



Management of fat reserves in tufted titmice *Baelophus bicolor* in relation to risk of predation

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ABSTRACT

Fat reserves are an important energy source for animals wintering in temperate zones. Long nights, low ambient temperature and often unpredictable food all increase the probability of death from starvation, and to survive, animals carry energy reserves as fat. Based on the assumption that extra weight makes birds more vulnerable to diurnal predators, it has been hypothesized that predation risk places an upper limit on avian fat reserves. The hypothesis leads to the prediction that birds should decrease their mass in response to increased risk of predation. We tested this prediction with a resident species, the tufted titmouse, *Baelophus bicolor*. During a 3-day period, we presented a taxidermic mount of a sharp-shinned hawk, *Accipiter striatus* (predator treatment) or a mourning dove, *Zenaida macroura* (control treatment) to seven titmice housed individually with food ad libitum. Even though vigilance and delay in time to resume foraging were significantly higher after exposure to the hawk model, the body mass of titmice after exposure to the hawk increased rather than decreased, a result opposite to that predicted. In particular, the birds significantly increased their evening body mass and mean daily mass gain during the treatment period. Our results suggest that risk-dependent foraging appears to regulate avian body fat reserves by limiting foraging time. When food is unlimited, as in our experiment, birds may be able to obtain high energy reserves even while maintaining intense vigilance for predators, and under such conditions, the energetic costs of flying may control upper level energy reserves.

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For many animals wintering in the temperate zone, fat reserves serve as an important buffer against starvation (e.g. Witter & Cuthill 1993). To minimize risk of starvation caused by long nights, low ambient temperatures, and limited and often unpredictable food supplies, animals should maximize the amount of energy reserves they carry as body fat (King 1972; Blem 1990). However, birds normally maintain much lower fat reserves than the maximum possible (Witter & Cuthill 1993), suggesting there must be costs to maintaining and/or carrying larger fat reserves. It has been hypothesized that risk of predation causes birds to maintain a lower amount of body fat (Lima 1986; McNamara 1990; McNamara & Houston 1990; Grubb & Pravosudov 1994), resulting in a trade-off between risk of starvation and risk of predation (Lima 1986). This assumption has been incorporated into a number of optimality-based theoretical investigations of the fat reserves birds should maintain under different ecological conditions (McNamara &

Houston 1990; McNamara et al. 1990, 1994; Houston & McNamara 1993; Bednekoff & Houston 1994a, b). That risk of starvation affects birds' fat reserves has recently been tested and supported (Ekman & Hake 1990; Bednekoff & Krebs 1995; Witter et al. 1995; Pravosudov & Grubb 1997). The effect of predation risk on fat reserves, however often assumed, has remained largely untested.

The hypothesized effect of predation risk on birds' fat reserves can be divided into two main components. The first component, predation risk-dependent body mass, holds that more fat reserves result in higher body mass which leads to higher predation risk by impairing birds' physical ability to fly. Heavier birds have been predicted to have reduced manoeuvrability and a slower maximum flight speed, which increases their chances of being attacked by an aerial predator (Witter et al. 1994; Metcalfe & Ure 1995; Kullberg et al. 1996). The other component of predation risk-dependent reserves concerns the extent of foraging bouts. To accrue and maintain higher fat reserves, a bird must spend more time foraging. Because birds are at higher risk of predation while foraging than while resting (Houston et al. 1993; Clark 1994), they may postpone foraging, and thus maintain the minimum necessary fat reserves.

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We investigated the predation risk-dependent body mass hypothesis by monitoring the body mass of birds under simulated high and low predation risk. Based on this hypothesis, the birds should show a decrease in body mass in response to increase in risk of predation.

METHODS

We caught seven male tufted titmice, *Baeolophus bicolor* (sexed by wing length, T. C. Grubb, unpublished data) at different locations in central Ohio and tested them individually in an outdoor aviary measuring $3 \times 8 \times 2$ m high. The aviary was open to the sky (except for wire netting), but was walled by translucent white fibreglass panels that isolated a bird visually and maintained wind speeds in the aviary at or near zero. One end of the aviary was roofed by a translucent white fibreglass panel 30 cm wide that protected a 'recording perch' and feeder from rain and snow (see below). The aviary contained five caching 'trees' fashioned from sugar maple, *Acer saccharum*, saplings, each bearing 20 evenly distributed holes 0.5 cm in diameter and 1 cm deep for the birds to use as cache sites. An observation chamber was situated at one end of the aviary, and separated from the aviary by a wall of one-way glass.

The experiments were conducted under prevailing photoperiods. Outdoor ambient temperatures were stored in a computer every 30 min ('Weather Wizard III'; and 'Weatherlink' software; Davis Instruments). An electronic balance (Mettler, Toledo, Ohio) inside the observation chamber was connected through the one-way glass wall to a perch in the aviary. As this perch was the highest available in the aviary, birds used it frequently during the day and always for roosting at night. Readings from the balance to the nearest 0.01 g were stored in a computer to provide a continual record of body mass. The system checked the balance every second and stored records of body mass and time of day whenever a bird was sitting on the perch. At night, the system recorded body mass and time every minute.

Procedure

We tested the seven titmice individually from mid-November 1996 to the beginning of March 1997. We followed a 9-day protocol consisting of three 3-day phases: pretreatment, treatment and post-treatment. Before being tested, each bird was isolated in a cloth-covered 1-m^3 holding cage for about 1 week followed by 4–5 days alone in the aviary with food ad libitum. During the entire experiment, food was provided ad libitum.

During the two control periods of the experiment, birds were exposed each day to a taxidermic mount of a mourning dove, *Zenaida macroura*, for one randomly chosen 4-min interval within each of four 2-h time blocks (see Pravosudov & Grubb 1997). In nature, mourning doves are ignored by tufted titmice (T. C. Grubb, personal observation). During the experimental period, the birds were exposed in a similar fashion to a taxidermic mount of a sharp-shinned hawk, *Accipiter striatus*, a common

predator of small passerines. The dove or hawk mount was introduced to the aviary through a small access door at the far end of the aviary from the observation chamber, placed by hand on a post 1.5 m tall, allowed to remain for 4 min, then removed by hand.

Data Collection and Analysis

To determine whether the titmice associated the hawk mount with increased risk of predation, we measured (1) vigilance and (2) time to resume foraging (foraging delay) following exposure to either mount. If the hawk mount represented an increase in predation risk to the titmice, they should have been more vigilant and more reluctant to resume foraging after exposure to the hawk mount than to the dove mount. To obtain a measure of vigilance, we recorded the number of times per minute that a bird looked up while handling and eating a sunflower seed (Pravosudov & Grubb 1995). To measure foraging delay, we recorded the length of time that a bird waited before resuming foraging after we had removed the hawk or dove mount from the aviary.

Body mass was recorded continually and daytime records were averaged to provide mean body mass for each 30-min interval. We employed four measures to test the predicted effect of treatment on a bird's body mass: (1) morning body mass, taken just before a bird first left its roosting perch in the morning; (2) mean daily body mass, calculated as the mean of the 30-min averages of a bird's body mass during the daytime period; (3) evening body mass, defined as a bird's body mass at the time it settled down for the night on the recording perch; (4) mean rate of mass gain, calculated as the overall mean of the 30-min mass gains throughout the day.

Because tufted titmice are food-caching birds, we also observed each bird to evaluate its caching behaviour. However, as in a previous experiment (Pravosudov & Grubb 1997), access to ad libitum food resulted in the birds abandoning caching behaviour.

Before reducing each bird's body mass records to mean values for an across-bird analysis, we checked each bird independently for any within-bird effects of ambient temperature using ANCOVAs with treatment as a factor and ambient temperature as a covariate. To check each bird for behavioural habituation to either the hawk or dove mount, we used analyses of covariance (ANCOVAs) with vigilance and foraging delay as dependent variables, treatment as a factor and number of days in the experiment as a covariate. After finding no differences between pre- and post-treatment control periods in analyses with the bird as the primary sampling unit, we compared the combined-control means with treatment means using Wilcoxon signed-ranks tests.

RESULTS

Ambient temperature during the experiment varied from -16.5 to $+16.30^\circ\text{C}$. There was no statistically significant effect of ambient temperature on the body mass of any of the birds (all $P_s > 0.2$). Titmice tended to begin night

Table 1. Changes in behaviour and body mass of seven tufted titmice exposed to taxidermic mounts of a mourning dove and sharp-shinned hawk

Variable	Z	P
Vigilance	2.37	0.02
Foraging delay	2.37	0.02
Morning body mass	0.08	0.93
Mean daily body mass	1.52	0.13
Evening body mass	2.37	0.02
Mean daily mass gain	2.37	0.03

Z and two-tailed P values are from Wilcoxon signed-ranks tests (treatment versus combined controls).

roosting about 6 min later during the treatment than during the two controls combined but the difference was not statistically significant ($P=0.08$). Neither vigilance nor foraging delay was significantly related to number of days in either treatment period or in the entire experimental replicate, a result indicating a lack of habituation to either the dove or the hawk mount.

All birds changed their behaviour significantly during the treatment phase of the experiment. During pre- and post-treatment control periods, birds always flew and foraged during a 4-min exposure to the dove mount. By contrast, birds usually ‘froze’ throughout the 4-min exposure to the hawk. Both vigilance and foraging delay were significantly greater during the treatment period than during the controls (Table 1, Fig. 1).

None of the body mass variables differed between the two controls ($Z<0.7$, $P>0.5$), but there were differences between the treatment and combined controls. Evening body mass and mean daily mass gain were significantly greater during the treatment than during the control periods (Table 1, Figs 2, 3). Mean daily body mass and morning body mass differed little between treatment and combined control periods (Table 1, Figs 4, 5).

DISCUSSION

To determine whether all titmice perceived the hawk mount as a predator, we compared each bird’s vigilance and foraging delay following removal of the hawk mount with those following removal of the mourning dove. Both of these measures indicated that the titmice responded much more strongly to the hawk mount, and therefore reflected direct responses to an increased threat of diurnal predation.

Contrary to the predictions, the titmice did not decrease their body mass when exposed to the hawk mount. Instead, across the seven birds there was a significant increase in both evening body mass and mean daily body mass gain after exposure to the hawk mount. The increase in gain rate suggests that the birds fed more intensively throughout the day during the treatment period. However, in the presence of the hawk model, the titmice stopped all foraging and feeding behaviour. It is possible that the increase in mass gain and evening body mass during the treatment was in response to

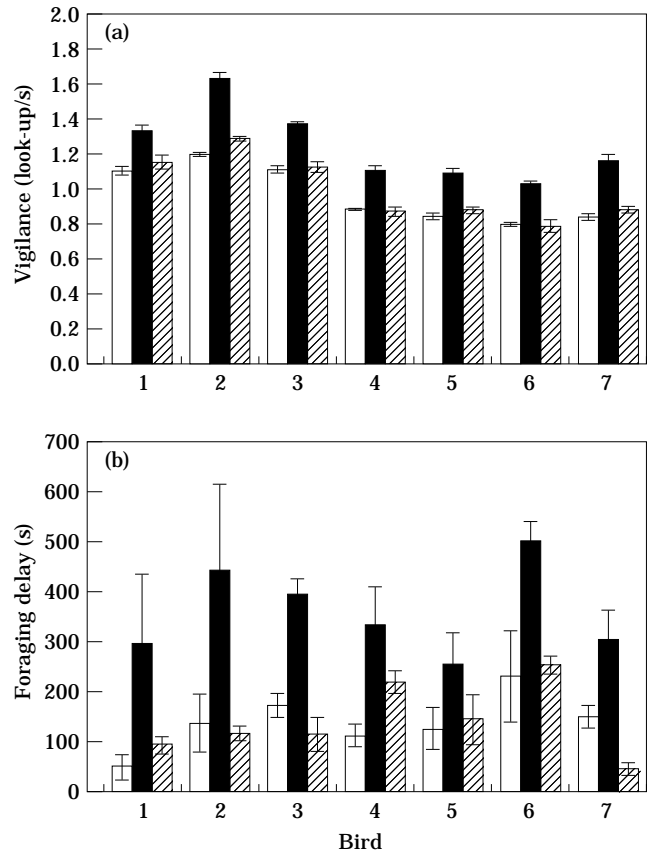


Figure 1. (a) Vigilance and (b) foraging delay of seven tufted titmice after exposure to a taxidermic mount of either a sharp-shinned hawk (predator) or a mourning dove (nonpredator). The mean(\pm SE) responses of the seven birds are arranged from left to right in the order tested over the course of one winter. \square , \square with diagonal lines: Means for the two 3-day control periods when each titmouse was exposed to the dove mount; \blacksquare : the intermediate 3-day period when birds were exposed to the hawk mount. Responses for both pre- and post-treatment controls are shown for each bird even though they were combined for analytical tests against treatment responses.

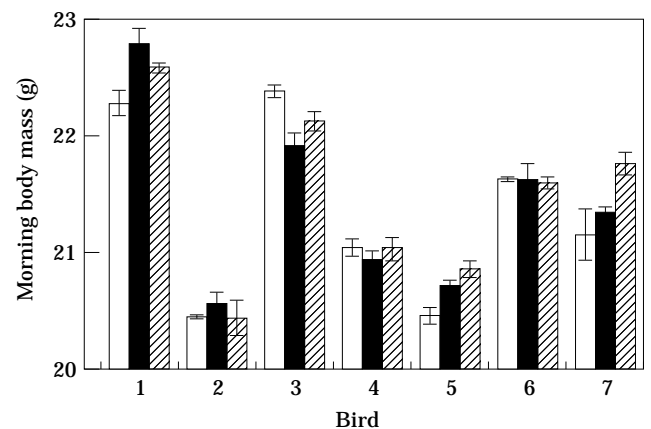


Figure 2. Morning body mass of seven tufted titmice. Annotation as in Fig. 1.

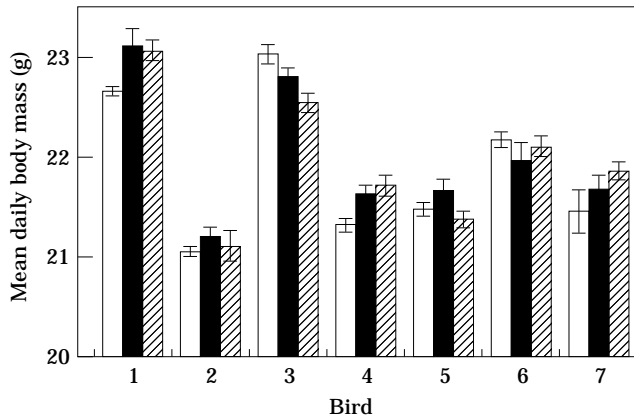


Figure 3. Mean daily body mass of seven tufted titmice. Annotation as in Fig. 1.

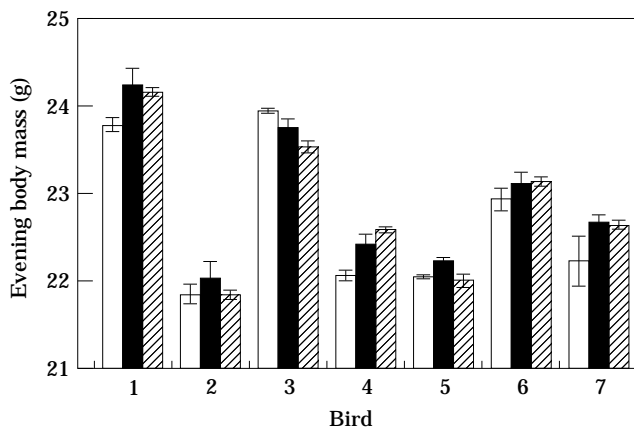


Figure 4. Evening body mass of seven tufted titmice. Annotation as in Fig. 1.

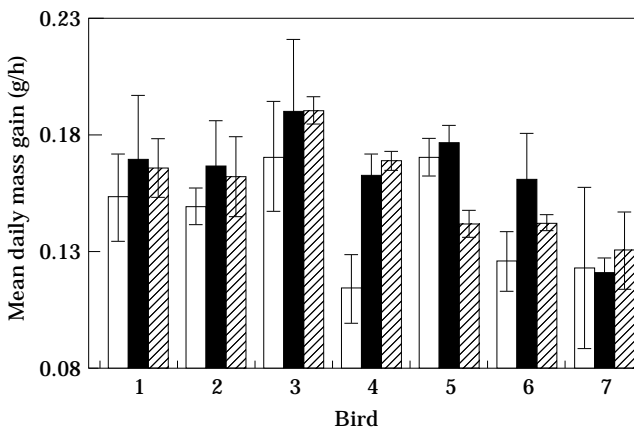


Figure 5. Mean daily rate of mass gain in seven tufted titmice. Annotation as in Fig. 1.

interruption of foraging opportunity rather than to the hawk model directly. Such an explanation seems unlikely, however, as the exposure to the hawk model totalled only 16 min per day when the birds were active for at least 8 h per day. The fact that evening body mass differed between treatment and control periods, but

morning mass did not, suggests that birds were losing more mass overnight during the treatment period.

A possible weakness in our experimental design was the rather short duration of each treatment period. We chose to use 3 days for each treatment because birds should be able to change their body mass quickly in response to predation risk and because responses to mounts during experimental periods longer than 3 days could have been increasingly confounded by habituation. Confirming that a 3-day duration was sufficient, the titmice significantly increased their evening mass and mean daily gain rate within the 3-day treatment and then often returned to their pretreatment mass during the post-treatment period.

Why might the birds have increased their body mass when they perceived a higher risk of diurnal predation? Such an inhibitory effect of extra mass on flight would seem to increase the risk of being killed by a predator. Other studies have demonstrated that birds increase their mass in the presence of protective cover (Witter et al. 1994) and carry less fat during years when the density of aerial predators is high (Gosler et al. 1995), again suggesting that birds might lower their mass in response to high predation risk.

While several investigators have obtained indirect evidence previous to this report, there has been only one direct test of the hypothesis linking lighter body mass to heightened predation risk (Lilliendahl 1997). Contrary to our results, Lilliendahl (1997) showed that greenfinches, *Carduelis chloris*, decrease their evening body mass in response to a mounted hawk. However, Lilliendahl (1997) used two groups of birds which he observed repeatedly after exposure to the mounted hawk, then treated several observations of each group as statistically independent. Therefore, the analysis may be compromised by pseudoreplication (Hurlbert 1984). Nevertheless, that the two groups of greenfinches showed a decrease in body mass is in line with prevailing hypothesis.

It is not clear why our results were so different. Perhaps, although mass per se might be inversely related to predation risk, different bird species might have different optimal strategies for predator escape, which could potentially overcome such a relationship. Although some workers have assumed that the most important escape tactic is to fly upwards at a steep angle (Witter et al. 1994; Metcalfe & Ure 1995; Kullberg et al. 1996), such a tactic may not be true for all birds. In one instance, a Eurasian nuthatch, *Sitta europea*, did not fly when attacked by a sparrowhawk, *Accipiter nisus* (V. V. Pravosudov, personal observation). Instead, the nuthatch 'ran' to and around a trunk. After several unsuccessful capture attempts, the hawk flew off. In many cases, both North American and Eurasian parids stop flying and remain stationary under cover while in the presence of an accipitrine hawk (personal observations). In many forest bird species such as titmice, birds do not seem to ascend or fly directly away when attacked, but, instead, make a very short horizontal or downward flight to the nearest cover (Lima 1993).

As noted earlier, body mass may be related in two ways to the risk of predation. First, body mass itself may be

dependent on predation risk given that heavier birds show reduced manoeuvrability (Lima 1986; McNamara & Houston 1990). Second, maintaining a higher body mass requires more foraging, and foraging involves higher predation risk than not foraging (Witter & Cuthill 1993; Clark 1994). Even though our results bear on both of these possible causal mechanisms, they have stronger implications for the first. The titmice clearly increased their mass during the treatment period, suggesting that carrying more weight, in and of itself, is not always associated with higher risk of predation.

Our results do not provide a strong test of the second hypothesis because all birds had an ad libitum food supply, which may have allowed the titmice to gain mass even while increasing vigilance and foraging delays after exposure to the hawk model. If we had presented the hawk model more often, it is possible that the birds would have reduced their foraging time below that required to maintain their level of reserves. Because our primary goal was to determine whether the birds' perceived predation risk was mass-dependent, we provided unlimited food and sufficient foraging time to allow the birds to maintain their desired level of reserves.

Our apparently contrary results become interpretable if a bird conceives predation risk as contributing to starvation risk. When parids know that a hawk is in the vicinity, they remain still in cover rather than foraging (personal observation). The length of such nonforaging bouts should be directly related to both incidence of hawk predators and to starvation risk. If birds can gather food quickly and efficiently (as under the ad libitum conditions in our aviary), they might always carry more fat as a buffer against fasting periods under cover whenever a hawk appears. By contrast, in nature, where food is limited and unpredictable in space and time, birds may not be able to increase their body mass quickly during intervals between predator appearances.

When food is unlimited, birds may be able to acquire and maintain energy reserves limited only by the energetic costs of flight. Therefore, we hypothesize that flying-related energy costs could depress avian body mass. This hypothesis could be easily tested by field data. For example, birds engaging in more flying during ordinary foraging should carry less fat than birds not so heavily dependent on flight. A swallow should carry less fat than a sparrow. Among wintering passerines, ground foragers seem to spend much less time flying than some tree-foraging birds like parids. In line with our hypothesis, ground-foragers carry relatively more fat than tree-foraging passerines (Rogers 1987; Rogers & Smith 1993). Furthermore, when these two foraging guilds were compared in areas of low (snow cover) and high (no snow cover) levels of food predictability, the ground-foragers still carried more fat (Rogers & Smith 1993).

In summary, our results directly contradict the prevailing hypothesis that higher predation risk causes birds to reduce body mass. It is clear, however, that in nature foraging as a process of acquiring energy reserves is dependent on degree of predation risk because foraging can only be done by sacrificing vigilance for predators (e.g. Houston et al. 1993). Thus, when food is not a

limiting factor, birds may easily obtain all the necessary reserves while increasing their vigilance for predators. When a food supply is limited and unpredictable, however, birds may not be able to maintain desired energy reserves because increased foraging would mean higher risk of predation. In this sense, body reserves are regulated as a trade-off between risk of predation and risk of starvation.

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References

- Bednekoff, P. A. & Houston, A. I. 1994a. Optimizing fat reserves over the entire winter: a dynamic model. *Oikos*, **71**, 408–415.
- Bednekoff, P. A. & Houston, A. I. 1994b. Avian daily foraging patterns: effects of digestive constraints and variability. *Evolutionary Biology*, **8**, 36–52.
- Bednekoff, P. A. & Krebs, J. R. 1995. Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology*, **9**, 457–462.
- Blem, C. R. 1990. Avian energy storage. *Current Ornithology*, **7**, 59–113.
- Clark, W. C. 1994. Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, **5**, 159–170.
- Ekman, J. B. & Hake, M. K. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. *Behavioral Ecology*, **1**, 62–67.
- Gosler, A. G., Greenwood, J. J. D. & Perrins, C. 1995. Predation risk and the cost of being fat. *Nature*, **377**, 621–623.
- Grubb, T. C., Jr & Pravosudov, V. V. 1994. Toward a general theory of energy management in wintering birds. *Journal of Avian Biology*, **25**, 255–260.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Houston, A. I. & McNamara, J. M. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica*, **24**, 205–219.
- Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B*, **341**, 375–397.
- King, J. R. 1972. Adaptive periodic fat storage by birds. *Proceedings of the 15th International Ornithology Congress*, pp. 200–217.
- Kullberg, C., Fransson, T. & Jakobsson, S. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proceedings of the Royal Society of London, Series B*, **263**, 1671–1675.
- Lilliendahl, K. 1997. The effect of predator presence on body mass in captive greenfinches. *Animal Behaviour*, **53**, 75–81.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology*, **67**, 749–755.
- Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attacks: a survey of North American birds. *Wilson Bulletin*, **105**, 1–47.

- McNamara, J. M.** 1990. The starvation–predation trade-off and some behavioral and ecological consequences. In: *Behavioral Mechanisms of Food Selection* (Ed. by R. N. Hughes), pp. 39–58. Berlin: Springer–Verlag.
- McNamara, J. M. & Houston, A. I.** 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheoretica*, **38**, 37–61.
- McNamara, J. M., Houston, A. I. & Krebs, J. R.** 1990. Why hoard? The economics of food storing in tits, *Parus* spp. *Behavioral Ecology*, **1**, 12–23.
- McNamara, J. M., Houston, A. I. & Lima, S. L.** 1994. Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287–302.
- Metcalfe, N. B. & Ure, S. E.** 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. *Proceedings of the Royal Society of London, Series B*, **261**, 395–400.
- Pravosudov, V. V. & Grubb, T. C., Jr.** 1995. Vigilance in the tufted titmouse varies independently with air temperature and conspecific group size. *Condor*, **97**, 1064–1067.
- Pravosudov, V. V. & Grubb, T. C., Jr.** 1997. Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behavioral Ecology*, **8**, 332–339.
- Rogers, C. M.** 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology*, **68**, 1051–1061.
- Rogers, C. M. & Smith, J. N.** 1993. Life-history theory in the nonbreeding period: trade-offs in avian fat reserves? *Ecology*, **74**, 419–426.
- Witter, M. S. & Cuthill, I. C.** 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 73–92.
- Witter, M. S., Cuthill, I. C. & Bonser, R. H. C.** 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Animal Behaviour*, **48**, 201–222.
- 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*. *Functional Ecology*, **9**, 568–574.