

The effects of latitude and day length on fattening strategies of wintering coal tits *Periparus ater* (L.): a field study and aviary experiment

VICENTE POLO, LUIS M. CARRASCAL* and NEIL B. METCALFE†

*Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain; *Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain; and †Ornithology Group, Division of Environmental and Evolutionary Biology, Graham Kerr Building, IBLS, University of Glasgow, Glasgow G12 8QQ, UK*

Summary

1. Cyclic daily fattening routines are very common in wintering small wild birds, and are thought to be the consequence of a trade-off between different environmental and state-dependent factors. According to theory, these trajectories should range from accelerated (i.e. mass increases exponentially towards dusk) when mass-dependent predation costs are the most important cause of mortality risk, to decelerated (i.e. the rate of mass gain is highest at dawn and decreases afterward) when starvation is the greater risk.
2. We examine if geographically separate populations of coal tits, wintering in Scotland and central Spain under contrasting photoperiods, show differences in their strategies of daily mass regulation. We describe population differences in wild birds under natural conditions, and experimentally search for interpopulation variation in diurnal body mass increase under common, manipulated, photoperiod conditions (LD 9 : 15 h vs. 7 : 17 h), controlling for temperature, food availability, predator pressure and foraging arena.
3. Winter diurnal mass gain of wild coal tits was more delayed towards the latter part of the daylight period in central Spain (i.e. the locality with longer winter days) than in Scotland. In both localities, the pattern was linked to the average mass at dawn, with mass increasing more rapidly in lighter birds. However, under the controlled photoperiod situation the pattern of daily mass gain was similar in both populations. Diurnal body mass gain was more accelerated at the end of the day, and the increase in body mass in the first hour of the day was considerably lower under the long (9 h) than under the short (7 h) photoperiod in both populations.
4. Wintering coal tits show patterns of mass gain through the day that are compatible with current theories of the costs and benefits of fat storage, with birds at lower latitudes (with longer winter days) having a greater tendency to delay mass gain until late in the day. The experimental study revealed that these patterns are plastic, with birds responding directly to the photoperiod that they experience, suggesting that they are continually making fine-scale adjustments to energy reserves on the basis of both inherent (e.g. state-dependent) and extrinsic cues.

Key-words: energy reserves, latitudinal variation, model of daily fattening, photoperiod, predation.

Journal of Animal Ecology (2007) **76**, 866–872
doi: 10.1111/j.1365-2656.2007.01270.x

Introduction

Cyclic daily fattening routines are very common in small birds in nature, and become especially pronounced in

winter, when on a daily basis birds must lay down enough fat reserves to deal with the harsh environmental conditions caused by the shortening foraging time, longer roosting time, increased fluctuation in resources and generally colder temperatures (Lehikoinen 1987; Haftorn 1989; Houston, McNamara & Hutchinson 1993; Witter & Cuthill 1993; Gosler 2002; Koivula, Orell & Lahti 2002). However, as a consequence of costs associated

with acquiring and maintaining higher levels of body reserves (e.g. Houston & McNamara 1993; Metcalfe & Ure 1995), birds generally maintain fat reserves below the maximum possible (Blem 1976; Witter & Cuthill 1993; Gosler 1996; Carrascal & Polo 2006).

There is theoretical and experimental evidence for plasticity in the shape of daily routines of body mass gain in small birds in relation to many environmental and individual variables (e.g. McNamara & Houston 1990; Gosler 1996; Pravosudov & Grubb 1997; Dall & Witter 1998; Lilliendahl 2000, 2002; Thomas 2000; Pravosudov & Lucas 2001; Gosler 2002; Koivula *et al.* 2002; Rogers & Reed 2003; Macleod *et al.* 2005b; Macleod, Gosler & Cresswell 2005a; Polo & Bautista 2006a,b). The shape of daily fattening routines is thought to be the consequence of a trade-off between different environmental and state-dependent factors that affect body mass in different ways (Macleod *et al.* 2005a,b; Polo & Bautista 2006a). Thus, these trajectories should range from accelerated (i.e. mass increases exponentially towards dusk) when mass-dependent costs are the most important cause of mortality, to decelerated (i.e. the rate of mass gain is highest at dawn and decreases afterward) when starvation is the greater risk (Bednekoff & Houston 1994; McNamara, Houston & Lima 1994; Pravosudov & Grubb 1997; Macleod *et al.* 2005a,b).

Within many animal species, geographically separate populations live under markedly different environmental conditions. Comparisons of populations that display geographical variation in behaviour can cast light on the mechanisms of adaptive divergence and the roles of phenotypic plasticity in determining patterns of behavioural evolution (Foster 1999). As the time available for feeding is a major factor limiting the acquisition of body reserves and the organization of foraging routines in small birds (Bednekoff & Krebs 1995; Lahti, Koivula & Orell 1997; Cresswell 1998; Dall & Witter 1998; Rogers & Reed 2003) and there are marked differences in day length at different latitudes, we might expect that populations wintering at different latitudes might regulate body mass in different ways (Rogers, Nolan & Ketterson 1993; but see King & Mewaldt 1981). However, to our knowledge, there have been no studies of the possible latitudinal effect of day length on the diurnal cycle of body mass gain.

In this study we examine if geographically separate populations of coal tits, wintering under contrasting photoperiods, show differences in their strategies of mass regulation. First, we describe population differences in wild birds under natural conditions, and compare these differences with the patterns predicted by latitudinal variation in day length. Secondly, we search for inter-population variation in diurnal body mass increase under common, manipulated, photoperiod conditions, controlling for temperature, food availability, predator pressure and foraging arena; this allows us to test whether there are differences between the populations indicative of local physiological adaptations. We therefore address the following questions: (1) Are there differences in the

shape of daily fattening between populations? (2) Can these differences be explained by the latitudinal differences in photoperiod? (3) Do individuals from contrasting populations show the same response when tested in a common environment?

Materials and methods

STUDY AREA, SPECIES AND MEASUREMENT OF NATURAL MASS TRAJECTORIES

The study areas were located in central Spain ('El Ventorrillo' field station, 1500 m a.s.l., 40°45'N 04°01'W, Sierra de Guadarrama), and in central Scotland (Scottish Centre for Ecology and the Natural Environment (SCENE), Glasgow University, Rowardennan, 20–70 m a.s.l., 56°8'N 4°37'W, Loch Lomondside). The area in Spain 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*. The area in Scotland is a mixed woodland of Scots pine and oak *Quercus petraea*. The field study was carried out from the end of autumn until mid-winter in one winter in each area (1998–99 in Ventorrillo, 2000–01 in Rowardennan). The sites were chosen to have a similar winter temperature range but contrasting photoperiod. During the date of the study (7 November–4 February in Ventorrillo and 20 October–9 February in Rowardennan), the ambient mean temperatures at noon were slightly lower in Ventorrillo (average 2.4 °C, range –4.5 to 6.7 °C) than in Rowardennan (average 6.6 °C, range 1–11 °C). Similar slight differences were observed at dawn (Ventorrillo: average –1.0 °C, range –5.6 to 3.5 °C; Rowardennan: average 3.7 °C, range –1 to 9.5 °C). Snowfall frequency was similar in Ventorrillo (15% of the days throughout the study period) and in Rowardennan (9%). However, there were marked differences in day length between Rowardennan and Ventorrillo field stations during the range of autumn–winter days used in the study (see above), being longer in Spain (range 9.28–10.25 h; average = 9.56 h) than in Scotland (range 6.94–9.92 h; average = 7.64 h).

The study species was the coal tit *Periparus ater* (L.), one of Europe's smallest resident birds (body mass 8–10 g) and so vulnerable to both predation and starvation. It is found at low to middle altitudes in temperate zones, becoming more montane at the southern edge of its range (Hagemeijer & Blair 1997; see Polo 2005; for more details of low latitude populations). In order to trap birds for measurement of mass, five rectangular funnel traps (40 × 40 × 60 cm) were placed in each study area, 50–100 m apart and hanging from branches 1.5 m above the ground. This kind of trap is especially efficient at capturing tit species and can be used under adverse weather conditions (Davis 1981; Senar *et al.* 1997). Funnel traps were permanently baited with two cylindrical feeders, hanging from the trap roof, which contained husked peanuts. A translucent plastic sheet

covered the roof of the traps to prevent birds becoming wet on rainy or snowy days. Trapping was conducted on an average of 14.3 and 12.2 days per month at Ventorrillo and Rowardennan, respectively. Daytime length and temperature at noon (to the nearest 0.1 °C) were recorded on each sampling day. The escape doors of the traps remained opened on noncapture days, so birds could use the peanuts as a supplementary food source, but they were closed during the capture days from dawn to dusk. On capture days, traps were inspected every 20–40 min, and the time at which each bird was captured was noted. Captured birds were given unique colour rings, weighed (with an electronic balance at the nearest ± 0.01 g) and released within the first 2–10 min after capture, depending on the number of birds caught during the capture procedure.

AVIARY EXPERIMENT

Nine coal tits were trapped in the third week of November 1999 at the Ventorrillo field site, while 10 coal tits were trapped in the corresponding week in November 2001 at Rowardennan. At each site, birds were colour banded for subsequent individual identification and randomly allocated to two metallic cages (100 × 50 × 40 cm). Each cage contained several pine branches with green needles, five plastic perches and four water dishes. Birds were provided with *ad libitum* food using four feeders filled with a grained mixture of pine seeds and dry kitten biscuits, and two feeders with peanuts. Cages were arranged in two different rooms, which were only illuminated with artificial light. Diurnal temperatures remained relatively constant in these rooms (Ventorrillo: range 3.1–6.6 °C; Rowardennan: range 5.7–10.2 °C). Prior to the experiments, the birds were kept in the cages for a 2-week period of acclimation with a natural light : dark (LD) cycle (Ventorrillo LD 9.75 : 14.25; Rowardennan LD 8.5 : 15.5). By means of this protocol, the birds were maintained under very similar conditions at the two study areas, so avoiding the logistical and ethical problems of moving them to a common experimental arena.

We then carried out the experiment in December (1999 in Spain, 2001 in Scotland) in the 4 weeks around the winter solstice. Birds spent 2 weeks in each of two different artificial LD cycles that matched the ambient photoperiods in Spain (LD 9 : 15, 'long' treatment) and Scotland (LD 7 : 17; 'short' treatment). Dawn and dusk were simulated by a gradual change in light levels lasting 15 min. In the first 2-week period, one group of five birds experienced the short photoperiod treatment while the other group experienced the long treatment. In the second 2-week period the photoperiods were reversed. During the first 7 days of each experimental phase, the coal tits were allowed to acclimatize to the artificial LD cycle without being disturbed. In the following 7 days the birds were captured and weighed with the aid of an electronic digital balance (precision ± 0.01 g) every hour, starting at 07.30 h GMT (10 times

per day in the long treatment and eight times per day in the short treatment). Less than 4 min was required to weigh each group, and birds resumed normal activities within 5 min of being re-released into the cages.

Immediately after the last weighing at the end of the day (14.30 h GMT in the short treatment, and 16.30 h in the long treatment) the birds of the same treatment group were placed into a cloth box (25 × 20 × 40 cm) to spend the night (i.e. the dark period). The two cloth boxes containing the two groups of birds were placed in the same room. The ambient temperature during the dark phase was roughly constant throughout the study (Ventorrillo: range 5.5–9.5 °C; Rowardennan: 5.7–11.3 °C). Birds at both locations were released back to the wild at the end of the experiment.

MODEL FOR THE HOURLY INCREASE OF BODY MASS

Small birds put on fat during the day in a manner that can be described by a double exponential model, characterized by a decelerated increase at the beginning of the day and an accelerated increase towards the end of the day (see Polo & Bautista 2006a for more details). While it is possible to measure the first part of daily body mass gain (i.e. the decelerated increase) in studies on captive birds. However, it is very difficult to capture wild birds at the beginning of the foraging period, when they have empty guts. Therefore, we have only used data recorded between 1 h after dawn and dusk in both the field and experimental (captive) studies, and use a simpler model to characterize the increase of body mass, W , in relation to ambient temperature at noon, T , daytime length, D , and time of day, t (hours from the beginning of the foraging period):

$$W = a + bT + c(D - D_0) + dt^e$$

Thus, we postulate inverse linear relationships between body mass and both the temperature at noon and the daytime length (constants b and c , respectively), but a power relationship with the time of day (one linear d , and another power exponent e) to describe curvilinear patterns of body mass gain through the day. The power exponent e provides a measure of the form of the daily trajectories of body mass gain: $e > 1$ for accelerated trajectories; $e < 1$ for decelerated trajectories; and $e = 1$ for constant hourly increase of body mass. D_0 represents the daytime length at winter solstice (9.3 h at Ventorrillo and 6.9 h at Rowardennan). Parameter a represents the predicted adjusted body mass of an individual on 21 December at the beginning of the foraging period for each individual bird and locality and at an ambient temperature of 0 °C.

STATISTICAL PROCEDURES

Regression analyses within each individual bird were carried out with the nonlinear estimation procedure

implemented in STATISTICA 6.0 (StatSoft 2001), using the Simplex and Quasi-Newton method to calculate regression coefficients. Although coefficients b and c for temperature at noon and daytime length were calculated in all regression analyses, they were not used in the subsequent analyses because they were entered as independent nuisance variables to control for their natural variation in comparisons between populations and experimental conditions in indoor aviary trials. Moreover, day length was not included in the regression analyses for the indoor experiments, under controlled conditions, because we artificially manipulated daytime duration using fixed treatments. Body mass at sunrise is only known in the experimental controlled conditions. Therefore, this value was used to estimate the body mass increase in the first hour, but not in the adjustment of body mass data to the exponential model.

The allometric exponent e of the body mass trajectories was log transformed in all data analyses, to attain linear relationships with predictor variables and normality in the residuals of the ANOVA–ANCOVAs and regression models. For the experiment using captive birds, ANOVA and ANCOVA tests and planned comparisons within birds were used to analyse the effect of daytime length on the shape of the trajectories of daily body mass, and on mean body mass. In these tests, bird was used as a random factor and the treatment as a fixed factor. Normality and randomness of residuals were checked with normal probability plots.

One-way ANOVAs and ANCOVA were employed in the analyses of body mass gain in the two study populations (Ventorrillo vs. Rowardennan) under natural conditions. Two-way repeated measures ANOVAs were carried out with data gathered in captivity, using day length manipulation as the within-subjects factor (7 : 17 h vs. 9 : 15 h day : night cycle) and population (Ventorrillo vs. Rowardennan) as a between-subjects factor. One-sample t -tests were used to examine significant deviations of power exponent e from 1 (i.e. linear increase of body mass throughout the day), both under natural conditions in the wild and under captivity in indoor experiments.

Results

PATTERN OF BODY MASS GAIN UNDER NATURAL CONDITIONS

A total of nine individually marked free-living coal tits at Rowardennan and 15 at Ventorrillo were captured often enough to provide data on their individual daily trajectories for body mass (mean number of captures per bird = 29, range = 11–70). The average body mass of the birds was similar in the two populations ($t = 1.65$, $P = 0.11$): 9.06 g (SD = 0.46 g, $n = 9$ birds) at Rowardennan and 9.37 g (SD = 0.41 g, $n = 15$ birds) at Ventorrillo (averaging all captures for each individually marked bird). However, the daily rate of mass gain, after controlling for natural variation in day length and temperature

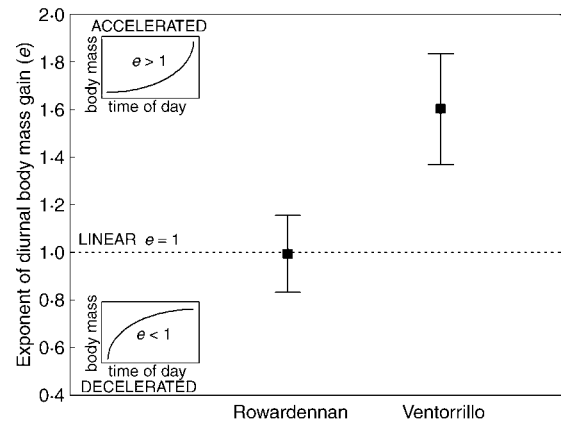


Fig. 1. Population differences in the exponent of diurnal body mass gain (power exponent e in the regression equation $\text{body mass} = a + b(\text{temperature at noon}) + c(\text{daytime length}) + d(\text{time of day})^e$) under natural conditions in free-living coal tits wintering at Rowardennan (Scotland) and Ventorrillo (Central Spain). The sample size is nine individual birds at Rowardennan and 15 at Ventorrillo. Vertical bars represent mean ± 1 SE.

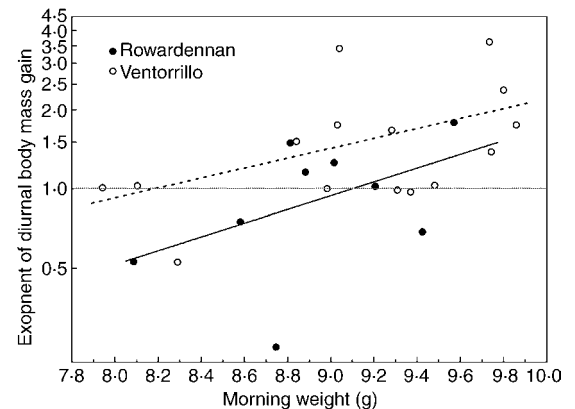


Fig. 2. Relationship between the exponent of diurnal body mass gain and body mass at the beginning of the day (morning weight; see Methods) for the Rowardennan (Scotland; open circles and dotted line) and Ventorrillo (Central Spain; filled circles and continuous line) coal tit populations.

at midday, was significantly more accelerated at Ventorrillo than at Rowardennan ($F_{1,22} = 4.406$, $P = 0.047$; see Fig. 1). Moreover, while the rate of diurnal body mass gain was indistinguishable from a linear pattern at Rowardennan (i.e. relatively steady body mass gain throughout the day; $t = 0.79$, $n = 9$, $P = 0.455$), at Ventorrillo it was clearly accelerated (i.e. with the highest body mass gain delayed until the last hours of the day; $t = 2.41$, $n = 15$, $P = 0.030$).

The exponent of hourly body mass trajectory was significantly and positively correlated with body weight at the beginning of the day (ANCOVA model; effect of covariate: $F_{1,21} = 6.80$, $P = 0.016$; see Fig. 2). The shape of this relationship did not differ between study areas ($F_{1,20} = 0.203$, $P = 0.657$).

In summary, these results show that the diurnal gain in body mass was more delayed until the latter part of the daylight period in the locality with longer winter days.

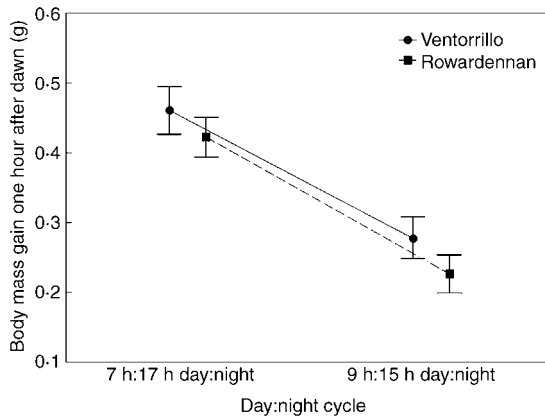


Fig. 3. Variation in body mass gain 1 h after dawn in captive coal tits from two populations [Rowardennan, Scotland ($n = 10$ birds) vs. Ventorrillo, Central Spain ($n = 9$)] under different day length regimes. Vertical bars represent mean \pm 1 SE.

In both localities, the pattern of diurnal body mass gain was linked to the average mass at dawn, with mass increasing more rapidly in lighter birds (Fig. 2).

BODY MASS CHANGES UNDER CONTROLLED CONDITIONS IN CAPTIVITY

The average body mass of coal tits in captivity was significantly higher ($t = 3.13$, $P = 0.006$) at Ventorrillo (mean = 9.89 g, SD = 0.55 g, $n = 9$ birds) than at Rowardennan (mean = 9.15 g, SD = 0.46 g, $n = 10$ birds; averaging all weights for each bird).

The increase in body mass in the first hour of the day was similar in birds from Spain and Scotland ($F_{1,17} = 1.24$, $P = 0.28$; Fig. 3). However, body mass gain at the beginning of the day was considerably higher under the LD 7 : 17 than under the LD 9 : 15 cycle in birds from both populations ($F_{1,17} = 124.55$, $P < 0.001$; Fig. 3). This pattern of morning mass gain in relation to daytime duration was similar in the two populations (population by photoperiod interaction: $F_{1,17} = 0.15$, $P = 0.70$).

The exponent of diurnal body mass gain did not differ between Ventorrillo and Rowardennan 1 h after dawn ($F_{1,17} = 1.25$, $P = 0.28$; Fig. 4). Nevertheless, it was larger (i.e. more accelerated at the end of the day) under the LD 9 : 15 cycle than under the LD 7 : 17 cycle in both populations (within-subjects effect: $F_{1,17} = 5.35$, $P = 0.033$; Fig. 4). The interaction between population and photoperiod was not significant ($F_{1,17} = 0.26$, $P = 0.62$).

The exponent of diurnal body mass gain under the 'natural' photoperiod for the respective population (i.e. Ventorrillo LD 9 : 15, and Rowardennan LD 7 : 17) was not significantly correlated with body mass at the beginning of the day (ANCOVA model; effect of covariate: $F_{1,17} = 1.79$, $P = 0.20$), nor did this differ between populations (test of parallelism: $F_{1,16} = 0.01$, $P = 0.91$).

The rate of daily mass gain was accelerated in both populations (i.e. the exponent was significantly larger than 1) under the LD 9 : 15 photoperiod ($P < 0.03$ in the two t -tests comparing the mean of observed exponents

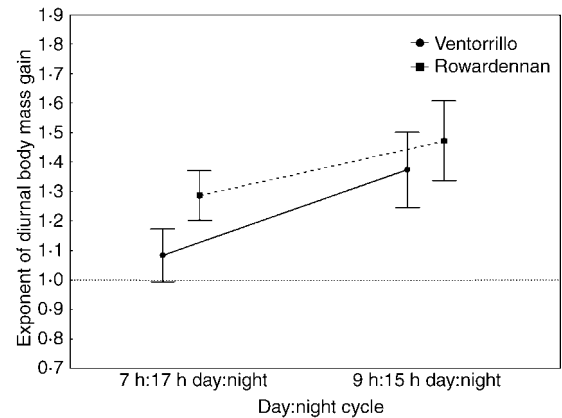


Fig. 4. Population differences in the exponent of diurnal body mass gain (see legend to Fig. 1) in captive coal tits under different day length regimes at Rowardennan (Scotland) and Ventorrillo (Central Spain). Sample sizes and data presented as in Fig. 3.

with the null hypothesis of $e = 1$). The same result was observed under the LD 7 : 17 cycle for the Rowardennan population ($P = 0.037$), but not for birds from Ventorrillo ($P = 0.26$).

Discussion

Small passerine birds are typically diurnal foragers and so use up energy (and hence mass) while unable to forage throughout the hours of darkness; therefore shorter day lengths in winter result in their having a shorter time to feed each day at the time of year when their food supply is usually lowest (and least predictable) and their energy demands for body maintenance are highest (Bednekoff & Krebs 1995; Lahti *et al.* 1997; Cresswell 1998; Dall & Witter 1998; Rogers & Reed 2003). Previous studies have demonstrated that such birds respond to these constraints by following a 'winter fattening strategy', characterized by an increase in mean daily body mass from early autumn to the winter solstice and then a decrease in body mass as days are becoming longer (Lehikoinen 1987; Haftorn 1989; Rogers & Rogers 1990; Meijer *et al.* 1996). This requires the birds to adjust the rate at which they lay down energy reserves during the day, increasing their hourly rate of mass gain when the day length is shorter. They therefore need to be very sensitive to day length, as this governs both the duration of the fasting period and the preceding length of time available for building up body reserves (McNamara & Houston 1990).

However, our results show that day length affects the pattern of mass gain through the day, as well as the average amount gained 1 h after dawn. Coal tits living at a latitude with a short winter day (Scotland) gained mass steadily throughout the daylight hours (exponent $e = 1$; see Koivula *et al.* 2002 for similar near-linear trajectories of daily mass gain in wintering wild willow tits *Poecile montana*, Conrad von Baldenstein 1827, living at northern latitudes). In contrast, those living in a similar temperature regime but further south in Spain showed an exponential pattern of mass gain (exponent

$e = 1.6$), putting on reserves at a slow rate in the morning but then accelerating towards dusk. These findings can be interpreted in terms of the costs of carrying fat reserves, which include a higher predation risk (Gosler, Greenwood & Perrins 1995; Carrascal & Polo 1999; Piersma, Koolhaas & Jukema 2003; Ydenberg *et al.* 2004; Macleod *et al.* 2005a,b), higher metabolic costs of activity (Lindström & Rosén 2003; Carrascal & Polo 2006) and lower flight manoeuvrability (Witter, Cuthill & Bonser 1994; Lee *et al.* 1996; Veasey, Metcalfe & Houston 1998). When time is less constrained (i.e. when the day length is relatively long even at the winter solstice), the optimal strategy is to postpone the major increase in body mass until late in the day, and so minimize the costs of carrying the reserves needed for overnight survival. However, at higher latitudes less time is available for foraging in midwinter (and the risk of starvation is higher), and so birds must feed intensively and lay down fat reserves throughout the day (Houston & McNamara 1993; Rogers *et al.* 1993; Bednekoff & Krebs 1995; Pravosudov & Grubb 1997; MacLeod *et al.* 2005a,b).

Therefore, there is a sound theoretical basis for the difference in the shape of the daily mass trajectories of Spanish and Scottish coal tits. At a proximate level, there are two potential explanations (which are not mutually incompatible) for these population differences. The first assumes that there is genetically based geographical variation in fattening strategies as a consequence of local adaptations to prevailing environmental conditions and reproductive isolation between populations. The second assumes that there are common physiological constraints that determine a small subset of behavioural solutions, and thus different populations should display the same solutions when experienced in the same environment. Our experimental results suggest that the observed differences in the patterns shown by wild birds at Ventorrillo and Rowardennan are mostly of environmental origin, as these differences disappeared when the birds were studied under identical circumstances in captivity; moreover, the differences in mass trajectories between the wild populations could be recreated experimentally by altering the day length (see also Rogers *et al.* 1993). Thus when the photoperiod was made to mimic the situation in Spain where daylight is less constrained, all birds delayed building up their body reserves until late in the day. In contrast, when the short winter days of Scotland were simulated, they responded by fattening at a high rate from dawn onwards (despite food being available *ad libitum*), such that the body mass increase 1 h after dawn was twice as high under the shorter day length (see Fig. 3). These results demonstrate convincingly that the daily trajectories for body mass in these contrasting populations are phenotypically plastic and dependent on environmental conditions (see also Macleod *et al.* 2005a).

Nevertheless, we found interesting population differences in the average body mass of the coal tits in captivity, with Scottish birds being lighter than Spanish

birds under the same controlled conditions of *ad libitum* food availability and relatively stable ambient temperatures. While this difference is consistent with the clinal variation in skeletal body size observed in the Western Palearctic, with the largest coal tits being found in Morocco and central Spain and the smallest birds in Scotland and Scandinavia (Cramp & Perrins 1993; Polo 2005), there were no corresponding differences in the winter body mass of the two populations coal tits in the wild; this suggests that the population living at higher latitude (Rowardennan) with a shorter day length may maintain a higher level of reserves under natural conditions.

The relationship between the rate of daily body mass increase and the length of daytime was modulated by differences in the initial level of body reserves at the beginning of the day. In both populations of wild birds there was a positive relationship between an individual's mean mass at the start of the day and the size of the exponent of its mass trajectory: thus individuals that were heaviest at the start of the day were more likely to delay gaining mass until later in the day. However, this relationship was only observed in free-living birds, and disappeared under the less-restrictive conditions in captivity, reinforcing the association between less-constrained internal body reserves or environmental conditions and an exponential daily pattern of body mass increase.

In summary, wintering coal tits show patterns of mass gain through the day that are compatible with current theories of the costs and benefits of fat storage, with birds at lower latitudes (with longer winter days) having a greater tendency to delay mass gain until late in the day; the experimental study revealed that these patterns are plastic, with birds responding directly to the day length that they experience. However, the variation between individuals in fattening strategy that was observed when they were in the wild (but not when they were brought into captivity) suggests that they are continually making fine-scale adjustments to energy reserves, on the basis of both state-dependent and extrinsic cues.

Acknowledgements

This study was funded by DGICYT project BOS2000-0993 of the Spanish Ministry of Education and Culture and by Glasgow University. The Biological Stations Ventorrillo (CSIC) and Rowardennan (Scottish Centre for Ecology and the Natural Environment – SCENE, Glasgow University) provided logistical support. Birds at Rowardennan were captured and temporarily taken into captivity under licence from Scottish Natural Heritage.

References

- Bednekoff, P.A. & Houston, A.I. (1994) Optimising fat reserves over the entire winter: a dynamic model. *Oikos*, **71**, 408–415.
- Bednekoff, P.A. & Krebs, J.R. (1995) Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology*, **9**, 457–462.

- Blem, C.R. (1976) Patterns of lipid storage and utilization in birds. *American Zoologist*, **16**, 671–684.
- Carrascal, L.M. & Polo, V. (1999) Coal tits, *Parus ater*, lose weight in response to chases by predators. *Animal Behaviour*, **58**, 281–285.
- Carrascal, L.M. & Polo, V. (2006) Effects of wing area reduction on winter body mass and foraging behaviour in coal tits: field and aviary experiments. *Animal Behaviour*, **72**, 663–672.
- Cramp, S. & Perrins, C.M. (1993) *The Birds of the Western Palearctic*, Vol. VII. Oxford University Press, Oxford.
- 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.
- 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.
- Davis, P.G. (1981) *Trapping Methods for Bird Ringers*. British Trust for Ornithology, Tring.
- Foster, S.A. (1999) The geography of behaviour: an evolutionary perspective. *Trends in Ecology and Evolution*, **14**, 190–195.
- Gosler, A.G. (1996) Environmental social determinants of winter fat storage in the Great Tit *Parus major*. *Journal of Animal Ecology*, **65**, 1–17.
- Gosler, A.G. (2002) Strategy and constraint in the winter fattening response to temperature in the great tit *Parus major*. *Journal of Animal Ecology*, **71**, 771–779.
- 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.
- Hagemeijer, W. & Blair, M. (1997) *The EBCC Atlas of European Breeding Birds Their Distribution and Abundance*. T&AD Poyser, London.
- Houston, A.I. & McNamara, J. (1993) A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica*, **24**, 205–219.
- Houston, A.I., McNamara, J. & 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-Biological Sciences*, **341**, 375–393.
- King, J.R. & Mewaldt, L.R. (1981) Variation of body-weight in gambel white-crowned sparrows in winter and spring – latitudinal and photoperiodic correlates. *Auk*, **98**, 752–764.
- Koivula, K., Orell, M. & Lahti, K. (2002) Plastic daily fattening routines in willow tits. *Journal of Animal Ecology*, **71**, 816–823.
- Lahti, K., Koivula, K. & Orell, M. (1997) Dominance, daily activity and winter survival in willow tits: detrimental cost of long working hours? *Behaviour*, **134**, 921–939.
- Lee, S.J., Witter, M.S., Cuthill, I.C. & Goldsmith, A.R. (1996) Reduction in scape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris*. *Proceedings of the Royal Society of London B – Biological Sciences*, **263**, 619–624.
- Lehikoinen, E. (1987) Seasonality of daily weight cycle in wintering passerines and its consequences. *Ornis Scandinavica*, **18**, 216–226.
- Lilliendahl, K. (2000) Daily accumulation of body reserves under increased predation risk in captive Greenfinches *Carduelis chloris*. *Ibis*, **142**, 587–595.
- Lilliendahl, K. (2002) Daily patterns of body mass gain in four species of small wintering birds. *Journal of Avian Biology*, **33**, 212–218.
- 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., Gosler, A.G. & Cresswell, W. (2005a) Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *Journal of Animal Ecology*, **74**, 956–964.
- Macleod, R., Barnett, P., Clark, J.A. & Cresswell, W. (2005b) Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *Journal of Animal Ecology*, **74**, 292–302.
- McNamara, J. & Houston, A.I. (1990) The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheoretica*, **38**, 37–61.
- McNamara, J., Houston, A.I. & Lima, S.L. (1994) Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 289–302.
- Meijer, T., Rozman, J., Schulte, M. & StachDreesmann, C. (1996) New findings in body mass regulation in zebra finches (*Taeniopygia guttata*) in response to photoperiod and temperature. *Journal of Zoology*, **240**, 717–734.
- 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-Biological Sciences*, **261**, 395–400.
- 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. (2005) Carbonero Garrapinos – *Parus ater*. *Enciclopedia Virtual de Los Vertebrados Españoles* (eds L.M. Carrascal & A. Salvador). Museo Nacional de Ciencias Naturales, Madrid. <http://www.vertebradosibericos.org/aves/parate.html>.
- Polo, V. & Bautista, L.M. (2006a) Daily routines of body mass gain in birds: 1. An exponential model. *Animal Behaviour*, **72**, 503–516.
- Polo, V. & Bautista, L.M. (2006b) Daily routines of body mass gain in birds: 2. An experiment with reduced food availability. *Animal Behaviour*, **72**, 517–522.
- Pravosudov, V.V. & Grubb, T.C. (1997) Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behavioral Ecology*, **8**, 332–339.
- Pravosudov, V.V. & Lucas, J.R. (2001) Daily patterns of energy storage in food-caching birds under variable daily predation risk: a dynamic state variable model. *Behavioral Ecology Sociobiology*, **50**, 239–250.
- Rogers, C.M. & Reed, A.K. (2003) Does avian winter fat storage integrate temperature and resource conditions? A long-term study. *Journal of Avian Biology*, **34**, 112–118.
- Rogers, C.M. & Rogers, C.J. (1990) Seasonal variation in daily mass amplitude and minimum body mass: a test of a recent model. *Ornis Scandinavica*, **21**, 105–114.
- Rogers, C.M., Nolan, V. Jr & Ketterson, E.D. (1993) Geographic variation in winter fat of dark-eyed juncos: displacement to a common environment. *Ecology*, **74**, 1183–1190.
- Senar, J.C., Doménech, J., Carrascal, L.M. & Moreno, E. (1997) A funnel trap for the capture of tits. *Butlletí del Grup Català d'Anellament*, **14**, 17–24.
- StatSoft (2001) *STATISTICA (Data Analysis Software System)*, Version 6.0. StatSoft, Inc., Tulsa, OK, USA.
- Thomas, R.J. (2000) Strategic diel regulation of body mass in European robins. *Animal Behaviour*, **59**, 787–791.
- Veasey, J.S., Metcalfe, N.B. & Houston, D.C. (1998) A reassessment of the body mass upon flight speed and predation risk in birds. *Animal Behaviour*, **56**, 883–889.
- Witter, M.S. & Cuthill, I.C. (1993) The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **340**, 73–92.
- 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.
- 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-Biological Sciences*, **271**, 1263–1269.

Received 26 December 2006; accepted 30 April 2007