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Rank-dependent winter fattening in the Willow Tit *Parus montanus*

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The body mass in tits increases in autumn towards a winter peak in December–January and then declines towards spring. I studied the winter fattening in the Willow Tit *Parus montanus* at two different sites in central Norway. Body mass data were collected in the early morning, late evening and partly at noon. To make the data comparable, they were transformed to body mass indexes. In rank-structured single-species flocks or aggregations of tits the body mass of each individual was compared with each one of the other members, using paired t-test (2-tailed) to control for seasonal and diurnal body mass fluctuations and impact of ambient temperature. Subordinate Willow Tits carried on the whole significantly more body fat than dominants throughout the day. Dominants do not utilize their actual capacity for fat storage, suggesting that fat storage is costly. Large fat deposits obviously reduce the risk of starvation, but whether the risk of predation at the same time is reduced because of constricted manoeuvrability is dubious. Since the dominants have priority to food resources, the subordinates are forced to carry more fat as an insurance against starvation. No consistent rank-dependent differences were found with regard to the diurnal body mass cycle.

1. Introduction

The body mass in tits increases towards a winter peak in December–January and thereafter declines towards the spring (e.g. Haftorn 1951, 1989, Owen 1954, Lehikoinen 1980). The rate of daily mass gain varies inversely with the day length and is roughly twice as high in mid-winter as in the autumn and the spring (Haftorn 1989). The fat depot gradually built up during the day is largely consumed the following night (Lehikoinen 1987, Haftorn 1992a).

When controlling for the daily build-up of reserves, Ekman & Lilliendahl (1993) recently found that Willow Tit *Parus montanus* subordinates outside Stockholm were heavier than dominants, although the latter had priority to food access. Similarly, Krams (1998) reported that Willow Tit males (alpha and beta individuals) and Crested Tit *P. cristatus* males in southeastern Latvia carried significantly less body reserves towards the end of their daily activity than their subordinate mates did. In contrast, at Oulu in Finland dominant Willow Tits were heavier than subordinates in the evening, but had about equal reserves in the morning (Koivula et al. 1995). Finally, Gosler (1996) showed that dominant Great Tits *P. major* at Oxford in England carried less fat than subordinates.

These findings suggest that reserves are under control of a foraging strategy and not simply constrained by food availability (Ekman & Lilliendahl 1993, Krams 1998).

Dominants do not utilize their actual capacity for fat storage, suggesting that fat storage is costly (e.g. King 1972). High body reserves obviously diminish the risk of starvation, but at the same time the higher wing-loading is suggested to reduce the manoeuvrability, resulting in increased predation risk (Metcalfe & Ure 1995). Consequently, birds should carry the minimum fat needed to survive periods of environmental stress, as for example a cold winter night. However, Kullberg (1998) recently showed that there was no measurable effect of body mass in take-off ability at dusk although Willow Tits were on the average 7.7% heavier by then than at dawn. This result indicates that the relatively small fat loads accumulated during a day by this species do not increase the predation risk due to reduced take-off ability. Similarly, Veasey et al. (1998) found that alarmed Zebra Finches *Taeniopyga guttata* increased their flight speed more when heavy than when light, and they therefore recommended caution in the use of weight as a predictor of predation risk in birds without examining its effect upon the flight speed of alarmed birds. Additionally, the Tufted Titmouse *Parus bicolor* was able to maintain a high vigilance for predators despite high body fat reserves (Pravosudov & Grubb 1998).

An important factor determining individual optimal reserve levels is the predictability of food supply relative to demand (Gosler 1996). For subordinates food availability is less predictable than for dominants, since dominants claim priority to food. Hence, according to theory, subordinates should deposit more fat than dominants, as an insurance against starvation during periods with increased energetic requirements. In such situations, dominants are likely to claim priority to food so that subordinates suffer from lack of food (Ekman & Lilliendahl 1993)

To study this matter in more detail I compared each individual in single-species, linear hierarchies of Willow Tits with each lower-ranked individual in the same hierarchy (flock). Based on theory and the findings above I predicted that in the matrix of dyads the dominant bird should weigh less than the subordinate.

2. Methods and materials

Data were collected throughout the winter at two different sites in central Norway, viz. in a predominantly coniferous forest at Klaebu (63°15´N) near Trondheim at about 160 m above sea level, and in the birch region at Venabu, Ringebu (61°40´N) at about 900 m above sea level. All birds were individually colour-ringed. Body mass was obtained in the early morning (just after roosting time) and in the late evening (just before roosting time) by using an electronic balance (Sartorius) with an accuracy of 0.1 g, kept in a windshield and fitted with a piece of solidified fat with embedded sunflower seeds to attract the birds. For each individual only the first record in the morning and the last one in the evening were used in the present analyses. A flashlight was necessary to read the colour rings and the balance scale properly in the poor morning and evening light in wintertime (see Haftorn 1989). At Klaebu the study covered one winter (1987–88), at Venabu two winters (1987–89). At Venabu I also collected weight data at noon during the first winter. At Venabu no artificial feeding took place in the periods between weighings. At Klaebu, however, sunflower seeds were unlimitedly available throughout the winter.

The social rank of each individual was determined from the outcome of pairwise interactions at feeders, using conventional methods (see Hogstad 1987a).

The sex and age of the birds were determined by wing length, form of the rectrices and reproductive behaviour (Laaksonen & Lehikoinen 1976, Haftorn 1982, 1999). Wing length was measured according to method (3) in Svensson (1992), i.e flattened and straightened wing. Usually each individual was captured only once (for ringing and measurements).

At Venabu each individual in separate Willow Tit flocks was compared, in descending order of rank, with each one of the other members within the flock, using paired t-test (2-tailed) to control for seasonal and diurnal body mass fluctuations and impact of temperature. In this way a matrix of dyads was established for each flock. At Klaebu intraspecific comparisons by the same statistical method were conducted, although without knowing the flock membership of individual birds.

Because the birds vary in size, their masses cannot be compared directly. Therefore, before comparisons were made all mass data were transformed into body mass indexes (BMI) by taking the ratio of body mass to the third power of the wing length (Summers 1989, Ekman & Lilliendahl 1993, Krams 1998), i.e. b/w^3, where b = body mass (g) and w = wing length (mm). However, as pointed out by Esa Lehikoinen (pers. comm.) BMI is still somewhat problematic and should be treated with caution.

Because the body mass usually peaks in December–January, I made analyses separately for the periods before and after New Year.

It should be noted that the same individuals are entered several times in the analyses, as exemplified in Table 1.

3. Results

3.1 Seasonal body mass

At Venabu one flock was studied during two consecutive winters. It consisted of four birds the first winter and five the next winter, of which three were the very same birds. The feeding table at which body mass data were collected was placed within the flock's winter territory. During the first winter the body mass was obtained at noon in addition to morning and evening. In analyses of dyads the subordinate flock member carried significantly more body reserves than the dominant at all three times of the day throughout the winter (Table 1).

The next winter the picture was largely the same (Table 2, flock 2), with the only exception that the old female (F-Y) weighed consistently more than its two subordinates (one young male and a young female).

In another flock at Venabu, containing four individuals, the dominant old male weighed significantly more than the second ranked old male, though significantly less than the two individuals at the bottom of the hierarchy (Table 2, flock 3). This flock belonged to a neighbouring winter territory of the first flock, but they both regularly visited the same feeding table.

Several Willow Tits visited my feeding table at Klaebu in January–April 1988. They certainly belonged to more than one flock, but I was not

Table 1. Mean body mass indexes (BMI) of four Willow Tits (two of each sex) forming a winter flock at Venabu 1987–1988. Each individual compared by paired t-test (2-tailed) to each one of the others in descending order of rank, with the dominant bird on top of each dyad. The letters M, N and E in the first column denote morning, noon and evening. M-B, m-YW etc. denote individuals by sex and age (M = adult male, m = young male, F = adult female, f = young female) and colour rings (the letters after the hyphen). Number of cases (dyads) in brackets. * = P < 0.05, ** = P < 0.01, *** = P < 0.001

		M-B	m-YW	F-Y
October–December				
M		39.0(15)		
	m-YW	41.1 ***		
N		41.0(11)		
	m-YW	42.8 ***		
E		43.2(14)		
	m-YW	44.6 ***		
M		39.0(17)	41.0(14)	
	F-Y	48.2 ***	48.3 ***	
N		40.8(15)	42.7(10)	
	F-Y	50.3 ***	50.7 ***	
E		43.2(16)	44.7(15)	
	F-Y	52.2 ***	52.5 ***	
M		38.7(1)	41.7(1)	
	F-YP	49.8	49.8	
N		41.1(2)	42.8(2)	50.8(2)
	F-YP	50.9 *	50.9 *	50.9 ns
E		42.9(1)	44.9(1)	52.8(1)
	F-YP	52.4	52.4	52.4
January–March				
M		38.2(20)		
	m-YW	41.2 ***		
N		39.4(16)		
	m-YW	42.4 ***		
E		41.1(19)		
	m-YW	44.4 ***		
M		38.2(22)	41.2(19)	
	F-Y	48.0 ***	48.1 ***	
N		39.4(16)	42.4(17)	
	F-Y	49.7 ***	49.7 ***	
E		41.1(17)	44.4(16)	
	F-Y	51.5 ***	51.4 ***	
M		38.1(21)	41.1(18)	48.0(20)
	F-YP	48.4 ***	48.5 ***	48.4 *
N		39.4(15)	42.5(16)	49.7(16)
	F-YP	50.5 ***	50.4 ***	50.4 **
E		40.9(14)	44.4(15)	51.3(14)
	F-YP	52.3 ***	52.4 ***	52.3 ***

able to distinguish the flocks. According to body mass, size and behaviour, seven were apparently females. With the exception of some non-significant differences, the subordinate bird was consistently heavier than the higher-ranking individuals, in the morning as well as in the evening (Table 2, flock 4).

The body mass relationships showed the same trend before and after New Year, as exemplified in Table 1.

3.2 Diurnal body mass cycle

The mean daily body mass increase and nightly decrease in wintertime are about 0.9–1.1 g in the Willow Tit (Haftorn 1992a). Daily increase and nightly decrease are balanced in healthy birds. Based on Table 1 in Haftorn (1992a), the correlation coefficient between daytime increase and nightly decrease was 0.77 ($P < 0.001$, $N = 14$). No consistent rank- dependent differences were found with regard to the diurnal body mass cycle, as exemplified in Table 3. It should nevertheless be mentioned that out of 44 daytime dyads 6 dyads showed a significant difference between individuals, of which the dominant bird increased its daily weight relatively more than the subordinate in 5 cases, the subordinate only in one (daytime weight gain in percentage of morning weight). Similarly, of 38 nighttime dyads 9 dyads provided a significant difference between the birds; in 6 cases the dominant bird lost relatively more weight than the subordinate, and vice versa in 3 cases (nightly loss in percentage of the evening weight).

4. Discussion

Tits are in many ways well adapted to winter life in harsh environments. They are highly flexible and react rapidly to environmental changes, for example ambient temperature. When the tits (Willow Tits, Marsh Tits *P. palustris*, Great Tits, Blue Tits *P. caeruleus*, Coal Tits *P. ater*) at Klaebu in Norway in February 1988 suddenly were exposed to a 20°C fall in temperature their body mass was hardly affected (Haftorn 1992b), showing that they immediately compensated strengthened energetic demands by increased food intake and maybe a higher degree of nocturnal hypothermia (Reinertsen & Haftorn 1984).

The prediction that subordinate tits carry more body reserves that dominant conspecifics was in the present paper tested by comparing each individual with each one of lower-ranked individuals in single-species flocks or aggregations of conspecifics at feeding tables. The prediction was strongly supported, regardless of sex and age. As many as 42 (70%) of 60 comparisons (dyads) significantly showed that the subordinate bird exceeded the dominant in body mass, whereas only 4 (7%) dyads demonstrated the opposite pattern.

The survey includes seven Willow Tits, prob-

Table 2. Summary of dyads obtained by paired t-tests (2-tailed) of three Willow Tit flocks at Venabu (1–3) and one aggregation of Willow Tits at Klaebu (here named flock 4). The dyads represent the outcome of comparisons of the mean body mass index (BMI) of each individual within the flock compared to the MBI of one by one of the others within the flock in descending order of rank, as shown in Table 1 (data of flock no. 1 are summarized from Table 1). Subord = subordinate individuals, dom = dominant individuals, > = significantly heavier than, NS = no significant difference.

	Morning			Evening		
Flocks	Subord > dom	Vice versa	NS	Subord > dom	Vice versa	NS
(1) 2 ♂♂ + 2 ♀♀	9	0	2	9	0	3
(2) 3 ♂♂ + 2 ♀♀	12	3	1	11	3	2
(3) 3 ♂♂ + 1 ♀	7	1	3	4	2	4
(4) 7 ♀♀	13	0	8	13	0	8
Total	41	4	14	37	5	17

ably all females, which most likely did not belong to the same flock. All seven birds visited my feeding table regularly in January–April and could easily be arranged into a linear hierarchy. The subordinate individual was significantly the heaviest in all dyads (Table 2, flock 4).

It seems therefore justified to conclude that subordinate Willow Tits in central Norway usually maintain more body reserves than dominants throughout the day. The evidence suggests that this pattern applies to birds in lowland coniferous forests as well as to those in the alpine birch region.

With respect to daytime body mass gain and nocturnal mass loss no consistent difference between ranks was found, although the dominant bird during daytime gained significantly more in body mass than the subordinate in 11 % of the dyads and lost significantly more during night in 16 % of the dyads. However, the daytime mass gain and nightly loss did not override the general pattern that subordinate Willow Tits were heavier than dominants in the evening as well as in the morning, in similarity with the situation outside Stockholm in Sweden (Ekman & Lilliendahl 1993), but in contrast to the findings at Oulu in Finland (Koivula et al. 1995). More specifically, when comparing the situation in "winter" (November–December) and "spring" (February–March), Koivula et al.(1995) showed that dominant Willow Tits at Oulu carried more fat reserves than subordinates in winter evenings, but about equal reserves in spring evenings; morning reserves did not differ significantly in winter or in spring. A similar investigation of Willow Tits at Venabu in Norway gave other results: subordinate birds had significantly higher morning and evening mass indexes compared to dominants in all dyads in "winter" (November–January) as well as in "spring" (February–March), as exemplified for one flock in Table 4.

For the Willow and Great Tits it is suggested that dominant individuals have a higher energy requirement than subordinates (Røskaft et al. 1986, Hogstad 1987b). While daytime metabolic rate of the Willow Tit was correlated with dominance rank, the nocturnal metabolic rate, in contrast, seemed to be independent of social rank (Reinertsen & Hogstad 1994). The largely rank-independent mass loss during night when the tits are prevented from food intake, as shown in the present study, supports this view.

From theoretic models it has been suggested that dominants postpone the daily build-up of body mass to maintain manoeuvrability during the day and thereby reducing predation risk (Lima 1986, Witter & Cuthill 1993). However, Willow Tits, independently of rank, weigh at noon significantly more than in the morning and have at that time achieved about half of the daily mass gain (Haftorn 1992a, this paper Table 1), and no consistent rank-dependent difference of body mass gain from morning to noon was found (Table 5).

The crucial question is why subordinates carry more body reserves than dominants in spite of the

Table 3. Mean daily body mass increase (DI) and nightly decrease (ND) (mass gain in percentage of the morning body mass and mass loss in percentage of the evening body mass) of four Willow Tits (two of each sex) forming a winter flock at Venabu 1987–1988. For further explanation, see Table 1.

		M-B	m-YW	F-Y
October–December				
DI		11.2(11)		
	m-YW	8.5 **		
ND		10.0(12)		
	m-YW	8.1 ***		
DI		11.1(12)	8.6(12)	
	F-Y	8.7 ***	8.8 ns	
ND		9.9(13)	8.3(12)	
	F-Y	7.7 ***	8.2 ns	
DI		–	–	–
	F-YP	–	–	–
ND		9.8(1)	7.0(1)	–
	F-YP	5.0	5.0	–
January–March				
DI		7.7(13)		
	m-YW	8.4 ns		
ND		7.2(17)		
	m-YW	7.4 ns		
DI		7.8(16)	8.4(13)	
	F-Y	7.3 ns	6.9 *	
ND		7.6(16)	7.5(13)	
	F-Y	6.7 *	6.4 *	
DI		7.7(13)	8.5(11)	7.3(13)
	F-YP	8.3 ns	8.1 ns	8.3 ns
ND		7.4(14)	7.9(13)	6.6(13)
	F-YP	7.8 ns	7.8 ns	7.8 *

fact that the latter have the benefit of priority to food resources. High body reserves diminish the risk of starvation, but could at the same time increase predation risk if high fat loads significantly reduce the flight speed as hitherto suggested (Metcalfe & Ure 1995). However, recent evidence makes it less likely that flight manoeuvrability is seriously affected by fat loads within normal limits (Kullberg 1998, Pravosudov & Grubb 1998, Veasey et al. 1998). It is therefore doubtful that subordinates suffer a higher predation risk than dominants due to larger body reserves. When subordinates nevertheless put on more body reserves than dominants it may be considered as an insurance against starvation during periods with increasing energetic requirements. In such situations, dominants are likely to claim priority to food so that subordinates might suffer from lack of food (Ekman & Lilliendahl 1993).

King (1972) has already pointed out that few birds possess sufficient stored fat at dusk to survive more than one night and part of the following day without food. It is interesting that subordinate tits in the present survey, start the new day with extra reserves compared to the dominants. This extra energy may be considered as a guarantee against shortness of food during the morning hours.

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Table 4. Mean body mass indexes (BMI) of four Willow Tits (two of each sex) forming a winter flock at Venabu 1987–1988. Winter: November–January. Spring: February–March. For further explanation, see Table 1.

		M-B	m-YW	F-Y
Winter				
M		38.9(17)		
	m-YW	41.4 ***		
E		42.6(17)		
	m-YW	44.7 ***		
M		38.9(17)	41.4(16)	
	F-Y	48.3 ***	48.3 ***	
E		42.7(16)	44.7(16)	
	F-Y	52.2 ***	52.2 ***	
M		38.8(7)	41.9(6)	48.4(6)
	F-YP	48.9 ***	48.9 ***	48.8 ns
E		41.9(4)	44.7(4)	51.9(4)
	F-YP	52.3 ***	52.3 ***	52.3 ns
Spring				
M		37.8(13)		
	m-YW	40.9 ***		
E		40.7(13)		
	m-YW	44.3 ***		
M		37.8(14)	40.8(12)	
	F-Y	47.8 ***	47.9 ***	
E		40.8(12)	44.3(12)	
	F-Y	51.3 ***	51.3 ***	
M		37.8(15)	40.9(13)	47.8(14)
	F-YP	48.3 ***	48.4 ***	48.2 ns
E		40.8(11)	44.4(12)	51.3(11)
	F-YP	52.3 ***	52.4 ***	52.3 ***

Selostus: **Hömötiaisten arvoasteikosta riippuva talvilihominen**

Hömötiaisen ruumiin paino nousee syksystä kohti joulu–tammikuun huippua, laskeakseen sen jälkeen kohti kevättä. Kirjoittaja tutki norjalaisten hömötiaisten ruumiin paino indeksin (body mass index) vaihtelua. Ravintorasvaresursseilla voidaan ehkäistä nälkiintymisen riskiä, mutta toisaalta yli-

Table 5. Mean relative body mass increase from morning to noon of four Willow Tits (two of each sex) forming a winter flock at Venabu 1987–1988 (mass gain in percentage of morning body mass). For further explanation, see Table 1.

	M-B	m-YW	F-Y
October–December			
	4.9(7)		
m-YW	4.1 *		
	4.4(10)	4.0(7)	
F-Y	3.8 ns	4.5 ns	
	–	–	–
F-YP	–	–	–
January–March			
	3.4(13)		
m-YW	3.6 ns		
	3.5(15)	3.5(12)	
F-Y	3.9 ns	3.8 ns	
	3.6(14)	3.3(12)	3.8(14)
F-YP	4.4 ns	4.4 *	4.4 ns

määräinen paino voi altistaa helpommin yksilön petojen saaliiksi jos ylimääräinen paino vaikuttaa esimerkiksi yksilön lentonopeuteen. Tutkimuksen mukaan arvoasteikossa alemalla tasolla (subdominantit) olevilla yksilöillä oli enemmän rasvaa kuin valta-asemassa (dominantit) olevilla yksilöillä sekä aamulla, päivällä että illalla. Dominantit yksilöt eivät siis käyttäneet valta-asemansa suomia mahdollisuuksiaan ylimääräisen rasvan hankkimiseen. Havainto viittaa siihen, että ylimääräisen rasvan varastoinnista aiheutuisi kenties ylimääräisiä kuluja. Runsaan rasvojen määrän voidaan kuitenkin olettaa vähentävän nälkiintymisen riskiä. Koska dominanteilla yksilöillä on etuoikeutettu mahdollisuus hyödyntää ravintoresursseja, ehkäistäkseen nälkiintymisen subdominantit yksilöt ovat todennäköisesti pakotettuja kantamaan enemmän rasvaa kuin valta-asemassa olevat yksilöt. Yleensä hömötiaisilla talvinen ruumiin paino nousee aamusta iltaan ja yön aikana paino laskee 0.9–1.1 g. Terveillä yksilöillä päivän aikainen lihominen ja yön aikainen laihtuminen on tasapainossa. Yksilöiden arvoasemalla ei havaittu olevan merkitystä tähän yksilöiden vuorokauden aikaiseen ruumiin painon vaihteluun. Norjassa subdominantit hömötiaiset näyttävät aloittavan uuden päivän runsaampien rasvavarastojen avulla kuin dominantit yksilöt. Tämä ylimääräinen rasva voi olla tärkeää subdominanteille yksilöille aamun tunteina, jolloin ravintoa on saatavilla vain vähän.

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