Fat reserves and perceived predation risk in the great tit, *Parus major*

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The fat reserves of small birds are built up daily as insurance against starvation. They are believed to reflect a trade-off between the risks of starvation and predation such that in situations of high predation risk birds are expected either to reduce their fat reserves in response to mass-dependent predation risk or to increase them in response to foraging interruptions. We assessed the effect on fat reserves of experimentally altering the perceived (but not the actual) risk of predation of wild great tits at a winter feeding site. The perceived predation risk was alternated between 'safe' and 'risky'. Increasing the perceived risk of predation involved 'swooping' a model sparrowhawk over the feeder at four unpredictable times each day, using a remote mechanism. We produce evidence that the experiment was successful in altering the perceived risk of predation. As predicted from the hypothesis of mass-dependent predation risk, great tits (*Parus major*) carried significantly reduced fat reserves during the 'risky' treatment. Furthermore, dominant individuals were able to reduce their reserves more than subordinates. As birds returned to feeders within seconds after a predator 'attack', the reduction in fat reserves cannot be attributed to an interruption in feeding.

Keywords: great tit; *Parus major*; starvation–predation trade-off; fat reserves; predation risk

1. INTRODUCTION

The fat reserves of small birds in winter can only sustain them for about one day (Blem 1976, 1990). They therefore show considerable circadian variation and the advantages to these birds of increasing their fat reserves in this season are self-evident. Until recently, it was assumed that increasing body-fat reserves inevitably increased survival probability (Fretwell 1969; King & Mewaldt 1981). However, there is growing evidence that this might not always be so, because an increase in mass resulting from elevated fat reserves is associated with a reduction in velocity or acceleration, angle of ascent and manoeuvrability in flight (Hedenström 1992; Witter *et al.* 1994; Metcalfe & Ure 1995; Kullberg *et al.* 1996), albeit only under certain circumstances (Kullberg *et al.* 1996; Kullberg 1998; Veasey *et al.* 1998). Therefore, the fat reserves stored by small birds are believed to reflect a trade-off between the risks of starvation and predation (reviewed by Witter & Cuthill 1993).

A number of recent studies have looked at the effect of predation risk on body mass in birds. Lilliendahl (1997) found that greenfinches, *Carduelis chloris*, lost mass when the perceived predation risk was experimentally increased, and Gosler *et al.* (1995) found that great tits (*Parus major*) were substantially heavier in years when their principal predator was absent. These results are consistent with a cost of fat storage. However, studies on the blackcap, *Sylvia atricapilla* (Fransson & Weber 1997), yellowhammer, *Emberiza citrinella* (Lilliendahl 1998), and tufted titmouse, *Baeolophus bicolor* (Pravosudov & Grubb 1998), found that body mass increased when the perceived predation risk increased. These results suggest that these birds might respond to the interruption to foraging caused by predators rather than to the predation risk *per se*, which is consistent with the 'interrupted foraging'

model of McNamara *et al.* (1994) under which birds gain mass when faced with increased foraging uncertainty.

In a study involving chasing coal tits, *Parus ater*, around an aviary, Carrascal & Polo (1999) found mass decreased as 'predation risk' increased. In addition, birds easily regained mass after a 1 h fast, making it unlikely that fat-reserve changes in predation experiments could be attributed to a reduction in the time available for feeding. Although these results are ambiguous because the increase in perceived predation risk cannot be separated from the increase in energy expenditure of the chased bird, Carrascal & Polo (1999) suggested that a slight decrease in the body mass of small birds may occur in the presence of predators, but if chased by predators this might be considerable.

So, in situations of high predation risk, birds might be expected to reduce their fat reserves. In addition, foraging strategies might differ between individuals of different dominance class since birds of different social status differ in feeding success (Pöysä 1988) and access to resources (Hogstad 1988; Koivula *et al.* 1994). Thus, the need to carry reserves as insurance against starvation should also differ. There is growing evidence (from a number of species) that subordinate individuals carry greater fat reserves than dominants (Ekman & Lilliendahl 1993; Gosler 1996; Hake 1996; Carrascal *et al.* 1998; Gosler & Carruthers 1999; Pravosudov *et al.* 1999). However, Lundberg (1985) and Piper & Wiley (1990) found no relationship between dominance and fat reserves in white-throated sparrows, *Zonotrichia albicollis*. This could be due to a different balance between the risks of starvation and predation, i.e. if the risk of predation was minimal, dominants might carry greater reserves than subordinates (Verhulst & Hogstad 1996). Indeed, Hake (1996) found that dominant greenfinches only carried higher fat reserves than subordinates in severe weather conditions. This could be explained if dominants reduced the food available to subordinates. Interaction between social dominance and environmental factors has also been

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Table 1. *Experimental design for the predation risk experiment*

date	trial	feeder treatment
2 November 1998 to 8 November 1998	pre-trial	—
9 November 1998 to 29 November 1998	1	risky
30 November 1998 to 20 December 1998	2	safe
4 January 1999 to 24 January 1999	3	risky
1 February 1999 to 21 February 1999	4	safe
22 February 1999 to 28 February 1999	post-trial	—

shown by Gosler & Carruthers (1999) who found that great tit fat reserves were negatively correlated with dominance in a dry, but not in a wet, winter.

Our study aimed to alter experimentally the perceived (but not the actual) risk of predation of wild great tits at a winter feeding site. Although a number of studies have previously attempted to increase the perceived risk of predation experimentally (Fransson & Weber 1997; Lilliendahl 1997, 1998; Pravosudov & Grubb 1998; Carrascal & Polo 1999; Van der Veen 1999), they have been conducted in aviaries and have often yielded inconclusive results. The only study undertaken so far on a natural population has been non-experimental (Gosler *et al.* 1995).

Our experiment addresses three questions: first, can the fat reserves of birds be manipulated by altering their perception of predation risk? Second, do great tit dominance classes differ in their fat reserves in relation to the 'perceived' risk of predation? Third, if fat reserves do vary with increasing perceived risk of predation, are they reduced, as predicted by the mass-dependent predation risk hypothesis, or increased, as predicted by the interrupted-foraging model?

2. METHODS

The experiment was undertaken during the winter of 1998–1999 as part of the long-term population study of the great tit in Wytham Woods near Oxford, UK (Perrins 1979; Gosler 1993). The experimental design involved alternating a peanut-feeder site between appearing to be predator 'safe' and predator 'risky'. The peanut feeder was positioned in a small clearing, surrounded by mixed deciduous woodland, where the shortest distance to cover was *ca.* 4 m. As the beech crop, which is an important natural food for the tits (Perrins 1979), was poor during this winter, it is likely that the feeder was an attractive food source. The perceived risk of predation was manipulated by presenting a flying plastic model of a sparrowhawk, the principal predator of great tits in Wytham, over the peanut feeder. The models measured *ca.* 40 cm from head to tail, with a 60 cm wing span, and were painted to resemble sparrowhawks (see §2(a)). The experiment was divided into four trials, each lasting three weeks, where the site was alternated between 'safe' and 'risky' (table 1). The feeder was filled from 1 October 1998 to attract sufficient birds prior to the experiment, and the first trial began five weeks later. Observations were made from a hide positioned nearby.

Birds were trapped by mist-nets between November and mid-March during both safe and risky trials. Mist-netting was carried out during the latter part of each trial to give birds time to adjust to the trial conditions. All individuals were given a unique colour

leg-ring combination consisting of one, two or three colour rings, plus a metal British Trust for Ornithology ring with a unique number. Birds were sexed and aged according to Svensson (1992) and fat in the tracheal pit was scored to the nearest half point on the six-point scale described by Gosler (1996). The time of processing was recorded to the nearest quarter hour passed, GMT. Dominance analysis was undertaken by age and sex class assuming that males are dominant over females, and adults are dominant over first years within each sex (Gosler 1996; Carascal *et al.* 1998; Gosler & Carruthers 1999).

Fat reserves covary with both mean temperature (at Oxford) and time of day (Gosler 1996). They were therefore standardized by regression using the equation

$$\text{fat} = 1.05 + (0.178 \times \text{time}) - 0.0368 \times \text{temperature} \\ (F_{2,832} = 80.24, p < 0.0001), \quad (1)$$

which explained 16% of the original variance. This regression was calculated from great tit data collected over three winters, two of which did not include the predation-risk experiment, to examine the background levels of fat reserves carried. The residual fat levels were compared across all great tits trapped during the experiment, and in a paired analysis for those individuals trapped during both safe and risky treatments, as birds that visited the feeder regularly should be more sensitive to changes in perceived predation risk. For birds trapped more than once during a treatment, the mean residuals of fat were used. Parametric statistics were used for analysis throughout as residual fat data did not depart significantly from a normal distribution (Gosler & Harper 2000).

(a) *Design of the mechanical predator*

The model predator consisted of a plastic box (60 cm × 60 cm × 100 cm) attached 6 m up a tree with a length of plastic-coated line running from the box, past the feeder, to a wire cage on the ground positioned some 35 m away in cover. The model predator was attached to the line by two pulleys on its back. The box housed the resting model predator, which made its 'attack' by swooping along the length of line and into the cage on the ground. A plastic curtain concealed the box entrance so that the model sparrowhawk could not be seen unless it was 'attacking'. The average speed of attack, 8.88 m s⁻¹, was within the range of real sparrowhawk attack speeds (Newton 1986).

The model sparrowhawk was maintained in the starting box by a length of fishing line that ran from the tail of the model to a fishing reel enclosed in another box on the ground. A catch was placed on the fishing reel, which, when released, allowed the model to 'swoop' past the feeder. The model sparrowhawks were returned to their starting positions by reeling in the fishing lines at the end of the day. The sparrowhawks were released remotely by using a wind-up alarm clock which, when activated, silently released the catch on the fishing reel, allowing the model predator to make its 'attack' without being associated with human activity.

During the risky trial, four model-predator attacks occurred each day. Four separate predator approach routes were constructed to reduce the disturbance to feeding birds through reeling back predators, and allowing predators to swoop at the feeder from four directions. Attack times and directions were randomized, but only one attack occurred in each direction each day. It is difficult to assess the background risk of sparrowhawk attack. However, Morse (1973) estimated that, on average, a tit

Table 2. Results of one-way ANOVAs showing the differences in three measures of latency to return to the feeder, or to resume the original feeding rate, between objects (sparrowhawk model or plastic bottle)

measure of latency	factor	d.f.	<i>F</i>	<i>p</i>	mean $\pm$ s.e.m. latency following sparrowhawk attack (s)	mean $\pm$ s.e.m. latency following bottle attack (s)
first bird	object	1,38	36.30	< 0.0001	39.15 $\pm$ 2.97	20.15 $\pm$ 1.06
first great tit	object	1,38	36.91	< 0.0001	64.55 $\pm$ 6.87	22.35 $\pm$ 1.04
original feeding rate	object	1,38	22.34	< 0.0001	151.60 $\pm$ 19.01	60.90 $\pm$ 2.62

flock in Wytham would suffer one encounter with a sparrowhawk each day. Our observations would suggest the same, so the four daily attacks by model hawks represented a substantial increase in perceived risk.

During both safe and risky treatments, daily visits were made at dusk (to minimize human disturbance) to fill the feeder. During risky trials, these visits were also used to reel back the sparrowhawks to their starting boxes and to reset the alarm clocks. The swooping-predator equipment was erected in September 1998, to ensure that it worked, and remained at the feeding site throughout the experiment, so that the only variable that changed during the trials was the presence or absence of model predators.

(b) Pre- and post-trial experiments

To test whether the model sparrowhawk increased the perceived risk of predation, rather than merely startling the tits, pre- and post-trial experiments were carried out that involved replacing the model sparrowhawk with a large (21) plastic bottle (as used by Lilliendahl 1997), which did not resemble a natural predator but was similar in overall size to the model sparrowhawk.

Pre- and post-trial experiments involved running the plastic bottle past the peanut feeder four times each day for seven days. Latency for the first bird of any species to return to the feeder, latency for the first great tit to return to the feeder and the time taken to resume the original feeding rate were recorded from the hide during both sparrowhawk trials and bottle trials. The original feeding rate was determined as 13 birds per minute (s.e.m. = 0.36), based on counts taken from 10 min periods over six days prior to the pre-trial experiment. We had also hoped to identify which individuals returned to the feeder first. However, in practice, birds visited the feeder so quickly that it was impossible to determine their colour-ring combinations.

3. RESULTS

Measures of latency following a model sparrowhawk 'attack' were significantly higher than those following a bottle 'attack' (table 2), indicating that model sparrowhawks were perceived as predators rather than as startling objects. In addition, there was no significant effect of date on any measure of latency (table 3), suggesting that the birds did not habituate to either object.

(a) Fat reserves during safe and risky treatments

In total, 39 great tits were trapped during the safe treatment and 30 during the risky treatment, with no significant differences between the treatments in the age or sex ratios of the birds trapped at the feeder (see figure 1 for totals). Out of these, 14 birds were trapped during

both feeder treatments. Across all birds, there was no significant difference between the residuals of fat reserves for safe (0.632 ± 0.205 , mean $\pm$ s.e.m.) and risky (0.077 ± 0.201) treatments, although there was a trend for fat to be reduced in the presence of a predator ($F_{1,67} = 3.60$, $p = 0.062$). An analysis of covariance (ANCOVA) incorporating both treatment and dominance status (covariate) for all birds found a weak treatment effect ($F_{1,65} = 3.79$, $p = 0.056$) and a highly significant dominance effect during the risky treatment ($F_{3,27} = 7.24$, $p = 0.009$) but not during the safe treatment ($F_{3,36} = 1.54$, $p = 0.218$) (figure 1). Interaction terms were omitted from these models as none were significant. Data have been analysed further at an individual level for those birds trapped during both safe and risky treatments ($n = 14$).

A two-way analysis of variance (ANOVA) carried out on residual fat data by treatment and individual bird, across birds trapped during both treatments, found a significant effect of treatment ($F_{1,13} = 9.69$, $p = 0.008$) and that individuals differed in their response to the change in treatment ($F_{13,13} = 2.55$, $p = 0.052$). However, individual differences could not be attributed to dominance class ($F_{3,10} = 0.29$, $p = 0.834$). Nevertheless, a trend for fat reserves to decrease with increasing dominance status (as described earlier in non-experimental studies by Gosler (1996) and Gosler & Carruthers (1999)) is suggested (figure 1), especially during the risky treatment, and the lack of statistical significance may be a type II error reflecting the small sample available.

4. DISCUSSION

All measures of latency were higher following a sparrowhawk attack than following a bottle attack, indicating that the experimental design successfully separated the effect of increased perceived predation risk from a startling effect. There was also no evidence that birds became habituated to the experiment, probably because treatments were only carried out for three weeks at a time.

Great tits carried significantly reduced fat reserves during the risky treatment (figure 1), and this was especially so for birds that remained near the feeder throughout the trials (trapped during both treatments). These findings are consistent with the prediction made by the mass-dependent predation hypothesis that carrying elevated fat reserves incurs a cost in the form of an increased risk of predation. Across all birds, all dominance classes carried less fat during the risky treatment except for first-year females. However, these followed the same trend as other dominance classes when only those

Table 3. *Product-moment correlations between three measures of latency and date*

measure of latency	object	<i>r</i>	<i>n</i>	<i>p</i>
first bird	sparrowhawk	0.055	40	0.734
	bottle	-0.185	40	0.253
first great tit	sparrowhawk	-0.054	40	0.741
	bottle	-0.199	40	0.218
original feeding rate	sparrowhawk	-0.077	40	0.639
	bottle	-0.119	40	0.464

trapped during both safe and risky treatments were analysed.

A significant effect of dominance on fat reserves was found for all birds trapped during the risky, but not the safe, treatment. Although there was no significant effect of dominance on fat reserves amongst the birds trapped during both treatments, the trend for dominant birds to carry the least fat, described for the unmanipulated population (Gosler 1996), is again supported during the risky treatment (figure 1). In addition, over both the whole data set, and in those trapped during both treatments, adult males (the most dominant class) carried significantly less fat during the risky treatment than first-year females (the least dominant class). However, during the safe treatment there was no significant difference. This is consistent with a situation in which food was in good supply (Gosler 1996).

In both the whole data set, and for the restricted set, it appears that the most dominant individuals (adult males) responded more to a change in predation risk than the least dominant individuals (first-year females). This is to be expected since the latter should be constrained in their choice of foraging times by the former.

The birds in our experiment reduced their fat reserves in the presence of a predator, presumably because under an increased risk of predation there is a cost to being fat. In this study, we found no evidence to support the interrupted-foraging model (McNamara *et al.* 1994; Lillendahl 1998), under which birds might gain fat in the presence of a predator because of the reduced probability of getting food. It could be argued that predator presence might prevent birds from storing more fat, i.e. that predator presence interrupts foraging to such an extent that feeding rates are reduced, constraining fattening. However, great tits took only 65 s overall to return to the feeder after a sparrowhawk attack (table 2). Therefore, the presence of a model predator reduced feeding by only *ca.* 4 min day⁻¹, which mostly represents time inactive in cover. As the reduction in fat reserves between treatments was as much as one fat-score unit, equivalent to about 0.4 g of fat (Gosler 1996), or more than 20% of a great tit's daily energy requirement (Gosler 1993), interruptions to foraging alone cannot explain the observed reduction in fat reserves.

Subordinates might carry greater fat reserves than dominants because they are the first to return to a feeder in a risky situation (De Laet 1985; Hegner 1985). However, they do so only a few seconds before dominants

Figure 1. Mean $\pm$ s.e.m. residual of fat reserve of great tits trapped during risky (shaded bars) and safe (open bars) treatments. (a) All birds (totals for safe treatment: 16 adult male, nine first-year male, 11 adult female and three first-year female; totals for risky treatment: 12 adult male, seven first-year male, eight adult female and three first-year female) and (b) birds trapped during both risky and safe treatments (totals: four adult male, five first-year male, three adult female and two first-year female). See §3(a) for statistical analysis.

and are displaced by the latter when feeding appears to be safe. Therefore, dominants lose only fractionally more feeding time than subordinates, which, again, cannot affect fat reserves to the extent observed (see above).

This is the first field-based experimental study to examine the effects of altering the perceived predation risk of a population of wild birds, and the first to separate perceived predation risk from energy expenditure. It demonstrates that, for the great tit at least, fat-reserve levels are set in response to the perception of predation risk rather than to actual predation events, which might incur energetic costs, or to interrupted foraging.

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