

Nocturnal loss of body reserves reveals high survival risk for subordinate great tits wintering at extremely low ambient temperatures

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Received: 5 February 2012 / Accepted: 3 October 2012 / Published online: 20 October 2012
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Abstract Winter acclimatization in birds is a complex of several strategies based on metabolic adjustment accompanied by long-term management of resources such as fattening. However, wintering birds often maintain fat reserves below their physiological capacity, suggesting a cost involved with excessive levels of reserves. We studied body reserves of roosting great tits in relation to their dominance status under two contrasting temperature regimes to see whether individuals are capable of optimizing their survival strategies under extreme environmental conditions. We predicted less pronounced loss of body mass and body condition and lower rates of overnight mortality in dominant great tits at both mild and extremely low ambient temperatures, when ambient temperature dropped down to -43°C . The results showed that dominant great tits consistently maintained lower reserve

levels than subordinates regardless of ambient temperature. However, dominants responded to the rising risk of starvation under low temperatures by increasing their body reserves, whereas subdominant birds decreased reserve levels in harsh conditions. Yet, their losses of body mass and body reserves were always lower than in subordinate birds. None of the dominant great tits were found dead, while five young females and one adult female were found dead in nest boxes during cold spells when ambient temperatures dropped down to -43°C . The dead great tits lost up to 23.83 % of their evening body mass during cold nights while surviving individuals lost on average 12.78 % of their evening body mass. Our results show that fattening strategies of great tits reflect an adaptive role of winter fattening which is sensitive to changes in ambient temperatures and differs among individuals of different social ranks.

Communicated by Mark Chappell.

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Keywords Fattening strategies · Great tit · Low temperatures · *Parus major* · Winter survival

Introduction

For quite some time it has been known that the body mass of many northern temperate birds increases during the autumn, reaches a peak in midwinter and declines as spring approaches (Lehikoinen 1987; Haftorn 1989). Superimposed on this seasonal variation there is a marked diurnal variation in body mass (Evans 1969; King 1972; Blem 1990), wherein birds deposit up to 10 % of their morning mass in fat as fuel for the coming night (Haftorn 1992). Ambient temperature affect birds directly by increasing energy demand (Walsberg 1986; Andreev 1999; Carey and Dawson 1999; Storey 2003; Broggi 2006) and smaller birds often have higher energy requirements for their size than

larger congeners (Calder and King 1974; Kendeigh et al. 1977; McNab 2002). The short period of daylight in mid-winter reduces available foraging time and results in a long nocturnal fasting period. In combination with restricted access to food due to snow and ice cover, this increases the risk of entering the nocturnal roosting period with insufficient energy reserves, thereby reducing the probability of survival till the next morning. This is especially true when ambient temperatures drop dramatically, as is often observed at high latitudes (e.g. Krams et al. 2010).

Wintering birds often maintain fat reserves below their physiological capacity, suggesting a cost involved with excessive reserve levels (Evans 1969; King 1972; Blem 1990). The optimal body mass hypothesis (Lima 1986) suggests a trade-off between the risks of starvation and predation (Suhonen 1993), the optimal solution to which should be the mass that minimizes the joint risk (Houston et al. 1993; Rogers and Smith 1993; Krams 2000; Hedenström and Rosen 2001). In line with this, it has been found that increased levels of perceived predation risk may reduce body mass and subcutaneous fat reserves (Lilliendahl 1997; Gentle and Gosler 2001; Krams 2002; Krams and Krama 2002). Fattening strategies have also been found to be related to social hierarchy (Haftorn 1989; Hake 1996; Verhulst and Hogstad 1996; Krams 1998a, b; Krams et al. 2001). To cope with both predation and starvation risks dominant individuals are usually able to carry lesser amounts of fat reserves than subordinates in relatively good environments in terms of the availability of food resources and thermoregulatory requirements (Gosler 1996; Krams 2000; Krams et al. 2010), because of their socially enforced higher predictability of access to food.

We studied overnight loss of body mass in free-ranging great tits (*Parus major* L.) in relation to their dominance rank and ambient temperature (which ranged from mild to extremely low). We predicted less pronounced loss of body mass and lower rates of overnight mortality in dominant great tits at both mild and extremely low ambient temperatures because of their higher predictability of food resources (Krams et al. 2010) and lower levels of physiological stress (Krams et al. 2012). We also predicted that dominant individuals would carry lesser amounts of body reserves at the end of the day than subordinates under mild conditions, but that the body reserves of dominant individuals should approach, or even exceed, evening reserve levels of subordinates under harsh conditions.

Materials and methods

Study place and the birds

We studied individually colour-ringed great tits wintering in the forest near the town of Krāslava, southeastern Latvia

(55°52'N, 27°12'E). Data were collected during the cold winters of 1978/1979, 1983/1984, 1995/1996, 1996/1997 and 2007/2008, when at least some weeks had average daytime temperatures around -14°C (range -37 to 3°C), and average temperatures at night around -18°C (range -43 to 2°C). The snow cover was 0.3–0.8 m deep. Day length at the winter solstice is less than 7 h.

During four study winters, members of 11 great tit flocks (number of flocks per winter: 2, 2, 3, 3, 1; $n = 56$ individuals in total across five winters) were captured by mist nets (Ecotone) or baited traps, measured (wing length), weighed (a 30-g Pesola spring balance), marked with colour rings, sexed and aged (as first winter or adult) either in the previous breeding season or a month before the study. Although flocks of great tits usually are not stable, our study sites were isolated from other populated areas by large forests, and local birds usually stayed together for some weeks in mid-winter as members of temporarily stable groups (Krams 1998b; Krams et al. 2006, 2010).

The birds were trained to come to the permanent feeders in their territories when hearing a specific sound signal, and food at feeders provided with sunflower seeds and fat was supplied only when we studied social behaviour and recorded body mass of the birds. As a result, the birds used mainly natural food, which made their food resources unpredictable.

Dominance hierarchies

Dominance order was measured within each flock using pairwise interactions between birds at the temporary feeders. A bird was dominant over another if it chased the other away from the food, caused the withdrawal of the other by approaching, or forced the other to wait by occupying the feeder (Koivula et al. 1993). The dominant won more interactions than the subordinate within each dyad (two-tailed sign-test, $P < 0.001$). A clear dominance hierarchy was found in all the basic flocks. With no exceptions adult males had the highest rank, because there is a site-related dominance in great tits (Delaet 1985; Krams 1998a). Furthermore, males were dominant over females in both age groups. This pattern was observed to be the same in free-ranging great tits (Krams 1998b, 2000).

Each flock member was assigned to one of five dominance categories (5 as the highest ranking individual and 1 as the most subordinate individual). Ten basic flocks had five permanent flock members for about 2 weeks, containing one adult male, one adult female, two juvenile males and one juvenile female. One basic flock consisted of six permanent flock members containing one adult male, one adult female, two juvenile males and two juvenile females. Since juvenile females were always subordinate to the subordinate males, we assigned juvenile females to the

same rank, which was always the lowest in the flock's dominance hierarchy. During cold spells many great tits leave the forests for human-supplied food (Orell 1989) and in our study area several temporary members joined the basic flocks as soon as temperatures dropped. We did not take them into consideration since these birds usually only appeared for some hours or days.

Body reserves

Each bird was captured 4 times during two sessions in the course of the study. The first session was carried out in January, when the weather forecast promised a subsequent serious cold spell but ambient temperatures were still thaw-like (within the range of -2 to 3 °C during the day and night: mean \pm SD = 0.49 ± 1.14 °C). Within 1 h after sunset, we captured great tits roosting solitarily in from five to seven nest boxes (Otter 2007; Velky et al. 2010) provided at the territory of each flock, usually within 200 m from the feeders. We recorded the bird's identity and measured its body mass. All measurements were completed within 2 min, after which the birds were put back into the nest boxes. The entrance hole of the nest boxes was left open for the duration of the night. We managed to capture 50 of the 56 colour-marked birds. One hour before sunrise when great tits were about to leave their roosting sites, we returned to the nest boxes. We opened the nest boxes to check whether the birds had successfully survived till the morning and recorded their body mass again. Four individuals had left their nest boxes before our second visit, which decreased our sample size from 50 to 46. The birds were recaptured within 13 h after the first sampling (13.51 ± 0.036 h, mean \pm SE).

As soon as a cold day arrived and the average temperature of the night dropped to the range of -43 to -25 °C (mean \pm SD = -31.51 ± 5.09 °C; with a mean daytime

temperatures from -27 to -19 °C; mean \pm SD = -22.74 ± 6.16 °C), we captured the birds again. This was usually done at the end of January or during the first days of February, and the birds were captured on average 14.72 ± 2.27 (mean \pm SD) days after the first capture. As in the first session, the birds were captured within 1 h after sunset and recaptured 1 h before sunrise. During the cold spell, we captured 45 out of the 46 great tits that were successfully weighed repeatedly in the first session. However, out of these 45 individuals, four birds left their nest boxes during the night (i.e. before our morning visit). This reduced our sample size to 41 individuals that were captured and weighed repeatedly during both the thaw period and the subsequent cold spell.

Variation in the birds' evening and morning body reserves was transformed to a body mass index (BMI) prior to analysis. BMI was calculated by dividing body mass by the third power of wing length (body mass/wing length $\times 10^3$). Extra fat may negatively affect escape behaviour, and hence wing length is of biological significance for fat reserves and, ultimately, predation risk (Ekman and Lilliendahl 1993; Hake 1996; Pravosudov et al. 1999; Hedenström and Rosen 2001; Krams 2002).

Results

Mild conditions

The body mass of great tits was within 17.0–20.0 g (18.57 ± 0.79 g, mean \pm SD) when they entered the roost sites during the thawing period. We found a significant positive relationship between evening body mass and dominance status during this period ($r_s = 0.472$, $P = 0.002$; Table 1; Fig. 1) suggesting that dominants were larger than subordinate individuals. However, the

Table 1 The results of the analysis of covariance

	Dominance				Mean temperature of the day or night			
	<i>F</i>	<i>r</i> ²	<i>df</i>	<i>P</i>	Slope	SE	<i>t</i>	<i>P</i>
Evening body mass under mild temperature	9.77	0.54	4,40	<0.001	0.13	0.06	0244	0.89
Evening body mass under low temperature	13.55	0.61	4,40	<0.001	0.28	0.74	0.26	0.57
Loss of body mass under mild temperature	17.18	0.69	4,40	<0.001	0.21	0.54	0.26	0.50
Loss of body mass under low temperature	18.24	0.68	4,40	<0.001	0.021	0.70	0.25	0.60
BMI under mild temperature	17.17	0.69	4,40	<0.001	0.04	0.06	0.04	0.87
BMI under low temperature	11.26	0.21	4,40	0.101	0.29	0.19	0.28	0.16
Loss of BMI under mild temperature	10.86	0.76	4,40	<0.001	0.22	0.85	0.08	0.68
Loss of BMI under low temperature	19.62	0.72	4,40	<0.001	0.08	0.02	0.50	0.36

Evening body mass, loss of body mass, body mass index (BMI) and loss of BMI as dependent variables, dominance rank as a factor, and mean temperatures of the day (for evening body mass and BMI models) or night (for loss of body mass and loss of BMI models) as a covariate under conditions of mild temperatures and extremely low ambient temperatures

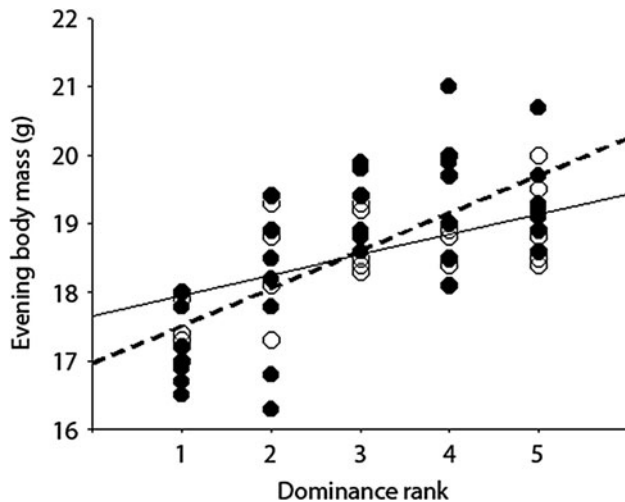


Fig. 1 The relationship between evening body mass and dominance rank in great tits under conditions of mild ambient temperature (*open circles, continuous line*) and extremely low temperature (*filled circles, dotted line*)

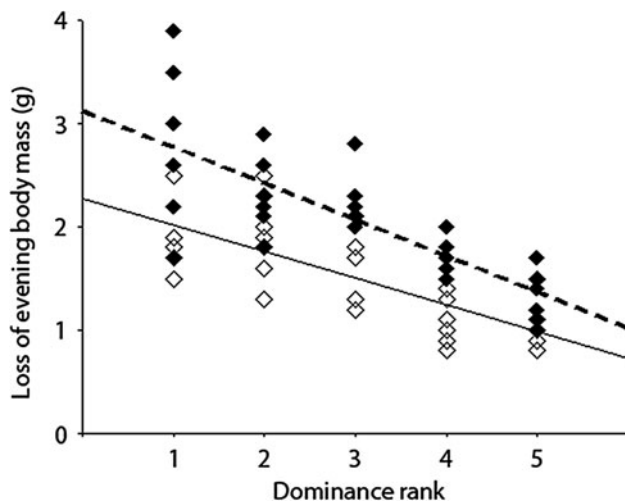


Fig. 2 The relationship between loss of evening body mass and dominance rank in great tits under conditions of mild ambient temperature (*open rhombuses, continuous line*) and extremely low temperature (*filled rhombuses, dotted line*)

evening body mass was not dependent on mean daily temperatures during the thaw [analysis of covariance (ANCOVA), Table 1].

On average great tits lost 1.49 ± 0.48 g (mean \pm SD; range 0.8–2.50 g) during their night roost. The decrease in body mass was not dependent on mean ambient temperature of the night (ANCOVA, Table 1), but we found a significant negative relationship between the loss of body mass and dominance rank ($r_s = -0.80$, $P < 0.001$; Fig. 2), which suggests that subordinate great tits lost more body mass than dominant individuals.

BMI was found to be within ranges of 0.0362–0.0496 g/cm³ (0.041 ± 0.003 g/cm³, mean \pm SD). There was a

significant negative relationship between BMI in the evening and dominance status ($r_s = -0.544$; Table 1; Fig. 3). BMI was not dependent on mean ambient temperature of the night (ANCOVA, Table 1) under mild conditions. Roosting great tits lost between 0.0019 and 0.006 g/cm³ (0.0032 ± 0.0013 g/cm³, mean \pm SD) of their BMI during the night under mild conditions. The loss of BMI was not associated with mean temperature of the night (ANCOVA, Table 1), but it was significantly negatively related to dominance rank of the roosting birds ($r_s = -0.833$, $P < 0.0001$; Table 1; Fig. 4). Thus, dominant great tits lost less body reserves during the roost.

Cold conditions

During cold spells evening body mass of the birds varied between 16.3 and 21.0 g (18.65 ± 1.13 g, mean \pm SD). This did not differ from their evening body mass under mild conditions (two-tailed paired t -test: $t = -0.81$, $df = 40$, $P = 0.42$; Fig. 1). However, subordinate individuals of the two lowest ranks decreased their evening body mass by 2.7 % from 18.11 ± 0.71 g under mild conditions to 17.63 ± 0.95 g under cold conditions (two-tailed paired t -test: $t = 3.18$, $df = 15$, $P = 0.006$; Fig. 1), while birds of the third, fourth and the fifth rank significantly increased their evening body mass by 2.4 % from 18.86 ± 0.54 to 19.32 ± 0.67 g (two-tailed paired t -test: $t = -8.00$, $df = 24$, $P < 0.0001$; Fig. 1). We found a significant positive relationship between evening body mass and dominance rank during cold spells ($r_s = 0.688$, $P < 0.001$; Table 1; Fig. 1). As before, the evening body mass was not affected by mean daily temperatures (ANCOVA, Table 1).

We found that great tits lost between 1.0 and 3.9 g (2.05 ± 0.63 g, mean \pm SD) during the night under harsh conditions. Consequently, birds, regardless of dominance rank, lost 38 % more body mass under low than mild ambient temperatures (two-tailed paired t -test: $t = -8.83$, $df = 40$, $P < 0.001$). In addition, there was a significant negative correlation between the loss of body mass and the dominance status of the roosting individuals during cold nights ($r_s = -0.849$, $P < 0.001$; Table 1; Fig. 2), but body mass loss was not explained by mean temperature of the night (ANCOVA, Table 1).

BMI varied within the ranges of 0.036–0.049 g/cm³ (0.041 ± 0.0024 g/cm³, mean \pm SD) in the evening under severe conditions. In contrast to mild conditions, we did not find any relationship between BMI in the evening and dominance status ($r_s = -0.258$, $P = 0.104$; Table 1; Fig. 3). This was because subordinate individuals of the first and second rank significantly decreased their evening BMI by 2.4 % from 0.043 ± 0.003 to 0.042 ± 0.003 g/cm³ (two-tailed paired t -test: $t = 2.746$, $df = 15$,

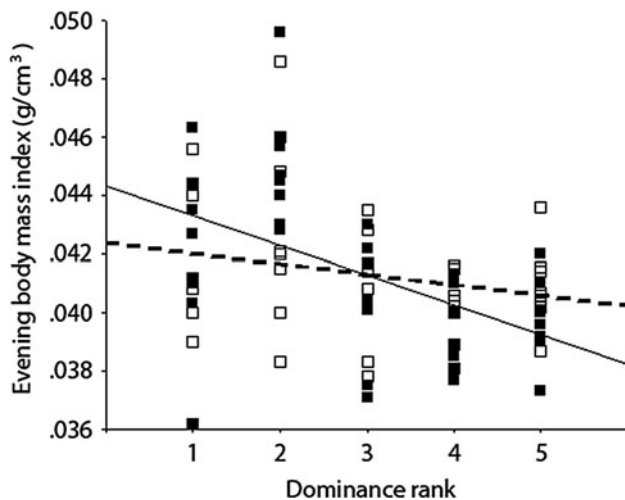


Fig. 3 The relationship between evening body mass index (g/cm^3) and dominance rank in great tits under conditions of mild ambient temperature (open squares, continuous line) and extremely low temperature (filled squares, dotted line)

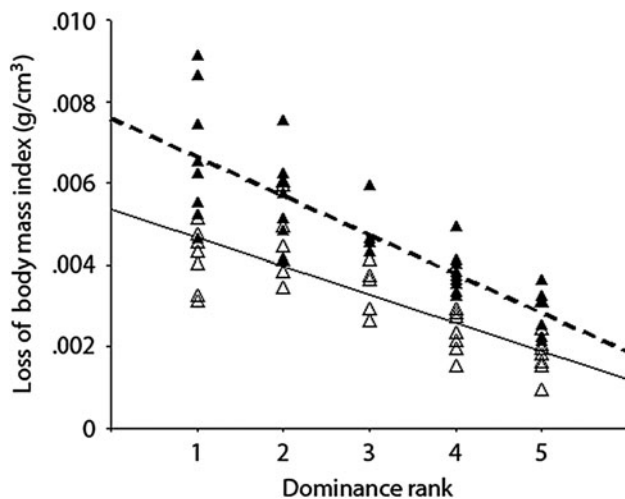


Fig. 4 The relationship between loss of evening body mass index (g/cm^3) and dominance rank in great tits under conditions of mild ambient temperature (open triangles, continuous line) and extremely low temperature (filled triangles, dotted line)

$P = 0.015$), while the individuals of the third, fourth and the fifth rank significantly increased their BMI in the evening by 2.5 % from 0.040 ± 0.002 to 0.041 ± 0.002 g/cm^3 (two-tailed paired t -test: $t = -7.10$, $df = 24$, $P < 0.0001$; Fig. 3). BMI was not dependent on mean temperature of the night (ANCOVA, Table 1) under cold conditions.

On average, great tits lost between 0.0021 and 0.009 g/cm^3 (0.005 ± 0.0017 g/cm^3 , mean \pm SD) of their BMI while roosting under severe conditions. This loss of BMI was 56 % greater than under mild roosting conditions (0.0032 ± 0.001 g/cm^3 ; two-tailed paired t -test: $t = -8.78$, $df = 40$, $P < 0.0001$). We also found that loss of

body reserves was significantly negatively associated with dominance status of the roosting birds ($r_s = -0.893$, $P < 0.0001$; Table 1; Fig. 4), but loss of relative body mass (i.e. BMI) was not associated with the mean ambient temperature of the night (ANCOVA, Table 1).

Survival

While none of the dominant great tits were found dead, we found five young females and one adult female dead in their nest boxes during the cold conditions. Neither the evening body mass (t -test: $t = 1.33$, $df = 14$, $P = 0.20$) nor BMI (t -test: $t = 1.39$, $df = 14$, $P = 0.17$) of the dead individuals differed from the evening body mass of individuals that survived. However, the morning body mass of dead individuals (14.28 ± 1.21 g, range 12.60–16.00 g) was 12 % lower than body mass (15.95 ± 0.83 g, range 14.00–16.80 g) of individuals of the same dominance rank that survived (t -test: $t = 2.491$, $df = 14$, $P = 0.026$), because the dead great tits had lost 17.45 ± 4.19 % (mean \pm SD, range 12.95–23.83 %) of their evening body mass during cold nights while surviving individuals lost on average 12.78 % (range 10.8–16.10 %) of their evening body mass. In line with this, BMI of the dead individuals (0.034 ± 0.004 g/cm^3) in the morning was 11 % lower than BMI of individuals of the same social rank, which survived until the next morning (0.038 ± 0.002 g/cm^3 ; t test: $t = 2.473$, $df = 14$, $P = 0.027$).

Discussion

Great tits confine feeding to daylight hours so that their fuel for overnight expenditures must be stored in advance (King 1972). Obviously, if a bird is unable to store sufficient amounts of energy or if its rate of fat utilization is so great that stores are depleted before it is able to feed again, death may follow. On the other hand, escaping from a predator is a matter of life and death, and leaner birds have been found to be quicker at take-off, which may increase the probability of successful escape upon a predator attack (Witter et al. 1994; Metcalfe and Ure 1995; Kullberg et al. 1996; Gentle and Gosler 2001; Krams 2002; Cresswell 2003; Ekman 2004). We showed that dominant males carry less body reserves than subordinate flock members, thus presumably being able to simultaneously balance the risk of starvation and the risk of predation in an optimal way (Krams 2000, 2002). They have priority of access to food, which likely increases predictability of foraging success whilst simultaneously reducing the probability of starvation. This may also mean that a better condition of dominant individuals when leaving the nest box allowed them to engage in less risky foraging behaviours in the morning. In

contrast, subordinate flock members must employ a strategy that decreases their risk of starvation at the expense of increased predation risk during the day. Thus, our study supports previous work in this great tit population, and also a number of previous studies, in demonstrating that dominant group members carry less energy reserves under conditions of relatively low energy expenditures and relatively high food availability (Lima 1986; Gosler and Carruthers 1999). However, our study adds to current knowledge in showing that this might be true also during very harsh environmental conditions. Dominant individuals could probably reduce their relative body mass because they had priority of access to food, higher predictability of foraging success, and, as a result, were at lower risk of starvation. Therefore, dominants can consistently reduce their energy reserves to reduce their mass-dependent predation risk without increasing their risk of starvation (Gentle and Gosler 2001; but see Nord et al. 2011).

However, energy demands increase considerably under the harsh conditions of cold spells when ambient temperatures drop dramatically, as is often observed at high latitudes. Under low ambient temperatures the energy requirements for nocturnal fasting and the attacks of predators may become equally unpredictable (Houston et al. 1993; Cuthill et al. 2000), which supposedly can explain the increased body reserves of dominant individuals (as evidenced by their greater evening body mass and BMI) in these conditions. This also supports the optimal body mass hypothesis in showing that extra reserves may facilitate the avoidance of starvation risk while the risk of predation may be avoided by choosing a less risky time for foraging. In our population, dominant great tits reduced predation risk by arriving at feeders later in the morning, and entering their roosting sites earlier in the evening than their subordinate flock mates (Krams 2000). In doing this, dominants probably minimized temporal overlap with both Eurasian sparrowhawks (*Accipiter nisus*) and pygmy owls (*Glaucidium passerinum*) which are the most important avian predator of passerine birds in our study area (Kullberg 1995; Krams 2000).

Our results show that changes in fattening strategies were largely dependent on dominance rank of the birds, and we did not detect any effect of a linear measure of ambient temperature within cold and mild periods. The absence of such an effect might be explained by the narrow range of temperature variables under both mild and severe conditions observed in this study (see “Materials and methods”). However, another possible explanation is that dominant individuals do not adjust their body reserves to gradual changes in ambient temperature. Instead, they might change their fattening strategies after reaching an ambient temperature threshold, below which they supposedly accumulate as much subcutaneous reserves as possible to cope with the harsh and unpredictable conditions in

deteriorating winter conditions (Krams et al. 2010). However, because we did not sample evenly across the temperature range used in our study (see “Materials and methods”), this hypothesis remains to be tested.

The body reserves and fattening strategies of subordinates cannot be always explained in terms of optimality models. Although subordinates may enjoy some benefits of group living, especially the reduced risk of predation by means of collective vigilance, sociality brings about costs such as an increased level of intraspecific competition for food and roosting sites (e.g. Krams et al. 2001). These costs may increase under extreme weather events, which is the most likely reason for the observed mortality in subordinate birds. Accordingly, recent evidence suggests that the heterophil/lymphocyte ratio, a reliable indicator of overall body condition (Krams et al. 2012), environmental harshness (e.g. Ilmonen et al. 2003; Müller et al. 2011) and survival prospects (Lobato et al. 2005; Kilgas et al. 2006), is higher in individuals of a lower dominance rank during sudden harsh cold spells (Krams et al. 2011). The heterophil/lymphocyte ratio sometimes also reflects physiological stress *sensu stricto* (i.e. levels of circulating corticosterone; the major avian stress hormone) (e.g. Maxwell 1993; Davis et al. 2008; but see Müller et al. 2011). High levels of stress hormones in the circulation are sometimes associated with a higher metabolic rate (Cohen et al. 2008; Giesing et al. 2010; Sloman 2010; but see Astheimer et al. 1992). Thus, it is possible that the higher body mass loss in subordinate birds in this study can be explained by a stress-related increase in energy turnover rates, which ultimately was not compatible with overnight survival in demanding environmental conditions. Alternatively, resting metabolic rate (and hence, overnight body mass loss) might have been up-regulated in subordinate females as a result of a higher diurnal work load (e.g. Nilsson 2002), which was likely required in the face of strong competition for food resources. Although the increased mortality in young females can likely be explained solely in terms of resource monopolisation by dominant individuals, variation in the quality of plumage should also be taken into account in future research, because subordinates are known to wear thinner plumage than more dominant great tits (Mayer et al. 1982; Reinertsen and Haftorn 1986; Broggi 2006; Broggi et al. 2011). Thus, it is possible that a poorer insulation capacity and the concomitantly higher cost of thermoregulation (e.g. Nilsson et al. 2011) can explain why females that died showed increased loss of body mass and BMI compared to surviving females of the same dominance category, despite non-significant differences in body mass and BMI at the beginning of the night.

Our results show that the fasting ability of subordinate individuals, and especially that of young females, is poor. In partially migratory species, such as great tits, only a part

of the population remains sedentary (Lack 1944; Gautreaux 1980, 1982). Females and juveniles normally constitute most of the migrants in this species (Gautreaux 1980). Our results suggest that this pattern might derive from the fact that migration may be less costly for females in comparison to spending the winter at higher latitudes, where survival is challenged by the costs of a lower dominance position (Krams et al. 2011, 2012; Cīrule et al. 2012).

Acknowledgments The Latvian Science Council supported Indriķis Krams and Tatjana Krama. The European Social Fund within the project Support for the Implementation of Doctoral Studies at Daugavpils University no. 2009/0140/1DP/1.1.2.1.2/09/IPIA/VIAA/015 supported Jolanta Vrublevska. We are thankful to Todd M. Freeberg for his critical comments and Inese Kivleniece for her help with figures. It would not have been possible to carry out this study without the help and support of Marta Krama and Alberts Krams.

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