67 ± 6.36	-3.41	< 0.002 *	389.4	0.223
		Body mass (g)	0.12 ± 0.03	4.56	< 0.001 *		
		Sex	19.26 ± 10.72	1.80	0.077		
		Mass*sex	-0.09 ± 0.04	-1.977	0.051		
Lean	~ BCI*sex	Intercept	214.51 ± 1.33	160.89	< 0.001 *	562.6	0.644
		BCI	12.28 ± 1.34	9.12	< 0.001 *		
		Sex	3.46 ± 2.07	1.67	0.099		
		BCI*sex	0.85 ± 2.22	0.38	0.702		
	~mass*sex	Intercept	24.13 ± 15.53	1.55	0.125	527.0	0.776
		Body mass (g)	0.78 ± 0.06	12.30	< 0.001 *		
		Sex	-28.60 ± 26.20	-1.09	0.279		
		Mass*sex	0.10 ± 0.11	1.00	0.323		

**denotes significant p-value at α = 0.05*

Table 3. Model coefficients for linear models testing whether a body condition index (BCI) derived from zygomatic width (ZW index) explains observed variation in fat and lean mass in black-tailed prairie dogs pre-winter. Reference group for sex: female.

Component	**Model**	**Independent terms**	**Estimate**	***t***	***p***	**AICc**	**Adjusted R^2**
Fat	~ BCI*sex	Intercept	517.47 ± 10.48	49.36	< 0.001 *	286.9	0.649
		BCI	69.42 ± 12.04	5.77	< 0.001 *		
		Sex	-21.91 ± 16.43	-1.33	0.195		
		BCI*sex	20.57 ± 25.45	0.808	0.427		
	~mass*sex	Intercept	-397.6 ± 128.5	-3.41	0.005 *	277.4	0.753
		Body mass (g)	0.628 ± 0.09	7.14	< 0.001 *		

		Sex	-109.1 ± 227.0	-0.48	0.635		
		Mass*sex	-0.00 ± 0.15	-0.00	0.999		
Lean	~ BCI*sex	Intercept	727.53 ± 12.38	58.79	< 0.001 *	295.9	0.817
		BCI	47.44 ± 14.21	3.34	0.003 *		
		Sex	201.26 ± 19.39	10.38	< 0.001 *		
		BCI*sex	-56.48 ± 30.04	-1.88	0.073		
	~mass*sex	Intercept	-56.00 ± 140.98	-0.40	0.695	282.4	0.889
		Body mass (g)	0.54 ± 0.10	5.57	< 0.001 *		
		Sex	675 ± 249.01	2.71	0.013 *		
		Mass*sex	-0.34 ± 0.16	-2.14	0.043		

**denotes significant p-value at α = 0.05*

Table 4. Model coefficients for linear models testing whether a body condition index (BCI) derived from right hind foot length (RHF index) explains observed variation in fat and lean mass in Columbian ground squirrels pre-winter. Reference group for sex: female.

Component	**Model**	**Independent terms**	**Estimate**	***t***	***p***	**AICc**	**Adjusted R^2**
Fat	~ BCI*sex	Intercept	116.42 ± 4.53	25.71	< 0.001 *	265.2	0.80
		BCI	15.68 ± 5.16	3.04	0.005 *		
		Sex	62.85 ±6.40	9.81	< 0.001 *		
		BCI*sex	1.78 ± 7.09	0.25	0.804		
	~mass*sex	Intercept	-49.70 ± 52.39	-0.95	0.352	266.7	0.80
		Body mass (g)	0.30 ± 0.09	3.18	0.004 *		
		Sex	-10.43 ± 93.38	-0.11	0.912		
		Mass*sex	0.04 ± 0.14	0.26	0.794		
Lean	~ BCI*sex	Intercept	388.37 ± 5.73	67.81	< 0.001 *	279.3	0.83
		BCI	34.54 ± 6.52	5.30	< 0.001 *		
		Sex	83.35 ± 8.1	10.29	< 0.001 *		
		BCI*sex	-14.23 ± 8.96	-1.89	0.124		
	~mass*sex	Intercept	12.61 ± 48.80	0.26	0.789	262.5	0.90
		Body mass (g)	0.67 ± 0.09	7.73	< 0.001 *		
		Sex	78.36 ± 87.00	0.90	0.376		
		Mass*sex	-0.14 ± 0.13	-1.053	0.302		

**denotes significant p-value at α = 0.05*

Table 5. Model coefficients for linear models testing whether a body condition index (BCI) derived from right hind foot length (RHF index) explains observed variation in fat and lean mass in Columbian ground squirrels in spring. Reference group for sex: female.

Component	Model	Independent terms	Estimate	*t*	*p*	AICc	Adjusted R^2
Fat	~ BCI*sex	Intercept	29.50 ± 2.03	14.56	< 0.001 *	664.6	0.59
		BCI	8.34 ± 2.23	3.74	< 0.001 *		
		Sex	30.16 ± 3.18	9.50	< 0.001 *		
		BCI*sex	0.50 ± 3.36	0.148	0.883		
	~mass*sex	Intercept	-35.48 ± 16.84	-2.11	0.038 *	664.9	0.59
		Body mass (g)	0.17 ± 0.04	3.87	< 0.001 *		
		Sex	23.41 ± 27.65	0.85	0.400		
		Mass*sex	-0.02 ± 0.06	-0.35	0.729		
Lean	~ BCI*sex	Intercept	310.09 ± 2.55	121.85	< 0.001 *	701.5	0.89
		BCI	34.54 ± 6.52	12.41	< 0.001 *		
		Sex	70.46 ± 3.99	17.67	< 0.001 *		
		BCI*sex	5.95 ± 4.22	1.41	0.163		
	~mass*sex	Intercept	22.57 ± 14.30	1.58	0.119	638.3	0.95
		Body mass (g)	0.76 ± 0.04	20.25	< 0.001 *		
		Sex	-2.22 ± 23.47	-0.10	0.925		
		Mass*sex	-0.001 ± 0.05	-0.15	0.880		

**denotes significant p-value at α = 0.05*

Table 6. Model coefficients for a set of linear models testing the interactive and singular effects of body condition index (BCI) or body mass (scaled within species) and species on fat and lean mass in red squirrels, prairie dogs, and ground squirrels (pre-winter and spring). Reference species: red squirrels.

Predictor	Component	Independent terms	Estimate	*t*	*p*	AICc	Adjusted R^2
BCI	Fat (g)	Intercept	6.70 ± 2.70	2.485	0.014 *	1981.6	0.98
		BCI	1.57 ± 2.84	0.53	0.596		
		Species (pre-winter prairie dogs)	501.84 ± 5.30	-94.78	< 0.001 *		
		Species (pre-winter ground squirrels)	-141.14 ± 5.10	27.70	< 0.001 *		
		Species (spring ground squirrels)	35.09 ± 3.77	9.31	< 0.001 *		
		BCI*species (pre-winter prairie dogs)	72.52 ± 6.63	10.94	< 0.001 *		
		BCI*species (pre-winter ground squirrels)	15.11 ± 5.55	2.73	0.007 *		
		BCI*species (spring ground squirrels)	7.05 ± 4.00	1.77	0.079		
	Lean (g)	Intercept	215.94 ± 5.74	37.70	< 0.001 *	2305.3	0.93
		BCI	12.56 ± 6.02	2.09	0.039 *		
		Species (pre-winter prairie dogs)	593.58 ± 11.24	52.80	< 0.001 *		
		Species (pre-winter ground squirrels)	214.10 ± 10.82	19.79	< 0.001 *		
		Species (spring ground squirrels)	122.85 ± 8.00	15.36	< 0.001 *		
		BCI*species (pre-winter prairie dogs)	22.24 ± 14.07	1.58	0.115		
		BCI*species (pre-winter ground squirrels)	14.43 ± 11.79	1.23	0.222		
		BCI*species (spring ground squirrels)	24.84 ± 8.48	2.93	0.004 *		
Body mass (scaled)	Fat (g)	Intercept	6.69 ± 2.54	2.64	< 0.001 *	1954.9	0.98
		Body mass (scaled)	1.40 ± 2.62	0.54	< 0.001 *		
		Species (pre-winter prairie dogs)	501.85 ± 54.98	100.84	< 0.001 *		
		Species (pre-winter ground squirrels)	141.15 ± 4.79	29.47	< 0.001 *		

	Species (spring ground squirrels)	35.10 ± 3.54	9.91	< 0.001 *		
	Mass *species (prairie dogs)	61.61 ± 65.16	11.93	< 0.001 *		
	Mass*species (pre-winter ground squirrels)	13.74 ± 4.95	2.77	0.006 *		
	Mass *species (spring ground squirrels)	6.92 ± 3.62	1.91	0.057		
Lean (g)	Intercept	215.83 ± 5.49	39.29	< 0.001 *	2287.3	0.94
	Body mass (scaled)	13.42 ± 5.67	2.37	0.019		
	Species (pre-winter prairie dogs)	593.69 ± 10.78	55.06	< 0.001 *		
	Species (pre-winter ground squirrels)	214.21 ± 10.38	20.65	< 0.001 *		
	Species (spring ground squirrels)	122.96 ± 7.67	16.03	< 0.001 *		
	Mass *species (pre-winter prairie dogs)	27.89 ± 11.18	2.47	0.014 *		
	Mass *species (pre-winter ground squirrels)	15.67 ± 10.73	1.46	0.146		
	Mass *species (spring ground squirrels)	23.89 ± 7.85	3.05	0.003 *		

**denotes significant p-value at α = 0.05*