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CHAPTER 3

ASSESSING BODY CONDITION IN BIRDS

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1. INTRODUCTION

Important biological concepts typically have many definitions. Body condition is no exception; it is a multi-level phenomenon that can be defined either conceptually or operationally. Although at this time there is no clear consensus on the definition for body condition, conceptually, the term in many cases describes the degree to which an organism's physiological state influences its performance (i.e., production, activity, or response to environmental conditions). Operational definitions for condition typically are based on some aspect of body composition (e.g., levels of nutrient stores or indirect indicators of such levels). Despite these complexities, numerous published studies have documented the effect of a bird's nutritional status on some aspect of Darwinian fitness. The primary goals of this chapter are to describe the available methods of assessing condition, evaluate their accuracy and utility, illustrate how these methods have been applied, and clarify how they satisfy operational and conceptual definitions of body condition. The result will be to provide a primer for researchers interested in

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obtaining condition estimates, as well as for those wishing to improve upon existing methods.

Section 2 begins by summarizing the general trends of empirical studies of body condition. Studies published during the last twenty years have been classified according to study organism, duration, condition index used, and purpose. The literature survey is intended to provide a historical perspective for body condition research and to enumerate the areas in which the greatest progress has been made. The survey also provides information on the areas of research that are not as well-known and that will deserve greater attention in future studies.

Section 3 examines the basic approach of the seven most commonly used condition indices. In describing the methods I distinguish between those that are direct, which provide values for the mass of specific nutrients (e.g., fat, protein), and those that are indirect, which act as indicators of nutritional state. Each method is also classified based on whether it requires invasive or noninvasive sampling. Special attention is given to the assumptions of each method, and how such assumptions may influence statistical analysis of condition data. The temporal context of each index, such as whether it provides information on past, current, or future body condition, is also described.

The surveyed indices vary in the degree of specificity with which they estimate condition. As a result, they differ in how well they quantify condition operationally and, as a consequence, how well they approach a conceptual definition of condition. Although I will not provide a concrete, single definition of body condition useful in the study of all possible questions, I do wish to provide a starting point for understanding how to begin when measuring condition in an empirical study. Therefore, I conclude this review by suggesting guidelines to use when investigating how body condition affects performance. These guidelines include careful consideration of the question to be asked, species to be studied, temporal aspects of the study, and financial constraints.

2. LITERATURE SURVEY OF BODY CONDITION RESEARCH

I surveyed the following thirteen journals (1974–1994) for studies addressing condition-related questions: *Animal Behaviour, Ardea, Auk, Canadian Journal of Zoology, Condor, Ecology, Ibis, Journal of Animal Ecology, Journal of Field Ornithology, Journal of Zoology, Ornis Scandinavica, Physiological Zoology,* and *Wilson Bulletin*. Studies were included in the review if they considered how nutritional state affects (or is affected by) production (breeding, molt), behavioral activ-

ity (mating, migration), or external factors (food availability, weather). Nutritional state was defined broadly on the basis of body composition, levels of nutrient reserves, or general indicators of these values. I also included studies that introduced or tested the accuracy of a technique used to assess nutritional state. The surveyed studies are listed in taxonomic order in the Appendix. Below I describe the overall patterns observed among the 244 reviewed studies in terms of their duration, purpose, condition index, and taxon investigated.

2.1. Frequency and Duration of Body Condition Studies

In general, the number of studies on body condition published per year has increased significantly in the past twenty years ($r^2 = .73$, $p < 0.001$) (Figure 1). In addition, recent studies have proposed new methods of assessing condition, such as ptilochronology (Grubb, 1989), profiling (Bolton *et al.*, 1991), and total body electrical conductivity (Walsberg, 1988). Thus, investigation of body condition has become an increasingly important aspect of avian research, a trend that is likely to continue.

Most studies surveyed (58%) were of short duration (usually less than 2 years), and fewer than 6% measured body condition in a single population over a period longer than 5 years (Figure 2). The lack of long-term body condition studies may indicate that researchers concentrate on short-term, rather than long-term, effects of condition on

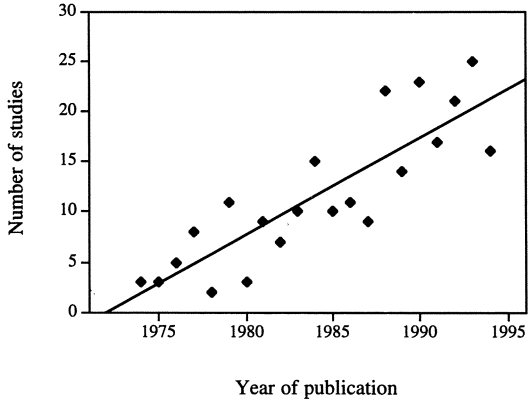

FIGURE 1. Linear regression of the number of studies of body condition published from 1974 to 1994 ($N_{total} = 244$), showing the positive relationship between frequency of published condition studies and date.

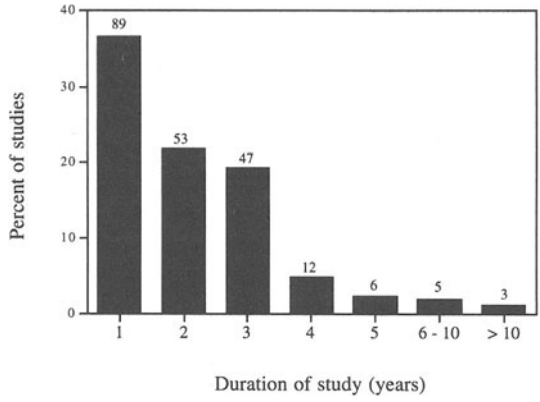

FIGURE 2. Duration, in years, of studies on body condition published from 1974 to 1994 (N_{total} = 186). Mean duration was 2.68 years (+ 0.17 SE).

activities such as breeding, migration, or molt. However, this trend may also result simply from the generally low frequency of long-term ecological studies, or from the fact that very few long-term studies consider body condition measurements in tandem with demographic and behavioral data.

The data on duration describe the number of years each population was measured. However, the number of animals measured in each study can be equally important. Low sample sizes can result in reduced statistical power and may be an unwanted consequence if adequate sampling is not done throughout a study. Although sample size was not analyzed for each study in this review, sample size obviously must be considered when designing a study utilizing condition estimates. Regardless of the number of years in which data are obtained, statistical analyses of condition data require sample sizes adequate for including each year in analyses, and particularly for understanding trends both within and among years. Thus, researchers should consider conducting *a priori* power analyses prior to initiating a study to better estimate the number of animals required to achieve adequate statistical power.

2.2. Purposes of Body Condition Studies

I created nine categories for analyzing objectives of body condition studies (Figure 3). Generally, studies addressed the interaction between condition and production (breeding, molt), activity patterns (migration, mating, social and wintering behavior), or external factors (diet, envi-

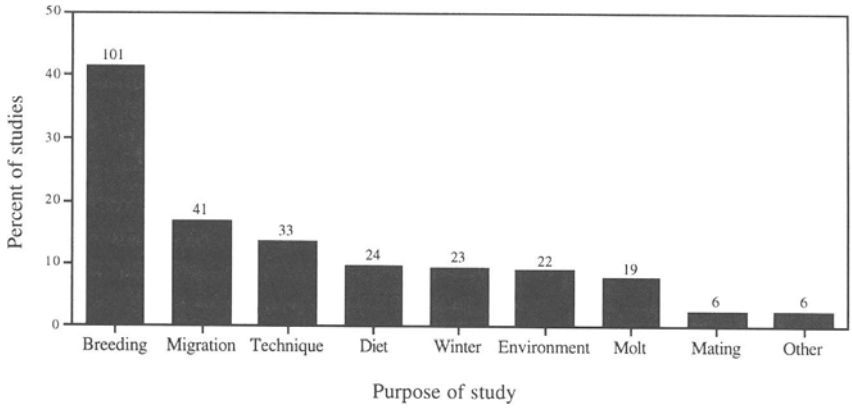

FIGURE 3. Purpose of body condition studies. Studies (N_{total} = 244) were included more than once if they investigated more than one relevant question. The category "Other" includes studies of social behavior, geographic range, captivity, and genetics. Number of studies in each purpose category is shown at the top of each bar.

ronmental conditions). In addition, a few studies considered the effects of captivity, geographic location, or genetic background on condition. Approximately 41% of the studies reviewed measured the interaction between body condition and reproductive performance, which probably is attributable to the strong dependence of breeding success on nutritional status, and the direct link between condition and Darwinian fitness. These studies included many classic investigations of waterfowl (Ankney and MacInnes, 1978), seabirds (Houston *et al.*, 1983), and passerines (Jones and Ward, 1976). Molt, another nutritionally expensive process, was studied less frequently (8% of studies) (Heitmeyer, 1988b; Murphy *et al.*, 1988; Ankney, 1979; Chilgren, 1977).

Periods of activity, such as mating or migration, can be nutritionally costly. Migratory birds must embark on a pathway, sometimes extending long distances through a potentially unfamiliar and unpredictable landscape in which feeding opportunities may be limited and nutritional demands of flight are high. Condition can determine the timing of departure for migration (Sandberg, 1994; Below, 1979; Baggott, 1975; Ward and Jones, 1977), stopover time between breeding and wintering sites (Morris *et al.*, 1994; Gauthier *et al.*, 1992; Geller and Temple, 1983), or the adequacy of an individual's nutrient reserves to complete the migratory journey (Johnson *et al.*, 1989; Smith *et al.*, 1986; Dick and Pienkowski, 1979). Birds may also produce condition-dependent display behaviors during mating, such as the courtship behavior of Sage Grouse (*Centrocercus urophasianus*) (Hupp and Braun,

1989) or of male harriers (*Circus cyaneus*) (Simmons, 1988). In addition, courtship may require production of costly morphological traits, such as feather or skin pigmentation (Piersma and Jukema, 1993; Burley *et al.*, 1992; Hill, 1990).

External environmental conditions, including captivity, food availability, and geographic variation, were the focus of approximately 20% of the remaining studies of body condition. This group was somewhat diverse and included investigations of the effects of temperature (Lovvorn, 1994; Grubb *et al.*, 1991; Dawson and Marsh, 1986; Owen and Cook, 1977), wetland acidification (Rattner *et al.*, 1987), and pesticide burden (White *et al.*, 1981).

2.3. Methods Used in Body Condition Studies

Table I briefly describes seven general categories of methods of condition assessment. The seven methods provide diverse measurements of nutritional status and vary in requirements and degree of accuracy. Important differences among the methods, as well as the costs and benefits associated with their application, are more fully described in section 3.

More than half of the studies surveyed used carcass analysis as the primary method (Figure 4). The next most common set of measures, morphological indicators, was diverse, and included body mass and mass corrected for structural size, as well as indices of damage (Jones, 1992) and condition-dependent advertisement (Piersma and Jukema, 1993; Burley *et al.*, 1992; Hill, 1990; Simmons, 1988). Subcutaneous fat scoring, a method of estimating body condition from the level of fat deposits, was employed frequently in conjunction with studies of migratory passerines (Morris *et al.*, 1994; Kaiser, 1993; Cherry, 1982; Finlayson, 1981). Methods of assessing condition from levels of key plasma or cellular indicators in blood were also used, often as means of sampling several nutrients noninvasively (Jenni-Eiermann and Jenni, 1994; Gavett and Wakeley, 1986). The three remaining techniques, conductance (section 3.6), ptilochronology, (section 3.7) and profiling (section 3.8) were represented by fewer studies, which may be the result of their recent introduction and, perhaps, of uncertainty about their accuracy.

The methods described in Table 1 represent varying levels of intrusion by researchers on their study animals. Some methods may require simple visual observations that can be conducted from a blind; others involve short-term handling after trapping; others, killing of study animals for carcass analysis. Methods that are less invasive and that allow

TABLE I
Methods of Assessing Body Condition

Method	Description	Index	Repeatable	Requires recapture	Requires calibration	Selected references
Carcass analysis	Assesses body composition through carcass homogenization, drying, lipid extraction, and combustion.	Lipid, protein, water, ash	No	No	N/A	Alisauskas *et al.*, 1990; Ankney and MacInnes, 1978; Jones and Ward, 1976; Krapu, 1981
Morphological indicators	Uses externally measured characteristics such as body mass, mass divided by structural size, or condition-dependent advertisement.	Mass, color, damage, performance	Yes	No	No	Burley *et al.*, 1992; Hill, 1990; Jones, 1992; Piersma and Jukema, 1993; Poole, 1985; Simmons, 1988
Fat scoring	Measures fat level by scoring fullness of the primary subcutaneous fat deposits in the furcular and abdominal regions.	Fat	Yes	No	No	Cherry, 1982; Krementz and Pendleton, 1990; Rogers, 1991; Kaiser, 1993
Blood indicators	Measures condition-dependent traits from the blood, e.g, hematocrit, white blood cell	Various plasma and cellular indicators	Yes	No	No	Bradley and Threlfall, 1974; Gauthier and Thomas, 1990; Nelsen

(*continued*)

TABLE I (*Continued*)

Method	Description	Index	Repeatable	Requires recapture	Requires calibration	Selected references
	count, circulating glucose, and other metabolites.					and Brandl, 1988; Rattner *et al.*, 1987
Conductance	Uses conductance of sound waves or electromagnetic current through the body to predict body composition.	TOBEC—Lean and lipid mass US—Pectoral muscle thickness	Yes	No	Yes	Castro *et al.*, 1990; Morton *et al.*, 1991; Roby, 1991; Sears, 1988; Skagen *et al.*, 1993; Walsberg, 1988
Ptilochronology	Induces feather growth and compares 24-hr growth bars in original and induced feathers.	Feather growth	Yes	Yes	No	Grubb, 1989, 1992; Murphy, 1992; White and Kennedy, 1992
Profiling	Estimates pectoral muscle or fat level through structural measurements and profiles of the surface of the keel or abdomen.	Pectoral muscle or abdominal fat	Yes	No	In some cases	Bolton *et al.*, 1991; van Eerden, 1991

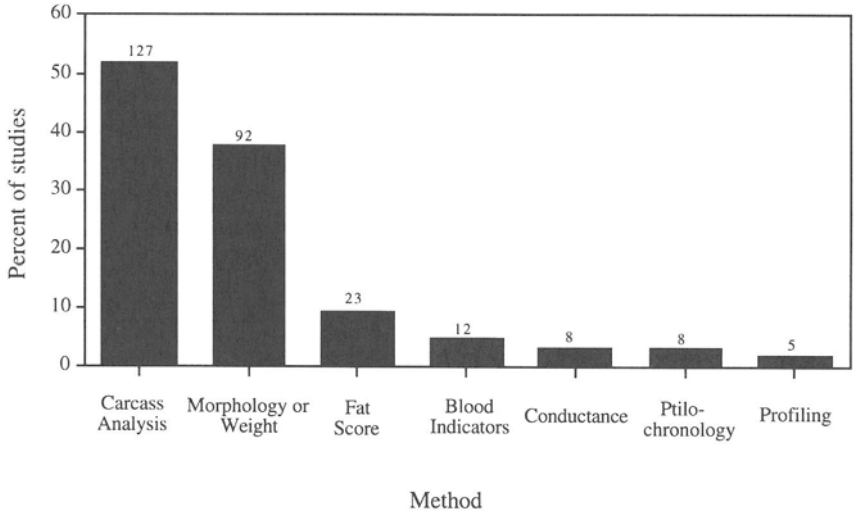

FIGURE 4. Assessment methods used in body condition studies (N_{total} = 244). Studies may be included more than once if they used multiple methods of assessing condition. The number of studies using each assessment method is shown at the top of each bar.

the animal to resume normal behavior after measurement are important for some research questions. This is even more critical when studying species over the long term, or species that are threatened or endangered. As a consequence of the development of indirect techniques, the potential for less invasive sampling has increased; thus the relative frequency of carcass analysis studies between 1974 and 1994 has decreased at a rate of approximately 1% each year (Figure 5). This trend is even more pronounced when comparing studies published before and after 1989, a year in which several new methods (such as ptilochronology and conductance) were introduced. Before that year, 62% (± 1.59%) of all studies used carcass analysis; thereafter, this figure was reduced by almost half (39 ± 0.15%) (Mann-Whitney U = 11, p = 0.008). Much of this change has occurred in conjunction with an increased awareness of ways in which experimental procedures are potentially harmful, accompanied by the advocacy of methods that reduce adverse effects on the animals studied (Animal Behavior Society, 1991; American Ornithologists' Union, 1988).

2.4. Taxonomic Distribution of Condition Studies

The species investigated in body condition studies are as diverse as the methods used. Some species are studied more often, either be-

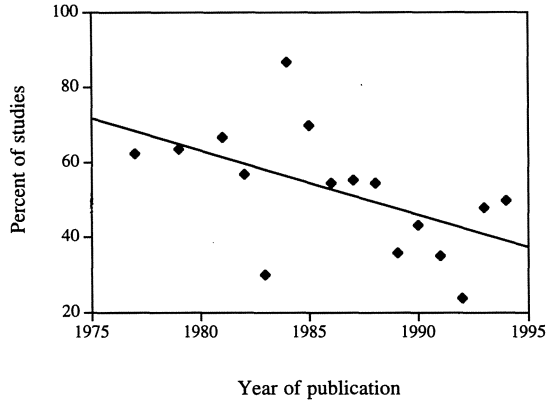

FIGURE 5. Percentage per year of studies that utilized invasive methods (including only years in which more than five studies were published).

cause of management practices, economic importance, or because they are more readily observed in the field. Condition studies show a strong taxonomic bias, as indicated in Figure 6; however, data in this figure are not corrected for frequency of published studies according to taxon. In general, four orders were most commonly represented in body condition studies: Anseriformes, Galliformes, Charadriiformes, and Passeriformes. The remaining orders, with the exception of the Falconiformes, are represented by three or fewer studies.

I considered whether carcass analysis was used more frequently in orders containing game species, which are often hunted. The results for the four most commonly studied orders showed that carcass analysis was used more often for the orders containing game species than those containing no game species (Table II; $\chi^2 = 15.81$, $p < .001$). One benefit gained from studies of game species is an increased knowledge of patterns of nutrient dynamics in these birds. Among waterfowl, numerous studies have described the role of nutrient reserves in limiting reproduction (reviewed by Ankney *et al.*, 1991), and these results are primarily based on data obtained from carcass analyses.

3. METHODS OF ASSESSING CONDITION

Methodology is often considered less important than are data; however, the rigor of the methods determines the quality of the data obtained. Techniques requiring capture and invasive sampling can alter

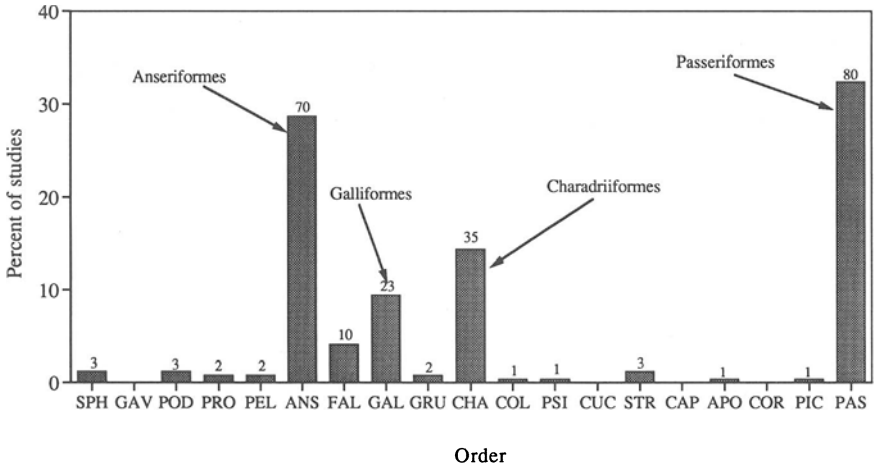

FIGURE 6. Taxonomic order of species used in body condition studies, listed by first three letters of the order: SPH, Sphenisciformes; GAV, Gaviiformes; POD, Podicipediformes; PRO, Procellariiformes; PEL, Pelecaniformes; ANS, Anseriformes; FAL, Falconiformes; GAL, Galliformes; GRU, Gruiformes; CHA, Charadriiformes; COL, Columbiformes; PSI, Psittaciformes; CUC, Cuculiformes; STR, Strigiformes; CAP, Caprimulgiformes; APO, Apodiformes; COR, Coraciiformes; PIC, Piciformes; PAS, Passeriformes. The number of studies of each order is shown at the top of each bar.

the normal behavior of an animal; sacrifice of study animals precludes any further observation of the same individual. If the study populations are threatened or endangered, researchers may be limited in the methods that can be used. Most indirect methods involve assumptions that, if violated, can affect the inferences that can be made from a particular data set. As a result, the simple problem of choosing a method becomes more complicated and is vital to the development of a good study. In the following sections, I describe the methods listed in Table I and provide specific examples from many studies. I also point out the pitfalls for each method and recommend how each method might be improved.

3.1. Carcass Analysis

Involving both dissection as well as more complicated methods of determining tissue composition, carcass analysis provides values for several different measures of nutrient stores, including fat, protein, and mineral deposits in the body. Carcass analysis is a logical starting point for describing the methods of assessing body condition for two reasons:

TABLE II
Comparison of Methods Used to Analyze the Four Most Commonly Studied Orders, Grouped according to Whether or Not They Include Species that Are Traditionally Hunted[a]

	Invasive	Noninvasive	Total
Game (Anseriformes, Galliformes)	65	28	93
Nongame (Charadriiformes, Passeriformes)	47	67	114

[a] $\chi^2 = 15.81$, $p < .001$

1) It has been the most commonly used method during the past twenty years, and 2) it is the standard against which all other assessment methods are compared. Although the results obtained from carcass analysis vary in complexity, all permutations of this method require killing birds and extensive processing of individual animals.

3.1.1. Methods of Analyzing Carcass Composition

Carcass analysis provides the most extensive and complete information about the body composition of an individual animal. Carcasses are most often obtained by active collection by researchers, although some studies have used hunter-shot (Hanson *et al.*, 1990), drowned (Piersma, 1984), or road-killed animals (Hirons *et al.*, 1984), or animals inadvertently killed during trapping (Piersma and Jukema, 1990). It should be noted that some methods of sampling (such as bait-trapping or hunting) may result in a biased sample of that segment of the population that is in poorer condition (Dufour and Weatherhead, 1991; Greenwood *et al.*, 1986), although sampling bias is a potential problem for all condition assessment methods. While values for protein, fat, lipid, water, and mineral content of an individual can all be obtained from a carcass analysis, the amount of information obtained depends on the degree of investment in processing. Some procedures yield only simple indices of nutrient levels, and others provide more exact values of fat, protein, and minerals.

In their seminal paper on the effects of nutrient reserves on reproductive performance, Ankney and MacInnes (1978) dissected Lesser Snow Geese (*Chen c. caerulescens*) and measured the mass of key nutrient depots as nutritional indices. Their study measured the wet mass of subcutaneous, mesenteric, and abdominal fat deposits as a lipid index; the dry mass of three primary muscle groups (the pectoral muscles, leg

muscles, and gizzard) as a protein index; and the fat-free mass of the leg bones and sternum as a calcium index. They also evaluated the reproductive condition of individual females through analysis of ovarian follicles, and they classified the potential clutch size of laying females and the actual clutch size of incubating females. Values for proteins, lipids, and minerals can also be corrected for structural size of the individual by dividing mass by a morphometric variable such as wing or tarsus length, or by a combination of size indicators (Bailey, 1985; Gauthier and Bedard, 1985).

Although different tissues capable of storing fat, protein, and calcium can be examined to assess nutrient levels as described above, deposits of these nutrients may remain undetected in other tissues. As a result, most studies since Ankney and MacInnes (1978) have used more refined and precise methods for determining neutral lipids, ash, and ash-free lean dry mass. More complex processing can also measure nutrient levels in the entire animal. Carcass grinding and homogenization is the first step in more complex procedures, followed by drying and lipid extraction of aliquots of homogenate to distinguish between proteins and lipids. In some circumstances, carcasses are instead separated to tissue level (for example, major muscle groups, heart, stomach, liver, etc.) and analyzed separately (Piersma *et al.*, 1996). Petroleum ether is the preferred solvent for lipid extraction because alternative solvents (e.g., chloroform) also remove non-energy structural lipids from cell membranes (Blem, 1990; Dobush *et al.*, 1985). Following lipid extraction, the homogenate is then burned to determine the ash or mineral component of the carcass (Afton and Ankney, 1991; Jones and Ward, 1976). More extensive processing methods may also use more complicated statistical procedures, such as principal components analysis, to incorporate morphometric variables and correct for variation in the reserve size due to variation in body size (Esler and Grand, 1994; Afton and Ankney, 1991).

3.1.2. Conclusions about Using Carcass Analysis to Measure Condition

Because carcass analysis yields the most complete information about body composition, this method is often viewed as the standard against which all other methods are compared. No other single technique can estimate the role of multiple nutrient reserves, including the more difficult-to-measure mineral reserves (Ankney and Alisauskas, 1991). Distinctions among different deposits of nutrients, as well as between utilizable and nonutilizable nutrients (such as structural vs.

stored lipids), can be made (Dobush *et al.*, 1985). To study the role of protein and lipid stores in egg production, carcass analysis can also combine information on nutritional status as well as reproductive traits (by determining the number and size of eggs produced) (Alisauskas and Ankney, 1994). As a result, carcass analysis can provide information on the current condition of an animal by quantifying the mass of nutrient stores at a single point in time, but may also be a good indicator of past and/or future reproductive performance. In addition, extensive research on waterfowl has provided a better understanding of the complexities of storage and use of nutrients throughout the annual cycle.

Although the primary benefit of carcass analysis is that it yields the most complete information on body composition, data are obtained at the cost of foregoing further study of these individual subjects. As a result, this method will not be appropriate for studies in which individual animals are to be sampled more than once, such as to determine the reproductive or survival consequences of a particular nutritional state. Further, it is unlikely to be useful in studies of rare or endangered species (Walsberg, 1988). In contrast, carcass analysis is used commonly in studies of pest species, such as European Starlings (*Sturnus vulgaris*) (Thompson *et al.*, 1993; Blem, 1981), House Sparrows (*Passer domesticus*) (Fleischer and Murphy, 1992; Krementz and Ankney, 1988; O'Connor, 1977), Brown-headed Cowbirds (*Molothrus ater*) (Scott and Ankney, 1980), Common Crows (*Corvus brachyrhynchos*) (Young, 1989), and Red-billed Quelea (*Quelea quelea*) (Jones and Ward, 1979; Ward and Jones, 1977), which are often culled to limit their population size.

3.2. Morphological Indicators

Morphological indicators include methods of assessing condition through a composite picture of the external appearance of an animal. Although indices such as fat scoring (section 3.4), ptilochronology (section 3.7), and profiling (section 3.8) also rely on characteristics that are measured externally (fat level, feather growth bars, and body contour, respectively), and could be included in this section as morphological indicators, I have excluded these methods from this category and given them separate consideration. In this section I describe two other types of morphological indicators: mass-based indices and condition-dependent advertisement. I also provide information on a third method, fluctuating asymmetry; this subject was not included in my literature survey, but has been suggested as a possible means of assessing condition in birds.

3.2.1. Mass and Mass Corrected for Structural Size

Body mass is often used as a condition index because it provides an easily obtained single value for the levels of all body nutrients without invasive sampling. Body mass varies throughout the year as a result of physiological demands placed on the organism, for example, through the gain or loss of fat reserves during migration or reproduction. Most changes in body mass are often assumed to reflect changes in fat levels, an assumption supported in a number of studies (e.g., McEwan and Whitehead, 1984; Slagsvold, 1982; Blem, 1981; see also Blem, 1990). However, changes in protein level also occur as body mass changes (e.g., Lindstrom and Piersma, 1993; Castro and Myers, 1990; Piersma and Jukema, 1990; Marsh, 1984; Jones and Ward, 1976). If single-point sampling is used, body mass provides a general index of current condition; however, if individuals are weighed multiple times, then body mass can be a better predictor of how past performance is correlated with condition.

To provide a better condition index, body mass should be expressed relative to the structural size of an individual. Structural size is the nutrient-reserve independent size of an individual, where nutrient reserves are tissues that can be utilized by the animal prior to starvation, and stores are accumulated prior to need (Lindstrom and Piersma, 1993; Piersma and Davidson, 1991). Incorporating structural size controls for the concomitant increases in tissue mass with increases in body size, and distinguishes more accurately between body nutrients that are utilizable (nutrient reserves and stores) and nonutilizable (structural components) (Piersma and Davidson, 1991). Common ratios include mass divided by wing length (Dufour and Weatherhead, 1991; Owen and Cook, 1977), tail length (Conway *et al.*, 1994; Slagsvold, 1982), tarsus length (Matthysen, 1989; Moreno, 1989) or bill length (Gatti, 1983; Slagsvold, 1982). Less plastic dimensions (such as skeletal features) are preferable to wing length because the latter varies with molt and physical wear. Alternatively, body mass indices can be corrected for by analysis of the residuals of the mass $\times$ size regression; individuals are then described relative to their expected body mass based on their structural size (Hochachka and Smith, 1991). In general, the results obtained from such corrections are expected to reveal differences in lipid mass among individuals.

More complex multiple regression models have been used to provide greater precision in the condition estimate based on body mass (Conway *et al.*, 1994; van der Meer and Piersma, 1994; Castro and Myers, 1990). Rather than calculating ratios, these models combine

structural measurements that best predict the variable of interest (e.g., lipid mass) and include them in the model. Structural size is often expressed as the product of several linear measurements (for example, tarsus length × wing length × bill length) to express the body size of an individual volumetrically (Castro and Myers, 1990). Predictive equations are usually evaluated using limited carcass analysis but, once calibrated by carcass analysis, can be applied using noninvasive body measurements.

Condition estimates based on body size may sometimes be inaccurate because assumptions of the method are violated. Ratios of body size to structural measurements assume that variation owing to body size is eliminated by this transformation. However, analyses of ratios can often create misleading results if the structural indicator does not vary isometrically with body size (Packard and Boardman, 1987; Blem, 1984). Further recommendations are described more explicitly in Piersma (1984), who suggests that structural size indicators should be three-dimensional (i.e., should scale volumetrically) and correlate well with mass of starved individuals (those that lack nutrient stores). Many researchers have stressed the importance of distinguishing among stores, reserves, and structural size (van der Meer and Piersma, 1994; Lindstrom and Piersma, 1993) and have described several regression models for which the assumptions are explicitly described. The reliability of these assumptions differs among species, and therefore it is suggested that researchers consider the assumptions underlying analytical procedures before making conclusions from body mass data (van der Meer and Piersma, 1994; Lindstrom and Piersma, 1993). In addition, regression models may be strongly geographically dependent, requiring development of different equations for different geographic regions in which structural size differences occur (Castro and Myers, 1990).

3.2.2. Condition-Dependent Advertisement

Morphological and behavioral traits that vary with general health have been proposed to be indicators of "good genes" because they provide a direct link between the degree of trait expression and body condition (Kodric-Brown and Brown, 1984; Hamilton and Zuk, 1982). Individuals that show a greater expression of energetically costly traits such as pigmentation or visual displays are predicted to be in better condition. As a result, these traits are expected to be used in mate choice. They can be scored by observers, sometimes without capture or disturbance, and compared both within and among individuals to estimate relative condition.

Several studies measured condition-dependent traits that were linked to resource availability, such as the carotenoid pigmentation in feathers of House Finches (*Carpodachus mexicanus*) (Hill, 1990) and bills of Zebra Finches (*Taeniopygia guttata*) (Burley *et al.*, 1992). More intense coloration patterns are produced only when individuals obtain critical amounts of key nutrients, which can be obtained only from exogenous sources (Hill, 1990). Visual displays, such as the in-flight U-displays of male Northern Harriers (*Circus cyaneus*) (Simmons, 1988), are also predicted to be honest indicators of male condition, as they are closely linked to food abundance on male territories and thus to a male's predicted rate of food delivery to mates. Alternatively, physical characteristics can be used by conspecifics (and by researchers) to identify individuals in poor condition. For example, holes and other damage to the foot webbing of Least Auklets (*Aethia pusilla*) have been shown to be linked to poor survival (Jones, 1992).

Although traits assumed to be accurate expressions of condition are useful morphological indicators that do not require invasive measurement, their use still relies on important assumptions. It is therefore necessary for researchers using such traits to consider these assumptions prior to making inferences about their utility as sexually-selected characters. In particular, it may be important to calibrate color, damage, or display rates with other condition estimates to determine whether or not they are honest condition indicators. If they appear to be reliable indices, they can then be used independently of other indices. However, the temporal context of condition-dependent advertisement must also be considered; thus, indices based on carotenoid pigmentation or damage should probably be used as indicators of past condition or past events, while display rates are more likely to be indicators of an animal's current condition.

3.2.3. Fluctuating Asymmetry

Fluctuating asymmetry (FA) occurs as small deviations from perfect morphological symmetry due to differential development of a structure that, if perfectly formed, is bilaterally symmetrical (Swaddle and Witter, 1994; Van Valen, 1962). Studies usually measure FA of a trait, such as tail length, as the difference in its size on the left side minus its size on the right side; values of FA are normally distributed about a mean of zero (Swaddle *et al.*, 1994; Møller and Pomiankowski, 1993). FA measures past condition of an animal during the time in which the trait was developed or acquired. Increased levels of fluctuating asymmetry have been associated in a number of species with both

genetic stressors, such as level of inbreeding (Lerner, 1954), as well as environmental stressors such as reduced food availability (Swaddle and Witter, 1994; Parsons 1990). The application of fluctuating asymmetry as a condition index originates mostly from studies of sexual selection (Watson and Thornhill, 1994), in which the degree of FA of an individual has been shown to act as a mechanism in mate choice and intrasexual mate competition (Møller, 1992, 1988; Andersson, 1982). Levels of FA have been shown to have a negative relationship with more common measures of condition, such as fat score (Swaddle and Witter, 1994).

Potential advantages of using FA as a measure of condition are that it is a low-cost non-invasive indicator, and is unique among methods in that the optimal condition state of an individual is known (perfect bilateral symmetry) (Møller and Pomiankowski, 1993). However, fluctuating asymmetry can at times be difficult to measure, and accuracy may be dependent on factors such as the absolute size of the trait (Møller, 1990). Statistical analyses of FA are strongly dependent on the degree of measurement error of the trait, and analysis may require that nonparametric procedures are applied (Palmer and Strobeck, 1986; Swaddle *et al.*, 1994).

3.3. Fat Scoring

Fat scoring is the estimation of fat level by comparing the color and fullness of the primary subcutaneous fat deposits in the interclavicular depression (furcula) and/or abdomen. This technique was first described in detail by McCabe (1943). However, even in its initial application, McCabe was quick to point out that he had "no precise measure of degree of fatness and can imagine none applicable to field work." This simple caveat is echoed in re-evaluations of accuracy of fat scoring (Rogers, 1991; Krementz and Pendleton, 1990).

3.3.1. Methods of Scoring Subcutaneous Fat

Most fat scoring regimes have been developed for use on passerines, although some researchers have applied this method to hawks (Smith *et al.*, 1986) and swans (Sears, 1988). Two advantages of the technique are that it does not require birds to be killed (but see Murton *et al.*, 1974), and it is relatively easy for a trained observer in the field without using special equipment. Scoring requires blowing aside the breast and abdominal feathers to expose the skin surface (see Rogers, 1991, for a complete description of the holding technique). Estimation

of visible fat (which is orange or yellow in appearance and contrasts with muscle tissue) is usually made on an interval scale (Hailman, 1965), and many different hierarchical schemes are available. Although scales ranging from 0–5 are most frequently used (usually based on Helms and Drury, 1960), scales may range from 0–3 (Smith *et al.*, 1986; Chandler and Muvilhill, 1992; Leberman, 1967) to 0–7 (Petersson and Hasselquist, 1985). A recent study has proposed that main classes between 0 and 8 be further broken down into three or four subclasses, thus increasing the number of possible fat levels from 5 to 31 (Kaiser, 1993).

3.3.2. Correlation between Fat Score and Lipid Mass

Although fat scoring may be qualitatively useful for measuring visible fat, it is necessary to demonstrate that visible fat accurately predicts total body fat. Five studies have calibrated the relationship between fat score and total lipid mass (Conway *et al.*, 1994; Kaiser, 1993; Rogers, 1991; Krementz and Pendleton, 1990; Rogers, 1987). Carcass analyses indicate that the proportion of variability in lipid mass explained by fat score ranged from a low value of 0.19 (Krementz and Pendleton, 1990) to a maximum of 0.66 (Kaiser, 1993). The ability of fat scores to predict total body fat differed among species. For example, Krementz and Pendleton (1990) found that the coefficient of determination from a mixed-species regression ($r^2 = 0.19$, 5 species) was lower than coefficients obtained from single-species regressions [0.429 for Pine Siskins (*Carduelis pinus*), and 0.697 for House Sparrows (*Passer domesticus*)]. Kaiser (1993), using different methods, showed that a species with a lower range of fat scores [Reed bunting (*Emberiza schoeniclus*), range 0.000–4.75] had lower coefficients of determination ($r^2 = 0.50$) than did a species with a larger range [Garden Warbler (*Sylvia borin*), range 1.00–7.25] ($r^2 = 0.82$).

Given such variation in the predictive power of fat scoring, researchers studying organisms for which this relationship has not been calibrated should first conduct sufficient carcass analysis to determine actual lipid mass. In addition, because these relationships may also vary depending on age, sex, geographic location, hour of day, and time of year, it may be necessary to repeat calibration for the same species in different studies. Fat scores may also be combined with body mass and other morphological indicators in regression models to obtain better predictors of body condition (van der Meer and Piersma, 1994). Krementz and Pendleton (1990) also advise against using fat scores to compare different species and suggest that for such comparisons a more

exact technique, such as carcass analysis, be used; they also suggest that fat scoring should not be used if it explains less than 60% of the variation in lipid mass.

3.3.3. Statistical Analysis of Fat Score Data

The quantitative treatment of subcutaneous fat score data was first described by Hailman (1965, 1969). Fat score may represent categorical assessments that do not correspond to an interval scale; that is, uniform transition from one level to the next, such as that from 1 to 2, does not necessarily equal the transition from 4 to 5. In addition, the sample distribution of fat score data is usually unknown, precluding examination of the assumption of normality required by parametric tests. As a result, Hailman (1965) suggested that fat score data be analyzed with nonparametric tests. Appropriate measurements of central tendency and variation for nonparametric data are the median and percentiles, not the mean and variance, and population samples should be compared using the Mann-Whitney U Test rather than the Student's t-test (Hailman, 1969; 1965).

Although these recommendations for statistical analysis of fat score data are well known, many studies have continued to compare fat scores using parametric tests without testing the data for the underlying assumption of normality (Conway *et al.*, 1994; Krementz and Pendleton, 1990; Rogers, 1987; Murton *et al.*, 1974). At least one author (Rogers, 1991) has suggested that fat score data may approach uniform interval data, based on a regression of lipid index against visible fat class in Dark-eyed Juncos (*Junco hyemalis*). Although Rogers (1991) suggests that these results allow use of parametric tests of fat score data, the assumption of uniformity must still be tested for other species (Greenwood, 1992). In studies where the relationship between lipid mass and fat score is calibrated, the form of the data (interval or ordinal) can be described and the correct statistical procedures applied.

3.3.4. Conclusions about Using Fat Scoring to Measure Condition

Primary concerns about the use of fat scores include the degree to which data obtained from this qualitative assessment are subject to observer bias, as well as the sensitivity of estimates of fat of individuals to short-term fluctuation. These concerns should be evaluated before use of fat scoring in any field study.

Several authors have stressed the fundamental importance of having highly-trained observers to control for among-observer variability

(Kaiser, 1993; Rogers, 1991; Krementz and Pendleton, 1990). Kaiser (1993) suggested that even complicated fat scoring regimes may be learned relatively quickly, with as little as 1–2 days of experience with approximately 100 birds. However, variability has been demonstrated, even among experienced observers. Krementz and Pendleton (1990) tested for such variability by comparing fat score data from 100 birds scored twice each by 5 different individuals who were given similar instructions. Within-observer variability was relatively low, but scores often varied among observers, depending on the species measured. This variation in scoring may increase with the number of scoring categories (Krementz and Pendleton, 1990). Recommendations for reducing such variability include limiting the number of individuals who participate in scoring, practicing the technique to ensure that all participants experience the full range of possible values, and statistical testing for observer effects in studies that must pool data from more than one observer (Rogers, 1991; Krementz and Pendleton, 1990).

The sensitivity of fat score data has also been questioned. Rogers (1991) studied changes in fat level that occur overnight in fasting Dark-eyed Juncos (*Junco hyemalis*). He scored birds entering evening roosts, kept the birds overnight, and then scored them again in the morning prior to release. Results indicated that birds experienced changes in visible fat owing to overnight fasting (with only 6.7% of birds showing the same fat class in both scoring episodes, and most registering a loss). However, this study also found that the lipid index (g lipid/g lean dry mass) for birds scored as having zero fat was significantly higher than that for starved zero-score birds known to have depleted their lipid reserve. These results suggest that fat score data can be used to compare individuals prior to and after a treatment, but that the method not be used for birds that have recently experienced extreme nutritional stress. As a result of the potentially rapid change in fat score within an individual, fat scoring is therefore likely to be a better indicator of past, rather than future, condition.

3.4. Blood Indicators

The use of blood indicators to measure condition is an indirect method, primarily because blood does not store nutrients but acts as a means of mobilization and transport. However, many authors suggest that hematological analysis provides an indicator of an organism's physiological response to its environment (e.g., Bradley and Threlfall, 1974; Atwal *et al.*, 1964) and that blood composition correlates strongly with health and condition (Gavett and Wakeley, 1986; Kronfeld and

Medway, 1969). Researchers commonly draw blood (usually by brachial venipuncture) after trapping, often to screen for the presence of parasites (Vehrencamp *et al.*, 1989) or for DNA analyses (Rabenold *et al.*, 1991). Blood sampling is therefore a well-tested, yet relatively noninvasive, procedure for estimating body condition.

3.4.1. Cellular Indicators of Condition

The cellular components of blood include erythrocytes, which are primarily responsible for transport of blood gases to and from tissues, and leukocytes, which respond to the effects of disease and stress (Sturkie and Griminger, 1986). Levels of these cellular components are usually measured by centrifugation of blood samples to obtain packed cell volume (hematocrit), or by blood dilution and cell counting (Sturkie and Griminger, 1986). Hematocrit reflects erythrocyte volume and production and is an important indicator of anabolism (Nelsen and Brandl, 1988). Leukocyte levels are more readily measured through blood dilution and cell counts because leukocytes are less abundant in blood than erythrocytes. Higher leukocyte counts are considered to be an indicator of poorer condition, primarily because of the association of these cells with disease or stress (Sturkie and Griminger, 1986).

The most common method used to assess the cellular component of blood is centrifugation to obtain hematocrit (Nelsen and Brandl, 1988; Rattner *et al.*, 1987; Gavett and Wakeley, 1986; Bradley and Threlfall, 1974). Hematocrit can be highly variable among individuals, although in at least one study this variability was attributable to low sample sizes (Bradley and Threlfall, 1974)). Age, date, and time of blood collection affected hematocrit of House Sparrows (*Passer domesticus*), but diet caused no effect (Gavett and Wakeley, 1986). Nelsen and Brandl (1988) found that weather influenced variation in hematocrit of Black-headed Gull chicks (*Larus ridibundus*) as a result of either stress during rainy, cold periods or of dehydration in the sun. Reduced hematocrit has also been shown to be a secondary effect of poor growth in Black Ducks (*Anas rubripes*) that fed in acidified wetlands where food production was low (Rattner *et al.*, 1987).

The efficacy of leukocyte levels as an indicator of condition has been tested in at least two studies (Lochmiller *et al.*, 1993; Bradley and Threlfall, 1974). Bradley and Threlfall (1974) measured leukocyte count and the area of the nucleus of individual cells of four alcid species; they concluded that these measurements were not useful in assessing condition because they showed extreme variation among and within individuals. However, small sample sizes and the lack of ade-

quate controls may have contributed to their results. Lochmiller *et al.* (1993) provided a more controlled study of immune response to diet quality in the Northern Bobwhite (*Colinus virginianus*). Bobwhite chicks given diets that varied in protein levels showed no difference in white blood cell count, but diet did cause an effect on cell-mediated immune system function. From these results, this group concluded that measurements of immunocompetence may be applied to future field studies in the same way that they are applied to studies of malnutrition in domestic animals (Klasing, 1988) and humans (Gibson, 1990).

3.4.2. Plasma Indicators of Condition

Plasma contains nutrients that have been synthesized, obtained from ingested material, or mobilized from body tissues (Sturkie and Griminger, 1986). Most studies estimating condition from plasma metabolites measure multiple components to obtain a more complete blood profile for each individual (Jenni-Eiermann and Jenni, 1994; Rattner *et al.*, 1987; Gavett and Wakeley, 1986). For example, several nutrients, such as lipids, proteins, and carbohydrates, can be measured from plasma. Blood glucose level is the most common indicator of carbohydrate status (Nelsen and Brandl, 1988; Rattner *et al.*, 1987); however, blood glucose can vary with time of day and time since food ingestion (Hazelwood, 1986). Plasma lipids include triglycerides and fatty acids (Jenni-Eiermann and Jenni, 1994), as well as more complex molecules such as cholesterol (Gavett and Wakeley, 1986). Differences in these indicators have been shown to correspond to changes in body mass (Jenni-Eiermann and Jenni, 1994) and food quality (Gavett and Wakeley, 1986). Plasma proteins are short-lived, although protein composition of blood can be measured through blood nitrogen or levels of specific proteins such as albumin, which can act as a protein reserve or a carrier of other nutrients (Griminger and Scanes, 1986). Levels of these indicators of protein status also change with diet and mass (Jenni-Eiermann and Jenni, 1994; Gavett and Wakeley, 1986).

Plasma water content may also be a useful indicator of condition. The isotope-dilution method of assessing fat reserves was used by Gauthier and Thomas (1990) based on the premise that, for a given body mass, fat content decreases the percentage of body water. A small amount of tritiated water was injected intraperitoneally in Cliff Swallows (*Hirundo pyrrhonota*), and later the percentage of tritiated water in plasma was measured. Unfortunately, this method, when calibrated by carcass analysis, was found to be too imprecise to use for an individual bird, but it would provide a means to compare groups of birds.

3.4.3. Conclusions about Using Blood Characteristics to Measure Condition

From blood characteristics a researcher can, relatively quickly, obtain a wide range of measurements of nutritional status in order to indirectly assess condition. However, blood may be a better indicator of short-term, rather than long-term, condition. Plasma carries newly absorbed nutrients and those being transported to the tissues, and it therefore provides an acute rather than long-term index of nutritional status (Gibson, 1990; Mertz, 1975). As a result, hematological analysis may work well for individuals in which performance is affected by rapid change in condition (Jenni-Eiermann and Jenni, 1994). However, two new techniques—glycosylated hemoglobin and stable-isotope analysis—may be useful in future studies measuring condition from blood characteristics. Measurements of glycosylated hemoglobin, which were originally used in studies of human diabetics (Means and Chang, 1982, Trivelli *et al.*, 1971), are predicted to be indicators of long-term condition because they describe the mean glucose level during the lifetime of red blood cells (between 30–50 days in birds) (Andersson and Gustafsson, 1995) Stable-isotope analysis, which measures the abundance of stable isotopes of carbon and nitrogen in body tissues, has previously been used only to assess diet of birds (Hobson and Clark, 1993). In the future, stable-isotope analysis may be applied to assess condition, owing to the association of isotope abundance with changes in body composition (Hobson *et al.* 1993).

In some circumstances, blood indicators may be influenced by time of day or by recent ingestion of food (Gibson, 1990). Researchers using indicators of condition obtained from blood can control for such variables by sampling at the same time of day, or prior to the animal's first foraging trip. An additional complication is that individuals may also have near-normal plasma nutrient concentrations, even under conditions of severe depletion of body stores, because some nutrient concentrations in plasma are strongly regulated (Gibson, 1990). Whether this complication is present in a particular study may be tested by determining the correlation between blood indicators and the results obtained from carcass analysis.

3.5. Conductance

The two primary methods of obtaining conductance estimates of condition share several features. All utilize the principle of transmission of either electromagnetic current or sound waves through animal tissue to obtain a value that is then correlated with lean mass, lipid

mass, and/or muscle thickness. Measurements require the use of specialized equipment that has been adapted from use either in hospitals or in the meat industry (Sears, 1988; Walsberg, 1988). These techniques are noninvasive, although they do require calibration by carcass analysis. The first conductance studies appeared in the literature in 1988 (TOBEC: Walsberg, 1988; Ultrasound: Sears, 1988), and there is still debate about appropriate analysis techniques and application. In addition, the overall utility of conductance is still in doubt, and many researchers recommend careful review of the costs and benefits of these methods prior to their application in a field study.

3.5.1. Total Body Electrical Conductivity

The use of total body electrical conductivity (TOBEC) as an indicator of body composition is based on the behavior of a magnetic field when registering the presence of ions in hydrated tissue (Presta *et al.*, 1983). The technique requires that an animal be placed in a chamber surrounded by a solenoid (e.g., the EM-SCAN Small Animal Composition Analyzer, EM-SCAN, Inc., Springfield, Illinois), and computerized output then measures change in the phase relation of voltage and current caused by the presence of the animal. This method is most useful for measuring the conductance of lean body tissue, which has higher conductivity than fat (Walsberg, 1988). Measurement of conductance in a live organism requires that the animal be restrained temporarily, and that several iterations of the measurement be obtained to calculate mean conductance. Lean mass is estimated from regression models using the TOBEC reading and known lean mass derived from carcass analysis of a small subgroup of animals.

There are several limitations on the utility of TOBEC in a field study. Many authors have suggested that the body size range of animals suited for TOBEC is limited, with a maximum determined by the size of the chamber (approximately 600 g, Walsberg, 1988). Walsberg (1988) predicted that the lower limit for TOBEC would be 40 g, and few studies have used TOBEC for small birds (Skagen *et al.*, 1993; Roby, 1991). The presence of leg bands may influence TOBEC readings, although evidence is mixed. Two studies have indicated no effect of metal bands (Roby, 1991; Castro *et al.*, 1990). Others have shown that bands increase measurement error by as much as 10% (Skagen, *et al.*, 1993), and the effect can increase or decrease depending on the size of the band (Scott *et al.*, 1991). Statistical comparisons of TOBEC readings to test for a band effect may be necessary prior to pooling data from banded and unbanded individuals.

Three other factors—hydration level, thermal state, and position of

the animal in the chamber—may also cause deviations in TOBEC readings. Lean mass estimates depend on hydration state of the animals measured because dehydrated animals register higher TOBEC readings (Roby, 1991; Walsberg, 1988) than normal. It has therefore been suggested that interpretation of measurements from wild-caught animals that may recently have completed a long flight or that may be experiencing heat stress be treated with caution (Roby, 1991). Conductivity is also affected by thermal state (Roby, 1991; Scott *et al.*, 1991; Castro *et al.*, 1990; Walsberg, 1988). In a study of several shorebird species, the TOBEC index changed by approximately 1.5% for each degree of change in body temperature; however, the authors suggest that analyses can correct for such deviations owing to temperature (Scott *et al.*, 1991). The position of the subject in the scanning chamber has also been shown to cause deviations in conductivity (Roby, 1991; Castro *et al.*, 1990; Walsberg, 1988); this effect may be reduced by properly restraining the animal and standardizing its position prior to obtaining a measurement.

Statistical analysis of TOBEC data is another much-debated issue. Obtaining a reading and developing predictive equations to measure lean and lipid mass are the standard requirements for a condition estimate. Because it was initially thought that TOBEC mostly measures the conductance of lean mass, it was believed that lipid mass could be obtained by subtracting lean mass from total mass (Castro *et al.*, 1990; Walsberg, 1988). However, coefficients of determination for lean mass regressions are more precise than values actually obtained for lipid mass (Skagen *et al.*, 1993; Morton *et al.*, 1991). There is greater relative error in calculating lipid mass because it is a smaller proportion of body mass (Morton, *et al.* 1991; Castro, *et al.* 1990). As a result of these differences between the relative error of measures of lipid and lean mass, it has been proposed that multiple regression models should incorporate body mass, because lipid mass is more strongly reflected in body mass (Skagen *et al.*, 1993). Comparison of the different equations for predicting lean mass and lipid mass reveals that use of TOBEC to correct for individual structural size or lean mass differences (in a method proposed by Morton *et al.*, 1991) also increases accuracy of the estimate of lipid mass (Skagen *et al.*, 1993).

3.5.2. Ultrasonic Conductance

Only two surveyed studies used ultrasonic conductance to assess body condition (Newton, 1993; Sears, 1988). Unlike TOBEC, which measures conductance of the entire animal, ultrasound uses conductance of sound waves through specific tissues, mainly large muscle

masses such as breast muscle. Breast muscle mass is the commonly used indicator of protein stores (Evans and Smith, 1975), and the thickness of the breast muscle is likely to be related to breast muscle mass (Sears, 1988). The pulse-echo method estimates breast muscle thickness by sending a sound pulse through the muscle and recording the time required for the pulse to reflect back from the bone plate of the sternum (Sears, 1988). Data are obtained with a portable ultrasonic meter and calibrated from carcasses by using a pin inserted in the muscle to measure actual thickness (Newton, 1993; Sears, 1988). A strong correlation between ultrasound reading and muscle thickness has been obtained ($r^2 = 0.90$, Newton, 1993), and there is a strong curvilinear relationship between muscle thickness and the lean dry mass of the entire pectoral muscle ($r^2 = 0.86$, Sears, 1988).

Ultrasonic conductance has been used primarily because of difficulties in obtaining condition estimates by other means. However, the amount of information obtained from this measurement is restricted to protein condition, in contrast to the range of data obtained from TOBEC or carcass analysis. Sears (1988) originally developed this method for use on Mute Swans (*Cygnus olor*) because of their size and because the time and cost required for carcass analysis of large numbers of samples was prohibitive. Newton (1993) extended ultrasonic conductance to use on Dippers (*Cinclus cinclus*) because the thick downy feathers that insulate these birds prevent fat scoring, and there is little annual variation in mean body mass. To determine the most accurate placement of the ultrasonic probe, both studies used several iterations of the measurement at a number of different sites and confirmed these results with limited carcass analysis.

3.5.3. Conclusions about Using Conductance to Measure Condition

Although the application of new techniques designed for hospital or industrial use represents an increase in the types of data that can be obtained from live animals, researchers will want to consider the costs of applying such methods to a field study. Significant financial investment is required to obtain the necessary equipment. Application of the methods may also require the added stress of transporting animals to the laboratory for measurement, unless portable equipment can be obtained and successfully used in field conditions. Additional costs result from the need to calibrate such indirect techniques through carcass analysis. In applying the methods and interpreting statistical results, care must be used to standardize estimates across samples. An important question is whether or not the information obtained by conductance methods will outperform other low-cost and less technically com-

plex methods (i.e., fat score, body mass). One study showed that the increased accuracy from measurements of conductance came at a cost of $1,200–$4,000 per 1% improvement in the fat estimate (Skagen *et al.*, 1993). Other studies that compared several methods of assessing fat level revealed that fat scoring outperformed TOBEC in predicting lipid mass and percent lipid (Conway *et al.*, 1994; Meijer *et al.*, 1994). One of these also showed only moderate correlation between TOBEC and lean body mass (Conway *et al.*, 1994). Results such as these suggest that although conductance measures may be technologically complex, the limited extent of the improvements in the resultant data should be considered before adopting the methods.

3.6. Ptilochronology

Although it is common to define an organism's body condition in terms of its composition (e.g., carcass analysis) or of specific deposits of key metabolites (e.g., fat score, conductance), an index of the consequences of differences in body condition is usually lacking in such measures. Condition estimates that include some measurement of ability to perform a certain task, such as breeding, migrating, or molting, can provide a better link between process and outcome. One such condition estimate, ptilochronology (literally, "feather timing"), which measures daily feather growth, was first proposed and applied by Grubb (1989). Ptilochronology assesses induced anabolism by measuring characteristics of feathers that birds produce to replace intentionally removed feathers. Since its introduction, this method has been applied frequently because of its ease, low cost, and relatively noninvasive sampling.

3.6.1. Description of the Method

Ptilochronology measures the width of characteristic feather growth bars as an index of condition. Bars of color occur along the length of feathers in a pattern of alternating light and dark bands (Wood, 1950), and each pair of bands is thus believed to represent 24 hrs of feather growth (Michener and Michener, 1938). Growth bars differ from fault bars, which result from stress due to handling the animal (King and Murphy, 1984). The method assumes that a reduction in growth bar width reflects a period of low nutrition (as shown in Grubb 1989, 1991; Hogstad 1992), and that any change in the nutritional status of an individual also registers concomitant changes in the

feather growth bar index. In the original paper describing ptilochronology (Grubb, 1989), this method was compared to the use of tree rings as a measure of growth (Fritts, 1976). Growth bars are most readily observed in the tail feathers (rectrices), and to a lesser degree in flight feathers and contour feathers. Growth indices are obtained by first removing a feather (usually the sixth rectrix) to promote new feather growth. Later, the same individual is recaptured to remove the induced rectrix, and original and induced feathers are compared (Grubb, 1989). The interval between removal of an original feather and the subsequent removal of the induced feather may correspond to periods of interest to the researcher, such as a breeding season, mating period, or winter. Comparisons are based not on the width of individual growth bars, but on a mean daily growth bar width obtained from ten growth bars at a standard position on the feather (Grubb, 1989). Thus, growth bar indices can be used as a record of the past nutritional state of an animal during the time in which an induced feather was grown, rather than an index of an animal's current or future condition. Although this method does not require calibration (by carcass analysis), it does require that individuals be caught at least twice to collect both the original and induced feather.

The application of ptilochronology is wide-ranging. The growth bar index has been used as a method of assessing the effects of social rank on foraging behavior and aggression in Willow Tits (*Parus montanus*) (Hogstad, 1992), brood size in European Starlings (White *et al.*, 1991), and ovary growth in Tree Sparrows (*Spizella arborea*) (White and Kennedy, 1992). The interaction between diet and nutritional condition has been the focus of several studies (Grubb *et al.*, 1991; Grubb, 1989). This method has also been used to measure the effect of external conditions (such as weather) on Northern Cardinals (*Cardinalis cardinalis*) (Grubb *et al.*, 1991).

3.6.2. Conclusions about Using Ptilochronology to Measure Condition

As with any indirect method of assessing body condition (i.e., fat score, profiling), ptilochronology is dependent on many critical assumptions. Several of the assumptions have been described elsewhere (Murphy and King, 1991), and two are especially important if ptilochronology is to be successfully used as a condition index: the assumption that the ability to make accurate comparisons among birds can be based on growth bar widths, and the assumption that changes in nutritional state and altered growth bar width are related.

The first assumption inherent in ptilochronology is that feather growth rate is accurate for comparisons among individuals. To satisfy this assumption, growth bars must be reliably detected and must follow a 24-hr cycle, and sampling must be possible at more than one time to enable comparisons of induced and original feathers. However, detection of growth bars can be difficult in some species, such as those that are large, have barred pigments, or are irregular in activity patterns (Grubb, 1995). In addition, the metabolic and biochemical factors that create growth bars, and the time scale on which these factors act, have not been studied (Murphy, 1992; Murphy and King, 1991). Although previous research using radiolabelled food to measure the incorporation of dietary sulfur into feathers (i.e., radio-ptilochronology) by Willow Tits has confirmed the 24-hr timetable of growth bar production for that species (Brodin, 1993), the cause of growth bars is still relatively unknown. Additional problems in using ptilochronology include the possible failure of the bird to grow a replacement feather and that the variation time lagging between feather removal and regrowth may result in variation among individuals (White *et al.*, 1991). Low recapture rates may also reduce sample size or prevent comparisons of original and induced feathers (White *et al.*, 1991).

A second assumption of ptilochronology is that a reduction in growth bar width reflects a period of poor nutrition, but Murphy (1992) listed several variables that may interfere with this relationship. Individual feather papillae can differ in responsiveness depending on season and hormonal state (Lucas and Stettenheim, 1972), thereby creating time lags or lack of regrowth. Non-nutritional stressors (i.e., handling) can also create differences in feather characteristics (King and Murphy, 1984). The presence of certain key body reserves may also counteract any reduction in growth rates (Grubb, 1992).

The known assumptions of ptilochronology require a more conservative interpretation of changes in feather growth index. However, they do not necessarily negate the potential impact of ptilochronology on research on body condition. Both critics and proponents of the technique suggest that the method requires further study to determine the causes of growth bars and the factors potentially influencing them (Grubb, 1995; Murphy, 1992). Testing the assumptions is vital to accurate interpretation of the results of ptilochronology in a field study.

3.7. Profiling

Profiling is the visual assessment of condition by estimating or measuring body contour. This method relies on the fact that many

nutrients, such as fat and protein, are stored in specific locations in the body. When deposits of stored nutrients are visible from external observations, profiling is a potentially useful method of assessing condition. However, as with many of the methods discussed in this review, body profiling techniques vary in complexity and accuracy depending on the degree of investment in calibration.

3.7.1. Methods of Assessing Condition from Profiles

Two distinct types of profiling, pectoral and abdominal, have been used. These methods assess different types of reserves and have been applied in investigating different kinds of ecological questions.

Abdominal profiling was introduced in a study of Barnacle Geese (*Branta leucopsis*) (Owen, 1981) , and since its introduction its use has been primarily restricted to waterfowl studies (Bowler, 1994; Van Eerden *et al.*, 1991 but see the wader/shorebird study by Wiersma and Piersma, 1995). Abdominal profiling estimates energy stores (fat) by scoring the roundness of the region of the body from the legs to the tail (see illustrations in Owen, 1981; van Eerden, 1991). Although originally developed as a four-category scale, corresponding to a range in appearance of the abdomen from a profile that is straight to one that is sagging and highly rounded, a more detailed scale has been proposed in order to assess intermediate levels between these two extremes (Wiersma and Piersma, 1995; van Eerden *et al.*, 1991). Abdominal profiles can be measured without handling or disturbance of the bird; however, doing so requires that observers control for posture, which can significantly alter an individual's profile (Owen, 1981). This method may also not work well for females that are close to or have begun egg-laying, as the presence of a large ovary or oviducal egg may alter the abdominal profile. Profiles correlate well with morphological indices of condition, such as mass divided by structural size (Bowler, 1994), and they fluctuate in response to changing environmental conditions (Owen, 1981). These relationships have been taken as evidence supporting the use of abdominal profiles in empirical studies.

Whereas abdominal profiles estimate energy reserves by estimating fat level, pectoral profiles are used to assess protein stores based on size and fullness of pectoral muscle. To date only two of the reviewed studies have estimated condition from pectoral profiles (Bolton *et al.*, 1991; Geller and Temple, 1983). Pectoral muscles (*pectoralis major* and *supracoracoideus*) have been shown to represent a significant proportion of body mass (Bolton *et al.*, 1991), and a strong negative relationship between muscle mass and stage of egg laying has been reported in

several species (Ankney and MacInnes, 1978; Jones and Ward, 1976). Although profiling can be used as a qualitative method of assessing the size of the pectoral muscle complex (Geller and Temple, 1983), a more quantitative technique of measuring condition from the cross-sectional area of profiles has recently been proposed by Bolton *et al.* (1991). The latter method involves numerous steps, including calculation of keel height, tracing of cross-sectional profiles, and estimation of condition from regression residuals. This improved technique is accurate yet non-invasive, requiring only initial calibration by carcass analysis of a subset of animals. Cross-sectional profiling has thus far been shown to have low variability in measurements obtained from the same individual (approximately 3%), and to have a good relationship with egg production in gulls (Bolton *et al.*, 1993). Although at least one study has shown that profiles are confounded only slightly by lipid deposits in muscle (Bolton *et al.*, 1991), lipid deposits may be more problematic in long-distance migrants or waterbirds that may have thick subcutaneous lipid stores (deVries and van Eerden, 1995). Pectoral profiling also yields estimates of muscle mass that are similar in accuracy to measurements obtained from ultrasound (Newton, 1993; Sears, 1988), thus making it an important, low-cost alternative to the latter method. However, the accuracy of pectoral profiling is much greater when comparing groups of animals (at least 10–15 individuals) rather than values for individual birds, and this may limit the types of questions that can be addressed.

3.7.2. Conclusions about Using Profiling to Assess Condition

Profiling represents a new development in assessing condition because it provides an index of specific reserves and does so with little or no invasive sampling or handling. In the studies included in the literature survey, profiling was used only for larger species, such as gulls (Bolton *et al.*, 1991), geese (van Eerden *et al.*, 1991), and hawks (Geller and Temple, 1983), for which other methods (such as fat scoring) are less often used. However, recent work has shown that abdominal profiling may be applied to smaller species, such as the Red Knot (*Calidris canutus*) (Wiersma and Piersma, 1995). Advances have also been made in obtaining pectoral profiles for smaller birds by making a reproduction of the pectoral muscle region using dental alginate, which can register the muscle shape of such birds more accurately than can wire (Selman and Houston, 1996). Such improvements help to increase the accuracy and broaden the applicability of available techniques.

Several additional limitations must be considered. For example, in

scoring profiles, researchers face similar statistical difficulties as in scoring fat (section 3.4.3). Abdominal and pectoral profile scores are qualitative values, and these values do not necessarily scale to equal incremental changes in fat or protein level. As a result, analyses of profile scores require nonparametric statistical procedures to test for differences among individuals. Profile scores should also be tested for across-observer reliability, a common cause for variability in fat scoring studies (Krementz and Pendleton, 1990). In addition, studies that rely on variation in qualitative profiles may also use calibration with results from carcass analysis to determine how accurately these values predict actual changes in mass of storage components, as well as whether or not profiles represent the full range of values possible for the species studied. The more sophisticated profiling technique developed by Bolton *et al.* (1991) may increase the sensitivity of this method to allow detection of within-individual changes that would be useful for long-term studies of condition.

4. CONCLUSIONS

Previous sections have provided information on the history of condition research. The literature survey reveals the types of problems that have been addressed and the areas that have received less attention (long-term studies, certain taxa). The methods that have been used illustrate the wide range of condition indices available to researchers, their basic requirements, and their underlying assumptions. One of the most significant questions remaining to be considered is how future condition studies can be designed utilizing the information provided by this review. Several important factors should be addressed when developing protocols for a condition study.

Consideration of the species to be used is an important first step in accurately assessing body condition. Many taxa are well-represented in the literature survey, and the information from earlier work can help support future research on these species. Less is known about the interplay between condition and fitness in other taxa, which may indicate that more condition research should be done on these orders. Traits of species will influence the choice of a condition index, as certain techniques will not work for some groups. Thus, techniques developed for passerines may or may not be directly applied to other species, and researchers should carefully fit their methods to fit their study organism.

The specific question to be studied also constrains the choice of method(s). Not all purposes (such as those described in section 2.2) will

necessarily call for the same experimental design. Methods that provide only one index, e.g., an estimate of lipid mass (fat scoring, abdominal profiling) or of lean or protein mass (conductance, pectoral profiling), will describe only the effect of a single nutrient store. Questions that address the function of multiple nutrients such as protein, fat, and minerals will require techniques such as carcass analysis, or perhaps the simultaneous application of several different techniques.

Temporal considerations should influence the design of a condition study in at least two ways. First, short- and long-duration studies may have different sample size requirements for statistical analyses and will be able to make inferences over either a few or many years. In addition, different methods will yield information about an animal's condition at different times. Some techniques will provide only an indicator of past condition, while others will provide an index of current or future condition.

Prior to applying any of the methods described in section 3, a researcher must determine whether the study will support and/or require invasive or noninvasive sampling, or some combination of the two. Some investigations may require invasive sampling and carcass analysis, e.g., if the goal is to measure multiple nutrient stores or to understand shifts in body composition throughout the annual cycle. Other studies may preclude invasive sampling, e.g., if long-term monitoring of the same individual is to be conducted or if threatened or endangered species are studied. A majority of studies may benefit from initial invasive sampling and noninvasive sampling; if the former verifies the accuracy of the latter then the invasive sampling can be discontinued. In addition, many of the methods described make critical assumptions that must either be tested, or at least considered. Although it may not be necessary to verify the assumptions of a particular technique in every study, failure to meet them can result in inappropriate or invalid conclusions.

One final question is how researchers can distinguish between conceptual and operational definitions of condition. Most frequently condition is defined conceptually in terms of its relation to Darwinian fitness (Blem, 1990), or as the ability of an animal to cope with current and future demands (Owen, 1977; Evans and Smith, 1975). Indices of nutritional condition are not useful unless they can be evaluated in the context of the nutritional requirements and physiological adjustments available to an animal (King and Murphy, 1985). Condition must be an index of fitness if the measurement is to give any insight into evolutionary processes; yet determining the relationship between condition and fitness is not always straightforward. For example, recent theoretical,

experimental, and observational studies of the tradeoffs between starvation and predation risk show different costs and benefits of variation in nutrient stores (Lucas, 1994; Ekman and Hake, 1990; Lima, 1986). The fact that such tradeoffs exist, and in turn are affected by health and ecological context, makes it very difficult to quantify the relationship between condition and fitness. Thus, the idea that "fatter is not always fitter" is a valid argument because there may be no single conceptual definition of body condition that can be agreed upon for all species, at each point in time, in every context, for every researcher. However, as this review has shown, the history of condition research reveals tremendous advances in developing techniques and a wealth of information that may help to refine how body condition is studied in the future.

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APPENDIX: LITERATURE SURVEY SUMMARY

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
ORDER SPHENISCIFORMES				
King Penguin *Aptenodytes patagonicus*	1	MO, BR BR	CA CA	Cherel *et al.* (1993) Cherel *et al.* (1994)
Multiple species	1	DIET	MORPH	Murphy *et al.* (1990)
ORDER PODICIPEDIFORMES				
Eared Grebe *Podiceps nigricollis*	1	MI	CA	Gaunt *et al.* (1990)
Great-crested Grebe *P. cristatus*	2 9	TECH MI	MORPH CA	Piersma (1984) Piersma (1988)
ORDER PROCELLARIIFORMES				
Black-browed Albatross *Diomedea melanophris* Grey-headed Albatross *D. chrystoma*	1	BR	MORPH	Prince *et al.* (1981)
Blue Petrel *Halobaena caerulea*	1	BR	MORPH	Chaurand and Weimerskirch (1994)

ORDER PELECANIFORMES				
Cape Gannet *Sula capensis*	3	BR	CA	Navarro (1992)
Double-crested Cormorant *Phalacrocorax auritus*	2	BR	CA	Dunn (1975)
ORDER ANSERIFORMES				
American Wigeon *Anas americana*	1 3	GENETIC TECH	CA MORPH	Rhodes and Smith (1993) Wishart (1979)
Bewick's Swan *Cygnus columbianus*	3	TECH	PROFILE	Bowler (1994)
Black duck *Anas rubripes*	7 1 1 1 3	WIN WIN DIET ENV BR	MORPH CA CA BLOOD CA	Krementz *et al.* (1989) Morton *et al.* (1990) Morton *et al.* (1994) Rattner *et al.* (1987) Reinecke *et al.* (1982)
Black Duck *Anas rubripes* Mallard *A. platyrhynchos*	1	ENV	CA	Hanson *et al.* (1990)
Blue-winged Teal *Anas discors*	2	ENV	CA	White *et al.* (1981)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Blue-winged Teal *Anas discors* Northern Pintail *A. acuta*	3	GEOG	CA	Thompson and Baldassare (1990)
Brant	2	MO	CA	Ankney (1984)
Branta bernicla	3	MO	MORPH	Boyd and Maltby (1980)
Canada Goose	3	MO	CA	Gates *et al.* (1993)
Branta canadensis	1	BR	CA	Joyner *et al.* (1984)
	2	BR	CA	Mainguy and Thomas (1985)
	1	MI	CA	McLandress and Raveling (1981)
	2	BR, MO	CA	Raveling (1979)
	1	BR	CA	Thomas and Peach Brown (1988)
Canvasback	4	BR	CA	Barzen and Serie (1990)
Aythya valisineria	1	WIN	CA	Hohman (1993b)
	2	ENV	CA	Lovvorn (1994)
Common Eider *Somateria mollissima borealis*	1	BR	CA	Parker and Holm (1990)
Emperor Goose *Chen canagicus*	1	BR	MORPH	Schmutz (1993)
Gadwall *Anas strepera*	1	BR	CA	Ankney and Alisauskas (1991)

Greater Snow Goose	1	DIET	MORPH, BLOOD	Boismenu *et al.* (1992)
Chen caerulescens atlantica	2	BR	CA	Gauthier *et al.* (1984a,b)
	2	TECH	CA	Gauthier and Bedard (1985)
	2	MI	CA	Gauthier *et al.* (1992)
Greater White-fronted Goose	2	WIN	CA	Ely (1992)
Anser albifrons frontalis				
Greylag Goose	1	MI	PROFILE	van Eerden *et al.* (1991)
Anser anser				
Lesser Scaup	4	BR	CA	Afton and Ankney (1991)
Aythya affinis	2	BR	CA	Austin and Fredrickson (1987)
Lesser Scaup	2	TECH	CA	Chappell and Titman (1983)
Aythya affinis				
Greater Scaup				
Aythya marila				
Lesser Scaup	3	DIET, MI	CA	Gammonley and Heitmeyer (1990)
Aythya affinis				
Bufflehead				
Bucephala albeola				
Lesser Snow Goose	2	BR	CA	Ankney (1977)
Chen c. caerulescens	2	MO	CA	Ankney (1979)
	2	BR	CA	Ankney and MacInnes (1978)
		BR	CA	Hamann *et al.* (1986)
	1	BR, MI	CA	Wypkema and Ankney (1979)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Mallard	3	BR	MORPH	Gatti (1983)
Anas platyrhynchos	1	TECH	CA	Greenwood *et al.* (1986)
	3	MO	CA	Heitmeyer (1988a,b)
	4	BR	CA	Krapu (1981)
	13	ENV	MORPH	Owen and Cook (1977)
	2	MO	MORPH	Panek and Majewski (1990)
	2	BR	MORPH	Pattenden and Boag (1989)
	1	WIN	CA	Pawlina *et al.* (1993)
	2	MO	MORPH	Pehrsson (1987)
	3	WIN	CA	Whyte and Bolen (1984)
	2	BR, DIET	CA	Young (1993)
Mottled Duck	2	WIN	CA	Moorman *et al.* (1992)
Anas fulvigula				
Mute Swan	–	TECH	CONDUCT	Sears (1988)
Cygnus olor				
Northern Pintail	2	BR	CA	Duncan (1988)
Anas acuta	2	BR	CA	Esler and Grand (1994)
	2	BR	CA	Mann and Sedinger (1993)
Northern Shoveler	2	BR	CA	Ankney and Afton (1988)
Anas clypeata				
Redhead	1	BR, TECH	CA	Bailey (1979)
Aythya americana	3	MO	CA	Bailey (1985)

Ring-necked Duck	5	BR	CA	Alisauskas *et al.* (1990)
Aythya collaris	3	BR	MORPH	Hohman (1986)
	1	WIN	CA	Hohman and Weller (1994)
Ruddy Duck	1	BR	CA	Alisauskas and Ankney (1994)
Oxyura jamaicensis	1	MO	CA	Hohman (1993a)
	3	BR	CA	Tome (1984)
Wood duck	–	BR	BLOOD, CA	Clay *et al.* (1979)
Aix sponsa	2	BR	CA	Drobney (1982)
	1	BR	MORPH	Harvey *et al.* (1989)
	3	BR	MORPH	Hepp *et al.* (1990)
ORDER FALCONIFORMES				
American Kestrel	2	MI	CA	Below (1979)
Falco sparverius		TECH	MORPH	Negro *et al.* (1994)
Eurasian Kestrel	10	BR, DIET	MORPH	Dijkstra *et al.* (1988)
Falco tinnunculus	9	BR, DIET	MORPH	Meijer *et al.* (1988)
Northern Harrier	3	MA	MORPH	Simmons (1988)
Circus cyaneus				
Osprey	1	BR, DIET	MORPH	Machmer *et al.* (1992)
Pandion haliaetus	4	MA	MORPH	Poole (1985)
Red-tailed Hawk	1	MI	PROFILE, SCORE	Geller and Temple (1983)
Buteo jamaicensis				
Spanish Imperial Eagle	3	BR	BLOOD	Ferrer (1992)
Aquila adalberti				

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Swainson's Hawk *Buteo swansonii* Broad-winged Hawk *B. platypterus*	12	MI	MORPH, SCORE	Smith *et al.* (1986)
ORDER GALLIFORMES				
Black Grouse *Tetrao tetrix*	1	TECH	CA	Willebrand and Marcstron (1989)
European Quail *Coturnix coturnix*	2	MI, BR	SCORE, CA	Boswell *et al.* (1993)
Northern Bobwhite *Colinus virginianus*	– 1	DIET TECH	BLOOD CONDUCT	Lochmiller *et al.* (1993) Roby (1991)
Northern Bobwhite *Colinus virginianus* Scaled Quail *Callipepla squamata*	1	DIET	CA	Leif and Smith (1993)
Norwegian Rock Ptarmigan *Lagopus mutus*	1	ENV	CA	Mortensen *et al.* (1985)
Red Grouse *Lagopus l. scoticus*	15	BR DIET	MORPH PROFILE	Moss *et al.* (1993) Savory (1983)

Rock Ptarmigan *Lagopus mutus repestris*	2	BR, WIN	CA	Thomas (1982)
Ruffed Grouse	1	DIET	MORPH	Beckerton and Middleton (1983)
Bonasa umbellus	3	BR	CA	Servello (1988)
Sage Grouse	3	MA	CA	Hupp and Braun (1989)
Centrocercus urophasianus	2	WIN, BR	CA	Remington and Braun (1988)
	3	MA	BLOOD, MORPH	Vehrencamp *et al.* (1989)
Sharp-tailed Grouse *Tympanuchus pallidicinctus*	3	BR	MORPH	Tsuji *et al.* (1994)
Spruce Grouse *Dendragapus canadensis*	3	BR	MORPH	Naylor and Bendell (1989)
Svalbard Ptarmigan *Lagopus mutus hyperboreus*	–	DIET	MORPH	Mortensen and Blix (1985)
Willow Grouse *Lagopus lagopus*	1	BR, DIET	CA	Brittas (1988)
Willow Ptarmigan	4	BR	MORPH	Robb *et al.* (1992)
Lagopus lagopus	2	BR	CA	Thomas and Popko (1981)
ORDER GRUIIFORMES				
American Coot *Fulica americana*	1	BR	CA	Alisauskas and Ankney (1985, 1987)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Coot *Fulica atra*	3	ENV	CA	Visser (1978)
Multiple species	1	BR	CA	Jones and Ward (1977)
Sandhill Crane *Grus canadensis*	2	MI, BR	CA	Krapu *et al.* (1985)
ORDER CHARADRIIFORMES				
American Woodcock *Philohela minor*	1	TECH	CONDUCT	Morton *et al.* (1991)
Bar-tailed Godwit *Limosa lapponica*	2 6	MI MA	CA MORPH	Piersma and Jukema (1990) Piersma and Jukema (1993)
Black-headed Gull *Larus ridibundus*	1	BR	BLOOD, MORPH	Nelsen and Brandl (1988)
Common Tern *Sterna hirundo*	3	BR, DIET	MORPH	Frank and Becker (1992)
Dipper *Cinclus cinclus*	1	TECH	CONDUCT	Newton (1993)
Dunlin *Calidris alpina*	4 2 2	MI, MO MI BR	MORPH CA CA	Holmgren *et al.* (1993) Mascher and Marcstrom (1976) McEwan and Whitehead (1984)

Dunlin *Calidris alpina* Red Knot *C. canutus*	1	CAP	CA	Davidson (1984)
Great Skua *Catharacta skua*	4	BR	MORPH	Hamer and Furness (1993)
Grey Plover *Pluvialis squatarola*	1	ENV	MORPH	Dugan *et al.* (1981)
Herring Gull *Larus argentatus*	3	ENV	MORPH	Coulson *et al.* (1983)
	3	BR	CA	Hario *et al.* (1991)
	7	BR	CA	Norstrom *et al.* (1986)
Least Auklet *Aethia pusilla*	3	BR	MORPH	Jones (1992)
Lesser Black-backed Gull *Larus fuscus*	1	TECH	PROFILE	Bolton *et al.* (1991)
	1	BR	CA	Houston *et al.* (1983)
Multiple species		TECH	BLOOD	Bradley and Threlfall (1974)
	3	MI	MORPH	Dick and Pienkowski (1979)
	2	BR	CA	Duncan (1988)
	1	BR	CA	Johnson and Morton (1979)
	1	MI	BLOOD	Klaasen *et al.* (1990)
	5	MI, TECH	CA, MORPH	Piersma and Van Brederode (1990)
	2	MI	CA	White and Mitchell (1990)
	3	MI, MO	MORPH	Zwarts *et al.* (1990)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Oystercatcher	6	BR, MI	MORPH	Dare (1977)
Haematopus ostralegus	1	ENV, WIN	CA	Swennen and Duiven (1983)
Pacific Golden Plover *Pluvialis fulva*	10	MI, WIN	CA	Johnson *et al.* (1989)
Purple Sandpiper *Calidris maritima*	1	MI	CA, MORPH	Summers *et al.* (1992)
Ring-billed Gull *Larus delawarensis*	1	BR	MORPH	Boersma and Ryder (1983)
Ruff *Philomachus pugnax*	12	MI	MORPH	Koopman (1986)
Sanderling *Calidris alba*	2	TECH	MORPH	Castro and Myers (1990)
Semipalmated sandpiper *Calidris pusilla*	3	MI	MORPH	Dunn *et al.* (1988)
Semipalmated Sandpiper *Calidris pusilla* White-rumped Sandpiper *C. fusciocollis*	1	MI, TECH	CONDUCT	Skagen *et al.* (1993)
Turnstone *Arenaria i. interpres*	14	MI, MO	CA, MORPH	Summers *et al.* (1989)

White-rumped Sandpiper *Calidris fuscicollis*		MI	MORPH	Harrington *et al.* (1991)
Wilson's Phalarope *Phalaropus tricolor* Red-necked Phalarope *P. lobatus*	3	BR	CA	Ellis and Jehl (1991)
ORDER COLUMBIFORMES				
Woodpigeon *Columba palumbrus*	3	BR	MORPH, SCORE	Murton *et al.* (1974)
ORDER PSITTACIFORMES				
Budgerigar *Melopsittacus undulatus*	1	DIET, ENV	CA	Wyndham (1980)
ORDER STRIGIFORMES				
Snowy Owl *Nyctea scandiaca*	10	ENV	MORPH	Kerlinger and Lein (1988)
Tawny Owl *Strix aluco*	11	BR, MO	CA	Hirons *et al.* (1984)
Tengmalm's Owls *Aegolius funereus*	2	BR	MORPH	Korpimaki (1990)
ORDER APODIFORMES				
Rufous Hummingbird *Selasphorus rufus*	11	MI	MORPH	Carpenter *et al.* (1993)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
ORDER PICIFORMES				
Downy Woodpecker *Picoides pubescens*	1	TECH, DIET	PTILO	Grugg (1989)
ORDER PASSERIFORMES				
American Goldfinch	5	ENV	CA	Dawson and Marsh (1986)
Carduelis tristis	5		MORPH, SCORE	Wiseman (1975)
Blackcap *Sylvia atricappila*	–	MI	MORPH	Wood (1982)
Blackcap *Sylvia atricapilla*	4	DIET	MORPH, SCORE	Jordano (1988)
Garden Warbler *S. borin*				
Blue Tit *Parus caeruleus*	2	BR	CA	O'Connor (1976)
Bluethroat *Luscinia s. svecica*	4	MI	MORPH	Ellegren (1992)
Brambling *Fringilla montifringilla*	–	ENV, WIN	CA	Jenni and Jenni-Eiermann (1987)
Brown-headed Cowbird	1	BR, DI	CA	Ankney and Scott (1980)

Molothrus ater	2	SOC	MORPH	Dufour and Weatherhead (1991)
	1	BR	CA	Scott and Ankney (1991)
Common Crow *Corvus brachyrhynchos*	1	BR	CA	Young (1989)
Dark-eyed Junco	1	MI	MORPH, SCORE	Chandler and Mulvihill (1992)
Junco hyemalis	5	WIN	MORPH, SCORE	Nolan and Ketterson (1983)
	4	BR	MORPH	Wolf *et al.* (1991)
	3	TECH	MORPH, SCORE	Rogers (1991)
	3	WIN	MORPH	Rogers *et al.* (1993)
Eastern Kingbird *Tyrannus tyrannus*	1	BR	CA	Murphy (1986)
Eurasian Nuthatch *Sitta europaea*	5	SO	MORPH	Matthysen (1989)
European Starling	1	WIN	CA	Blem (1981)
Sturnus vulgaris	1	BR	CA	Riklefs and Hussell (1984)
	3	BR	MORPH	Smith *et al.* (1993)
	1	SO	CA	Summers *et al.* (1987)
	1	BR	CA	Thompson and Flux (1988)
	1	BR	MORPH, PTILO	White *et al.* (1991)
Field Sparrow *Spizella pusilla*	4	BR	CA	Olson and Kendeigh (1980)
Garden Warbler *Sylvia borin*	1	MI, TECH	BLOOD	Jenni-Eiermann and Jenni (1994)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Golden-crowned Kinglet *Regulus satrapa*	1	WIN	CA	Blem and Pagels (1984)
Gray Jay	1	WIN	PTILO	Waite (1990)
Perisoreus canadensis	1	ENV, WIN	MORPH, SCORE	Waite (1992)
Great Tit *Parus major*	3	BR, ENV	CA	Mertens (1987)
Grey-backed Camaroptera *Camaropter brevicaudata*	3	BR	CA	Fogden and Fogden (1979)
Grey-breasted Silvereye *Zosterops lateralis*	1	MI	CA	Chan (1994)
Hooded Crow	–	BR	MORPH	Loman (1984)
Corvus corone cornix	4	TECH	CA, MORPH	Slagsvold (1982)
House Finch *Carpodacus mexicanus*	2	MA	MORPH	Hill (1990)
House Sparrow	1	ENV	CA	Fleischer and Murphy (1992)
Passer domesticus	1	DIET	BLOOD	Gavett and Wakeley (1986)
	–	TECH	CA	Jones (1991)
	3	BR	CA	Krementz and Ankney (1986, 1988)
House Wren *Trglodytes aedon*	3	BR	MORPH	Freed (1981)

House Wren *Troglodytes aedon* European Starling *Sturnus vulgaris*	2	BR	CA	Thompson *et al.* (1993)
Magpie *Pica pica*	1	BR	CA	Tatner (1984)
Multiple species	1	TECH	CONDUCT	Castro *et al.* (1990)
	2	MI	MORPH, SCORE	Diamond *et al.* (1977)
	3	ENV	MORPH, SCORE	Finlayson (1981)
	–	TECH	SCORE	Kaiser (1993)
	1	TECH	SCORE	Krementz and Pendleton (1990)
	2	WIN	MORPH	Lefebvre *et al.* (1992)
	2	MI	MORPH, SCORE	Morris *et al.* (1994)
	3	BR	CA	O'Connor (1977)
	–	DIET	MORPH, SCORE	Rogers (1987)
	12	WIN, DIET	MORPH, SCORE	Rogers and Smith (1993)
	3	MI	MORPH	Winker *et al.* (1992)
	1	BR, MI	MORPH	Yong and Moore (1994)
Northern Cardinal *Cardinalis cardinalis*	3	ENV	MORPH, PTILO	Grubb *et al.* (1991)
Northern Wheatear *Oenanthe oenanthe*	3	DIET	MORPH	Moreno (1989)
Pied Flycatcher *Ficedula hypoleuca*	2	BR	CA	Silverin (1981)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Red-billed Quelea *Quelea quelea*	1 1 1	BR BR MI	CA CA CA	Jones and Ward (1976) Jones and Ward (1979) Ward and Jones (1977)
Red-winged Blackbird *Aegelaius phoeniceus*	1	TECH	BLOOD	Gauthier and Thomas (1990)
Redpoll *Acanthis flammea* Robin *Erithacus rubecula*	2	MI, MO	BLOOD	Frelin (1974)
Robin *Erithacus rubecula*	2	MI	MORPH, SCORE	Sandberg (1994)
Siskin *Carduelis spinus*	2	WIN	MORPH	Senar *et al.* (1992)
Snow Bunting *Plectrophenax nivalis*	1	WIN	CA	Vincent and Bedard (1976)
Song Sparrow *Melospiza melodia*	7	BR	MORPH	Hochachka and Smith (1991)
Dark-eyed Junco *Junco hyemalis* Tree Sparrow *Spizella arborea*	–	DIET	MORPH, SCORE	Stuebe and Ketterson (1982)

Tree Sparrow *Spizella arborea*	1	TECH	MORPH, PTILO	White and Kennedy (1992)
Tree Swallow *Tachycineta bicolor*	1	BR	CA	Lozano (1994)
White-bellied Swiftlet *Collocalia esculenta*	1	BR	MORPH	Hails and Turner (1985)
White-breasted Nuthatch *Sitta carolinensis*	1	ENV, TECH	PTILO	Zuberbier and Grubb (1992)
White-crowned Sparrow *Zonotrichia l. leucophrys*	3 1 1 1	MI MO MO TECH	SCORE, MORPH CA MORPH MORPH	Cherry (1982) Chilgren (1977) Murphy *et al.* (1988) Murphy *et al.* (1989)
White-throated Sparrow *Zonotrichia albicollis*	3	TECH	MORPH, SCORE	Westneat (1986)
Willow Tit *Parus montanus* Marsh Tit *P. palustrus*	–	TECH	PTILO	Brodin (1993)
Willow Warbler *Phylloscopus trochilus*	2	MO	CA	Baggott (1975)
Wood Thrush *Hylocichla mustelina*	1	TECH	SCORE, MORPH, CONDUCT	Conway *et al.* (1994)

(*continued*)

APPENDIX (*Continued*)

Species	Duration of study (years)[a]	Purpose[b]	Method of assessing condition[c]	Source
Zebra Finch *Taeniopygia guttata*	1	DIET	MORPH	Burley *et al.* (1992)
MULTIPLE ORDERS				
Multiple species	2	MI	SCORE	Dyrcz (1987)
	1	WIN	PTILO	Grubb and Cimprich (1990)
	1	ENV	CA	Marcstron and Mascher (1979)
	1	BR	CA	Osborn and Harris (1984)
		TECH	CA	Perdeck (1985)
		TECH	CONDUCT	Walsberg (1988)

[a]This category left blank if duration of study was not explicitly stated.
[b]Purpose of study includes the following: BR = Breeding behavior/reproductive success, MI = Migration, TECH = Test of a technique of measuring condition, DIET = Diet or foraging behavior, WIN = Wintering behavior, SO = Social behavior, ENV = Environmental conditions such as weather or pollution, MO = Molt, MA = Mating.
[c]Method of assessing condition includes the following: CA = Carcass analysis, MORPH = Morphology or mass, SCORE = Fat scoring, BLOOD = Blood indicators, CONDUCT = Conductance, PTILO = Ptilochronology, PROFILE = Profiling.

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