JOHN R. SPEAKMAN

Introduction

Interest in the body condition of animals in the wild has long been an important aspect of animal ecology. Perhaps because there is an intuitive feeling that understanding something about the status of an animal – in terms of its body 'condition' – might provide a suitable window through which we can start to perceive components of an animal's fitness. The underlying premise behind this belief appears to be that an animal that is in 'good' condition is more likely to be a fitter member of the population than an animal that is in 'poor' condition. This notion may derive from the impression that the individual in 'good' condition has had the ability to not only satisfy all its requirements but also to take good care of itself. In addition, the animal may also have had time to deposit a healthy fat store that would see it through times of food scarcity. In contrast, the poor animal may be suffering from the ravages of a disease or simply be incapable of securing a living at the same time as managing to maintain itself. Intuitively therefore, by quantifying body condition, we may also be quantifying in a single measure these diverse factors that comprise our understanding of the term 'fitness'. Moreover, measuring the body conditions of the animals that live in a given area may not only tell us something about the animals but can perhaps also inform us about the area itself: its productivity, and the extent to which it can supply resources to sustain the population of animals that are living there.

More recently these notions have been added to by a body of work that has explicitly attempted to address the question of the adaptive nature of fat storage. In particular, these models have considered the level of fat that animals should store in their bodies (assuming they are not nutrient limited). The models predict that fat storage should be a responsive trait

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to fluctuations in the levels of predation along with the risks of starvation. When the risks of future shortfalls in energy supply increase, animals are predicted to elevate their body fat storage to enable them to ride out periods of difficulty. Conversely, if there is an increased risk of predation engendered by carrying around a large fat store, when predation risk is generally elevated animals might do better to carry around less fat.

Whatever the reasons, it is clear that there is a considerable and continuing demand among animal ecologists for methods that allow an assessment of the body condition (compositions) of their subject species. Probably one of the most popular methods for 'measuring' body composition of animals is to calculate some form of 'condition index'. The underlying premise of this method is the clear fact that individual animals are not all the same size. Hence, although measuring body mass gives a good indication of the total amount of tissue that an animal is carrying around, one might anticipate that bigger individuals would be heavier simply by virtue of their greater size. Overall body mass may be a poor measure of condition, but if one could somehow take size out of the equation, one would have an easily utilized method for 'measuring' animal body condition. The classical manner in which this has been done is to measure a linear aspect of the animals' body size (such as the length of its body) and then calculate a 'condition' index simply by dividing the mass by the length.

This was exactly the method I used in a paper in 1986 to express the body condition of immature bats and to try and relate spatial variations in this condition index (a) to differences in habitat quality around their roosts and (b) to the likelihood of the male individuals becoming sexually mature (Speakman and Racey, 1986). In that case we used body mass divided by the length of the bat's forearm to calculate a 'condition index'. Forearm length in bats is a repeatable and frequently used measure of 'size'. I think that most ecologists nowadays would be aware of the problems of scaling relationships and the difficulties that are attached to the derivation of such simple ratio based indices when the scaling is not isometric (although papers regularly still appear that ignore these problems) (see Packard and Boardman, 1987 for a full discussion). One might imagine that the difficulties attached to derivation of ratios are eliminated by utilizing more appropriate and sophisticated statistical approaches – such as regression analysis followed by the derivation of residuals. In their thought-provoking chapter in the first part of this book, Jack Hayes and Scott Shonkwiler (Chapter 1) show us the fallacy of relying on this reasoning and how even condition indices that appear to be derived using sophisticated statistical methods are, in fact, fraught with difficulties in derivation and interpretation.

What then is the animal ecologist expected to do? The obvious alternative is to resort to a more direct form of measurement, the most direct of which is chemical analysis. Chemical analyses of body composition have a long pedigree, particularly in the agricultural arena. Appropriate methods which minimize errors in the determinations have been worked out, and these have been summarized by Scott Reynolds and Tom Kunz in their chapter (Chapter 2). By adopting these methods, there is no doubt that the result is a precise and accurate breakdown of the body into its constituent aspects, providing in detail all the information an ecologist might need. Although this method beats the body condition index hands down when it comes to accuracy and precision, it has a clear drawback. The animal involved dies to give us the answer. Apart from the clear ethical concerns that such actions may pose, particularly where the subject species is rare or endangered, this action closes off the opportunity to explore the factors which influence variation in body composition within individuals over time.

One is therefore faced with a choice between two very different approaches: an approach that is completely non-invasive that may be dogged by problems of derivation and interpretation, or an ultimately invasive procedure that may be ethically dubious, incompatible with other aspects of the study, but precise and accurate. In the gap between these two alternatives are a group of methods that form the focus of the second part of this book. These are non-destructive methods that allow individual estimates of body composition, of varying accuracy and precision, but without the need to kill the subject to get the answer. However, before we get carried away on a wave of ethical self- congratulation, it is perhaps important to point out immediately that many animals do die in the process of validating these methods against the gold standard of chemical analysis. The methods may not therefore be quite as benign as they initially appear – a point that will be reiterated at several points throughout the text. Nevertheless, the methods do open up the possibilities of repeated measurements that are closed off by chemical analysis, and for most techniques they do provide a reduction in the degree to which animals are killed, compared with the numbers that might be destroyed if chemical analysis were the only alternative available.

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The non-invasive methods included in this book fall into three natural groups. First, there are the methods that are based on some form of dilution principle. These include isotope-based methodologies that are the focus of my own contribution to the volume, which was co-authored by Henk Visser, Sally Ward and Ela Król (Chapter 3), and the lipid soluble gas methods explained by Brian Henen (Chapter 4). The second group of methods are those which exploit the electrical properties of body tissues to assess their composition – these include the chapter by Ian Scott, Colin Selman, Ian Mitchell and Peter Evans (Chapter 5), which concerns total body electrical conductivity (TOBEC) and the chapter by Wouter van Marken Lichtenbelt that covers bio-impedance analysis (BIA), a method used frequently in the clinical setting but increasingly being used with animals. Finally, the last two methods are based on the absorption and reflection properties of different tissues. These include a chapter by Matthias Starck, Maurine Dietz and Theunis Piersma on ultrasound imaging (Chapter 7) and finally a chapter by Tim Nagy on dual-energy X-ray absorptiometry (Chapter 8), recent machine developments of which have opened up tremendous opportunities for the study of small animals.

I am aware that, in selecting these methods, I have omitted several very powerful approaches to the non-destructive determination of body composition. These include, for example, computed tomography (CT) and magnetic resonance imaging (MRI) methods. I chose to omit these deliberately because, at present, these methods are effectively unavailable for the small animal ecologist, partly because the machines are generally prohibitively expensive, but also because even when they are available they are not portable, meaning animals have to be transported to the machines, rather than the reverse. In my mind, this sets them apart from the methods that are included in this volume because they are primarily laboratory methods rather than field methods.

Throughout the book we have attempted to standardize the use of a number of terms to avoid confusion. Body mass: is the total body mass including gut contents if present. Several different models have been used to subdivide the total body mass into separate components. These models have generally been called the two-, three- and four-compartment models reflecting the different numbers of compartments into which the body is subdivided. An unfortunate problem is that similar terms are used within each of these models to describe compartments that are not exactly equivalent. Hence the lean component of the body under the two-compartment model is not the same as the lean compartment under the

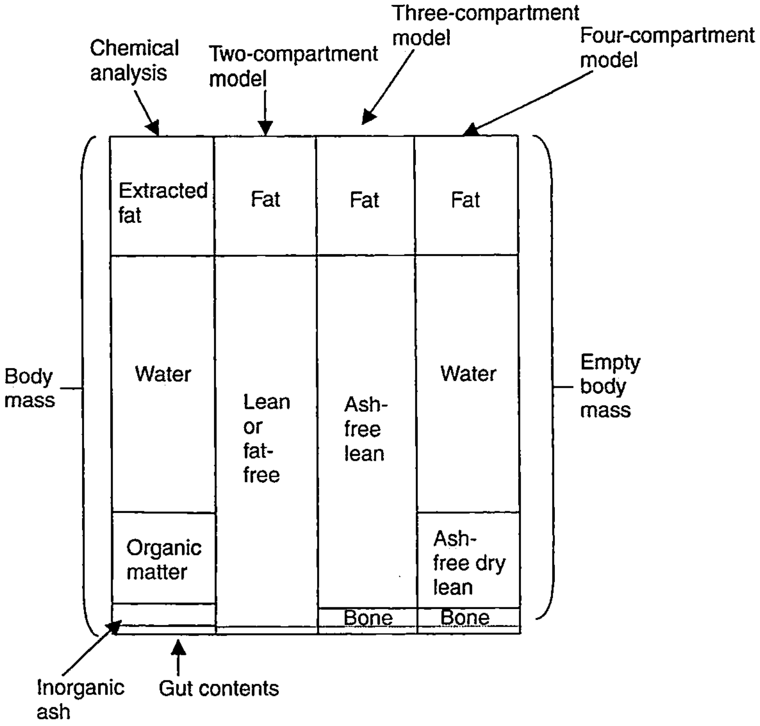

Fig. 1. Inter-relationships of different terms describing body composition analysis.

three- or four- compartment model. The subdivision of the body under different models is illustrated in Fig. 1, alongside the relationship of these divisions to the subdivision of the body when using chemical analysis. During chemical analysis, the gut contents are generally separated from the rest of the body. The mass of the remaining body is often called the 'empty body mass'. The mass of the gut contents can vary enormously, depending on the species under study. In ruminants, it can comprise a considerable portion of the total body mass. In animals that have been starving, they may be undetectable. The remaining body is separated into four constituents – extracted fat, water, organic matter and inorganic ash. Because the fat is extracted chemically, it is important to recognize that some of this fat will consist of structural lipids that are unavailable for utilization as an energy source by the animal in question. Inorganic ash derives principally from the skeleton. However, there is also a contribution from inorganic molecules spread throughout the body. Inorganic

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ash will therefore generally exceed the bone mineral content. In addition, the 'ash' does not exist as such within the body because the result of chemical analysis is to oxidize the inorganic ions. There is consequently an addition of atmospheric oxygen to the mass during this process of oxidation. In the two-compartment model, the body is subdivided into fat and non-fat compartments. The fat compartment is equivalent to the extracted fat from chemical analysis. This is generally called the 'fat mass' or the 'body fat mass'. It is important to distinguish this from the 'fat tissue mass' which is the mass of the fat tissues dissected out from the carcass. Fat tissue contains not only fat but all the cellular components in which the fat is stored and a complex supply of nervous tissue and blood. Consequently, fat tissue includes a variable proportion of non-fat organic matter and water. The non-fat compartment contains everything that is not fat (often including gut contents) and is also frequently referred to as the 'lean mass', the 'lean body mass' or the 'fat-free mass'. In the three-compartment model, the non-fat compartment is subdivided into the bone mineral content, which is sometimes also referred to as the skeletal mass, and the balance which consists of the body water and non-fat organic matter. This is also generally termed the 'lean mass' or 'lean body mass' or more correctly the 'ash-free lean mass'. As with fat mass and fat tissue mass, the bone mineral content is not directly equivalent to bone tissue mass, which is the mass of bones dissected out from a carcass. Bone tissue mass includes a considerable portion of organic tissue and water, above the mineral content. Finally, in the four-compartment model, the water content of the lean portion of the body is separated out – leaving the non-fat organic fraction, which is sometimes referred to as the 'dry lean mass' or 'ash-free dry lean mass'.

I selected authors for the chapters who have considerable practical experience with the methods that they have written about. This was important because each chapter contains not only a theoretical overview of the underlying principles by which each method works, but also invaluable practical advice on what to look out for when utilizing the methods in the field or laboratory. All the chapters were peer reviewed, normally by two independent referees who also had experience in the given field, in one case by only one referee, and for one chapter (TOBEC) by three referees, at the request of the publisher.

I sincerely hope you will find this book useful to guide you about decisions over what methods may suit your own study, and as a practical handbook during execution of any particular piece of work.

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JACK P. HAYES AND J. SCOTT SHONKWILER

1

Morphometric indicators of body condition: worthwhile or wishful thinking?

Introduction

External measures of animal size, e.g. body mass, wing chord, foot length, and so on are often used by ecologists to develop body condition indices, e.g. body mass/length. Body condition indices are thought to reflect variation in diverse aspects of organismal quality, e.g. health, nutritional status, fat content and even Darwinian fitness (Krebs & Singleton, 1993; Brown, 1996; Viggers *et al.*, 1998). Body condition indices are generally easy to compute, so if they are highly correlated with variables, such as fatness or health, that are difficult to measure, they may be useful to ecologists for at least two reasons. First, they may be indicators of variables, e.g. fat content, that are difficult to measure accurately without harming an animal. Secondly, they may be more efficient or experimentally simpler to measure than variables that are hard to quantify, such as health or Darwinian fitness.

Ecologists seeking rapid non-destructive methods for estimating body condition have used two basic approaches for estimating body condition from external morphology. These two approaches are based on the construction of ratio variables, e.g. body mass divided by length, and the generation of residual variables, e.g. residuals from the regression of mass on length. Use of both kinds of condition indices requires considerable care to prevent errors in inferring the biology of interest, i.e. to prevent drawing erroneous conclusions about the biology being studied. One serious problem with the use of condition indices is that apparently subtle differences in the method used to compute the condition index may lead to vastly different conclusions about an animal's condition. A second problem is that researchers use condition indices to mean differ-

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ent things biologically. For example, condition indices are used as proxies for an animal's fat mass, health, survival, and so on. Thus the term condition index often is used imprecisely, which may lead to confusion in understanding what a condition index means. A third problem is that condition indices are sometimes used to capture biological concepts that are articulated imprecisely, e.g. well-being, health or quality. These problems lead to difficulties in evaluating the validity of condition indices in general. This chapter examines some of the commonly used condition indices based on external morphology. Our examination of the current usage of condition indices leads us to three conclusions. First, in many cases, the use of condition indices should be abandoned entirely. Secondly, when condition indices can be validated, and hence are still useful, greater care should be paid to the statistical analysis of condition indices formulated as either ratios or as residuals. Thirdly, we advocate the direct analysis of data used to generate condition indices as an alternative to the indirect, and often problematic, formulation of ratio or residual indices of condition.

What is body size?

Body size is an essential feature of condition indices, but the best measure of an animal's body size is a matter of debate (Rising & Somers, 1989; Freeman & Jackson, 1990; Piersma & Davidson, 1991; Wiklund, 1996). In reality, animals do not have a single size; they have many sizes (Bookstein, 1989). For example, a bird has a wet mass, a fat-free mass, a wing chord, a tarsus length, and a bill depth, all of which are measures of size. Which measure of size is the best probably depends on the biological question being asked. Yet, regardless of the size metric that is used, it is important to specify precisely what one means when referring to organismal size. A major feature of different measures of body size is that they may have different dimensions. For example, size can be assessed in dimensions of length, e.g. wing chord of a bird, snout–vent length of a lizard, standard length of a fish, total length of a mammal, and dimensions of mass. Throughout this chapter, unless specifically stated otherwise, we use the term mass to mean body mass. Mass is an indirect indicator of volume because an animal's mass equals its density multiplied by its volume. In geometrically similar objects, area increases in proportion to length squared, and volume in proportion to length cubed. If an object's density does not change with size, its mass increases in proportion to length

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cubed as well. The primary data for estimating body size are almost always measures of length or mass or some transformation of them.

Besides direct measures of size, such as mass, length, and so on, so-called structural size is an often used indirect measure of size, particularly for birds and mammals. Structural size is usually the first principal component (PC) from a principal components analysis of several measures of body length. Imagine that several measures of body length are available, e.g. bill length, bill depth, and tarsus length. A principal components analysis resolves the original *n* variables into *n* principal components so that (i) each PC score for an individual animal is a sum resulting from the linear combination of each of the original variables, e.g. $PC1 = 0.498$ times bill length + 0.6 times bill depth + 0.7 times tarsus length, (ii) the principal components are all uncorrelated with one another, and (iii) the variance of the first PC is greater than the variance of the second PC and so on (Manly, 1986). If the first PC explains a large fraction of the cumulative variation in the lengths and if all the measures of length have positive loadings on the first PC, the first PC is often considered an overall metric of size and is called structural size. Clearly, an estimate of structural size depends on which body measurements are used to construct it, so again it is important to specify precisely how structural size is determined (Bookstein, 1989).

Condition indices and size

The condition indices, discussed in this chapter, are based on external measures of size. Two types of condition indices, ratios and residuals, are in common use. Ratio indices are one measure of size divided by a second measure of size. Ratio indices of condition include (i) mass divided by length, i.e. a linear measure of size; (ii) mass divided by length cubed; (iii) the cube root of mass divided by length; (iv) mass divided by length raised to an empirically determined power; (v) mass divided by mass predicted from length; (vi) log mass divided by log length; and (vii) log mass divided by log mass predicted from log length. Residual indices of condition are the difference between an observed measure of size and that predicted by a regression equation. Residual indices include (i) residuals from regressions of mass on length; (ii) residuals from regressions of mass on length cubed; (iii) residuals from regressions of mass on length raised to an empirically determined power; and (iv) residuals from regressions of log mass on log length. Hence, a multitude of alternative condition measures