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ARTICLE

Factors influencing the fat load variation in three wintering bird species under stable food access conditions

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Abstract Winter is one of the crucial periods of the bird's year-round life cycle. Fat reserves in bird species are prone to a wide range of factors, with weather conditions and a bird's social status being two major ones. In our study we analysed the variation in fat reserves in birds with stable, constant access to food resources in three of the most common wintering species: the great tit *Parus major*, the blue tit *Cyanistes caeruleus* and the greenfinch *Chloris chloris*. The highest mean value of fat score was found in the greenfinch, whereas in both species of tits these values were equally lower. For all three species the amount of fat reserve was correlated with the same factors. It increased together with the decrease of mean average temperature, and with the course of daytime as well as the season-site index (calculated as data collected at a given site in a particular year). Contrary to many previous surveys we did not find dependence of the fat score level on individual dominance status, which is probably linked to the abundance of food in catching sites.

Keywords Bird feeders · Fat score · Poland · Great tit · Blue tit · Greenfinch

Introduction

Winter is one of the crucial periods of the bird's year-round life cycle (Cuthill and Houston 1997). During this period the length of the day is shortest, so that birds have less time to find food and they have limited access to it when snow cover is present (Siriwardena et al. 2008; Goławski and Kasprzykowski 2010). Moreover, energy consumption grows when the weather conditions deteriorate (the decrease of temperature, snow and rainfall, wind, freezing rain, etc.). Fat reserves in birds are adaptively adjusted to increased requirements by winter fattening (Lehikoinen 1987; Haftorn 1989; Ekman and Hake 1990), but are also influenced by social factors (Haftorn 1989; Gosler and Carruthers 1999). It is well known that in each

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species there is a hierarchy connected with sex and age — males dominate females and older individuals dominate younger ones (Ekman 1989; Hogstad 1989). In many studies, dominant individuals were found to have lower fat deposits than the subordinates (Verhulst and Hogstad 1996; Haftorn 2000; Krams 2002), but in other studies, the dominants were fatter than the subordinates (Gosler 1996). Moreover, birds must find a trade-off between weight gain and their manoeuvrability, which allows them to escape predators (Witter et al. 1994; Kullberg et al. 1996; Gentle and Gosler 2001). Some birds, such as greenfinches *Chloris chloris* and great tits *Parus major* lost mass when a perceived predation risk was present (Gosler et al. 1995; Lillendahl 1997). The speed and agility with which small birds can take flight are crucial in determining whether or not they will survive an attack by a predator. Natural diurnal variation in mass has a highly significant impact on flight performance, as stated for zebra finches *Taeniopygia guttata* (Metcalfe and Ure 1995). Good body condition after winter is especially important for females, which need much energy for egg laying in the breeding season (Saino et al. 2004; Studds and Marra 2005).

Bird feeders, serving as a stable source of food in the hardest period of the year, are crucial for successful survival of many bird populations (Robb et al. 2008). This is quite a popular method of providing additional food for birds in urban areas, from big cities to small villages (e.g. Jones and Reynolds 2008; Polakowski et al. 2010; Tryjanowski et al. 2015). Easily available resources of high energy food (especially pork fat and sunflower seeds) attract many species, often forming large foraging flocks (Goławski and Dombrowski 2011). Moreover, the use of bird feeders may be a factor reducing flight initiation distance and hence reducing the relative cost of flight and increasing body condition (Møller et al. 2015). If bird feeders are regularly refilled by their owners it contributes to the constant presence of flocks in the vicinity of the feeder (Berner and Grubb 1985). Much is known about the factors affecting the fitness of birds using feeders in Western European regions (Jones and Reynolds 2008), whereas only a low number of papers from Central and Eastern European countries deal with this issue. Meanwhile, the behaviour of wintering birds is mainly affected by the weather, which is much milder in Western Europe than in Central and Eastern Europe (Domonkos and Piotrowicz 1998). Under such mild winter conditions, the strong influence of rainfall on the fatness of great tits in Ireland was found (Gosler and Carruthers 1999).On the other hand, there was a lack of easy correlation between the temperature and the amount of fat accumulated by yellowhammers *Emberiza citrinella* in England (Evans 1969). Thus, it is important to study this phenomenon in other parts of Europe, where winters are colder and snowy, to develop our knowledge about wintering birds.

In this paper we studied the three most common wintering species in the whole of Central Europe, numerously found close to human settlements, and especially keen on bird feeders: great tit, greenfinch and blue tit *Cyanistes caeruleus*. We analysed the adjustment of fat reserves in birds with constant access to food resources, in relation to several factors, primarily the bird's social status and changeable weather conditions.

Study area

Study plots were located in five human settlements in Poland (Fig. 1), ranging from small villages to large cities (Table 1). The rural areas (two places) were located at least 18 km away from big cities with over 100,000 inhabitants. Przebendowo village was situated in northern Poland, with the research site located in an overgrown park by an old manor house. Wapnica village was also located in the same part of the country with traps placed in a garden separated from the village by a forest. Studies in Białystok (eastern Poland) took place in the suburbs of the city, in a detached house district. A study in central Poland was conducted in the centre of Bydgoszcz city, in the botanical garden. Another botanical garden was also used as a study plot in the centre of Kraków city (southern Poland).

Materials and methods

The data were collected in the following seasons: Wapnica: 2009–2012, Przebendowo: 2009–2012, Białystok: 2005–2007 and 2008–2009, Bydgoszcz: 2009–2012, and Kraków: 2009–2012. The study was conducted from the beginning of December to the end of February. Bird ringing was performed once per fortnight, 7–8 times during one study season, with about 10-day breaks. Birds were caught with mist-nets and ringed with aluminium rings over 5 h, starting from sunrise (6 or 7 am). The nets were located close to bird feeders, with sunflower seeds, refilled daily through the course of the whole winter. In each study plot the position of the nets was the same during each study season. The total length of nets was as follows: Przebendowo, 40 m; Wapnica, 10 m; Białystok, 30 m; Bydgoszcz, 16 m; Kraków, 12 m. The fat score of ringed birds was assessed according to a 9-point scale, from 0 to 8 (Busse and Kania 1970). This method, based on the appearance of the belly, furculum and pectoral muscles is explained as follows: 0 — belly without visible fat or only red fat traces, air sac visible inside furculum; 1 — furculum filled with fat, air sac not visible; 2 — belly with unconnected fat belts, guts visible; 3 — almost whole belly covered with

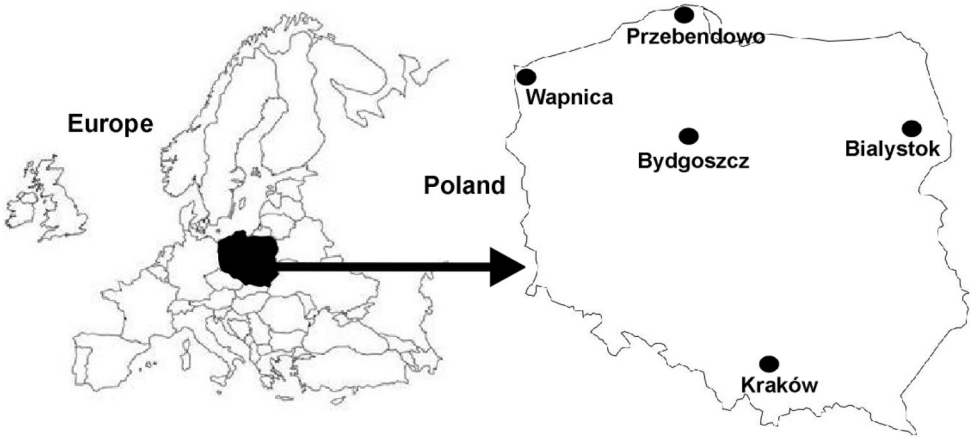

Fig. 1 Distribution of study sites in Poland

Table 1 Location and characteristic of the study plots in Poland

Name of city/ village	Population (thousands)	Location of the study plot	Urbanization degree	Habitat
Przebendowo	0.05	54°43′N 17°50′E	Rural	Park
Wapnica	0.4	53°52′N 14°26′E	Rural	Garden
Białystok	294.4	53°06′N 23°12′E	Urban	Orchard
Bydgoszcz	363.9	53°07′N 18°01′E	Urban	Botanical garden
Kraków	758.3	50°03′N 19°57′E	Urban	Botanical garden

fat, guts not visible, liver visible; 4 — whole belly covered with fat, concave fat layer inside furculum; 5 — whole belly covered with fat, convex fat layer inside furculum, lateral sides of the pectoral muscles without fat streaks; 6 — lateral sides of the pectoral muscles with fat streaks; 7 — the pectoral muscles partly covered with fat; 8 — the pectoral muscles wholly covered with fat.

We caught and ringed 7113 birds belonging to 40 species. We analysed only the three dominant species: great tit, greenfinch and blue tit, samples of which allowed for statistical elaboration.

We studied several factors which were expected to influence the amount of fat reserve in birds: (1) weather conditions — we analysed average temperature (°C), precipitation (mm) and average wind speed (km/h) in study areas on ringing days. Weather data were obtained from the website http://www.tutiempo.net. The distance between meteorological stations and study sites did not exceed 30 km in any case; (2) social status (dominance) — following Gosler (1996), age and sex have been combined in one variable called 'ranked status' where 1st-year females are coded as "1", adult females as "2", 1st-year males as "3", and adult males as "4"; (3) hour of catching — full hours between 7 am and 2 pm; (4) study plot — 5 areas; (5) season (year) — 6 winters in years 2005–2012 (except 2007/2008).

The relationship between the fat score in birds and weather conditions, ranked status, season and site parameters were examined using generalized linear mixed models (GLMMs) with an identity link function and normal error distribution in the module provided by Statistica 10.0 software (StatSoft 2012). The effect of each variable was first tested separately through univariate models, and only significant variables were chosen for further testing. The explanatory variable was the index of fat score. We included the weather conditions (average temperature, precipitation and average wind speed) as continuous covariates. The ranked status of birds was introduced as a fixed effect. The hour of catching was also included as a random effect. Since our survey design contained some gaps — not all of the sites were active in every year of the study — we were not able to test the effects of site and year separately. Instead, we adopted the effect of a data set, i.e. data collected at a given site in a particular year, as a random factor in the analyses (season-site index). As some birds were caught more than once in a season, we included only the data of the first catching to avoid pseudoreplication. Values reported are mean ± 1 SE. Only results with a probability of $p \leq 0.05$ were assumed to be statistically significant.

Results

Altogether we caught and ringed 3641 individuals of the three species considered: great tit, 69.0 %; greenfinch, 18.6 %; and blue tit, 12.4 %. The highest mean value of fat

Table 2 Results of the GLMM showing factors affecting the fat score in three bird species wintering in Poland

Effect	*Parus major*			*Cyanistes caeruleus*			*Chloris chloris*		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Temperature	1,13.6	6.33	0.025	1,28.8	13.26	0.001	1,10.9	13.46	0.004
Rainfall	Out of analyses			1,57.5	2.73	0.103	1,31.6	2.61	0.116
Wind	1,13.4	0.98	0.340	1,20.4	0.02	0.886	1,15.0	1.87	0.192
Ranked status	3,21.2	0.72	0.551	3,1.4	0.52	0.725	3,0.4	18.55	0.399
Hour	7,47.7	3.06	0.010	7,10.1	5.02	0.011	7,10.6	2.84	0.062
Season-site index	11,49.8	4.53	0.001	11,11.9	2.93	0.039	11,6.1	13.27	0.002
Interaction term: ranked status × hour	21,146.0	1.33	0.167	19,64.1	0.47	0.966	21,27.5	0.76	0.743
Interaction term: ranked status × season-site index	33,77.0	2.00	0.007	33,76.7	0.93	0.580	29,58.0	0.52	0.972
Interaction term: hour × season-site index	51,55.5	4.06	0.001	47,45.1	1.41	0.124	40,72.2	1.19	0.334
Interaction term: ranked status × hour × season-site index	133,2250.0	0.89	0.796	56,272.0	1.13	0.266	62,499.0	1.16	0.199

score was found in greenfinch (2.6), whereas in both species of tits these values were lower and equal at 1.8. For all three species the amount of fat reserve was influenced by the temperature (GLMM analysis; Table 2): it increased with the decrease of mean average temperature. The strongest correlation was found in greenfinches ($r = -0.43$, $p < 0.001$, $n = 676$), was weaker in blue tits ($r = -0.22$, $p < 0.001$, $n = 452$) and weakest in great tits ($r = -0.16$, $p < 0.001$, $n = 2513$, Fig. 2). Coefficients of correlation did not differ significantly between the two species of tits ($p = 0.181$), whereas it differed significantly between greenfinches and both tits ($p < 0.001$ for both comparisons). Time of day also influenced the fat score of the two tit species. There was a clear tendency of the fat score to increase as daytime passed. This trend was statistically significant for great and blue tits, whereas for greenfinches it was close to significance ($p = 0.062$). In all the species the fat score was lowest in the first hour of catching (7.00) and highest in the last hour (14.00). Compared with greenfinches, the daily increase of fat score was more linear for both tits, and it reached 1.04 for great tits, 1.01 for blue tits and 1.59 for greenfinches (Fig. 3). The GLMM analysis revealed that the season-site index influenced the fat score in all species. The relationship between the fat score and interactions: ranked status × season-site index and hour × season-site index occurred only in great tits (Table 2). There was no influence of the ranked status on the fat score in any species (Table 2).

Discussion

Our results show that the fatness of these three species influenced the same factors. The fat score increases with the decrease of average temperature on the day of catching, was dependent on season-site index, and increased with the course of the day, which is rather obvious. The negative correlation of fat score and average temperature is connected with the higher energy demands of a bird's body when it is colder. Birds need to accumulate enough fat to survive the night, when the temperature falls significantly (Meijer et al. 1996; Brodin 2000; Gosler 2002). The strongest correlation was found for the greenfinch, which roosts in open fields, perching in bushes or tree crowns. It seems to be therefore more exposed to frost than tits, which roost in tree hollows or nest boxes (Kempenaers and Dhondt 1991; Christe et al. 1994). For example, the great tits actively explored roosts before the final choice of sleeping site. Selected roosts had higher average temperature as well as the temperature at dawn (Velky et al. 2010). In our study greenfinches lost more fat through night than tits. Thus, the greenfinch relies on its fat resources more than tits and must accumulate fat more efficiently when the temperature decreases. An alternative explanation is the compromise between carrying body reserves and an insurance against starvation (Ekman and Hake 1990). This is connected with reducing the risk of starvation in conditions when energy intake is impossible as well as with a relatively high cost of locomotion while an individual is carrying a large load of fat. Due to a higher predation risk when the greenfinch is fat, the bird modifies its body mass and fat reserve to be able to escape from predators and increase survival probability (Lilliendahl 1997). However, in urban habitats where the study plots were located, the predation risk was slight, and birds seemed to spend time mainly feeding compared to other activities, such as watching for predators (Houston and McNamara 1993). In contrast, tits, which do not gather in such large and dense flocks as greenfinches, can be more prone to predator attacks and therefore cannot risk accumulating a higher fat load. The tits have to respond by reducing the maximal fat reserves and body mass to the optimal level to allow them fast and agile flight, which limits the risk of being killed by a predator. One of the most common predators in urban habitats is the Eurasian sparrowhawk *Accipiter nisus* (Chace and Walsh 2006;

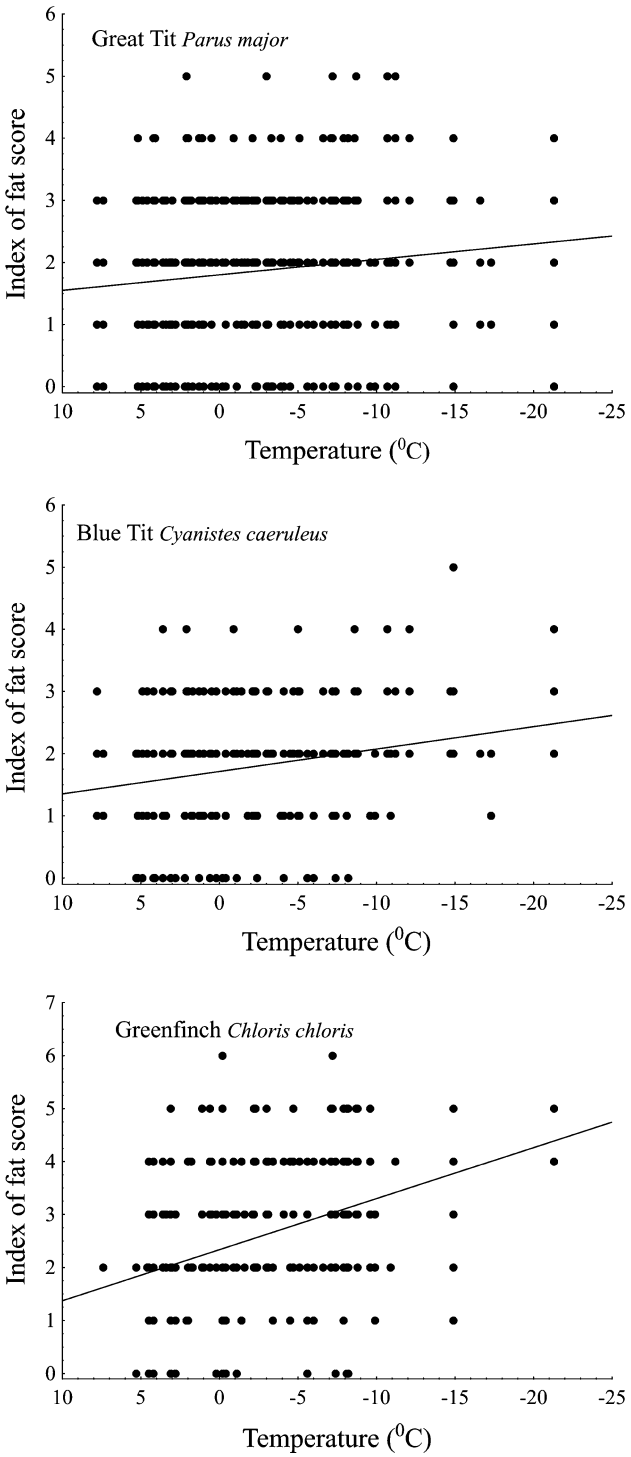

Fig. 2 Effect of the average temperature on the fat score in three bird species wintering in Poland

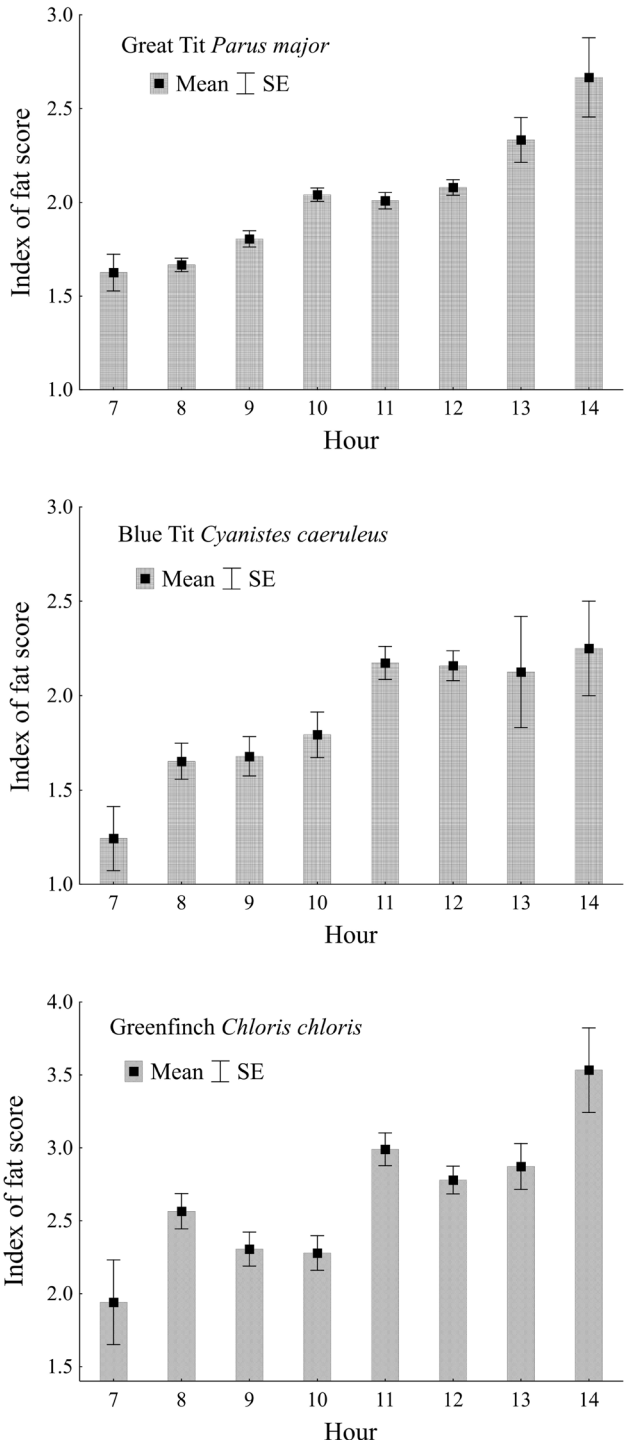

Fig. 3 Fat score variation with time of day in three bird species wintering in Poland

Shaw et al. 2008) and tits are major components of its diet (Zawadzka and Zawadzki 2001). When we were catching the birds, the sparrowhawk was seen several times at each site. However, its winter abundance is rather low in the settlements in Poland, e.g., in eastern Poland it had been seen for a quarter of all surveys in detail studied three villages (Goławski and Dombrowski 2011), while in the UK this species is numerous (Chamberlain et al. 2009). Moreover, the greenfinch as a larger and more aggressive species, when occupying bird feeders in flocks may take over the food

resources and not allow other species to forage efficiently enough to accumulate higher fat loads (Wojczulanis-Jakubas et al. 2015). The greenfinch, being naturally granivorous, has perhaps a more efficient digestive system to deal with seeds and metabolize them into fat. In contrast, tits, as natural insectivores (Cramp 1998), seem to be less effective in this matter.

We found that the season-site index significantly influenced fat reserves, probably due to the different climate conditions in various parts of the country. The western part of Poland has milder weather with less snow; the coastal and southern areas have the highest temperatures, while the harshest is the continental climate of northeastern Poland (Domonkos and Piotrowicz 1998). Also, each season had different sequences of weather conditions which might, like the location of study plots, significantly affect the fat load in birds. An additional important factor is the presence of potential predators which may differ between locations and seasons, influencing the fat score in birds that need to adjust their body weight to be able to escape from predators (Gosler et al. 1995).

No influence of ranked status of birds on fat score seems rather surprising (Ekman and Lilliendahl 1993; Haftorn 2000; Krams 2002). Perhaps food in bird feeders was provided ad libitum, more than the birds could eat and metabolize, therefore all individuals could "eat their fill" and consequently there were no differences between the status groups. Without human influence, the temperature seems to affect the fat level much more. This has been confirmed by Krams et al.'s studies (2010) on the great tit, where dominant individuals gained a greater fat load than subordinate ones in strong temperature decrease conditions, whereas no differences were found in fat scores of individuals of different social status during mild temperatures. Similar tendencies in the fat load levels in great tits of various dominance groups were described in terms of food supplies; if there was plenty of food, all the birds gained much less fat load than in seasons with low food availability, when differences in fat load between individuals were much larger (Gosler 1996). This corresponds well with the results of our study.

In conclusion, our study showed that the average temperature is the main factor affecting the fat score of all species of birds. Comparison with other studies suggests that under the conditions of Central or Northern Europe it is the most important meteorological factor for the birds, as in other parts of Europe (Gosler 1996), where, however, birds may also strongly react to rainfall with the amount of fat accumulated (Gosler and Carruthers 1999). We found no correlation between the fat score and the degree of dominance in all species described here, although many studies have proven such a dependence (Hake 1996; Lange and Leimar 2004; Krams et al. 2010). Meanwhile, when energetic requirements increase and food becomes less available in winter, social priority to food access should be important, particularly among birds that form flocks. Possible reasons for our study not fitting those of others in this respect was abundance of food in the feeders, sufficient for all foraging birds, and low predation risk.

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