



Measurement of mass change in breeding birds: a bibliography^S and discussion of measurement techniques

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Studies detailing how energy reserves change over the course of the breeding season can give us valuable insights into environmental and physiological factors affecting the life-history strategies of birds. Here, we bring together a reference collection of studies that have measured reproductive mass changes in 132 species. We discuss how data collection, recording and reporting can be refined to offer a detailed insight into the evolution of avian reproductive strategies.

In the late 1920s, anecdotal observations (Myers 1928, Taber 1928) suggesting that birds differed in mass according to season as well as time of day led ornithologists to measure these changes in mass over time (eg Hesse 1921, Graf Zedlitz 1926, Esten 1931, Kendeigh 1934, Linsdale & Sumner 1934a, 1934b, 1937, Nice 1937, 1938, Stewart 1937, Kirkpatrick 1944, Höhn 1947, review by Baldwin & Kendeigh 1938). Before long, these observers noticed that individuals not only differed from one measurement to the next (Marples 1935), but mass variation also existed in relation to time of year, time of day, sex, age, and location. Furthermore, birds tended to show very different masses during their breeding season, when compared to other times of the year (Mountfort 1935, Baldwin & Kendeigh 1938). Since then, as detailed in Table 1 (<http://www.bto.org/ringing/rmj/rmj-23-1.htm>), numerous studies have recorded how body mass changes over the course of the breeding season.

Why is it useful for us to understand how energetic reserves change over the course of the breeding season? It has been shown in theoretical studies that an understanding of how energetic reserves change over the course of a day or season (McNamara *et al* 1994, Houston & McNamara 1999), or during migration (Hedenström & Ålerstam 1997, Houston 1998), can give us valuable insights into many aspects of how evolution has shaped the life histories of birds. In the context of breeding, one important concept is that a trade-off exists between current and future reproductive

success: if an animal invests a certain amount of resources and time in a current reproductive attempt, it may then be reducing its ability to survive and invest in future reproductive attempts. This is commonly called the 'cost of reproduction' (Williams 1966, Reznick 1985, Lessells 1991, Roff 1992, Stearns 1992). If we are able to measure the costs associated with a reproductive attempt, we may be able to understand the processes that determine how selection has acted upon species' life histories.

Unfortunately, measuring the cost of reproduction is problematic (see eg Bell 1980, Reznick 1985, Bryant 1988, Clutton-Brock & Godfray 1991, Partridge 1992, Lessells 1993) – it is notoriously difficult to quantify long-term measures of fitness, such as the effects of a particular behaviour upon the survival and reproductive success of both the focal parent and the offspring (and subsequent generations) that are affected by its behaviour. Instead of these long-term measures, short-term surrogates recording current effort are often used instead, such as measuring how energy reserves change over the course of the breeding season (Bryant 1988). These short-term measures are more useful, because they offer a potential means of identifying the stage at which costs are incurred, as well as the causal agent and the scale of these costs. Furthermore, their measurement is much more amenable in short-term ecological studies. However, despite their usefulness, these short-term measures must first be proven as reliable indicators of long-term changes in fitness – if not, they may provide unreliable information about the trade-offs between current and future reproductive success that could be occurring (Sibly & Calow 1984, Bryant 1988).

^SThe bibliography (Table 1) is only available online at <http://www.bto.org/ringing/rmj/rmj-23-1.htm>

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Changes in body mass – the consequences of decisions made by the parent about how it should maintain its own reserves (such as stores of fat or protein distributed around the body), and how these should be allocated during reproductive attempts – have often been considered to reflect a cost of reproduction. A variety of patterns are seen during reproduction, which can be related to life-history strategies (Moreno 1989a, Rands 2000). Individuals within a species tend to show highly conserved patterns of mass loss during reproduction. It can be argued that this loss will have an effect on an individual's future survival (and hence its chances of going on to reproduce). Therefore, examining this short-term effect on an individual may give us a chance to predict the resulting long-term effects.

The differences in ecology and physiology between species may, therefore, affect how the cost of reproduction is manifested. For example, body size may have large effects upon the reserve allocation strategies of a species. Body size to body area scaling constraints will mean that there will be different metabolic expenditures and physiology in species of different sizes, and this may well have an effect upon strategy. If we consider bird breeding strategies (Baicich & Harrison 1997, Harrison & Castell 1998), species that migrate to a distant breeding site, incubate constantly without feeding once there, and that have precocial chicks that are moderately self-sufficient, such as ducks and geese, are usually large birds. Smaller birds such as passerines tend to have altricial chicks, will take feeding recesses during incubation, and engage in central-place foraging for the chicks. Having large body reserves would suggest that an individual can fund a long period of incubation without the need to forage (Moreno 1989a), and reserve changes should reflect this.

Ideally, we should be able to conduct a comparative analysis of how ecology and physiology affect the patterns of mass loss in species: however, mass-loss strategies tend to be similar in closely related species, so similarity associated with shared phylogeny must be statistically separated from similarity resulting from common adaptation. The comparative method (Harvey & Pagel 1991, Martins 1996, Harvey & Nee 1997) offers a means of separating the effects of shared common ancestry from the ecological factors that we are interested in, and has been used effectively to explore many aspects of avian life-history strategies (Bennett & Owens 2002). However, for the comparative method or meta-analytic techniques to be applied usefully, data from different species and studies must be equivalent.

Table 1 (<http://www.bto.org/ringing/rmj/rmj-23-1.htm>) presents a bibliography of studies that have explicitly quantified mass changes over the breeding

period. Combining these studies together, in order to pick apart the processes and conditions that have shaped the evolution of mass change strategies, is complicated by several factors. On their own, these factors are usually not important in affecting the conclusions that we can draw from the individual study of a species or group of species, but mean that we would run into problems if we are comparing large numbers of studies. These factors include the recording of mass, time of day and pseudoreplication.

Recording mass

Mass (or some measure of body condition) has been recorded in many different ways. Some of the data come from live individuals, whilst others have been killed by various means (notably the waterfowl, where many of the data sets come from studies that also present detailed information on the masses and physical components of various internal organs), which could greatly affect the masses recorded as the age of the cadaver increases. In the studies that have examined live individuals, two forms of mass measurement are possible. In studies where the birds are trapped, direct handling and measurement of a bagged bird with a spring balance is probably the most common method. In addition to any direct effect of trapping and handling, the procedure can also have substantial long-term effects (Nicholson *et al* 2000, Rogers *et al* 2004). It is possible that some of these effects arise because birds respond to trapping in the same way as they respond to an unsuccessful attack by a predator. (For discussion of the optimal response to attacks, see McNamara *et al* 2005.) Furthermore, mass loss can be extremely rapid in response to a stressful event (Rands & Cuthill 2001), and so the masses measured from trapped specimens may change rapidly after the moment when the bird is trapped.

Therefore, if we are measuring mass changes in response to a carefully controlled breeding parameter, handling and trapping may add unwanted noise to the experiment. However, it is also arguable that if all trapped individuals are treated in the same way (as is likely during a capture session), then their responses to a stressor should be of a similar intensity and duration, and so it is legitimate to compare individuals within a study (although it is less simple to compare different species that may respond to the same treatments in different ways; similarly, different researchers conducting the same technique may impose different stresses within individuals of the same species). One solution that avoids imposing any extra stress is to allow the bird to measure itself, either by attracting the bird to a feeder or perch placed on a balance (*eg* Moreno 1989b, Vézina *et al* 2001), or if possible by placing the balance under

the nest, which ensures that a centrally-foraging parent weighs itself regularly over the course of the day. Many systems now exist that allow these measurements to be recorded remotely, and downloaded to a computer at a time that is convenient to both the researchers and the birds (eg Szép *et al* 1995, Reid *et al* 1999, Criscuolo *et al* 2000).

Time of day

Time of day may be important in determining the measured mass of the bird, but has only been taken into account in a few of the studies given in Table 1 (eg Haukioja 1969, Bryant 1975, Korpimäki 1990, Williams 1996). Outside the breeding season, birds show a huge amount of variation in mass over the course of the day (eg Cresswell 1998, Rands & Cuthill 2001, MacLeod *et al* 2005), and there are good reasons to expect such trends. For example, carrying a large amount of extra mass (such as energy reserves, or semi-digested food) may increase the bird's predation risk, as this extra weight makes the bird less agile in take-off and flight (eg Witter & Cuthill 1993, Kullberg *et al* 1996, Lind 2001), and maintaining these high reserves may mean that the bird has to spend more time exposed to danger whilst foraging. However, a bird carrying too little energy will expose itself to an elevated risk of starving, and so the energy reserves it carries should represent a trade-off between predation and starvation risk. Theoretical work has predicted that during harsh periods such as the winter months, where the bird faces a long period of night in which it is unable to forage, it should aim to build up its energy reserves gradually through the day, so that it has a large amount of reserves to survive through the night, and relatively low reserves for much of the day (eg Houston & McNamara 1993, Bednekoff & Houston 1994, McNamara *et al* 1994, Houston & McNamara 1999). Experimental work has confirmed these predictions (Cresswell 1998, Thomas 2000, MacLeod *et al* 2005), showing that fluctuations in an individual's energy reserves throughout the day should not be ignored, as this can be used to measure how the bird is responding to environmental stressors.

Because temporal variation in mass is important outside the breeding season, we should not underestimate its potential importance during parental care. It could be argued that including time of day as an extra measurement consideration is relatively unimportant when we are considering much larger changes in mass over the course of the breeding season, and taking our results from a large sample of individuals (where there is likely to be more variation between than within the individuals). Also, many capture protocols are likely to involve capture and weighing during a short

time-window of the day, negating the need to consider time of day. Therefore, although it is extremely useful to quantify and report the timing of measurements, careful consideration of time of day may only be an issue of concern when we are studying a small number of individuals repeatedly over time, or comparing different species where there may be a systematic bias in the time at which measurements are made (eg nocturnal *versus* diurnal species).

Pseudoreplication

In some studies, the experimental protocol has not been recorded in sufficient detail to ensure that data are not pseudoreplicated. Pseudoreplication in this context (as discussed in detail by Hurlbert 1984) would result from recording multiple data points from the same individual, and then presenting data for different individuals in a way that does not take account of this repetition. An individual is much more likely to be similar to itself at a future date or time than to a different individual, and so if repetition is not taken into account, this can substantially underestimate the variation between individuals and have a huge impact on whether a tested manipulation or environmental effect shows a statistically meaningful result. If data are being collected from ringed, identifiable individuals then pseudoreplication need not be an issue, provided that care is taken to ensure that multiple observations of the same individual within and between breeding seasons are dealt with in a statistically suitable manner. Through careful refereeing and an increased awareness of pseudoreplication, it is very unlikely that papers published in the last decade or so have presented data that is pseudoreplicated. Furthermore, in some cases it can easily be ascertained from the protocol whether pseudoreplication is possible (for example, repeated observations of the same individuals would not be possible in studies where birds have been shot and then measured). It is likely that many early papers have not presented pseudoreplicated data, but unfortunately the limited information about the protocols used makes it impossible to conclude this with certainty.

DISCUSSION

Therefore, we urge researchers collecting mass change data during reproduction to be careful in designing their experiment and collecting their data. As we have argued, it is unlikely that neglecting to record time of day is important in most studies, but pseudoreplication is something that could and should be avoided (usually by careful description in the methods sections of

papers). Different species of bird will require different methods of capture, and so it is arguable that if we wish to conduct comparative analyses of reserve allocation during the breeding season, this is an unavoidable problem that we simply have to work around. However, although we have urged caution, we cannot overemphasise the usefulness of mass-change data from any species of breeding bird. Table 1 (<http://www.bto.org/ringing/rmj/rmj-23-1.htm>) lists 132 species that have been examined to varying degrees of detail, but there are significant biases to the list, with a distinct emphasis on seabirds and wildfowl. As would be expected, bias is also distinctly European and North American with little coverage of tropical species, but, even from the European records, noticeable gaps include the woodpeckers, nightjars, swifts, most of the Ciconiiformes, Gruiformes and Coraciiformes, and a large proportion of the passerines (as well as the cuckoos, where any data that could be tied to breeding stage would be very interesting!). Especially useful would be detailed multiple observations of mass changes within individuals coupled with time of day, phase of breeding, and parental activity: information of this form would be enlightening from even the commonest of species. If these observations are made with suitably rigorous measurements such as those described in this paper, we may eventually be able to piece together a fuller picture of the evolution of avian parental care.

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