

Nocturnal body mass loss in coal tits *Periparus ater*: the combined effects of ambient temperature and body reserves^{*}

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Abstract The environmental temperature and the level of body reserves have been described as important regulating factors of the amount of energy used at resting (i.e. nocturnal body mass loss). However, because these variables are associated in natural conditions, previous studies have not made a clear distinction between the separate effect of ambient temperature and body reserves on nightly energy management. To investigate whether ambient temperature acts as a proximate factor on nocturnal body mass regulation in captive coal tits *Periparus ater*, the day-to-day and day-to-night changes in environmental temperatures were experimentally manipulated, under unrestricted food availability. The experiment was conducted within the normal autumn range of temperature variation in a mountain area of continental Mediterranean climate in Central Spain. Nocturnal body mass loss depended on the level of body mass at dusk and daily body-mass gain in the previous day. The largest rates of body mass loss at night were recorded when birds ended the previous day-time period with the highest levels of body reserves obtained after high rates of diurnal body mass increase. However, unpredictable changes in current environmental temperatures did not influence night body mass loss in the coal tit, as it would be expected following a pure physiological energetic balance. These results suggest that birds try to maintain body reserves within narrow ranges when some environmental factors, as the ambient temperature, become unpredictable [Acta Zoologica Sinica 54 (4): 615–621, 2008].

Key words Coal tit, *Periparus ater*, Body mass loss, Body reserves, Night, Temperature, Winter

环境温度和体内储备物共同影响煤山雀夜间体重的下降^{*}

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摘要 环境温度和体内储备物水平被认为是鸟类在静止状态下能量利用的重要调节因子(夜间体重降低)。然而,以往的研究没有把环境温度和体内储备物对夜间能量维持加以明确的区分。为了研究环境温度是否是为煤山雀(*Periparus ater*)夜间体重调节的直接因子,在自由取食条件下,实验室控制日-日和日-夜环境温度。温度变化模拟西班牙中部地中海山区秋季日-夜温度的变化。夜间体重取决于黄昏时的体重以及前一天体重的增加值。当前一日白天煤山雀体重增加最大时,记录夜间体重最大降低的比率。然而,环境温度的不可预见性没有影响煤山雀夜间体重降低,可以解释煤山雀内在的生理能量平衡。这些结果提示,当一些环境因子如温度变得不可预见时,鸟类在狭小范围内保持体内储备物[动物学报 54(4): 615–621, 2008]。

关键词 煤山雀 体重下降 体内储备物 夜晚 温度 冬季

Wintering birds in cold temperate regions must attain high metabolic rates in order to maintain normothermic body temperatures during times of extreme cold, shorter daylength, and reduced food availability. Accordingly, small birds typically carry high levels of body reserves (Lehikoinen, 1987; Haftorn, 1989), and pectoralis

muscle thickness (i.e. a measure of body condition) is usually higher at localities with more severe environmental conditions (Carrascal et al., 1998). These reserves are used as an additional source of energy to survive the longer and colder nights and the beginning of the subsequent day (King, 1972; Blem, 1976), when

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internal reserves are at their minimum and foraging success is unpredictable due to weather variability.

Body mass loss at night-time has been described in very few occasions in terms of ambient temperature and actual body reserves (e.g. Lehtikoinen, 1987; Bednekoff et al., 1994; Thouzeau et al., 1999). Studies on nocturnal energy regulation in birds have not made a clear distinction between the separate effects of these two variables. Under natural conditions, diurnal and nocturnal temperatures are usually related, and thus birds can adjust their reserve levels to anticipate the expected energy demands at night-time (e.g. Caraco et al., 1990; Gosler, 1996; Cresswell, 1998). Following a pure physiological model, a decrease in body reserves, due to night resting metabolism, should be expected when ambient temperature drops (Calder and King, 1974; Reinertsen and Haftorn, 1986).

By means of an experiment, this paper analyses the separate effects of environmental temperatures and diurnal body weight on nocturnal weight loss in coal tits. Winter midday temperature has a negative significant effect on diurnal body mass of coal tits, although it accounts for a low proportion of observed variability (Carrascal and Polo, 2006). Working indoors with coal tits, we simulated unpredictable day to day and day to night changes in environmental temperatures, within the normal autumn range of the study area (mountain area in Central Spain of continental Mediterranean climate), under unrestricted food availability. We investigate if, under these experimental conditions, both the intensity of cold during the night and the level of body reserves at dusk are positively related with nocturnal body mass loss, according to well known and deterministic metabolic equations (Calder and King, 1974; Kendeigh et al., 1977).

1 Material and methods

1.1 Procedure

Twelve coal tits (six adults and six juveniles) were captured at 'El Ventorrillo' field station (1500 m above sea level, 40°45'N, 04°01'W, Sierra de Guadarrama, central Spain) in the second half of November 2001. They were colour banded for individual identification and introduced into a large outdoor aviary prior to the experiment (for more details on the study area and capture methods see Carrascal et al., 1998; Carrascal and Alonso, 2006). The aviary was placed in a small forest clearing of 15 – 20 m, and was covered by translucent fiberglass panels to protect the birds from snow and rain. The twelve coal tits were randomly assigned in triads to four cages (2 m × 2 m × 2 m) where they lived for a two weeks period of acclimation to the captivity experimental conditions. Each cage contained a nest box and several pine and cedar branches fully covered by green needles, which the birds used for perching, roosting and

sheltering. Birds were given access to water for bathing to prevent any plumage deterioration throughout the experiment. Coal tits were maintained with ad libitum diet of water with vitamins, dry kitten cookies, peanuts, sunflowers and pine seeds. They were accustomed to our presence as we visited the cages every 2 – 3 days to change the water and the food. Coal tits were cared for in accordance with guidelines of the Guide for the Care and Use of Laboratory Animals (1996, National Academy Press, 2101 Constitution Ave. NW, Washington, DC 20055, USA) and the Spanish laws regarding animal experimentation.

We performed the experiment during the following 3 weeks (29 November to 18 December 2001). Birds were individually housed indoors in small cages (0.5 m × 0.4 m × 0.3 m). The experimental cages were located in two large rooms of 6 m × 4 m near large windows (6 cages in each room). Therefore, birds experienced the natural light cycle of study area on a 8 h 56 min L:15 h 4 min D light regime ($SD = 0.19$ h: variation was mainly attributable to natural day-length variation across the study period). Each cage had four perches, two drinking bottles and one feeder. Coal tits were maintained with ad libitum diet of water with vitamins, and a mixture of dry kitten cookies, peanuts, sunflowers and pine seeds for all the experiment. Drinking bottles and feeders were replenished at night-time on the experimental days to avoid any disturbance on bird behaviour (see below). There was no evidence of plumage deterioration with time in the 3-week experimental trial.

At sunset (16 h 56 min GMT on average), coal tits were captured in nearly complete darkness to catch them easily and to reduce the stress of capture (we closed the shutter of the windows and waited 3 minutes, after which period birds remained still in the cages). Immediately afterwards, birds were moved to another room and weighed with an electronic balance (at the nearest 0.01 g) and housed in cloth (cotton) boxes (0.4 m × 0.2 m × 0.2 m), without food and water, where they spent the night into a small dark thermal chamber. All the birds were processed by two researchers in order to minimize the time devoted to handling them. The manipulation of the birds can induce some avian stress (i.e. possible increase in stress hormones). However, we suppose not bias in the interpretation or the results because all birds were manipulated in same way.

Ambient temperatures were controlled by using electronic stoves during day-time and a small dark thermal chamber (1 m × 1 m × 0.7 m) at night time. The temperatures throughout every night (at the nearest 0.1°C) or day (at the nearest 1°C) were maintained constant and chosen at random within specified ranges (see below). Approximately 15 h after (see above), at sun rising, birds were captured again from the cloth boxes in complete darkness, they were weighed and immediately

released to their metallic cages in the experimental rooms with the windows opened. Coal tits did not suffer any other interference from the researchers throughout the study period. This procedure was repeated three days per week (Tuesday, Wednesday and Thursday), so birds were not bothered from Friday to Monday when they remained into the experimental cages with the windows opened and natural non-controlled temperatures. On Tuesday of each experimental week, birds were captured and weighed at sunrise (approx. 8 h GMT). Measurement of masses at the beginning of the three-day per week experimental period was necessary to calculate the rates of diurnal body mass gain (see below).

Nocturnal temperature ranged between -1°C and 7.6°C (Mean = $4.4^{\circ}\text{C} \pm 2.5$ SD), remaining constant in each night-time period. Diurnal temperature in the experimental rooms was controlled by means of opening the windows to equal ambient temperature outdoors, or using electronic stoves. It was measured at midday (12 h GMT). Day-time temperature in the experimental rooms was randomly settled, ranging from 5°C to 18.5°C (Mean = $9.8^{\circ}\text{C} \pm 4.1$ SD; it followed the natural diurnal variability, from low temperatures at dawn and $3^{\circ}\text{C} \pm 10^{\circ}\text{C}$ higher in the evening). The range of variation of nocturnal and diurnal temperatures in the study was selected to mimic the natural variation of the environmental temperatures in the study area during autumn. As diurnal and nocturnal temperatures were randomly selected, their covariation was completely decoupled ($r = 0.024$, $n = 9$ experimental days, $P = 0.951$), and birds had no clue to predict the temperature they were to experience the following night considering the previous day.

Diurnal rate of body mass gain for each individual bird was calculated as the difference between body mass at dusk minus body mass at dawn, divided by the time elapsed (expressed in g/h). In the same way, night-time body mass loss (expressed in g/h) was calculated as the difference between body mass at dusk (end of the day at sunset) minus the body mass at the beginning of the following day (dawn), divided by night-time duration.

1.2 Statistical analyses

We used a mixed-model ANCOVA to analyze night-time body mass loss (dependent variable) in relation to ambient temperatures at night and in the preceding day, daytime rate of body mass gain and body mass at dusk in the preceding day (covariate variables) and coal tit identity as a random factor (BIRD; 12 individual birds). We used the unconstrained parameters model to test significance of the covariates in the mixed ANCOVA (Voss, 1999; Quinn and Keough, 2002). In this approach, the error terms for the effects of covariates were the interactions of each covariate \times the random factor BIRD. This analytical procedure is very conservative, because it solves the problem of inflated sample sizes by

reducing the degrees of freedom of the error terms and avoids any kind of pseudoreplication (i. e. the proper sample unit for the fixed effects is the individual bird and not every measurement obtained in the cages). Repeatability was computed from the mean squares of one-way ANOVAs (Lessells and Boag, 1987) using BIRD as factor.

2 Results

Average body mass at dawn (8 h GMT) of the 12 studied individual birds was $9.17 \text{ g} \pm 0.42 \text{ g}$ (Mean \pm SD, the same below. Range: $8.59 \text{ g} - 9.76 \text{ g}$), while average body mass at dusk (17 h GMT) was 9.98 ± 0.43 (range: $9.41 - 10.61 \text{ g}$; see Table 1). Thus, the average rate of body mass gain during the 9 hours of daytime was $0.090 \text{ g} \pm 0.008 \text{ g/h}$ (range: $0.079 - 0.104 \text{ g/h}$), and the average rate of body mass loss in the 15 hours of night-time was $0.053 \text{ g} \pm 0.005 \text{ g/h}$ (range: $0.047 - 0.062 \text{ g/h}$). Repeatabilities were highly significant ($P < 0.01$), although they were higher for body mass at dawn and dusk ($r_i > 0.75$) than for rates of diurnal body mass gain and nocturnal body mass loss (r_i around 0.2).

The interindividual variation in nocturnal body mass loss was highly significant, explaining nearly one-fourth of the total variance (Table 2). Nocturnal and diurnal temperatures were not significantly associated with night-time body mass loss, accounting for a very low proportion of the observed variability ($< 1\%$). The main variable responsible for body mass loss at night was body mass at dusk (26.4% of the original variance): the largest rates of body mass loss at night were recorded when birds ended the previous day-time period with the highest levels of body reserves. Previous day-time body mass gain also played an important role determining nocturnal body mass loss (15.1% of variance explained): the days with large rates of body mass increase were followed by nights with large rates of body mass loss. The relationships within each experimental bird between the rate of night-time body mass loss and the rate of diurnal body mass gain and body mass at dusk are shown in Fig.1 and 2, respectively.

3 Discussion

We have simultaneously analyzed the separate effects of body reserves and current ambient temperatures on the nocturnal energy management (i. e. body mass loss) of a small bird wintering at temperate latitude characterized by cold and long nights. These variables were experimentally decoupled to prevent possible confounding effects, due to the strong covariation among body mass, ambient temperature and day length under natural conditions (Lehikoinen, 1987; Meijer et al., 1994; Cresswell, 1998; Gosler, 2002; Rogers and Reed, 2003; Macleod et al., 2005; Carrascal and Polo, 2006; Polo et al., 2007).

Table 1 Inter and intra individual variation in body mass (in g) at dawn (8 h GMT) and at dusk (17 h GMT), and body mass gain (g/h for a daytime of 9 h) and loss (g/h for a night-time of 15 h) of 12 coal tits living in indoor aviaries

Bird	Body mass at dawn (g)		Body mass at dusk (g)		Daytime gain (g/h)		Night-time loss (g/h)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	9.71	0.15	10.45	0.10	0.082	0.02	0.049	0.01
2	9.27	0.10	10.02	0.10	0.084	0.02	0.050	0.01
3	9.18	0.10	9.93	0.12	0.084	0.01	0.050	0.00
4	8.85	0.16	9.68	0.17	0.093	0.02	0.054	0.01
5	9.70	0.08	10.57	0.13	0.097	0.02	0.059	0.01
6	8.69	0.24	9.41	0.32	0.081	0.02	0.048	0.01
7	8.59	0.22	9.47	0.30	0.098	0.02	0.056	0.01
8	9.76	0.33	10.61	0.40	0.095	0.02	0.054	0.01
9	8.74	0.15	9.62	0.13	0.098	0.01	0.058	0.00
10	8.88	0.11	9.59	0.16	0.079	0.01	0.047	0.01
11	9.29	0.12	10.06	0.12	0.085	0.02	0.051	0.01
12	9.38	0.19	10.31	0.21	0.104	0.01	0.062	0.01
Mean	9.17		9.98		0.090		0.053	
SD	0.42		0.43		0.008		0.005	
r_i	0.82		0.79		0.22		0.17	
F	43.08		35.77		3.49		2.88	
P	<0.001		<0.001		0.0004		0.003	

Sample size is 9 days for every bird. r_i : repeatability; F and P are the results of one-way ANOVAS comparing the twelve coal tits.

Table 2 Mixed-model ANCOVA of night-time body mass loss (expressed in g/h) with respect to bird identity (BIRD), diurnal and nocturnal ambient temperatures, daytime gain (in g/h) and body mass at dusk (evening weight)

	df	beta	F	P	% var.
BIRD	11, 92		5.80	<0.001	23.4
Covariates:					
Body mass at dusk	1, 11	0.43	25.33	<0.001	26.4
Daytime body mass gain	1, 11	0.28	12.05	0.005	15.1
Diurnal temperature	1, 11	-0.08	1.73	0.215	0.5
Nocturnal temperature	1, 11	-0.05	0.42	0.530	0.9

Sample size is 108 days for 12 individual birds (9 days per bird). df : degrees of freedom (effect, error term). % var.: percentage of variance accounted for by each effect (GLM with type III sum of squares). beta: standardized regression coefficient for covariates.

In our experiment, an important proportion of the within-individual variation in nocturnal body mass loss (41.5%) was related to the level of body reserves (i. e. evening body weight and daily body mass gain in the preceding day). Coal tits decreased body mass loss during the night when they carried lower level of fat reserves at dusk or when they gained less mass during the previous day. These results are in agreement with theoretical predictions of dynamic models of fat reserves in small birds (McNamara and Houston, 1990; Pravosudov and Lucas, 2000) and with the results in other field and experimental studies (e. g. Lehtikoinen, 1987; Haftorn,

1992; Bednekoff et al., 1994). Moreover, the pattern of diurnal body mass gain in the Coal tit is also linked to the average mass at the start of the day, with mass increasing more rapidly in lighter birds (Polo et al., 2007). All these results are consistent with behavioural changes of birds to prevent present and future risk of starvation (Polo and Bautista, 2002).

Theoretical and experimental evidence supports the idea that ambient winter temperature may act as a proximate factor operating on fat reserve levels in the short term (McNamara and Houston, 1990; Gosler, 2002; Macleod et al., 2005). Following a pure physiological

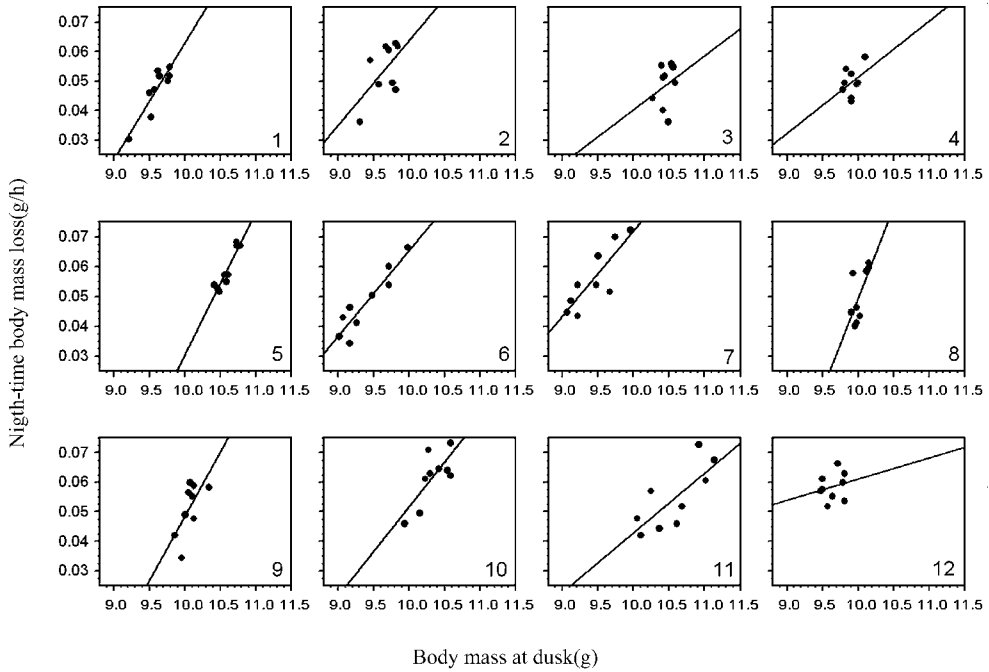


Fig.1 Within-individual relationship between the rate of night-time body mass loss and body mass at dusk

Sample size is 9 days for every individual coal tit. In the right lower corner of each scatterplot is the number code of each individual bird (see Table 1).

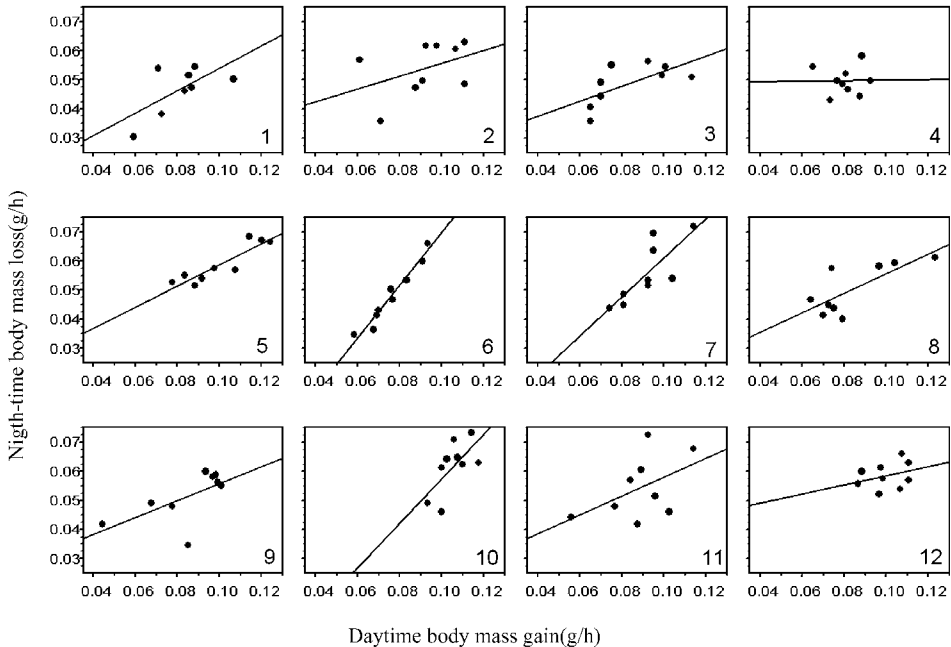


Fig.2 Within-individual relationship between the rates of nocturnal body mass loss and diurnal body mass gain

Each scatterplot corresponds to a different coal tit. (see Fig.1 for details).

argumentation derived from allometric models for small birds, relating energy expenditure to body mass and temperature (see Calder and King, 1974; Reinertsen and Haftom, 1986; Reinertsen, 1986; Lehikoinen, 1987), the maximum variation of 9°C in nocturnal temperature used in our experiment should translate into a nocturnal body mass loss variation of circa 20%. Nevertheless, diurnal and nocturnal temperatures had no significant

effects on the night body mass loss in the coal tits, explaining a negligible amount of variance in this variable (1.4%). Similarly, current ambient temperature was not a good predictor of mean daily fat levels in the great tit *Parus major* (Bednekoff et al., 1994; Gosler and Carruthers, 1999; Gosler, 2002; but see Lilliendahl et al., 1996; Lehikoinen, 1987). In an experimental study, Bednekoff and colleagues (1994) used both a

warm overnight temperature of 15.5°C and a cold one of 1.5°C and found a similar night weight loss in great tits, not dependent upon overnight temperature.

On the light of our results a question arises: how do birds adjust overnight body mass loss independently of unpredictable current temperatures? The adjustment of overnight body mass loss in relation to previous and current body reserves may be a direct consequence of the increase in resting metabolism with larger body reserves (Reinertsen, 1996), and has been reported in free-living individuals of all *Parus* species (see Haftorn, 1992). Facultative nocturnal hypothermia (Haftorn, 1972; Reinertsen, 1996) could be the only adequate mechanism to explain the observed pattern of nocturnal body mass loss. Hypothermia is an efficient and widely distributed energy-saving mechanism in small diurnal birds living in very cold environments (Swanson, 1990, 1993; Reinertsen, 1996; McKechnie and Lovegrove, 2002), that may result in a 10% – 50% reduction in nocturnal energy expenditure (Haftorn, 1972; Reinertsen and Haftorn, 1983, 1984, 1986; Chaplin, 1974, 1976; Mayer et al., 1982; Waite, 1991; Cooper and Gessaman, 2005). There is also experimental evidence that birds living in warmer environments can use hypothermia to save energy during the night (Hainsworth et al., 1977; Maddocks and Geiser, 1997). However, we have not evidence for this body temperature control in our birds. This interesting possibility remains to be directed in further studies.

A potential confounding effect of our results might arises if birds in our study, since food was provided ad libitum, showed differences in feeding access immediately prior of going to roost in relation to daytime temperatures. If birds ingested more food prior to roosting on colder than on warmer days, then body mass at dusk would be artificially elevated and mass loss due to digestion and elimination of the ingested food would contribute to overall nocturnal mass loss, thus causing mass loss rates to be inflated relative to birds going to roost without prior feeding. However, previous information in body weight gain of birds of the same species (Polo et al., 2007) during the last hour of the day (i. e. the hour prior going to roost) have shown not intra-individual differences in this variable in relation to natural daily temperatures. In addition, the body mass gained in this last hour of the day is less than 15% – 18% of the total body mass gained during the day (Polo and Bautista, 2006a, b). Thus, we do not imagine significant confounding effect caused by this reasons.

Inter-individual differences in nocturnal body mass loss explained nearly one-fourth of the total variance in this variable. It may be that birds do show great individual variation that is related to their size. Since large birds with large organ and muscle masses would be expected to show highest absolute mass losses over night,

the significant effect of “bird” may simply reflect bird lean mass, that are simply related to differences in body size. To discard this last possibility we have correlated the residuals of the mixed ANCOVA model in Table 2 analyzing night-time body mass loss, with mass at dawn the following morning. This correlation was not significant ($r = 0.016$, $n = 144$, $P = 0.829$), so interindividual differences in nocturnal body mass loss are not simply due to differences in body size. Perhaps, inter-individual differences in body mass loss might reflect some variation in nocturnal body temperatures. This possibility remains to be evaluated in further studies.

In conclusion, this study supports evidence on the proximate effect of body reserves at the beginning of the night and diurnal body mass gain in the preceeding day, but not current ambient temperatures, on the overnight body mass loss of a population of coal tits wintering in the Mediterranean region. The surprising negligible effect of temperature on nocturnal body mass loss could be explained if the most probable mechanism for the control of night body mass loss is the use of nocturnal hypothermia.

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References

- Bednekoff PA, Biebach H, Krebs JR, 1994. Great tit fat reserves under unpredictable temperatures. *J. Avian Biol.* 25: 156 – 160.
- Blem CR, 1976. Patterns of lipid storage and utilization in birds. *Am. Zool.* 16: 671 – 684.
- Calder WA, King JR, 1974. Thermal and caloric relations of birds. In: Farmer DS, King JR ed. *Avian Biology*. Volume IV. New York: Academic Press, 259 – 413.
- Caraco T, Blanckenhorn WU, Gregory GM, Newman JA, Recer GM, Zwicker SM, 1990. Risk-sensitivity: ambient temperature affects foraging preferences. *Anim. Behav.* 39: 338 – 345.
- Carrascal LM, Alonso CL, 2006. Habitat use under latent predation risk. A case study with wintering forest birds. *Oikos* 112: 51 – 62.
- Carrascal LM, Polo V, 2006. Effects of wing area reduction on winter body mass and foraging behaviour in coal tits: field and aviary experiments. *Anim. Behav.* 72: 663 – 672.
- Carrascal LM, Senar JC, Mozetich I, Uribe F, Domenech J, 1998. Interaction between environmental stress, body condition, nutritional status and dominance in Mediterranean great tits *Parus major* during winter. *Auk* 115: 727 – 738.
- Chaplin SB, 1974. Daily energetics of the black-capped chickadee *Parus atricapillus* in winter. *J. Comp. Physiol.* 89: 321 – 330.
- Chaplin SB, 1976. The physiology of hypothermia in the black-capped chickadee *Parus atricapillus*. *J. Comp. Physiol.* 112: 335 – 344.
- Cooper SJ, Gessaman J, 2005. Nocturnal hypothermia in seasonally acclimatized mountain chickadees and Juniper Titmice. *Condor* 107: 151 – 155.
- Cresswell W, 1998. Diurnal and seasonal mass variations in blackbirds *Turdus merula*: consequences for mass-dependent predation risk. *J. Anim. Ecol.* 67: 78 – 90.
- Gosler AG, Carnuthers T, 1999. Body reserves and social dominance in the great tit *Parus major* in relation to winter weather in southwest Ireland. *J. Avian Biol.* 30: 447 – 459.
- Gosler AG, 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *J. Anim. Ecol.* 65: 1 – 17.

- Gosler AG, 2002. Strategy and constraint in the winter fattening response to temperature in the great tit *Parus major*. *J. Anim. Ecol.* 71: 771 – 779.
- Haftorn S, 1972. Hypothermia of tits in the arctic winter. *Ornis Scand.* 3: 153 – 166.
- Haftorn S, 1989. Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. *Wilson Bull.* 101: 217 – 235.
- Haftorn S, 1992. The diurnal body weight cycle in titmice *Parus* spp. *Ornis Scand.* 23: 435 – 443.
- Hainsworth FR, Collins BG, Wolf LL, 1977. The function of torpor in hummingbirds. *Physiol. Zool.* 50: 215 – 222.
- Kendeigh SC, Dol'nik VR, Gavrilov VM, 1977. Avian energetics. In: Pinowski J, Kendeigh SC ed. *Granivorous Birds in Ecosystems*. New York: Cambridge University Press, 127 – 204.
- King JR, 1972. Adaptive periodic fat storage by birds. In: Voous KH ed. *Proc. XV International Ornithological Congress*. Brill: Leiden, 200 – 217.
- Lehikoinen E, 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scand.* 18: 216 – 226.
- Lessells CM, Boag PT, 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116 – 121.
- Lilliendahl K, Carlson A, Welander J, Ekman, JB, 1996. Behavioural control of daily fattening in great tits *Parus major*. *Can. J. Zool.* 74: 1612 – 1616.
- Lima SL, 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in wintering birds. *Ecology* 67: 377 – 385.
- Macleod R, Barnett P, Clark JA, Cresswell W, 2005. Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *J. Anim. Ecol.* 74: 292 – 302.
- Maddocks TA, Geiser F, 1997. Energetics, thermoregulation and nocturnal hypothermia in Australian silvereyes. *Condor* 99: 104 – 112.
- Mayer L, Lustick S, Battersby B, 1982. The importance of cavity roosting and hypothermia to the energy balance of the winter acclimatized Carolina Chickadee. *International Biometeorology* 26: 231 – 238.
- McKechnie AE, Lovegrove BG, 2002. Avian facultative hypothermic responses: a review. *Condor* 104: 705 – 724.
- McNamara JM, Houston AI, 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheor.* 38: 37 – 61.
- Meijer T, Möhring FJ, Trillmich F, 1994. Annual and daily variation in body mass and fat of starlings *Sturnus vulgaris*. *J. Avian Biol.* 25: 98 – 104.
- Polo V, Bautista LM, 2002. Daily body mass regulation in dominance-structured coal tit *Parus ater* flocks in response to variable food access: a laboratory study. *Behav. Ecol.* 13: 696 – 704.
- Polo V, Bautista LM, 2006a. Daily routines of body mass gain in birds: 1. An exponential model. *Anim. Behav.* 72: 503 – 516.
- Polo V, Bautista LM, 2006b. Daily routines of body mass gain in birds: 2. An experiment with reduced food availability. *Anim. Behav.* 72: 517 – 522.
- Polo V, Carrascal LM, Metcalfe N, 2007. The effects of latitude and day length on fattening strategies of wintering coal tits *Periparus ater* (L.): a field study and aviary experiment. *J. Anim. Ecol.* 76 (5): 866 – 872.
- Pravosudov VV, Lucas JR, 2000. The cost of being cool: a dynamic model of nocturnal hypothermia by small food-caching birds in winter. *J. Avian Biol.* 31: 463 – 472.
- Quinn GP, Keough MJ, 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.
- Reinertsen RE, Haftorn S, 1983. Nocturnal hypothermia and metabolism in the willow tit *Parus montanus* at 63°N. *J. Comp. Physiol.* 151: 109 – 118.
- Reinertsen RE, Haftorn S, 1984. The effect of short-time fasting on metabolism and nocturnal hypothermia in the willow tit *Parus montanus*. *J. Comp. Physiol.* 154: 23 – 28.
- Reinertsen RE, Haftorn S, 1986. Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol.* 156: 655 – 663.
- Reinertsen RE, 1996. Physiological and ecological aspects of hypothermia. In: Carey C ed. *Avian Energetics and Nutritional Ecology*. London: Chapman and Hall, 125 – 157.
- Rogers CM, Reed AK, 2003. Does avian winter fat storage integrate temperature and resource conditions? A long-term study. *J. Avian Biol.* 34: 112 – 118.
- Swanson DL, 1990. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the dark-eyed junco *Junco hyemalis*. *Auk* 107: 561 – 566.
- Swanson DL, 1993. Cold tolerance and thermogenic capacity in dark-eyed juncos in winter: geographic variation and comparison with American tree sparrows. *J. Therm. Biol.* 18: 275 – 281.
- Thouzeau C, Duchamp C, Handrich Y, 1999. Energy metabolism and body temperature of barn owls fasting in the cold. *Phys. Bioch. Zool.* 72: 170 – 178.
- Voss DT, 1999. Resolving the mixed models controversy. *Am. Stat.* 53: 352 – 356.
- Waite TA, 1991. Nocturnal hypothermia in gray jays *Perisoreus canadensis* wintering in interior Alaska. *Ornis Scand.* 22: 107 – 110.