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Food composition of wintering great tits (*Parus major*): habitat and seasonal aspects

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Abstract. The winter diet of the great tit (*Parus major*) was examined in mixed and deciduous forest in central Slovakia during three winters. Using a faecal samples analysis, in 105 sampled roosting individuals (in nest-boxes) at least 37 taxa of invertebrates were found. Apart from the invertebrates, plant material was identified in dissected birds' droppings as well. There were no significant differences in the winter food composition between sexes. Generally, plant material was the most frequent and the most dominant winter food. This component was followed by moths, beetles and dipterans. While comparing the relative volume between two distinct habitats, the most significant difference was found in Lepidoptera adults and plant material. Birds from mixed forest foraged less on Lepidoptera adults in contrast to individuals from deciduous forest. This could be compensated by bigger consumption of seeds and buds there. Regarding seasonal changes, within five winter months (from November to March), the relative volume and frequency of some invertebrate groups (Heteroptera, Homoptera and Lepidoptera) significantly increased with the temperature but no correlations were found with other weather characteristics. Invertebrates exhibited the opposite seasonal pattern compared to the plant material.

Key words: birds, food, droppings, faecal analysis, invertebrates, plant material

Introduction

Less favourable environmental winter conditions require various adaptations of animal species. In birds, foraging strategies remain unchanged but foraging territories are subjected to changes (Enoksson & Nilsson 1983, Hedenstrom 2008). On the other hand, the residents, in particular insectivorous species of temperate zone, have to alter their diet spectrum. That is due to the deficit in arthropods caused by low air temperature or snow cover in the area (Grubb 1975, 1978, Robinson et al. 2007). In such a case, the invertebrate part of the food is supplemented by plant material, e.g. seeds, nuts, buds (Van Balen 1980, Vestjens 1983, Chamberlain et al. 2007). Great tits (*Parus major*) preferably forage on invertebrates in all developmental phases (e.g. Lepidoptera, Araneidea, Hemiptera, Diptera, Hymenoptera, Coleoptera) during their breeding and post-breeding (Betts 1955a, Inozemtsev 1962, Ceballos 1972, Kristín 1992). With the arrival of spring and breeding period, when vegetation starts growing, the plant food is used less, despite its high availability (Betts 1955a). The food components in the breeding season and their nutritional importance have been well studied (e.g. Royama 1970, Eguchi 1980, Kiziroglu 1982). However, in cold winters in the temperate zone, when the invertebrate food supply is limited (Pravosudov & Grubb 1997), the plant material should represents the major component of the diet (Van Balen 1980, Vestjens 1983, Sasvári 1988, Otter 2007). It is represented mainly by seeds and buds of beech, hazel, oak and other plant species and often also by non-native seeds provided at bird tables (Perrins 1966, Van Balen 1980, Källander 1981, Gosler 1993).

The role of invertebrates in the winter diet has not been studied sufficiently. We expect that the winter diet of the great tit does not contain plant material components only, but that the birds are able to supplement it with protein-rich invertebrates, despite their low availability at that time. Our main focus was variability of invertebrates in the diet during the harsh winter period. Hence, we analysed 1)

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composition 2) habitat influence and 3) weather-dependent and seasonal changes in the winter diet of great tit populations roosting in two forests in central Slovakia. We bring new information that the great tits are able to forage on various invertebrate taxa also during the harsh winter period.

Material and Methods

Data collection

The diet composition was examined using dissection of faecal samples (e.g. Rosenberg & Cooper 1990). Birds' droppings, containing the food remains, were collected from birds roosting singly in the nest-boxes during three winter periods from mid-November to mid-March (2006/2007, 2007/2008 and 2008/2009). Samples were obtained during the night, 1-4 hours after sunset, when the individuals were already lethargic in their sleeping position. Birds were carefully caught by hand (sex and possible age were determined), then ringed and transferred into the cotton bag for defecation. Apart from droppings found in the bag, some fresh ones (still having wet surface) from the nest-box were also collected and stored in 70 % ethanol. A sample consists of 1-3 fresh present-day droppings from one individual. Data from each particular individual were used only once. These droppings should represent the food consumed during the last 1-2 hours before roosting (Betts 1955b, Gibb 1956, 1957, Morton 1979, own unpublished results), when the winter basal metabolic rate and digestion of food increases with decrease of air temperature (Broggi et al. 2007, 2009, Caro & Visser 2009).

The sampling was conducted in two distinct forest habitats in central Slovakia (7.3 km from each other), where the winter abundance of the great tit was similar: 1) 110-year-old mixed stand with dominancy of coniferous trees, in the following text "mixed forest" (Kováčová; N 48°38′08″, E 19°04′05″; 480 m a.s.l.; fir 42 %, beech 40 %, others 18 %; area 4.2 ha; 166 trees (diameter in breast height exceeding 10 cm)/ha; 60 nest-boxes controlled; distance between the nest-boxes 50-70 m); 2) 80-year-old, prevalently deciduous stand, in the following "deciduous forest" (Stráže; N 48°34′23″, E 19°05′57″; 320 m a.s.l.; hornbeam 48 %, oak 46 %, others 6 %; area 3 ha; 378 trees/ha; 28.7 tree cavities/ha; 30 nest-boxes controlled; distance between the nest-boxes 50-70 m). No supplementary food or bird tables were placed directly in studied forests habitats. However, their presence is possible in the vicinity (outside the forest), where territories of some birds can extend.

Data analysis

Dissection of faecal samples was performed under a binocular enhancer (magnification scale 6-30×). Diet components were identified thanks to undigested tissues of invertebrates and plants respectively. Regarding the plants, only sunflower seeds were identified properly, while other plant tissues were specified and labelled as undetermined plant material. Composition was classified up to the lowest possible taxonomical level, usually as the family and order, less as genus and only exceptionally as the species (Appendix 1). For the quantitative comparison we pooled determined components into ten main groups (mainly based on taxonomic relatedness). Since birds can digest different groups at significantly different rates (e.g. hard exoskeleton of beetles versus soft cuticle in aphids) we used two different methods to estimate food quantity. Frequency of groups' occurrence was based only on their presence or absence in a sample, whereas estimation of relative volume should also relate to abundance and body size of consumed prey items. The total volume of a sample (100 %) was divided between estimated volume of invertebrates and the plant material which occurred there. Consecutively, the relative volume of a particular invertebrate group (I_k) was calculated as follows:

$$I_k = \frac{(a_k \cdot s_k) \cdot (100 - P)}{\sum_{i=1}^{n} (a_k \cdot s_k)}$$

where a_k is the abundance of consumed individuals of the particular invertebrate group k; s_k is the potential body size of the particular invertebrate group k; and P is the estimated volume of plant material in the sample. Abundance of consumed individuals was estimated as the number of unique body parts, i.e. a head, thorax, etc. in the sample (Rosenberg & Cooper 1990), while potential body size was taken as the average in particular group of invertebrates. Percentage values of the frequency of occurrence and of the relative volume were applied in two sample sets (i.e. two habitats). Quantitative data was correlated to the actual weather characteristics (average temperature, amount of precipitations, and depth of snow cover), provided from the nearest (2 km distant) local weather station (© Slovak Hydro-Meteorological Institute). Tested weather characteristics represented sampling day average and since insects' activity can differ according to the course of weather, also an average from the last three days before the sampling. Depending on actual weather condition, birds do not roost in the boxes equally during the whole winter period (Veľký

2006). Hence pooling of unequally field collected samples (from three winter seasons) was necessary to obtain sufficient number of material for the analysis of overall winter seasonal aspects (from November to March). To suppress possible bias due to different years, the seasonal pattern was plotted with long-term (19 years) averages of month temperatures (freely downloaded from http://www.weatherbase.com/).

Since data departed from normality, distribution-free non-parametric tests were applied in all cases. For a "post-hoc" testing in a non-parametric Kruskal-Wallis ANOVA we have used standardized values Z (Mann-Whitney *U*-test) in pair-wise comparisons. Computations were performed in STATISTICA 7 (© StatSoft, Inc.).

Results

Diet composition and distinct habitats

During the winter seasons 105 individuals of the great tit were sampled (mean = 2.7 droppings per sample). Altogether, at least 37 taxa of invertebrates were found. In some groups larvae or pupae were determined, too. Apart from invertebrates, plant material (mainly unidentified remains, except for sunflower seeds foraged on bird tables) and occasionally also gastrolites were present in the faecal samples (Appendix 1). In ten quantitative diet groups (compared separately) we did not find any significant differences between the sexes (Mann-Whitney *U*-test, n = 73 males, 32 females samples) and thus further analyses were performed without such reference. Generally, the plant material (undetermined plant species) was the most frequent and the most dominant in winter food of the great tit. This component was followed by moths (Lepidoptera), beetles (Coleoptera) and dipterans (Diptera). Despite the relatively higher frequency of foraging on spiders (Arachnida) or bugs (Heteroptera), these items comprised lower volume than other invertebrates in samples (Fig. 1). While comparing the relative volume between mixed and deciduous forests, the most significant difference was found in Lepidoptera adults and plant material. Birds of the mixed forest (n = 28 samples) foraged significant less for Lepidoptera adults in contrast to individuals from the deciduous one (n = 77 samples; Mann-Whithey *U*-test, Z = –5.30, p < 0.001) which was compensated by significantly higher consumption (volume) of plant material there (Z = 3.22, p < 0.001). In addition, Heteroptera also had significantly higher frequency in the mixed forest, but here in total volume it formed an unimportant part (Z = 2.74, p < 0.01). However, the frequency of the plant material did not differ significantly in droppings between mixed and deciduous forests (Fig. 1B). Besides a relatively smaller volume and also lower frequency of Lepidoptera adults (Z = –3.12, p < 0.001), higher foraging frequency on other groups was in mixed forest (significant in Heteroptera, Z = 3.32, p < 0.01, and Lepidoptera larvae and pupae, Z = 2.64, p < 0.01).

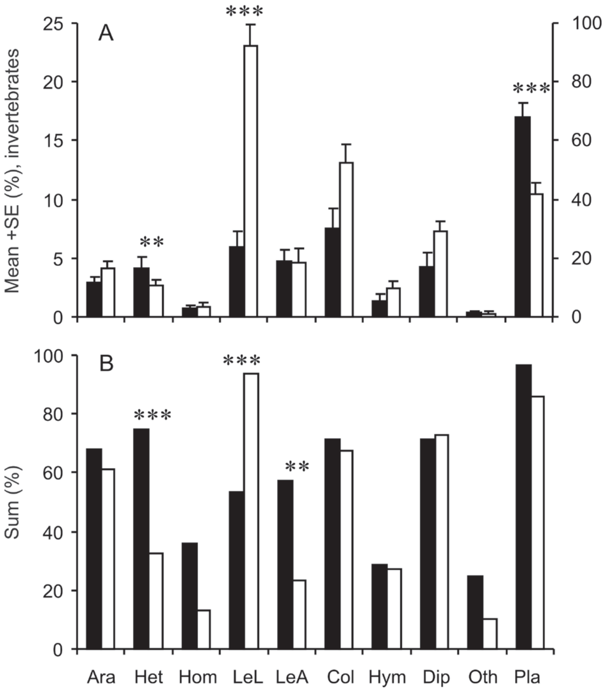

Fig. 1. *Relative volume per sample (A) and the total frequency of occurrence in all samples (B) of particular food items of the great tit during the winter season in two distinct forest habitats. Black columns – mixed forest (n = 28 samples, 2.7 droppings per individual), white columns – deciduous forest (n = 77 samples, 2.7 droppings per individual); Ara – Arachnida, Het – Heteroptera, Hom – Homoptera, LeL – Lepidoptera larvae and pupae, LeA – Lepidoptera adults, Col – Coleoptera, Hym – Hymenoptera, Dip – Diptera, Oth – Other invertebrate groups, Pla – Plant material. Significant differences between two habitats are indicated: ** – p < 0.01, *** – p < 0.001 (Mann-Whitney U-test).*

Seasonal changes in winter diet

Compared to the plant material, all analysed groups of invertebrates exhibited an opposite seasonal pattern in winter diet (Fig. 2). An increase in plant material decreases a share of invertebrates. In the coldest months of the mid-of-winter period (from December to February), the remarkable decrease in the relative volume of invertebrates contrasted with an increase of the plant material. Of the main invertebrate groups, intra-seasonal changes were significant in Arachnida (Kruskal-Wallis ANOVA, $H_{4,105}$ = 16.12, p < 0.01),

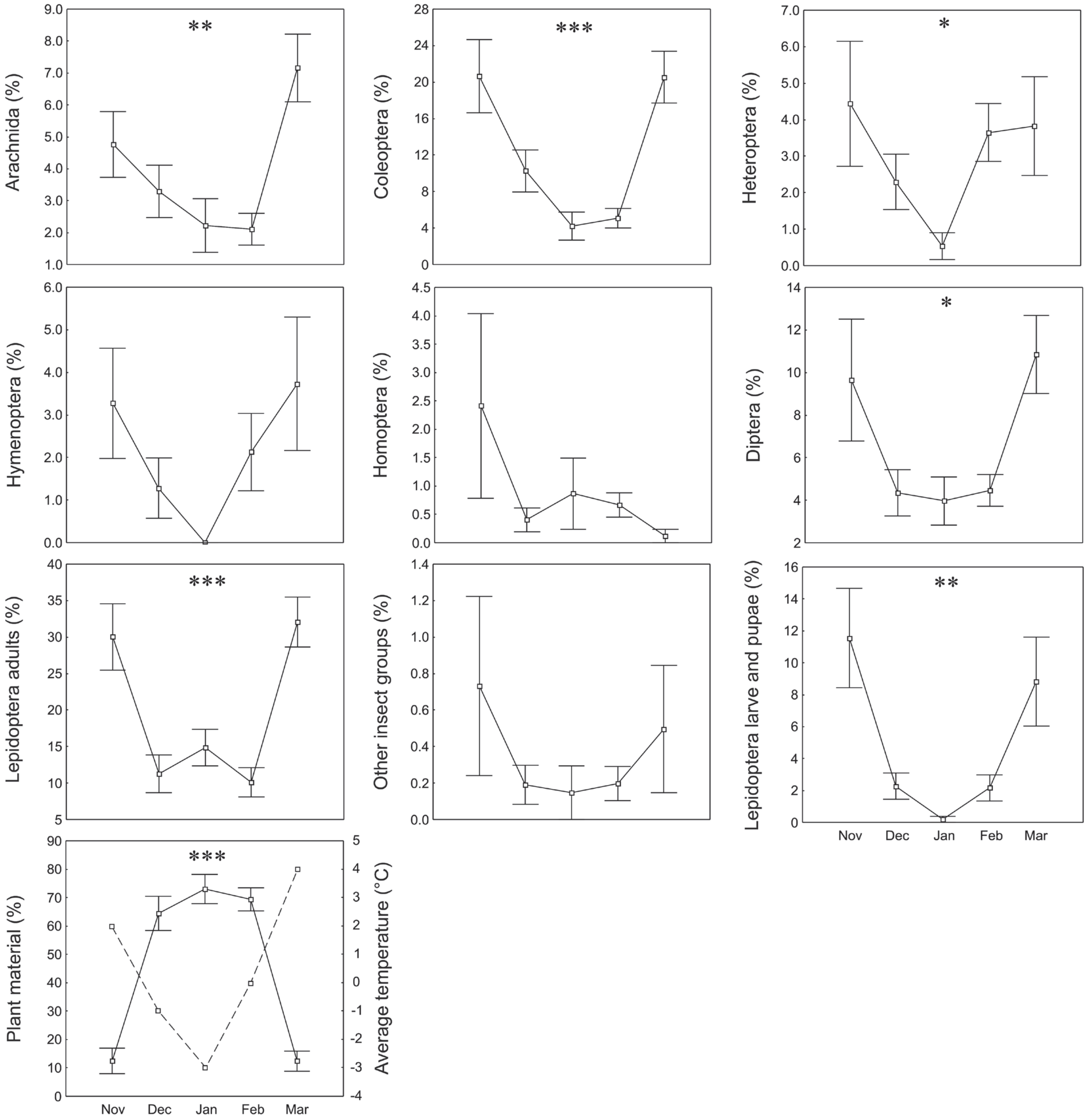

Fig. 2. *Changes in the relative volume of particular food items in the diet of the great tit during the winter season (means ± SE). Significant differences among months are indicated: * – p < 0.05, ** – p < 0.01, *** – p < 0.001 (Kruskal-Wallis ANOVA). The last figure includes also the long-term average month temperature in the study area (based on 19 years).*

Lepidoptera adults ($H_{4,105}$ = 35.86, $p < 0.001$), Coleoptera ($H_{4,105}$ = 29.65, $p < 0.001$), Lepidoptera larvae and pupae ($H_{4,105}$ = 13.90, $p < 0.01$), Heteroptera ($H_{4,105}$ = 10.34, $p < 0.05$) and Diptera ($H_{4,105}$ = 10.79, $p < 0.05$). Similarly, significant changes in the plant material were found ($H_{4,105}$ = 56.89, $p < 0.001$). The overall increase of the invertebrates' volume in March was consistent with the beginning of the vegetation period. The discovered pattern clearly corroborates the long-term averages of month temperatures in the study area (Fig. 2, the last plot). However, in Lepidoptera adults a somewhat different pattern was found. In pair-wise comparisons of Z-values differences, statistically significant higher volume in November and March versus December, January or February was found (Z = 3.64-4.71, $p < 0.001$). Simultaneously, the relative volume did not differ between the beginning (November) and the end

Table 1. *Correlation between measures (volume and frequency) of particular food items found in great tit faecal samples and average air temperature during the day of sampling (Spearman ranks, * – significant at p < 0.05).*

Food items	Relative volume	Frequency of occurrence
Arachnida	0.05	0.09
Heteroptera	0.20*	0.28*
Homoptera	0.20*	0.21*
Lepidoptera adults	–0.21*	–0.17
Lepidoptera larvae and pupae	0.33*	0.34*
Coleoptera	–0.12	–0.11
Hymenoptera	0.08	0.09
Diptera	–0.08	0.00
Other invertebrate groups	0.15	0.15
Plant material	0.18	0.12

(March) of winter season (0.16-2.70). This indicates that mainly moths are enriching the winter diet of the great tit in this time (Fig. 2).

When looking for some correlations with actual weather characteristics, only the average air temperature of the sampling day resulted in weak correlations (Table 1). Relative volume and frequency of some invertebrate groups (Heteroptera, Homoptera and Lepidoptera adults, larvae and pupae) increased with this temperature. However, a slight increase of Lepidoptera adults was consistent with decreasing temperature, probably caused by the above-mentioned pattern in January. However, taking average temperature of three days before sampling into account, no correlation was found there generally. Similarly, relative volume and the frequency of occurrence correlated neither with amount of precipitations, nor with depth of snow cover.

Discussion

Diet composition

In the central European winter, plant material represented the most important food component, enriched by moths, beetles and dipterans (Fig. 1). Our results corroborated the hypothesis that the great tit is able to forage on invertebrates also during the harsh winter period, but plant material dominated in winter food (Fig. 1) because invertebrates are limited (Van Balen 1980, Vestjens 1983, Otter 2007). Their availability is affected by outdoor temperature, depth of snow cover and less mobility of particular species. Highly proteinaceous invertebrates are replaced mainly with seeds (Van Balen 1980, Vestjens 1983) or buds (Otter 2007), and this plant material can compensate the lack of nutrients and so increase the winter survival of tits (Jannson et al. 1981, Orell 1989). Altogether, more than 40 various plant families have been found in the winter diet of the great tit (Perrins 1966, Van Balen 1980, Källander 1981), although birds might forage less on wild seeds and buds when sunflower seeds and other supplementary food is provided at bird tables. In northern Russia, an unexpectedly low proportion of plant material was found in the winter period (0.4 % of relative abundance), while Coleoptera (48.0 %) and Hemiptera (47.2 %) dominated (Petrov 1954). Similarly, in Mediterranean Spain, where the proportion of all plant material was also low (3.5 %), Coleoptera represented 27.1 % (Ceballos 1972). However, in central Russia a significantly higher proportion of plant material during winter was found (38.5 %), but Lepidoptera was the most dominant food component (49.5 %; Inozemstev 1962). Such discrepancies, comparing with our data suggest that proportions of particular components can differ among distinct sites according to local habitat and weather conditions. Different proportions of plant material in winter food can correlate with its different availability during winter period and seed size of several main tree species, i.e. beech, oak, hornbeam (Perrins 1966, Perdeck et al. 2000). Moreover, it should be considered also that different methods of food analysis can result in some differences. Methods identifying food remains found in the droppings can underestimate some less sclerotic tissues (Obeso 1988, Mouritsen 1994, Scheiffarth 2001). Thus some invertebrates (spiders or bugs) can be found in droppings in higher relative frequency, but lower relative volume (Rosenberg & Cooper 1990). However, due to the destructive effect of gut content analysis, the faecal analysis method is more appropriate in modern times (cf. Cramp & Perrins 1993, Matthysen 1998).

Influence of season, weather and habitat

Plant material was the most important diet component from December to February with the relative volume fluctuating around 70 % (Fig. 2). A similar pattern to our temperate continental climate was found in the Netherlands (Van Balen 1980), where the maximum values reached up to 90 % in the mid-winter. We found that before the coldest months (in November), the plant material can account for merely 10 %, while

Lepidoptera and Coleoptera dominated. The presented trend clearly corresponded to the local long-term temperature history (Fig. 2, the last plot).

Seasonal changes in the birds' diet depend on the activity of invertebrates responding to the actual weather circumstances (Hromada & Krištín 1996). The plant material (e.g. seeds) can be energy biased under some unsuitable weather conditions (low temperature), mainly because of its better availability than invertebrate food (Gibb & Betts 1963, Gosler 1993, Otter 2007). Our results demonstrate that air temperature of the sampling day was the only factor possibly enhancing winter activity in particular invertebrate species (Table 1). There was no influence of other weather characteristics (amount of precipitations, depth of snow cover). The subzero temperatures induce crystallisation of water in invertebrate bodies and physiological changes (Duman et al. 1991, Bale 1993, Storey & Storey 2000), whereas increasing air temperature (0-5 ºC) can encourage or start the activity of some invertebrate groups like moths and spiders during the winter period (Wolda 1988, Leather et al. 1993). In phytophagous moths (including also larvae and pupae) changes in activity are more complicated. Most of these species are overwintering as caterpillars in central Europe (Patočka & Kulfan 2009). Their winter activity depends on the roosting site (deciduous or coniferous tree). Caterpillars, overwintering on deciduous trees, do not have an increasing activity, not even during short-term temperature increase, which is caused by the absence of leaves, i.e. their primary food (Leather et al. 1993). However, on conifer-dependent species that consume needles, a smaller warming has more pronounced impact on activity (Han et al. 2005, Dvořáčková & Kulfan 2009). On the other hand, higher consumption of invertebrates during the warming can be caused by increased searching activity of primarily insectivorous birds (Grubb 1975, 1978, Broggi 2006).

Regarding the influence of habitats on the winter diet composition, it is necessary to consider that we solely investigated the influence of the roosting site habitat (food samples were collected from roosting birds). Indeed, the study species is very faithful to the roosting site during the winter period (Krištín et al. 2001). While in daylight the tits can collect the food in more distant (up to 1 km) and different habitats (Tokka 2006), droppings from birds captured at their roosts are related to the surrounding habitat only, since they collect the food at least one hour before the evening twilight already there (Gibb 1957, Von Haartman 1975, own unpublished data).

We found differences in the winter diet composition between mixed and deciduous forests, with significantly higher relative volumes of plant material found in birds originated from the mixed (fir-beech) forest. This could have been caused by complicated searching of invertebrate food on coniferous trees there, which may also explain unexpectedly higher consumption of bugs (Heteroptera) in the mixed forest, despite a higher bug diversity and abundance on deciduous trees in the vegetation period (Ammer & Schubert 1999). On the other hand, a significantly higher relative volume and frequency of occurrence of Lepidoptera in tits inhabiting deciduous (oak-hornbeam) forests may corroborate higher abundance of moth species living on oak trees (Patočka et al. 1999, Murakami et al. 2007, Patočka & Kulfan 2009). During the breeding season, food composition is similar in the two forest habitats. In general, the predominant food item (relative abundance and frequency) is Lepidoptera, followed by Arachnida, occasionally Coleoptera and Diptera, and only seldom other invertebrates (Betts 1955a, Bösenberg 1964, Kabisch 1965, Krištín & Patočka 1997).

Our study contributed to better knowledge of winter food composition of the great tit in central European deciduous and mixed forests. We found that despite the harsh winter condition the birds can find and consume invertebrates. Regarding seasonal changes, within five winter months (from November to March), the relative volume and frequency of some invertebrate groups (Heteroptera, Homoptera and Lepidoptera) significantly increased with the temperature. Some invertebrates can be found in the droppings even during the coldest days, although at that time, lack of invertebrates is compensated by various plant materials.

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Appendix 1. *Food remains in the droppings of the great tit during the winter season. Estimated numbers of food items in all containing samples/number of all containing samples from deciduous forest (n = 77 birds, 2.7 droppings per individual) and mixed forest (n = 28 birds, 2.7 droppings per individual), respectively.*

Gastropoda (2 food items/2 containing samples from deciduous forest, 0 food items/0 containing samples from mixed forest); Arachnida (Acarina 2/2, 1/1; Pseudoscorpionidea 3/3, 7/7; Lycosidae 1/1, 0/0; Araneidea indet. 52/46, 24/19); Heteroptera (Pentatomidae 9/8, 6/5; Miridae 4/3, 7/6; Heteroptera indet. 18/16, 16/14);

Homoptera (Aphidoidea 31/10, 12/10; Cicadidae 1/1, 3/3); Lepidoptera (Noctuidae adults 1/1, 0/0; Tortricidae adults 1/1, 0/0; Microlepidoptera adults 1/1, 1/1; Psychidae larvae 2/1, 0/0; Lepidoptera adults indet. 98/72, 17/14; Lepidoptera pupae indet. 0/0, 4/4; Lepidoptera larvae indet. 21/16, 14/13); Neuroptera (Hemerobiidae 1/1, 0/0); Coleoptera (Curculionidae indet. 64/28, 16/11; *Phyllobius* sp. 13/3, 0/0; *Dorytomus* sp. 2/1, 0/0; Carabidae 2/2, 2/2; Elateridae adults 1/1, 0/0; Elateridae larvae 1/1, 1/1; Chrysomelidae 2/2, 2/1; Tenebrionidae 0/0, 1/1; *Aphodius distinctus* 0/0, 1/1; Coleoptera adults indet. 39/36, 22/18; Coleoptera larvae indet. 4/3, 2/2); Hymenoptera (Ichneumonidae 7/5, 1/1; Braconidae 8/6, 1/1; Formicidae 17/14, 6/5; *Vespula* sp. 0/0, 2/1; Hymenoptera indet. 3/3, 1/1); Diptera (Syrphidae 0/0, 2/2; Nematocera indet. 74/55, 19/15; Tipulidae 1/1, 6/1; Brachycera indet. 3/3, 3/3; Diptera pupae 0/0, 1/1); undetermined plant material: 178/67, 49/26; sunflower seeds 7/7, 7/7; other seeds 14/1, 0/0; gastrolites: max. length > 1 mm 10/4, 3/1; max. length < 1 mm 1/1, 3/2.