Moving Beyond Body Condition Indices as an Estimate of Fitness in Ecological and Evolutionary Studies

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PERSPECTIVE
Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies

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Summary
1. Body condition indices, measures of body ‘plumpness’ or mass relative to frame size, are often used as a proxy for lipid reserves or fitness-related traits of animals and assumed to be positively related to fitness.
2. The quantification and analysis of body condition indices has been the subject of debate for decades. Here, we summarize three additional concerns with the use of body condition indices.
3. First, body condition index is often poorly correlated with lipid content in animals. Second, even if body condition index and lipid content are correlated, lipid content of an animal may not be the most important aspect of body composition influencing fitness. Finally, neither body condition index nor lipid reserves are likely to be directly positively related to fitness in animals, as many animals homeostatically regulate intermediate levels of condition index or lipid reserves, with both higher and lower values incurring fitness costs.
4. A wide range of analytical methods, including some relatively inexpensive and simple measures, are available for more detailed measures of animal body composition or fitness-related traits. Replacing body condition indices with more direct measures of body composition – even relatively simple measures – can inform understanding of the physiological mechanisms underlying animal responses in a wide range of behavioural, ecological and evolutionary studies.

Key-words: body condition index, fitness, lipid

Introduction
Fitness and fitness-related traits are of key interest in many studies of behaviour, ecology and evolution. Yet, fitness itself can be difficult to define and even more difficult to quantify, and hence, surrogates are often used to estimate fitness or fitness-related traits (Jakob, Marshall & Uetz 1996; McGraw & Haswell 1996; Thompson et al. 2011). While measurements such as lifetime reproductive success may be strongly correlated with fitness, more indirect surrogates may be much less reliable as they are often contingent on a number of assumptions or intermediate relationships.

Body condition indices are frequently used as surrogate of fitness or fitness-related traits (Fig. 1; Jakob, Marshall & Uetz 1996; Speakman 2001; Stevenson & Woods 2006). While the metrics used to quantify body condition index vary, it is often measured by comparing two aspects of an animal’s size: one that is relatively fixed or varies through growth over a long time-scale (e.g. some measure of skeleton or exoskeleton size) with another measure that is more likely to vary in response to short-term changes in fat storage or recent feeding (e.g. mass or girth) (Bolger & Connolly 1989; Hayes & Shonkwiler 2001; Stevenson & Woods 2006). In other words, body condition index often provides a measure of ‘plumpness’ or body size relative to frame size and is often used as a surrogate of lipid content and/or assumed to be directly positively related to fitness (Fig. 1; Jakob, Marshall & Uetz 1996; Speakman 2001; Stevenson & Woods 2006). While the usefulness and quantification of body condition indices have been the subjects of critical debate for decades (Jakob, Marshall & Uetz 1996; Kotiaho 1999; Marshall, Jakob & Uetz 1999; Speakman 2001; Stevenson & Woods 2006; Labocha, Schutz & Hayes 2014), these indices still remain commonly used in a range of behavioural, ecological and evolutionary studies. Much of the debate on the use of body condition indices in the literature over the past several decades has focused
on the quantification and analysis of these indices (Garn, Leonard & Hawthorne 1986; Jakob, Marshall & Uetz 1996; Kotiah 1999; Marshall, Jakob & Uetz 1999; Green 2001; Hayes & Shonkwiler 2001; Schulte-Hostedde, Millar & Hickling 2001; Schulte-Hostedde et al. 2005; Peig & Green 2009, 2010; Labocha, Schutz & Hayes 2014). At least 17 different indices have been developed, and there is little consensus on which, if any, is best (Jakob, Marshall & Uetz 1996; Kotiah 1999; Marshall, Jakob & Uetz 1999; Peig & Green 2009, 2010; Labocha, Schutz & Hayes 2014). This is an important discussion because the particular method chosen can affect interpretations of data and overall conclusions. While the debate over the analysis and quantification of body condition index has yet to be resolved, there are other more significant problems with body condition indices that have received less attention in the literature (Speakman 2001; Stevenson & Woods 2006; Peig & Green 2009, 2010).

We discuss three additional problems associated with the use of body condition indices as a surrogate for fitness or fitness-related traits (Table 1). We contend that the problems associated with quantifying, analysing and interpreting body condition indices outweigh their benefits. More direct measurements or estimates of the physiological state, composition or fitness-related traits of animals can be relatively simple and inexpensive and provide a greater ability to integrate animal physiology with behaviour, life history, ecology and evolution (Table 2).

Problems with body condition indices

Does body condition measure lipid content or reserves?

A significant problem with body condition indices is that they assume that changes in the volume or mass of an animal’s body are due to a single or primary cause, such as lipid content (Table 1). While several studies have found significant relationships between body condition index and lipid content of animals, these relationships are often weak (Krebs & Singleton 1993; Schulte-Hostedde, Millar & Hickling 2001; Labocha, Schutz & Hayes 2014). For example, body condition index (i.e. residual of body length vs. mass) was more strongly related to lean tissue ($r^2 = 0.14-0.45$) and water content ($r^2 = 0.26-0.69$) than fat content ($r^2 = 0.07-0.10$) in five species of small mammals (Schulte-Hostedde, Millar & Hickling 2001). In another study that compared 17 different body condition indices, all were poor predictors of body fat content in mice (Labocha, Schutz & Hayes 2014). Multiple regression models that incorporated measurements of several morphological traits were better at predicting fat content but only had $r^2$ values of 0.17–0.55, showing that even these better models often explained less than half of the variation in body fat content (Labocha, Schutz & Hayes 2014). The low ability of body condition to predict lipid content is likely because variation in the size or volume of animal bodies can be due to a number of different factors including gut contents (i.e. undigested food), lipid reserves, protein (e.g. muscle, protein storage), water, reproductive status and parasite load (Wang, Pierson & Heymsfield 1992; Speakman 2001; Moya-Larario et al. 2008). In particular, water and lipid contents of animals are often negatively correlated with each other (Speakman 2001). Animal bodies are multivariate and the many components that can change along with their interrelatedness complicate the interpretation of body

Table 1. Summary of the problems associated with body condition indices

<table>
<thead>
<tr>
<th>Problem</th>
<th>Evidence</th>
<th>Consequences</th>
<th>Solution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Does body condition measure lipid content or reserves?</td>
<td>Low correlation coefficients between BCI and fat content&lt;sup&gt;1,2,3,4&lt;/sup&gt;</td>
<td>BCI are coarse and not sensitive to small changes in body composition</td>
<td>Use more direct measures of fat content or body composition (Table 2)</td>
</tr>
<tr>
<td>Is body lipid an appropriate currency?</td>
<td>Negative correlation between fat and water contents&lt;sup&gt;5&lt;/sup&gt;</td>
<td>Animals can have the same BCI but different health or fitness&lt;sup&gt;6,7,8&lt;/sup&gt;</td>
<td>Test the relationship between body composition (lipid and other measures) and fitness (Fig. 2)</td>
</tr>
<tr>
<td>Does maximization of body condition index or lipid equate to maximal fitness?</td>
<td>Fitness can be related to other aspects of body composition&lt;sup&gt;7,8,9&lt;/sup&gt;</td>
<td>Interpretations based on lipid data alone may be misleading</td>
<td>Test the relationship between BCI (or other surrogates) and fitness or use a more direct measure of fitness or health (Table 2)</td>
</tr>
</tbody>
</table>

<sup>1</sup>Krebs & Singleton (1993); 2Schulte-Hostedde, Millar & Hickling (2001); 3Labocha, Schutz & Hayes (2014); 4Garn, Leonard & Hawthorne (1986); 5Speakman (2001); 6Yajnik & Yudkin (2004); 7Ahima & Lazar (2013); 8Romero-Corral et al. (2008); 9Barry & Wilder (2013); 10Liu & Manson (2001); 11WHO Expert Consultation (2004); 12Stern & Elser (2002); 13Frost et al. (2005); 14Persson et al. (2010).
condition indices and their ability to detect changes in any one aspect of animal body composition (e.g. lipid content; Speakman 2001).

**IS BODY LIPID AN APPROPRIATE CURRENCY?**

Body condition indices are often used as a proxy for lipid content of animals, and both body condition index and lipid content are assumed to be proxies for animal fitness (Table 1, Fig. 1; Jakob, Marshall & Uetz 1996). To achieve high fitness, an animal must survive a range of challenges (e.g. starvation, abiotic conditions, predators, parasites and disease) long enough to reproduce and accumulate sufficient resources to produce offspring. Lipid can enhance fitness in several ways, including as energy reserves (e.g. for hibernation, migration or to avoid starvation); insulation against harsh abiotic conditions; and protection from injury. However, lipid content is not the only aspect of body composition that affects fitness. An animal can have plenty of lipid but have low reproductive success if it is deficient in other nutrients (e.g. protein, vitamins, minerals), needed to reproduce (e.g. Nie et al. 2014) or maintain healthy metabolic function (e.g. immune system; Ponton et al. 2013).

There may be many situations where lipid content is not a predictor of fitness-related traits. For example, in a study where praying mantids were fed one of two different diet treatments, the female mantids with higher lipid content in their bodies had half as many eggs and were much less attractive to males than the females with lower lipid content (Barry & Wilder 2013). The females with high lipid content in their bodies had fed on higher lipid diets. Presumably, this diet had more lipid and less protein than the females needed for egg production, and females stored the excess

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**Table 2. Alternatives to body condition indices for measuring composition and physiology**

<table>
<thead>
<tr>
<th>Measure</th>
<th>Assay</th>
<th>Benefits</th>
<th>Disadvantages/Costs</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body Composition</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fat Lean Tissue and Bone Content</td>
<td>Dual X-ray Absorptiometry&lt;sup&gt;1,2,3&lt;/sup&gt;</td>
<td>Accurate, noninvasive</td>
<td>Expensive machine, only two sizes: large (human-sized) and small (rodent-sized)</td>
</tr>
<tr>
<td>Lipid</td>
<td>Bioelectrical Impedance&lt;sup&gt;4,5,6&lt;/sup&gt;</td>
<td>Portable, noninvasive estimate of fat content, more reliable than BCI</td>
<td>Needs to be calibrated, primarily used for mammals</td>
</tr>
<tr>
<td>Lean Body Content</td>
<td>Gravimetric Lipid Assay&lt;sup&gt;7&lt;/sup&gt;</td>
<td>Direct measure of fat, inexpensive</td>
<td>Destructive sampling</td>
</tr>
<tr>
<td>Protein</td>
<td>Bradford Assay&lt;sup&gt;8&lt;/sup&gt;</td>
<td>Relatively inexpensive</td>
<td>Can be less reliable on samples with skewed amino acid compositions, especially arginine, lysine and histidine</td>
</tr>
<tr>
<td>Amino Acids or Fatty Acids</td>
<td>Mass Spectrometer&lt;sup&gt;10,11&lt;/sup&gt;</td>
<td>Precise data on amino acid and fatty acid content</td>
<td>Expensive machine</td>
</tr>
<tr>
<td>Elements</td>
<td>High-Performance Liquid Chromatography (HPLC)&lt;sup&gt;12,13&lt;/sup&gt;</td>
<td>Precise data on amino acid and fatty acid content</td>
<td>Expensive machine</td>
</tr>
<tr>
<td></td>
<td>Carbon, Hydrogen and Nitrogen Analysis (CHN)&lt;sup&gt;14&lt;/sup&gt;</td>
<td>A single, small sample (&lt;2 mg) can provide data on all three elements</td>
<td>Expensive machine</td>
</tr>
<tr>
<td>Physiology</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gene Expression</td>
<td>qRT-PCR&lt;sup&gt;15&lt;/sup&gt;</td>
<td>Can be used to measure a wide range of traits</td>
<td>Can require significant optimization for less well-studied species</td>
</tr>
<tr>
<td>Immune Response</td>
<td>Phenoloxidase, Lysozyme, Encapsulation Assay, etc.&lt;sup&gt;16&lt;/sup&gt;</td>
<td>Can provide information on constitutive and induced defences of animals</td>
<td>It is important to consider multiple aspects of the immune system as they can respond differently to treatments</td>
</tr>
<tr>
<td>Hormones</td>
<td>Hormone Assays&lt;sup&gt;17&lt;/sup&gt;</td>
<td>Can be used to assay a range of factors related to health including stress (e.g. cortisol)</td>
<td>There are many hormones, and it is important to understand which may be more important for the goal of a study</td>
</tr>
</tbody>
</table>

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<sup>1</sup>Svendsen et al. (1993); <sup>2</sup>Pietrobelli et al. (1996); <sup>3</sup>Nagy (2001); <sup>4</sup>Lichtenbelt (2001); <sup>5</sup>Hwang, Lariviére & Messier (2005); <sup>6</sup>Barthelmess, Phillips & Schuckers (2006); <sup>7</sup>Reynolds & Kunz (2001); <sup>8</sup>Zor & Selinger (1996); <sup>9</sup>Strug et al. (2014); <sup>10</sup>Vetter & Thurnhofer (2007); <sup>11</sup>Maleknia & Johnson (2012); <sup>12</sup>Hill et al. (1979); <sup>13</sup>Chaytor (1987); <sup>14</sup>Sterner & Elser (2002); <sup>15</sup>VanGuilder, Vrana & Freeman (2008); <sup>16</sup>Schulenburg et al. (2009); <sup>17</sup>Loraine & Bell (1971).
lipid and did not produce as many eggs (Barry & Wilder 2013). Hence, females with lower lipid content had higher fitness-related traits. For reproducing females, especially species that only live for 1 year or that are semelparous, high lipid reserves may not be necessary as most nutrients and energy should be invested into offspring production.

Even if lipid is an important measure in an animal, whole-body lipid content (e.g. measured directly or estimated by body condition index) may be poorly correlated with health or evolutionary fitness due to the health consequences of different lipid storage deposits. For example, in humans, intra-abdominal fat deposits are more strongly correlated with obesity-related health consequences than subcutaneous fat (Fox et al. 2007). The health consequences of different fat deposits are one important reason why BMI (body mass index, which is a body condition index for humans) is a poor predictor of morbidity and mortality in humans and why people with similar BMI can have different metabolic health (e.g. metabolically healthy obese; Romero-Corral et al. 2008; Ahima & Lazar 2013; Roberson et al. 2014; Solon-Biet et al. 2014).

**DOES MAXIMIZATION OF BODY CONDITION INDEX OR LIPID EQUATE TO MAXIMAL FITNESS?**

Body condition indices typically assume that body condition index and lipid content are positively and monotonically related to fitness or some component of fitness. However, in some situations, this is clearly not the case. For example, the body condition index of reproducing females changes with reproductive status. Following fertilization, females gain significant amounts of weight and increase in body condition as they synthesize eggs or gestate offspring. Then, at birth or egg laying, females experience a rapid loss of body condition index and may return to a level similar to that before reproduction. Yet, despite similar body condition indices, prereproductive and postparturition females have very different fitness. In natural populations, measuring body condition index values without accounting for reproductive state or offspring production can provide misleading estimates of fitness (e.g. low condition females may have just produced offspring) or highly variable data (e.g. nonsynchronously reproducing species). While accounting for reproduction may be easier in species with parental care, it may be difficult or impossible in many other species, especially many arthropods.

More generally, there is evidence that the relationship between body condition index and measures of lipid reserves and fitness is nonlinear (Table 1). For example, many animals will homeostatically regulate their body composition (e.g. C:N, % lipid) to avoid extremes when possible (Sterner & Elser 2002; Frost et al. 2005; Persson et al. 2010). Animals use a range of preigestive (e.g. diet regulation) and postigestive (e.g. enzymes, thermoregulation) mechanisms for regulating their body composition (Frost et al. 2005; Clissold et al. 2010; Simpson & Raubenheimer 2012). The ability to regulate lipid reserves to particular levels is especially pronounced in hibernating species. These animals maintain relatively lower lipid reserves in the active season and much higher levels preceding hibernation as energy reserves (Hilderbrand et al. 2000; Bartness, Demas & Song 2002; Król et al. 2005). For example, in some rodents, these lipid set points are regulated by photoperiod such that under longer day lengths, the lipid content of individuals is maintained at a level up to three times higher than the same animal under short day lengths (Hilderbrand et al. 2000; Bartness, Demas & Song 2002; Król et al. 2005). Hence, many animals do not attempt to maximize their lipid content or body condition index (i.e. relative ‘plumpness’ and ratio of mass to skeleton size). Animals likely have an optimum or peak body condition index value at which fitness is maximized. Peak body condition index values are unlikely to be generalizable and may differ according to sex (Lease & Wolf 2011), developmental stage (Chyb & Simpson 1990), season (Raubenheimer et al. 2007), epigenetics (McMillen & Robinson 2005; Gluckman & Hanson 2006a) and population-level differences (Warbrick-Smith et al. 2006; Kristensen et al. 2011).

Animals may regulate body condition index or lipid content to intermediate values because there can be negative fitness consequences of very low (e.g. malnutrition) and high (e.g. obesity) values. This is well known in humans where there is a U-shaped relationship between body mass index and morbidity and mortality (Liu & Manson 2001; WHO Expert Consultation 2004). A U-shaped relationship between body condition index and morbidity or mortality may also exist for other animals besides humans. Negative health consequences of too high lipid content, including obesity and reduced immune function, have been observed in companion animals and a wide range of wild animals (McNamara & Houston 1990; Crane 1991; McNamara et al. 2005; Goodchild & Schwitzer 2008; German et al. 2010; Klimentidis et al. 2011; Raubenheimer et al. 2015).

It remains unclear how often animals gain excessive weight in nature (i.e. not due to eggs or offspring). Some evidence suggests that the average weight of companion animals, laboratory animals and wild animals in anthropogenically disturbed environments has been increasing over time (Klimentidis et al. 2011; Raubenheimer et al. 2015). However, in many natural environments, normal homeostatic regulation of food and nutrient acquisition would be expected to limit the extent to which animals gain excessive weight or lipid reserves, as will limited availability of food or other constraints on feeding. Nevertheless, the assumption that high body condition indices or high lipid content equates to high levels of fitness or lifetime reproductive success needs to be tested on a case-by-case basis (Speakman 2001; Labocha, Schutz & Hayes 2014).

**When is measuring body condition index appropriate?**

Measures of body condition index relate the mass or volume of an animal to a fixed measure of the animal’s
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Compositional Measures

Body condition index is often used as a surrogate of lipid content. Lipid is one of several common measures of body composition, which also includes skeleton mass or density (exo- or endoskeleton), protein content, muscle mass and water content. Measures of body composition can be useful because they can indicate the pool of available resources to fuel metabolic activities or attributes that may be related to fitness (e.g. muscle mass or skeleton density). There are many different compositional and physiological assays (Table 2; Speakman 2001; Wagner et al. 2013). In many cases, especially early stages of study, it may be unclear which aspects of physiology or composition will change with experimental treatment or be correlated with an ecological variable. In addition, only measuring particular small-scale variables can potentially miss other unexpected but important variables. In these cases, a hierarchical approach involving multiple measurements of physiology or composition that transitions from coarser to finer scales of resolution may be useful (e.g. Fig. 1 in Wilder 2011). For example, preliminary studies could examine broad scales of body composition (e.g. lipid, protein and water) and further studies or measurements can be made at higher resolutions (e.g. fatty acids, amino acids and micronutrients) (Table 2). Recent technological and methodological advances have increased the availability and decreased the cost of a wide range of assays to measure the biochemical composition and physiology of animals at different scales (Speakman 2001; Wagner et al. 2013). Even relatively simple measures can provide useful information about the body composition of animals. For example, weighing animals before and after drying and before and after soaking in chloroform or a similar solvent can provide data on the water, lipid and lean mass contents of animals (Table 2). More detailed analyses (e.g. protein, amino acid and fatty acid) can then be done to further explore body composition. Speakman (2001) and Wagner et al. (2013) provided overviews and details of a range of measures of animal composition and physiology including some noninvasive techniques.

One of the strongest arguments for using body condition indices, despite their limitations, is that they are noninvasive and do not require injuring or killing study animals. This may be particularly important for ethical reasons (Stevenson & Woods 2006) or studies in which repeated measurements or manipulations are conducted over time. There are two potential solutions to this problem. First, there are many detailed measures of animal physiology or composition that can be conducted without killing animals (reviewed in Speakman 2001; Stevenson & Woods 2006). These techniques include measures of blood chemistry (e.g. circulating stress hormones, nutrients or immune response), isotopic dilution, bioelectrical impedance, dual-energy X-ray absorptiometry and magnetic resonance imaging (Speakman 2001; Stevenson & Woods 2006). The benefits and costs of each of these techniques are summarized in detail in Table 2. Secondly, for those assays that require sacrificing animals (e.g. total body composition), investigators can increase the initial sample size of individuals in a study and randomly sacrifice a subset of animals at sampling periods to gain more detailed data on how animal physiology or composition changes with time. A relatively small increase in sample size (i.e. to accommodate periodic destructive sampling to measure body composition) can significantly increase the information on the physiological consequences of experimental treatments in ecological and evolutionary studies.

Testing the Relationship Between Composition and Fitness

The body composition of an animal is very likely to have important consequences for fitness. Consequently, maintenance of body composition should be relatively homoeostatic all else being equal (Sterner & Elser 2002; Frost et al. 2005; Persson et al. 2010). Any variation in body composition is likely due to external factors or genetic differences that influence the acquisition, allocation or use of...
resources in the body (Boggs 2009) and these, in turn, can affect fitness. For example, low food availability typically results in low lipid reserves. While low lipid reserves reduce starvation tolerance, other consequences of low food availability (e.g. changes in metabolic rate, activity levels and hormone levels) could interact with, intensify or dampen the effects of low lipid reserves on starvation. In spiders, extended periods of starvation result in reductions in metabolic rate that buffer the effects of food limitation on starvation tolerance by decreasing the rate at which lipid reserves are depleted (Stoltz, Hanna & Andrade 2010; Wilder 2011). Hence, body composition should be viewed as one among several mechanisms through which external factors or genotypes can influence fitness. We therefore recommend a multistage approach to testing the consequences of body composition for fitness in which investigators test the relationship between external factors or genotype and body composition and then the relationships between body composition, external factors or genotype and fitness (Fig. 2).

Multivariate response surfaces may be particularly useful for examining the relationships between external factors, body composition (e.g. lipid and protein contents) and fitness. Response surfaces of fitness measures and other variables of interest can be mapped onto experimentally-generated or naturally occurring bi-coordinate arrays of protein (e.g. \(x\)-axis) vs. lipid (e.g. \(y\)-axis) derived from populations of individuals subjected to different treatments or external influences. For example, Wilder et al. (2013) tested whether the trophic level of an arthropod (\(z\)-axis) was related to the protein (\(x\)-axis) and lipid (\(y\)-axis) contents of its body (see Fig. 1 in Wilder et al. 2013). Statistical analysis can be performed using multivariate (e.g. how is a factor related to body lipid and protein as responses) or univariate (e.g. how is body lipid and protein related to a measure of fitness) generalized linear or additive models (GLM or GAM).

A variant of this approach is needed when measures of composition and fitness have to be taken from separate cohorts of individuals (e.g. when destructive sampling of composition is necessary). For example, Lee & Jang (2014) tested the relationship between body composition and starvation tolerance by feeding Drosophila melanogaster a range of diets, assaying separate sets of individuals on each of their treatments for body composition (lipid and lipid-free body mass) and starvation tolerance, and plotting the relationship between these variables using a nutritional landscape (see Figure 6 in Lee & Jang 2014). Alternatively, investigators could choose fitness measures that can be done simultaneously with compositional measures. For example, in a study of praying mantids, investigators sacrificed individuals after a fixed treatment period, counted the number of eggs within the ovaries as a surrogate for reproductive output and used the bodies and eggs for compositional analyses (Fig. 2b; Barry & Wilder 2013).

**Conclusions**

Body condition indices have been attractive metrics in studies of behaviour, ecology and evolution because they are easy to measure and have been presumed to provide an estimate of fitness or fitness-related traits (Jakob, Marshall & Uetz 1996). However, body condition indices are often not strongly correlated with lipid reserves, lipid reserves may not be a good proxy of fitness, and intermediate lipid reserves or body condition index may be better for fitness than maximization of these values. These critiques cast doubt on the veracity of body condition indices as estimates of fitness or fitness-related traits. Further study of a range of related questions is necessary to resolve the relationships between body condition, composition and fitness, including: Which aspects of animal body composition are correlated in their response to various experimental treatments? What are the importance of lipid and other nutrient reserves for animal fitness? and Are there intermediate values of lipid reserves, relative body mass, food and nutrient intakes, etc. at which fitness is maximized and how do these intermediate values vary among animals and across time?

Because of these problems, body condition indices are open to a wide range of interpretations and provide relatively little insight into fitness-related traits of animals and their physiological basis. In the worst case, interpretations based on body condition index or lipid reserves can conflict with fitness-related traits (e.g. mantids with higher lipid reserves had fewer eggs and attracted fewer males; Barry & Wilder 2013). Echoing calls from previous work (Speakman 2001; Labocha, Schutz & Hayes 2014), we recommend that measures of body condition index largely be abandoned in ecological or behavioural studies. More direct measures of animal composition (e.g. Table 2;
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