

L.M. Bautista · S.J. Lane

Coal tits increase evening body mass in response to tawny owl calls

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Abstract Current theory predicts small birds should have a reduced body mass when daytime predation risk is high. However, the influence that nighttime predators might have on changes in body mass or daytime foraging behaviour has not been addressed. We therefore studied the effect of changes in perceived nocturnal predation risk on the body mass of captive coal tits. In a sound-proof room, eight coal tits were housed in individual cages and an experiment was performed in which the birds were subjected to two treatments. First, morning and evening body mass was monitored following nights that were quiet. Second, these parameters were measured following nights when the call of a tawny owl had been played once per hour. Evening body mass was 3% greater on days following owl-disturbed nights, but morning body masses did not differ between treatments. To ensure this result was a response to the owl calls per se, and not a general response to increased disturbance, a second experiment was necessary. Here the coal tits were exposed hourly to the calls of a nightjar, a non-predatory nocturnal bird, but no increases in body mass were observed compared to quiet nights. We suggest the coal tits increased body mass in response to owl calls to offset increased nighttime energy expenditure in attentive behaviour.

Key words Predation risk · Body mass regulation · Coal tit · *Parus ater* · Tawny owl · *Strix aluco* · Nightjar · *Caprimulgus europaeus*

Introduction

Small wintering passerine birds typically increase their body mass by 5–15% between dawn and dusk (e.g. Lehtikoinen 1987; Haftorn 1989, 1992; Metcalfe and Ure 1995; Kullberg 1998). Such increases in body reserves, mostly in the form of fat deposits (Chaplin 1974; Webster 1989; Blem 1990), are necessary to enable small birds to survive night-time periods of fasting without starving. However the weight attained at dusk is generally below that which is physiologically possible (Witter et al. 1994; Gosler et al. 1995), which suggests there is a price to be paid for maximising body reserves (Witter and Cuthill 1993).

Recent theoretical studies have suggested that a trade-off exists between the risks of starving and being preyed upon (e.g. McNamara et al. 1994). Since increased body mass can impair flight ability disproportionately, heavier individuals might be less proficient at escaping a predatory attack (Metcalfe and Ure 1995; Bednekoff 1996; Kullberg et al. 1996; but see Fransson and Weber 1997; Lilliendahl 1998; Pravosudov and Grubb 1998), although body mass increase must be large enough to induce a decrease of survival by predation (Kullberg 1998). In the presence of predators it is suggested that it is advantageous for small birds to be lighter and there is a good array of studies with similar findings and suggestions (i.e. Lima 1986; Lima and Dill 1990; McNamara and Houston 1990; Witter and Cuthill 1993; Bednekoff and Houston 1994; Witter et al. 1994; Bednekoff and Krebs 1995; Gosler et al. 1995; Lilliendahl 1997; Polo and Carrascal 1997; Adriaensen et al. 1998; but see also Kullberg 1998; Veasey et al. 1998).

In contrast, when diurnal predators are absent, small birds can afford to be heavier, thus reducing starvation risks, though maximum weights may still be constrained by other costs such as increased energy requirements associated with greater body masses (Witter and Cuthill 1993). This idea of mass-dependent predation implies a facultative decision on the part of the prey to maintain lower body masses when predators are in the area, even

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L.M. Bautista (✉) · S.J. Lane
Departamento de Ecología Evolutiva,
Museo Nacional de Ciencias Naturales, CSIC,
José Gutiérrez Abascal 2, E-28006 Madrid, Spain
e-mail: lmbautista@mncn.csic.es
Tel.: +34-9-1411328, Fax: +34-9-15645078

when food supplies are readily available. Lower body masses may also occur as a result of lost foraging time (Lima 1986; Rogers 1987; McNamara and Houston 1990; Cresswell 1998), although in the long term an increase in body mass is predicted to cope with future foraging interruptions (McNamara and Houston 1990).

The findings described above are specific to daytime circumstances and, in contrast, the response of small birds to the presence of nocturnal predators has not yet been addressed. Nocturnal predation risk on small birds is smaller than diurnal predation risk, but some owl species do forage occasionally on small birds (Mikkola 1983). For instance, tawny owls (*Strix aluco*) prey upon both young and adult birds from open nests, nest boxes, and holes that may be checked regularly, especially when snow cover or rain make other forms of hunting difficult (Beven 1965, 1969; Cramp and Perrins 1993). Indeed 70–80% of their diet might consist of small birds (Leppänen 1970; Mikkola 1983), although smaller percentages are more common (Uttendörfer 1939, 1952; see references in Mikkola 1983). If reducing body mass is a general phenomenon when perceived predation risks are greater, then weights of small passerines should also be lower following nights when a nocturnal predator is present.

However, an increase in evening body mass may be a suitable solution to increase nocturnal survival under predation risk. A decrease in body mass during the night may be the result of an increase in energy expenditure due to an increase in attentive behaviour. When a small bird is disturbed in the night, it is able to raise its body temperature and therefore its energy expenditure (Haftorn 1972; Reinertsen and Haftorn 1984). A higher body temperature implies a higher state of alertness and presumably a smaller risk of being surprised by predators. A larger evening body mass and a greater decrease in body mass during the night are expected after disturbed nights than after quiet nights. The energy used during the night may be a compromise between maintaining as high a state of alertness as possible and, at the same time, saving sufficient energy to survive the night. Birds prepared to survive the night period may derive an anti-predator benefit from using more of their reserves (Bednekoff et al. 1994).

Here we look for evidence of body mass changes in a small bird when perceived nocturnal predation risk is increased. We exposed coal tits (*Parus ater*) to the call of a tawny owl in a controlled laboratory environment. The coal tit is a small (8–10 g) woodland passerine that frequently forms part of the diet of tawny owls (López-Gordo 1974; López-Gordo et al. 1976), as well as of a number of other diurnal avian predators. Consequently it could be expected that foraging strategy of coal tits might be determined, at least partly, by a predation-starvation risk trade-off. Our aims were to determine the effects, if any, of owl 'presence' on dawn and dusk body masses of coal tits, and also on their food intake and daily activity.

General Methods

In a soundproof room located in the Natural History Museum (Madrid, Spain), eight coal tits were housed in individual cages-measuring 50×40×30 cm arranged such that the birds were visually, but not acoustically, isolated. The light-dark cycle was 9:15 (L:D). In the daytime period, the lights were brightened and dimmed gradually to simulate dawn and dusk. Birds were habituated to these conditions for 2 months prior to the start of this work. Each cage had two perches, but no shelter for the birds was provided. Fresh water via bottles was always available. Dry kitten cookies (The IAMS Company, Dayton, Ohio, USA), ground and sieved to small pieces of a constant weight of 0.04 g, were provided as food.

Temperature was controlled and ranged between 20°C and 25°C to remove the thermoregulation costs. Various tits (*Parus* spp.) are able to modulate their energy consumption during the night, decreasing their body temperature (Reinertsen et al. 1983; Reinertsen and Haftorn 1984, 1986; Bednekoff et al. 1994). Obviously hypothermia must have a cost since small birds avoid it under normal circumstances. Predation risk is a likely cost. Hypothermia is very likely to reduce the ability of a small bird to detect and avoid nocturnal predators such as owls (Bednekoff et al. 1994). The magnitude of an effect of nocturnal predation risk on body mass should be greater in cold nights than in mild nights, and therefore we performed a conservative test of our hypothesis.

Food was not available *ad libitum* in the experiment. In each cage, food pellets were available between 0930 and 1800 hours in a small tray below a hopper fitted to the cage wall. The hopper was connected to a computer-controlled pellet dispenser (Camden Instruments, Loughborough, UK) by a plastic tube. A light next to the hopper indicated to the bird that a food reward could be obtained if it pecked a key adjacent to the light. The light was illuminated for 10 s. When the bird pecked the key within 10 s, the computer switched off the light and delivered a food pellet. Elapsed time between the light turning off (either by itself or because the bird had pecked the key) and the beginning of a new cycle was 30 s. Maximum food delivery could reach 29.3 g/day in this system, 12 times higher than the mean daily intake of 2.3 ± 0.1 g/day established prior to this work. An Acorn RiscPC-600 microcomputer running Arachnid experimental control language (CeNeS Cognition 1990) controlled the stimulus events (light) and response contingencies (food delivery) and recorded quantity of food delivered per day. The birds were trained to obtain food using an autoshaping procedure (Staddon 1983) in a 2-month habituation period. Birds lived in a closed economy (Collier 1983), obtaining all their food through the experimental schedule.

Experiment 1: effect of owl calls

Methods

To test for the effect of nocturnal predation risk, the presence of a tawny owl was simulated using call playbacks. In field conditions owls are more likely to be detected aurally than visually. Owl calls were presented by a Sony CD player and a 10-W speaker placed circa 2 m from the cages. The intensity of the sound broadcast by the speaker was adjusted with a Realistic Sound Pressure Meter (Fast setting, A weighted) so that it reached the cages at 80 dB (range 78–82 dB, equivalent to the intensity of a call emitted by a tawny owl located at approximately 10 m). Tawny owls typically perform periodic calls during the night (Mikkola 1983; Cramp and Perrins 1993) and so we attempted to duplicate this by playing

the first call 5 min after the lights had been switched off and then setting the CD player to replay the call at intervals of 60 min until dawn (14 calls per night).

The trial lasted 16 days. For the first 8 days no owl calls were played, thereafter the birds were subjected to the calls on all subsequent nights. Each day the birds were caught at 0930 hours (dawn) and 1800 hours (dusk) and weighed to the nearest 0.001 g. Between 4 and 9 min were needed to complete this task depending on whether or not we were both present. These data were used to calculate diurnal body mass gain and nocturnal body mass loss for each individual. We also recorded daily food intake by subtracting spilled food (collected from the cage floors at 1800 hours) from the weight of food dispensed. Finally the activity of birds was recorded as the number of hops between perches and cage walls in a period of 10 min. We observed one bird per hour such that every bird was observed at least once in each hour of daylight in both treatments. To prevent undue disturbance these data were collected by watching the birds from outside the room through a one-way window.

Treatment differences of body mass, body mass change, intake rate, and activity were assessed with Wilcoxon signed rank tests (T^+). The occurrence of a relationship between body mass gain and food intake in either treatment was determined with Spearman rank correlation tests (r_s , Siegel and Castellan 1988). Data obtained in the last 5 days of each treatment were averaged to give a mean value for each bird: thus, $n=8$ birds in paired tests. We took probability values directly from statistical tables rather than rely on those provided by our software (Mundry and Fischer 1998). Results are presented as means and standard errors.

Results

Activity, measured as number of hops per minute, peaked during the first hours of the day and again at the end of the day (Fig. 1), but there was no significant difference between treatments (control: mean \pm SE=10.4 \pm 3.3 hops/min; owl call: 11.3 \pm 2.8; $T=23$, $P=0.55$, $n=8$). Although there was an apparent decrease of hopping activity at dawn and dusk when owl calls were played, the differences were not significant (first hour of the day, last hour or both hours pooled; all three Wilcoxon signed rank tests: $P>0.75$).

In both treatments foraging started immediately after the feeders were activated by the computer. Feeding in-

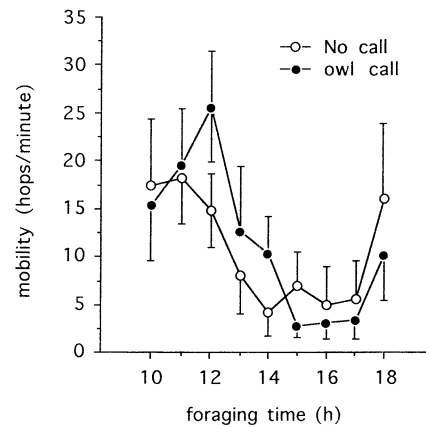


Fig. 1 Mobility (mean \pm SE) of eight coal tits with an owl call played during the night (filled symbols) and without the owl call (empty symbols) during the day

tensity was greatest in the first 30 min of the day, decreasing afterwards (Fig. 2). Coal tits requested food 19 \pm 1% (mean \pm SE) of the times food was offered in the owl treatment, but they used only 16 \pm 1% of the opportunities in the control treatment. The difference in the daily intake between control and experimental treatments (Table 1) was not significant ($P=0.08$). However, foraging intensity was greater during the first and the last hours in the day after an “owl night” (33.4 \pm 1.8% and 21.2 \pm 5.7%, respectively) than after a “control night” (22.8 \pm 2.1% and 14.6 \pm 9.4%, respectively; $T^+=36$, $P<0.01$, $n=8$, in both first and last hours).

Morning body masses did not differ between treatments, but the birds were significantly heavier at dusk on days following nights when owl calls were played (Table 1). Weight change during the night was significantly greater when owl calls were played (Table 1), which is suggestive of increased energy expenditure. Daily mass gains per bird were significantly correlated both with food intake in the control treatments ($r_s=0.976$, $P<0.01$, $n=8$) and in the owl call treatments ($r_s=0.643$, $P=0.05$, $n=8$).

To test for possible habituation to the owl calls over the 5-day duration of this treatment we performed a planned comparison in a repeated-measurements ANOVA test of body mass at dusk against number of days since the owl calls were first broadcast. Differences were not significant ($F_{1,7}=0.73$, $P=0.419$). However, one bird increased with day of treatment its response to the owl calls. When the

Table 1 Mean changes (\pm SE) in body mass and daily food intake of eight coal tits in control conditions and following night-time exposure to owl calls. T^+ and two-tailed P values are from Wilcoxon signed ranks tests (control vs. treatment)

Variable	Control	Owl calls	Difference ^a (%)	T^+	P
Daily food intake (g)	2.12 \pm 0.13	2.38 \pm 0.06	15.46 \pm 7.91	31	0.078
Morning body mass (g)	8.67 \pm 0.25	8.79 \pm 0.20	1.51 \pm 1.09	25	0.383
Evening body mass (g)	9.65 \pm 0.30	9.89 \pm 0.21	2.77 \pm 1.78	33	0.039
Nocturnal body mass loss (g)	-0.97 \pm 0.07	-1.06 \pm 0.05	10.96 \pm 5.32	35	0.016

^a Difference between control and owl calls=[(owl-control)/control] \times 100%. The differences are the averages of individual differences; hence they do not match the percentage change between the mean results

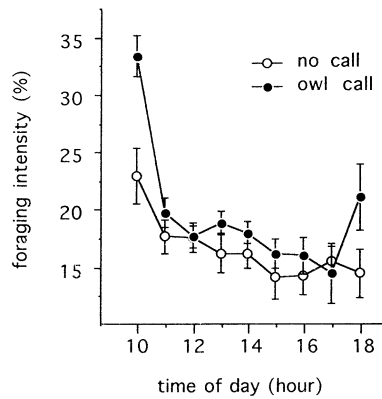


Fig. 2 Percentage (mean \pm SE) of food offered by the system each hour that was requested by eight coal tits on days with an owl call played during the night (filled symbols) and without the owl call (empty symbols)

anomalous individual was removed from the sample, the analysis detected a significant decrease in body mass at dusk ($F_{1,6}=8.14$, $P=0.029$) suggesting that most birds habituated to the simulated presence of a nocturnal predator.

Experiment 2: effect of nightjar calls

Methods

The effect seen in experiment 1 may have been a general response to night-time disturbance and not necessarily a specific reaction to the owl call. To eliminate this possibility we therefore performed an identical experiment except that the owl calls were replaced by those of a nightjar (*Caprimulgus europaeus*). Nightjars are insectivorous, nocturnal birds whose presence is of presumably little consequence to coal tits. Nightjars are present in the area where coal tits were trapped so these individuals may have prior experience of their call (Luis M. Carrascal, personal communication). A period of 30 days elapsed between experiments 1 and 2 during which the birds were maintained in an outdoor aviary (2 \times 2 \times 2 m).

Results

Food intake, morning body masses, and nocturnal mass losses did not differ between treatments (Table 2). All

Table 2 Mean changes (\pm SE) in body mass and daily food intake of eight coal tits in control conditions and following night-time exposure to nightjar calls. T^+ and two-tailed P values are from Wilcoxon signed ranks tests (control vs. treatment)

Variable	Control	Nightjar calls	Difference ^a (%)	T^+	P
Daily food intake (g)	2.41 \pm 0.30	2.54 \pm 0.38	3.98 \pm 3.62	25	0.383
Morning body mass (g)	8.58 \pm 0.11	8.57 \pm 0.12	-0.07 \pm 0.30	19	0.946
Evening body mass (g)	9.73 \pm 0.13	9.70 \pm 0.14	-0.36 \pm 0.14	32	0.055
Nocturnal body mass loss (g)	-0.83 \pm 0.03	-0.81 \pm 0.02	-2.26 \pm 1.37	27	0.250

^a difference between control and nightjar calls=[(nightjar-control)/control] \times 100%. The differences are the averages of individual differences; hence they do not match the percentage change between the mean results

though differences in evening body mass approached significance, the birds were heavier during the period when no calls were played. This is the converse of the result in experiment 1. When results were compared between owl call and nightjar treatments, nocturnal body mass loss was significantly greater in the former ($T=36$, $P=0.008$).

Discussion

Coal tits reacted to the playback of tawny owl calls by increasing their evening body masses. That they did not react to nightjar calls suggests they were able to discriminate between predator and non-predator calls. These results indicate that nocturnal predation risk may play a role in daily body mass regulation. Although a weight increase is counter to the expectations of the current theory of mass-dependent predation risk during the daytime, it may pay to be heavier in the context of nocturnal predation risk.

Speed and agility are likely to be important when flying routinely during the day in successfully escaping a predator; and a number of theoretical and empirical studies have predicted or shown that increased mass will reduce flight performance (Pennycuik 1975, 1989; Norberg 1990, 1996; Metcalfe and Ure 1995; Kullberg et al. 1996), perhaps making birds more vulnerable to predation. Some studies have not found the expected benefit of a reduced body mass in escape flights as opposed to routine flights (Kullberg 1998; Veasey et al. 1998). These studies suggest that the advantage of being lighter when escaping from predators does not operate when the bird is motionless. Furthermore, at night a rapid escape flight would be a risky strategy for avoiding owl predation as injuries could be sustained through collisions with unseen obstacles, and the probability of being detected is increased when the bird is flying. Small birds most probably escape hunting owls through concealment, perhaps by retreating into a nook in a trunk or into denser foliage (Cramp and Perrins 1993). However, being awake and vigilant may be a necessary prerequisite to allow this response, but at the cost of increased energy expenditure through increased activity and sleep loss (Reinertsen 1996). This would account for the greater nocturnal body mass change observed in our study. When owls are present in an area we suggest small birds will compensate for increased energy expenditure in vigilant activities by small but significant increases in evening body mass. With our experimental setup we cannot

exclude stress as another factor accounting for the body mass increase when owl calls were played. The coal tits experienced tawny owl calls from just 10 m away repeatedly during the nights. The closeness of the "owl" together with a lack of shelter in the cages may have been a very stressful situation, and stress is a well-known factor causing a body mass reduction. Therefore the results may be due to an anticipation of stress instead of an anticipation of a higher predation risk. The nightjar treatment suggests that the coal tits do in fact discriminate between stress and higher predation risk.

Coal tits could achieve a greater body mass at dusk by either reducing their daytime energy expenditure or increasing energy intake or both. Since they were similarly active in both treatments we reject the first of these mechanisms. The daily shape of foraging activity was also similar in both treatments with a peak at the beginning of the day. However there was a difference in the level of food requested throughout the day. Overall, coal tits requested more food during the period owl calls were played. This seems to be the likely mechanism in which greater body mass was attained despite the fact that the difference in actual daily food intake between treatments was not significant ($P=0.078$).

Although our study was the first to suggest a potential link between night predation risk and daytime foraging strategy, we are not the first to show that small birds increase body mass in response to predation risk. For example, two other studies also found small increases in body mass when perceived predation risks were increased, though both were in daytime situations. Sixteen captive yellowhammers *Emberiza citrinella* increased evening body mass from 28.1 g to 28.4 g on average (0.96%, see Fig. 2 in Lilliendahl 1998) after a stuffed sparrow hawk *Accipiter nisus* was displayed to the birds in the morning. In another study, seven tufted titmice *Baeolophus unicolor* increased evening body mass from 22.8 g to 22.9 g on average (0.69%, see Fig. 4 in Pravosudov and Grubb 1998) after they were exposed to a mount of a sharp-shinned hawk *Accipiter striatus*. Lilliendahl (1998) proposed the yellowhammers increased their body mass in preparation to leave a dangerous area and Pravosudov and Grubb (1998) suggested increases in titmice weight occurred to cope with periods of interrupted foraging. These studies, and the results presented here, suggest that weight reductions are not necessarily a general phenomenon in small birds in response to predator presence. It is conceivable that under some circumstances small increases in mass are appropriate to survive the night (Reinertsen and Haftorn 1984; Bednekoff et al. 1994). In winter small tits can enter a state of hypothermia during the night to save energy (Reinertsen 1996). Hence it is expected they increase evening body mass as a response to high predation risk in a larger proportion than our results suggest. Moreover, several authors have also suggested that small gains in body mass have little impact on flight performance (Kullberg 1998), particularly when birds are alarmed (Veasey et al. 1998), casting doubt on the mass-depen-

dent predation risk hypothesis when birds are motionless during the night. An increase of evening body mass may be an adaptive response to increased night predation risk. The results of this study should serve to update the theory of optimal body mass of small birds (e.g. McNamara and Houston 1990) living under constant predation risk (i.e. diurnal and nocturnal).

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