Coal tits, *Parus ater*, lose weight in response to chases by predators

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Theoretical models predict that birds should decrease their body mass in response to increased predation risk because lighter birds take off faster and are more manoeuvrable. We studied the effect of predation risk by chasing coal tits in large outdoor aviaries thus simulating an attempt to capture them. With this increase in predation risk, both perceived and actual, coal tits lost significantly more weight than in a control situation when they were not pursued. This pattern was attributable to a smaller gain in weight only during the day; nocturnal weight did not change in relation to diurnal predation risk. The lower daily weight gain was not consistent with predictions from models of interrupted foraging, but was consistent with predictions from risk adjustment models. Moreover, there was no difference in weight gain over 2-h periods that included a 1-h fast and those in which feeding was ad libitum, suggesting that coal tits could easily regain their body mass after a predator had interrupted their feeding. Our results therefore suggest that pursuit by predators leads to a decrease in the body mass of small birds.

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The survival value of fat reserves is governed by a trade-off between starvation and predation risk, and, as a consequence, birds normally maintain much lower fat reserves than the maximum possible (Lima 1986; Witter & Cuthill 1993). Although fat reserves serve as an important buffer against starvation in winter to cope with long nights and low temperatures (Blem 1990), there are costs associated with maintaining and/or carrying large fat reserves. One of these costs is related to predation risk: this may cause birds to carry lower fat reserves (Lima 1986; McNamara & Houston 1990), because take-off ability is dependent on body mass (i.e. the higher the fat level, the smaller the angle of ascent; Kullberg et al. 1996) and is crucial for escaping a predator. Moreover, heavier birds have higher wing loadings, and wing loading correlates negatively with flight speed (e.g. Norberg 1995 and references therein). Recently, theoretical studies have predicted that predation risk, in terms of reduced flight performance, increases with body mass (McNamara & Houston 1990; Hedenström 1992; Witter & Cuthill 1993). Heavier birds would be less manoeuvrable and slower, so less able to escape (Witter et al. 1994; Metcalfe & Ure 1995; Kullberg et al. 1996). Nevertheless, two recent studies found no measurable effect of fat loads on take-off

ability when small birds were subjected to increased predation risk (Kullberg 1998; Veasey et al. 1998). Furthermore, Kullberg (1998) and Kullberg et al. (1998) did not find that the natural increase in weight between dawn and dusk affected flight velocity, acceleration or angle of ascent during take-off in two tit species (willow tit, *Parus montanus*, and great tit, *P. major*).

Although theoretical models predict that body mass will change with predation risk, empirical data are scarce and the results are not consistent. Gosler et al. (1995) showed that British great tits weighed less in years when the density of their principal predator, the sparrowhawk, *Accipiter nisus*, was high. Similarly, Lilliendahl (1997) showed experimentally that, with an increase in perceived predation risk (a moving stuffed predator), greenfinches, *Carduelis chloris*, lost weight. On the other hand, in three recent experimental studies with stuffed predators (Fransson & Weber 1997 with the blackcap, *Sylvia atricapilla*, as prey; Lilliendahl 1998 with the yellowhammer, *Emberiza citrinella*; Pravosudov & Grubb 1998 with the tufted titmouse, *Baelophus bicolor*) birds gained weight when hawks were shown, contrary to the prediction of the trade-off between fat reserves and predation risk. These results are consistent with predictions of the interrupted foraging model (McNamara et al. 1994): birds will gain more weight when faced with the uncertainty of getting food. The birds might have treated the stuffed hawks as an interruption to their foraging (and remained in cover instead of feeding) rather than as

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an increase in predation risk. This effect of interrupted foraging caused by the appearance of a predator may overwhelm other predation effects (Lilliendahl 1998), and compensatory feeding when the predator is absent may cause birds to gain weight.

We tested the prediction that increased risk of predation results in lower body mass of a social, small passerine that usually forages hidden among foliage: the coal tit. To do this we performed an experiment in which the 'predator' pursued the prey, which escaped by flying and/or hopping through branches in an aviary. Previous experiments have tried to assess the effect of stuffed predators that were either still or moved in a limited way. Although these predators may be perceived as threats, they do not attack or pursue the prey. In our experiment, we chased the birds ourselves simulating an attempt to capture them (see Lilliendahl 1997 for an effect of human handling on weight loss in greenfinches). Control and experimental groups had experience with the same 'predator' (humans). Experimental birds saw and were pursued by the 'predator' during the day, while control birds heard the alert chirrups of experimental birds but did not see the 'predator' and were not pursued. We postulate that when birds are forced to flee from a predator's attack, manoeuvrability and maximum flight speed become relevant, leading to a weight loss to increase the birds' chances of avoiding the attacks (Witter et al. 1994; Metcalfe & Ure 1995; Norberg 1995; Kullberg et al. 1996). Consequently, diurnal weight gain should be lower in experimental birds, their weight should decrease, and night-time weight loss should be the same for control and experimental birds, as 'predator' attacks occurred only during the day.

METHODS

We captured 12 coal tits (seven adults and five juveniles) at the 'El Ventorrillo' field station (1500 m above sea level, 40°45′N 04°01′W, Sierra de Guadarrama, central Spain) in the second fortnight of December 1997. They were colour banded for individual identification and introduced into a large outdoor aviary placed in a small forest clearing of 15×20 m. The aviary was covered by translucent fibreglass panels to protect the birds from snow and rain, and divided into two cages of $2 \times 2 \times 2$ m separated by a thick, green, plastic net (birds in one cage could hear, but not see, the birds in the other). Each cage contained several pine and cedar branches fully covered by green needles, which the coal tits used for perching, roosting and sheltering from humans. We randomly assigned two groups of six coal tits to the two cages. Prior to the experiments, the birds were kept in the aviary cages with an ad libitum diet of peanuts and sunflower seeds, and water with vitamins, for 14–21 days. They were accustomed to our presence as we visited the cages every 2–3 days to change the water and the food. After this 2–3-week period of acclimation to the outdoor aviary, we performed the experiment during the following 2 weeks (see below). We believe our handling protocol and experimental design (the birds were accustomed to our presence prior to the experiment) were successful in separating the startling effect (i.e. the stress response to handling and acclimation) from the effect of increased predation risk.

The predation risk experiment was performed in the second and third weeks of January 1998. During these 2 weeks the coal tits could feed ad libitum on peanuts and sunflower seeds. In the first week of the experiment, one group of six coal tits experienced increased predation risk, while the other group was the control. In the second week, the 'control' group in the first week was under the 'experimental' treatment, and the 'experimental' group in the first week was treated as the 'control' group. Every experimental–control phase lasted 3 days as in previous studies (e.g. Pravosudov & Grubb 1998). We measured ambient temperature at 1200 hours GMT in the outdoor aviary (1300 hours local time). Average daytime ambient temperature was identical for the 12 coal tits in the combined experimental–control trials ($\bar{X} \pm \text{SE} = 5.7 \pm 0.95°$C, $N=6$ days). After the first experimental–control phase, the coal tits were left in the outdoor aviary without being disturbed, for 4 more days, before the second experimental–control phase.

We captured the coal tits with a butterfly-collecting net at the end of each day of the predation risk experiment (1703 hours GMT on average), and weighed them with an electronic digital balance (precision ± 0.01 g) within 15 min. The six birds belonging to each group were placed in a cloth box of 25 (high) $\times 20 \times 40$ cm. The two cloth boxes were placed together in the same nonheated room for the night. The ambient temperature of the 'sleeping' room remained constant throughout the study period ($\bar{X} \pm \text{SE} = 7.0 \pm 0.13°$C, $N=6$ days). Fifteen minutes before sunrise (0723 hours GMT on average), we weighed the coal tits and released them into their cages in the outdoor aviary.

To simulate a predator, we tried to capture the experimental coal tits by hand for 6 min on four occasions throughout the day (at intervals of 1 h 56 min; total of 24 min or 4.1% of daytime) on each of the 3 days. Since they were individually marked, we could chase each bird for the same amount of time. When the experimental birds were being chased, the control coal tits were left alone. They could not see us although they were alerted by the chirps of the experimental birds and interrupted their feeding. Both control and experimental coal tits were captured once every day (at dusk) for weighing, so experimental birds were chased five times per day (four experimental chases and one capture at dusk). We estimated weight loss after 3 days of chases as the difference in weight at dawn between days 1 and 4. Diurnal weight gain and nocturnal weight loss were calculated as the average change observed over the 3 control and 3 experimental days.

The experimental birds might put on less weight than the controls because they had ca. 50–60 min less time for feeding (24 min of pursuit, and ca. 30 min of feeding delay after we had pursued them; personal observation and data in Pravosudov & Grubb 1998). To investigate this possibility, we did another experiment. In the first fortnight of February 1998 we studied the coal tits' weight increase in 2-h periods in two treatments: 1 h of fasting

(all food removed in the first hour and food ad libitum during the second), and 2 h without fasting (with food ad libitum). The birds were put into metallic cages of 0.4×1.0 m $\times 0.5$ m high in groups of four (randomly assigned). We did not perform this experiment in the large outdoor aviary because coal tits store food (Cramp & Perrins 1993) and it was very difficult to control their access to stored food hidden in the roof, metallic walls and ground of the aviary, and among the pine and cedar branches. Seven days elapsed between the end of the predation risk experiment and the beginning of the food deprivation experiment. During this period the birds were allowed to acclimate to the new cages before the food deprivation experiment started. Water and food (peanuts and sunflower seeds) were provided ad libitum during both the settling period and the experiment.

All the birds were studied for 5 days in each of the two food availability conditions. The two treatments were interchanged during the 10 days of the food deprivation experiment (beginning with the food ad libitum treatment). Data from the 5 sampling days were averaged for each bird. The three metallic cages were in a naturally illuminated, nonheated room at a nearly constant temperature of 7°C. We captured and weighed the birds at 1100 hours GMT on each day, and immediately afterwards released them into the metallic cages. At 1200 and 1300 hours GMT on each day they were captured and weighed again. The birds were put back into the metallic cages after the weighing at 1300 hours GMT. After this experiment, the birds were put back in the aviary for 7 days prior to their release.

Individual birds cannot be treated as fully independent statistical units in the predation risk experiment because they were arranged in two cages of six birds each. To overcome this problem, we used a two-way ANOVA model with cage as a between-subject blocking factor and predation risk as a within-subject factor. With this ANOVA model the main repeated measures effect (control and increased predation risk) was estimated controlling for the main effect of group of birds. The same two-way ANOVA model was used for the data from the second experiment (three metallic cages as the levels of the blocking factor); we compared weight increase between 1100 and 1300 hours and between 1200 and 1300 hours GMT in the nonfasting situation with the 1-h fasting condition (working with averages obtained for 5 days in each treatment). This statistical approach provided results with the same significance as combining in a unique probability estimate the results of simple one-way repeated measures ANOVAs on the data obtained within each cage (single test of combined probabilities from independent tests of significance; Sokal & Rohlf 1981).

We released the 12 coal tits at the place of capture after the experiments. The experiments had no obvious effects on the birds' body condition apart from the weight changes described in the Results (i.e. they were in good body condition throughout the study period). We compared weights the first day the predation risk experiment began, with those at the end of the food deprivation experiment, 31 days later, at the same time of day (dawn).

The repeated measures ANOVA was not significant ($F_{1,11}=0.613$, $P=0.450$). Therefore, our experimental protocol did not induce any measurable decrease in the birds' body condition.

RESULTS

Predation Risk Experiment

Morning body weight decreased significantly more in the 3-day experimental predation risk treatment than in the control treatment (average decrease in body mass: $\bar{X} \pm SE=2.6 \pm 0.64\%$, $N=12$; Fig. 1a; two-way repeated measures ANOVA with the cage as a blocking factor: $F_{1,10}=9.64$, $P=0.011$; the blocking factor was not significant: $F_{1,10}=3.40$, $P=0.095$). The percentage of variance in this weight loss accounted for by the predation risk treatment was 15.8%. This weight decrease was attributable only to a lower average diurnal weight gain in the experimental predation risk treatment (Fig. 1b; two-way repeated measures ANOVA with the cage as a blocking factor: $F_{1,10}=20.80$, $P=0.001$; the blocking factor was not significant: $F_{1,10}=2.50$, $P=0.145$). The percentage of variance in diurnal weight gain accounted for by the predation risk treatment was 7.2%. Nocturnal weight loss did not differ significantly between treatments (Fig. 1c; two-way repeated measures ANOVA with the cage as a blocking factor: $F_{1,11}=0.67$, $P=0.43$; the blocking factor was not significant: $F_{1,10}=0.05$, $P=0.835$). In summary, when predation risk, both perceived and actual, was increased, coal tits lost significantly more weight than in the nonpursuit situation and this pattern was attributable to less weight gained during the day.

Food Deprivation Experiment

The weight gain between 1100 and 1300 hours GMT did not differ significantly between the 2-h period with 1 h of fasting ($\bar{X} \pm SE=0.10 \pm 0.010$ g/h, $N=12$) and the 2-h period with feeding ad libitum ($\bar{X} \pm SE=0.11 \pm 0.004$ g/h, $N=12$; two-way repeated measures ANOVA with the metallic cage as a blocking factor: $F_{1,9}=0.36$, $P=0.56$; the blocking factor was not significant: $F_{2,9}=0.66$, $P=0.54$). Nevertheless, in the last half of the trial the weight gain was faster after 1 h of fasting ($\bar{X} \pm SE=0.32 \pm 0.013$ g/h, $N=12$) than after 1 h feeding ad libitum ($\bar{X} \pm SE=0.11 \pm 0.007$ g/h, $N=12$; two-way repeated measures ANOVA with the metallic cage as a blocking factor: $F_{1,9}=300.39$, $P<0.001$; the blocking factor was not significant: $F_{2,9}=0.78$, $P=0.49$). Therefore, the coal tits could easily regain weight after a 1-h nonfeeding period. It is therefore unlikely that body mass changes in the predation risk experiment can be attributed to a reduction in time available for feeding.

DISCUSSION

Both theoretical models and experimental data suggest that birds are able to increase their intake rate and
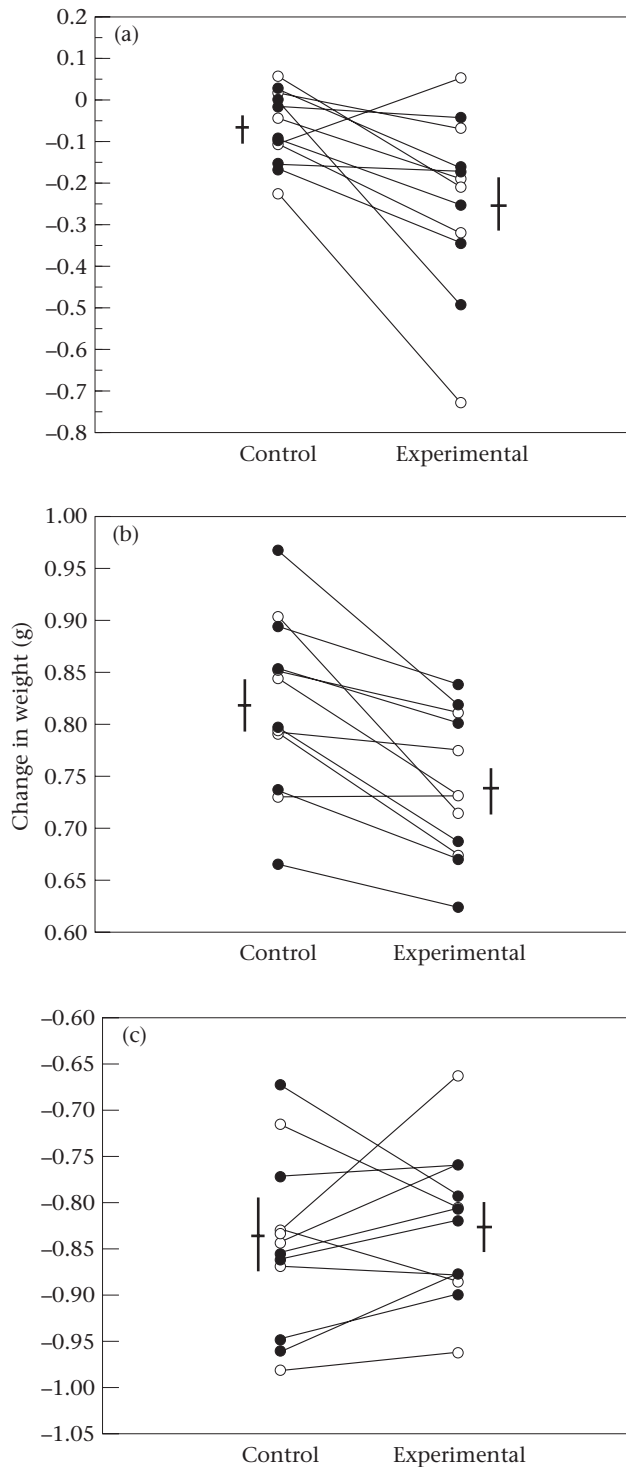
Figure 1. Average changes in weight of coal tits over a 3-day period. (a) Changes in morning weight. (b) Changes in weight during a day lasting 9 h 40 min. (c) Changes in weight during a night lasting 14 h 20 min. Twelve coal tits were used: six in the experimental treatment first, then in the control treatment (○); six in the control treatment first then in the experimental treatment (●). In the experimental treatment we chased each bird for four periods of 6 min/day for 3 days, simulating a predator; in the control treatment the birds were left alone. Lines join data points for each individual bird. Means±SE are also shown for each treatment.

compensate quickly for interrupted foraging (Bednekoff & Houston 1994; Bednekoff & Krebs 1995). The results of our food deprivation experiment support this prediction. Nevertheless, we did not detect any significant increase in weight after a foraging interruption of 1 h, time equivalent to that lost by the experimental coal tits when pursued by us. This result has two implications. First, it rules out the explanation that coal tits lost weight in our pursuit experiment because access to food was restricted. Second, it does not support the prediction from McNamara et al.'s (1994) model that body mass should increase when foraging is interrupted as a means of coping with the uncertainty of getting food. The discrepancy between this prediction and our results may lie in the different timescales involved: between different days in McNamara et al.'s (1994) model, and 2 h on the same day in our study.

We think the pursuit effect simulated in our experiment is relevant for coal tits in our study area. On many occasions we have observed coal tits fleeing from sparrowhawks, jays, *Garrulus glandarius*, tawny owls, *Strix aluco*, and red squirrels, *Sciurus vulgaris*. Moreover, predation risk affects their foraging and scanning behaviour (Mozetich & Carrascal 1995): they spend less time at feeders and scan for longer when foraging far from cover (see also Valone & Lima 1987; Lima & Dill 1990). Coal tits thus seem to be sensitive to variation in predation risk in the form of pursuits and regulate their weight in accordance with the perceived level of risk. The most likely proximate mechanism for the weight loss seen in our study is a voluntary decrease in food intake (Lilliendahl 1997), as diurnal weight gain was significantly lower with increased predation risk.

To date, three studies (Gosler et al. 1995; Lilliendahl 1997; this study) out of six have shown a significant effect of predation risk on the body weight of small birds. Results may differ because: (1) species differ in their response to predators (Fransson & Weber 1997; Lilliendahl 1998; Pravosudov & Grubb 1998); (2) the studies were done under different manipulative scenarios (large aviary in this study versus small cages of less than 0.5 m³ where flight was impaired); (3) predation risk levels varied between studies (from 4.1% of the daytime in this study, to 0.1%); and (4) the effect of predation risk on the regulation of body is very subtle. Accordingly, those experimental studies that have not simulated predator chases have failed to show the decrease in body mass (but see Lilliendahl 1997) predicted by theoretical models and observational studies (Lima 1986; McNamara & Houston 1990; Houston & McNamara 1993; Gosler et al. 1995). Our results show that a high predation attack rate can lead to a low, although detectable, decrease in body mass (2.6%). Therefore, any decrease in body mass caused by increased predation risk would probably be undetectable in an experiment (statistical type error II), if the predators do not pursue the experimental subjects, do not promote escape behaviour requiring flight (since weight determines take-off acceleration and manoeuvrability), and are present for only a short period.

Acknowledgments

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