



Effects of wing area reduction on winter body mass and foraging behaviour in coal tits: field and aviary experiments

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Theoretical and experimental evidence suggests that an increase in flight costs will decrease flight performance, and that birds should trade-off the benefits of body reserves to minimize these costs. Alternatively, birds could avoid starvation by increasing food intake, thereby maintaining body reserves, and/or decreasing flight activity to compensate for the greater per unit flight costs. To test the effect of increased flight costs on body mass regulation and on flying and feeding activity, we experimentally manipulated wing area in a free-ranging wintering population of coal tits, *Parus ater*, and in captive birds living in a less restrictive environment (large outdoor aviaries). In the field, body mass decreased when wing area was reduced, but heavier birds lost more weight than lighter birds as a consequence of an allometric increase in flying costs. However, wing area reduction had no effect on body mass in the aviaries. Birds also flew less when wing area was reduced and those with higher wing loadings decreased flying frequency more markedly. We suggest that the goal of small resident birds living in a Mediterranean montane climate would be to maintain daily fat reserves within narrow limits during autumn and winter, even under contrasting ecological conditions.

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Nonmigrating small passerines at high latitudes acquire fat reserves in daily and seasonal routines in response to harsh winter conditions ('winter fattening'). Most of the fluctuation in body reserves may be explained by circadian variation in fat stores, as daily body mass gain accounts for 5–12% of total body mass (Lehikoinen 1987; Haftorn 1989, 1992; Polo & Carrascal 1997; Broggi et al. 2003). These reserves are used on a short-term basis to cope with high metabolic costs derived from low winter temperatures, reduced and unpredictable food availability and long winter nights (Blem 1990). Nevertheless, body mass gain involves costs dependent on the level of fat reserves (Gosler et al. 1995; Gosler 1996; Lindström & Rosén 2003; Ydenberg et al. 2004; reviewed in Witter & Cuthill 1993 and references therein). Thus, the level of fat reserves carried throughout the day, and reached at dusk, should amount to a compromise between realized costs and future benefits (Lima 1986; McNamara & Houston 1990).

Among the costs of carrying fat reserves is the interaction between the metabolic cost of flight and body mass. Flight is the most energetically expensive activity in

small birds (Pennycuik 1990; Norberg 1995). The ascending force generated by the wings is directly proportional to the wing surface and inversely proportional to body mass. Therefore, any change in wing loading (via body mass or wing area) will affect both the power required to fly and the speed of flight (Pennycuik 1990; Norberg 1995). An increase in body fat deposits will increase wing loading, with a consequent decrease in flight performance (Witter et al. 1994; Lee et al. 1996; see, however, Kullberg 1998; Kullberg et al. 1998; Veasey et al. 1998) and an increase in the power required for flight (Norberg 1995).

With increased uncertainty about access to food resources it should be advantageous to reduce activities such as flight that are more costly in terms of energy expenditure, thus minimizing energetic demands (Dall & Witter 1998). Nevertheless, reducing flying would decrease the area explored while foraging, lowering encounter rates with potential food patches, and therefore would increase the risk of starvation (Naef-Daenzer 2000). To survive winter conditions, animals must explore their environment, to familiarize themselves with the changing location of food and water sources. None the less, a high exploration rate may be costly in terms of the flight activity it entails and the greater exposure to predators (Ekman & Hake 1990; Witter & Cuthill 1993). In these conditions, the maintenance of an appropriate level of fat reserves may

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limit the risk of starvation when sufficient food is not found quickly (Blem 1990). Several empirical and experimental studies have established the relation between the level of internal reserves and costs dependent on weight (e.g. predation risk: Lima 1986; Gosler et al. 1995; Carrascal & Polo 1999; Piersma et al. 2003; Ydenberg et al. 2004; Macleod et al. 2005; metabolic costs: Lindström & Rosén 2003), as well as between body fat and the risk of starvation (Bednekoff & Krebs 1995; Dall & Witter 1998). Nevertheless, few field studies have explored the trade-off between these two opposite strategies, allowing for the testing of the predictions of theoretical models (McNamara & Houston 1990; Houston et al. 1997).

We analysed the variation in the average daily body mass of a wintering population of coal tits, *Parus ater*, living in a mountain area of central Spain. We manipulated the coal tits' wing area, and thus wing loading, to test the effect on body mass. Although we did not manipulate flight costs per se, we assume that flight costs are likely to increase after a reduction in wing area (Norberg 1990; Pennycuik 1990). We studied a free-ranging population, living in a coniferous forest, to understand processes involved under natural conditions of ecological relevance (i.e. natural food resources, interactions among tits, predation risk). Because a control for food ingestion and flying activity is not possible under wild conditions, we also studied captive birds in large outdoor aviaries.

There are two possible strategies regarding reduction of wing area and, thus, an increase in wing loading. (1) If birds maintain their food encounter rate (i.e. they choose to maintain a constant food intake rate), they should not modify exploring activity, and they should maintain flying rate. They will then incur greater flying costs because of the diminished wing area, resulting in a lower level of internal reserves (Cresswell 1999), and thus body mass, because a similar food intake is associated with a higher energy expenditure. (2) On the other hand, if body mass remains unchanged after the reduction in wing area birds would be seeking to maintain a stable reserve level so as not to increase the risk of starvation. This would oblige them to increase food intake rate to compensate for increased flying costs (reviewed in Witter & Cuthill 1993). If resources were predictable in the environment, birds might maintain constant levels of fat reserves being less active. Thus, the increasing risk of starvation caused by a reduction in foraging activity would be compensated for by more predictable access to food. This would minimize the energetic flying cost during daytime. Therefore, we need to know more about the range of possible behaviours adopted and their ecological correlates, and whether they are compensatory.

Furthermore, if individuals maintain isometric relation in their body proportions (i.e. variation in the size of birds does not imply a change in shape in adult birds of the same species), the larger birds would fly less efficiently because wing loading increases with the power 0.333 of weight (McMahon & Bonner 1983). Therefore, do coal tits lose mass when wing area is reduced and is the decrease in mass state dependent?

METHODS

Study Area and General Procedures

The study area lies in Madrid Province, central Spain ('El Ventorrillo' field station, 1500 m above sea level, 40°45'N, 04°01'W, Sierra de Guadarrama). The area is a 6-ha mixed forest dominated by Scots pine, *Pinus sylvestris*, chestnut, *Castanea sativa*, maples (*Acer* sp.), poplars (*Populus* sp.) and Pyrenean oak, *Quercus pyrenaica*. During the end of autumn and in mid-winter the ambient mean temperatures are regularly below zero at dusk (average -1.0°C , range -5.6 to 3.5°C) and a little above zero at noon (average 2.4°C , range -4.5 to 6.7°C ; data obtained during sampling days). There is snow cover on a quarter of all days. Daylength at the winter solstice is 8.8 h.

Six rectangular funnel traps (40×60 cm and 40 cm high) were placed in the area, hanging from branches at 1.5 m above the ground. The funnel traps had an extension area of 10 cm at the front which was essential for birds to find the entrance hole once the trap was set. The metal framework was covered on all sides, except the base, by 1.5-cm wire-mesh net. The wire-mesh net on the bottom was 0.5 cm, allowing the birds to walk more easily on it. The funnel (8×8 cm) was on the bottom at the front, leading 20 cm into the trap. The end of the funnel was closed but roofless, so that the birds could get into the trap through the small (8×8 cm) hole in the funnel roof. Once in the trap, the birds could not find the way out. A translucent plastic sheet covered the roof of the trap to avoid birds getting wet on rainy days. The opposite end of the frontal part of the trap had a 1.5-cm meshed door of 40×40 cm that could be raised, allowing the birds freely to use the feeders in the trap; or it could be lowered, so that the birds could enter the trap only through the funnel. On this door, a cloth sleeve was attached to allow the researcher to put his hand and arm in to catch the birds. Funnel traps were baited with two cylindrical feeders (made of 4.5-mm wire-mesh net) containing husked peanuts and hanging from the trap roof in the middle of the trap. Thus, birds could use them as a supplementary source of food. For more details on this kind of trap see Senar et al. (1997).

Traps remained opened on noncapture days, and were closed on capture days from dawn to dusk. They were checked every 20–40 min (30 min on average). If birds were inside the trap, the researcher slowly approached it and caught the birds through the cloth sleeve. The birds were immediately put into a cloth collector whose interior was in complete darkness. We ringed and weighed the birds in a nearby house (30–100 m away), releasing them immediately after. The time elapsed between the capture and the release was 5–10 min depending on the birds captured (3–5 min outdoors and 2–5 min inside the house). No bird died during the capture procedure.

Two large outdoor aviaries were placed in the study area within small forest clearings. The aviaries were divided into five and four cages, respectively, of 10.5 m^3 (1.75×2 m and 3 m high), separated by a thick, green, plastic net (birds in one cage could hear, but not see, the birds in the other). Each cage contained a nestbox and several pine and cedar branches fully covered by green

needles, which the birds used for perching, roosting and sheltering. Aviaries were covered by translucent fibreglass panels to protect birds from snow and rain.

Field Study

The field study was conducted by means of recaptures of 17 coal tits from 1 November 1996 to 31 January 1997. In the first capture, birds were colour banded for subsequent individual identification, if not already banded, weighed with an electronic balance (+0.01 g), and their tarsus and wing lengths were measured with a digital calliper (+0.01 mm).

Birds were routinely captured and weighed throughout this 3-month period. We recorded body mass, date, time of day (0700–1700 hours GMT) and ambient temperature for each bird capture. After 5 December we plucked the right and left seventh primary feathers of each bird before releasing it. This manipulation was equivalent to a reduction of 5–7% in wing area (Polo 1999). Average number of captures per bird before wing area manipulation (control treatment) was 5.9 (range 1–39). The recapture period in the experimental treatment spanned from 5 December to 31 January. The average number of captures per bird in this period was 9.0 (range 2–37). As coal tits in the same area and season began to regenerate primary feathers 20–30 days after they were plucked (Polo & Carrascal 1998), body masses were obtained within the 30-day period after the removal manipulation.

The main concern in our experimental approach was the lack of a control in the field experiment, since all birds were first unmanipulated and then manipulated: treatment is thus confounded by season (i.e. date). To improve our field experiment, we used data from coal tits measured and weighed in the previous winter (November 1995 to January 1996; birds were caught 4–63 times). These birds thus formed a 'control' group. The data for these 2 years are part of a long-term study on body condition and winter survival in a Mediterranean population of coal tits. Of the 17 coal tits manipulated in the second winter, 12 had been repeatedly captured and weighed in the autumn–winter of 1995–1996. Therefore, the final sample size in our field experiment was reduced from 17 to 12 birds. For each bird, we divided the body masses recorded in the first autumn–winter (1995–1996) into two groups, recorded before and after 5 December, which was the date on which we removed the same bird's feathers in the experimental year 1996–1997. The average dates for capture and weighing of individuals matched in the treatment and control years.

We used a mixed ANCOVA model to analyse body mass variation in the wild (dependent variable) in relation to date of capture (Day, included as number of days from the winter solstice, 21 December), time of day, ambient temperature at noon (covariates), coal tit identity as a random factor (Bird, $N = 12$), and wing area reduction treatment (Treatment) and period before–after manipulation date (Before–After) as fixed factors. We used the unconstrained parameters model to test significance of the fixed effects in the mixed ANCOVA (Voss 1999; Quinn

& Keough 2002). In this approach, the mean square (MS) of the interaction terms Bird * Treatment and Bird * Before–After are used, respectively, as the MS error terms of the main effects Treatment and Before–After; for the main effect Bird and the interaction terms Bird * Treatment and Bird * Before–After, the whole interaction Bird * Treatment * Before–After was used as the error term. Finally, the error terms for the effects of covariates were the interactions of each covariate with the random factor Bird. This analytical procedure is conservative, because it solves the problem of inflated sample sizes by reducing the degrees of freedom of the error terms and avoids pseudoreplication (i.e. the proper sample unit for the fixed effects is the individual bird and not every weight obtained in the field). Adjusted body masses for each bird and fixed factors (controlling for the effects of date of capture, time of day and temperature at midday) were obtained from the previous ANCOVA model. The differences between mean adjusted body masses before and after wing area reduction were regressed against tarsus length in both the control and manipulation years, to test for allometric effects in body mass regulation.

Aviary Experiment

Nine coal tits were captured on 8 October 2001. We measured and colour banded them by using the same protocol as in the field study (see above). We also drew the wing perimeter by placing the ventral side of the extended right wing on a sheet of paper. Wing area was obtained from these drawings by scanning and measuring them with Image Tool for Windows 1.28 (The University of Texas Health Science Center, San Antonio, TX, U.S.A.). Individuals were randomly housed in nine aviary cages and maintained with an ad libitum diet of water with vitamins, dry kitten cookies, peanuts, sunflowers and pine seeds.

After a week to allow the birds to acclimatize to the aviary cages, we reduced wing area by taping primary remiges six and seven together ('experimental' treatment) in four of the nine coal tits. The taped remiges were positioned such that their rachises lay side by side. This is the normal spatial relationship of the three feathers when the wing is folded. We then cut a rectangular notch from the feather vanes on each side of the rachises along the feather shaft. Then, a 2-mm strip of tape was attached to the two remiges within the notched area, around the rachises. This wing manipulation was reversible and equivalent to a reduction of 5–7% in wing area in the field study. The remaining five coal tits ('control' birds) also had the notch from the feather vanes cut, but no tape was added (i.e. no wing manipulation was done). See figure 1 in Senar et al. (2002) for more details and a picture of this manipulation.

Prior to experimental data recording, all birds in the control and experimental groups spent 4 days adapting to the new conditions in their cages. After this period, all the birds were studied for the next 3 days. At sunset of the fourth day of acclimatization, and for the next 3 days, we caught both control and experimental coal tits at, on average, 1635 hours GMT. We used a butterfly-collecting

net to ensure no damage to wing and tail feathers during the capture. Immediately afterwards, birds were housed in two cloth (cotton) boxes (0.2 × 0.4 m and 0.2 m high) without food and water, where they spent the night at an ambient mean temperature of 12.8°C (range 10.8–14.3°C). Birds were weighed at sunrise (0620 hours GMT on average) and released in their respective aviary cages. These body mass measurements allowed us to estimate daily body mass gain (body mass at dusk minus that at dawn).

We also measured feeding and flying activity by recording the number of visits to the feeders and the number of flights longer than 0.5 m made by each bird within 10-min sampling periods. We observed individual activity by sitting immobile in front of the aviary at a distance of 5–7 m. We waited for 10 min before recording data, enough time for birds to resume their routine activity. Six to nine samples per day were obtained throughout the daytime for each bird (20–29 10-min samples per tit).

In the second week we untied the sixth and seventh primaries in the experimental group and manipulated the wings in the control group by taping the sixth and seventh primaries together. The experimental group of birds thus changed to the control treatment, while the previous control bird group changed to the experimental treatment (within-subjects approach). We monitored the ambient temperature at noon each day throughout the study period.

We also applied a mixed-model ANCOVA to analyse body mass at sunset and daily body mass gain in the aviary (dependent variables) in relation to midday temperature (covariate), bird identity (random factor) and treatment (fixed factor). Feeding and flying rates (visits to feeders and flights/min, respectively) were also analysed in relation to bird (random factor), treatment (fixed factor) and cubic polynomial effect of time of day (covariates; to account for possible nonlinear circadian rhythms).

To control for treatment order we had two orders of treatments (the experimental trial in the first week and the control treatment in the second week in four coal tits; first control and second experimental in the other five coal tits). Although we did not anticipate any significant treatment order effect, we tested for it in the aviary experiment by including 'treatment order' in the mixed ANOVA models. The order of treatments (first week–second week) was included in the mixed ANOVA models to analyse its effect, together with bird identity. The combined effect of the order and the treatment per se could not be tested because of lack of data (i.e. control and experimental trials were not carried out simultaneously in the first and second weeks, see above). The influence of treatment order was not significant on the four dependent variables analysed in the aviary experiment ($P > 0.15$ in the four mixed ANOVAs with 1,8 *df* for the term 'order of treatment').

Ethical Note

Coal tits were in good body condition throughout the study period, as their body masses did not fall below those observed in the field (see Polo & Carrascal 1998 for

a comparison with birds in the wild). After the experiment, coal tits were released at the place of capture. We compared body weights the first day of the experiment with those the day when birds were released (15 days later at the same time of day). A repeated measures ANOVA showed that coal tits on average gained 0.15 g (1.7%) throughout the study period ($F_{1,8} = 5.87$, $P = 0.042$). This small variation in body mass at dawn was consistent with the winter fattening strategy when daylength is becoming shorter (e.g. Lehikoinen 1987; Haftorn 1989). The feather manipulations did not appear to impair the flight of the birds when they were released. Wild birds during moult often simultaneously lose one or two feathers, and they have the ability to adjust and cope with such events (see below). Furthermore, the proportion of experimental birds recaptured in the next winter after the year of the treatment (i.e. feather plucking) was not different from the typical 'surviving' proportion between successive years. There was no evidence that the probability of catching birds in the outdoor aviaries depended on whether they had the feathers taped. Furthermore, many birds with the primary feathers plucked were repeatedly caught in the funnel traps in the field experiment. Therefore, (1) our feather manipulation cannot be considered a severe and unusual situation, (2) we do not think that plucking or taping the remiges introduced a bias in probability of capture, and (3) we assume that our experimental procedures did not have deleterious effects on the birds. The study was approved by the Spanish Ministry of Science & Technology.

RESULTS

Body Mass Changes in the Wild

A mixed-model ANCOVA (all effects: $F_{50,367} = 38.23$, $P < 0.001$; 83.9% of the variance accounted for; Table 1) shows that time of day (positive relation) and midday

Table 1. Results of a mixed-model ANCOVA of coal tit body mass in the wild in relation to date (Day), time of day and ambient temperature at noon (covariates), bird identity (Bird, $N = 12$, random factor), experimental reduction in wing area (Treatment, fixed factor) and period within year before and after the manipulation was made (Before–After, fixed factor)

	Sum of squares	<i>df</i>	<i>F</i>	<i>P</i>	% Variance
Day	0.17	1,11	2.80	0.122	0.2
Time of day	13.67	1,11	321.62	<0.001	16.9
Midday temperature	1.39	1,11	17.84	0.001	1.7
Bird	17.39	11,11	20.07	<0.001	21.4
Treatment	0.03	1,11	1.79	0.208	0.0
Before–After	0.01	1,11	0.35	0.564	0.0
Bird * Treatment	0.20	11,11	0.24	0.988	0.3
Bird * Before–After	0.39	11,11	0.45	0.898	0.5
Treatment *	0.39	1,11	4.94	0.048	0.5
Before–After					
Bird * Treatment *	0.87	11,367	2.21	0.013	1.1
Before–After					

The effect sizes are also given as % of variance explained. For more details on error term definitions, see Methods.

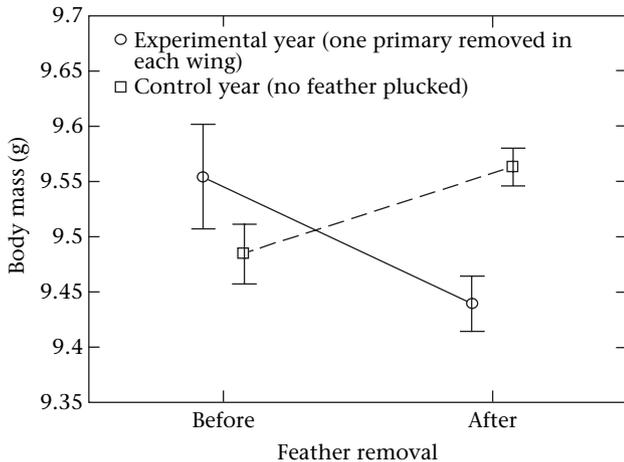


Figure 1. Mean \pm SE body mass of coal tits in the wild before and after the date of feather removal in the control year (no feather plucked) and experimental year (one primary removed in each wing). $N = 12$ birds (using mean adjusted body masses derived from the ANCOVA mixed model in Table 1).

temperature (negative relation) had significant effects on body mass. Clear interindividual differences in body mass were observed accounting for most of the explained variance. The main fixed factors Treatment and Before–After were not significant, although their interaction reached significance, showing that the change in body mass before and after the manipulation date (5 December) had a different effect in the control (feathers not plucked) and experimental (the same birds with one primary removed in each wing) groups. Body masses were not different in the control and experimental years before feather removal (planned comparison: $F_{1,11} = 0.86$, $P = 0.373$; Fig. 1). However, when birds were manipulated (i.e. wing area reduced) body mass decreased significantly with respect to the control situation (planned comparison: $F_{1,11} = 7.86$, $P = 0.017$; Fig. 1). Finally, there was a significant three-way interaction, denoting marked interindividual differences in the changes in body mass between treatment years and periods within a year.

Tarsus length was correlated with the decrease in body mass after wing area reduction (Pearson correlation: $r_{10} = 0.657$, $P = 0.020$; Fig. 2), but there was no significant relation between tarsus length and temporal change in body mass in the control group ($r_{10} = -0.037$, $P = 0.909$).

In summary, on average body mass decreased when wing area was reduced (i.e. flying costs probably increased), and the magnitude of this effect differed between birds: heavier birds lost weight, while light birds did not change body mass.

Body Mass Changes in Aviaries

Body mass ranges of the aviary birds were 8.66–9.74 g and 8.63–9.73 g at the beginning of the day and 9.56–10.56 g and 9.50–10.50 g at sunset in the control and experimental situations, respectively. Body mass at sunset was not significantly affected by the experimental decrease in wing area (Table 2). Nearly all variance in this

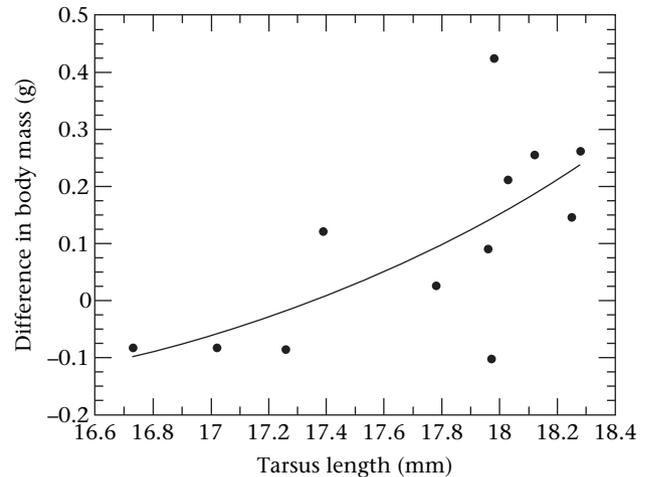


Figure 2. Relation between body size of coal tits (measured by tarsus length) and the differences in body mass before and after wing area reduction (using mean adjusted body masses derived from the ANCOVA mixed model in Table 1). $N = 12$ birds. The regression line shows the relation using log tarsus length.

variable was accounted for by interindividual differences. There were no significant differences between birds in their responses to treatment effects (interaction bird * treatment). Midday temperature did not affect body mass at sunset. A large proportion of the variance in body mass at sunrise was accounted for by all the effects considered in Table 2 (88.5%, all effects: $F_{18,44} = 18.85$, $P < 0.001$). Similar results were obtained for body mass at the beginning of the day (i.e. not affected by the experimental decrease in wing area: $P = 0.620$; large interindividual differences: $P < 0.001$).

Differences between body masses in the control and experimental treatments were not correlated with body size (i.e. log tarsus length) either at the beginning of the day (Pearson correlation: $r_7 = 0.000$, $P = 0.999$) or at dusk ($r_7 = -0.138$, $P = 0.724$).

Diurnal body mass gain (increase in body mass from sunrise to sunset) was not significantly correlated with midday temperature (Table 3). Interindividual differences and the bird * treatment interaction were not significant. Experimental reduction in wing area did not show a significant trend. Thus, diurnal body mass gain was not

Table 2. Results of a mixed-model ANCOVA of coal tit body mass at sunset in outdoor aviaries in relation to ambient temperature at noon (covariate), bird identity (Bird, $N = 9$, random factor) and experimental reduction in wing area (Treatment, fixed factor)

	Sum of squares	df	F	P	% Variance
Bird	4.72	8,8	21.41	<0.001	82.3
Treatment	0.00	1,8	0.00	0.954	0.0
Bird * Treatment	0.22	8,44	1.84	0.095	3.8
Temperature	0.01	1,8	0.45	0.519	0.1

The effect sizes are also given as % of variance explained. For more details on error term definitions, see Methods.

Table 3. Results of a mixed-model ANCOVA of coal tit diurnal body mass gain in outdoor aviaries in relation to ambient temperature at noon (covariate), bird identity (Bird, $N = 9$, random factor) and experimental reduction in wing area (Treatment, fixed factor)

	Sum of squares	df	F	P	% Variance
Bird	0.17	8,8	1.42	0.316	9.8
Treatment	0.01	1,8	0.43	0.530	0.4
Bird * Treatment	0.12	8,35	0.36	0.933	6.9
Temperature	0.00	1,8	0.20	0.665	0.3

The effect sizes are also given as % of variance explained. For more details on error term definitions, see [Methods](#).

significantly explained by any of the effects in [Table 3](#) (17.2% of the variance accounted for; $F_{18,35} = 0.404$, $P = 0.978$).

In summary, variability in body mass at sunset was highly predictable, but was explained only by interindividual differences. The experimental reduction in wing area had no effect on body mass. Body mass change, caused by experimental reduction in wing area, was not related to body size of individuals (i.e. there was no clear allometric effect).

Flying and Feeding Frequency in Aviaries

[Table 4](#) shows the results of the ANCOVA of flying frequency (61.6% of the original variance explained, all effects: $F_{28,432} = 24.75$, $P < 0.001$). Number of flights/min was significantly explained by a third-order polynomial of time of day, as linear, quadratic and cubic terms were significant. Flight frequency abruptly increased from sunrise to 1000 hours, then decreased to a minimum at 1530 hours, and finally showed a small increase towards sunset ([Fig. 3](#)). Time of day accounted for 25.4% of variance in flying frequency and interindividual differences 33.4%. Treatment effect was also significant, showing that birds flew less when wing area was reduced ([Fig. 4a](#)). The change in flight frequency caused by the experimental reduction in wing area was not uniform across the nine coal tits (bird * treatment interaction).

Table 4. Results of a mixed-model ANCOVA of flying frequency (flights/min) in outdoor aviaries in relation to bird identity (Bird, $N = 9$, random factor), the experimental reduction in wing area (Treatment, fixed factor) and cubic polynomial effects of time of day to account for possible nonlinear circadian rhythms (HGMT: linear; $HGMT^2$: quadratic; $HGMT^3$: cubic effects)

	Sum of squares	df	F	P	% Variance
Bird	16156.1	8,8	14.62	<0.001	33.4
Treatment	2076.3	1,8	15.03	0.005	4.3
Bird * Treatment	1105.2	8,440	3.07	0.002	2.3
HGMT	4544.3	1,8	32.41	<0.001	9.4
$HGMT^2$	4133.6	1,8	28.60	<0.001	8.5
$HGMT^3$	3654.0	1,8	24.57	0.001	7.5

The effect sizes are also given as % of variance explained. For more details on error term definitions, see [Methods](#).

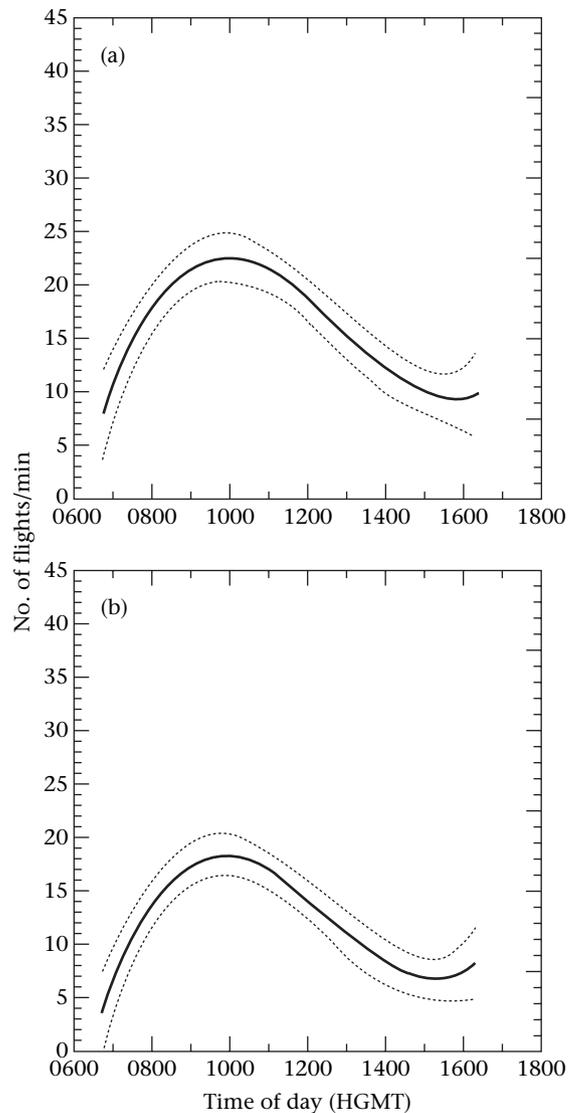


Figure 3. Circadian variation in flying frequency (flights/min) in nine coal tits in outdoor aviaries. HGMT: hours in GMT. Regression lines are the average models for nine coal tits, obtained after fitting a cubic polynomial in (a) control and (b) experimental (reduced wing area) treatments (dashed lines: confidence bands at $P = 0.05$). Control: $Y = -209.14 + 59.41 \times HGMT - 4.90 \times HGMT^2 + 0.13 \times HGMT^3$; experimental: $Y = -227.155 + 63.79 \times HGMT - 5.35 \times HGMT^2 + 0.14 \times HGMT^3$.

Wing loading in the control treatment significantly explained 72.9% of interindividual differences in flying frequency changes between the control and the experimental treatment (wing area reduction; Pearson correlation: $r_7 = 0.854$, $P = 0.003$ using the natural logarithm of wing loading; [Fig. 5](#)). When we repeated the analysis using tarsus length as a measurement of body size, we obtained the same result ($r_7 = -0.723$, $P = 0.028$, using log tarsus length). Birds with higher wing loadings thus decreased flying frequency more markedly when wing area was reduced. The difference between diurnal body mass gain in the experimental and control treatments was not significantly correlated with either wing loading ($r_7 = 0.062$,

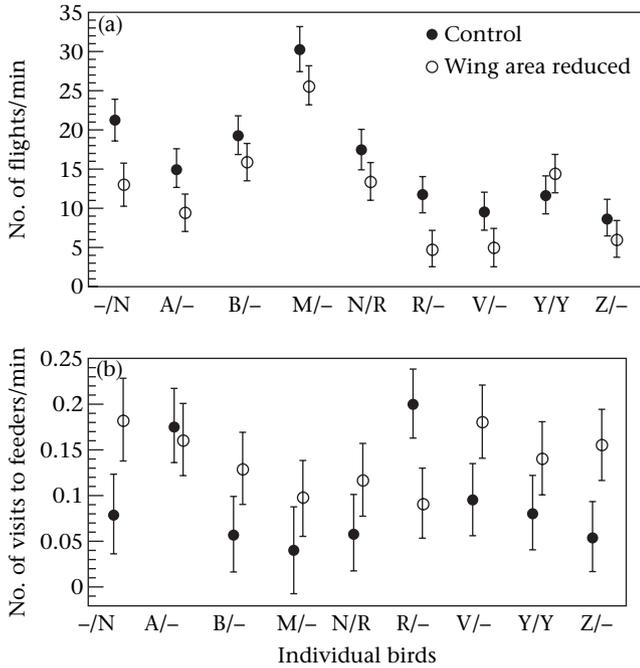


Figure 4. Mean \pm SE (a) flying frequency (no. of flights/min) and (b) feeding frequency (visits to feeder/min) of nine coal tits in outdoor aviaries.

$P = 0.874$) or flight frequency ($r_7 = 0.106$, $P = 0.786$) in the control treatment.

The general linear model in Table 5 explained 24.4% of original variance in feeding frequency, measured as the frequency of visits to the feeders (all effects: $F_{21,439} = 6.74$, $P < 0.001$). The experimental reduction in wing area had a significant effect on feeding frequency: in general, all other things being equal, birds ate more when wing area was reduced (Fig. 4b). This pattern was not homogeneous across birds, as shown by the significance of the interaction term bird * treatment. Feeding frequency was not significantly correlated with flying frequency. Interindividual differences in feeding frequency were not significant.

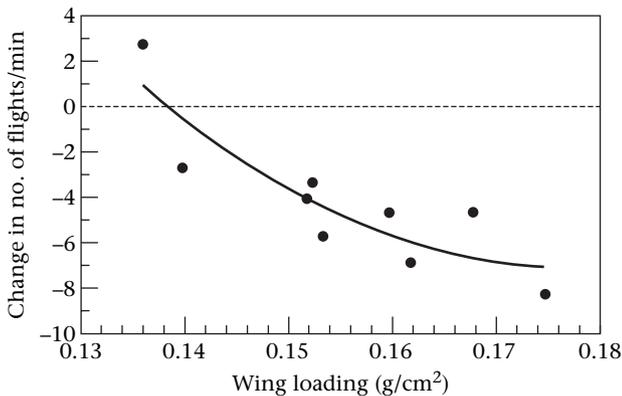


Figure 5. Relation between wing loading in the control treatment (unmodified wing area) and the interindividual differences in flying frequency between the control and the experimental treatments (wing area reduction) in nine coal tits in outdoor aviaries. The regression line shows the relation using log wing loading.

Table 5. Results of a mixed-model ANCOVA of feeding frequency (visits to feeders/min) in outdoor aviaries in relation to bird identity (Bird, $N = 9$, random factor), the experimental reduction in wing area (Treatment, fixed factor), flying frequency (covariate) and cubic polynomial effects of time of day to account for possible nonlinear circadian rhythms (HGMT: linear; HGMT²: quadratic; HGMT³: cubic effects)

	Sum of squares	df	F	P	% Variance
Bird	9.75	8,8	0.98	0.509	8.7
Treatment	6.55	1,8	5.29	0.050	5.8
Bird * Treatment	9.90	8,439	6.42	<0.001	8.8
Flight frequency	0.99	1,8	2.07	0.188	0.9
HGMT	0.00	1,8	0.01	0.933	0.0
HGMT ²	0.01	1,8	0.05	0.829	0.0
HGMT ³	0.03	1,8	0.13	0.731	0.0

The effect sizes are also given as % of variance explained. For more details on error term definitions, see Methods.

Feeding frequency did not show any significant relation with time of day ($P > 0.7$ in the three F tests analysing linear, quadratic and cubic relation).

In summary, flight and feeding frequency were significantly affected by the experimental reduction in wing area: birds flew less and ate more when wing area was reduced. Flight showed a clear circadian rhythm, with a step increase from a minimum at sunrise to a midmorning peak, and a subsequent gentle decrease to a second minimum 1 h before sunset, before a less marked increase towards sunset.

DISCUSSION

Some studies have shown that birds do not carry maximum fat deposits during winter because of mass-dependent costs: maintenance costs of large fat reserves caused by increased metabolism, greater exposure to predators while feeding caused by higher energy requirements and impaired escape ability with higher body mass (see Cuthill & Houston 1997 and references therein). Several theoretical studies predict that mass-dependent costs and starvation risk interact in a trade-off, moulting daily patterns of mass increase even during winter (Lima 1986; McNamara & Houston 1987, 1990; Rogers & Smith 1993; Houston et al. 1993; Bednekoff & Houston 1994; McNamara et al. 1994). Therefore, a strategic reduction in body mass caused by experimental reduction in wing area should be expected (Witter & Cuthill 1993). This prediction has been experimentally confirmed by Swaddle & Witter (1997) and by Lind & Jakobsson (2001) in comparisons between individuals, and by Senar et al. (2002) using a within-individuals design in the wild. Our experiment with the coal tit under wild conditions also demonstrates a trade-off, although the magnitude of its effect is low (see the interaction term Treatment * Before–After in Table 1 and Fig. 1). However, our experiment under controlled conditions in outdoor aviaries suggests that body mass is not subjected to a clear trade-off to maintain wing loading during autumn–winter. Nevertheless, another possibility is that this trade-off always exists (at least theoretically)

but how it is manifested depends on the circumstances: birds could have the ability to compensate in a dimension other than body mass. In other words, birds could compensate behaviourally instead of compensating by reducing body mass (see below).

The discrepancies between our study and those by Lind & Jakobsson (2001) and Senar et al. (2002) clearly show the nongeneralized effect of the same phenomena in different taxonomic, experimental and environmental situations. We suggest that discrepancies can arise from two different, nonexclusive, explanations. First, birds experienced more severe treatments in the other studies (three remiges in each wing were taped together or cut), and second, differences in prevailing environmental conditions could determine the magnitude of body mass decreases caused by experimental manipulations. In our experiment, birds were studied during winter, in conditions of reduced natural food availability, low temperatures (especially at night), and short days and long nights. These conditions contrast with those in Senar et al.'s (2002) and Lind & Jakobsson's (2001) experiments, carried out during moult at the end of summer and mid-autumn, respectively.

In small wintering birds, the fattening strategy involves daily increases in body mass that range from 7 to 15% of the bird's fat-free body mass (Lehikoinen 1987; Haftorn 1989; Polo & Carrascal 1997; Kullberg 1998). In our study area, and under control situations in outdoor aviaries (i.e. no wing reduction), coal tits experienced an average wing loading increase of 8.9% from daily fattening. This percentage was slightly higher than the 5–7% of wing area reduction resulting from our experimental manipulation of birds. Therefore, our manipulation was within the limits of natural variation in wing loading.

Surprisingly, the amount of wing area reduction was not of great ecological importance for body mass changes of the coal tits studied, as the average decrease in body mass caused by the wing reduction was small in both outdoor aviaries and under wild conditions (see also Hedenström & Sunada 1999; Lind 2001 for small detrimental effects of moult gaps on escape ability and aerodynamic performance). However, body mass decrease showed an allometric pattern, as this decrease was proportional to bird size before the reduction in wing area in the field experiment (Fig. 2): the five largest birds reduced 2.7% of their body mass with respect to the unmanipulated situation. Nevertheless, this effect was not found in the aviary experiment. Normally, the opposite effect is predicted because when birds are put into aviary conditions with food ad libitum many ecological constraints are released, enabling the birds to compensate for treatments for which they could not compensate in the wild. This unexpected result leads to the question what made the birds compensate differently in these two situations.

Although the effective sample size to discuss this question is only two experiments, it makes sense to conclude that the two different responses occurred because of different ecological conditions. This is an important conclusion because there is a general lack of appreciation in antipredation studies particularly with mass-dependent predation risk experiments, that the

conditions under which they occur determine the direction of the results. Variation in predictability of foraging (i.e. husbandry conditions), the state of the birds caught (i.e. high or low initial mass) and time of year (i.e. whether starvation risk, predation risk or territory holding is considered as the priority for the bird) can all vary in a simple way to account for the discrepancy between the different results in mass-dependent predation studies.

We suggest that the goal for our coal tits was to maintain body mass within narrow limits during autumn and winter under natural conditions of light and temperature, even in favourable foraging conditions as in the outdoor aviaries. This goal could not be attained by the larger coal tits under wild, restrictive, conditions in terms of low food availability and presence of predators (sparrowhawk, *Accipiter nisus*) and competitors (conspecifics and great tits, *Parus major*, crested tits, *Lophophanes cristatus*, and Eurasian nuthatches, *Sitta europaea*, which are dominant species over the coal tits; see Carrascal & Moreno 1992). The difficulties associated with living within a natural foraging environment possibly constrained the larger bird's ability to maintain their initial body reserves after wing area reduction, owing to allometric effects of body mass on flying costs. Under a much less restrictive environment, when birds were maintained in the aviary (more food and more predictable availability, predation risk reduced because predators do not visit the aviary and without competition pressure), allometric costs were also present but the larger birds with higher wing loadings compensated by flying less (Fig. 5). Therefore, the larger birds should face higher flying costs in the wild, owing to allometric effects (see below), leading to greater reductions in body mass.

At the intraspecific level, body proportions in adult birds do not deviate much from what would be expected from isometric similarity (McMahon & Bonner 1983). As a result of this isometric rule, wing loading increases with the power 0.333 of body mass (quotient between body mass, l^3 , and wing area, l^2). Thus, a greater detrimental effect of the experimental manipulation in larger birds would be expected (McMahon & Bonner 1983). Negative effects of body mass increase on flight performance have been observed in small birds, both under natural changes in wing loading (daily changes in body mass: Metcalfe & Ure 1995; Norberg 1995; Veasey et al. 1998; but see Kullberg 1998; Kullberg et al. 1998; van der Veen & Lindström 2000; wing feather moult: Swaddle & Witter 1997; and migratory fuel load: Kullberg et al. 1996; Lind et al. 1999) and experimental manipulations (Witter et al. 1994; Swaddle et al. 1999). Cresswell (1999) also found a negative association between flying activity and body mass in wild blackbirds, *Turdus merula*, during mid-winter. Therefore, as a direct consequence of allometric energetic demands, larger birds should have higher flying costs than smaller birds. Our results support this prediction: larger manipulated coal tits suffered a marked decrease in fat reserves while foraging in the wild under restricted food availability and they reduced flying frequency without modifying body mass in the captive environment with abundant food where they did not need to explore the home range.

The circadian rhythm of activity showed a clear pattern for flying frequency. There was a rapid increase in flying frequency towards a peak 2 h after dawn, followed by a gentle decrease towards the end of the day with a slight increase 1 h before dusk (see also Aschoff 1966; Daans & Aschoff 1975 for other bird species). In contrast, feeding frequency remained unchanged with time of day. If feeding frequency remains unchanged throughout the day, then a linear diurnal increase in body mass should be expected. However, coal tits showed a general pattern of exponential increase in body mass during the day in the study area; which has a Mediterranean montane climate, with an increasing rate of body mass gain from the beginning (0.04 g/h) to the end (0.12 g/h) of the day (Polo 1999; see also Pravosudov & Grubb 1998). Diurnal changes in flight activity may explain this exponential increase in body mass. Coal tits may fly less frequently as the day proceeds as a result of increased travel costs derived from higher body mass (e.g. Hedenström 1992; Metcalfe & Ure 1995), and the reduction in energy spent in flight would contribute to an increase in body mass at the end of the day.

It has been widely recognized that avian fat storage entails costs mainly associated with predation risk, and thus body mass reflects the outcome of this trade-off (Witter & Cuthill 1993; Cuthill & Houston 1997; Cresswell 1998; Houston & McNamara 1999). Animals can compensate for increased predation risk in different ways. First, birds in particular may compensate by decreasing their mass because this is likely to increase their ability to escape from predators (Witter & Cuthill 1993; Kullberg et al. 1996; Lind et al. 1999). Second, animals generally may compensate for increased predation risk simply by avoiding the predator, spatially (Durant 2000; Rettie & Messier 2001) or temporally (van der Veen 2000). Third, animals may compensate for increased predation risk by allocating more time to antipredation behaviours (Whitfield 1988; Wolff & Van Horn 2003). In our experimental study in outdoor aviaries the predation risk was minimized, so a complementary/alternative explanation for the lack of change in body mass is that coal tits probably did not trade-off the starvation–predation risk dilemma because of a low perceived predation risk in aviaries where predators were excluded.

Finally, the trade-off paradigm between opposite forces determining average body mass has been widely accepted among biologists studying winter fattening strategies of small birds. Our results show a trade-off between wing area reduction and body mass (in the field) and between wing area and flying frequency (in the aviaries), both mediated by allometric effects of body size. They also lead to the conclusion that the goal of small resident birds would be to maintain daily fat reserves within narrow limits during autumn and winter, even under different ecological conditions.

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References

- Aschoff, J. 1966. Circadian activity pattern with two peaks. *Ecology*, **47**, 657–662.
- Bednekoff, P. A. & Houston, A. I. 1994. Dynamic models of mass-dependent predation, risk-sensitive foraging, and premigratory fattening in birds. *Ecology*, **75**, 1131–1140.
- Bednekoff, P. A. & Krebs, J. R. 1995. Great tit fat reserves: effects of changing and unpredictable day length. *Functional Ecology*, **9**, 457–462.
- Blem, C. R. 1990. Avian energy storage. *Current Ornithology*, **7**, 59–113.
- Broggi, J., Koivula, K., Lahti, K. & Orell, M. 2003. Seasonality in daily body mass variation in a hoarding boreal passerine. *Oecologia*, **137**, 627–633.
- Carrascal, L. M. & Moreno, E. 1992. Proximal costs and benefits of heterospecific social foraging in great tit *Parus major*. *Canadian Journal of Zoology*, **70**, 1947–1952.
- Carrascal, L. M. & Polo, V. 1999. Coal tits, *Parus ater*, lose weight in response to chases by predators. *Animal Behaviour*, **58**, 281–285.
- Cresswell, W. 1998. Diurnal and seasonal mass variation in blackbirds *Turdus merula*: consequences for mass-dependent predation risk. *Journal of Animal Ecology*, **67**, 78–90.
- Cresswell, W. 1999. Travel distance and mass gain in wintering blackbirds. *Animal Behaviour*, **58**, 1109–1116.
- Cuthill, I. C. & Houston, A. I. 1997. Managing time and energy. In: *Behavioural Ecology: an Evolutionary Approach*. 4th edn. (Ed. by J. R. Krebs & N. B. Davies), pp 97–120. London: Blackwell Science.
- Daans, S. & Aschoff, J. 1975. Circadian-rhythms of locomotor activity in captive birds and mammals: their variations with season and latitude. *Oecologia*, **18**, 269–316.
- Dall, S. R. X. & Witter, M. S. 1998. Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Animal Behaviour*, **55**, 715–725.
- Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.
- 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. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology*, **65**, 1–17.
- Gosler, A. G., Greenwood, J. J. D. & Perrins, C. M. 1995. Predation risk and the cost of being fat. *Nature*, **377**, 621–623.
- Haftorn, S. 1989. Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. *Wilson Bulletin*, **101**, 217–235.
- Haftorn, S. 1992. The diurnal body weight cycle in titmice *Parus* spp. *Ornis Scandinavica*, **23**, 435–443.
- Hedenström, A. 1992. Flight performance in relation to fuel load in birds. *Journal of Theoretical Biology*, **158**, 535–537.
- Hedenström, A. & Sunada, S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology*, **202**, 67–76.
- Houston, A. I. & McNamara, J. M. 1999. *Models of Adaptive behaviour: an Approach Based on State*. Cambridge: Cambridge University Press.

- Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B*, **341**, 375–397.
- Houston, A. I., Welton, N. J. & McNamara, J. M. 1997. Acquisition and maintenance costs in the long-term regulation of avian fat reserves. *Oikos*, **78**, 331–340.
- Kullberg, C. 1998. Does diurnal variation in body mass affect take-off ability in wintering willow tits? *Animal Behaviour*, **56**, 227–233.
- 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.
- Kullberg, C., Jakobsson, S. & Fransson, T. 1998. Predator-induced take-off strategy in great tits (*Parus major*). *Proceedings of the Royal Society of London, Series B*, **265**, 1659–1664.
- Lee, S. J., Witter, M. S., Cuthill, I. C. & Goldsmith, A. R. 1996. Reduction in escape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris*. *Proceedings of the Royal Society of London, Series B*, **263**, 619–624.
- Lehikoinen, E. 1987. Seasonality of the daily weight cycle in passerines and its consequences. *Ornis Scandinavica*, **18**, 216–226.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology*, **67**, 377–385.
- Lind, J. 2001. Escape flight in moulting tree sparrows (*Passer montanus*). *Functional Ecology*, **15**, 29–35.
- Lind, J. & Jakobsson, S. 2001. Body building and concurrent mass loss: flight adaptations in tree sparrows. *Proceedings of the Royal Society of London, Series B*, **268**, 1915–1919.
- Lind, J., Fransson, T. & Jakobsson, S. 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behavioral Ecology and Sociobiology*, **46**, 65–70.
- Lindström, Å. & Rosén, M. 2003. The cost of avian winter stores: intra-individual variation in basal metabolic rate of a wintering passerine, the greenfinch *Carduelis chloris*. *Avian Science*, **2**, 139–144.
- Macleod, R., Barnett, P., Clark, J. A. & Cresswell, W. 2005. Body mass change strategies in blackbirds *Turdus merula*: the starvation–predation risk trade-off. *Journal of Animal Ecology*, **74**, 292–302.
- McMahon, T. A. & Bonner, J. T. 1983. *On Size and Life*. New York: Scientific American Books.
- McNamara, J. M. & Houston, A. I. 1987. Starvation and predation as factors limiting population size. *Ecology*, **68**, 1515–1519.
- McNamara, J. M. & Houston, A. I. 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheoretica*, **38**, 37–61.
- 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.
- Naef-Daenzer, B. 2000. Patch time allocation and patch sampling by foraging great and blue tits. *Animal Behaviour*, **59**, 989–999.
- Norberg, U. M. 1990. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Berlin: Springer Verlag.
- Norberg, U. M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology*, **9**, 48–54.
- Pennycuik, C. J. 1990. *Bird Flight Performance*. Oxford: Oxford University Press.
- Piersma, T., Koolhaas, A. & Jukema, J. 2003. Seasonal body mass changes in Eurasian golden plovers *Pluvialis apricaria* staging in the Netherlands: decline in late autumn mass peak correlates with increase in raptor numbers. *Ibis*, **145**, 565–571.
- Polo, V. 1999. Factores que determinan el ciclo diario de ganancia de peso en una población de carboneros garrapinos (*Parus ater*). Ph.D. thesis, Universidad Complutense, Madrid.
- Polo, V. & Carrascal, L. M. 1997. El ciclo diario de ganancia de peso durante el invierno en una población silvestre de *Parus cristatus* en el centro España. *Ardeola*, **44**, 215–224.
- Polo, V. & Carrascal, L. M. 1998. Relación entre la condición física invernal y la capacidad de regenerar plumas en el carbonero garrapinos (*Parus ater*). *Ardeola*, **45**, 203–213.
- Pravosudov, V. V. & Grubb, T. C. 1998. Management of fat reserves in tufted titmice (*Parus bicolor*): evidence against a trade-off with food hoards. *Behavioral Ecology and Sociobiology*, **42**, 57–62.
- Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.
- Rettie, W. J. & Messier, F. 2001. Range use and movement rates of woodland caribou in Saskatchewan. *Canadian Journal of Zoology*, **79**, 1933–1940.
- Rogers, C. M. & Smith, J. N. M. 1993. Life-history theory in the non-breeding period: trade-offs in avian fat reserves? *Ecology*, **74**, 419–426.
- Senar, J. C., Domènech, J., Carrascal, L. M. & Moreno, E. 1997. A funnel trap for the capture of tits. *Butlletí del Grup Català d'Anellament*, **14**, 17–24.
- Senar, J. C., Domènech, J. & Uribe, F. 2002. Great tits (*Parus major*) reduce body mass in response to wing area reduction: a field experiment. *Behavioral Ecology*, **16**, 725–727.
- Swaddle, J. P. & Witter, M. S. 1997. The effects of moult on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. *Canadian Journal of Zoology*, **75**, 1135–1146.
- Swaddle, J. P., Williams, E. V. & Rayner, J. M. V. 1999. The effect of simulated flight moult on escape take-off performance in starlings. *Journal of Avian Biology*, **30**, 351–358.
- van der Veen, I. T. 2000. Daily routines and predator encounters in yellowhammers *Emberiza citrinella* in the field during winter. *Ibis*, **142**, 413–420.
- van der Veen, I. T. & Lindström, K. M. 2000. Escape flights of yellowhammers and greenfinches: more than just physics. *Animal Behaviour*, **59**, 593–601.
- Veasey, J. S., Metcalfe, N. B. & Houston, D. C. 1998. A reassessment of body mass upon flight speed and predation risk in birds. *Animal Behaviour*, **56**, 883–889.
- Voss, D. T. 1999. Resolving the mixed models controversy. *American Statistician*, **53**, 352–356.
- Whitfield, D. P. 1988. Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering turnstone *Arenaria interpres* and redshank *Tringa totanus*. *Ibis*, **130**, 284–287.
- 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**, 73–93.
- Witter, M. S., Cuthill, I. C. & Bonser, R. H. C. 1994. Experimental investigation of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Animal Behaviour*, **48**, 201–222.
- Wolff, J. O. & Van Horn, T. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology*, **81**, 266–271.
- Ydenberg, R. C., Butler, R. W., Lank, D. B., Smith, B. D. & Ireland, J. 2004. Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proceedings of the Royal Society of London, Series B*, **271**, 1263–1269.