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The ecological costs of avian fat storage

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SUMMARY

Avian fat storage is associated with both benefits and costs. Although the benefits of maintaining higher energetic reserves have long been considered, the associated costs have received far less attention. Spatial and temporal patterns of fat storage, together with experimental data, indicate that birds are capable of actively regulating their energetic reserves at levels below physiological or environmental maxima. This regulation implies that fat storage entails a cost. Evidence of potential costs are reviewed and discussed under the following headings: mass-dependent metabolism, mass-dependent predation risk, mass-dependent risk of injury, mass-dependent foraging, pathological costs and reproductive costs. Although the evidence that fat storage is costly is convincing, key empirical data are lacking. We indicate the sorts of data which need to be gathered and suggest ways in which this might be done. We go on to discuss the interaction of these costs and their relevance to between-individual patterns of fat storage and the interpretation of 'condition indices'. Because many of the purported costs of fat storage are dependent upon changes in body mass, or wing loading, our review is also relevant to other phenomena which may involve mass-dependent costs, such as gonadal hypertrophy, transport of food items and primary moult.

1. INTRODUCTION

The benefits of avian fat storage have been widely addressed in the ecological, ornithological and behavioural literature, with respect to the quantity, composition and morphological distribution of the fat stored (for reviews see King (1972); Blem (1976, 1990); Pond (1978); Lehikoinen (1986)). However, the costs of fat storage in wild populations are rarely considered. This is unfortunate, as a number of recent theoretical models which assume that fat storage has associated costs have led to insights into fat reserve dynamics (e.g. Lima 1986; McNamara & Houston 1990), energy storage strategies (e.g. McNamara et al. 1990), population-size regulation (e.g. McNamara & Houston 1987), migratory strategies (e.g. Alerstam & Lindström 1990; Lindström & Alerstam 1992) and the organization of daily behavioural routines (e.g. Houston et al. 1987; McNamara et al. 1987; Hutchinson et al. 1993).

Purported benefits of fat storage include body insulation (e.g. Blem 1974; Mortensen & Blix 1986), mechanical support, protection, buoyancy and both sexual and social signals (Pond 1978). However, the most widely acknowledged benefit of storing fat, and likely to be the most generally applicable, is the energy it liberates when metabolized. Although birds may utilize a number of energetic substrates (Blem 1990), lipid depots are the major energy reserve of most birds (Griminger 1986). Body temperature and resting metabolic rates are high in birds, even in comparison to other endotherms (e.g. Bennett & Harvey 1987; Prinzinger et al. 1991). Additionally, the predominant mode of locomotion amongst avian species is flapping flight, the most energetically expensive mode of locomotion per unit time. Stored fat can

fuel this high demand for energy during periods when such requirements cannot be met directly from environmental sources. Such circumstances may arise, for example, during a long migratory flight, due to periods of inclement weather, or simply due to the stochastic nature of foraging success. Although such benefits are readily apparent, the costs associated with avian fat storage have received only relatively sparse attention in the literature, and have not before been reviewed in detail (but see Pond 1981). This is surprising considering that it has long been realized that it is the trade-off between the benefits and costs of fat storage which determine the optimal level of reserves to carry (e.g. King 1972; Blem 1975; Pond 1978, 1981).

Recent models incorporating costs of fat storage (e.g. Lima 1986; McNamara & Houston 1987, 1990) have highlighted mass-dependent costs (i.e., costs caused by the increase in body mass associated with fat storage). In particular, mass-dependent metabolic expenditure and mass-dependent predation risk, have been suggested as potentially important costs of maintaining higher energetic reserves. An assumption behind these costs is that increased fat storage will be associated with an increase in body mass. Comparing across individuals, a variety of studies have found significant, positive correlations between body mass and lipid reserves (e.g. Blem 1981; McEwan & Whitehead 1984; Johnson et al. 1985; Blem & Shelor 1986). However, the storage of a given mass of fat will not always be associated with the same increment in body mass if other components of mass change when fat is stored. Although a number of studies have found non-fat components of birds to remain the same during fat deposition (e.g. Connell et al. 1960; Odum et al. 1964; Rogers & Odum 1964; Odum 1965; Helms

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et al. 1967; Johnston 1973; Mascher & Marcström 1976), other studies have found increases in water and/or protein content (e.g. King 1967; Moreau & Dolp 1970; Fry *et al.* 1972; Ward & Jones 1977; Blem 1980; Marsh 1984; Piersma & Jukema 1990; Lindström & Piersma 1993). If non-fat components of body mass necessarily have to increase during fattening then this may impose additional loading costs.

Although we concentrate on fat storage, mass-dependent costs will not only be associated with increased fat reserves, but would also apply to other phenomena which involve increased wing loading (the ratio of body mass to wing area) or body mass. Such examples include gonadal hypertrophy during the breeding season, carrying undigested food in the gut, or carrying prey to a nest or cache. Enhanced wing loading costs may also be incurred due to a decrease in wing area, as occurs during moult, or as the result of feather abrasion. Although each of these changes may have quantitatively different mass-dependent costs because, for example, the distribution of the load may differ between fat and food in the gut, or because moult and feather abrasion alter the shape of the wing in addition to its area, they may still usefully be viewed as qualitatively similar.

In addition to considering the evidence behind fat- and mass-dependent costs, we discuss the problems inherent in their study, suggest some possible directions for future research and propose hypotheses relating to the consequences of costly fat storage. We find that much of the key empirical work remains to be done. Nevertheless, a detailed knowledge and understanding of the nature of such costs may be critical to an understanding of, for example, fat reserve dynamics, strategic body mass regulation, the morphological distribution of fat, energy storage strategies (e.g. depositing fat versus caching food), types of energy budgeting (e.g. torpor versus non-torpor), the circadian and circannual organization of behaviour, and life-history decisions, particularly those involving energy allocation between self and offspring and strategies of parental mass allocation.

We discuss the purported costs of being fat under the following general headings, although clearly these costs are highly interrelated: mass-dependent metabolism, mass-dependent predation risk, mass-dependent risk of injury, mass-dependent foraging, pathological costs and reproductive costs. In the discussion we speculate on how costs and benefits may interact to produce observed population-level patterns of fat storage. Firstly, however, we discuss the evidence for avian body mass regulation, as regulation of mass has typically been taken as the first line of evidence in favour of the hypothesis that fat storage does entail some cost (e.g. Lima 1986; McNamara & Houston 1990; Ekman & Hake 1990; Krebs & Kacelnik 1991).

2. STRATEGIC REGULATION OF BODY MASS

The energetic yield of a fat store, considered alone, would imply that the optimal level of fat to be carried should be the maximum allowed by either physiological capacity or environmental availability, as the energetic value of the fat reserve is an increasing function of the size of reserve (the risk of starvation being a decreasing function of the size of reserve). However, a number of authors have noted that, most of the time, birds maintain stable levels of reserves that are apparently well below these maxima (e.g. King & Farner 1966; King 1972; Blem 1976). Circumstantial evidence in favour of this view stems from a consideration of temporal and spatial patterns of fat storage, or body mass change, exhibited by a wide variety of species. For example, the fat reserves within a species generally increase with increasing latitude (e.g. Dolnik 1967; Blem 1975). Individuals in many species become fatter during winter months compared to summer (e.g. Nice 1938; Bartleson & Jensen 1955; King & Farner 1966; Helms 1968; King 1972; Blem 1976; Haftorn 1976; King & Mewalt 1981; Lehikoinen 1986; Haftorn 1989). Even within winter, the highest reserves of fat have been found during the coldest periods (e.g. Baldwin & Kendeigh 1938; Odum & Perkinson 1951; Helms & Dury 1960; Helms 1968; Newton 1969; Evans 1969; Blem & Shelor 1986). Fat reserves may also increase with decreasing daylength (Kendeigh *et al.* 1969; Haftorn 1989) and decreasing time available to feed (Kacelnik 1979; Bednekoff 1992). Because food is liable to be less abundant during the winter, the above trends in energetic reserves are unlikely to be a simple 'passive' reflection of environmental food availability. Of course, there may be periods when food availability directly limits energetic reserves, although the prevalence of such circumstances may have been overestimated in the literature (King & Murphy 1985). The observed spatial and temporal patterns of fat storage are consistent with the hypothesis that birds are regulating their energetic reserves actively with respect to their needs. Consistent with this view is the observation that birds with low fat reserves do not utilize all available feeding opportunities (Lehikoinen 1986).

Birds may regulate their body fat, or body mass, in a 'preprogrammed' manner, at specific times in the circannual cycle, in anticipation of their energetic requirements for, say, breeding (e.g. Mrosovsky & Sherry 1980; Sherry *et al.* 1980) or migration (King & Farner 1965, 1966; Moore *et al.* 1982; Gwinner 1986; Alerstam 1990). Theoretical analysis also predicts that the optimal level of fat to store is dependent upon environmental factors such as temperature or food availability (Lima 1986; McNamara & Houston 1990). Consistent with this prediction, Rogers (1987), in a comparative study of a variety of small birds, found that species which exploit an unpredictable food source during the winter store higher levels of fat than those species which have a more predictable food source. Gosler's (1987) finding that dominant great tits, *Parus major*, store less fat than subordinants provides further circumstantial evidence in favour of adaptive regulation of reserves. Dominants may store less fat because they have a more predictable food supply or higher mean energetic gain. Subordinate individuals, which have a higher chance of being displaced or excluded from a source of food, have to

store higher levels of fat as an 'insurance' against interruptions or an overall reduction in the rate of energy intake. However, factors such as food availability or social environment may not always be predictable, so birds may have to regulate reserves in direct response to environmental cues, rather than following a fixed endogenous strategy. Currently available experimental evidence suggests that some species are able to alter the amount of fat they store appropriately to experimental manipulations of food predictability. For example, Ekman & Hake (1990) found that greenfinches, *Carduelis chloris*, responded to a short period of unpredictable access to food by increasing stores of body fat. Furthermore, Ekman & Lilliendahl (1993) found that removal of dominant willow tits, *Passer montanus*, resulted in a decrease in mass of subdominants.

Various measures of temperature show a general negative correlation with body mass (e.g. Newton 1966, 1969; Evans 1969; Chaplin 1974; Haftorn 1976; Lehikoinen 1986; but see O'Connor 1970; Biebach 1977). King & Farner (1966) have urged caution in the interpretation of the correlation between body mass, or size of fat reserve, and environmental temperature as representing evidence of proximate causation. They point out that temperature may be the ultimate cause of winter fattening patterns, rather than a proximate cue. Consistent with this hypothesis is the observation that the fat content of wintering American goldfinches, *Carduelis tristis*, on a particular date is best predicted by multi-year mean temperatures rather than, say, the actual temperature at time of capture, or on days prior to capture (Dawson & Marsh 1986). On the other hand, Blem & Shelor (1986) found larger correlation coefficients for 20 day averages of temperature and lipid reserves than average temperatures based on 1 to 32 years for the white-throated sparrow, *Zonotrichia albicollis*. Similarly, experimental manipulations of temperature have produced a range of results. Ekman & Hake (1990) found that greenfinches responded to an experimental decrease in temperature by storing more fat. However, some studies have found a decrease in total body mass or no significant change in response to a reduction in temperature (e.g. Kendeigh 1949; Chaffee & Mayhew 1964). These apparent inconsistencies may represent real between-species differences. Whether it is better to regulate body fat in direct response to environmental change or evolve a more fixed pattern of fat storage related to long-term trends must depend, in part, on between-season constancy and the extent to which between-season changes are predictable ('contingency'). Wingfield *et al.* (1992) have used the contingency–constancy approach to predictability to generate hypotheses about the control of gonadal cycles in birds. This approach may also be useful for understanding the regulation of avian fat storage. For studies performed in the field, the relationship between fat reserves and temperature will also depend on the availability of food; that is, upon whether or not birds are able to attain their optimal level of energetic reserves.

The above examples of energetic reserve regulation can be taken to imply a cost of fat storage (e.g. Lima 1986; McNamara & Houston 1990; Ekman & Hake 1990; Krebs & Kacelnik 1991), because these birds are maintaining stable levels of reserves below the maximum attainable. This is consistent with the view that the amount of fat stored is set by the apparent cost–benefit relationship of fat storage. That is, storing an amount of fat in excess of current, or expected, requirements is penalized by counteracting costs. It is the possible nature of these costs to which we now turn.

3. MASS-DEPENDENT METABOLISM

Fat storage might be expected to have a number of consequences for avian metabolism. We pay particular attention to the energetic costs of increased body mass associated with flight, as this is likely to have the largest influence on metabolic expenditure. It must be remembered, however, that it is difficult to accurately determine *a priori* what the energetic consequences of increased loading are for the flight costs of any particular individual. The relationship between the mechanical power requirements of flight, body mass and wing loading has an extensive theoretical base. However, the complicating issues of biomechanical and physiological constraints, the potential for mass-dependent metabolic efficiency, changing flight strategy and adjustments of physiological capacity, preclude an accurate generalization about the effects that increased body mass will have on energetic expenditure during flight of individuals of any particular species. Two approximate approaches have typically been employed in modelling these mass-dependent costs; using the theoretical relationship between body mass and the mechanical power requirements of flight (e.g. Pennycuick 1969, 1975; Houston 1986, 1990; McNamara & Houston 1987, 1990) or empirically derived formulae of the sort given in Norberg & Rayner (1987) and Rayner (1990). We discuss each of these below. The costs of other locomotory activities are also briefly considered. In principle, fat storage could also incur metabolic costs during periods of inactivity perhaps due to enhanced maintenance costs associated with the fat reserve, or due to enhanced musculature related to a higher body mass. Alternatively, fat reserves may have insulatory benefits which could depress the resting metabolic rate at low ambient temperatures. We also discuss these possibilities, and then go on to speculate on the necessarily more tenuous relationship between body mass and total daily metabolic expenditure.

(a) *Mass-dependent energetics of locomotion*

The mass-dependent energetics of flight have received extensive theoretical treatment, and have been considered in detail by a number of previous authors (e.g. Pennycuick 1968, 1975; Rayner 1979, 1990; Norberg 1981, 1990; Houston 1986; Norberg & Rayner 1987; Rayner *et al.* 1989; Pennycuick 1990). Hence, here, we only briefly consider how mass influences the power requirements of flight within an

individual, as this is most appropriate for analysing the costs of fat storage. A variety of treatments indicate that the mechanical power requirement of flight, at some characteristic velocity, is an accelerating function of body mass. A number of simple derivations, based on isometric scaling (e.g. Norberg 1981; Hughes 1990), indicate that the mechanical power requirements of flight (P) scale with body mass (M) as

$$P \propto M^{1.5}$$

Rayner (1990) calculated the mechanical power requirements of flight for a range of birds flying at maximum range velocity (V_{mr}) and related these power requirements (P_{mr}) to morphology (see Norberg & Rayner (1987) for details of the method employed). He derived the following equation

$$P_{mr} = 27.21 \ M^{1.590} \ B^{-1.818} \ S^{0.275},$$

where M is body mass, B is wing span and S is wing area. Within individuals, where B and S are constant, the equation predicts that the mechanical power requirement increases with body mass with an exponent of 1.590, a value close to that based on isometric scaling given above.

The equations above suggest that the mechanical power requirements of flight are an accelerating function of body mass, thus one may propose that the actual metabolic requirements of flight increase by at least this much. Pennycuick (1975) and Tucker (1974) have presented models of the metabolic requirements of flight which incorporate basal metabolism and costs of providing the flight musculature with energy and oxygen. However, as pointed out by Rayner (1990), a particular difficulty with the approach is the estimation of muscular efficiency. This has typically been assumed to be constant. Rayner (1990) argues that, because efficiency is determined by muscle contraction strain rate and stress, then efficiency must change with velocity because changes in velocity are necessarily related to wing-beat frequency and amplitude. By analogous reasoning, efficiency must be related to changes in body mass, even at a fixed velocity, since wing-beat frequency and amplitude change with body mass. However, since we are unaware of any work relating efficiency to changes in body mass within individuals we will not consider this potentially important issue further.

Given that it is difficult to determine accurately how the metabolic power requirements of flight change with body mass from purely a theoretical view, we now consider the empirical data on metabolic power requirements during flight. Rayner (1990) has also derived equations relating body mass, and other morphological variables, to metabolic power requirements of flight (P_{met}) based on available empirical measurements. The general equation for birds, which is consistent with theoretical predictions, is given below

$$P_{met} = 98.39 \ M^{1.505} \ B^{-2.539} \ S^{0.236}.$$

Thus, according to this extrapolation from between-individual patterns, within individuals the metabolic power requirements of flight are predicted to increase with body mass with an average exponent of 1.505. However, between avian taxa this value changes markedly. For example, for passerines the exponent is 1.930, while for non-passerines the exponent is 0.834. This may represent a real between-taxa difference (c.f. Aschoff & Pohl 1970), but pooling data across the non-passerine taxa may depress the allometric exponent (c.f. Harvey & Pagel 1991). Additionally, it should be noted that the sample size for non-passerines is small relative to that of passerines (see Masman & Klaasen 1987; Rayner 1990).

The techniques described above for relating body mass to the power requirements of flight, although appealing from the point of view of generality, are clearly a poor substitute for direct empirical measurement of the effects of experimentally manipulated wing loadings on individual birds. Unfortunately, direct measurements of the influence of body mass on metabolic rates during flight in birds are rare. Gessaman & Nagy (1988) studied the metabolic rate of homing pigeons, *Columba livia*, carrying transmitter loads of 2.5% or 5% of body mass. They found increases in metabolic expenditure in excess of what one would predict purely on the basis of the mass increment. However, the enhanced drag created by the transmitter would also increase the metabolic power requirements of flight, so it is difficult to determine the effect of mass change per se. Gessaman *et al.* (1991) have more recently attempted to investigate the effects of transmitter loads on tippler pigeons. In this case, they found no significant difference in metabolic expenditure between birds flying with and without a transmitter. They noted, however, that the relatively small sample size and high between-individual variability in metabolic rate precluded a good test of the influence of transmitter load on energetic expenditure.

The mass-dependent mechanical power requirements of flight, which we discussed above, apply to birds which are performing active flapping flight at some characteristic velocity on the velocity-power curve (c.f. Pennycuick 1975; Rayner 1979). Clearly, there is some scope for changing the relationship between the power requirements of flight and body mass by altering parameters of flight performance. Adoption of intermittent flight strategies (e.g. undulating or bounding flight; see Rayner 1985; Norberg 1990) or changes in flight velocity may complicate the relationship between body mass and power requirements. For example, Videler *et al.* (1988) found that European kestrels, *Falco tinnunculus*, responded to increased wing loading by decreasing flight velocity from near the predicted maximum range speed to near the predicted minimum power speed. Videler *et al.* considered that this shift took place because the kestrels were approaching their maximum sustainable power output, and decreased speed to reduce power requirements. The power output of the flight musculature may be increased by hypertrophy during periods of excessive, premigratory fattening (see Marsh 1984).

The relationship between power requirements of

flight and $M^{1.5}$ implicitly assumes that birds are mechanically or physiologically capable of maintaining optimal performance under increased load. Hughes & Rayner (1991) investigated the effect of changing wing loading on flight performance in the long-eared bat, *Plecotus auritus*. They found that *P. auritus* decreased flight velocity with increased loading, and suggested that this was the result of some undetermined physiological or mechanical constraint. With increased loading, the difference between predicted V_{mp} and observed velocity increased, resulting in a large increase in the mechanical power requirements of flight. This increase in power was approximately double that which would have occurred had the animal been able to adopt V_{mp}. It is difficult to ascertain how general constraints, such as maximum stresses, are for avian flight performance. Potentially at least, increased loading could result in more profound increases in the power requirements of flight than theory predicts if birds are unable to maintain optimal velocity.

The metabolic power requirements of other locomotory activities are also likely to be mass-dependent, although the costs in these cases are unlikely to be an accelerating function of mass. Running and walking in birds and mammals are remarkably similar, at least in terms of metabolic expenditure. Both taxa can be represented fairly accurately by the same regression equation relating body mass to energy requirements (e.g. Taylor *et al.* 1982; Peters 1983). Taylor *et al.* (1980) studied the influence of load carrying on oxygen consumption within individuals in a variety of mammals. They found that oxygen consumption increased in direct proportion to the mass of the load being carried, irrespective of the speed or size of the animal. We know of no comparable data for birds, but given the similarity in running and walking in the two groups, a similar relationship is likely to hold (Norberg 1981). Similarly, the energetic costs of other activities, which do not involve flight, such as hanging from branches to feed, are also likely to increase energetic expenditure in direct proportion to mass increment (see Mass-dependent foraging).

(b) Fat-dependent resting metabolism

Fat storage may have a number of influences on metabolic rate during periods of inactivity. For example, high levels of fat storage, associated with flight muscle hypertrophy (see Piersma 1990) could elevate BMR because of increased maintenance costs. Alternatively, subcutaneous fat deposits may provide insulation which could reduce resting metabolic rate at low ambient temperatures. Blem (1990) suggested that this may be why subcutaneous fat is first to be deposited but the last to be utilized. However, an insulatory function of fat has not been experimentally demonstrated in birds (Blem 1990), although some suggestive data exists (see Blem 1974; Mortensen & Blix 1986). For most small birds, metabolic adjustments appear to be more important than insulation in determining cold acclimation (e.g. Dawson & Carey 1976; Heldmaier *et al.* 1989). Increases in insulation
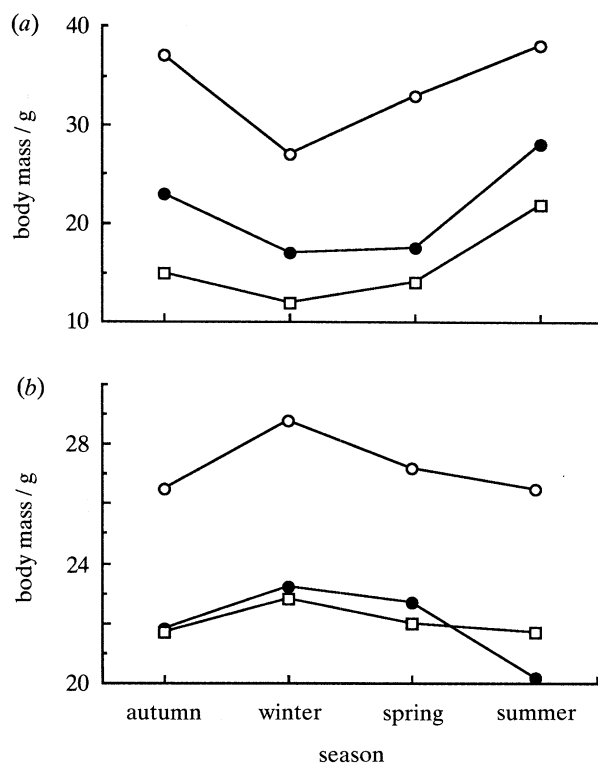

Figure 1. Seasonal change in body mass in (*a*) three small non-hibernating mammals: (open circles) *Phodopus sungorus* (Heldmaier & Steinlechner 1981), (filled circles) *Microtus pennsylvanicus* (Iverson & Turner 1974), (open squares) *Clethrianomys rutilus* (Seolander 1966); and (*b*) three small non-migratory birds: (filled circles) *Melospiza melodia*, (open circles) *Dryobates pubescens*, (open squares) *Parus bicolor* (Baldwin & Kendeigh 1938).

may actually be disadvantageous for birds during flight, when large amounts of heat have to be dissipated.

The metabolic costs of maintaining the fat reserve itself while inactive are poorly known (Lima 1986), but are probably small in comparison to the maintenance costs of muscle tissue or the mass-dependent costs associated with activity (see Kersten & Piersma 1987). A variety of small non-hibernating mammals show seasonal patterns of mass change very different from that exhibited by small birds (see figure 1). During autumn, body mass falls rapidly by between 30% and 50% to a new low winter level (e.g. Mezhzherin 1964; Zejda 1971; Heldmaier & Steinlechner 1981). This mass loss is paradoxical because it increases the surface area to volume ratio and reduces the size of energetic reserves. However, Heldmaier & Steinlechner (1981) found that this mass reduction decreased total energetic requirements because less heat needed to be generated to warm a smaller body (i.e. although the mass-specific metabolic rate increases, the reduction in body mass results in a decrease in total metabolic expenditure (see Heldmaier 1989)). We do not know whether a large fat reserve similarly increases thermoregulatory costs in birds. However, given the very different seasonal pattern of mass change which birds adopt it seems likely that if such a cost exists then it is out-weighed by the benefits of an increased energetic reserve.

(c) Fat storage and daily metabolic expenditure

Given that an increase in body mass, associated with fat storage, is likely to increase metabolic expenditure, particularly during locomotory activities, how might this manifest itself in the daily energy expenditure of the bird? Bryant & Tatner (1991) examined the influence of change in body mass on total daily energetic expenditure in a variety of birds. They found that for three species energetic expenditure and change in body mass were positively related, in one species the relationship was negative and in four there was no change. The relationship between energetic expenditure and change in body mass is necessarily related to any associated changes in behaviour. If the bird's behaviour does not change with body mass, then the change in its metabolic expenditure will be related in a relatively simple manner to the proportion of its time it spends active and any relevant increase or decrease in BMR. Of course, as a given bird changes in body mass its behaviour is unlikely to remain the same. The increase in active metabolic expenditure associated with an increase in body mass places extra energy demands on the individual. This implies that the animal must obtain more food from the environment, or process food more efficiently. Obtaining more food from the environment could be achieved in a number of ways (e.g. increasing feeding intensity, increasing the total time spent feeding or switching feeding site). Potentially, each of these methods of enhanced food intake may be associated with an increased risk of predation (e.g. Lima 1986; Gilliam & Fraser 1987; McNamara & Houston 1987, 1990). Of course, increased time spent feeding not only affects predation risk, other costs are also involved. There is less time to spend on other activities such as defending a territory, finding a mate or maintaining plumage. Hutchinson *et al.* (1993) present a stochastic dynamic programming model of a bird singing to attract a mate (see also McNamara *et al.* 1987). In this case, the increase in energetic requirements brought about by increased body mass is penalized because it reduces the time which birds have available to sing. It may be that if birds are highly time constrained, increasing feeding intensity may be favoured over increasing total time spent feeding.

Whether the predominant cost of increased energetic expenditure is lost opportunity or exposure to predation, it is clear that birds might be expected to exhibit behaviours which minimize metabolism-related costs. There are a number of possible strategies which birds may be able to employ. Earlier we considered how changes in flight strategy may influence mass-dependent metabolic costs of flight. Additionally, changes in the time allocated to different activities, particularly flight, may lessen the effects that increased body mass has on energetic requirements. It is difficult to ascertain the influence that body mass has on activity patterns from natural fluctuations in mass because of the large number of potentially confounding variables. Even studying time budgets of birds with experimentally manipulated body mass is problematic as such a manipulation not only alters body mass but also the energetic state of the animal (Witter 1993), which itself could influence the time allocated to different activities. Perhaps the most profitable approach is to consider the effects of artificial loads on behaviour. A number of studies have examined the effects of radio transmitters on time budgets. For example, Hooge (1991) found that the attachment of 4.5 g (5.1%–5.9% of body mass) transmitters to acorn woodpeckers, *Melanerpes formicivorous*, resulted in decreased flight time, decreased flycatching behaviour and increased time spent feeding compared to individuals with no transmitter and, more interestingly, individuals with a 3 g (3.5%–3.9% of body mass) transmitter. These types of behavioural change are what one might predict (i.e. a reduction in time allocated to activities which are highly mass-dependent, but an increase in total time spent feeding). However, this pattern is by no means universal. For example, Brigham (1989) found that total flight time did not change in female barn swallows, *Hirundo rustica*, with transmitters of 4.1%–5.6% body mass; the length of each foraging bout increased with transmitter load, but fewer bouts were made. Clearly, however, the mass increase brought about by the attachment of a transmitter may have rather different effects from the increase in body mass due to fat storage. Additionally, the finding that the attachment method itself influences time budgets (see Hooge 1991) places a further constraint on the validity of extrapolation.

4. MASS-DEPENDENT PREDATION RISK

The metabolic costs of fat storage may have important implications for the time spent exposed to predation, as discussed above. However, a number of authors have suggested that individuals with large fat reserves may also be at a greater risk of predation per unit time, because of an impaired ability to escape following an attack (Blem 1975; Pond 1978, 1981; Stuebe & Ketterson 1982; Nolan & Ketterson 1983; Pienkowski *et al.* 1984; Lima 1986; McNamara & Houston 1987, 1990; Hedenström 1992). It would seem likely that increased fat reserves could impair ability to escape from a predator for at least two distinct, but related, reasons: (i) due to a reduced take-off ability; and (ii) due to impaired performance in flight. We discuss the effect of changes in body mass on each of these below and then discuss their possible implications for predation risk.

(a) Take-off ability

A number of hypotheses have been proposed regarding the relationship between lift production, take-off ability and morphology, in a between-species context. Savile (1957) proposed that enhanced lift production and take-off ability are associated with low wing loading, high aspect ratio, and slotting of the distal primary feathers. Work by Pennycuick (1969), Rayner (1979) and Ellington (1984), for example, suggests that maximum lift production should be inversely proportional to the square-root of the wing

disc loading. Hartman (1961) has suggested an important role for flight muscle ratio (flight muscle mass/total body mass) in determining take-off ability. Such relationships have been investigated by Marden (1987), who added successively increasing amounts of weight to a variety of birds, bats and insects, and was able to determine maximum lift production (but see Ellington 1991) and take-off angle. He found that across all taxonomic groups with conventional wingbeat (i.e. not 'clap-and-fling' wingbeat; see Weis-Fogh 1973; Ellington 1984), take-off ability was dependent upon flight muscle ratio. Marginal take-off ability occurred with flight muscle ratios around 0.16–0.18. Flight muscle ratio was also found to have a profound effect on take-off angle, low flight muscle ratios being associated with low take-off angles. It seems likely that changes in body mass, within individuals, would result in similar changes in take-off ability. If a predator attack is detected, the development of maximum force would be expected if perceived risk is high (cf. Ydenberg & Dill 1986), since this would maximize the probability of escape. An increase in body mass would result in decreased acceleration, in accordance with Newton's second law, if similar take-off angles are employed. Additionally, high take-off angles may not be possible at high wing loadings, if maximum lift becomes limiting, as in Marden's (1987) experiment. Such reduced take-off angle, and reduced maximum acceleration brought about by the increase in body mass, could be costly during an escape response from a ground predator, where, presumably, the main objective would be to reach some safe height, or area of cover, as rapidly as possible.

Although these results are suggestive of a major impairment of take-off ability due to increased loading, caution must be exercised in extrapolating these results to natural take-off ability. Marden (1987) was primarily interested in the maximum lift generated by the active flapping of the wings, thus the birds were unable to utilize their legs during take-off. Work by Heppner & Anderson (1985) on the pigeon, has suggested an important role for the initial leap during take-off. However, Blem (1975) noted a reduced take-off ability in artificially loaded house sparrows, *Passer domesticus*, which were free to use their legs. Fry *et al.* (1970), from observations on a range of small passerines during premigratory fattening, noted poor take-off ability following release from the hand. Similarly, Hedenström & Alerstam (1992) have recorded reduced climb rates in shorebirds with high fat loads. Jones (1986) has experimentally increased the body mass of sand martins, *Riparia riparia*, and found heavy birds took longer to reach ascending flight following release.

(b) *Flight performance*

Predator attacks may take place not only on the ground but also during flight. Increased mass is expect to reduce maximum acceleration, maximum velocity and maximum rate of climb (Alerstam & Lindström 1990). In addition to these effects, increased wing loading and body mass are also expected to reduce manoeuvrability and agility. Both are predicted to decline with increases in mass (see Norberg 1990; Hedenström 1992). However, there is not a great deal of associated empirical evidence in the ornithological literature. Blem (1975) found that House sparrows with added weights were easier to catch in a net, which may reflect a decrease in manoeuvrability. A number of relevant loading studies have been performed on bats. For example, Aldridge & Brigham (1988) found that addition of artificial loads of between 5% and 30% of body mass to *Myotis yumanensis* significantly reduced ability to negotiate an obstacle course. However, Hughes (1990) examined the effects of wing loading on aerial manoeuvrability, by flying loaded and unloaded bats through an obstacle course and comparing the fraction of successful negotiations. However, no difference in this measure of manoeuvrability was observed, although wing loading was increased by up to 30%. Recently, we have found decreases in aerial manoeuvrability associated with elevated body mass, within their natural range, in the European starling, *Sturnus vulgaris* (Witter *et al.* 1993).

Earlier we discussed the results of Videler *et al.* (1988) and Hughes & Rayner (1991), who found that flight velocity decreased with increased loading. Although this would suggest an impaired escape performance, there is no way of knowing whether this reflects the response which would have occurred under conditions of 'maximum effort' as would be expected during a predator escape response. For example, Hughes & Rayner (1991) suggested that their bats may have reduced flight velocity to maintain some 'safety margin' against, say, muscular stress or strain. *A priori*, one may hypothesize that this safety margin would be reduced during an escape response. More generally, caution should be exercised in the extrapolation of the results of increased body mass in one context to an other.

(c) *Predation risk*

If increased wing loading has the general detrimental effects on avian flight performance predicted by theory, which empirical evidence suggests, how do these changes in flight performance affect the risk of predation? Observations of predation events, and behavioural decisions made under the risk of predation, may indicate which parameters of flight performance are important in determining escape ability. We examine this below, and discuss some of the complicating and confounding issues involved.

The consequences of an impaired take-off ability on the probability of escape from a terrestrial predator may seem apparent on common-sense grounds. However, with regard to the details of the take-off strategy, the bird is faced with a trade-off between maximizing its linear acceleration and maximizing its rate of climb. Taking a low take-off angle allows rapid acceleration, lift generation being assisted by the forward motion of the bird, but rate of ascent is reduced. Alternatively, a high take-off angle allows a

more rapid vertical climb, but acceleration is necessarily penalized because of the extra work done against gravity. It is difficult to determine *a priori* which would be the best policy to adopt, since the rate of acceleration in flight, and the rate of vertical climb from the predator, both appear to be attractive currencies to be maximized. The optimal policy might be expected to depend on, for example, the detailed nature of the predator's attack, the proximity of protective cover and the presence or absence of conspecifics. Studies of starlings flying to protective cover, following a startle stimulus, in the laboratory have suggested that these birds 'defend' escape velocity as body mass increases by reducing their rate of ascent (Witter *et al.* 1993). However, Cade (1960) has suggested that rate of climb may be important for waterfowl escaping from peregrine falcons, *Falco peregrinus*. Cade noted that the birds would often try to outclimb the peregrines; if they could remain above the falcon they would be safe. Further data on predator escape strategies of different species, or differential responses of individuals to different predators, may reveal more details of the nature of this trade-off.

There are a number of examples illustrating behavioural changes associated with predation risk and the use of protective cover (e.g. Barnard 1980; Caraco *et al.* 1980; Ekman & Askenmo 1984; Schneider 1984; Ekman 1987; Lima *et al.* 1987; Lazarus & Symonds 1992). Generally, the birds in these studies prefer to feed near areas of cover, presumably because it represents an area of safety which can be rapidly reached in the event of a predator attack. (Although this benefit may be traded-off against the risk of an attack from within cover (Carey 1985; Lima 1987; Lazarus & Symonds 1992).) It seems reasonable to assume that increasing the time to reach cover, as would occur under conditions of increased wing loading because of decreased maximum acceleration and velocity, increases the associated risk of predation. The increase in travel time would have a similar effect to feeding further away from protective cover, which is believed to be associated with increased perceived predation risk (e.g. Todd & Cowie 1990). This example also highlights the possibility that habitat-use may be affected by increased fat storage, because of decreased escape ability (see Lima 1992).

The importance of manoeuvrability in determining the chance of evading predation can be gleaned from a number of observations of raptor attack strategies. For example, Bijlsma (1990) outlines a number of tactics employed by raptors when hunting around the Mauritanian coast for waders. Bijlsma (1990) noted the following response to a fast low level falcon attack: '. . . waders invariably took flight and tried to evade the falcon by twisting and turning in dense aerial flocks.' Bijlsma noted one case where the falcon made 19 swoops at prey before finally giving up. Intuitively, one may suppose that speed and manoeuvrability could be substituted for each other in a prey's repertoire to evade predation (see Howland (1974) for a formal model). The relative roles of each will depend on the details of the predator–prey interac-

tion. For example, the Peregrine, *Falco peregrinus*, may reach speeds of 39 m s^{-1} during a dive (Alerstam 1987). If detected, manoeuvrability is likely to be of the utmost importance in determining the chances of escape, as most intended prey would be unable to attain such speeds. However, the precise role of speed versus manoeuvrability will not only depend upon the relative flying abilities of the predator and prey, but also, for example, the distance at which the predator is detected. If detected at long range, it may be possible to out-run the predator. However, if the attack is detected when the predator is relatively close, then manoeuvrability may be critical. This is believed to be the case for moths evading attacking bats (Roeder 1963).

There is some evidence regarding the role of acceleration in flight for evading predation. As discussed earlier, flight muscle ratio is an important determinant of linear acceleration capacity (Marden 1987). Kenward (1978) found that wood pigeons with low flight muscle ratios were more prone to predation by goshawks. Of course, low flight muscle ratio would also adversely affect other flight performance characteristics. However, Kenward's observations suggest that the ability to out-accelerate the goshawk was a critical determinant of escape ability. Kenward also suggested that the increase in predation success around dusk was due to the increase in body mass of the pigeons as they pack their crop before roosting. However, other explanations are also compatible with this data, because no account was taken of changes in light intensity or pigeon behaviour (e.g. vigilance) at dusk. Additionally, Mueller (1973) found that circadian changes in hunger of two falconiform birds, *Falco sparverius* and *Buteo platypterus*, can generate a late afternoon peak in feeding in the absence of changes in the mass of prey. More generally, caution must be exercised in the interpretation of correlative data relating levels of fattening or body mass to predation, if body mass has not been experimentally manipulated. Although an increase in body mass within individuals would be predicted to increase predation risk (other things being equal), the relationship may not hold across individuals, say, if individuals take predation risk into account in determining the optimal fat reserve. For example, only individuals with large flight muscles, or with flight plumage in good condition, may store high levels of fat. The data of Grant (1965) suggests that predation risk may be taken into account in determining fat storage strategy. Comparisons of the mean fat levels of eleven species of small passerines on Tres Marias islands and the nearby mainland of Mexico revealed that in ten of the species higher levels of fat were present in the island subspecies (figure 2). Because food supply on the island and mainland was similar, Grant found the difference difficult to account for. Blem (1976) suggested that as islands are often associated with predator release, then this observation is consistent with the view that reduced predation risk is associated with higher fat reserves. Consistent with this proposition, we have found that starlings maintained in outdoor aviaries overwinter varied their fat reserves according
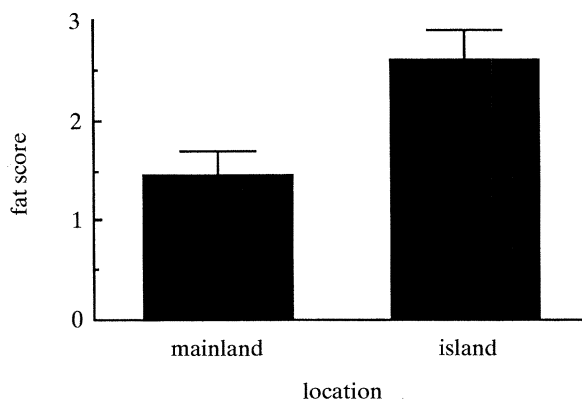
Figure 2. Mean fat scores (± s.e.) for eleven species of birds on Tres Marias Island and on the adjacent mainland of Mexico. Data from Grant (1965).

to the availability of protective cover (Witter *et al.* 1993). Where most cover was present, fat reserves were highest.

In future studies, how could mass-dependent predation risk be directly, experimentally investigated? The staging of predation events similar to the work of Kenward (1978) is one possibility, although it is questionable on ethical grounds (Huntingford 1984; Cuthill 1991). Any such direct approach must, firstly, involve an experimental manipulation of fat reserves since natural variation in fat may be confounded by escape ability. More critical to the direct approach, however, is the point raised by McNamara & Houston (1987) and McNamara (1990), that realized rates of predation are a poor indicator of actual predation risk. For example, fat individuals may take their increased body mass into account and exhibit behaviours which reduce predation risk compared to lean individuals. Thus, in addition to recording predation rates on lean and fat manipulations, convincing data would have to be gathered to show that both groups are behaving similarly (i.e. that it is only body mass which differs between the groups). Given the range of ways in which behavioural differences may manifest themselves (foraging group size, vigilance, microhabitat selection, etc.), we believe that it would be difficult to unequivocally demonstrate an effect of body mass on predation risk directly. Indeed, it would be surprising if manipulating fat reserves did not result in associated changes in behaviour because there is good experimental evidence for the role of energetic state in determining the extent of anti-predatory behaviours (for a review, see Lima & Dill (1990)). Thus, whereas the pursuit of such direct evidence is a worthwhile aim, there seems sound ethical and theoretical justification for taking an indirect approach, studying the effects of body mass on behaviours likely to be important in determining the ability to escape predation (for a discussion, see Witter *et al.* (1993)).

5. MASS-DEPENDENT RISK OF INJURY

Increased body mass may increase the risk of injury due to collision during flight and landing. In the previous section we described how increased body mass can reduce manoeuvrability and agility. These

changes in flight performance may increase the risk of collision while flying through a cluttered environment such as dense vegetation. Additionally, severity of any particular collision is determined by the bird's momentum (the product of mass and velocity, MV) at the moment of impact. So, in addition to increasing the chance of a collision, the severity of a collision at any particular velocity will increase linearly with body mass. Cuthill & Guilford (1990) noted that increased risk of collision may not manifest itself as an increase in the number of collisions because the increased risk may be traded-off against other components of fitness. They were able to demonstrate experimentally a trade-off between collision risk and rate of food intake. Consistent with this, Aldridge (1985) and Aldridge & Rautenbach (1987) found that manoeuvrability was an important determinant of habitat selection across a range of bats. Only the most manoeuvrable species fed in dense vegetation. So, just as rates of predation may be a poor indicator of predation risk (McNamara & Houston 1987), Cuthill & Guilford's (1990) results argue that rates of collision may similarly be a poor indicator of collision risk.

Landing can involve a number of complex manoeuvres which reduce horizontal and sinking velocity in order to avoid a hard impact on the landing substrate (Norberg 1990). Landing can be particularly difficult for large birds, where the power required for slow flight is not available. Increases in body mass of individuals may also make landing more difficult or mean that landing may have to take place at a higher velocity. The ability to land on substrates such as branches and twigs may be more adversely affected by increases in body mass because accurate pre-landing manoeuvres will be more difficult. These changes in landing ability may result in changes of the choice of landing substrate as body mass increases. For birds which are known to utilize a variety of landing sites, examining choice of landing substrate at different body masses may be a useful way to test this hypothesis.

6. MASS-DEPENDENT FORAGING

The manner and degree to which foraging ability is impaired by increased body mass will clearly depend on the details of the species and the foraging niche it occupies. For example, probing in the soil for invertebrates may be less affected by changes in body mass than hovering to glean fruit or insects. Two modes of foraging which are likely to be particularly impaired by increased body mass are arboreal foraging and feeding on the wing. Below we concentrate predominantly on mass-dependent arboreal foraging. Birds which feed on the wing will be penalized by increases in body mass because of the adverse affects of increased wing loading on flight performance which we discussed in the previous two sections.

(*a*) *Mass-dependent foraging ability*

Many studies have illustrated how subtle differences in morphology can result in differential use of micro-

habitat in between-species comparisons (e.g. Partridge 1976; Norberg 1979; Moermond & Howe 1986). Body mass may be a critical morphological variable in determining microhabitat selection. On common-sense grounds, it is clear that body mass must place certain limits on the arboreal activities of birds. Heavy birds are necessarily unable to feed from the thinnest twigs. Thus, we postulate that changes in body mass of a given individual may subtly alter either feeding-station selection, foraging efficiency or both. Lehikoinen (1986) suggested essentially this point in relation to winter fattening in tits, *Parus* spp.; 'Fat birds feeding by hanging on branches and twigs are probably not as efficient foragers as the leaner ones.'

Arboreal foraging efficiency may be particularly impaired for activities which involve shifting the centre of gravity away from the perch or hanging under branches. For any particular hanging position, the moment of the muscle force necessary to maintain position is directly proportional to the weight of the bird (Norberg 1979). This implies at least a reduced foraging efficiency, since more energy needs to be expended to obtain a food item. However, if the force becomes limiting then hanging may no longer be possible. Similar reasoning can be applied to a bird which reaches horizontally outwards from a branch. The observation that birds sometimes have to use 'corrective' behaviours, such as flapping their wings, to return to an upright position (e.g. Snow & Snow 1990), may imply that the maximum forces which can be developed in the legs are indeed attained during this form of foraging. Thus, changes in body mass may place direct limits on the distance which birds are able to reach away from their perch. This would be expected to directly affect the accessibility of food items. Accessibility *per se* may be an important determinant of food selection (e.g. Denslow & Moermond 1982; Moermond & Denslow 1983, 1985).

However, the types of arboreal feeding behaviour which are affected by increases in body mass may not be limited to hanging or leaning from branches, but would also include hovering to glean insects, seed or fruit. Low wing loading is advantageous for very slow flight and hovering, and birds which utilize such behaviours frequently during feeding may be particularly heavily penalized by increases in body mass because of the sharp increase in energetic costs associated with such flight. The increase in body mass may even preclude hovering because the necessary power is no longer available. Under circumstances where such behaviours are frequently employed, the types of patches or microhabitats which can be exploited may be particularly influenced by body mass changes. Norberg (1979) has addressed a similar issue, but in a between-species context, in relation to feeding station selection of the coal tit, *Parus ater*, the crested tit, *Parus cristatus*, the willow tit, *Parus montanus*, the goldcrest, *Regulus regulus*, and the treecreeper, *Certhia familiaris*. *C. familiaris* and *R. regulus*, both of which have low wing loading, are observed to hover while feeding. *P. ater* which also has relatively low wing loading does not hover, but often hangs while feeding and, like *R. regulus* can exploit the outermost

branches for food. *P. montanus* and *P. cristatus* have higher wing loading than the other species, and most often feed on the main branches, although there is some feeding station overlap (Haftorn 1956). Similarly, Newton (1967) found body mass to be an important determinant of microhabitat selection among British finches.

Unfortunately, little data exist regarding within-species niche separation brought about by changes in body mass, but such niche separation may occur in an analogous manner to between-species separation. For example, Gustaffson (1987) found that feeding station selection was highly dependent on body mass in coal tits, *Parus ater*. Similarly, Loria & Moore (1990) found that lean red-eyed vireos, *Vireo olivaceus*, broadened their use of microhabitat and increased their foraging repertoire compared to fat individuals. Although Loria & Moore (1990) suggested that these changes were in response to increased energy demands, Alerstam (1990) noted that they may be due to reduced agility in the individuals with large fat stores. Other potential explanations also exist. For example, lean and fat migrants may be trading-off food intake against the increased predation risk associated with increased body mass. Lindström (1990) found that predation risk may be an important determinant of stopover habitat selection in bramblings, *Fringilla montifringilla*. Interpreting changes in feeding station which correlate with changes in body mass as examples of mass-dependent foraging must necessarily remain speculative until controlled experiments, able to unconfound correlated phenomena, have been performed.

(b) *Mass-dependent foraging behaviour*

The effects of mass-dependent costs on foraging behaviour have been investigated with particular reference to loads such as food in the gut (DeBenedictis *et al.* 1978; Schmidt-Hempel *et al.* 1985; Kacelnik *et al.* 1986; Tamm 1989). The cost of carrying fat will be analogous, although, since not as labile, the effects of a fat load are unlikely to be manifested in patch by patch changes in behaviour. Nevertheless, changes in body mass would be predicted to influence various parameters of foraging behaviour. Kacelnik & Houston (1984) have investigated theoretically the effects of energy costs on foraging behaviour. For a bird which flies to a patch and then feeds by perching or walking, increases in mass are predicted to increase optimal patch residence times and optimal load sizes. For any type of forager, increasing mass would generally reduce the net rate at which energy can be collected or delivered. Norberg (1981) and Houston (1986) have examined theoretically the influence of adaptive mass loss in parental birds. Additionally, the observation that parents often feed the young most intensely in the early part of the day (e.g. O'Connor 1984) is consistent with the view that the parents are reducing the impact of mass-dependent costs by foraging most intensely when their body mass is low. Of course, chicks may also be hungrier at this time of day, following the overnight fast. Morning hunger,

however, does not provide a full explanation of the diurnal pattern of parental feeding, because if the parents fed the young more intensely late in the day, they would not be so hungry in the morning (Bednekoff 1992).

Many species may employ strategies to avoid paying mass-dependent foraging costs in a similar manner to our example of temporal feeding patterns of parental birds. Consider the temporal pattern of hoarding and retrieval in tits, *Parus* spp (e.g. Gibb 1954; Haftorn 1956). Detailed studies on marsh tits, *P. palustris*, have revealed higher levels of caching in the morning than afternoon, with the reverse being true for retrieval (Stevens & Krebs 1986). The initial foraging for food may entail mass-dependent foraging ability costs, but this is often carried out through the early parts of the day when body mass is low. During the latter parts of the day, fat has to be stored in preparation for the night. During this time, body mass must presumably increase. By retrieving food from stores at this time, the tits may be evading the mass-dependent costs associated with storing fat earlier in the day. The results of the stochastic dynamic programming model of McNamara et al. (1990) indicate that mass-dependent costs may be critical for generating this pattern of behaviour (see also Hurly 1992). The effect of mass-dependent foraging ability, not considered in their model, can be seen as analogous to their mass-dependent metabolism, since both act to reduce the net rate of energetic gain with increasing body mass. However, mass-dependent foraging ability could act in addition to the mass-dependent metabolism and mass-dependent predation considered in their model, and may provide an additional selection pressure favouring this pattern of storage and retrieval, if mass-dependent foraging costs are only 'paid' during the initial foraging and not during retrieval.

7. PATHOLOGICAL COSTS

The relationship between high levels of body fat and increased human mortality has long been of interest. Obesity, usually defined as adipose tissue amounting to 20% of body mass in men and 25% of body mass in women (Schwandt 1990), has been found to be associated with, for example, cardiovascular disorders, diabetes mellitus, gall and kidney stone diseases, cancer and arthritis (for recent reviews, see Bjorntörp & Brodoff (1992)). Much of this work has been carried out with reference to human epidemiological studies and mammalian animal models so it is difficult to ascertain how directly relevant many of these results are for wild birds. However, the levels of fat stored during premigratory fattening in small birds (e.g. Lindström 1986) would be considered pathological in many mammals. Possibly obesity has such detrimental effects in the above examples because the level of fat stored is beyond the natural range to which these animals are adapted. Small birds, naturally exposed to high fat reserves on a regular basis, may be able to employ specialized physiological strategies to avoid pathological costs. For example, the absence of

fat storage around the heart (Odum & Perkinson 1951) may be one such strategy. However, high levels of avian fat storage may entail equally damaging pathological costs, but since elevated levels of body fat are maintained for only short periods during premigratory fattening, the effects may be minimal. Alternatively, pathological costs may be substantial, but have simply not been investigated by ornithologists. Domestic chickens, *Gallus gallus*, are known to develop hypoxic pulmonary hypertension which can cause rapid death (Burton et al. 1968). Food restriction can improve arterial oxygenation and reduce this form of mortality (Reeves et al. 1991). However, food restriction is believed to reduce pulmonary hypertension by reducing growth rate, rather than, say, reducing fat content. Nevertheless, excessive obesity in humans is often associated with hypoventilation (Pickwickian syndrome). The hypothesis that large deposits of fat impair respiration because they interfere with respiratory muscles and decrease compliance of the thoracic cage may have some relevance to migratory birds where large amounts of fat are stored throughout the body. However, the importance of these costs to natural populations cannot be determined until relevant work, on non-domesticated, wild birds, has been performed.

Increases in body mass may place extra stress on the muscular and skeletal systems, particularly during flight where enhanced wing loading is predicted to be associated with increased wingbeat frequency and amplitude. There are a number of possible consequences of these phenomena. The most extreme possibility is that increased loading results in yield or failure of the flight skeleton or damage to the flight musculature. However, given the rather obvious fitness consequences of, say, skeletal failure, physiological or behavioural measures are likely to be adopted which minimize this risk. Rayner (1986, 1987) has argued that minimizing stress on the wing surface and moments at the wing root may be important determinants of wingbeat kinematics in bats. Earlier, we discussed the results of Hughes & Rayner (1991), who suggested that the observed flight velocity and wingbeat kinematics of Long-eared bats flying with enhanced load resulted from the maintenance of some 'safety margin' with regard to maximum stresses on the flight muscles, flight skeleton or wing surface. Thus, in this case, the risk of muscular, skeletal or wing membrane damage was minimized, but this resulted in the power requirements of flight being greatly enhanced (see also Rayner et al. 1989). Risk of damage to the flight skeleton may also be minimized by remodelling the bone during periods of enhanced loading (c.f. Lanyon et al. 1982). Despite the long history of this hypothesis (e.g. Wolff 1892), the phenomenon remains controversial (see Bertram & Swartz 1991). Rubin & Lanyon (1984, 1985) found that atrophy–hypertrophy of the ulna of turkeys depended on the magnitude of load applied, the rate of application and the number of loading cycles. Artificial loads, within the natural range of wing loading, applied at only four cycles per day were sufficient to maintain bone mass. Higher cycles of

application resulted in enhanced bone deposition. Although seasonal changes in bone histology have long been recognized in birds (e.g. Meister 1951), we know of no data from wild bird populations indicating adaptive remodelling in response to increased natural load. Such data may give an indication of the relevance of this phenomenon as a response to natural changes in wing loading.

8. REPRODUCTIVE COSTS

The trade-off between reproductive and somatic investment is central to life-history theory (Williams 1966; Stearns 1976, 1989; Partridge 1989). Whereas somatic investment includes the balancing of metabolic expenditure, growth, immunocompetence and tissue maintenance, the accumulation of fat reserves is an obvious mechanism by which residual reproductive value can be enhanced (Calow 1979, 1984). The corollary of this is that fat accumulation has life-history costs in terms of energy diverted from current reproductive effort, or indeed other 'maintenance' functions. Although there is strong tradition of ornithological investigation into putative 'costs of reproduction' (reviews by Nur 1988a, Linden & Møller 1989; Partridge 1989), rather less attention has been focused on the mechanisms through which these costs act. Although it is easier to model life-history decisions as the outcome of alternative allocations of energy *per se* (e.g. Kacelnik & Cuthill 1990; Kozlowski 1991), with parental fat reserves as the principal determinant of residual reproductive value, the effects of current reproductive effort on future mortality or fecundity could be mediated via changes in other physiological variables, such as protein levels or the immune system. Alternatively the costs may act through changes in time allocation which may, say, increase exposure to predation (e.g. McNamara & Houston 1990). Most of the accepted demonstrations of costs of reproduction in birds (see Nur 1988a; Linden & Møller 1989; Dijkstra *et al.* 1990) do not specify the state variable (*sensu* Houston & McNamara 1992) through which costs act. As costs of reproduction can be in terms of either fecundity or survival, and either inter- or intra-seasonal, here we identify only those costs in which depletion of fat stores is the likely proximate agent. It is these components of residual reproductive value that are most likely to be involved in the trade-offs determining optimal fat levels.

For convenience, we will consider a seasonal breeder with effects acting at increasing remoteness from the current breeding attempt, namely reduced intra-seasonal fecundity (second or subsequent clutches within the same breeding season), over-winter survival, and inter-seasonal (next year's) fecundity. First, however, we note that the trade-off between fat storage and reproductive effort can have effects within a given breeding attempt. Unpredictable cold weather may be associated with interruptions in laying sequence, 'missed days', due to diversion of reserves away from egg production towards replenishment of depleted fat stores (e.g. Dhont *et al.* 1983). Similar effects will delay initiation of the

entire clutch, with the consequence of the reduced recruitment that is characteristic of later breeding (Perrins & Birkhead 1983; Daan *et al.* 1990). Just as individual differences in absolute food availability, or the ability to acquire it, may constrain 'low quality' individuals to initiate breeding later (Price *et al.* 1988; Perrins 1991), so too may individual differences in the need for self-allocation due to, say, increased metabolic expenditure correlated with body size, parasite load, or exposure of the breeding site.

Intra-seasonal costs of reproduction appear to be more marked than inter-seasonal (Linden & Møller 1989; Nur 1988a; Tinbergen & Daan 1990; Dijkstra *et al.* 1990). Many brood manipulation experiments indicate that increased current reproductive effort delays initiation or size of the second clutch (reviewed by Arcese & Smith (1988); Dhindsa & Boag (1990); Hörnfeldt & Eklund (1990)). As the time between independence of the first brood and initiation of the second clutch can be a matter of days, it seems plausible that the costs of an enlarged first brood act directly through parental fat reserves. Fat loss, or that inferred from a reduced body mass, is a common feature of breeding birds, but its interpretation is controversial.

A simple proximate interpretation of mass loss as reproductive stress (Nice 1938; von Haartman 1958) has given way to a functional perspective (see Moreno 1989a). Mass loss has been interpreted by many as a direct measure of the cost of reproduction, reflecting differential allocation of energy away from the parent to the young, in analogous fashion to the reallocation seen at the level of individual feeding decisions (e.g. Jones 1988; Kacelnik & Cuthill 1990). However, Freed (1981) and Norberg (1981) have argued that weight loss during breeding does not represent a cost, but an 'adaptive' reduction favoured by the saving in flight costs that lowered wing-loading brings (see § 3). Indeed, as Moreno (1989a) notes, mass loss during breeding may represent a return to 'normal' levels of fat reserves, with pre-laying hypertrophy favoured by long stints of brooding. From this perspective, the 'cost' of reproduction is perhaps better reflected in the need to gain mass prior to breeding, rather than the mass loss when the chicks hatch. Simple models of parental food allocation, which presume residual reproductive value to be an increasing function of parental energy reserves (e.g. Kacelnik & Cuthill 1990), ignore the costs of mass gain. Norberg (1981) notes one such cost, which acts to reduce the value of the current brood through reduced provisioning efficiency, but the other costs of fat accumulation outlined in this paper can affect both current and residual reproductive value. Furthermore, Norberg (1981) does not model the cost to the parent, in terms of starvation risk, of reduced body fat. As Moreno (1989a) argues, without an explicit life-history model taking into account the costs as well as benefits of fat accumulation, from pre-laying through incubation to chick rearing, our understanding of the function of different avian strategies of mass change during breeding is unlikely to be advanced.

Although it is rare for empirical studies to investi-

gate the proximate mechanism whereby first brood effort affects the likelihood, timing and productivity of a second brood, measures of increased parental energetic expenditure (Masman *et al.* 1989; Dijkstra *et al.* 1990; Bryant & Tatner 1991) do suggest a direct role for fat reserves. However, for inter-seasonal trade-offs, fat depletion is unlikely to be directly implicated. First, the nature of the costs are unclear. For example, Gustafsson & Part (1991) and Gustafsson & Sutherland (1989) have demonstrated reduced future fecundity in collared flycatchers, *Ficedula albicollis*, but not over-winter survival. Nur (1984, 1988*b*, 1990) has shown effects on both future fecundity and survival in blue tits, *Parus caeruleus*. However, Pettifor *et al.* (1989) argue that these are artifacts of the analysis, and claim that there are no inter-seasonal costs of reproduction in tits. Even if we accept the existence of inter-seasonal costs (reviewed by Dijkstra *et al.* (1990)), the turnover of fat reserves is in the order of days for the small passerines in the above studies, so reductions of fat stores during the breeding season are unlikely to have a direct effect on the fat storage that influences over-winter survival and next year's breeding condition. The possibility of indirect effects, say through depleted fat stores delaying moult (e.g. Meijer 1990) or migration to wintering grounds, remains open.

To summarize, the most likely reproductive costs of fat are in intra-seasonal trade-offs. Short-term changes in weather, or differences in individual metabolic demands, may delay clutch initiation or interrupt the laying sequence. Increased reproductive effort may act via fat reserves to delay initiation or productivity of a second brood, but inter-seasonal costs, if they exist, are likely to be due to deterioration of other aspects of physiological condition than fat stores.

9. DISCUSSION

When the costs of fat storage, which we have presented, are invoked or experimentally investigated it should be remembered that many of the hypotheses refer to changes in fat content, or body mass, within individuals. For experimental investigations, these predictions would apply directly to 'repeated measures' designs (e.g. Mead 1988). However, this is a rather limited perspective. If one is interested in between-individual patterns, or if repeated measures are difficult to obtain (as they may be in the field), it is necessary to consider how within-individual predictions translate into between-individual predictions. We have considered how between-individual differences, correlated with variation in fat reserves, may confound experimental tests of the mass-dependent predation risk hypothesis (see Mass-dependent predation risk). However, this covariation between fat reserves and phenotypic quality is also relevant to any investigations of the consequences of fat storage and the interpretation of between-individual patterns of fat reserves (e.g. 'condition indices').

Within individuals, other things being equal, increasing fat reserves may, for example, hinder flight performance or foraging efficiency. However, comparing across a population, the fattest individuals may

not be, say, the most prone to predation or the worst foragers, since we expect each individual to optimize its own fat reserves. Thus, we would predict that the population pattern of fat storage will depend on the relative cost–benefit ratio of fat storage of the individuals which make up that population. Clearly, from this hypothesis, a continuum of possible outcomes are feasible. However, a lack of consideration of the costs of maintaining higher fat reserves, in many previous studies, has led to a rather one-sided interpretation of fat variation within, and between, populations. Implicit in a number studies, we believe, is the hypothesis that the benefit of storing fat and food limitation, together, can explain observed variation in fat reserves. That, often, only the benefits of fat storage are considered is well illustrated by the calculation of so-called 'survival potentials' (e.g. Reinecke *et al.* 1982; Albright *et al.* 1983; Whyte & Bolen 1984). The 'survival potential' is a measure of the amount of time an animal could survive without food before dying of starvation. However, this measure gives no indication of the possible detrimental effects of fat storage on other sources of mortality, such as predation, nor does it take into account the probability of actually having to endure such an extended period of deprivation. Below we present a cost–benefit perspective of between-individual variation in fat reserves, based on the models of Lima (1986) and McNamara & Houston (1987, 1990).

(a) *Between-individual variation in fat reserves*

Interest in between-individual patterns of fat storage has most often focused on 'physiological condition', although the latter appears to be a rather poorly defined concept. Ultimately, we suppose, condition must refer to fitness or measurable components of fitness (c.f. Blem 1990). Using the size of energy reserve as a measure of condition must, therefore, presuppose that a positive monotonic relationship exists between size of energy reserve and fitness. A number of studies have found positive correlations between energy reserves, or body mass, and various measures which are likely to correlate with fitness, such as survival rate and reproductive potential (e.g. Ankney & MacInnes 1978; Raveling 1979; Krapu 1981; Haramis *et al.* 1986; Hepp *et al.* 1986; Conroy *et al.* 1989). Within-individuals, a positive monotonic relationship between fat reserves and fitness would clearly be contrary to the hypotheses we have presented and a number of theoretical models (Lima 1986; McNamara & Houston 1987, 1990). However, between individuals, such a relationship does not in itself contradict the hypothesis of costly fat storage or adaptive regulation of energetic reserves. Indeed, we suggest that between-individual differential costs may be vital for generating a positive relationship between the size of fat reserve and fitness.

McNamara & Houston (1990) considered how changes in environmental and physiological parameters influence optimal reserves. We consider the significance of their results for between-individual patterns of fat storage. From their models it is clear

that differential costs and benefits of acquiring and maintaining fat reserves can generate either a positive or negative relationship between aspects of 'quality' (which we use rather than 'condition', since, to many, 'condition' is synonymous with fat reserve) and size of the fat reserve. The analytical model in McNamara & Houston (1990) indicates that the 'quality-dependent' pattern of fat storage is highly sensitive to the ways in which differences in quality may manifest themselves. For example, if predation risk is greater in low quality individuals, then high quality individuals have larger optimal fat reserves, because obtaining a given level of reserves is more costly (in terms of predation) to the low quality individuals. Such an effect may arise, for example, because dominants are able to displace subordinants from 'safe' feeding sites (Lima *et al.* 1987). Similarly, De Laet (1985), Hegner (1985) and Hogstad (1988) have found that subordinants return to a feeder, following a startle stimulus, before dominants, increasing their risk of predation. Alternatively, low 'quality' individuals may be inefficient foragers or feed at low quality sites (Ekman & Askenmo 1984). This again produces a positive correlation between 'quality' and optimal fat reserves (even with constant predation rate), in this case, because acquiring higher reserves results in a longer period exposed to predation. Helms (1968) suggested that adult great tits may maintain higher levels of fat reserves than first-winter birds because they could acquire the reserves more rapidly, and thus spend proportionately less time exposed to predators. The analytical model of McNamara & Houston (1990) formally confirms this line of reasoning. These, or similar effects, may be important determinants of the often found positive relationship between dominance and fat reserves (e.g. Baker & Fox 1978; Piper & Wiley 1990). More generally, it appears that differential costs may be vital to the generation of a positive relationship between fat reserves and 'quality', which the condition index assumes. However, the reverse relationship, if we assume dominance to be related to 'quality', has also been found (e.g. Gosler 1987; Ekman & Lilliendahl 1993). This pattern can be explained in terms of differential food predictability (see § 2; Ekman & Lilliendahl 1993).

In all the cases considered above, individuals of high 'quality', of course, show the lowest levels of mortality. Importantly, however, they show lower levels of mortality whether or not they have the highest fat reserves. This indicates the potential difficulty with 'survival potentials', which we discussed above. However, these outcomes are discussed for illustrative purposes only. The key point is that both the qualitative and quantitative between-individual patterns of fat storage predicted by cost–benefit analysis are highly dependent upon the ways in which differences in 'quality' may manifest themselves. Although the above models only consider the consequences of fat reserves for starvation and predation, clearly, the same cost–benefit reasoning could be applied to other consequences of fat storage. For example, Moreno (1989*b*) suggested that male wheatears, *Oenanthe oenanthe*, may maintain low levels of fat reserves prior to breeding because increased body mass was detrimental to display flights. This may decrease their likelihood of pairing early or pairing with a good female, either of which might decrease their reproductive success.

There is, however, the danger, in these sorts of cost–benefit arguments, of 'Panglossian' reasoning (*sensu* Gould & Lewontin 1979), as almost any population level pattern could potentially be explained, *post hoc*, by individual optimization. What are required are detailed empirical studies which make, ideally quantitative, *a priori* predictions about both the benefits and costs of changes in fat reserves. In addition, the models assume that food does not directly limit the size of energetic reserve. Food availability may, of course, place direct limits on fat reserves under certain circumstances. However, what is clear from this discussion is that the existence of differential levels of fat reserves cannot be invoked as evidence of food limitation. If food limitation is to be invoked, independent evidence that birds are unable to attain their optimal level of reserves is required. This, of course, necessitates determining what the optimal levels of reserves are. King & Murphy (1985) make the point succinctly: 'It seems to us unjustified to assume, and even more so to conclude, that there is "not enough" when "enough" has not been defined.'

Where a positive relationship between 'quality' and fat reserves holds, the condition index has descriptive utility. However, there are further logical difficulties with the condition index concept for assessing temporal variation in 'condition'. For example, in what sense can birds be considered to be in better 'condition' during the winter rather than summer, or during premigratory fattening rather than during other periods of the annual cycle, if there is temporal variation in the optimal level of reserves? As Ormerod & Tyler (1990) point out, during the premigratory period or winter, when fat reserves (and, hence, condition index) are high, a small deficit between attained and optimal reserves may have large fitness consequences, even though the condition index is either higher or comparable to other periods of the annual cycle. In general, comparisons of 'condition' from different periods of time (or different sites) are meaningless if reserve optima vary, as we expect they would. The shifting benefits of storing fat at different points in the annual cycle (e.g. overwinter versus breeding versus moult) are readily apparent. Costs are also expected to change (e.g. Freed 1981; Norberg 1981; King & Murphy 1985). Thus, the optimal levels of reserves are bound to change in association. Ormerod & Tyler (1990) have suggested that it may be possible to adjust condition indices, to take into account the above complexities, in order to give a better indication of the bird's 'condition'. This could be achieved by taking the functional approach which we have advocated. For example, the deviation between optimal and observed reserves may give a better indication of 'condition' than simply the size of fat reserve. No doubt, such an undertaking would be difficult. However, not only might it give a better measure of condition, it may also teach us rather more about the complexities of avian energetic strategies

than the simple assertion that 'fat is fit' (c.f. Lehikionen 1986). We have not attempted to present an exhaustive list of possible reasons for the maintenance of between-individual differences in fat reserves. Instead, we have simply attempted to advocate what seems to us a particularly fruitful approach. We hope that presenting our reasoning in this way encourages others to be more explicit in predicting between-individual patterns of fat storage and the relationship between fat reserves and 'condition'.

(*b*) *Conclusion*

The concept that fat storage entails associated costs has long been acknowledged (e.g. King 1972; Blem 1975; Pond 1978, 1981), and there has been a growing appreciation of the trade-off between the costs and benefits of fat storage both theoretically (e.g. Lima 1986; McNamara & Houston 1987; Alerstam & Lindström 1990; McNamara *et al.* 1990) and empirically (e.g. Stuebe & Ketterson 1982; Nolan & Ketterson 1983; Rogers 1987; Ekman & Hake 1990; Lindström & Alerstam 1992). Nevertheless, there remain many studies which have either not considered, or paid only passing lip-service to, the costs of fat storage. The 'benefits only' approach is unable to convincingly explain a variety of observed variation in fat storage, within and between individuals. Also problematic is the finding that costs often seem only to be invoked when differential benefits fail to explain the data. Obviously, benefits and costs do not represent two different levels in a hierarchy of potential explanations. The two should be considered together, since it is the net result which determines the optimal level of reserves to maintain. Although cost–benefit reasoning is able to account for the wide variation in fat storage, the role of food limitation in determining between-individual differences remains an empirical question. However, we have argued that invoking food limitation demands an assessment of optimal reserves, and thus necessitates cost–benefit reasoning. Despite the potential importance of the costs which we have discussed, there have been remarkably few empirical studies to investigate them. To provide support for our arguments, we have considered a range of studies, many of which were not performed in this context. In some cases, the data appears convincing, but extrapolation necessarily means that much of the evidence is circumstantial or anecdotal. Considering the degree of interest in fat and energy storage strategies in birds (see Blem 1990) and their potential importance for a variety of ecological and behavioural phenomena, the lack of unequivocal, experimental evidence for a number of the cost that we have considered is a matter of some concern. We hope that this review has gone some way towards highlighting the sorts of data which needs to be gathered to test the assumptions and consequences of costly fat storage, and has indicated the ways in which this might be done.

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