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Physiological condition of incubating and brood rearing female Great Tits *Parus major* in two contrasting habitats

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Abstract. Little is known about the physiological causes and consequences of habitat choice decisions in birds. We compared size-corrected body mass, hematocrit, plasma albumin, beta- and gamma-globulin and triglyceride concentrations, as well as the albumin/globulin ratio of female Great Tits breeding in deciduous and coniferous forests in Estonia. Females were sampled during incubation and during the chick-rearing period. Whereas the nest box occupation rate and clutch size were higher in the deciduous habitat, the female nutritional condition during incubation was better in the coniferous habitat. This habitat difference in condition was not explained by the differences in the start of egg-laying or clutch size. Females lost more mass from incubation to the chick-rearing stage in the coniferous than in the deciduous forests. Although the values of most blood parameters changed from incubation to the chick-rearing stage, no habitat-related change was observed. There were no habitat differences in the number and quality of fledglings or in female condition during the chick-rearing period. Our results indicate that incubating female Great Tits are in a worse nutritional state in the preferred deciduous habitat fragments than those in the non-preferred coniferous habitat. However, habitat-related differences in condition during incubation seem to be unrelated to habitat-specific reproductive decisions.

Key words: Great Tit, *Parus major*, habitat differences, plasma proteins, triglycerides, hematocrit, breeding cycle

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INTRODUCTION

Due to the loss and fragmentation of natural forest habitats, the ecological quality of the remaining plots changes (reviewed in Ewers & Didham 2006). With such decrease in the amount of optimal habitat, increased proportion of individuals is often forced to move to normally avoided or non-preferred habitats (Battin 2004). Sometimes birds are attracted to non-preferred habitats also by conservationists and researchers who use some wildlife management techniques, e.g., providing nest boxes for secondary cavity-nesting birds (Rodenhouse et al. 1997, Semel & Sherman 2001, Schlaepfer et al. 2002). However, our knowledge about the individual physiological causes and consequences of habitat choice decisions in such mosaics of optimal and sub-optimal habitat is still very limited (e.g., Mazerolle & Hobson 2002, Suorsa et al. 2003, 2004, Wikelski & Cooke 2006, Bańbura et al. 2007, Johnson 2007).

Several hole-nesting passerines, including the Great Tits, prefer to breed in deciduous woodlands instead of coniferous forests (van Balen 1973, Klomp 1980, Mänd et al. 2005; reviewed in Newton 1998). Coniferous forests are considered to be less attractive for breeding as a result of nest hole shortage and lower food abundance (van Balen et. al 1982, Perrins 1991). Also the breeding success of Great Tit has generally been shown to be higher in deciduous habitats compared to coniferous habitat (Sanz 1998; but see Lundberg et al. 1981, Catalan & Haeger 1996, Mänd et al. 2005).

In our study area, situated in north-eastern Europe, it has recently been shown that the occupancy of the nest boxes by Great Tits is higher and clutch and egg sizes are larger in the fragments of deciduous habitat compared to managed pine forests (Mänd et al. 2005). Unexpectedly, the number of offspring and their condition turned out to be higher in coniferous habitat in most years

(Mänd et al. 2005). Furthermore, adults' physiological condition during nestling feeding period tended to be better in the coniferous habitat compared to the deciduous habitat (Kilgas et al. 2006). However, it has remained unsolved whether such habitat differences in adult condition arise during nestling feeding period or already in earlier breeding phases.

The decrease of body mass during breeding is a commonly observed phenomenon in female birds (e.g., Freed 1981, Merilä & Wiggins 1997, Cichoń 2001). Much less is known about changes of physiological parameters throughout the different reproductive phases in free-living birds (e.g., Hõrak et al. 1998a, Vanderkist et al. 2000, Kern et al. 2005, Gayathry & Hedge 2006). However, to our knowledge, the studies examining temporal changes in physiological condition indices of breeding birds simultaneously in different habitats are absent.

In the current study we compared the nutritional and immunological condition and body size of breeding female Great Tits in deciduous and coniferous forests of a heterogeneous habitat mosaic. Blood samples were taken in the middle of the incubation period and in the second half of the nestling period. We also recorded breeding data (see Material and Methods) to see whether habitat-related differences in physiological condition are also in correspondence with the habitat-specific reproductive decisions. We also followed individual changes in condition indices from incubation to chick rearing stage in both habitats. Based on our previous results (see above), it was predicted that female condition during incubation is better in preferred deciduous habitat than in non-preferred coniferous habitat. The opposite was predicted for chick rearing period. As indicators of female physiological condition, we used size-corrected body mass, hematocrit, plasma albumin, beta- and gamma-globulin and triglyceride concentrations, and albumin/globulin ratio.

MATERIAL AND METHODS

General field procedures

Data were collected in the surroundings of Kilingi-Nõmme in Estonia (58°7′N, 25°5′E), NE Europe, in 2003. The study area is approximately 50 km^2 with two contrasting forest types — deciduous and coniferous (see Mänd et al. 2005 for the scheme of the study area). Fragments of young deciduous forests, surrounded by agricultural landscape, grow on fertile soils that have a rich deciduous understorey. The most common tree species are Grey Alder *Alnus incana* and Silver Birch *Betula pendula*. The coniferous habitat is a typical continuous managed pine forest on nutrient-poor sandy or peat (in the lower parts of the terrain) soil. Dominant tree species are Scots Pine *Pinus sylvestris*, which sometimes occur in mixed stands of Norway Spruce *Picea abies* on sandy soils or of Downy Birch *Betula pubescens* on peat soils.

Great Tits bred in wooden nest boxes with cavity measurements of 11×11×30 cm and an entrance diameter of 3.5–4 cm. Nest boxes were mounted on tree trunks at a height of 1.5–2 m. The nest boxes were arranged in lines, and each line consisted of some tens of nest boxes. Distance between nest boxes was 50–60 m. Old nest material was removed every year before the start of nest building. All nest boxes were visited twice (with one-week interval) during the nest-building period, in order to record those occupied by Great Tits. Each occupied nest box was thereafter inspected with 1–2-day intervals during the whole egg-laying period.

Incubating females were weighed on the fifth day after the clutch completion with a Pesola spring balance to the nearest 0.1 g and their tarsi were measured with a sliding caliper to the nearest 0.1 mm. Blood samples (ca. 100–150 microliters) were taken from the tarsal or brachial veins and collected into heparinized capillary tubes and kept cool until centrifugation few hours later. 37% of incubating females abandoned the nest after the capture and blood sampling. There were no differences in incubation body mass or blood parameters between deserters and non-deserters (T-test, all $p > 0.1$). Females that did not abandon their nests were sampled again when their nestlings were 8–15 days old. Physiological parameters of females were not significantly associated with the time of sampling or the age of nestlings (Pearson correlation, all $p > 0.1$). Fledglings' mass and tarsus length were measured at day 15 post-hatch.

Laboratory analyses

Plasma was separated from blood cells after 10 min centrifugation at 10 000 rpm, and was stored at -20°C until analysed. Hematocrit was measured with a sliding caliper to the nearest 0.1 mm. Standard agarose gel electrophoresis with REP System (Helena Laboratories) was used for detection of major protein groups. Gels were stained with Ponceau S stain using REP Gel processor, and were densitometrically scanned at a wavelength of 525 nm. Due to difficulties in separating the pre-albumin fraction from albumin, summed concentration was used and termed as albumin concentration, similarly to Ots et al. (1998). Concentration of triglycerides was determined using a quantitative enzymatic test (Sigma Diagnostics). Exactly the same methods for protein and triglyceride detection have also previously been used in Great Tits (Ots et al. 1998, Kilgas et al. 2006, Tummeleht et al. 2006).

Blood parameters studied

Hematocrit measures the relative amount of red blood cells in total blood volume. It reflects the oxygen carrying capacity of the blood. Its low values (anemia) are indicative of bacterial or parasite infections, but also reflect deficiencies in nutrition, especially the scarcity of some micronutrients such as Fe, Cu and vitamin B_{12} (Svensson & Merilä 1996, Coles 1997). Hematocrit value can also rise with hard physical exercise (Saino et al. 1997) and decrease in egg laying birds (reviewed in Williams et al. 2004).

A decrease in albumin concentration in the blood plasma accompanies almost any diseases and is also an indicator of malnutrition (e.g., Kawai 1973, Ots et al. 2001, Hõrak et al. 2004). The gamma-globulin fraction of the serum includes most of the known antibodies (immunoglobulins) involved in the immune response to protozoan, bacterial and viral infections. The concentration of gamma-globulins increases with both acute and chronic infections. The beta-globulins include several acute phase proteins. An increase in beta-globulin concentration in blood plasma is expected with acute inflammation (Coles 1997). Healthier individuals in general have higher albumin/globulin ratios (Kawai 1973, Coles 1997, Hõrak et al. 2004).

Triglyceride concentration in blood plasma reflects the rate of lipid transport into adipose tissues and can be considered as an estimate of the amount of lipids absorbed during the few hours before blood sampling (e.g., Jenni-Eiermann & Jenni 1997).

Statistical analyses

Statistical analyses were performed using the statistical package Statistica 7.0 (StatSoft Inc.). GLM analysis was used to study the effect of habitat on body mass, body size and blood parameters. In order to normalize the distribution of the dependent variables, original values of blood parameters, except hematocrit, were ln-transformed. To control for structural size when analysing the variation of adult body mass, the cubed tarsus length was included as a covariate in the model (García-Berthou 2001). Sample sizes differ slightly for different variables, since not all measures could be obtained for all individuals. When analyzing the effects of habitat on the number of fledglings, depredated or deserted nests were omitted from the analysis. The brood mean nestling body mass and tarsus length were used in analyses.

RESULTS

The nest box occupation rate by Great Tits was higher in deciduous (23.4% of 380 nest boxes) than in coniferous (10.8% of 776 nest boxes) habitat (χ^2 analysis, $\chi^2 = 31.8$, df = 1, $p < 0.001$). The Great Tit females breeding in deciduous forests laid slightly larger clutches than those breeding in coniferous forests (deciduous: mean ± SD = 11.43 ± 1.27; coniferous: 10.81 ± 1.26; GLM, habitat: $F_{1,\,65} = 3.99$, $p = 0.050$). This result, as well as all the following results, was unchanged when laying initiation date was included in the models as a covariate. However, laying initiation date itself remained always non-significant and was therefore not included in final models. The mean date of laying start also did not differ between habitats (T-test, $t_{1,\,65} = 0.13$, $p = 0.9$).

During incubation, females breeding in coniferous habitat had higher size-corrected body mass, hematocrit, albumin/globulin ratio and albumin concentration, compared to those breeding in deciduous habitat (GLM, Table 1). There was no significant effect of habitat on tarsus length and globulin and triglyceride concentrations (GLM, Table 1).

The inclusion of clutch size in the models as a covariate did not change the previous results. As the effect of clutch size on condition indices was not significant (results not shown), it was not included in final models.

In the case of blood parameters, the results remained unchanged when female body mass was included in the models as a covariate (results not shown). As the effect of body mass was non-significant in all initial models, it was not included in final models (Table 1).

There was no significant effect of habitat on the number of fledglings, and their tarsus length and body mass (GLM, all $p > 0.1$). There were also

Table 1. The effect of habitat on condition indices and tarsus length of female Great Tits measured during incubation (GLM analysis). Presented are untransformed means. In case of body mass, the cubed tarsus length of females was included in the model as a covariate ($F_{1,64} = 3.85$, $p = 0.05$).

	Coniferous forest			Deciduous forest			F	p
	Mean	SD	N	Mean	SD	N		
Tarsus (mm)	19.73	0.53	32	19.77	0.51	36	0.12	0.73
Mass (g)	20.59	0.79	32	20.02	0.89	35	8.28	0.005
Hematocrit	0.46	0.03	31	0.44	0.03	33	7.26	0.009
Albumin (g/L)	21.79	8.31	27	16.33	5.06	32	10.42	0.002
Beta-globulin (g/L)	7.23	2.39	27	6.39	1.53	32	2.23	0.14
Gamma-globulin (g/L)	2.89	1.18	27	2.78	0.99	32	0.16	0.69
Albumin/globulin ratio	1.47	0.34	27	1.19	0.30	32	11.57	0.001
Triglycerides (mg/dL)	252.40	142.90	27	221.50	82.60	32	0.15	0.70

no significant effects of habitat on female tarsus length and condition indices measured during chick rearing phase (GLM, all $p > 0.1$).

None of the blood parameters measured in females during incubation was correlated with respective values measured during nestling phase (Pearson correlation, all $p > 0.1$). However, female body mass measured during incubation was positively correlated with body mass measured during nestling phase ($r = 0.66$, $n = 37$, $p < 0.001$).

There was a significant decrease in female body mass from incubation to chick rearing stage (Repeated measures GLM, Table 2, Fig. 1). This change was significant in both habitats separately (Tukey test, deciduous habitat $p < 0.001$ and coniferous habitat $p < 0.001$), although the significant breeding stage x habitat interaction term indicated that the decrease was more pronounced in coniferous habitat (Table 2, Fig. 1). Female hematocrit and albumin/globulin ratio increased, and triglyceride and beta-globulin concentrations decreased from incubation to chick rearing phase (Table 2). There was no significant change in albumin or gamma-globulin concentrations (Table 2). Changes in blood parameters between different breeding stages did not differ between habitats; therefore the habitat term was not included in the final models (Table 2).

DISCUSSION

Habitat differences of condition indices

We found that, during incubation, Great Tit females in coniferous habitat had higher size-corrected body mass, hematocrit, plasma albumin/globulin ratio and albumin concentration, compared to those breeding in deciduous habitat. These results indicate that females were in a better nutritional condition (see Material and Methods) during incubation in coniferous than in deciduous habitat. Several studies have used hematological parameters and plasma chemistry to examine habitat differences in physiological condition of adult free-living birds (e.g., Mazerolle & Hobson 2002, Suorsa et al. 2004, Owen et al. 2005, Kilgas et al. 2006, Tummeleht et al. 2006). However, almost nothing is known about possible temporal patterns of habitat differences in physiological condition (reviewed in Johnson 2007).

Table 2. Changes of condition indices from incubation stage to chick rearing stage in female Great Tits (Repeated measures GLM). Presented are untransformed mean values. The values are pooled over habitat since this factor did not have significant interactions with breeding stage. In case of body mass, the term time x habitat was included in the model ($F_{1,35} = 7.53$, $p = 0.009$).

	Incubation		Chick rearing		N	F	p
	Mean	SD	Mean	SD			
Mass (g)	20.40	0.91	18.00	0.90	38	411.80	< 0.0001
Hematocrit	0.45	0.03	0.50	0.04	35	67.30	< 0.0001
Albumin (g/L)	18.64	7.13	18.14	3.06	24	0.04	0.85
Beta-globulin (g/L)	7.16	1.87	5.63	1.44	24	14.90	< 0.001
Gamma-globulin (g/L)	2.85	1.07	2.41	0.89	24	3.11	0.09
Albumin/globulin ratio	1.26	0.34	1.56	0.28	24	16.30	< 0.001
Triglycerides (mg/dL)	244.90	126.40	153.40	68.50	26	13.90	< 0.001

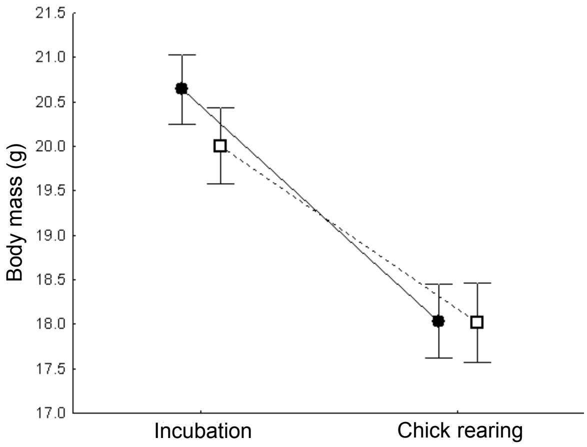

Fig. 1. Body mass (mean ± 95%) of female Great Tits during incubation and during chick rearing in coniferous and deciduous habitat. Filled symbols: coniferous habitat, empty symbols: deciduous habitat.

Our finding is of particular interest in the light of numerous studies that clearly show that Great Tits prefer deciduous habitats to coniferous habitats (e.g., van Balen 1973, Klomp 1980, Cramp & Perrins 1993, Mänd et al. 2005, this study). The fact that females usually have less and smaller eggs per clutch in coniferous than in deciduous habitat (Sanz 1998, Mänd et al. 2005, current study) may lead one to the assumption that the observed habitat-specific variation in female condition is just the result of a lower investment in egg production (Williams 2005) or of lower incubation costs (Hanssen et al. 2005) in coniferous habitat. However, inter-habitat differences in body mass and blood parameters of females persisted even when clutch size was included in the model as a covariate. This indicates that the effect of habitat on female condition is probably independent of the egg-laying and incubation costs, and is apparently caused by some other habitat-related factors.

We cannot exclude the possibility that the habitat-related differences in female condition existed already before egg laying. This could be possible if only females in superior condition usually settle into non-preferred coniferous habitat. However, individuals in prime condition are generally expected to settle into preferred habitats (Newton 1998, Stamps 2006).

It is also possible that foraging conditions early in the season are actually better in coniferous habitat than in deciduous habitat. In the Netherlands, it has been found that the caterpillar abundance during nestling feeding stage is higher in mature oakwoods, compared to pinewoods (van Balen 1973). However, in Finland, there seemed to be no differences between birch forests and coniferous forests in caterpillar abundance during incubation period (Rytkönen & Orell 2001). Similarly, Mägi (2007) has found no differences between habitats in caterpillar biomass during incubation period for our study area. As the breeding density of Great Tits in our study area is much higher in young deciduous habitat fragments compared to coniferous habitat (Mänd et al. 2005, this study) it is possible that the *per capita* amount of food is actually higher in coniferous habitat.

Females lost ca. 0.5 g more mass from incubation to chick rearing period in coniferous compared to deciduous habitat. This could indicate that possible favorable conditions in coniferous habitat early in season are not prevalent anymore in chick-rearing stage. Consistent with this prediction, there was also no habitat effect on breeding success or female condition during the chick-rearing period. Previous studies in the same population have also failed to observe any habitat differences in the body mass (Mänd et al. 2005, Kilgas et al. 2006) or tarsus length (Mänd et al. 2005) of chick rearing females. However, we have shown earlier that brood-rearing adults tended to have a better immunological state in coniferous habitat compared to deciduous habitat (Kilgas et al. 2006). The differences between the studies may be caused by annual differences in foraging conditions, since body condition and immune parameters of birds within one population can differ considerably between years (Acquarone et al. 2002, Sánches-Guzmán et al. 2004, Kern et al. 2005, Kilgas et al. 2006). Similarly, the habitat-related differences in reproductive performance in Great Tits vary considerably yearly (Mänd et al. 2005, Pimentel & Nilsson 2007).

Variation in blood parameters in relation to stage in the breeding cycle

Although the values of most blood parameters showed remarkable changes between the two breeding phases, no habitat-specific changes could be revealed. The higher values of beta-globulins and lower values of albumin/globulin ratio during incubation, observed in this study, may indicate higher acute inflammatory response and the lower health state at this breeding phase (Kawai 1973, Coles 1997), compared to chick rearing period. There was however no significant change with breeding phase in gamma-globulin concentrations. Thus investments into humoral immune defence did not differ between the two reproductive phases. It has previously been shown in birds that immunoglobulin production increases during egg laying, in order to facilitate passive immunoglobulin transfer to eggs (Saino et al. 2001, Gasparini et al. 2002). However, it has also been shown in Barn Swallows *Hirundo rustica* that circulating immunoglobulin concentrations drop to prelaying levels with clutch completion (Saino et al. 2001).

Plasma triglyceride concentrations depend strongly on food intake (Jenni-Eiermann & Jenni 1997, Cerasale & Guglielmo 2006), therefore higher triglyceride concentration during incubation may indicate females' superior nutritional status compared to that during chick rearing phase. This is in accordance with higher body mass observed during incubation compared to chick rearing period. Triglyceride concentrations also increase in egg-laying birds (Vanderkist et al. 2000, Challenger et al. 2001). However, it has been shown in the European Starling *Sturnus vulgaris* that triglyceride values decreased to prebreeding levels with clutch completion (Challenger et al. 2001). In Pied Flycatchers *Ficedula hypoleuca*, no differences were found in triglyceride concentrations between incubation and chick rearing stages (Kern et al. 2005). We also found no differences between breeding stages in albumin concentration, an indicator strongly associated with protein nutrition (Kawai 1973, Coles 1997).

Females had also higher hematocrits during chick rearing than during incubation. Hematocrit typically declines in egg-laying birds and sometimes it does not recover upon cessation of egg production, remaining low even at incubation (reviewed in Williams et al. 2004). However, it has also been shown in Great Tits that experimental brood increment increases parents' hematocrit (Hõrak et al. 1998b). Therefore, higher hematocrit during brood rearing, compared to incubation stage, may also be a response to the requirement of elevated oxygen-carrying capacity of the blood during increased workload.

In conclusion, our results indicate that, although Great Tits prefer deciduous habitat to coniferous habitat, the nutritional condition of incubating females was better in the non-preferred coniferous habitat in our study area. The decline of female body mass from incubation to chick rearing phase was more pronounced in coniferous habitat compared to deciduous habitat. Although the values of most blood parameters changed from incubation to chick rearing stage, no habitat related change was observed. There were also no habitat differences in breeding success and female condition at chick rearing stage. These findings show that the critical period that causes the habitat-related variation in physiological condition in Great Tits may lie at a much earlier stage of breeding than the brood-rearing stage. This study also suggests that habitat related differences in nutritional state during incubation could be unrelated to habitat-specific reproductive decisions.

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STRESZCZENIE

[Parametry fizjologiczne samic bogatki podczas wysiadywania jaj i wychowu młodych w dwóch środowiskach leśnych]

Celem pracy było porównanie kondycji i wielkości ciała ptaków gniazdujących w mozaice środowisk. Badania prowadzono w Estonii w 2003. Badano bogatki gniazdujące w skrzynkach lęgowych w dwóch silnie różniących się środowiskach — młodych lasach liściastych z olszą szarą i brzozą, oraz gospodarczych lasach sosnowych. Ptaki łapano dwukrotnie, podczas wysiadywania (5 dnia po zakończeniu składania jaj) oraz karmienia 8–15 dniowych piskląt. Ptaki mierzono, ważono i pobierano próbki krwi, które odwirowano, aby zmierzyć hematokryt, zaś w osoczu zmierzono stężenie: albuminy, beta i gamma globuliny oraz trójglicerydów. 37% samic wysiadujących jaja, od których pobrano krew porzuciło swe lęgi.

Częstość zajęcia skrzynek lęgowych oraz wielkość zniesienia były większe w lasach liściastych, natomiast parametry kondycji samic podczas wysiadywania (m. in. ciężar ciała, hematokryt, stężenie albumin) były wyższe w lasach sosnowych (Tab. 1). Różnice te nie były związane z terminem rozpoczęcia składania jaj lub wielkością zniesienia.

Ciężar ciała samic zmniejszał się istotniej w okresie między wysiadywaniem a karmieniem piskląt w lasach sosnowych niż w liściastych (Tab. 2, Fig. 1). Wartość większość parametrów krwi zmieniała się między okresem wysiadywania i wychowem piskląt, ale nie stwierdzono, aby zmiany te związane były z różnicami środowisk. Nie stwierdzono także różnic między środowiskami w liczbie i kondycji piskląt (długość skoku, masa ciała) oraz samic karmiących młode.

Wyniki pracy wskazują, że wysiadujące samice z preferowanych przez ten gatunek lasów liściastych są w gorszej kondycji, niż te w środowiskach nie preferowanych i sugerują, że powstawanie różnic w kondycji ptaków gniazdujących w porównywanych środowiskach może zachodzić na początku sezonu lęgowe.