Review

Theoretical models of adaptive energy management in small wintering birds

Anders Brodin*

Department of Theoretical Ecology, Lund University, Ecology Building, 223 62 Lund, Sweden

Many small passerines are resident in forests with very cold winters. Considering their size and the adverse conditions, this is a remarkable feat that requires optimal energy management in several respects, for example regulation of body fat reserves, food hoarding and night-time hypothermia. Besides their beneficial effect on survival, these behaviours also entail various costs. The scenario is complex with many potentially important factors, and this has made ‘the little bird in winter’ a popular topic for theoretic modellers. Many predictions could have been made intuitively, but models have been especially important when many factors interact. Predictions that hardly could have been made without models include: (i) the minimum mortality occurs at the fat level where the marginal values of starvation risk and predation risk are equal; (ii) starvation risk may also decrease when food requirement increases; (iii) mortality from starvation may correlate positively with fat reserves; (iv) the existence of food stores can increase fitness substantially even if the food is not eaten; (v) environmental changes may induce increases or decreases in the level of reserves depending on whether changes are temporary or permanent; and (vi) hoarding can also evolve under seemingly group-selectionistic conditions.

Keywords: energy reserves; small birds; adaptive fat regulation; food hoarding; nocturnal hypothermia; theoretical models

1. INTRODUCTION

(a) *The little bird in winter*

In the boreal taiga forest, temperatures may be -20°C or even -30°C for prolonged periods in winter. Still several species of small passerine birds such as the willow tit (*Parus montanus*), the Siberian tit (*Parus cinctus*) and the boreal chickadee (*Parus hudsonicus*) are resident throughout the winter in their year-round territories. Since northern winter nights are long, there are only a few hours available for foraging. Unlike larger birds, such as ptarmigan (Irving *et al.* 1967), small birds cannot sustain themselves on food carried in the gut overnight. Instead, on a daily basis, they will build-up reserves of subcutaneous fat that are metabolized overnight. Each day, a bird with a body mass of 10–20 g must gain 7–12% of its morning body mass as fuel for the coming night (Haftorn 1992). The unfavourable surface-to-volume ratio makes small animals lose relatively more heat to the environment than large animals, and in this review I will consider only species of this size to be ‘small birds in winter’.

The fact that small birds can winter under these conditions is even more astonishing if one considers the poor availability of food that these species eat, for example invertebrates, seeds and nuts. Not surprisingly they must spend most of the day foraging. The boreal taiga zone may seem to be an extreme example, but the demands for special adaptations are analogous but less

extreme also for species that winter in moderately cold regions.

Flying animals require special adaptations since they need to minimize the mass they are carrying. This is expressed, for example, in the light skeletons that flying birds possess, but also in the fact that they normally carry much smaller body fat reserves than the potential maximum level. It has been known for long that there must be costs associated with reserves that are larger than necessary (King 1972). This knowledge in combination with the understanding that selection must be strong for optimal energy regulation has made ‘the little bird in winter’ the subject of a number of theoretical models (Lima 1986; McNamara & Houston 1987, 1990, 1994; McNamara *et al.* 1990, 1994, 2004, 2005; Lucas & Walter 1991; Houston & McNamara 1993; Houston *et al.* 1993, 1997; Bednekoff & Houston 1994a–c; Grubb & Pravosudov 1994; Clark & Ekman 1995; Bednekoff 1996; Brodin & Clark 1997; Brodin 2000, 2001; Lucas *et al.* 2001; Pravosudov & Lucas 2001a,b; Welton *et al.* 2002). My aim with this article is to review this literature and to summarize the insights and predictions that we have gained from the models.

The models I discuss relate to a large number of empirical studies that I do not aim to cover fully here. I will discuss these primarily in the context of the models that I review. Various aspects of avian energy regulation in winter have been reviewed thoroughly, for example the costs of fat storage (Witter & Cuthill 1993), adaptive energy management in general (Pravosudov & Grubb 1997) and food hoarding (Källander & Smith 1990).

*anders.brodin@teorekol.lu.se

However, none of these reviews focus on the theoretical work and none is recent.

(b) *What is adaptive energy management in wintering small birds?*

I will consider three forms of adaptive management of energy: (i) regulation of body fat reserves, (ii) food hoarding, and (iii) night-time hypothermia. Before I discuss the theoretical models, let me motivate the choice of these topics by some examples.

Great tits (*Parus major*) in Britain were fatter during years when there was a low population of their main aerial predator, the sparrowhawk (*Accipiter nisus*), compared to when sparrowhawks were common (Gosler *et al.* 1995). The authors interpreted this observation as adaptive adjustment of body fat reserves; in the absence of predators the tits could afford to carry larger reserves than when predators were present. Species that primarily forage on the ground usually carry larger fat reserves than arboreal foragers. The suggested explanation for this was that the ground will become covered by snow more frequently than foraging substrates in trees, which will make ground foraging species experience more variation in food availability than arboreal foragers (Rogers 1987). In order to hedge against this variation, ground foraging species should carry more fat. Intuitively, one would think that dominant individuals would take advantage of their rank privileges and build-up larger reserves than subordinate individuals. However, dominant individuals in flocks of willow tits (Ekman & Lilliendahl 1993) and European starlings (*Sturnus vulgaris*) (Witter & Swaddle 1995) carried smaller fat reserves than subordinate flock members. The authors considered this to be a strategic 'choice'. Due to their more reliable food access, dominants could reduce mass-dependent costs by staying lighter than subordinates (see §2e). These studies provide strong evidence for adaptive adjustments of body fat reserves because when the authors removed the dominants, the subordinates decreased their fat reserves to 'dominant levels'.

Also, the significance of food storing has been demonstrated in many empirical studies. Those species of small passerines that are able to withstand the extreme conditions that prevail in winter in the northernmost boreal taiga zone are all large-scale food hoarders. Willow tits, Siberian tits, black-capped chickadees (*Poecile atricapillus*), boreal chickadees and the Siberian race of the Eurasian nuthatch (*Sitta europaea asiatica*) store thousands of food items in the autumn, for later use as winter food (Haftorn 1974; Pravosudov 1985; Källander 1993; Brodin 1994b, 2005). The climatic conditions in this region in winter probably make food hoarding a prerequisite for survival.

A third way to optimize energy use is to regulate expenditure. Small birds can save energy by entering a state of hypothermia, or reduced body temperature, during cold nights. A general model showed that the fitness gain of this strategy can be larger than that expected from simple energetic considerations (Houston & McNamara 1993). By reducing the body temperature by 10 °C or more, species like willow

tits and mountain chickadees (*Parus gambeli*) and black-capped chickadees can reduce overnight energy expenditure considerably (Haftorn 1972; Chaplin 1976; Cooper & Swanson 1994; Reinertsen 1996; Cooper 2002).

(c) *Types of models*

Most theoretical models for foraging in birds from the 1970s to 1980s were optimal foraging theory (OFT) models that dealt with energy optimization problems (cf. Stephens & Krebs 1986). Such models cannot accurately describe the complex situation the 'little bird in winter' faces. Most models published after 1990 have been dynamic state variable models (DSVMs, also called stochastic dynamic programming models) (Mangel & Clark 1988; Houston & McNamara 1999; Clark & Mangel 2000), although there are also some simpler analytical ones. The ability of DSVM to incorporate many factors makes it possible to model this problem with some realism. Such models can simultaneously incorporate stochastic variables for weather conditions, predation risk and foraging success at the same time as they include temporal dynamics and behaviour that depend on the state of the animal. Two papers are typical game theoretical models (Smulders 1998; Brodin *et al.* 2001) and one is a DSVM in a game theoretical setting (Clark & Ekman 1995).

2. MODELS OF BODY FAT REGULATION

(a) *The modelling framework*

In this section, I will primarily discuss models on regulation of body fat that will not include food hoarding or hypothermia (Lima 1986; McNamara & Houston 1987, 1994; Ekman & Lilliendahl 1993; Houston & McNamara 1993; Houston *et al.* 1993, 1997; Bednekoff & Houston 1994a-c; McNamara *et al.* 1994, 2004, 2005; Bednekoff 1996; Brodin 2001). The models on this topic that were published before 1993 were summarized in Houston *et al.* (1993).

Since it will be costly to gain and carry large fat reserves (e.g. Lima 1986; Witter & Cuthill 1993), birds should not carry more fat than they need (King 1972). In two early papers, Lima (1985, 1986) made some assumptions that provided a basic framework for later models. He assumed that: (i) birds store energy as body fat, and carrying fat will incur costs; (ii) death is due to either starvation or predation and these risks depend on the level of fat; (iii) birds will optimize body mass, so that total mortality from both starvation and predation over the winter is minimized; and (iv) the environment is stochastic, for example with respect to food availability and weather conditions. Point (ii) is a core assumption in many later models; there is an obvious trade-off between the costs and benefits provided by fat reserves. Lima's (1986) framework has been adopted and refined in later more complex models. Some common assumptions in these are that: (i) food availability and overnight metabolic cost vary stochastically; (ii) both metabolic costs and predation risk may increase with body mass; (iii) just as in other behavioural models, optimization is useful since natural selection has favoured strategies that maximize

fitness; and (iv) time and energy that are allocated to foraging could otherwise be invested in other behaviours that are important.

Lima predicted that fat reserves should: (i) increase with increasing frequency or harshness of unfavourable periods; (ii) increase with the general level of food availability; (iii) decrease with increasing predation risk; and (iv) decrease with increasing temperature. Later models support many of these predictions but also produce a more complex picture. A positive correlation between fat reserves and environmental conditions implies that the level of reserves has been restricted by food availability. It is important to make a distinction between conditions when fat reserves are restricted by food availability and when they are under strategic control of the forager (e.g. Verhulst & Hogstad 1996). Thus, increasing food availability could trigger reductions in body fat reserves rather than increases (McNamara & Houston 1990, 1994). The reason is that birds will need smaller reserves in a rich environment than in a harsh environment.

(b) The trade-off between starvation and predation

Weather may vary unexpectedly, and the larger the fat reserves a bird carries, the smaller the risk of starvation will be. On the other hand, it may be costly to carry large fat reserves since this may increase metabolism and predation risk. This means that an optimally foraging bird must balance the risks of starvation and predation against each other and find the trade-off that gives the smallest mortality. The existence of such a trade-off in wintering birds has long been assumed (King 1972) although it was not examined in detail at that time.

The optimum in the predation/starvation trade-off (i.e. the minimum total probability of dying from these two sources) is not where these risks are equal, but where their marginal rates of change (or derivatives) are equal (McNamara & Houston 1987, 1990). The reason for this is obvious if one considers mortality to be a function of body mass. The total mortality is the sum of one component that decreases with increasing fat reserves (starvation) and one that increases with the level of reserves (predation). Clearly, the optimum will be at minimum total mortality, that is, where its derivative is zero. This derivative can only be zero where its two components cancel each other out, that is where the decrease in starvation risk (a line with a negative slope) is of the same magnitude as the increase in predation risk (a line with a positive slope). At this equilibrium, death by predation will usually be much more common than death by starvation. This prediction conforms nicely with field observations: most birds that die in winter die of predation, not starvation (Jansson *et al.* 1981). Only unusually extreme conditions will result in starvation. Also, starvation and predation may interact and result in higher mortality than expected since the combined effect on mortality may exceed the sum of their individual effects (McNamara & Houston 1990). This becomes clearer if one considers the effect of a given increase on instantaneous predation risk. A bird in good condition may not suffer as much from this increase as a bird that

Figure 1. Food availability and starvation (dashed curve) may be positively correlated even though total mortality (solid curve) shows the expected negative correlation. This may occur if the probability of predation is a decelerating function of mean gain (McNamara & Houston 1987) or if starvation only constitutes a very small fraction of total mortality. I have plotted this as McNamara & Houston, with the *x*-axis showing 'energy needed' even though they modelled it also for 'energy available'.

has very small energy reserves. Alternatively, a bird may be able to compensate for deterioration in the environment by foraging more intensively as long as predation risk remains low.

Since it is the total mortality risk from both these factors that matters, predictions may be directly wrong if only one of them is considered in isolation from the other (McNamara & Houston 1987). For example, starvation may decrease when food requirement increases (figure 1). The reason is that the forager minimizes total mortality, not only starvation. Depending on the relationship between predation and foraging, starvation may correlate to food availability in an unexpected way, especially if it accounts for only a small part of total mortality. This shows that when several parameters affect fitness simultaneously (probably the rule in nature), a model can disentangle the effects of single factors, one at a time. In some cases, predictions coming from models may be opposite to those coming from intuitive guesses.

Not only can starvation and food availability correlate in a counterintuitive way but even more unexpected is the possibility of a positive correlation between the level of body fat reserves and starvation. This may occur when conditions of increasing stochasticity cause birds to increase their fat reserves. Under conditions where increases in fat reserves incur accelerating costs (see §2c for a discussion on this), birds will not increase fat levels high enough to compensate fully for the increased starvation risk (figure 2). Thus, fat reserves and starvation can show this surprising positive correlation (Houston & McNamara 1993).

Another phenomenon that would be hard to understand without a model is that optimal gain rate may increase or decrease when food availability increases. If the improvement is temporary, the bird should forage more intensively to grab its share of resources that otherwise disappears. If the improvement is permanent, foraging intensity should instead decrease since

Figure 2. The optimal level of fat reserves as a function of increasing environmental stochasticity under conditions of accelerating mass-dependent costs (dashed curve). The solid line shows full compensation, that is when fat reserves increase so that starvation risk is kept constant. Due to accelerating costs, birds will not compensate fully and starvation will increase even though reserves increase. Based on Houston & McNamara (1993).

the bird needs smaller reserves in a richer environment (McNamara & Houston 1994). This insight has a general aspect: predictions will frequently be opposite if changes in the environment are permanent compared to when they are ephemeral (see Brodin *et al.* 2001 and the discussion of contingency/constancy in Witter & Cuthill 1993).

Some experiments in which predation has been increased by manipulation have produced responses in which birds have increased the level of fat reserves instead of decreasing them in accordance with predictions from the predation/starvation trade-offs (Lilliendahl 1998; Pravosudov & Grubb 1998). This has been interpreted either as if these birds perceived this as an interruption in foraging rather than as an elevation of the general predation risk (Lilliendahl 1998; Pravosudov & Grubb 1998; van der Veen & Sivars 2000; Rands & Cuthill 2001; McNamara *et al.* 2005) or that species that are not resident in winter should gain fuel and leave the area where the predator is present (Lilliendahl 1998). An alternative interpretation is that this response may depend on the birds having been disturbed and handled during the experiments (van der Veen & Sivars 2000).

(c) The costs of fat storage

The ecological costs of body fat storage contain two important components, increased metabolic rate and increased predation risk per time unit (e.g. Lima 1986; Witter & Cuthill 1993). Fat birds will have higher metabolism than lean birds, for example when they are flying. This means that they need to spend more time foraging, which in turn means that they may become more exposed to predators. There can also be a direct increase in predation risk per time unit if fat birds are less good at escaping attacking predators (e.g. Norberg 1989; Hedenström 1992; Metcalfe & Ure 1995; Kullberg *et al.* 1996). This could depend on impaired take-off ability, reduced manoeuvrability, or both (Witter & Cuthill 1993). These two components, metabolic rate and

predation risk, are usually referred to as mass-dependent costs (e.g. Houston & McNamara 1993). It is a common assumption that such costs are an accelerating, for example quadratic, function of body mass although linear increases in many cases will produce similar results (Houston *et al.* 1993; Bednekoff & Houston 1994a).

In the models I discuss in this review, the word 'risk' means the risk of getting killed by a predator. In earlier OFT models, it usually referred to the risk of not finding sufficient food, that is, to the variance in the availability of the resource. It is not obvious how these two types of risks will interact on foraging behaviour. A model showed that accelerating mass-dependent costs would have a strong effect (Bednekoff & Houston 1994a) and make fat birds even more risk-averse than predicted by OFT models.

Empirical studies suggest that the effect of small or moderate increases of body fat reserves on predation risk may be weak. There are several possible reasons for this. First, the actual risk experienced by the birds may not always correlate strongly to body mass (McNamara 1990). One possibility is that fat birds may behave differently from lean birds in order to decrease the predation risk. For example, starlings stayed longer in protective cover when they were heavy compared to when they were light (Witter *et al.* 1994).

Second, small increases in body mass do not seem to have a strong effect on performance during escape flight (although it may for performance during more relaxed flight). A number of experiments (Kullberg 1998; Kullberg *et al.* 1998; Veasy *et al.* 1998; van der Veen 1999; van der Veen & Lindström 2000) suggests that acceleration and take-off angle are not noticeably affected by 7–10% increases in body mass. This may seem impossible since increased load will impair acceleration and/or take-off angle according to physical laws (e.g. Hedenström 1992). Also, in European starlings, attached artificial loads will significantly decrease take-off trajectories (Witter *et al.* 1994). A possible explanation would be that birds possessed the ability to compensate for increases in body fat reserves (figure 3), for example by gaining muscle tissue in parallel to fat (Witter *et al.* 1994; Brodin 2001) or by increased wing-loading, known for example in bats (Hughes & Rayner 1991). The latter mechanism, however, seems less likely for birds that depend on acceleration and rapid climb to escape from attacking predators since these always should fly at maximum power. Observations of zebra finches (*Taeniopygia guttata*) suggest that priorities will differ between predator-induced and spontaneous take-off. Increasing fat reserves significantly decreased take-off speed in unalarmed finches (Metcalfe & Ure 1995; Veasy *et al.* 1998), while no such impairment occurred in finches that were startled to take off (Veasy *et al.* 1998).

Flight muscle hypertrophy as a response to increases in body fat has been known for sometime (e.g. Lindström & Piersma 1992), but it has not yet been demonstrated that wintering passerines can do this fast enough to follow their daily fluctuations in fat reserves. Interestingly, the starlings that were equipped with artificial loads seemed to be able to compensate for

Figure 3. Predation risk per time unit as a function of body fat reserves. The dashed curve shows a case when flight muscle tissue gain in parallel to body fat compensates for the extra mass up to some level, the solid curve shows a case with no such compensation. In the latter case, predation risk reflects the effect of gravity on acceleration. After Brodin (2001).

the extra mass if they were allowed to carry it for some days before they were tested (Witter *et al.* 1994).

On the other hand, the effect of increased body mass on experienced predation risk can sometimes be stronger than suggested by physical laws. Foraging birds cannot scan continuously for predators. If less time is allocated to predator scanning, this may increase the reaction time when a predator attacks. A delay before take-off may also make small reductions in acceleration ability dangerous (Bednekoff 1996). Still, the difficulty in detecting effects of small increases in fat reserves on take-off performance suggests that such a 'reduced vigilance' effect may be more important in cases when birds carry large reserves. One possible example is premigratory fattening when small birds will carry considerably more fat than during the daily build-up of night fuel (e.g. Kullberg *et al.* 1996). Also, it is possible that manoeuvrability may be more important than acceleration and take-off angle for a small bird trying to escape from an aerial predator. Rapid alterations of direction may be easier for a bird that is not flying at maximum speed. Most empirical studies that aim to evaluate the effect of fat load on predation risk have only measured acceleration and trajectory. Witter *et al.* (1994), however, found that starlings hit significantly more obstacles not only when they were equipped with artificial weights but also when they were fatter. The fact that the starlings did not fly slower, however, suggests that the starling prioritized acceleration and speed during escape.

If birds possess the ability to compensate for moderate increases of fat reserves (for example by flight muscle hypertrophy), this will have consequences for the question of whether birds should choose to increase foraging time or foraging intensity when they need to increase their level of reserves (e.g. Witter & Cuthill 1993). In such a case, small birds should choose to forage longer rather than to increase foraging intensity (Brodin 2001). The reason is that they can afford to forage for a long time as long as their compensation ability makes it possible to outperform

an attacking predator. Below some upper levels of fat reserves, a foraging bird will have a good chance of escaping as long as it can scan frequently for predators (figure 3). Increasing foraging intensity, on the other hand, may be dangerous. Even if the foraging bird still can maintain high escape performance ability, effective predator scanning may be difficult. A long bout of foraging under very low risk will be better than a short bout under high risk.

(d) The effect of variation

Variability is an important component in foraging models. Variation can be deterministic, for example predictable daily and seasonal changes, but variation can also be non-deterministic, that is, stochastic. It is obvious from §2a (and in the term 'stochastic dynamic programming') that stochasticity is a key factor in the DSVM. Predation is a stochastic event in all such models I discuss in this review. Foraging success is considered to be stochastic in most of them although it has been modelled as deterministic in models where stochastic energy expenditure has been considered to incorporate sufficient variability (Bednekoff & Houston 1994c; Clark & Ekman 1995). Other variables that have been treated as stochastic include daytime weather changes or interruptions to foraging (Houston *et al.* 1993; Brodin 2000, 2001; McNamara *et al.* 2005), premature termination of foraging (Houston *et al.* 1993), stochastic night-time energy expenditure (Brodin 2000, 2001) and seasonal changes (Houston *et al.* 1993). In some models, energy gain is a combination of two stochastic variables: food encounter and energy contents of food items (Houston & McNamara 1993; Welton *et al.* 2002). Most models consider death by starvation to be a step-function when fat reserves fall to 0, but some treat this as a stochastic event for birds that carry small fat reserves (Lucas & Walter 1991; Lucas *et al.* 2001; Pravosudov & Lucas 2001a). McNamara *et al.* (2005) modelled predation risk (not predation events) as a stochastic variable that depended on whether a predator was present.

Several empirical studies show that foraging birds respond adaptively to increased stochasticity by adjusting body fat reserves. Great tits increased their fat reserves under constant mean conditions if foraging (Bednekoff & Krebs 1995) or overnight temperatures (Bednekoff *et al.* 1994) became less predictable. Although European starlings may not be typical for the category 'little birds in winter', they responded both to greater unpredictability of the food supply and greater overnight stochasticity by increasing dusk reserves (Cuthill *et al.* 2000).

Species that differ from this category of birds may show entirely different responses to increased stochasticity than adjustment of body fat reserves. For example, large birds such as crows (*Corvus corone*) and magpies (*Pica pica*) did not increase their fat levels when stochasticity increased (Acquarone *et al.* 2002; Cucco *et al.* 2002). Neither did zebra finches show such a response (Dall & Witter 1998), but these are nomadic Australian seed-eaters that differ in many respects from typical small wintering birds. The interpretation of the evidence for adaptive regulation of body fat may further be complicated by the fact that the response to

stochasticity can be season or condition dependent (Witter *et al.* 1995; Witter & Swaddle 1997). In general, however, stochasticity will increase the level of reserves, regardless of how it has been incorporated in models. For example, small birds will normally carry fat reserves that are considerably larger than needed for average requirement (see below) since they must be prepared to meet worse than average conditions.

Conditions will change over time, both in a long- and short-term perspective. For example, overnight energy expenditure will increase gradually to a mid-winter maximum, and then decline. Not surprisingly, theory predicts that the level of fat reserves should follow seasonal changes in energetic requirements (Bednekoff & Houston 1994c) since this variation is predictable. The effect of increased stochastic variation in this model is more interesting since it explains the occurrence of winter fattening. Lehikoinen (1987) defined true winter fattening as when not only evening reserves, but also average dawn reserves are larger in winter than in other seasons. The model predicted that optimal dusk reserves should exceed the average requirement, and this safety margin should increase with increasing stochastic variation in nocturnal energetic requirements (Bednekoff & Houston 1994c). Except for mornings after really cold nights dawn reserves will be substantial. Also, it may be beneficial to further increase dawn reserves to hedge against poor foraging success during the next day.

Most small birds fast overnight, intuitively suggesting that they should forage most intensively in the morning and in the afternoon. Empirical studies agree with this prediction; the common pattern is bimodal with peaks of foraging activity around dawn and dusk (see references in McNamara *et al.* 1994). However, the selective forces shaping this pattern may be complex (McNamara *et al.* 1994). Spreading predation risk evenly over time will in many cases minimize total predation risk (e.g. Houston *et al.* 1993). To hedge against daily stochastic events, foraging should take place early in the day, but in order to minimize total predation risk a bird should forage in the afternoon (McNamara *et al.* 1994). Thus, the bimodal pattern may primarily be an adaptation to stochasticity and mass-dependent predation risk rather than to daily variations in energy requirement or food availability.

Pravosudov & Lucas (2001b) suggested that predation risk may vary in a predictable way over the day, but since this model also includes food storing I will discuss it later. As mentioned in §2b, birds that are exposed to a predator will sometimes respond by reducing their fat reserves (Lilliendahl 1997; Gentle & Gosler 2001), and at other times by increasing them (Lilliendahl 1998; Pravosudov & Grubb 1998). This shows that it is important how the appearance of a predator is perceived by the birds. McNamara *et al.* (2005) incorporated predation risk as a variable that depended on the presence/absence of predators. They found that the presence of a predator could be predicted to either increase or decrease the optimal level of reserves. If risk increases only during the period when the predator is seen, this will have the same effect as a stochastic interruption and increases the optimum level. If, on the

other hand, the risk is high after a predator has been spotted (but disappeared out of sight), foraging (and fat reserves) will decrease afterwards. Later, however, foraging may increase to even higher levels than before the predator was spotted.

The opportunity to forage strategically may be reduced by constraints. For example, restrictions in digestive capacity will spread out feeding more evenly over the day (Bednekoff & Houston 1994b). This restriction may interact with increased stochastic variation and select for larger fat reserves. The effect of a factor such as this is suitable to evaluate in a model since it would be extremely hard to test empirically. The bimodal foraging pattern that prevails in nature made it possible for Bednekoff & Houston to conclude that foraging birds are affected more by environmental stochasticity than by digestive constraints.

(e) *Dominance rank*

As mentioned earlier, dominant willow tits and European starlings carried smaller fat reserves than subordinate birds even though they have prior access to food (Ekman & Lilliendahl 1993; Witter & Swaddle 1995; Cuthill *et al.* 1997). Outside the breeding season, willow tits live in small, coherent flocks and dominant flock members exclude subordinate individuals from the best habitat (Ekman & Askenmo 1984). A model based on such a social system showed that dominants should prefer safe low-gain habitats before risky high-gain habitats during normal days (Clark & Ekman 1995). During cold days, dominants should instead forage in the rich but risky habitat, thereby excluding subordinates from it. To hedge against this exclusion, subordinates must carry more fat than dominants. Since subordinates will experience less predictable access to food, this can be seen as a specific case of a general prediction that birds should meet harsher or more stochastic conditions by increasing their reserves when the environment allows them to do so (e.g. Lima 1986).

Some studies of dominance rank effects have produced results that contradict predictions from adaptive fat regulation theories. Dominant willow tits at northern latitudes carry larger fat reserves than subordinates (Koivula *et al.* 1995; Verhulst & Hogstad 1996). The authors proposed that the birds were restricted by a harsh environment in which the dominants should use their prior access to food. In another experiment, removal of dominant great tits resulted in increased fat levels in the remaining birds (Lange & Leimar 2003). However, this was an aviary experiment in which the birds were moved between consecutive aviaries in order to decrease social stability.

Also, the principle that subordinates need to hedge for 'rank privileges' exercised by dominants appears to be general. Brodin *et al.* (2001) reached similar conclusion in a game theoretical model of rank effects on food hoarding behaviour that I will discuss in §3.

It is noteworthy that Clark & Ekman (1995) predicted that dominants should choose to stay on low fat levels even though the model did not include mass-dependent costs! Arguing that mass-dependent costs is a fundamental factor in this type of model, Houston *et al.* (1997) point out that the factor limiting

Figure 4. When winter starts, passerines will increase their minimum level of fat to a higher average level, a phenomenon called winter fattening (Lehikoinen 1987). During this process, which occurs for 2 days in this example, between the hatched lines, the birds must forage at high rates. This will entail extra 'acquisition' costs. Fat must be gained also for daily usage, but the birds will then forage at normal intensities and only pay 'maintenance' costs. Both types of costs may have mass-dependent components. After Houston *et al.* (1997).

fat deposits in this model may have been a ceiling effect rather than a strategic choice by the bird. In order to clarify this, Houston *et al.* proposed a distinction between costs of acquisition and costs of maintenance. A bird that is foraging at high intensity to gain substantial fat reserves will pay higher costs than a bird foraging at its long-term average intensity. For example, this bird may have less time to scan for predators. However, acquisition and maintenance costs may sometimes be hard to separate since also daily maintenance means that fat must be gained. This makes it necessary to define these concepts in order to make them useful. For wintering birds, the distinction can be made between energy that is gained on a daily basis and energy that is gained to elevate the long-term level, for example winter fattening. Figure 4 shows a hypothetical example of winter fattening. Under autumn conditions, the bird will maintain its minimum level of fat by compensating night-time energy loss by daytime energy gain. When winter comes (indicated by the left dashed line), the bird must forage intensively for 2 days in order to elevate its long-term fat level. When the bird reaches the right dashed line, it has acquired sufficient minimum winter fat and it will now be possible to forage in a more relaxed way.

(f) Heat substitution

A bird has to move in order to forage, and much energy is lost as heat during movement. For flying organisms, such as birds, movement will be especially energy demanding. Most models I discuss have assumed that metabolic expenditure increases as an accelerating function of body mass. However, substitution occurs when surplus heat that is produced during movement can be used to keep the bird warm and thus reduce metabolic expenditure. Substitution has been included in several models (Brodin & Clark 1997; Brodin 2000)

as a factor that reduces the metabolic costs of activity, but only one model focuses specifically on it (McNamara *et al.* 2004). It shows that substitution will decrease metabolic costs and that at some level of reserves, or threshold, the heat generated by activity may completely replace the heat that is needed for thermogenesis. The model suggests that below this level, the effect of substitution will be to increase the optimal level of reserves compared to what its value would have been in the absence of substitution. Another prediction of this model is that threshold should increase as the environment becomes cooler. The take-home message is that thermoregulatory substitution will reduce the effect of increased body mass on metabolism.

(g) Conclusions

Adaptive body fat regulation is an important component in most theoretical models of the 'little bird in winter', and many models focus exclusively on this topic. Some predictions are intuitive and simple, whereas others would be difficult to make without the predictive powers of a model. The level of fat reserves is decisive for the trade-off between two important sources of mortality, starvation and predation. This trade-off has become generally accepted as a driving factor behind energy storing strategies in small birds in winter. There are many ways in which the optimum in this trade-off has been experimentally manipulated to test predictions from models of adaptive regulation of body fat. Examples of factors that have been manipulated include: predation risk, dominance rank (with subordinates expecting less predictable access to food) and different forms of environmental variability.

The optimal level of fat is not where mortality from starvation and predation are equal, but where the slopes, or derivatives, are equal (e.g. McNamara & Houston 1987). At this equilibrium, death by predation is usually much more common than the death by starvation. Also, erroneous predictions could be made if one of these factors is considered in isolation from the other.

Another important insight is that the optimal level of reserves can correlate both positively and negatively with food availability in the environment depending on whether changes are constant or ephemeral (e.g. McNamara & Houston 1994). This reversal of the response depending on whether changes are constant or temporary appears to be a general phenomenon (e.g. Witter & Cuthill 1993; Brodin *et al.* 2001).

Increasing fat reserves may increase both metabolism and predation risk (e.g. Lima 1986; Witter & Cuthill 1993). Most experiments have failed to detect any effects on take-off ability of small to moderate increases in fat level, but this cannot be interpreted as if mass-dependent costs are irrelevant. Instead, impairments in escape ability could be so dangerous that they must be avoided by some sort of compensation. One possibility is that fat birds behave differently from lean birds, for example scan more intensively or increase their wing-loading. Another possibility is that they will gain flight muscle tissue in parallel to fat (Brodin 2001). Mass-dependent costs are important components in

this type of model, both during acquisition and maintenance of fat reserves (Houston *et al.* 1997).

3. MODELS OF FOOD HOARDING

(a) *Short-term hoarding versus body fat*

Hoarding birds provide an interesting case of adaptive energy regulation since fat and external food stores to some degree are alternative energy storing strategies with different costs and benefits. In two early dynamic models, hoards are assumed to disappear within one or few days after storing (McNamara *et al.* 1990; Lucas & Walter 1991). The models produced a number of interesting predictions but the short longevity of the caches may explain some differences compared to later models with long lasting hoards (Brodin 2000; Pravosudov & Lucas 2001a). Even under very conservative assumptions, such as lack of mass-dependent predation risk or brief persistence of hoards, hoarding will be the optimal strategy. The explanation for this is that there will still be costs in the form of mass-dependent metabolism and stored food will not increase body mass (McNamara *et al.* 1990). Also, high body fat levels may act to inhibit not only foraging and eating but also caching. The reason is that behaviour other than foraging becomes more important as the bird gets fatter (Lucas & Walter 1991). Examples of such behaviour include preening, exploratory behaviour, singing and resting.

To hedge against variation in foraging success, a bird must either maintain large body reserves or use stored food. The acorn woodpecker (*Melanerpes formicivorus*) does not occur in regions with boreal winters and it is larger than typical species that belong to the 'little bird in winter' category. I still include it here since a theoretical model on storing in this species shows an important benefit of hoarding. The woodpeckers invest heavily in storing acorns even though stored food only constitutes a small fraction of the total energy that the birds need (Koenig & Mumme 1987). Stored food will hedge against stochastic variation in the environment and also a small amount of stored food can increase fitness substantially (Hitchcock & Houston 1994). The model suggests that stored food can be more important as insurance than as an energy source. The presence of stored food will allow hoarding willow tits to stay on body fat levels that would be dangerously low for non-hoarders, thereby minimizing mass-dependent costs (Brodin 2000). In case the weather remains good for a long period, these caches may have acted as insurance against stochastic events even though they were not consumed. Since they permitted hoarders to reduce their body fat reserves they still improved fitness.

McNamara *et al.* (1990) suggested that hoarders should gain fat later in the day than non-hoarders in order to minimize mass-dependent costs over the whole day. Field evidence suggests the opposite; three hoarding species gained fat at a higher rate in the morning than a non-hoarding species (Lilliendahl 2002). Two later models (Brodin 2000; Pravosudov & Lucas 2001a) show that this pattern could occur under reasonable assumptions. Due to the safety provided by cached supplies, hoarders will carry smaller fat reserves than non-hoarders. Since these two models assumed

Figure 5. Linear (solid line) and accelerating (dashed curves) predation risk in Brodin (2000) and Pravosudov & Lucas (2001a).

that caches remained overnight, this also applies to morning fat reserves. In the morning, a hoarder will be left with small reserves and the optimal behaviour will be to start the day by eating thereby gaining fat to hedge for uncertainty and metabolism for the rest of the day. An important reason for this discrepancy was that McNamara *et al.* had constructed their model with short-term hoarding marsh tits (*Parus palustris*) in Britain in mind, assuming that caches disappeared overnight. In that case, hoarders must carry the same overnight reserves as non-hoarders, meaning that they in most cases will start the day with substantial fat reserves. Field experiments on long-term hoarding willow tits in Scandinavia (Brodin 1993a, 1994b) show that caches remain intact for much longer in the boreal forest, which was the habitat where Lilliendahl made his observations.

Also, some additional assumptions were needed to produce the patterns observed by Lilliendahl (2002). One was that the increase in direct predation risk with mass must be small at low fat levels (Brodin 2000; Pravosudov & Lucas 2001a), something predicted already by Lucas & Walter (1991). Even though Brodin's and Pravosudov & Lucas' models produced similar results, they treated mass-dependent costs differently. Pravosudov & Lucas gave predation risk a low value (figure 5), while Brodin hypothesized that there could be some limit under which the birds could compensate for the increased load (figure 3). Although predictions almost are opposite, the key factor is similar in Brodin & McNamara *et al.* since the temporal foraging patterns in these models depend on that the birds are minimizing mass-dependent costs.

Pravosudov & Lucas (2001a) suggested that the pattern of fat gain in hoarders and non-hoarders that Lilliendahl found in the field can arise under a wider set of conditions than Brodin suggested. Given the similarity of the models, such qualitative different predictions seem strange. Instead, the main difference seems to lie in the assumptions of the models. Brodin sought a pattern when hoarders gain more fat than non-hoarders in the morning, whereas Pravosudov & Lucas sought a more general pattern in which both categories gain more fat in the morning than in the afternoon.

Not surprisingly, a general pattern will appear under a wider set of assumptions than a pattern that differs in a specific way between the categories. Also, there appears to be no stochasticity in nocturnal energy expenditure in the model of Pravosudov & Lucas. Surely, this must be a key factor in an investigation of how fat gain should be distributed over a day.

(b) *The longevity of stored food*

Field studies suggest that long-term hoarding is important in parids (titmice and chickadees) that inhabit boreal regions. Such species store tens of thousands of food items per individual each year (Haftorn 1959; Pravosudov 1985; Brodin 1994b, 2005). These items constitute a large proportion of the winter food (Haftorn 1956; Jansson 1982; Nakamura & Wako 1988; Brodin 1994b) meaning that much of the stored food will be eaten months after it was stored (Brodin 1994a). Some models consider caches to be relatively long-lived (e.g. Hitchcock & Houston 1994; Pravosudov & Lucas 2001a) but only one model specifically addressed long-term hoarding in a seasonal environment (Brodin & Clark 1997). In this model, long-term caches was treated as a variable that was separate from short-term caches. Several field experiments show that long-term hoarding willow tits also use a distinct short-term hoarding strategy, when caches have a half-life of around 7 h (Brodin 1992, 1993a,b). This species must optimize management of energy reserves at four dimensions: fat reserves, short-term caches, long-term caches and night-time hypothermia (see §4). As expected, the model of Brodin & Clark predicted large-scale hoarding during the autumn when food is abundant to increase the supply of winter food.

A hoarder that remembers caching locations can retrieve stored food immediately when it is needed. If, on the other hand, caching locations are not remembered, a hoarder must search for and locate caches before they can be consumed. Also, the proportion of the stored food that can be retrieved will be larger if exact positions of caches are remembered. Considering the large number of food items stored and the long interval between storing and retrieval, it is not likely that all long-term caches can be retained in memory, especially in species such as the willow tit that has a rapid memory decay (Brodin & Kunz 1997; Smulders & Dhont 1997).

Brodin & Clark (1997) suggested that caches were remembered when they were stored, but that they were forgotten as an exponentially decreasing curve. Forgotten 'short-term' caches would still benefit the hoarder since they increased the general supply of winter food in the hoarder's territory. The model showed that forgotten caches may confer almost the same fitness benefits as those that are remembered (Brodin & Clark 1997). Forgotten caches can be seen rather as an enrichment of the foraging habitat while remembered short-term caches can be seen as 'externally' stored body fat. The strong effect on survival of forgotten caches depends on that food availability is elevated from a level where the birds face a high risk of starvation. If these caches had been retained in memory, retrieval would have been more efficient, but

Figure 6. Fitness as a function of the amount of stored food in a winter territory of a hoarding small bird. 'A' symbolizes the food that is available without any stored food, 'B and C' are the stored food. 'B' is the proportion that can be retrieved even if caching locations are not remembered and 'C' is the additional gain from more accurate retrieval that would occur if all caching locations had been remembered. The increase in amount of food retrieved is the same for 'B and C', but the fitness gain is much larger for 'B'.

the additional fitness gain of the extra food recovered may be smaller than expected. The reason is that the fitness gain from additional food will be a curve of diminishing returns (figure 6). The fitness gain from increasing storing effort 'one unit' in figure 6 is larger in region B than in region C. In region D, additional storing will even decrease fitness since the bird already has all the winter food it needs.

In winter, very little food may be available for storing but the model (Brodin & Clark 1997) predicted that the birds still should continue storing. The proportion of the total food that these stores will account for is very small, but short-term caches retained in memory are valuable since they act as insurance against stochastic variation. Marsh tits responded to increasing variability by storing more food rather than by increasing fat reserves (Hurly 1992).

(c) *The effect of pilfering*

It seems obvious that birds facing increased pilfering should compensate for this by hoarding more or by increasing their fat deposits. A theoretical examination, however, showed that the response to pilfering can be complex, especially under elevated levels of predation risk (Lucas *et al.* 2001). Small pilfering rates can be counteracted by increased hoarding rates but at higher pilfering it pays less to try to compensate and birds should increase resting instead. Pilfering will also reduce the effects of predation on body mass. The reason is that predation will have a strong effect on body mass only when pilfering is so high that birds cease caching. At intermediate levels of pilfering, changes in predation risk will instead correlate to changes in hoarding rates while body mass remains essentially constant (Lucas *et al.* 2001).

A game theoretical model that compared hoarding and cache pilfering as alternative strategies predicted that hoarding will not be evolutionarily stable unless it

is more advantageous to hoarders than to conspecific non-hoarding pilferers (Andersson & Krebs 1978). The reason is that the hoarder pays costs of hoarding, for example energy expenditure and exposure to predators during hoarding transports. The evolution of hoarding under conditions when caches are shared equally between hoarders and non-hoarders may seem to require group selection. A more elaborate model shows that this may not necessarily be true for the social structure that dominates among species that belong to 'the little bird in winter' category (Smulders 1998). Species such as boreal parids live in small, territorial groups consisting of individuals that are not closely related (Ekman 1989). In such a 'small-group' system, hoarding may evolve even if caches are shared equally between hoarders and non-hoarders (figure 7). Even under conditions when non-hoarding is the best strategy in a single group in isolation, the average fitness of non-hoarders in the whole population may be lower than the one of hoarders. Many groups may consist of only non-hoarders and these will have very low fitness since there are no hoarders to pilfer from. The low global fitness of the non-hoarding genotype will then 'flood' the fitness of the non-hoarders in the small group.

This might be easier to understand with an imaginary example. The important thing here is not the magnitude of the absolute numbers, but their relative values. I assume that flock size is as in figure 7, i.e. four from all groups. Individuals can only move in their own territories, meaning that they have access to own caches and caches made by other members of their own flock. For example, let the basic fitness without any hoarded supplies be 5, the gain from one individual's hoarding 12 and the cost of hoarding -2 . The fitness of a single hoarder in a group with three non-hoarders (the territory within the dashed border in figure 7) will be $5 + 12/4 - 2 = 6$. Here, 12 is divided by 4 as caches are shared equally by all four flock members. If we look at this group in isolation, the fitness of its non-hoarders will be $5 + 12/4 = 8$. In other groups that consist of only non-hoarders, the non-hoarders will instead have a fitness of 5. While the non-hoarders in the dashed territory appear to have higher fitness than hoarders, the global fitness for the non-hoarding genotype must be averaged over all territories. According to figure 7, this gives them a fitness of $(16 \times 5 + 3 \times 8)/19 \approx 5.5$. This is lower than the fitness of the hoarder, 6. The result will be a mixed evolutionary stable strategy since non-hoarders always can invade a population of pure hoarders (cf. Smulders 1998).

(d) The effect of variation

Predation risk is a fundamental factor in most models I discuss here, but few of them acknowledge that predation risk may vary over the day. For example, a predator may be most active in the morning, at midday, or in the afternoon. As expected, a model including varying but predictable predation risk predicted that birds should avoid high-intensity eating during periods when predation risk was high (Pravosudov & Lucas 2001b). In reality, predators may respond to the behaviour of their prey, but this was not incorporated

Figure 7. A rare mutant playing a hoarding strategy (filled circle) can invade a population of non-hoarders (open circles) if these live in small, territorial groups even if the hoarder would have lower fitness than non-hoarders in its own group in isolation (surrounded by a dashed border). Under such a territorial system, a hoarding strategy can invade even if there is no recovery advantage for hoarders. The reason is that hoarded supplies will only be shared between group members but not with conspecifics outside the group. See the text for an example calculation.

in the model. I discuss the case when predation risk depends on the behaviour of the predator in §2e.

Predictions concerning hoarding behaviour were less obvious. When predation risk peaks at midday, birds should cache in the afternoon rather than in the morning. Food hoarders will be leaner than non-hoarders in the morning since they can afford to carry smaller fat reserves. They should start the day by eating to buffer their metabolism for the rest of the day, a pattern also predicted by Brodin (2000). After gaining sufficient fat to buffer the rest of the day, hoarders can cache later in the day.

Pravosudov & Lucas (2001b) found that the temporal pattern of cache retrieval should not be affected by daily variations in predation risk: birds should primarily retrieve caches in late afternoon. McNamara *et al.* (1990) reached the same conclusion for evident reasons since they assumed that unused caches disappeared overnight. It is more unexpected that Pravosudov & Lucas would predict the same temporal pattern even though they assumed that caches were long-lived.

(e) Dominance rank

As mentioned earlier, a game theoretical model that investigated the effects of dominance rank on optimal hoarding investment (Brodin *et al.* 2001) is conceptually similar to the model of optimal fat regulation in relation to rank (Clark & Ekman 1995). In the model, a period of food surplus when food can be stored (the autumn) is followed by a lean period when stores can be retrieved (the winter). The relationship between the ranks is one-sided; dominants can pilfer caches of subordinate birds but not the other way around. Not surprisingly the model predicted that subordinates

should store more than dominants to compensate for the pilferage from dominants.

The model also predicted that this difference should decrease if environmental conditions in winter gets worse. The reason is that foraging efficiency becomes more important as the environment becomes harsher. The dominant should decrease pilfering and increase own storing in order to increase its efficiency, since retrieval of own caches gives a higher energetic gain than to search for other's caches.

This prediction was only valid in cases when the deterioration was predictable, in which case the birds could store optimally. If conditions got worse in an unpredictable way, the dominant should instead steal more food from the subordinate. The reason is that the dominant has not stored enough for harsh conditions and has to grab what it can. Here, a parallel can be drawn to predictions of responses in fat acquisition to conditions of ephemeral and permanent changes in the environment (see §2b and McNamara & Houston 1994).

(f) *Conclusions*

Food storing may be very beneficial, shown by the fact that it will occur even under conditions when fat does not incur mass-dependent predation costs and caches disappear fast (McNamara *et al.* 1990). Species that store food externally can decrease fat reserves and thereby reduce metabolic costs (McNamara *et al.* 1990; Hitchcock & Houston 1994; Brodin 2000; Pravosudov & Lucas 2001a). Stored food is not only valuable as a regular source of energy but the presence of hoarded food will also hedge against rare stochastic events in the environment (Hitchcock & Houston 1994; Brodin 2001). Hoarders should store in a way that minimizes mass-dependent costs and predation risk. Low ranked birds should build-up larger energy reserves than high ranked ones, not only in the form of body fat (Clark & Ekman 1995) but also in the form of stored food (Brodin *et al.* 2001). The reason is that they must compensate for despotic behaviour from dominants. Predictions about reactions to environmental changes in hoarding behaviour may vary to the degree that they are opposite depending on the underlying assumptions. For example, hoarders should be predicted to eat most intensively in the afternoon if caches are short-lived (McNamara *et al.* 1990) but in the morning if caches are long-lived (Brodin 2000; Pravosudov & Lucas 2001a). Also, the effect of permanent changes in the environment on caching decisions may be opposite to the effects of temporary changes (Brodin *et al.* 2001).

4. MODELS OF NIGHT-TIME HYPOTHERMIA

(a) *The models*

Clark & Dukas (2000), Pravosudov & Lucas (2001a) and Welton *et al.* (2002) have developed dynamic models of optimal hypothermia. In all three models, the authors assume that hypothermia saves energy but increases predation risk. Re-warming when leaving a state of hypothermia will take at least 15 min, during which time a bird will be helpless against predators (Reinertsen & Haftorn 1986). Considering the similarity of the models, it is not surprising that they

reached similar conclusions; hypothermia is beneficial when variation is high and conditions severe but should be avoided under more benign conditions.

There are some differences between the models. Pravosudov & Lucas and Welton *et al.* considered hypothermia to be a single drop in temperature while Clark & Dukas treated the depth of hypothermia as a variable that could be optimized. On the other hand, Pravosudov & Lucas included hoarded supplies as an alternative to fat, whereas the other models had only one storing variable, body fat. All three models considered increased predation risk to be the main cost of hypothermia but Welton *et al.* (2002) added a warming-up cost in their model. This produced a qualitatively new prediction: there would be a threshold level of fat under which hypothermia would not occur. This threshold should become increasingly important as dawn approached. The reason is that the gain from hypothermia becomes less important in relation to the warming up cost as the night progresses.

(b) *Conclusions*

It is hard to evaluate these models since the costs of nocturnal hypothermia are poorly known. Neither is it known how frequently small birds use nocturnal hypothermia; it can either be an adaptation to a temporary deficit of energy reserves or everyday behaviour. During empirical measurements, the subject birds have probably been disturbed, for example by insertion of thermometers, compared to conditions during natural roosting. This makes it hard to evaluate predictions from these models with existent data. The significance of the strategy is shown by the fact that not only small birds in winter, but also hummingbirds use overnight hypothermia on a regular basis, at least in environments such as the Andes (Hainsworth 1981; Carpenter & Hixon 1988).

5. GENERAL CONCLUSIONS

Since Lima's model was published in 1986 a number of empirical studies have been designed based on predictions from models I discuss in this review (Lucas & Walter 1991; Ekman & Lillendahl 1993; Lucas 1994; Metcalfe & Ure 1995; Witter *et al.* 1995; Kullberg *et al.* 1996, 1998; Lee *et al.* 1996; Lillendahl 1997, 1998; Kullberg 1998; Veasy *et al.* 1998; van der Veen 1999, 2002; Cuthill *et al.* 2000; Lillendahl 2000, 2002; Thomas 2000; van der Veen & Lindström 2000; van der Veen & Sivars 2000; Brodin 2001; Rands & Cuthill 2001; Brodin & Lundborg 2003; Lange & Leimar 2003; Lundborg & Brodin 2003; Macleod *et al.* 2005). Thus, the understanding of adaptive energy management in wintering birds has been substantially improved by these models. The subject is well suited for modelling since it is a complex phenomenon with many interacting factors.

Many predictions are obvious without theoretical models, for example, birds should build-up larger energy reserves when conditions get worse or when environmental stochasticity increases, and they should avoid behaviour incurring high predation risk unless energy shortage forces them to. The benefit from the models is instead that they have helped us make

predictions and draw conclusions that are not obvious. For example:

- starvation and predation risks may interact in complex ways creating counterintuitive effects if only one of these risks is considered;
- the equilibrium in the predation–starvation trade-off is where their marginal (not absolute) values are equal;
- at this equilibrium, death by predation is much more common than death by starvation. Death by starvation is unavoidable when resources are depleted, whereas death by predation is a stochastic risk;
- changes in the environment may have opposite effects on storing decisions depending on whether the change is ephemeral or permanent;
- accelerating mass-dependent costs may create unexpected effects, for example birds may face an increasing starvation risk even when they increase body fat reserve;
- stored food may improve fitness substantially even if it is not eaten since it hedges against rare stochastic events;
- increases in direct predation risk with body mass are smaller than suggested by physical laws, but this may depend on the fact that such costs are important and compensated for.

6. SUGGESTIONS FOR FUTURE MODELS

Apparently, the optimal solution to the trade-off between starvation and predation is where the marginal changes in these two components are equal (McNamara & Houston 1987, 1990). However, this problem is still not fully understood since it is not always clear what the marginality refers to. Sometimes it may refer to foraging intensity and at other times to the level of fat reserves. It may be worthwhile to explore the interaction between foraging intensity and level of fat reserves in more detail than it has been done previously, as for example in Houston & McNamara (1993). For example, a lean bird may have to forage intensively to avoid starvation. It may then experience high predation risk due to poor scanning for predators at the same time as it will be good at escaping once it spots a predator due to its low mass.

Energy reserves may not always be the best indicator of condition in a wintering bird. Especially, fat deposits but also the stored food of a small bird will change relatively fast making it unlikely that long-term trade-offs can be mediated by energy reserves alone. Thus, it could be important to include conditional variables other than energy reserves in models.

In a field study, Stoutjesdijk (2003) found that small birds sometimes are able to absorb more heat than they lose even during cold winter days and that a bird that perches in the sun may get thermally stressed. This depends on the excellent absorption and insulation properties provided simultaneously by feathers. This suggests that sun-basking may be an important behaviour also under boreal winter conditions. This

has not been incorporated in any models so far and the consequences are poorly known.

DSVM can be quite complex with many interacting parameters and this can make them hard to test (Hutchinson & McNamara 2000). Such models will be more useful for empiricists designing experiments if they produce simple and testable predictions. Thus, it should be up to modellers to design their models so that these produce testable predictions, rather than to empiricists to disentangle complex models.

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REFERENCES

- Acquarone, C., Cucco, M., Li Cauli, S. & Malacarne, G. 2002 Effects of food abundance and predictability on body condition and health parameters: experimental tests with the hooded crow. *Ibis* **144**, E155–E163. (doi:10.1046/j.1474-919X.2002.t01-2-00094.1.x)
- Andersson, M. & Krebs, J. 1978 On the evolution of hoarding behaviour. *Anim. Behav.* **26**, 707–711. (doi:10.1016/0003-3472(78)90137-9)
- Bednekoff, P. A. 1996 Translating mass dependent flight performance into predation risk: an extension of Metcalfe & Ure. *Proc. R. Soc. B* **263**, 887–889.
- Bednekoff, P. A. & Houston, A. I. 1994a Dynamic models of mass-dependent predation, risk-sensitive foraging, and premigratory fattening in birds. *Ecology* **75**, 1131–1140.
- Bednekoff, P. A. & Houston, A. I. 1994b Avian daily foraging patterns: effects of digestive constraints and variability. *Evol. Ecol.* **8**, 36–52. (doi:10.1007/BF01237664)
- Bednekoff, P. A. & Houston, A. I. 1994c Optimizing fat reserves over the entire winter: a dynamic model. *Oikos* **71**, 408–415.
- Bednekoff, P. A. & Krebs, J. R. 1995 Great tit fat reserves: effects of changing and unpredictable feeding day length. *Ecology* **9**, 457–462.
- Bednekoff, P. A., Biebach, H. & Krebs, J. 1994 Great tit fat reserves under unpredictable temperatures. *J. Avian Biol.* **25**, 156–160.
- Brodin, A. 1992 Cache dispersion affects retrieval time in hoarding willow tits. *Ornis Scand.* **23**, 7–12.
- Brodin, A. 1993a Low rate of loss of willow tit caches may increase the adaptiveness of long-term hoarding. *Auk* **110**, 642–645.
- Brodin, A. 1993b Radio-ptilochronology—tracing radio-actively labelled food in feathers. *Ornis Scand.* **24**, 167–173.
- Brodin, A. 1994a The disappearance of caches that have been stored by naturally foraging willow tits *Parus montanus*. *Anim. Behav.* **47**, 730–732. (doi:10.1006/anbe.1994.1100)
- Brodin, A. 1994b The role of naturally stored food supplies in the winter diet of the boreal willow tit *Parus montanus*. *Ornis Svecica* **4**, 31–40.
- Brodin, A. 2000 Why do hoarding birds gain fat in winter in the wrong way? Suggestions from a dynamic model. *Behav. Ecol.* **11**, 27–39. (doi:10.1093/beheco/11.1.27)
- Brodin, A. 2001 Mass-dependent predation and metabolic expenditure in wintering birds: is there a trade-off between different forms of predation. *Anim. Behav.* **62**, 993–999. (doi:10.1006/anbe.2001.1844)
- Brodin, A. 2005 Hippocampus volume does not correlate to food hoarding rates in the field in two closely related bird species, the black-capped chickadee *Poecile atricapilla* and the willow tit *Parus montanus*. *Auk* **122**, 819–828.

- Brodin, A. & Clark, C. W. 1997 Long-term hoarding in the Paridae: a dynamic model. *Behav. Ecol.* **8**, 178–185.
- Brodin, A. & Kunz, C. 1997 An experimental study of cache recovery by hoarding willow tits after different retention intervals. *Behaviour* **134**, 881–890.
- Brodin, A. & Lundborg, K. 2003 Rank-dependent hoarding effort in willow tits (*Parus montanus*): a test of theoretical predictions. *Behav. Ecol. Sociobiol.* **54**, 587–592. (doi:10.1007/s00265-003-0661-9)
- Brodin, A., Lundborg, K. & Clark, C. W. 2001 The effect of dominance on food hoarding: a game theoretical model. *Am. Nat.* **157**, 66–75. (doi:10.1086/317008)
- Carpenter, F. L. & Hixon, M. A. 1988 A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* **90**, 373–378.
- Chaplin, S. B. 1976 The physiology of hypothermia in the black-capped chickadee, *Parus atricapillus*. *J. Comp. Physiol.* **112**, 335–344.
- Clark, C. W. & Dukas, R. 2000 Winter survival strategies for small birds: managing energy through hypothermia. *Evol. Ecol. Res.* **2**, 473–491.
- Clark, C. W. & Ekman, J. 1995 Dominant and subordinate fattening strategies: a dynamic game. *Oikos* **72**, 205–212.
- Clark, C. W. & Mangel, M. 2000 *Dynamic state variable models in ecology—methods and applications*. New York, NY: Oxford University Press.
- Cooper, S. J. 2002 Seasonal metabolic acclimatization in mountain chickadees and juniper titmice. *Physiol. Biochem. Zool.* **75**, 386–395. (doi:10.1086/342256)
- Cooper, S. J. & Swanson, D. L. 1994 Seasonal acclimatization of thermoregulation in the black-capped chickadee. *Condor* **96**, 638–646.
- Cucco, M., Ottonelli, R., Raviola, M. & Malacarne, G. 2002 Variations of body mass and immune function in response to food unpredictability in magpies. *Acta Oecol.* **23**, 271–276. (doi:10.1016/S1146-609X(02)01154-2)
- Cuthill, I. C., Hunt, S., Cleary, C. & Clark, C. 1997 Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*). *Proc. R. Soc. B* **264**, 1093–1099. (doi:10.1098/rspb.1997.0151)
- Cuthill, I. C., Maddocks, S. A., Weall, C. V. & Jones, E. K. M. 2000 Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behav. Ecol.* **11**, 189–195. (doi:10.1093/beheco/11.2.189)
- Dall, S. R. X. & Witter, M. S. 1998 Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Anim. Behav.* **55**, 715–725. (doi:10.1006/anbe.1997.0749)
- Ekman, J. 1989 Ecology of non-breeding social systems of *Parus*. *Wilson Bull.* **101**, 263–288.
- Ekman, J. B. & Askenmo, C. E. H. 1984 Social rank and habitat use in willow tit groups. *Anim. Behav.* **32**, 508–514.
- Ekman, J. B. & Lilliendahl, K. 1993 Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. *Behav. Ecol.* **4**, 232–238.
- Gentle, L. K. & Gosler, A. G. 2001 Fat reserves and perceived predation risk in the great tit, *Parus major*. *Proc. R. Soc. B* **268**, 487–491. (doi:10.1098/rspb.2000.1405)
- Gosler, A. G., Greenwood, J. J. D. & Perrins, C. 1995 Predation risk and the cost of being fat. *Nature* **377**, 621–623. (doi:10.1038/377621a0)
- Grubb, T. C. J. & Pravosudov, V. V. 1994 Toward a general theory of energy management in wintering birds. *J. Avian Biol.* **25**, 255–260.
- Haftorn, S. 1956 Contributions to the food biology of tits especially about storing of surplus food. Part III. The willow tit (*Parus atricapillus* L.). *Kgl. Norske Vidensk. Selsk. Skrifter* **3**, 1–80.
- Haftorn, S. 1959 The proportion of spruce seeds removed by the tits in a Norwegian spruce forest in 1954–55. *Kgl. Norske Vidensk. Selsk. Forh.* **32**, 121–125.
- Haftorn, S. 1972 Hypothermia of tits in the arctic winter. *Ornis Scand.* **3**, 153–166.
- Haftorn, S. 1974 Storage of surplus food by the boreal chickadee *Parus hudsonicus* in Alaska, with some records on the mountain chickadee *Parus gambeli* in Colorado. *Ornis Scand.* **5**, 145–161.
- Haftorn, S. 1992 The diurnal body weight cycle in titmice *Parus* spp. *Ornis Scand.* **23**, 435–443.
- Hainsworth, F. R. 1981 Energy regulation in hummingbirds. *Am. Sci.* **69**, 420–429.
- Hedenström, A. 1992 Flight performance in relation to fuel load in birds. *J. Theor. Biol.* **158**, 535–537.
- Hitchcock, C. L. & Houston, A. I. 1994 The value of a hoard: not just energy. *Behav. Ecol.* **5**, 202–205.
- Houston, A. I. & McNamara, J. M. 1993 A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scand.* **24**, 205–219.
- Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour. An approach based on state*. Cambridge, UK: Cambridge University Press.
- Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993 General results concerning the trade-off between gaining energy and avoiding predation. *Phil. Trans. R. Soc. B* **341**, 375–397.
- Houston, A. I., Welton, N. J. & McNamara, J. M. 1997 Acquisition and maintenance costs in the long-term regulation of avian fat reserves. *Oikos* **78**, 331–340.
- Hughes, P. M. & Rayner, J. M. V. 1991 Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance. *J. Exp. Biol.* **161**, 285–298.
- Hurly, T. A. 1992 Energetic reserves of marsh tits (*Parus palustris*): food and fat storage in response to variable food supply. *Behav. Ecol.* **3**, 181–188.
- Hutchinson, J. M. C. & McNamara, J. M. 2000 Ways to test stochastic dynamic programming models empirically. *Anim. Behav.* **59**, 665–676. (doi:10.1006/anbe.1999.1362)
- Irving, L., West, G. C. & Peyton, L. J. 1967 Winter feeding program of Alaska willow ptarmigan shown by crop contents. *Condor* **69**, 69–77.
- Jansson, C. 1982 The year round diets of the willow tit *Parus montanus* Conrad and the crested tit *P. cristatus* L. Ph.D. thesis, Göteborgs Universitet, Göteborg.
- Jansson, C., Ekman, J. & von Brömssen, A. 1981 Winter mortality and food supply in tits *Parus* spp. *Oikos* **37**, 313–322.
- Källander, H. 1993 Hamstrände nötväckor klarar vintern bättre (Hoarding nuthatches copes better with the winter). *Fauna Flora* **88**, 23–27.
- Källander, H. & Smith, H. G. 1990 Food storing in birds: an evolutionary perspective. *Curr. Ornithol.* **7**, 147–207.
- King, J. R. 1972 Adaptive periodic fat storage by birds. In *Proc. 15th Int. Ornithol. Congr.* (ed. K. H. Voous), pp. 200–217. Leiden, The Netherlands: E.J. Brill.
- Koenig, W. D. & Mumme, R. L. 1987 *Population ecology of the cooperatively breeding acorn woodpecker*. Princeton, NJ: Princeton University Press.
- Koivula, K., Orell, M., Rytkönen, S. & Lahti, K. 1995 Fatness, sex and dominance; seasonal and daily body mass changes in willow tits. *J. Avian Biol.* **26**, 209–216.
- Kullberg, C. 1998 Does diurnal variation in body mass affect take-off ability in wintering willow tits? *Anim. Behav.* **56**, 227–233. (doi:10.1006/anbe.1998.0765)

- Kullberg, C., Fransson, T. & Jakobsson, S. 1996 Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proc. R. Soc. B* **263**, 1671–1675.
- Kullberg, C., Jakobsson, S. & Fransson, T. 1998 Predator-induced take-off strategy in great tits (*Parus major*). *Proc. R. Soc. B* **265**, 1659–1664. (doi:10.1098/rspb.1998.0485)
- Lange, H. & Leimar, O. 2003 Social stability and daily body mass in great tits. *Behav. Ecol.* **15**, 549–554. (doi:10.1093/beheco/arh044)
- Lee, S. J., Witter, M. S., Cuthill, I. C. & Goldsmith, A. R. 1996 Reduction in escape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris*. *Proc. R. Soc. B* **263**, 619–623.
- Lehikoinen, E. 1987 Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scand.* **18**, 216–226.
- Lilliendahl, K. 1997 The effect of predator presence on body mass in captive greenfinches. *Anim. Behav.* **53**, 75–81. (doi:10.1006/anbe.1996.0279)
- Lilliendahl, K. 1998 Yellowhammers get fatter in the presence of a predator. *Anim. Behav.* **55**, 1335–1340. (doi:10.1006/anbe.1997.0706)
- Lilliendahl, K. 2000 Daily accumulation of body reserves under increased predation risk in captive greenfinches *Carduelis chloris*. *Ibis* **142**, 587–595.
- Lilliendahl, K. 2002 Daily patterns of body mass gain in four species of small wintering birds. *J. Avian Biol.* **33**, 212–218. (doi:10.1034/j.1600-048X.2002.330302.x)
- Lima, S. L. 1985 Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* **66**, 60–67. (doi:10.1007/BF00378552)
- Lima, S. L. 1986 Predation risk and unpredictable feeding conditions: determination of body mass in birds. *Ecology* **67**, 377–385.
- Lindström, Å. & Piersma, T. 1992 Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* **135**, 70–78.
- Lucas, J. R. 1994 Regulation of cache stores and body mass in Carolina chickadees (*Parus carolinensis*). *Behav. Ecol.* **5**, 171–181.
- Lucas, J. R. & Walter, L. R. 1991 When should chickadees hoard food? Theory and experimental results. *Anim. Behav.* **41**, 579–601.
- Lucas, J. R., Pravosudov, V. V. & Zielinski, D. L. 2001 A reevaluation of the logic of pilferage effects, predation risk, and environmental variability on avian energy regulation: the critical role of time budgets. *Behav. Ecol.* **12**, 246–260. (doi:10.1093/beheco/12.2.246)
- Lundborg, K. & Brodin, A. 2003 The effect of dominance rank on fat deposition and food hoarding in the willow tit *Parus montanus*—an experimental test. *Ibis* **145**, 78–82. (doi:10.1046/j.1474-919X.2003.00124.x)
- Macleod, R., Barnett, J. A., Clark, K. & Cresswell, W. 2005 Body mass strategies in blackbirds *Turdus merula*: the starvation–predation risk trade-off. *J. Anim. Ecol.* **74**, 292–302. (doi:10.1111/j.1365-2656.2005.00923.x)
- Mangel, M. & Clark, C. W. 1988 *Dynamic modeling in behavioral ecology*. Princeton, NJ: Princeton University Press.
- McNamara, J. M. 1990 The starvation–predation trade-off and some behavioural and ecological consequences. In *Behavioural mechanisms of food selection* (ed. R. M. Hughes). NATO ASI Series A, Life Sciences, pp. 39–59. New York, NY: Springer.
- McNamara, J. M. & Houston, A. I. 1987 Starvation and predation as factors limiting population size. *Ecology* **68**, 1515–1519.
- McNamara, J. M. & Houston, A. I. 1990 The value of fat reserves and the tradeoff between starvation and predation. *Acta Biotheor.* **38**, 37–61. (doi:10.1007/BF00047272)
- McNamara, J. M. & Houston, A. I. 1994 The effect of a change in foraging options on intake rate and predation rate. *Am. Nat.* **144**, 978–1000. (doi:10.1086/285721)
- McNamara, J. M., Houston, A. I. & Krebs, J. R. 1990 Why hoard? The economics of food storing in tits, *Parus* spp. *Behav. Ecol.* **1**, 12–23.
- McNamara, J. M., Houston, A. I. & Lima, S. L. 1994 Foraging routines of small birds in winter: a theoretical investigation. *J. Avian Biol.* **25**, 287–302.
- McNamara, J. M., Ekman, J. & Houston, A. I. 2004 The effect of thermoregulatory substitution on optimal reserves of small birds in winter. *Oikos* **105**, 192–196. (doi:10.1111/j.0030-1299.2004.12188.x)
- McNamara, J. M., Barta, Z., Houston, A. I. & Race, P. 2005 A theoretical investigation of the effect of predators on foraging behaviour and energy reserves. *Proc. R. Soc. B* **272**, 929–934. (doi:10.1098/rspb.2004.3037)
- Metcalf, N. B. & Ure, S. E. 1995 Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc. R. Soc. B* **261**, 395–400.
- Nakamura, H. & Wako, Y. 1988 Food storing behavior of willow tit *Parus montanus*. *J. Yamashina Inst. Ornithol.* **20**, 21–36.
- Norberg, U. M. 1989 Vertebrate flight. In *Zoophysiology*, vol. 27, pp. 1–291. Berlin: Springer.
- Pravosudov, V. V. 1985 Search for and storage of food by *Parus cinctus lapponicus* and *P. montanus borealis* (Paridae). *Zool. Zh.* **64**, 1036–1043.
- Pravosudov, V. V. & Grubb, T. C. J. 1997 Energy management in passerine birds during the nonbreeding season. *Curr. Ornithol.* **14**, 189–234.
- Pravosudov, V. V. & Grubb, T. C. 1998 Management of fat reserves in tufted titmice *Baeolophus bicolor* in relation to predation risk. *Anim. Behav.* **56**, 49–54. (doi:10.1006/anbe.1998.0739)
- Pravosudov, V. V. & Lucas, J. R. 2001a A dynamic model of short-term energy management in small food-caching and non-caching birds. *Behav. Ecol.* **12**, 207–218. (doi:10.1093/beheco/12.2.207)
- Pravosudov, V. V. & Lucas, J. R. 2001b Daily patterns of energy storage in food-caching birds under variable daily predation risk: a dynamic state variable model. *Behav. Ecol. Sociobiol.* **50**, 239–250. (doi:10.1007/s002650100361)
- Rands, S. A. & Cuthill, I. C. 2001 Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*. *Proc. R. Soc. B* **268**, 1783–1790. (doi:10.1098/rspb.2001.1653)
- Reinertsen, R. E. 1996 Physiological and ecological aspects of hypothermia. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 125–157. London, UK: Chapman & Hall.
- Reinertsen, R. E. & Haftorn, S. 1986 Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol.* **156**, 655–663.
- Rogers, C. M. 1987 Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* **68**, 1051–1061.
- Smulders, T. V. 1998 A game theoretical model of evolution of food hoarding: applications to the *Paridae*. *Am. Nat.* **151**, 356–366. (doi:10.1086/286124)
- Smulders, T. V. & Dhont, A. A. 1997 How much memory do tits need? *Trends Ecol. Evol.* **12**, 417–418. (doi:10.1016/S0169-5347(97)01200-7)
- Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory*. Princeton, NJ: Princeton University Press.

- Stoutjesdijk, F. 2003 Birds in the cold: the effects of plumage structure and environment on operative temperature, shown by spherical models. *Ornis Svecica* **13**, 123–136.
- Thomas, R. J. 2000 Strategic diel regulation of body mass in European robins. *Anim. Behav.* **59**, 787–791. (doi:10.1006/anbe.1999.1360)
- van der Veen, I. T. 1999 Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (*Emberiza citrinella*). *Behav. Ecol.* **10**, 545–551. (doi:10.1093/beheco/10.5.545)
- van der Veen, I. T. 2002 Seeing is believing: information about predators influences yellowhammer behavior. *Behav. Ecol. Sociobiol.* **51**, 466–471. (doi:10.1007/s00265-002-0464-4)
- van der Veen, I. T. & Lindström, K. M. 2000 Escape flights of yellowhammers and greenfinches: more than just physics. *Anim. Behav.* **59**, 593–601. (doi:10.1006/anbe.1999.1331)
- van der Veen, I. T. & Sivars, L. E. 2000 Causes and consequences of mass loss upon predator encounter: feeding interruption, stress or fit-for-flight. *Funct. Ecol.* **14**, 638–644.
- Veasy, J. S., Metcalfe, N. B. & Houston, D. C. 1998 A reassessment of the effect of body mass upon flight speed and predation risk in birds. *Anim. Behav.* **56**, 883–889. (doi:10.1006/anbe.1998.0880)
- Verhulst, S. & Hogstad, O. 1996 Social dominance and energy reserves in flocks of willow tits. *J. Avian Biol.* **27**, 203–208.
- Welton, N. J., Houston, A. I., Ekman, J. & McNamara, J. M. 2002 A dynamic model of hypothermia as an adaptive response by small birds to winter conditions. *Acta Biotheor.* **50**, 39–56. (doi:10.1023/A:1014761227478)
- Witter, M. S. & Cuthill, I. C. 1993 The ecological cost of avian fat storage. *Phil. Trans. R. Soc. B* **340**, 73–92.
- Witter, M. S. & Swaddle, J. P. 1995 Dominance, competition, and energetic reserves in the European starling, *Sturnus vulgaris*. *Behav. Ecol.* **6**, 343–348.
- Witter, M. S. & Swaddle, J. P. 1997 Mass regulation in juvenile starlings: response to change in food availability depends on initial body mass. *Funct. Ecol.* **11**, 11–15. (doi:10.1046/j.1365-2435.1997.00041.x)
- Witter, M. S., Cuthill, I. C. & Bonser, R. H. C. 1994 Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim. Behav.* **48**, 201–222. (doi:10.1006/anbe.1994.1227)
- Witter, M. S., Swaddle, J. P. & Cuthill, I. C. 1995 Periodic food availability and strategic regulation of body mass in the European starling, *Sturnus vulgaris*. *Funct. Ecol.* **9**, 568–574.