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Evaluating methods to assess the body condition of female polar bears

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Abstract: An animal’s body condition provides insight into its health, foraging success, and overall fitness. Measures of body composition including proportional fat content are useful indicators of condition. Isotopic dilution is a reliable non-destructive method for estimating the body composition of live mammals, but measurements can potentially be affected by field conditions. Body condition indices (BCI) and energy density models can also be used to assess body condition based on morphological measurements, but may not reliably reflect an animal’s energy stores. Here we evaluate BIA, BCI, and an energy density model in measuring the energy stores of female polar bears (Ursus maritimus). We examine the relationship between total body fat (TBF) derived from isotopic dilution to these alternative methods for 9 female polar bears from 14 captures on the sea ice of the southern Beaufort Sea in April 2014–2016. An energy density model, BCI, and BIA-derived measures of TBF were poor predictors of TBF derived from isotopic dilution. We suggest energy density, BCI, and BIA may not be predictive of an animal’s body fat at fine scales (e.g., among individuals within the same sex, reproductive status, and season). In particular, BIA should provide similar measures of body composition as isotopic dilution, but it failed to reliably measure TBF of individual bears. These limitations in the precision of body condition measures should be considered when planning future studies.

Key words: bioelectrical impedance analysis, body composition, body condition index, body fat, energy density, isotopic dilution, polar bear, Ursus maritimus


Body condition provides an indication of an animal’s energy stores (Speakman 2001, Schulte-Hostedde et al. 2005). Measures of condition are useful to evaluate individual health, foraging success, reproductive potential, and overall fitness as well as to evaluate environmental conditions experienced by the individual (Virgl and Messier 1992, Atkinson and Ramsay 1995, Atkinson et al. 1996, Winstanley et al. 1999, Speakman 2001, Stevenson and Woods 2006, Molnár et al. 2011). In population studies, condition may be one of the first parameters to exhibit measureable change before reproduction and survival (vital rates) effects are detectable (Derocher et al. 2004, Williams et al. 2013, Obbard et al. 2016). Measures of an animal’s energy stores are of particular importance for species that store (and use) large amounts of energy in the form of body fat–adipose tissue as part of a life-history adaptation for dealing with seasonal variation in food availability.

Polar bears (Ursus maritimus) undergo dramatic changes in storage energy as an adaptation to living in an environment where food availability is highly seasonal (Ramsay and Stirling 1988, Stirling and Øritsland 1995). In the late spring and early summer, when access to lipid-rich marine mammal prey such as ringed seals (Pusa hispida) increases, polar bears become hyperphagic and their adipose tissue deposits undergo extensive hypertrophy (Ramsay and Stirling 1988). The percent body fat of most individuals peaks by late summer or autumn and varies according to sex, age class, and reproductive status, with adipose tissue among pregnant females comprising up to half of their total body mass (Atkinson and Ramsay 1995, Atkinson et al. 1996). During other seasons, food availability is less predictable and hence storage of body fat is more variable (Atkinson and Ramsay 1995, Atkinson et al. 1996). Superimposed on this annual cycle of

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body fat are the potential effects of declines in Arctic sea ice, which in some areas appear to be reducing polar bear foraging success (Regehr et al. 2007, 2010; Cherry et al. 2009; Patyk et al. 2015). Given this changing ecosystem, reliable measures of body condition (in particular, energy stores) are needed to evaluate the effects of declines in sea ice on polar bear condition, health, and population viability (e.g., Stirling and Derocher 1993; Stirling et al. 1999; Obbard et al. 2006, 2016; Rode et al. 2010, 2012, 2014b; Patyk et al. 2015).

Various methods have been used to assess the body condition of polar bears, including body condition indices (Stirling et al. 1999, Cattet et al. 2002), lipid content of adipose tissue (Thieman et al. 2006, McKinney et al. 2014, Sciullo et al. 2016), energy density models (Molnár et al. 2009), and measures of body composition (Arnould and Ramsay 1994, Atkinson and Ramsay 1995, Atkinson et al. 1996, Sciullo et al. 2016). These methods differ from one another in the way body condition is conceptualized and in the assumptions associated with measuring it (e.g., Cattet 1990, Green 2001, Speakman 2001, Barthelmess et al. 2006, Schamber et al. 2009, Hwang et al. 2015). In comparison with other methods of condition assessment, body composition analyses facilitate a more direct and absolute evaluation of the amount of stored energy in an animal, especially in species such as polar bears that are known to store energy in large deposits of adipose tissue. Whole-body chemical extraction provides the most accurate measure of body composition (Speakman 2001), but requires sacrificing the animal.

Two methods for empirically measuring the body composition of live animals are isotopic dilution and bioelectrical impedance analysis (BIA). These methods assume an animal’s mass consists of 2 compartments: fat mass and fat-free (lean body) mass with water restricted to the animal’s fat-free mass (Speakman 2001). Based on this assumption, isotopic dilution and BIA can be used to estimate an animal’s total body water (TBW) content, which, in combination with the animal’s body mass and regression equations derived from chemical extraction (e.g., Farley and Robbins 1994), can be used to predict total body fat (TBF) and protein content.

Isotopic dilution has been used for decades to measure the body composition of mammals (Richmond et al. 1962, Nagy and Costa 1980), including wild brown bears (U. arctos) and polar bears (Atkinson and Ramsay 1995; Atkinson et al. 1996; Hilderbrand et al. 1999, 2000; Gau and Case 2002; Harlow et al. 2002; McKinney et al. 2014; Sciullo et al. 2016). Bioelectrical impedance analysis involves measuring the electrical conductance of the body using a known alternating current across electrodes positioned at distal ends of the body (Kushner 1992, Marken Lichtenbelt 2001). This provides a measure of electrical resistance across the body, which, in combination with a measure of the distance between the electrodes and a measure of body mass, can be related to TBW, which is often derived from isotopic dilution (Kushner 1992, Farley and Robbins 1994, Marken Lichtenbelt 2001). Bioelectrical impedance analysis can be rapidly performed, but can be prone to errors depending on the animal’s body position, depth of anesthesia, injuries, ambient and body temperature, and moisture on or in contact with the animal’s body (Farley and Robbins 1994, Marken Lichtenbelt 2001). The last 3 factors are of particular concern for using BIA to measure the body composition of polar bears on the sea ice because of the combination of low and variable ambient temperatures and the potential for water, snow, or ice to affect resistance measures. For example, Farley and Robbins (1994) reported erroneous results in using BIA when bears were resting in standing water. These potential sources of error led Vongraven et al. (2012) to conclude that BIA was unsuitable as a standard monitoring tool for polar bears. Yet, BIA has been used for polar bears on land (Atkinson and Ramsay 1995, Sciullo et al. 2016) and on the sea ice (McKinney et al. 2014). Sciullo et al. (2016) found weak but significant correlations between TBF in polar bears derived from BIA and lipid content in adipose tissue and energy density. Nevertheless, Sciullo et al. (2016) concluded that potential sources of error in the field make BIA impractical for...
monitoring body condition of polar bears. However, unlike lipid content in adipose tissue or energy density models, BIA measures an animal’s body composition following a 2-compartment model and, hence, weak correlations may reflect differences in how these methods assess condition rather than measurement errors. In fact, body composition measures from BIA conducted on polar bears on the sea ice have yet to be evaluated in comparison with body composition measures using techniques that also assume a 2-compartment model (e.g., isotopic dilution).

Given the potential value of BIA as a rapid measure of polar bear body composition, we conducted isotopic dilutions and BIA measurements of female polar bears of the Southern Beaufort Sea subpopulation captured on the sea ice. We used percent TBF as an indicator of bears’ energy stores and evaluated the reliability of body composition measures from BIA in comparison with similar metrics derived from isotopic dilution. We also compared estimates of percent TBF from these 2 methods with estimates of condition derived from a body condition index (Cattet et al. 2002) and an energy density model (Molnar et al. 2009). Both of these alternative condition metrics have been used to monitor changes in body condition within polar bear subpopulations (Obbard et al. 2006, 2016; Rode et al. 2010, 2012, 2014a, b).

**Methods**

We captured adult (≥4 yr) and subadult (2–3 yr) female polar bears without dependent young on the sea ice north of Prudhoe Bay, Alaska, USA, during April 2014–2016. We located polar bears from a helicopter and immobilized them with a rapid-injection dart (Palmer Cap-Chur Equipment, Douglasville, Georgia, USA) containing zolazepam–tiletamine (Telazol®; Zoetis, Parsippany, New Jersey, USA) containing zolazepam–tiletamine (Telazol®; Zoetis, Parsippany, New Jersey, USA [Stirling et al. 1989]). In 2015 and 2016, bears were recaptured 8–11 days later as part of a separate study. We measured total body mass (TBM) at each capture using an electronic load cell suspended from an aluminum tripod. We measured straight-line body length (SLBL) as the straight-line distance from the tip of the nose to the end of the last tail vertebra while bears were sternally recumbent. We measured snout-to-vent length (SVL) following the dorsal contours (Farley and Robbins 1994). Bears that had not been previously captured were aged based on counts of cementum annuli from an extracted vestigial premolar (Calvert and Ramsay 1998). Procedures were approved by the Animal Care and Use Committees of the U.S. Geological Survey, Alaska Science Center and the University of California, Santa Cruz. Research was approved under U.S. Fish and Wildlife Service Marine Mammal Permit MA690038.

**Bioelectrical impedance analysis**

With immobilized bears positioned in sternal recumbency, we attached anterior electrodes to the upper lip at the level of the canines while we attached posterior electrodes to needles positioned approximately 3 cm on either side of the base of the tail (Farley and Robbins 1994). We measured resistance (R) using a Quantum X analyzer (RJL Systems, Clinton Township, Michigan, USA) using an alternating current of 425 μA at 50 kHz. The analyzer has a resistance range of 0–1,000 ohms and a resolution of 0.1 ohms. We took 3 separate resistance measurements and used the average. In 2015–2016, we took BIA, SVL, and TBM measurements at both the initial capture and recapture. Bears were completely immobile and relaxed at the time of measurement.

We calculated TBW from resistance and SVL measurements using the regression equation for polar bears derived from Farley and Robbins (1994), where $\text{TBW} = -1.86 + 0.231 \times (\text{SVL}^2/R) + 0.074 \times (\text{TBM})$. We used measures of TBW to determine measures of TBF based on Farley and Robbins (1994), where $\%\text{TBF} = 98.01 - 1.28 \times (\%\text{TBW})$.

**Isotopic dilution**

Following BIA measurements, we inserted a jugular catheter to facilitate blood sampling and administration of isotopes. We collected an initial blood sample to serve as a baseline measure of D$_2$O. We then injected the bear intravenously with a precisely weighed (±0.01 g; Ohaus Scout Pro, Parsippany, New Jersey, USA) dose of 0.06–0.14 g/kg of 99.9% enriched D$_2$O (Isotec, Inc., Miami–burg, Ohio, USA or Cambridge Isotope Laboratories, Inc., Tewksbury, Massachusetts, USA) with NaCl added to make it 0.9% isotonic and sterilized using a 0.2-μm Millipore filter (Corning, Inc., Corning, New York, USA). On injection, we back-washed the syringe with blood 3 times to ensure all D$_2$O had been injected into the bear. We kept the bear immobilized for 90–120 minutes after the injection of D$_2$O to allow isotope equilibration (Arnould 1990; Farley and Robbins 1994; D.P. Costa, University of California, Santa Cruz, personal communication). We collected serial blood samples 60 minutes, 90 minutes, and 120 minutes after dosing to evaluate equilibration curves (Speakman 1997). Bears recaptured in 2015 and 2016 were again subject to isotopic dilution as described above to measure potential changes in composition. At recapture, we assessed the disappearance rates of D$_2$O between capture and recapture by collection of an initial
blood sample and serial blood samples collected 60 minutes and 90 minutes after dosing of D₂O. We collected blood in evacuated tubes without anticoagulants and centrifuged tubes to separate serum from red blood cells. We stored serum frozen in cryogenic vials at −20°C until analysis.

We analyzed serum samples for D₂O concentration (Metabolic Solutions, Inc., Nashua, New Hampshire, USA). We calculated TBW as the ratio of the amount of D₂O injected to the concentration of D₂O in the body at equilibration per the plateau method (Speakman 1997, eq. 17.11). We used measures of TBW to determine measures of TBF based on Farley and Robbins (1994), where

\[ \%\text{TBF} = 96.85 - 1.33 \times (\%\text{TBW}) \]

**Body condition metrics**

Using data on TBM and SLBL, we used 2 metrics to estimate the body condition of female polar bears captured in this study. The first was an energy density model developed by Molnár et al. (2009). This model estimates structural mass from SLBL and storage mass from SLBL and TBM (Molnár et al. 2009). The model uses body composition measures from previous studies and energy density estimates of fats and proteins to convert storage mass to storage energy (MJ; Molnár et al. 2009). We converted measures of TBM and SLBL to storage energy (E) using the equation for adult female polar bears, where

\[ E = 26.14 \times \text{TBM} - 390.53 \times \text{SLBL}^3 \]  

(Molnár et al. 2009). We converted storage energy to energy density (MJ/kg) by dividing by lean body mass based on the equations of Molnár et al. (2009). We excluded measures from subadult females because storage energy equations have not been developed for this group (Molnár et al. 2009).

The second metric was a residual body condition index (BCI: Cattet et al. 2002). This index uses the standardized residuals from the regression of TBM and SLBL as a measure of condition, with a potential range of −3 to +3 (Cattet et al. 2002). Rode et al. (2014a) used measures of TBM and SLBL from polar bears captured in the Southern Beaufort Sea subpopulation between 1982 and 2013 to develop a BCI for polar bears in the Southern Beaufort Sea subpopulation using the methods of Cattet et al. (2002). We applied the equation from Rode et al. (2014a) to the TBM and SLBL measurements from the bears captured in this study, where

\[ \text{BCI} = (\ln\text{TBM} - 2.29 \times \ln\text{SLBL} + 6.7) / (2.58 - 0.45 \times \ln\text{SLBL}) \]

**Statistical analyses**

Large amounts of food in the stomach (i.e., gut fill) can cause erroneous measures of body composition using either BIA or isotopic dilution (Farley and Robbins 1994, Hilderbrand et al. 1999); therefore, we excluded measurements from bears that were identified to have full stomachs at capture based on stomach palpation. We used paired t-tests to compare estimates of TBW and TBF derived using BIA versus isotopic dilution. We then used linear regressions to evaluate the relationships between (1) BIA and isotopic dilution in their estimates of TBW and TBF; (2) resistance and SVL²/ resistance (i.e., conductor volume) with isotopic dilution-derived TBW (Farley and Robbins 1994) to assess whether measurements of SVL or equations derived from Farley and Robbins (1994) might influence our TBW measurements derived using BIA; (3) BIA-derived TBW and TBF and isotopic dilution-derived TBW and TBF with TBM to assess whether body mass alone is a suitable predictor of body composition; and (4) energy density and BCI compared with TBF derived from isotopic dilution and from BIA. We conducted all analyses in Program R (R Core Team 2014), and considered differences of \( P \leq 0.05 \) to be significant. For regressions, we report the coefficient of determination (\( r^2 \)) and the standard error of the estimate (SEE).

**Results**

We captured 4 adult female polar bears in 2014, 3 adult female and 1 subadult female polar bears in 2015, and 2 adult female polar bears in 2016. In 2015, we recaptured 3 of these bears 9–11 days later. In 2016, we recaptured both bears 8–9 days later. One adult female in 2014 was identified to have a full stomach at capture and was excluded from analyses. Therefore, we used paired BIA and isotopic dilution measurements from 14 captures of 9 individuals. One individual had only a single BIA resistance measurement; all others received 3 resistance measures. Bioelectrical impedance analysis resistance measures within individuals differed by ≤5.8 ohms with a maximum standard error in BIA-derived percent TBF of 1.6% (Fig. 1). Snout-to-vent length measures differed between capture and recapture of individuals by an average of 6.5 cm (SE = 2.1, n = 5). D₂O equilibration occurred within 90 minutes for all measurements (Fig. 2). Measures of TBM, TBW, and TBF were all greater in adult bears than in the subadult (Table 1). Total body water derived from BIA differed significantly from estimates made by isotopic dilution (\( t_{13} = -3.6, P = 0.003 \)). Percent TBF derived from BIA did not differ significantly from estimates made by isotopic dilution (TBF: \( t_{13} = 1.5, P = 0.15 \)).

METHODS TO ASSESS POLAR BEAR BODY CONDITION • Pagano et al. 175

Fig. 1. Mean (± SE) percent total body fat (TBF) determined by bioelectrical impedance analysis based on 3 separate resistance measurements from female polar bears (Ursus maritimus) captured on the sea ice of the southern Beaufort Sea in April 2014–2016.

Kilograms of TBW derived from BIA accounted for 70% of the variation in kg TBW as measured by isotopic dilution (SEE = 8.70, P < 0.001; Fig. 3a), but there was no relationship in percent TBW between the 2 methods ($r^2 = 0.12$, SEE = 2.55, $P = 0.22$; Fig. 3b). Similarly, kg TBF were weakly related between the 2 methods ($r^2 = 0.28$, SEE = 8.39, $P = 0.05$; Fig. 3c), but there was no relationship for percent TBF ($r^2 = 0.12$; SEE = 3.39, $P = 0.22$; Fig. 3d).

Bioelectrical impedance analysis resistance and SVL$^2$/resistance accounted for 63% and 65%, respectively, of the variation in kg TBW derived from isotopic dilution (BIA resistance: SEE = 9.77, $P < 0.001$; SVL$^2$/resistance: SEE = 9.45, $P < 0.001$). Total body mass accounted for 91% of the variation in kg TBW derived from isotopic dilution (SEE = 4.80, $P < 0.001$; Fig. 4a), but only 66% of the variation in kg TBW derived from BIA (SEE = 11.73, $P < 0.001$; Fig. 4b). Total body mass accounted for 58% of the variation in kg TBF as measured by isotopic dilution (SEE = 6.38, $P = 0.002$; Fig. 4c), but was not related to kg TBF derived from BIA ($r^2 = 0.18$, SEE = 15.02, $P = 0.13$; Fig. 4d). Neither percent TBF derived from isotopic dilution nor percent TBF derived from BIA were related to TBM ($r^2 = 0.04$, SEE = 3.54, $P = 0.47$; $r^2 = 0.02$, SEE = 7.95, $P = 0.65$, respectively).

There was a strong relationship between energy density and BCI ($r^2 = 0.99$, SEE = 0.05, $P < 0.001$; Fig. 5). Energy density was related to percent TBF based on BIA ($r^2 = 0.56$, SEE = 5.81, $P = 0.005$; Fig. 6a), but was not related to percent TBF based on isotopic dilution ($r^2 = 0.19$, SEE = 3.37, $P = 0.16$; Fig. 6b). Similarly, BCI was related to BIA-derived percent TBF ($r^2 = 0.40$, SEE = 6.20, $P = 0.02$; Fig. 6c), but not percent TBF derived from isotopic dilution ($r^2 = 0.05$, SEE = 3.53, $P = 0.44$; Fig. 6d). Body condition index was related to kg TBM ($r^2 = 0.51$, SEE = 19.98, $P = 0.004$), but energy density was not related to kg TBM ($r^2 = 0.25$, SEE = 20.2, $P = 0.10$).

Discussion
Our results indicate that BIA may be useful to detect large-scale variations in the body composition of wild polar bears.

Table 1. Mean (± SE) body mass, total body water (TBW), and total body fat (TBF) from female polar bears (Ursus maritimus) captured on the sea ice of the southern Beaufort Sea in April 2014–2016. Bears were both dosed with deuterium oxide (isotopic dilution) and sampled by bioelectrical impedance analysis (BIA).

<table>
<thead>
<tr>
<th>Age class</th>
<th>N</th>
<th>Body mass (kg)</th>
<th>TBW (kg)</th>
<th>TBF (kg)</th>
<th>BIA TBW (kg)</th>
<th>TBF (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ad</td>
<td>12</td>
<td>183.9 ± 6.4</td>
<td>107.4 ± 3.1</td>
<td>35.3 ± 2.9</td>
<td>116.7 ± 5.0</td>
<td>30.8 ± 4.8</td>
</tr>
<tr>
<td>Subad</td>
<td>2</td>
<td>133.6 ± 7.0</td>
<td>75.1 ± 3.2</td>
<td>29.5 ± 2.5</td>
<td>82.6 ± 4.7</td>
<td>25.2 ± 0.9</td>
</tr>
</tbody>
</table>

Fig. 2. Equilibration of deuterium oxide (D$_2$O) enrichment levels (mean ± SE; parts per million) in 9 female polar bears (Ursus maritimus), captured on the sea ice of the southern Beaufort Sea in April 2014–2016, prior to and following an intravenous injection of D$_2$O.
Fig. 3. Relationships between (a) kg total body water (TBW) determined by bioelectrical impedance analysis (BIA) and isotopic dilution (Dilution; $y = 28.49 + 0.66x$), (b) percent TBW determined by BIA and isotopic dilution, (c) kg total body fat (TBF) determined by BIA and isotopic dilution ($y = 25.30 + 0.31x$), and (d) percent TBF determined by BIA and isotopic dilution from female polar bears (*Ursus maritimus*) captured on the sea ice of the southern Beaufort Sea in April 2014–2016. ‘SEE’ is standard error of the estimate.

Polar bears, but may not reflect the fine-scale individual variations in body composition that were apparent using isotopic dilution. Total body water and TBF measured using BIA and isotopic dilution were related when values were unscaled by body mass, which suggests that both methods distinguished differences between overall larger and smaller TBW and TBF pools resulting from differences in body mass. Additionally, there was no difference in percent TBF using either method in a pairwise comparison. However, there was no relationship between percent TBW or TBF estimated by BIA and isotopic dilution. This suggests that BIA may provide a reasonable measure of mean body composition among groups of polar bears (e.g., between sexes and bears of different reproductive statuses), but errors resulting from measurements in the field may affect the resolution of body composition.
METHODS TO ASSESS POLAR BEAR BODY CONDITION

Pagano et al. 177

Fig. 4. Relationships between (a) total body mass (TBM) and kg total body water (TBW) determined by isotopic dilution (Dilution; \( y = 8.95 + 0.53x \)), (b) TBM and kg TBW determined by bioelectrical impedance analysis (BIA; \( y = 10.68 + 0.58x \)), (c) TBM and kg total body fat (TBF) determined by isotopic dilution (\( y = -11.91 + 0.26x \)), and (d) TBM and kg TBF determined by BIA from female polar bears (Ursus maritimus) captured on the sea ice of the southern Beaufort Sea in April 2014–2016. ‘SEE’ is standard error of the estimate.

estimates, thus limiting the utility of BIA in discerning the condition of individual bears within groups (e.g., individuals of the same sex, reproductive status, and season) or in monitoring changes within the same individual over time. Bowen et al. (1999) similarly found BIA suitable for measuring mean TBW among groups of grey seals (Halichoerus grypus), but a poor measure for discerning TBW of individual seals. Thus, caution may be needed in attempting to use BIA as a long-term monitoring tool for polar bears.

The use of BIA for estimating TBW is based on equations in which resistance readings and body length are related to TBW estimated from isotopic dilution (Farley and Robbins 1994). In our study, the relationship between resistance and TBW derived from isotopic dilution was considerably weaker than previously reported (Hoffer et al. 1969, Farley and Robbins 1994, Gales et al. 1994, Bowen et al. 1999). Other studies have shown that relationships between BIA and TBW derived using isotopic dilution can provide suitable measures of TBF in brown and black bears (Farley and Robbins 1994, Hilderbrand et al. 1998). However, calculations of TBF are based on relationships with percent TBW (Farley and Robbins 1994), and given the weak relationship we found between percent TBW using BIA and isotopic dilution,
we would expect a similarly weak relationship in TBF predictions.

Field conditions in our study, which are more extreme for polar bears compared with other bear species, may have affected estimates of TBW using BIA. Moisture, ambient temperature, body temperature, and gut fill are known to affect BIA measurements (Farley and Robbins 1994, Hilderbrand et al. 1998, Marken Lichtenbelt 2001) and may be particularly problematic when using BIA on polar bears on the sea ice in the spring. For example, impedance is known to decline with both skin and body temperature (Marken Lichtenbelt 2001). Ambient temperatures in this study varied by 31°C, rectal temperatures of bears varied by 3°C, and bears were processed while lying on snow and ice. Though other studies have used plastic sheets underneath animals to potentially reduce the loss of electrical current to the ground (Farley and Robbins 1994, Atkinson and Ramsay 1995, Bowen et al. 1999, Sciullo et al. 2016), no data exist to assess whether ground insulation improves the accuracy of resistance measures. Other factors that could affect BIA and our other metrics are common issues in field studies of ursids, whether conducted on the sea ice or land. Wet fur could affect BIA resistance measures as well as inflate body mass measures, which would affect all of our metrics. However, it may be a less likely source of error in our study because bears were relatively dry and swam infrequently (0.3% of the time; A.M. Pagano et al., U.S. Geological Survey, unpublished data). Additionally, gut fill could inflate body mass measures, which would similarly affect all of our metrics. We palpated animals’ stomachs to assess gut fill and excluded the one animal that was assessed to have fed recently. Urine in the bladder has the potential to minimally affect TBW measurements using isotopic dilution (Nagy and Costa 1980), but we were unable to account for this potential source of error. Lastly, field morphometric measures are difficult to measure accurately and have been found to be associated with considerable error among individual researchers (Cattet et al. 1997), which could further affect the accuracy of measures using BIA, energy density models, or BCI metrics; but such measures are not required.
in estimating body composition using isotopic dilution. Although Hilderbrand et al. (1998) found strong correlations between BIA and whole-body chemical extraction in black and brown bears, they found stronger correlations using isotopic dilution and concluded that isotopic dilution was more suitable for field applications given the potential sources of error in using BIA in the field. Our results further support this conclusion, with the caveat that use of isotopic dilution more than doubled our typical processing time of solitary female polar bears, requiring an average of 152 minutes compared with our typical average of 69 minutes (A.M. Pagano et al., unpublished data).

Energy density and BCI also were not related to percent TBF derived from isotopic dilution. Percent TBF differed by <10% among individuals based on isotopic dilution, which may have been insufficient variation to detect significant relationships using indirect measures of condition (i.e., energy density and BCI). Total body fat estimated from BIA was more closely correlated with energy density and BCI than was TBF based on isotopic dilution, which may be a result of BIA, energy density, and BCI all incorporating morphometric measurements in their derivations. Nevertheless, the relationship between percent TBF derived from BIA and energy density was weak ($r^2 = 0.56$) and similar to the relationship reported by Sculillo et al. (2016; $r^2 = 0.49$) from a larger data set of polar bears captured onshore in the Western Hudson Bay subpopulation. Energy density includes both the energetic content of body fat as well as that of non-structural lean tissue (Molnár et al. 2009). Similarly, Cattet et al. (2002) validated the BCI against individual masses of fat and skeletal muscle from dissected polar bears, which would include fat, protein, and some amount of water and would not include lipids contained at the cellular level. Hence, our weak correlations of percent TBF with BCI and energy density may in part be related to differences in the tissues being used to assess body condition. Additionally, both energy density and BCI metrics were developed using data from bears of varying reproductive status, from different seasons, and across a wider range of body masses (and presumably composition) than we used in the current study. Energy density and BCI strongly correlated with one another, which was also reported by Rode et al. (2014a). Our results from isotopic dilution suggest that, at fine scales (i.e., within the same individual or same group, e.g., individuals of the same sex, reproductive status, and season), energy density and BCI may not be predictive of an animal’s body fat. Nevertheless, energy density has been shown to be a strong predictor of reproductive output in polar bears from the Western Hudson Bay subpopulation (Molnár et al. 2011). Further, both energy density and BCI have been found to vary in expected ways, such as females with cubs-of-the-year having lower measures than lone females and females with older cubs, and among seasons (Molnár et al. 2009, Rode et al. 2014a, Obbard et al. 2016). Hence, despite the lack of ability of these metrics to predict TBF at fine scales, energy density and BCI appear to be suitable for evaluating broader, population-level differences and changes in body condition.

Our results indicate that BIA, when used on female polar bears lying on the snow or ice, only coarsely measures body composition and is likely no more advantageous in evaluating polar bear body condition than is the use of an energy density model or BCI, which only require standard morphometric measurements. Most capture studies routinely collect morphometric measurements, so energy density models or BCI can also be used to monitor changes in body condition from historical cross-sectional data sets. However, our results found both the energy density model and BCI failed to predict the percent body fat of lone female polar bears, which suggests that these metrics should not be used to evaluate the condition of polar bears at fine physiological scales or in longitudinal studies.

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