



The use of mass and fat reserve measurements from ringing studies to assess body condition

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The mass of birds can be used as an index of condition and of a bird's survival probability or fitness. If many birds are sampled and average patterns of condition appear, we can draw conclusions about how ecological factors affect condition and population dynamics. Mass can be negatively or positively correlated with fitness, depending on the environmental conditions that determine the relative costs and benefits of energy reserves: fat reserves act as insurance against starvation but are costly to gain and maintain, and increase predation risk. Environmental conditions that affect foraging predictability and so increase starvation risk, such as habitat quality, season, and weather, tend to lead to increased mass, whereas increased predation risk leads to decreased mass, except in good-quality habitats, where mass may increase. Mass change can reflect environmental conditions directly from the perspective of the bird species, and the monitoring of bird mass via a comprehensive and computerised ringing scheme takes the utility of birds as environmental indicators to a new and very powerful level.

Measures of a bird's mass and fat stores are routinely taken when birds are captured for ringing. These provide an estimate of condition or the degree to which an individual has stores of energy, and can be used as an index of fitness – how long, how often and how successfully an individual will reproduce in its life. Under a given set of environmental conditions, individual birds will vary in body condition because individuals vary genetically and so have phenotypes that may confer differences in their ability to deal with particular conditions (Cresswell 1998b). For example, when food is limited some individuals will be better competitors and so more able to meet their foraging needs (Cresswell 2001, Cresswell *et al* 2001). Relative body condition can then be used to draw conclusions about the relative probability of survival of an individual bird or its reproductive performance under these particular conditions. If many birds are sampled and average patterns of condition appear, then we can draw general conclusions about how environmental conditions affect population dynamics. For example, most individuals will be in poor condition when foraging is very difficult, and this may lead to declining populations (eg Anteau & Afton 2008). Alternatively, average body condition can be used as an index of environmental conditions because the proportion of a population that can optimise their body condition will depend on the environment (eg MacLeod *et al* 2008).

Any conclusions with respect to body condition based on mass, of course, depend on a clear understanding of

the causal relationship between fitness and mass. In some cases it may be straightforward: a bird of very low mass in cold weather (eg Brown & Brown 1998), or an unusually low-mass chick in a nest (eg Bukacinski *et al* 1998) may be in the process of starving to death. In other cases it is more complicated: a lower mass than average may indicate an individual with high survival probability, that can meet all its foraging requirements without having to store excess fat. Fat is costly (see below) but provides insurance for potential poor foraging, which less competitive individuals are more likely to encounter, in the future (eg Cresswell 2003).

So although mass will usually reflect condition, mass can be negatively or positively correlated with fitness, depending on the environmental conditions that determine the relative costs and benefits of energy reserves. This means that a good understanding is needed of the costs and benefits of increased energy reserves in birds. In particular, the circumstances that cause the cost and benefits to change need to be fully appreciated before any simple measures of energy reserves in birds such as mass can be translated into a measure of survival probability or environmental quality. For example, high mass can indicate relatively poor or good condition for wintering passerines dependent on the level of predation risk and the quality of the foraging environment (MacLeod *et al* 2007). Mass may not even directly correlate with fitness if other factors, that affect fitness in the opposite direction to mass, come into play to compensate. For example, in Blackbirds *Turdus merula*, overwinter mass correlates negatively with territory size, because the costs of maintaining high mass are

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probably lower for individuals that have small territories. In this case, mass would correlate with fitness only if the confounding effects of territory size were also considered (Cresswell 1999).

THE COSTS AND BENEFITS OF ENERGY STORES

Anyone that has caught species such as Blackbirds in winter will know that birds may weigh up to one third more than in the breeding season (eg Cresswell 1998a), without any apparent immediate consequences for survival in either season (Miller *et al* 2003). This is because when foraging intake is reduced and energetic demands increase, a bird that weighs more for its size will be able to survive much longer (Pravosudov *et al* 1997). Indeed most small birds and many larger species respond to any deterioration of foraging conditions by adding extra mass: counter-intuitively, as food becomes scarcer, so birds become fatter. We know from many ringing studies, particularly of waders, that in severe weather conditions, those birds with larger fat reserves are more likely to survive (eg Davidson & Evans 1982).

So why don't all birds carry extra mass against any chance of reduced foraging opportunity? The straightforward answer is that energy reserves are costly (Witter & Cuthill 1993), both in terms of the extra foraging time needed to acquire the extra reserves and to maintain them, because fatter birds have higher metabolic rates, all other things being equal (Houston *et al* 1997). There is also a cost in terms of predation risk because a fatter bird will have to spend more time foraging and therefore exposed to predation risk (rather than roosting safely in a bush, for example) (Brodin 2001). Mass may also increase predation risk because fatter birds accelerate more slowly when taking flight and so are less likely to initially outrun attacking predators such as Sparrowhawks *Accipiter nisus* (eg Kullberg *et al* 1996).

As a general rule, any animal that minimises its costs will have more resources to allocate to reproduction and so will be favoured by natural selection (Lessells *et al* 1991). Therefore animals should be selected to be very sensitive to cost-benefit trade-offs, and fat reserves in birds provide a classic example of this. Because increased energy reserves carry both a cost and a benefit, a trade-off will be important if birds are to maximise their fitness. If the benefits of energy reserves are high, for example to ensure survival during a cold-weather period, and the costs are relatively low, for example where the risk of being attacked by a Sparrowhawk is low, then birds will have relatively large fat reserves. But if the benefits decline, for example the weather ameliorates so that fat reserves are not needed, then the relative risk of being killed by a Sparrowhawk as a consequence of being fatter may exceed the relative risk of starving as a consequence of

being thinner. Then birds will lose their energy reserves (see Houston *et al* 1993).

Even if foraging conditions are poor, a bird forced to forage in an environment where predation risk is always very high, such as House Sparrows *Passer domesticus*, may only ever put on small fat reserves (MacLeod *et al* 2006). In areas of high predation risk we expect birds to minimise their chance of capture and so to minimise mass. In these circumstances there will be a negative correlation between mass and fitness because those birds that are the best competitors (*ie* perhaps the best foragers) will be able to manage successfully without fat reserves (Cresswell 2003). In areas of low predation risk we might predict the opposite.

Whether the benefits of fat reserves outweigh the costs of increased energy use and predation risk will depend on a number of factors that determine foraging predictability – in particular time of day, weather, and habitat quality or the availability of resources.

Time of day

Time of day provides a good example of how body mass reflects condition, and how this relationship can be positive or negative depending on the time of day and predation risk (McNamara *et al* 1994). Mass increases diurnally for both temperate and tropical birds to compensate for mass loss overnight when foraging is not possible (Cresswell 1998a, Goulart & Rodrigues 2007, Brandt & Cresswell 2009). Night length increases midwinter in temperate regions, when temperatures will also be at a minimum, so increased fat reserves at dusk become essential. For small birds such as tits, such energy reserves will determine whether a bird survives the 18-hour freezing dark period of a northern temperate winter (Blem & Power 1990). Fat reserves at dusk therefore are likely to correlate positively with fitness (eg Thomas 2000). This is also likely to apply just before dawn. A Robin *Erithacus rubecula*, for example, with high fat reserves at dawn will be able to sing from within a dense bush and enhance its reproductive potential with relatively low predation risk (see Thomas & Cuthill 2002, Thomas *et al* 2003). But high fat reserves after dawn during territorial patrol and defence activities which expose the Robin to predators will carry a relatively high predation risk. Any bird that cannot hide from predators completely during the day will also have a higher predation risk if they have higher fat reserves. As a result mass tends generally to be added later during the day in small birds, becoming early only as foraging becomes less predictable (Bednekoff & Houston 1994a): mass during most of the day then correlates negatively with fitness. The relationship between condition and mass reverses again as dusk approaches, when fat reserves again become positively correlated with fitness for all species.

Weather

Weather has one of the most obvious effects on mass as an index of body condition. Low temperatures, high winds and frozen conditions affect both the amount of energy needed by a bird to survive and its ability to gain that energy. Snow cover, frozen ground and high winds will decrease prey activity and detectability and so availability. This makes foraging unpredictable, and in combination with the extra energy demands of maintaining body temperature that severe weather entails, reduces the chance of a bird meeting its daily energy budget. Consequently, in most temperate passerine birds mass is put on seasonally, with fat reserves increasing during the winter, so that shortfalls in energy budgets can be met from the increased energy stores (Pravosudov *et al* 1997).

During severe weather, when foraging is impossible or unpredictable, and when predation risk becomes relatively unimportant, there will be a positive correlation between mass and fitness. For example, lower-mass waders are more likely to die during cold weather (eg Davidson & Evans 1982). There are, however, few instances where predation risk can be ignored completely. Therefore, although severe weather will lead to an increase in average mass of a population, individual birds should maintain the lowest mass they can: consequently body mass is likely to be correlated negatively with fitness except in the severest weather (Brodin 2007).

Habitat quality

Habitat quality also affects mass as an index of body condition in the same way that weather does. Weather can be considered as a component of habitat quality in any case, with severe weather acting to reduce habitat quality generally. If habitat quality deteriorates then birds may not be able to maintain condition and starve to death, or in more subtle cases they may not be able to reach reproductive condition or continue to feed their chicks (Weimerskirch & Lys 2000). In poor quality or 'sink' areas we would then predict a positive relationship between mass and habitat quality (eg Burton *et al* 2006). However, in areas of reasonable habitat quality we would predict a negative relationship with habitat quality because, as foraging predictability decreases, so mass should be added as insurance (eg Brown *et al* 2002). But such effects of habitat quality will also depend on predation risk.

In favourable environments, small birds can respond to increased predation risk by avoiding foraging at times and in places of higher predation risk but, because foraging opportunities become more constrained as a result, individuals need increased energy reserves to avoid an increased risk of starvation: this is known as the interrupted foraging response (Lima 1986, Lilliendahl 1998). In poor environments, however, individuals may have no choice

but to continue to feed at times and in places of higher predation risk. In this case, individuals can respond by reducing energy reserves, and therefore body mass, and predation risk is reduced not by avoidance but by reducing foraging exposure time and/or increasing flight performance and chance of escape when attacked: this is known as the mass-dependent predation response (Witter & Cuthill 1993, Bednekoff & Houston 1994b, Lilliendahl 1997). Reducing energy reserves to reduce predation risk entails a trade-off with an increased starvation-risk cost, however, so the mass-dependent predation response should be selected only when the foraging environment is too poor to allow the individual to meet its energy requirements during the reduced foraging opportunities that an interrupted foraging response would require. Therefore, high mass in areas of high predation risk will probably indicate a good environment, whereas low mass will indicate a poor environment (MacLeod *et al* 2007).

LIFE HISTORY AND BODY CONDITION

At certain life-history stages the absolute benefits of fat reserves may be particularly high, leading to strong positive correlations between mass and fitness: these might include terrestrial courtship (eg Hagelin 2003), egg production (eg Hanssen *et al* 2002), incubation (eg Cresswell *et al* 2004), moult (eg Perez-Tris *et al* 2001) and migration (eg Inger *et al* 2008). Similarly, but in reverse, certain life-history stages may have high costs to high mass: these might include aerial courtship, territory defence and foraging while feeding young. An incubating Eider *Somateria mollissima* in the Arctic, for example, may need to be very fat in all circumstances because otherwise it will not sustain incubation (Bolduc & Guillemette 2003), although such strategies evolve only where predation risk is very low (in line with the notion of a trade-off).

Migrating birds similarly cannot cross oceans or deserts without large fat reserves; the predation risk posed by Eleonora's Falcons *Falco eleonora* hunting a less manoeuvrable fat migrant over the Mediterranean (Hedenstrom & Rosen 2001) is probably relatively unimportant compared to the risk of a thin migrant not having sufficient reserves to get across the sea. The relationship between mass and condition will therefore be species- and life-history-stage-specific, dependent on mating system, foraging strategy, adult survival rate, reneating potential, whether the young need parental feeding, moult timing and duration, migration strategy and so on, and there will also be an interaction with environmental conditions, habitat characteristics and predation risk. Key examples of this are mass changes directly in response to reproduction, moult and migration.

Reproduction

Mass will often be correlated with fitness during reproduction, but the direction of this relationship will depend on stage of breeding and on species. For example, contest courtship such as lekking may require high mass in the competing sex for any reproductive success, although alternative successful strategies associated with lower body condition may be possible (eg Andersson 1994). Females of any species with low body reserves during egg production are likely to be in poor condition: body mass may then indicate lifetime reproductive success in females but not males (eg Jensen *et al* 2004). The breeding success of capital-breeding species in particular may be positively correlated with mass, but short-lived species may show the reverse, because fledgling mass is maximised rather than adult condition (Horak 2003). Long-lived species may need to reach a threshold of body condition before commencing breeding (eg Becker *et al* 2001), when body condition then declines; after breeding there may be a period when body condition is regained (eg Weimerskirch & Lys 2000). But, in some species, such mass loss post-breeding may be adaptive because low mass will promote flight and foraging efficiency when feeding chicks (Ritz 2007). The chance of fledglings surviving their first year usually depends on high mass at fledging (eg Both *et al* 1999), although, for small species at some point during their first few months, starvation risk decreasing below predation risk may reverse this relationship (eg Brotons & Broggi 2003).

Moult

Increased mass may allow for more rapid moult, or may be traded off against moult duration and frequency so that there is no direct relationship between mass and fitness (eg Senar *et al* 1998, Bojarinova *et al* 1999), or may be reduced during moult to compensate for reduced flying ability (Lind & Jakobsson 2001, Senar *et al* 2002).

Migration

High mass is a very important predictor of migration speed (eg Izhaki & Maitav 1998), timing (eg Battley *et al* 2004) and success when crossing barriers (eg Rubolini *et al* 2002), and so is likely to be correlated positively with fitness during migration time (eg Morrison *et al* 2007), but again this may vary, for example with a stronger effect for pre-breeding migration, when arrival dates and condition are more likely to determine breeding success than migration at other times.

SYNTHESIS: THE VALUE OF RINGING STUDIES THAT MEASURE CONDITION

Mass data collected from ringing studies presents a great opportunity for monitoring bird populations and

habitat quality. For example, body mass in Blackbirds has been shown to correlate with individual competitive ability (Cresswell 2003). Body mass in albatrosses, in conjunction with its interaction with environmental conditions, has been shown to be a good predictor of adult and chick survival and overall lifetime reproductive success (Weimerskirch *et al* 2001). Body mass in Redshanks *Tringa totanus* has been shown to be associated with habitat availability (Burton *et al* 2006) and winter weather conditions (Mitchell *et al* 2000). Body mass in Great Tits *Parus major* has been shown to be an index of predation risk (MacLeod *et al* 2005) and Sparrowhawk abundance (Gosler *et al* 1995). Similarly, mass gain or loss with respect to predation risk (as measured by Sparrowhawk abundance) in 26 common species monitored by ringing in the UK over a ten-year period has been shown to predict population declines (MacLeod *et al* 2007). Body mass, within a wider study of all the important factors that affect its use as an index of condition, can therefore be used to provide a valuable monitoring tool that can predict the survival of individuals, population dynamics and habitat quality and change (Piersma & Lindström 2004).

But, as this review illustrates, mass can be used to make predictions about fitness, population dynamics or the environment only with a thorough knowledge of the natural history of the species concerned and so how the relative costs and benefits of mass vary. Mass data are most usefully collected within the context of an integrated monitoring programme, where breeding parameters, population density, density of predators, and survival are collected on a national scale. If such data are computerised then it is possible to carry out very powerful analyses efficiently. Such mass data and all of the ancillary data that allow us to interpret mass changes have been collected by the BTO for the last century, but it is only now, with advances in our theoretical understanding and more powerful computing and statistical techniques, that these data are beginning to be used to their full potential.

The BTO's bird monitoring schemes are acknowledged to be, more or less, a model of how bird data can contribute to wider environmental monitoring and so our understanding of how humans affect and manage ecosystem services. Ringing data are crucial and all ringers should continue to collect and computerise mass and biometric data from the birds they capture, with these data referenced by individual, time of day, habitat and site location. But some other aspects of mass data collection in ringing could be emphasised, particularly the value of multiple captures of the same individual at different times: intra-individual comparisons control for many of the confounding factors that affect the relationship between mass and condition. Local monitoring of weather conditions and other specific local conditions

that affect the mass and condition relationship, such as supplemental feeding at a ringing station would be a valuable addition to the ringing database. A record of the number of Sparrowhawks and other predators observed per person per hour at a ringing station would also increase the resolution of the data and our ability to infer local population and environmental changes.

With increasing pressure to understand and manage environmental change due to anthropogenic effects on ecosystem functions, any ways that we can monitor change are valuable. Mass data have been collected for a long time and over a very large spatial scale by ringing schemes and the value of these data has only recently begun to be realised. For example, we could potentially use mass data collected by European ringers over the last century as an accurate index of change in environmental quality. Although many sites have been monitored directly for some of the time (so allowing us to ground-truth the use of mass data as an index of environmental quality), many more have not. Direct environmental and population monitoring takes time and money and is often complicated. In contrast, collection of bird mass data is being pursued by enthusiasts already over a large spatial and temporal scale, and is straightforward to carry out. But, perhaps best of all, mass change (as a properly understood index of body condition and fitness) reflects environmental conditions directly from the perspective of the bird species, integrating all of the environmental factors that are important to the bird. Birds have always been acknowledged as indicator species, but monitoring of bird mass via a comprehensive and computerised ringing scheme potentially takes their utility as indicators to a new and very powerful level.

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