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THE HABITAT-RELATED VARIATION OF REPRODUCTIVE PERFORMANCE OF GREAT TITS IN A DECIDUOUS-CONIFEROUS FOREST MOSAIC: LOOKING FOR CAUSES AND CONSEQUENCES

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers referred to in the text by their Roman numerals. As all papers are the result of a collective effort of different members of our study group, where each person was usually responsible for different aspects of the whole study, only certain aspects were included in the present thesis from some papers (**IV**, **V**, **VI**). This is specified in the Results section of the main part of the thesis. Original papers are reproduced with permission from the publishers.

I. Mägi, M. & Mänd, R. 2004. Habitat differences in allocation of eggs between successive breeding attempts in great tits (*Parus major*). *Ecoscience* 11: 361–369.

II. Mägi, M., Mänd, R., Tamm, H., Kilgas, P. & Tilgar, V. Seasonal and habitat-related variation in great tits' reproductive parameters, provisioning rate and food abundance: what is behind the contrasting breeding patterns? (submitted manuscript)

III. Mänd, R., Tilgar, V., Kilgas, P. & Mägi, M. 2007. Manipulation of laying effort reveals habitat-specific variation in egg production constraints in great tits (*Parus major*). *Journal of Ornithology* 148: 91–97.

IV. Tummeleht, L., Mägi, M., Kilgas, P., Mänd, R. & Hõrak, P. 2006. Antioxidant protection and plasma carotenoids of incubating great tits (*Parus major* L.) in relation to health state and breeding conditions. *Comparative Biochemistry and Physiology C: Toxicology & Pharmacology* 144: 166–172.

V. Tilgar, V., Mänd, R. & Mägi, M. 2002. Calcium shortage as a constraint on reproduction in Great Tits *Parus major*: a field experiment. *Journal of Avian Biology* 33: 407– 413.

VI. Kilgas, P., Mänd, R., Mägi, M. & Tilgar, V. 2006. Hematological parameters in brood-rearing great tits in relation to habitat, multiple breeding and sex. *Comparative Biochemistry and Physiology A*: *Molecular & Integrative Physiology* 144: 224–231.

The author's contribution to the papers:

The order of the authors' names reflects their involvement in the paper. In papers **I** and **II**, I participated in planning experiments and in data collection, performed all analyses and was responsible for writing manuscripts. In papers **III**, **V** and **VI**, I was involved in data collection (since 1999 in the case of paper **V**) and analysis and participated in finishing the manuscripts. In paper **IV**, I performed the laboratory and statistical analysis of the data on caterpillar abundance and was involved in finishing the manuscript.

1. INTRODUCTION

Intensive forest or agricultural management and wetland draining leading to habitat fragmentation or degradation have caused the decline in numbers of many bird species and have become the leading threats to biodiversity worldwide (Meffe & Carroll 1994; Newton 1998; Debinski & Holt 2000; Owens & Bennett 2000). Moreover, long-range studies in bird ecology examining recent changes in global climate have revealed the decrease of the reliability of cues that have previously been used by birds for making reproductive decisions (Visser *et al*. 2006). Due to changes in climate, there have also been shifts in the distribution of many avian species (Thomas & Lennon 1999; Carrillo *et al.* 2007). Such changes could potentially result in colonization of newly available climatically suitable habitats. All changes induced by human activity or climate may become expressed in worsened feeding conditions or increased interference, which may lower the breeding performance of populations. Therefore, knowledge about species adaptations to proximal and ultimate constraints in different quality habitats in a heterogeneous landscape is of high conservational value.

Individuals suffering from habitat destruction or degradation are forced to occupy formerly unoccupied areas, whose quality is often unknown. In some cases, resettlement of species into new areas by humans is the only conservational measure to preserve and protect threatened species (Ausden 2004). One should consider that habitat management or resettlement of a species could potentially be advantageous as well as harmful to populations and ecological processes. Therefore, it is important to learn to reliably predict the outcome of such activities and to study how to achieve the best results with minimal harm (Ausden 2004). Before any conservational action is undertaken, one must be sure that knowledge about the species ecology is adequate and how the new habitat corresponds with species requirements. According to Sutherland *et al.* (2004), typical questions that should be asked before taking any actions are: what are the foraging condition like in new area; are there sufficient appropriate nesting sites; are there predators, competitors or diseases that may have an affect on the survival or reproductive success of species?

The lack of proper knowledge about what the limitations for the species in a non-traditional habitat are, may result in creating so-called ecological traps – poor habitats that are preferred by animals, but whose true quality is less suitable for reproduction or survival than that of others (Gates & Gysel 1978; Kokko & Sutherland 2001; Schlaepfer *et al.* 2002). Such ecological traps have obvious management implications – a trap may become an “attractive sink” if the mortality in the habitat exceeds the birth rate (Delibes *et al.* 2001a; Delibes *et al*. 2001b). Any situation that attracts organisms to inferior habitat can lead to population decline, and theoretical modelling has shown that even modest amounts of trap habitat can pose a significant danger to population persistence (Schlaepfer *et al.* 2002; Battin 2004).

One possible mechanism by which a habitat can be turned into an ecological trap is when novel elements that mimic the traditional cues for habitat choice are introduced there (Schlaepfer *et al.* 2002). For example, provision of nest-boxes is the prevailing technique to increase nest site availability and quality for secondary cavity-nesting birds (reviewed in Newton 1998), and this technique has also been used for biological control of insect pests by attracting hole-nesting passerines to managed coniferous forests or orchards (*e.g.*, Mols & Visser 2002). Given that cavities are a major cue for nest-site selection of hole-nesters (Hildén 1965), abundant nest-boxes should make an area very attractive for many of them. The boxes are often placed in such habitats where hole-nesters otherwise cannot breed (Newton 1998). However, some researchers have recently reported that in certain cases this practice can yield undesired results (*e.g.*, Semel & Sherman 2001; Pöysä & Pöysä 2002; Mänd *et al.* 2005). For example, Semel & Sherman (2001) reported that erecting nest-boxes for wood ducks *Aix sponsa* in clusters over open marshes, instead of their usual hidden places in woods, had detrimental effects on reproduction because it exposed the nests to a supra-normal level of intra-specific brood parasitism. Pöysä & Pöysä (2002) provided another example where density-dependence negated the desired benefits of providing nest-boxes for common goldeneyes *Bucephala clangula*. One possible mechanism behind such negative outcomes is local crowding of breeders in spatially constrained populations due to the provision of nest-boxes (Rodenhouse *et al.* 1997). Hence, to avoid undesirable results, it is important for conservationists, before applying any measures, to learn to recognize the true quality of a habitat from the point of view of animals, to understand the rules that animals use in habitat selection. In particular, the consequences of conservation management techniques should be studied thoroughly from the viewpoint of the ecological trap concept. As stressed recently by Robertson & Hutto (2006), an improved library of such kinds of empirical studies will be essential if we are to develop a more synthetic understanding of the mechanisms that can trigger maladaptive behaviour in general and the specific conditions under which ecological traps might occur. Until now, such investigations are very scarce.

Wildlife conservationists are often placed in situations where decisions have to be made quickly, without enough time for specific research. Moreover, to perform a study on threatened species is often difficult due to a lack of resources (generally money) or time, which may be a critical factor for species sustainability. Therefore, besides the direct observation of endangered animal species, more thorough investigations of non-endangered model species are often helpful for revealing general rules. Several hole-nesting bird species accept and sometimes even prefer artificial nest-boxes for breeding instead of natural cavities (Bortolotti 1994; Ludwichowski 1997; Brouwer & Komdeur 2004; Gaedecke & Winkel 2005). Therefore secondary cavity nesters have served as popular model species in many bird ecology studies. Studies of habitat effects on breeding behaviour of tits and flycatchers are continuously actual (*e.g.*, Blondel *et al.* 2002; Tremblay *et al.* 2003; Eeva & Lehikoinen 2004; Lambrechts *et al.* 2004; Török *et al.* 2004; Eeva *et al.* 2005; Simon *et al.* 2005; Stauss *et al.* 2005). One widely exploited species for nest-box studies is the great tit (*Parus major*).

In the northern temperate zone, forests can be divided mainly into coniferous, deciduous or mixed ones. Forest management can greatly influence changes in avifauna. Management usually results in a reduction in tree species diversity, simplified structure, diminished abundance of mature trees and dead wood and, as a consequence, lowers the value of the stand for birds (Ausden 2004). Due to intensive forestry, the cover of mature deciduous forest has been greatly reduced both in temperate and boreal Europe (Riddington & Gosler 1995; Angelstam *et al.* 1997; Esseen *et al.* 1997). Also, availability of suitable nest cavities has decreased in managed stands (Newton 1998). Deciduous woodlands are typically smaller and younger (due to shorter rotation) than coniferous stands in the boreal vegetation zone and remain mainly as fragments between agricultural lands (*e.g.*, Huhta *et al.* 1998). For many species, like great tits, managed coniferous forests are still less attractive for breeding than deciduous forests, most likely due to a shortage of suitable nest holes and lower food abundance (Van Balen 1973). Previous studies have revealed consistent differences in breeding parameters of individuals breeding in coniferous forests, compared to those breeding in deciduous woodlands (Van Balen 1973; Sanz 1998; Mänd *et al.* 2005).

The nest-boxes for birds are often placed in small, young secondary deciduous stands (which presumably do not provide as much resources for breeding as old mature forests) or in managed conifer woods where hole-nesters normally cannot breed (Newton 1998) and which therefore represent novel habitats for them. Thus the risk of an ecological trap exists in both habitats. For example, the Estonian State Forest Management Centre has issued a decree to encourage the provisioning of nest-boxes in managed pinewoods, yet nobody has sufficiently explored the ecological consequences of this practice (Mänd *et al.* 2005). Recently, a six-year-long study of great tits was carried out in a heterogeneous landscape in SW Estonia, with the aim to compare the reproductive success of this species in young deciduous woods with that in managed coniferous forests of the same area, after the cavity shortage had been eliminated from both habitats by adding a surplus of nest-boxes (Mänd *et al.* 2005). The results of this study indicated that great tits preferred the deciduous habitat for breeding and invested relatively more in this habitat at the start of the breeding season, as judged by the relatively higher nest-box occupation, earlier egg-laying and larger clutches and eggs. Yet the final breeding outcome (number of fledglings per pair, fledglings' quality and recruitment rate) was consistently higher in the coniferous habitat (Mänd *et al.* 2005). A similar tendency was observed in some other studies performed in other regions with great tits (Lundberg *et al.* 1981; Catalan & Haeger 1996). Mänd *et al.* (2005) hypothesized that the preference for deciduous habitat may have a historical basis, and therefore nest-boxes in the preferred habitat had caused a supra-optimal breeding density leading to a maladaptive outcome (ecological trap). At the same time, nest-boxes had probably drastically improved the breeding conditions in the non-preferred coniferous habitat, but birds were incapable of exploiting the breeding habitat fully (Mänd *et al.* 2005).

There are, however, still more questions than answers. What is actually behind the above-described habitat-specific breeding patterns and the apparently non-adaptive investments? What role is played and what is the relative importance of proximate constraints versus strategic decisions? Food availability is considered to be one of the main environmental factors limiting avian reproduction (Newton 1998). Until recently, most avian studies have assumed that egg production is relatively inexpensive and that total reproductive costs consist mainly of costs of chick rearing (reviewed in Williams 2005). Therefore, some authors believed that birds' reproduction is not limited by the amount of resources available to females at the time of laying, and, instead, they use information from the environment prior to egg laying to anticipate feeding conditions when they rear young (Lack 1954; Ewald & Rohwer 1982; Perrins 1991; Arnold 1994). Recent investigation has revealed that egg production is in fact costly in several respects (*e.g.*, Monaghan & Nager 1997; Nager *et al.* 2001; Nilsson & Råberg 2001; Visser & Lessells 2001; Williams 2005). Such costs often reflect nutritional constraints (Monaghan *et al.* 1998; Clifford & Anderson 2001; Blount *et al.* 2004) and depend on environmental conditions at the time of laying (Visser & Lessells 2001). Therefore, the costs of egg production cannot be ignored when assessing optimal reproductive strategy of birds in different environments. Some authors have even suggested that it is difficult for birds to precisely predict future food availability, and that females always lay as many eggs as they can in a particular environment (Perrins 1970; Nur 1987; Eeva *et al.* 2000). To answer all these questions, we need a more thorough investigation and experiments, aimed at looking for specific constraints acting in different habitats during different phases of the breeding cycle.

One of the weaknesses of the above-mentioned study of Mänd *et al.* (2005) is that it took into account only data of the first breeding attempt. However, great tits, similarly to many other avian species in our region, are known as facultative double breeders – it means that females may lay a second clutch within the same breeding season after the successful rearing of the first brood. The number of breeding attempts during a season is considered to be an important life history trait affecting the offspring number in birds (*e.g.*, Tinbergen 1987; Friesen *et al.* 2000; Thompson *et al.* 2001; Visser *et al.* 2003). Moreover, in most cases the question is even more complicated. The first and the second breeding attempt often differ from each other with regard to such parameters as clutch size, egg size, fledging success, *etc.* (Ojanen *et al.* 1979; Orell & Ojanen 1983; Haftorns 1985; Den Boer-Hazewinkel 1987; Sasvari &

Hegyi 1994; Hõrak *et al*. 1995; Verhulst *et al*. 1995; Verhulst & Hut 1996; Christe *et al*. 2001; Dhondt *et al*. 2002). Thus, besides deciding whether to breed once or twice during a breeding season, the double breeders must also decide how to allocate their reproductive investment between successive breeding attempts (*e.g*., how many eggs to lay in the first clutch as compared to second clutch). Although data are available about the effects of habitat differences on the frequency of second broods (*e.g*., Kluijver 1951; Den Boer-Hazewinkel 1987; Cramp *et al*. 1993; Holmes *et al*. 1996), studies on other aspects of multiple breeding in different habitats are nearly absent. Thus, to be able to answer the above questions, one must certainly consider the data from the whole breeding season, including the second breeding attempt.

Our study area in Estonia differs from most of the other study areas of this species, representing a spatially heterogeneous deciduous-coniferous forest mosaic. The almost random distribution of contrasting habitat patches (see the map of study area in **I**) makes the investigation of habitat effects, methodically especially suitable here. At the same time, the situation that is characteristic to our region, where deciduous woodland exists mainly in the form of isolated fragments, while the more continuous forests are mainly managed conifers, is typical of extensive areas of the northern temperate zone. Therefore the investigation of the above-mentioned problems in this habitat system might be of great importance from the point of view of conservation biology in this whole region.

The general aim of the present thesis was to acquire a better understanding of the causes and consequences of the habitat-specific breeding patterns and apparent non-adaptive reproductive investments of a hole-nesting forest passerine – the great tit – in a deciduous-coniferous habitat system. The specific goals of the thesis were:

1) To explore whether there exist any consistent habitat-specific patterns in reproductive performance in great tits breeding in a deciduous-coniferous forest mosaic of the northern temperate zone;
2) To study whether various aspects of breeding in this species are limited to a different extent in different habitats and/or during different stages of the breeding cycle.

To address these goals, some basic reproductive parameters and the physiological condition of adult great tits were monitored for several years in the two contrasting habitats during successive breeding attempts. Besides this, data about possible calcium limitation during egg-laying and food limitation during brood rearing were collected. Both experimental and comparative approaches were used.

2. MATERIAL AND METHODS

2.1. Study species

The Great tit is a widespread, small (ca. 19 g), insectivorous, socially monogamous, secondary cavity-nesting passerine bird, living throughout the Palearctic region (Perrins 1979; Gosler 1993). It inhabits various woodlands – deciduous forests, older conifers, hedgerow trees, parklands and gardens, yet prefers deciduous forest as breeding habitat (Van Balen 1973; Ulfstrand *et al.* 1981; Lemel 1989; Cramp *et al.* 1993; Mänd *et al.* 2005). However, it is able to reproduce in managed coniferous forests as well when nest-boxes are added. In Estonia, great tits usually start egg-laying at the end of April or at the beginning of May, producing about 8–12 eggs per clutch (Hõrak *et al.* 1995; **I**). The eggs are incubated for up to 15 days and the offspring fledge after a 16–22 days. During the breeding period, great tits forage mainly in the tree canopy (Rytkönen & Krams 2003). Their diet consists of a variety of insects, especially of lepidopteran and sawfly larvae and spiders (Cramp *et al.* 1993; Gosler 1993). During egg laying and brood rearing periods, they have to search for additional calcium-rich food items, mainly snail shells (Graveland *et al.* 1994; Graveland & Van Gijzen 1994; **V**). Both breeding partners feed the nestlings. In our study area usually 40–70 % of females lay a second clutch during the same breeding season (Fig. 1, **I**).

2.2. Study system

The study was conducted in the surroundings of Kilingi-Nõmme (58° 7’ N, 25° 5’ E) in SW Estonia in 1999–2005. The study area (see the map in **I**) is approximately 50 km^2 in size and is situated in the transitional zone from base-rich (moraine plateau) to base-poor soils (sedimentary sand dunes). The forests in the area can be divided into two main types – deciduous and coniferous. Deciduous forests occur mainly as isolated patches (approximately 0.25–0.5 km^2) in the agricultural landscape or as 250–500m wide galleries along roads and stream valleys. These forests are mostly unmanaged and grow on fertile soil with a rich deciduous understorey. The most common tree species are grey alder *Alnus incana* and silver birch *Betula pendula*, with an age of about 40–50 years, and in the understorey, bird cherry *Padus avium* is very common. The coniferous habitat is typically a managed pine forest on nutrient-poor sandy or peat (in the lower parts of the terrain) soil. The dominant tree species is Scots pine *Pinus sylvestris* with an age of about 60–80 years, which sometimes forms mixed stands with Norway spruce *Picea abies* on sandy soil and downy birch *Betula pubescens* on peat soil. In the field layer, dwarf shrubs of bilberry

Vaccinium myrtillus and cowberry *Vaccinum vitis-idaea* are the most frequent species.

Great tits bred in wooden nest-boxes with cavity measurements of 11 x 11 x 30 cm and an entrance diameter of 3.5–4.0 cm. Altogether about 500–600 wooden nest-boxes were erected in deciduous woods and 1200–1300 nest-boxes in the coniferous forests in the mid-1970s (Mänd *et al.* 2005). Damaged nest-boxes have been repaired regularly or replaced with new ones as necessary, and the number of boxes has remained approximately the same throughout the study period. Nest-boxes were mounted on tree trunks at a height of about 1.5–2.0 m, and were arranged in lines. Each line generally consisted of some tens of nest-boxes in a homogeneous (either coniferous or deciduous) habitat. The distance between nest-boxes was 50–60m. All boxes were cleaned of old nest material every year before the start of the breeding season. Previous research has shown that, during the first breeding attempt, there exist consistent differences in several breeding traits between great tits breeding in different habitats of this study area (Tilgar *et al.* 1999).

2.3. General field methods

Nest-boxes were checked as often as necessary to record laying date of the first egg, clutch size, hatching date and the number of fledglings. The eggs of both first and second clutches were photographed, using a special apparatus. A graphic digitizer was used for the input of egg contours from photos, and egg volume was estimated using the method described in Mänd *et al.* (1986). The nestlings were weighed on day 15 post-hatch to an accuracy of 0.1 g using a Pesola spring balance, and their tarsus length (in 2005 also wing length) was measured to the nearest 0.1 mm (wing – to 1 mm), using a sliding calliper. Adults were captured during the second half of the nestling period, and their sex was determined by brood patch. Adults were also weighed and their tarsus (in 2005 also wing) measured. Each adult and fledgling was marked with an individual metal ring. The true age class of adult birds was determined by ringing data. Additional details on general field methods are described in the original papers.

The first and the second breeding attempts were clearly distinguishable from each other because there was no time overlap between dates of laying first and second clutches. Distance between successive nests of the same pair during the first and the second breeding attempt was less than 300 m (mean distance 73 m), and pairs did not move from one habitat to another between breeding attempts (**I**).

2.4. Study of feeding behaviour (II)

The adult provisioning rates to the offspring were recorded by filming nest-boxes with a video camera. All recordings were conducted only in dry weather between 08:00 a.m. – 15:00 p.m. Each nest was filmed on two sequential days, at exactly the same time of day. The first filming at each nest took place when nestlings were nine days old, because in this developmental stage the energy requirement of great tit nestlings has been shown to be the highest (Perrins 1965; Van Balen 1973). The aim of the first filming was to record adults' normal feeding activity at this stage. On the next day, the entrance of the nest-box was closed with a piece of cardboard for 2 hours before filming, and reopened when filming started. It was expected that hungrier chicks should beg more intensively, which forces parents to increase their feeding effort. It was predicted that if food availability in a particular habitat during a particular breeding attempt is low and the normal feeding rate of parents is close to the upper limit of their capability, the opportunities for parents to compensate for the increased hunger level of chicks by increasing their provision rate is more limited than in the case when food is abundant and parents normally do not have to work too hard. See more details on the method in **II**.

2.5. Experimental manipulation of laying effort (III, IV)

An experimental manipulation of the investment of females in egg-production was carried out during the laying of first clutches in 2002–2003, and during the laying of second clutches in 2005. Each nest-box occupied by great tits was inspected with 1–2-day intervals during the whole egg-laying period. In both habitats separately, pairs of clutches with the same laying initiation date were formed. In each pair, one of the pair-members was randomly assigned as the experimental and the other as the control clutch. The laid eggs were numbered with non-soluble marker pen, to mark the relative position of the egg in the laying sequence. In the experimental group, four eggs were removed from each clutch during egg-laying. Earlier studies had shown that great tits tend to lay additional eggs when some eggs are removed during the laying (Kennedy 1991; Oppliger *et al.* 1996; Visser & Lessells 2001). It was assumed that if egg production is relatively more constrained in coniferous habitat than in deciduous habitat, the different costs of increased laying effort should be reflected in the number and/or size of the extra eggs laid in these habitats. See more details on the method in **III**.

2.6. Estimation of food abundance (II)

Caterpillars usually form the majority of the great tit nestlings' diet (Gibb & Betts 1963; Royama 1970; Van Balen 1973; Cramp *et al.* 1993; Rytkönen & Krams 2003). Changes in caterpillar abundance were monitored by frass-fall method (*e.g*., Seki & Takano 1998; Visser *et al*. 2006). In 2004 and 2005 five collecting sites in each habitat were randomly selected, with each site containing four collectors (round plastic funnels 30 cm in diameter) placed beneath trees or bushes about 40 cm above the ground. Funnels fed a 1 x 4 paper coffee machine filter, where the frass accumulated during the collection period. Filters were collected and replaced after every five days. Filters with contents were dried at 35–40ºC and stored in plastic bags. Later the frass was separated from the litter, kept at 60ºC for 48 hours and weighed to an accuracy of 0.1 mg. For one data point, the mean of four funnel frass samples collected during five days in the same collecting place was calculated. Caterpillar biomass was calculated from these data, as shown in Tinbergen & Dietz (1994).

2.7. Haematological methods (VI)

In 2000–2001, blood samples for haematological measurements were taken from the tarsal or brachial veins in adults immediately after the capture of the bird. Adults were sampled during both breeding attempts. Blood samples were collected into heparinized capillary tubes. Plasma was separated from blood cells after 10 min centrifugation at 10621 g and stored at –20ºC. Hematocrit was measured with a sliding calliper to the nearest 0.1mm. Standard agarose gel electrophoresis with REP System (Helena Laboratories) was used for the detection of major protein groups. For identification of leukocytes, a drop of blood was smeared on a microscope slide, air-dried, fixed in absolute methanol and stained with azure-eosine. The proportion of heterophiles and lymphocytes was assessed under 1000× magnifications on the basis of an examination of a total of 100 leukocytes in oil immersion. Differential leukocyte concentrations were obtained by multiplying their proportion with total white blood cell count per 10000 erythrocytes. Plasma chemistry values (triglyceride, albumin and globulin concentration and albumin/globulin ratio) were available only for the year 2000. See more details on the method as well as on the interpretation of different haematological parameters in **VI**.

2.8. Manipulation of calcium availability (V)

Most passerine birds, including great tits, lay relatively large clutches containing much more calcium than is stored in the female skeleton prior to laying and they have to rely predominantly on external sources of calcium such as calcium-rich invertebrates and snail shells (Graveland *et al.* 1994; Graveland & Van Gijzen 1994; Bureš and Weidinger 2000). Previous studies in our study area had revealed that the abundance of land snails was significantly smaller in coniferous than in deciduous habitat (Tilgar *et al.* 1999; Mänd *et al.* 2000b, a). To explore how the natural calcium shortage affects breeding parameters of great tits in different habitats during different breeding attempts, a calcium provisioning experiment was carried out during both breeding attempts in 1999 (**V**). Small metal feeders were mounted on the nest-boxes. Feeders on experimental nest-boxes were filled with small fragments of domestic chicken eggshells about two weeks before the start of nest building. The feeders attached to occupied nest-boxes were regularly monitored and refilled, so that birds of the experimental group were always provided with *ad libitum* calcium-rich material. Feeders on the control group's nest boxes were empty. Visual observations as well as the analysis of nest material confirmed that birds consumed the provided calcium-rich items from the feeders (Tilgar *et al.* 1999). See more details on the method in **V**.

3. RESULTS

3.1. Habitat differences in seasonal breeding patterns, reproductive output and parental condition (I, II VI)

Although in four of the five study years, females breeding in coniferous forests tended to lay a second clutch more often than those breeding in deciduous forests (Fig. 1), the between-habitat difference in the probability of double-breeding was not statistically significant in our study area (χ^2=2.81, df=1, P=0.093). Only in 2004 were the second broods nearly significantly more frequent in coniferous habitat than in deciduous habitat (Fig. 1; χ^2=3.55, df=1, P=0.06).

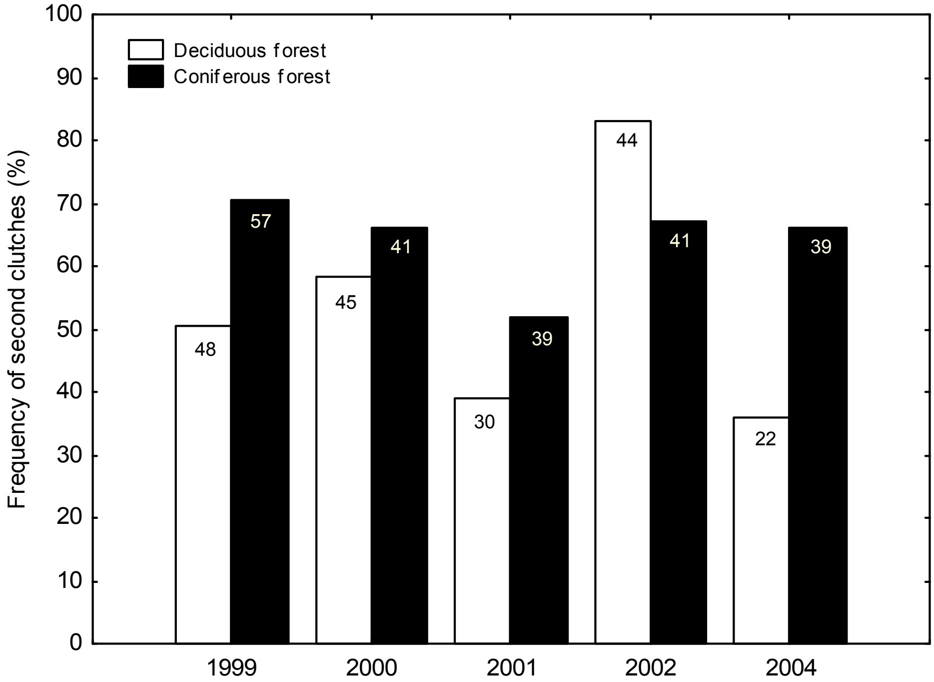

Fig.1. Frequency of second clutches in great tits breeding in deciduous and coniferous forests in SW Estonia during 1999–2002 and 2004. Numbers denote pairs laying a second clutch.

First clutches were started earlier in deciduous than in coniferous forest (**I**, **II**). Also second clutches were generally started earlier in deciduous than in coniferous forest, but the mean first-egg lay-date difference between habitats was smaller during the first breeding attempt than during the second breeding attempt (**I**). Thus the interval between successive breeding attempts tended to be shorter in deciduous forest than in coniferous forest (**I**).

First clutches were larger than second clutches (**I**, **II**). However, the significant interaction term between breeding attempt and habitat (**I**, **II**) indicates that the decline in clutch size between the two breeding attempts was greater in deciduous than in coniferous forest (Fig. 2, **I**, **II**). While first clutches were, on average, larger in deciduous than in coniferous habitat, second clutches tended to be larger in coniferous as compared to deciduous habitat (Fig. 2, **I**, **II**).

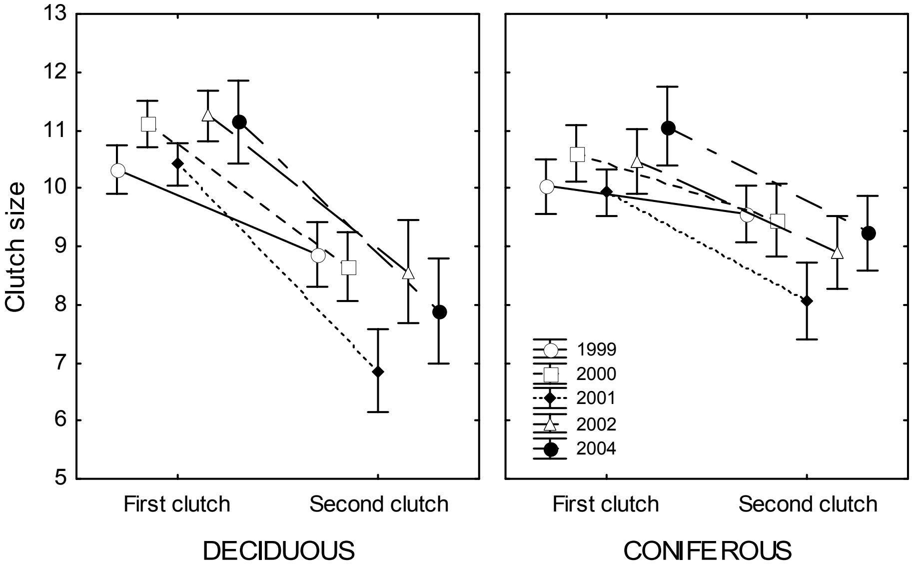

Fig. 2. Mean size of first and second clutches of great tits in deciduous and coniferous forest during 1999–2002 and 2004. Whiskers denote 95% confidence limits.

Mean egg volume was significantly larger in second than in first clutches, and significantly larger in deciduous than in coniferous habitat (**I**, **III**). There was no significant habitat*breeding attempt interaction on egg size.

The number of fledged young was higher in first than in second broods (**I**). Habitat had no significant main effect on the number of fledglings during 1999–2002 (**I**), but the number of offspring was significantly smaller in deciduous as compared to coniferous habitat in 2004 (**II**). When all five years were included into the same model, a slight tendency to have more offspring in coniferous compared to deciduous habitat remained non-significant ($F_{1,417}$=2.8, P=0.09).

Overall, fledglings from second broods were on average heavier ($F_{1,432}$=4.5, P=0.034) and had longer tarsi ($F_{1,429}$=18.8, P<0.001) than those from first broods (**I**, **II**). Fledglings from coniferous habitat tended to be heavier ($F_{1,432}$=13.1, P<0.001; **I**, **II**) and with longer tarsi and wings (**II**) than those from deciduous habitat . However, when different breeding attempts were analysed separately, significant between-habitat differences in fledglings' parameters were found to occur only in first broods (**I**, **II**). Between-habitat difference in fledglings' parameters disappeared in second broods, because of a significant increase in the values of fledglings' parameters from the first to the second breeding attempt in deciduous habitat (**I**, **II**), while fledglings' parameters remained at the same level for both breeding attempts in coniferous habitat (Fig. 3, **I**, **II**).

Adult male body mass and tarsus length and female body mass did not differ significantly between habitats (**I**). Also, body parameters did not differ between single and double breeders (**I**). Older females laid a second clutch more often than yearlings, but the age composition of the breeding population did not differ between habitats (**I**). The only independent parameter that had significant effect on the probability of double breeding was lay-date: early breeders laid a second clutch more often than late breeders (**I**). Adult body mass was lower during the second breeding attempt than during the first breeding attempt, but this seasonal decline was significant only in deciduous and not in coniferous habitat (**VI**). In double breeders, only females (not males) lost weight significantly between successive breeding attempts (**VI**).

Adult great tits breeding in coniferous habitat had higher hematocrit, higher albumin/globulin ratio and lower total globulin concentration, lower heterophile concentration and, during the first breeding attempt, also lower lymphocyte concentration than those breeding in deciduous habitat (**VI**). None of the measured haematological condition parameters affected the probability of laying a second clutch (**VI**).

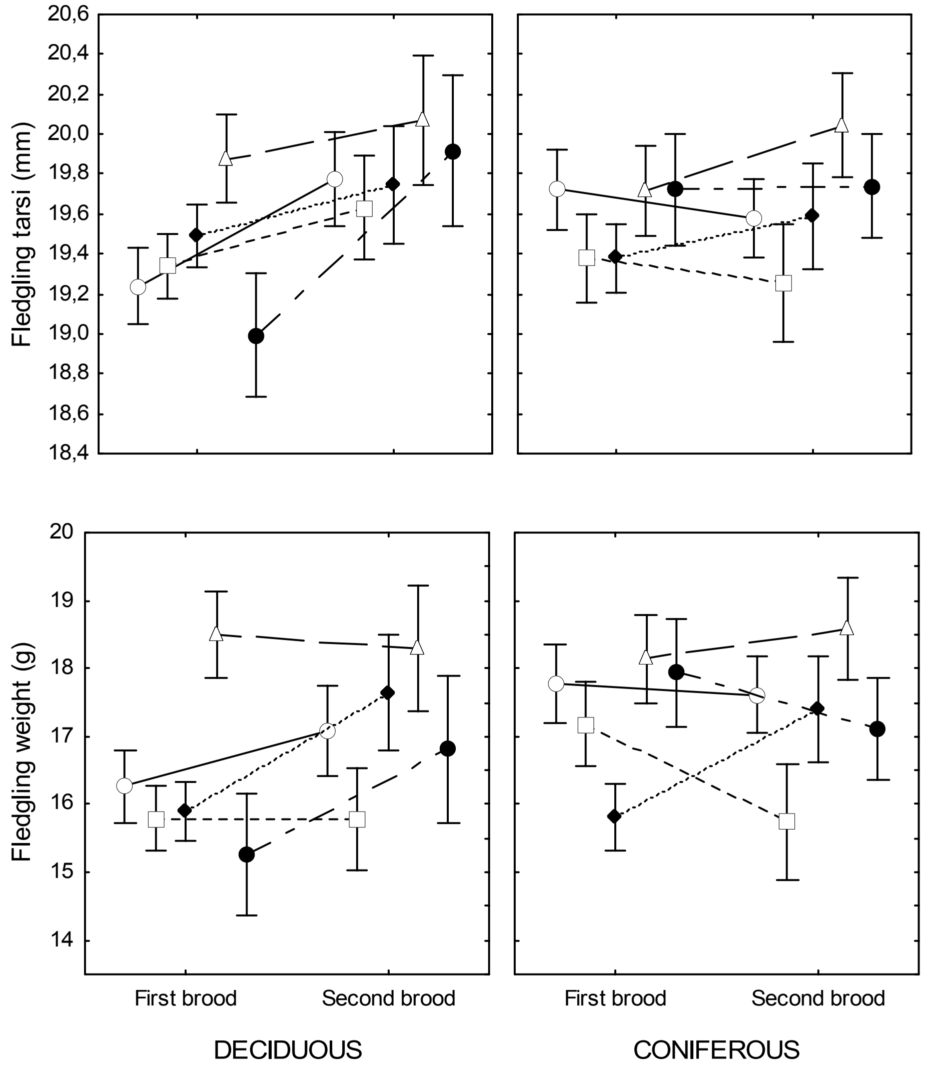

Fig. 3. Fledgling tarsus length and body weight in first and second broods of great tits in two different habitats in 1999–2002 and 2004. Whiskers denote 95% confidence limits. Years are denoted with the same symbols as in Fig. 2.

3.2. Food and calcium availability as possible factors affecting seasonal breeding patterns (II, IV, V)

Caterpillar abundance increased significantly during the breeding season, being significantly higher during second broods than during first broods (**II**, **IV**, Mänd *et al.* unpubl). However, in 2004, this increase was significant only in coniferous forests, but not in deciduous ones (**II**). In both study years, the estimated caterpillar abundance during second broods was significantly ($P<0.001$) higher in coniferous habitat as compared to deciduous habitat (**II**, **IV**, Mänd *et al.* unpubl.).

Provision of supplementary calcium before egg-laying in 1999 significantly increased clutch size and number of fledglings in great tits during both the first and the second breeding attempts (**V**). During the first breeding attempt, fledglings from calcium-supplemented nests also had longer tarsi than those from control nests (**V**). The effect of extra calcium on breeding parameters did not differ between different habitats, because no habitat*calcium interaction term was significant. The probability of laying a second clutch did not depend on extra calcium during the first breeding (unpubl.).

3.3. Habitat and seasonal differences in parental provisioning rate (II)

The main effect of breeding attempt on parental feeding frequency was not significant when controlled for brood size, but feeding frequency was significantly higher in deciduous than in coniferous habitat. However, the difference between habitats was significant only during the first broods and not during the second broods. This was because feeding frequency per nestling tended to decrease between two successive breeding attempts in deciduous habitat and, at the same time, to increase in coniferous habitat, although, when taken separately, the change was not significant either in deciduous or in coniferous habitat. The feeding rates of different sexes did not differ significantly from each other.

After experimental food deprivation of broods, parents significantly increased their provisioning frequency, compared with that in the previous day. When different sexes were analysed separately, the increase was significant in females, but not in males. However, the sex*experiment interaction term was not significant. The effect of manipulation did not differ between habitats or breeding attempts, as the interactions between these factors and 'experiment' were not significant.

Provisioning rate was not related to body parameters of parents when both sexes were included in the same model. However, when different sexes were analysed separately, it was negatively related to the male's body weight.

Fledglings' body parameters at day 15 were all significantly and negatively related to male's provisioning frequency when controlled for habitat type and breeding attempt. At the same time, fledglings' weight and tarsus length were not related to female's provisioning frequency. Exeptionally, there was a significant positive relationship between female's feeding frequency and fledglings' wing length.

3.4. Habitat and seasonal differences in the effect of experimentally increased laying effort (III, IV)

Manipulated females laid approximately one egg more than control females during the first breeding attempt (**III**), but manipulation had no effect on the number of eggs laid during the second breeding attempt (**IV**). The effect of manipulation on the number of extra eggs did not differ between the habitats. However, the relative size of extra eggs compared with the mean size of earlier laid eggs of the same clutch was smaller in the coniferous habitat than in the deciduous habitat, while there was no habitat-related difference in the relative size of last-laid eggs of control clutches (**III**). Such a difference between two habitats indicates that egg production may be more resource limited in coniferous habitat than in deciduous habitat.

4. DISCUSSION

4.1. Habitat differences in seasonal breeding patterns

The frequency of second broods in great tits in our study area is relatively high (usually 40–70 per cent of females lay second clutches – **I**, **II**). In four out of five years the frequency of second clutches was higher in coniferous than in deciduous forest, although this difference was statistically not significant. The higher frequency of second broods in coniferous than in deciduous forest has been reported also by other researchers (Kluijver 1951; Den Boer-Hazewinkel 1987; Cramp *et al.* 1993). Yet many authors (Tinbergen 1987; Smith *et al.* 1988; Geupel & De Sante 1990; Verhulst 1995; Verhulst *et al.* 1995; Verboven & Verhulst 1996; Verboven *et al.* 2001; Brinkhof *et al.* 2002; **I**) have also shown that the probability of laying a second clutch is the greater, the earlier first clutches are laid at the beginning of the breeding season. Since previous research has recorded generally earlier breeding onset in deciduous than in coniferous habitat in our study area (Tilgar *et al.* 1999) and elsewhere (Sanz 1998), one would predict that the frequency of second broods is greater in deciduous habitat. However, as shown above, data from our study area support the conclusions of previous authors rather than the latter prediction.

The time interval between breeding attempts tended to be slightly shorter in deciduous than in coniferous habitat. However, the latter effect disappeared when only those pairs who produced two clutches during a season were considered. Thus the observed population-level habitat difference in this trait was probably due to a slightly higher proportion of single breeders in deciduous habitat who started first clutches relatively late (**I**). The variation of several other breeding parameters of great tits with habitat and breeding attempt in our study area generally resembled that described for other areas (Ojanen *et al.* 1979; Orell & Ojanen 1983; Haftorns 1985; Den Boer-Hazewinkel 1987; Sasvari & Hegyi 1994; Hõrak *et al.* 1995; Verhulst *et al.* 1995; Verhulst & Hut 1996; Seki & Takano 1998; Christe *et al.* 2001; Dhondt *et al.* 2002), although some of these results are contradictory. The main objective of this study, however, was to check for possible interactions between breeding attempt and habitat, to determine whether the pattern of allocation of reproductive investment between successive breeding attempts differed between habitats.

During the first breeding attempt, great tits breeding in deciduous forests started egg-laying earlier than those breeding in coniferous forests, and their clutch size tended to be slightly larger in the deciduous compared to the coniferous forests (**I**, **II**). However, despite this relatively better start in the deciduous forest, both the fledging success and the body condition of fledglings were significantly worse in deciduous than in coniferous habitat (**II**), as was previously shown also by Mänd *et al.* (2005). During the second breeding attempt, in contrast, tits breeding in deciduous forests laid less eggs on average than those in coniferous forests, while the body condition of their chicks was significantly better than that of the first broods of the same habitat, and similar to chicks in coniferous forests (**I**, **II**). The fledging success of the second broods did not differ between contrasting habitats, as was the case with the first broods. Thus, second breeding attempt seems to mitigate the negative effect of the apparently non-adaptive reproductive decision in great tits in the deciduous habitat of this study system, which was demonstrated in Mänd et al. (2005) as well as in this study.

Hence, clutch size was allocated between two successive breeding attempts more equally in coniferous than in deciduous forests, and fledglings' body parameters showed a significant seasonal trend in deciduous habitat, but remained quite stable in coniferous habitat (**I**, **II**). This is the first observation where such a difference in seasonal breeding patterns between adjacent habitats has been documented in birds. While previous authors have pointed to a greater frequency of second broods in great tits in coniferous habitat, current data demonstrate that coniferous habitat differs even more clearly from deciduous habitat by a more equal allocation of reproductive investment between two breeding attempts. Note that a similar habitat-related variation in allocation of reproductive investment between successive breeding attempts was recently discovered by Pimentel & Nilsson (2007) in great tits in a substantially different habitat system in the Mediterranean region, suggesting that the described patterns are widespread phenomena.

4.2. Are the observed patterns related to a habitat-specific variation in the quality of breeders?

No systematic differences in morphology or age composition of adults breeding in the different habitats were found (**I**). Thus, the habitat effect does not appear to be related to the quality of breeders. Also, none of the physiological condition indices measured during the first breeding attempt had an effect on the parental decision to start a second clutch (**VI**). Similarly, other studies (Smith *et al.* 1987; Lindén 1988; Verboven & Verhulst 1996) have found that the probability of great tits laying a second clutch does not depend as much on the quality of individuals, but more so on the timing of breeding. The finding that older females lay second clutches more often than yearlings (**I**) coincides with the findings of Perrins (1979), De Laet & Dhondt (1989) and Holmes *et al.* (1996). However, this observation is probably not the main cause of the habitat differences observed, because, as noted above, differences in age composition of breeders were not observed between different habitats. The observed population-level effects of habitat seemed not to be subject to the slightly different proportions of double breeders in the compared habitats, because the main results concerning clutch size and fledgling parameters held also when only those pairs who produced two clutches during a season were considered in the analysis (**I**).

The only parameters of adults that were systematically worse in deciduous habitat compared to coniferous habitat were several haematological health state indices in brood-rearing parents (**VI**), indicating that great tits were in a worse health state in deciduous than in coniferous habitat. This finding is worth considering carefully in the context of the ecological trap hypothesis (Mänd *et al.* 2005), as well as in the context of the habitat-specific variation of reproductive patterns observed in this study.

4.3. Are the patterns in food abundance consistent with the patterns of reproductive performance in this study system?

Food availability is one of the main environmental factors limiting avian reproduction (Newton 1998). Earlier investigators have pointed to the obvious link between multiple breeding and the dynamics of food availability in different habitats. For example, it has been suggested that a relatively low but steady food availability during the breeding season in coniferous forest, compared to deciduous forest, where the food peaks at the beginning of breeding season and then notably declines, is the reason for the overall greater frequency of second clutches in great tits in coniferous habitat (Van Balen 1973; Gosler 1993). Indeed, a lower level of food availability has been observed in coniferous forests at the beginning of the breeding season as compared to deciduous forests (Van Balen 1973; Slagsvold & Lifjeld 1985; Huhta *et al.* 1998; Sanz 1998). Food availability in deciduous woods has been found to decline remarkably after the first breeding attempt, but food availability in coniferous woods remains fairly stable during the entire breeding season (Van Balen 1973; Slagsvold & Lifjeld 1985; Gosler 1993) or peaks later during the breeding season (Eeva *et al.* 2000; Rytkönen & Orell 2001). Providing that this may be the case also in our study area, this could potentially also help to explain the above-mentioned contradiction between later breeding and increased probability of multiple breeding in coniferous habitat. Verboven *et al.* (2001) showed that multiple breeding occurs with increasing frequency when tits breed earlier relative to the seasonal food peak, yet there were no additional effects of absolute lay-date. If food supply peaks in coniferous forests significantly later than in deciduous forests, then laying onset of tits, relative to this food peak, may be earlier in coniferous forests even though the absolute date of laying is somewhat later. Perhaps in our study area this has an even larger effect on the allocation of clutch size between two successive clutches rather than on the probability of laying a second clutch?

Although the analysis of caterpillar frass fall data revealed substantially different food dynamics in our study system than those described earlier in other areas (**II**), it is still quite consistent with the above model. While in 2004 the caterpillar abundance in deciduous habitat stood relatively stable throughout the breeding season (except only a slight and insignificant increase toward the end of season), there was a remarkable increase in caterpillar abundance during the second breeding attempt in coniferous habitat (**II**). Although the caterpillar abundance during second broods increased significantly in both habitats in the next year, the increase was still relatively smaller in deciduous than in coniferous forests (**IV**). Unfortunately, the frass fall method is not equally suitable for comparing the absolute values of caterpillar supply between habitats, since estimates may be biased due to substantial differences in the canopy structure of different forest types. Therefore one cannot be quite sure whether the food availability during first broods is indeed at about the same level in both habitats, as it appears to be in the respective graph in **II**. Other authors have usually observed higher food availability at the beginning of the breeding season in deciduous than in coniferous forests (Van Balen 1973; Slagsvold & Lifjeld 1985; Huhta *et al.* 1998; Sanz 1998). Note that also Mänd *et al.* (2005) have earlier found, in the same study system, that there are more caterpillars in deciduous than in coniferous habitat during first broods. However, the latter conclusion rests on sampling caterpillars in only the lowest stratum of the stand (Mänd *et al.* 2005), and thus may also be biased. Hence, although one cannot be sure about the exact ratio of caterpillar biomasses in the compared habitats, it is clear that it increases dramatically during the second broods in coniferous habitat and much less, or almost not at all, in deciduous habitat.

However, an additional problem is the fact that it is not clear whether the estimated abundance of caterpillars reflects actual food availability for birds. There may exist, for example, a seasonal decline either in the nutritional value or palatability of caterpillars (*e.g.*, an increase in the content of some poisonous or distasteful compounds or development of special defensive morphological structures later in summer) or in the effectiveness of finding or in the consumption of caterpillars (*e.g.* due to foliage development, increased interference, parasites, heath stress *etc.*). In such a case the available portion of food may decline towards the end of the season, even if the general food abundance stays at the same level (as it was in deciduous habitat). On the other hand, the available food may stay constant despite an increase in general food abundance (as in coniferous habitat). However, it was found that, simultaneously with caterpillar abundance, plasma carotenoid levels of females also increased seasonally (**IV**). This is indirect proof that frass fall reflects actual caterpillar abundance, since lepidopteran larvae serve as a main source of dietary carotenoids for breeding great tits (Partali *et al.* 1987; Eeva *et al.* 1998). On the other hand, in such case higher plasma carotenoid levels should also have been observed in coniferous habitat, which was not the case (**IV**). A possible explanation is that the carotenoid content in the needles of coniferous trees is generally lower than in the leaves of deciduous trees (Czeczuga 1987), so that despite the overall higher food availability in conifers, birds get relatively less carotenoids from the same amount caterpillars eaten. Despite all these problems with the interpretation of the frass fall data, it is still clear that the seasonal food dynamics in contrasted habitats is different, and this difference seems to benefit second broods in coniferous habitat.

A shortage of natural calcium sources (*e.g.* land snails) also may limit reproduction in forest passerines (*e.g.*, Graveland & Van Gijzen 1994; Tilgar 2002; Reynolds *et al.* 2004), especially in naturally calcium-poor areas like our study area (Tilgar 2002). Snails are more abundant in deciduous forests as compared to coniferous habitat during the first breeding attempt in our study area (Mänd *et al.* 2000a, b; **V**). Although there are no data on snail availability in our study area during the second half of the breeding season, the results of our calcium-supplementation experiment (**V**) indicate that calcium-shortage limits breeding of great tits not only during the first breeding attempt, but also during the second breeding attempt. However, as no habitat-specific differences in calcium-limitation were detected (**V**), there is not sufficient evidence to claim that the habitat and/or seasonal variation in availability of calcium-rich food items somehow contributes to creating the above-described patterns of reproductive performance in great tits in our study system.

4.4. Is parental capability to feed nestlings responsible for the observed patterns of reproductive performance in great tits?

As noted above, food availability is one of the main factors limiting avian reproduction (Newton 1998). Usually it has been assumed that the costs of chick rearing represent a major part of total reproductive costs (reviewed in Williams 2005). It has been hypothesized that the provision of nest-boxes in the preferred deciduous habitat may raise the density of great tits to a supra-optimal level, causing relative food shortage (Rodenhouse *et al.* 1997; Sanz 2001; Mänd *et al.* 2005). This is probably not the case in the non-preferred coniferous habitat, where the density remains relatively low even despite the addition of the same amount of nest-boxes (Mänd *et al.* 2005). Such a “density trap” (named after Rodenhouse *et al.* 2006) may thus lie behind the relatively poor breeding performance of tits in the deciduous habitat during the first breeding attempt. If this is the case, one should expect that the ability of parents to feed their broods is more limited in deciduous than in coniferous habitat. Correspondingly, if food availability in a particular habitat during a particular period is low and the normal feeding rate of parents is close to the upper limit of their capability, the chances of parents to compensate for the increased need of chicks by increasing their provision rate should be more limited than in the case when food is abundant and parents normally do not have to work too hard (as found, *e.g.*, by Sanz *et al.* 2002; Stauss *et al.* 2005). On the other hand, having relatively small broods with well-attended young during the second breeding attempt in deciduous habitat may be a tactical decision on the part of females who had performed poorly during the first breeding attempt, when they had relatively large broods (**I**).

As shown above, the results of haematological studies of parents indicated that brood-rearing great tits were in a worse health state in deciduous than in coniferous habitat (**VI**), which is consistent with the above trap-hypothesis. However, the results of the experimental manipulation of the chicks' hunger level were not consistent with the above suggestion (**II**). Although parents increased their feeding frequency significantly after the temporary food deprivation of chicks, the effect of manipulation did not differ either between compared habitats or between breeding attempts (**II**). Of course, it is possible that the duration of the food deprivation was too short to cause sufficient increase in chicks' begging intensity, and therefore the parental response remained too weak to reveal the habitat and seasonal differences in the food limitation. An alternative explanation, however, is that food shortage during brood rearing is not responsible for the relatively poor breeding performance in deciduous habitat, and other factors should be considered. Note that recent data from our study population, suggesting the inferior physiological condition of females in deciduous habitat already during the early incubation stage (Tilgar *et al.* unpubl.), is consistent with this second assumption.

Despite the negative result of the experiment, our correlative study revealed a remarkably clear, although somewhat unexpected, correspondence between habitat-specific patterns of parental provision rates and body parameters of the offspring (**II**). This suggests that the parental feeding frequency and the nestlings' growth may still be somehow related. The relatively high feeding rate of parents in deciduous habitat during the first breeding attempt resulted in a relatively low weight and shorter tarsus and wing of offspring in the same habitat during the same period (**II**). At the same time, in deciduous habitat, an increase in average body size of offspring from the first to the second broods was accompanied by a slight decline in parental provisioning frequency. In coniferous habitat, the corresponding trends were the opposite. As a result, neither parental feeding rate nor offspring size differed significantly between the two habitats during the second breeding attempt (**II**). In short, it seems that the lower the parental feeding rate in great tits is, the better their chicks grow.

There are at least two possible and non-exclusive explanations for such an inverse relationship between parental provisioning frequency and offspring size. First, although many authors have used feeding frequency as a direct measure of parental provisioning effort (*e.g.*, Conrad & Robertson 1992; Christe *et al.* 1996; Hurtrez-Bousses *et al.* 1998; Radford *et al.* 2001; McCarty 2002; Tripet *et al.* 2002; Biard *et al.* 2005), other researchers have shown that this is not always reliable (*e.g.*, Nour *et al.* 1998; Grieco 2001; Grieco 2002; Tremblay *et* *al.* 2005). Lower feeding frequency does not necessarily indicate lower food supply and/or lower provisioning level of chicks. In certain circumstances, parents may spend more time in looking for more energetically valuable food items (Betts 1955; Royama 1970; Nour *et al.* 1998; Grieco 2001; Grieco 2002; Stauss *et al.* 2005), which ensures better growth and higher survival of offspring (Tremblay *et al.* 2005). Thus a relatively low feeding frequency may actually mean a higher selectivity and, accordingly, also a relatively higher amount of food brought to chicks per unit of time. It is also possible that in a particular habitat during a particular period, the food items are on average smaller and parents therefore need to feed nestlings more frequently there than in another habitat or during another period. Such correlations between habitat type, food item size and parental feeding frequency in passerines were demonstrated, *e.g.*, by Stauss *et al.* (2005) and Tremblay *et al.* (2005). Schwagmeyer & Mock (2003) found that house sparrows reduced their per-chick delivery rates as the season progressed, because very large lepidopteran larvae became more common prey items later in summer. Perhaps the same was the reason for the seasonal decline in feeding frequency in great tits in deciduous forest?

Parents may also adjust their feeding effort with respect to the current condition of nestlings. When the chicks are in a good condition and grow well, they are also less hungry and beg less intensively (Kölliker *et al.* 1998; Grieco 2001). Correspondingly, parents may decrease the provisioning of such high-quality offspring (Kölliker *et al.* 1998; Grieco 2001). Note that the finding that male's feeding frequency was negatively correlated with fledglings' body parameters (**II**) is consistent with the above suggestion. A negative relationship between feeding rate and nestling growth has recently been observed by Stauss *et al.* (2005) also in blue tits *Parus caeruleus* (but see Moreno *et al.* 2004). In Corsica, blue tits' nestlings experimentally infected with ectoparasites were fed more frequently by their parents, but grew more slowly than parasite-free nestlings (Blondel *et al.* 2002; Banbura *et al.* 2004, Simon *et al.* 2004). Recent research has revealed that nestlings' growth and condition may be subject to several maternal effects via eggs (*e.g.*, Dzialowski & Sotherland 2004; Veiga *et al.* 2004; Verboven *et al.* 2005; Szigeti *et al.* 2007). Thus one cannot exclude the possibility that the observed habitat-related and seasonal differences in parental feeding rates and offspring parameters actually reflect some differences in the number of ectoparasites in the nests, or even in the quality of eggs. For example, a trade-off may exist between the number and quality of eggs laid by a female (Lessells *et al.* 1989; Cichoń 1997; Williams 2001; Sanchez-Lafuente 2004). As shown above, clutch size in deciduous habitat drops more dramatically from the first to the second breeding attempt than in coniferous habitat (**I**, **II**). If such a marked decline in clutch size is accompanied by a simultaneous increase in egg quality, this can explain why parental feeding rate decreases while the offspring parameters still improve significantly between successive breeding attempts in deciduous but not in coniferous habitat. Again, the finding from our study area that during the first breeding attempt the females in deciduous habitat are in a relatively worse physiological condition during the early incubation stage (Tilgar *et al*., unpubl.) is consistent with the second explanation, suggesting that the reasons for the described patterns of reproductive performance may actually lie in a much earlier stage than the brood rearing period. To address this problem, an experimental approach is needed, including manipulation of the overall condition of chicks and swapping broods between different habitats, accompanied by recording not only the feeding frequency of parents, but also the size and quality of food items brought to chicks in different habitats during different breeding attempts.

4.5. Is there any habitat-specific or seasonal variation in egg-laying costs?

The equivocal relationship between parental feeding frequency, food abundance and nestling growth suggests that the habitat-related differences in general breeding patterns in birds should not be too easily attributed to the variation in food abundance during brood rearing, and an alternative possibility that the true reasons for such differences lie at an earlier stage of the breeding season, should be considered. Until recently, most avian studies have assumed that egg production is relatively inexpensive and that total reproductive costs consist mainly of the costs of chick rearing (reviewed in Williams 2005). Recent investigation has revealed that egg production is also costly (*e.g*., Monaghan *et al*. 1998; Nager *et al*. 2001; Nilsson & Råberg 2001; Visser & Lessells 2001; Williams 2005). Such costs may reflect nutritional constraints (Monaghan & Nager 1997; Clifford & Anderson 2001; Blount *et al*. 2004) and depend on environmental conditions at the time of laying (Visser & Lessells 2001). Therefore, the costs of egg production cannot be ignored when assessing optimal reproductive behaviour in different habitats of a heterogeneous environment.

To test this possibility on great tits in our study system, part of the females were experimentally manipulated to increase their laying effort (**III**). Provided that females have a limited ability to maintain egg quality when laying more than their normal clutch size (Nager *et al*. 2000; Williams & Miller 2003; Williams 2005), it was presumed that if the relatively small clutches in coniferous forests during the first breeding attempt are caused by relatively higher costs of egg production in this habitat, then either the number or the quality of extra eggs laid by the manipulated females should be smaller there than in deciduous habitat. Given that the size of an egg generally reflects its nutrient content (reviewed in Rosivall *et al*. 2005), egg size was used as an indirect measure of egg quality. As a result of the experiment, the manipulated females laid approximately one egg more than control females in both habitats (**III**). However, the relative size of extra eggs compared to the mean size of earlier laid eggs of the same clutch was smaller in the coniferous habitat than in the deciduous habitat, while there was no habitat-related difference in the relative size of last-laid eggs in control clutches (**III**). Such a difference between two habitats indicates that some kind of proximate limitation during the egg-laying period can indeed contribute to the relatively small clutches and eggs in coniferous habitat.

However, why did this manipulation affect the size and not the number of additional eggs laid? The ability of small passerines to accumulate energy and nutrients in their body before reproduction is quite limited (*e.g*., Houston *et al.* 1995; Meijer & Drent 1999), and they must obtain most of the energy and nutrients required for egg formation on a daily basis. In the pine forests, the availability of calcium (necessary for eggshell formation) is much lower than in deciduous forests, both during egg laying and nestling periods (Tilgar *et al.* 1999; Mänd *et al.* 2000a; **V**). Therefore, it may be that, at the final stage of egg-laying, the exhausted females breeding in coniferous habitat are unable to find enough food and/or calcium per day both for restoring their own body reserves and for producing a large nutrient-rich egg. The relatively large size of last-laid eggs in passerines is generally thought to be adaptive, representing a maternal mechanism aimed to compensate for the detrimental effect of asynchronous hatching and to enhance the survival of the last-hatched offspring (Slagsvold *et al.* 1984; Cichoń 1997; Hillstrom 1999; Rosivall *et al.* 2005; Ferrari *et al.* 2006). Thus it is not reasonable to lay large clutches with relatively small last eggs, because the survival probability of last-hatched chicks in such nests is low (Hillstrom 1999; Rosivall *et al.* 2005). Therefore it is likely that females normally stop egg-laying before exceeding the critical point of their physiological state, where clutch size and egg size must be traded against each other. Hence, this may be the reason for relatively small clutches in coniferous forests. The situation was different in our experimental case because an unusually small number of eggs in the nest could be such a strong stimulus for manipulated females that they did not stop laying even when the egg size dropped below the usual limit. However, this is only one possible mechanism and one cannot rule out some other explanations. For example, manipulated females in poor habitat could sacrifice the size of the last eggs to maintain body condition for more effective parental care at later reproductive stages.

Whatever the exact mechanism is, this study provides experimental evidence that egg production in great tits during the first breeding attempt is in some way more constrained in coniferous than in deciduous habitat. One can suggest, therefore, that proximate limitation during the egg-laying period may contribute to the relatively small clutches and eggs in coniferous habitat. However, this does not exclude the possibility that chick-rearing costs later in the season have an additional ultimate effect on egg-laying decisions of females.

It is noteworthy that an attempt to manipulate egg-laying effort of great tits during the second breeding attempt was unsuccessful, since the number of eggs laid by the birds in the experimental group did not exceed that of the control birds (**IV**). It may be that during the second breeding attempt the birds refrained from increasing their reproductive effort due to time constraints (Verboven & Verhulst 1996; Visser *et al*. 2003). Moreover, second clutches are significantly smaller than first clutches (**I**, **II**), and Haywood (1993) has found in blue tits that the smaller the clutch, the earlier the disruption of follicular growth. The same author has also demonstrated that the proportion of female blue tits that cease to lay increases when higher temperatures occur towards the end of laying (Haywood 1993), and mean ambient temperature is always higher during the second clutches than during the first clutches.

4.6. Proximate constraints or strategic decisions?

A specific question concerns the relative role of proximate and ultimate factors behind the observed habitat-specific breeding patterns. According to the proximal limitation hypothesis, it is difficult for birds to precisely predict future food availability (*e.g*., Nur 1987; Seki & Takano 1998; Eeva *et al*. 2000) and adaptive changes in clutch size are not possible (Seki & Takano 1998). Therefore females, who are directly constrained by the availability of food and/or nutrients at egg-laying and/or during the nestling period, always lay as many eggs (and perhaps also raise as many young) as they can in a particular breeding attempt in a particular habitat. However, because both clutch and egg size have been found to be food-limited in tits (*e.g*., Nager 1993; Föger & Pegoraro 1996; Ramsay & Houston 1997; Mänd & Tilgar 2003; **V**), why then are second clutches significantly smaller in deciduous as compared to coniferous forests, but the eggs of these clutches are not (**I**)? Secondly, if the second breeding attempt is more food-limited in deciduous than in coniferous habitat (judged by clutch sizes as well as by differences in seasonal food dynamics between contrasting habitats – **II**), then why is body condition of second brood fledglings better than that of first brood fledglings in deciduous habitat, but not in coniferous habitat (*i.e*., no difference in body size among first and second brood fledglings – **I**, **II**)?

It seems that direct food limitation alone cannot create the above-mentioned patterns, and that birds breeding in different habitats make different strategic decisions. Naef-Daenzer *et al*. (2001) and Götmark (2002) have shown that, due to increased predation, survival of juveniles in some tit species decreases dramatically towards the end of the breeding season and that juvenile survival is then strongly dependent on body size. Because selection for larger fledging size is much stronger later in the season than earlier (Naef-Daenzer *et al*. 2001), it may be more beneficial for parents to invest in the quantity of offspring rather than in quality during the first breeding attempt and in quality rather than in quantity in the second breeding attempt. It can be that such a strategy is more beneficial in deciduous rather than in coniferous forests. Breeding density of great tits and many other passerines is, on average, greater in deciduous forest fragments than in coniferous forests in our study area (Mänd *et al.* 2005) as well as elsewhere (Van Balen 1973; Ulfstrand *et al.* 1981; Cramp *et al.* 1993; Solonen 1996; Newton 1998), and predators are often concentrated in this attractive habitat, significantly increasing the predation risk (Schlaepfer *et al.* 2002). Furthermore, the value of a second brood depends on the competition that the second-brood fledglings face from first brood fledglings, which is stronger in areas with higher tit density (Verhulst 1992; Both 1998). Indeed, Both (1998) demonstrated experimentally that the proportion of great tits starting second broods was affected by breeding density. Thus, great tits breeding in a heterogeneous environment may choose different behavioural tactics depending on habitat composition, seasonal dynamics of food availability, predation risk, and competition risk from first brood fledglings. This strategy can lead to the different allocation patterns that were observed in our study. That different breeding patterns may indeed be adaptive to different habitats, was demonstrated by Orell & Ojanen (1986), who found that production of two broods per season by great tits is more profitable in terms of fitness in a conifer-dominated area than in deciduous woodland in northern Finland. Hence, habitat-specific allocation of reproductive investment between successive breeding attempts probably plays a role in optimising breeding tactics by facultative multiple-brooded bird species in a heterogeneous environment, potentially serving as a useful mechanism facilitating their adaptation to novel habitats. However, more data about predation risk and inter-brood competition in different habitats is necessary to draw more definitive conclusions about causes behind the observed patterns.

SUMMARY

A better knowledge of the constraints playing a role in different habitats of heterogeneous landscapes and about adaptations of species to these variable conditions possesses high conservational value. To reveal general rules, it is reasonable to use some well-studied model species as study objects. In this thesis, the great tit (*Parus major*), a common facultative multiple-brooding forest passerine, was studied. The great tit as a hole-nesting species willingly occupies artificial nest-boxes, being therefore methodically easy to manipulate and serving as a popular model in avian ecology.

The aims of the present thesis were: (1) to explore whether there exist any consistent habitat-specific patterns in reproductive performance in great tits breeding in a deciduous-coniferous forest mosaic of the northern temperate zone; (2) to study whether various aspects of breeding in this species are limited to a different extent in different habitats and/or during different stages of the breeding cycle. To address these goals, basic reproductive parameters and the condition of adult great tits were monitored for several years during successive breeding attempts in two contrasting habitats in SW Estonia. Besides this, data about possible calcium limitation during egg-laying and about food limitation during brood rearing were collected. Both experimental and comparative approaches were used.

Consistent differences in seasonal breeding patterns between adjacent habitats, which have not been described in birds before, were revealed. Clutch size was allocated between two successive breeding attempts more equally in coniferous than in deciduous forests, and fledglings' body parameters remained quite stable in coniferous habitat, but showed a significant seasonal trend in deciduous habitat. While it has been shown that during the first breeding attempt, breeding performance in great tits tends to be better in coniferous than in deciduous habitat, the breeding performance was found to be much more similar between different habitat types during the second breeding attempt. Thus, the second breeding attempt seems to mitigate the negative effect of the apparently non-adaptive reproductive decision in great tits in the deciduous habitat of this study system. Similar patterns in birds breeding in other habitat systems in substantially different regions have been discovered.

The above habitat effect does not appear to be related to the age structure or morphological parameters of breeders, because no systematic differences in these traits in adults breeding in the different habitats were found. However, the analysis of haematological indices showed that, during the brood rearing period, great tits breeding in deciduous habitat were in a worse physiological condition compared to those breeding in coniferous habitat.

The study of the abundance of caterpillars revealed completely different food dynamics in this habitat system than described earlier in other areas. There is a remarkable increase in caterpillar abundance during the second breeding

attempt in coniferous habitat, while the increase is much smaller and sometimes almost missing in deciduous habitat. Thus the habitat-specific pattern of food dynamics seems to be a possible candidate partly responsible for the above-mentioned breeding patterns.

Snails (natural calcium source for eggshells and fledglings' skeleton growth) are more abundant in deciduous forests as compared to coniferous habitat during the first breeding attempt in this study system. The results of a calcium supplementation experiment indicate that calcium shortage limits breeding of great tits not only during the first breeding attempt, but also during the second breeding attempt. However, given that no significant habitat-specific differences in calcium limitation were detected, it is not clear whether the variation in availability of calcium-rich food items contributes to the above-described patterns of reproductive performance in great tits in this study system, or not.

A relationship between habitat-specific patterns of parental provision rates and body parameters of offspring was revealed. The relatively high feeding frequency of parents in deciduous habitat during the first breeding attempt resulted in relatively small-sized offspring. In deciduous habitat an increase in average body size of offspring from the first to the second broods was accompanied by a slight decline in parental provisioning frequency, while in coniferous habitat the opposite trends occurred. Thus, the parental feeding frequency seemed to be negatively correlated to the growth of chicks. Parental ability to compensate for experimentally increased hunger level of nestlings by increased feeding rate did not differ between habitats or breeding attempts. The above-described variation in the dynamics of food availability seemed not to be consistent with the respective patterns in offspring growth and parental feeding rates. These findings suggest that the habitat-specific differences in breeding performance in birds should not be too easily attributed to the variation in food abundance during brood rearing, and that the true reasons may lie at earlier stages of the breeding season.

An experiment where some eggs were removed from the clutches during laying forced the manipulated females to increase their investment in egg production in both habitats during the first breeding attempt, but not during the second breeding attempt. The relative size of extra eggs compared to the mean size of earlier laid eggs of the same clutch was smaller in the coniferous habitat than in the deciduous habitat, while there was no habitat-related difference in the relative size of last-laid eggs in control clutches. This indicates that egg production in great tits is in some way more constrained in coniferous than in deciduous habitat, and that this limitation can contribute to the relatively small clutches and eggs in coniferous habitat during the first breeding attempt. Besides, this result clearly emphasizes the formerly underestimated need to take egg production costs into account when attempting to understand the reasons for the variation in reproductive parameters of birds breeding in heterogeneous landscapes.

It is likely that proximate constraints alone cannot create the habitat-related patterns described above, and that birds breeding in different habitats may adopt different tactics during the breeding season. Habitat-specific allocation of reproductive investment between successive breeding attempts probably plays a role in optimising breeding tactics by facultative multiple-brooded bird species in a heterogeneous environment, potentially serving as a useful mechanism facilitating their adaptation to novel habitats.

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KOKKUVÕTE

Sigimisnäitajate elupaigaline varieeruvus rasvatihasel okaspuistu-lehtpuistu süsteemis: otsides põhjusi ja tagajärgi

Täielikumad teadmised liikidele mõjuvaist piirangutest ja nende kohastumustest heterogeensete elupaikade erikvaliteedilistes osades omavad suurt looduskaitselist väärtust. Üldiste seaduspärasuste väljaselgitamiseks on otstarbekas kasutada hästiuuritud mudelliike. Käesoleval juhul uuriti rasvatihast kui parasvöötme puistutes arvukalt esinevat fakultatiivset korduvpesitsejat värvuliseliiki, kes suluspesitsejana asustab kergesti tehispesi ja kellega seetõttu on metoodiliselt lihtne opereerida. Käesoleva väitekirja eesmärkideks oli uurida, (1) kas ja millised regulaarsed elupaigaspetsiifilised sigimiskäitumise mustrid esinevad rasvatihasel põhja-parasvöötme lehtpuistu-okasmetsa mosaiikides; (2) kas selle liigi pesitsemise erinevad aspektid on eri biotoopides ja/või sigimisperioodi erivates faasides limiteeritud erineval määral. Selleks jälgiti mitme aasta vältel kogu pesitsussesooni jooksul liigi sigimisedukust kahes erinevas elupaigas Edela-Eesti uurimisalal. Lisaks koguti andmeid võimaliku munemisaegse kaltsiumidefitsiidi esinemise ning toidupuuduse limiteeriva mõju kohta pesakondade kasvatamise ajal. Rakendati nii eksperimentaalset kui ka võrdlevat lähenemist.

Sesoonsetes sigimismustrites ilmnesid regulaarsed, lindudel seni kirjeldamata elupaikadevahelised erinevused. Okasmetsades oli kurna suurus järjestikuste sigimiskordade vahel jaotunud oluliselt võrdsemalt kui lehtmetsades. Ka linnupoegade kasv püsis okasmetsas kahe pesitsuskorra vahel samal tasemel, kuid lehtmetsa poegade kasvuparameetrites ilmnes esimese ja teise pesitsuskorra vahel selge tõusutrend. Kui esimesel pesitsuskorral oli rasvatihaste pesitsusedukus okasmetsas kõrgem kui lehtmetsas, siis teisel pesitsuskorral oli elupaikade vaheline erinevus suuresti nivelleerunud. Seega näib, et teine pesitsus aitab leevendada seda, mille põhjustab lehtelupaigas pesitsevate rasvatihaste ilmselt mitteadaptiivse sigimisotsuse negatiivseid tagajärgi. Tänaseks on samasuguseid mustreid analoogilistes elupaigasüsteemides teiste autorite poolt kirjeldatud juba ka teistes regioonides. See viitab võimalusele, et korduvpesitsemine võib lindudel mängida olulist rolli sigimistaktikate optimeerimisel heterogeensetes elupaigasüsteemides.

Kirjeldatud elupaikadevahelised erinevused ei paista olevat seotud seal pesitsevate lindude vanuselise koosseisu ega morfoloogiliste näitajatega, kuna lehtmetsa ja okasmetsa tihaste asurkondades puudusid süstemaatilised erinevused nende tunnuste osas. Hematoloogilised analüüsid näitasid aga samas, et pesakonna toitmise perioodil on lehtmetsas pesitsevad rasvatihased kehvemas füsioloogilises seisundis kui okasmetsa linnud.

Röövikute kui rasvatihase pesapoegade toidusedeli olulisima komponendi rohkuse uuringud paljastasid antud uurimisüsteemis oluliselt teistsuguse sesoonse toidurohkuse dünaamika, kui on eelnevalt kirjeldatud maailma teistes regioonides. Okasmetsas tõusis teise pesitsuse ajal röövikute biomass märgatavalt, lehtmetsas oli aga tõus väga väike või puudus hoopis. Seega võib eespool mainitud pesitsusmustrite taga tõepoolest vähemalt osaliselt peituda elupaigaspetsiifiline toidurohkuse dünaamika.

Esimese pesitsusperioodi ajal on maismaatigude (looduslik kaltsiumiallikas munakoorte moodustamiseks ja poegade skeleti kasvuks) arvukus lehtmetsas oluliselt kõrgem kui okasmetsas. Kaltsiumi-lisasöötmise eksperiment näitas aga täiendavalt, et kaltsiumipuudus ei ole rasvatihasel limiteerivaks teguriks mitte ainult esimese, vaid ka teise pesitsuskorra ajal. Kuna aga kaltsiumilimitatsiooni puhul ei ilmnenud elupaigaspetsiifilisi erinevusi, pole selge, kas kaltsiumirikaste toiduobjektide arvukuse elupaigaline varieeruvus võib olla seotud rasvatihase eespool mainitud pesitsusmustritega või mitte.

Poegade kasvunäitajate ja vanalindude toitmissageduse elupaigaliste mustrite vahel ilmnes mõnevõrra ootamatu seos. Kuigi esimese pesitsuse ajal oli poegade toitmissagedus lehtmetsas suhteliselt kõrge, olid lennuvõimestunud järglased seal suhteliselt väikesekasvulised. Teise pesitsuse ajal lehtmetsa poegade toitmissagedus langes, võrreldes esimese pesitsuskorraga, samas kui poegade kasvunäitajad paranesid oluliselt. Männikus kaldusid vastavad trendid olema vastupidised, mistõttu teise pesitsuskorra ajal elupaikade vahelised erinevused kadusid. Seega – mida harvemini poegi toideti, seda paremini nad kasvasid. Vanalindude võimekus kompenseerida poegade eksperimentaalselt suurendatud näljatunnet toitmissageduse tõstmise teel ei erinenud ei pesitsuskordade ega elupaikade vahel. Eespool kirjeldatud toidurohkuse sesoonne dünaamika ei olnud vastavuses poegade kasvu ja toitmissageduse elupaigaliste mustritega. Need tulemused näitavad, et elupaigaspetsiifilisi erinevusi lindude sigimiskäitumises ei tohiks liiga kergekäeliselt seostada toidurohkuse varieerumisega poegade kasvatamise perioodil, nagu seda varem on tihti tehtud, ning et tegelikud põhjused võivad peituda juba varasemates pesitsusfaasides.

Eksperiment, mille käigus eemaldati kurnadest munemise ajal osa mune, põhjustas esimese pesitsuse ajal nii lehtmetsas kui ka okasmetsas emaslindude munemispingutuse suurenemise, mis väljendus lisamunade munemises. Teise pesitsuse ajal emased aga mainitud manipulatsioonile ei reageerinud. Okasmetsas munetud lisamunad olid võrreldes sama kurna eelmiste munadega suhteliselt väiksemad kui vastavad munad lehtmetsas. Samas aga ei erinenud kontrollgrupi viimaste munade suhteline suurus elupaikade vahel. See näitab, et rasvatihasel on munemine okasmetsades mingil põhjusel enam piiratud kui lehtmetsades ning see piirang võib tõenäoliselt seletada suhteliselt väikeste kurnade ja munade munemist okasmetsas võrreldes lehtmetsa omadega esimesel pesitsuskorral. Ühtlasi näitab see tulemus, kuivõrd seniarvatust olulisem on lisaks poegade toitmise aegsetele piirangutele arvestada ka munemispingutuse hinda, mõistmaks heterogeensetes elupaigasüsteemides pesitsevate lindude sigimisparameetrite muutlikkuse põhjusi.

On tõenäoline, et eespool kirjeldatud elupaigalisi sigimismustreid ei põhjusta üksnes proksimaalsed piirangud, ja et linnud rakendavad erinevais elupaigus erinevaid taktikalisi otsuseid. Sigimisinvesteeringu elupaigaspetsiifiline jaotus erinevate sigimiskordade vahel mängib fakultatiivselt korduvpesitsevail linnuliikidel tõenäoliselt rolli sigimistaktika optimeerimisel heterogeensetes elupaigasüsteemides, olles potentsiaalselt kasulik ka lindude kohanemisel ebatraditsiooniliste elupaikade tingimustega.

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PUBLICATIONS

II

Mägi, M., Mänd, R., Tamm, H., Kilgas, P. & Tilgar, V.
Seasonal and habitat-related variation in great tits' reproductive parameters,
provisioning rate and food abundance: what is behind the contrasting
breeding patterns? (submitted manuscript)

HABITAT-RELATED VARIATION IN GREAT TITS' REPRODUCTIVE PARAMETERS, PROVISIONING RATE AND FOOD ABUNDANCE: WHAT IS BEHIND THE CONTRASTING BREEDING PATTERNS?

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ABSTRACT

Previous studies have revealed a consistent habitat variation in seasonal reproductive patterns in great tits in a mosaic of deciduous woodland fragments and managed coniferous forests. In deciduous forests, clutch size declines remarkably and offspring parameters improve significantly between two successive breeding attempts, whereas in coniferous forests the decline in clutch size is less steep and there is no seasonal trend in nestlings' parameters. In this study, we explored whether these patterns can be explained by habitat-specific dynamics of food abundance and parental provisioning ability. We found an inverse relationship between seasonal patterns of offspring growth parameters and parental feeding rates in different habitat types. Parental ability to compensate for experimentally increased hunger level of nestlings by increased feeding rate did differ neither between habitats nor breeding attempts. Habitat-related variation in seasonal dynamics of food availability was not consistent with the respective patterns in offspring growth and parental feeding rates. These findings suggest that the habitat-related and seasonal differences in breeding performance in birds should not be too easily attributed to the variation in food abundance during brood rearing, and that true reasons may lie at earlier stages of the breeding season.

Keywords
Caterpillar abundance, deciduous-coniferous forest mosaic, multiple breeding, nestling growth, *Parus major*, provisioning frequency

INTRODUCTION

Many bird species are able to use different types of habitats of a heterogeneous landscape for breeding. Due to habitat loss, birds are often forced to occupy alternative habitats instead of traditional ones (reviewed in Newton 1998). Sometimes such habitat switches may even occur as a result of certain nature management activities, e.g., providing nest boxes for cavity-nesting species in habitats where they normally do not breed (Newton 1998, Mänd et al. 2005). In order to understand the extent of variable and novel breeding conditions a species is able to cope with, it is essential to learn about the variability of its breeding performance among different habitats and the adjustment of its behavior and physiology to conditions prevailing in different breeding environments.

Great tit (*Parus major*) is a facultative double-breeding passerine that prefers deciduous woodland as breeding habitat, but is also able to reproduce in managed conifers in case nest-boxes are provided (van Balen 1973, Cramp et al. 1993, Mänd et al. 2005, Pimentel and Nilsson 2007). Earlier investigators have described a clear habitat-related variation in a number of breeding parameters in this species (e.g., Sanz 1998). Our study area in Estonia represents a mosaic of deciduous woodland fragments and managed coniferous forests (quite typical for large areas of boreal and northern temperate zones). Previous studies in our area have revealed a consistent habitat variation in seasonal reproductive patterns in great tits. During the first breeding attempt, great tits breeding in deciduous forests (preferred habitat) had larger clutches than the ones breeding in coniferous forests. However, the number of fledglings as well as recruits per pair was higher in coniferous than in deciduous habitat (Mänd et al. 2005). During the second breeding attempt, on the contrary, clutch size was relatively higher in coniferous habitat, whereas the condition of the fledglings was better in deciduous habitat. There was no significant difference in the number of the offspring among habitats (Mägi and Mänd 2004). Note that a similar habitat-related variation in allocation of reproductive investment between successive breeding attempts was recently discovered by Pimentel and Nilsson (2007) in great tits breeding in a substantially different habitat system in the Mediterranean region, suggesting that the described patterns might be a widespread phenomenon. Both these authors and Mägi and Mänd (2004) suggest that such different patterns may play an important role in optimizing breeding tactics in different environments.

However, the actual reasons for the patterns described above are far from being clear – are they solely determined by some proximal limitation mechanisms, or are there some strategic decisions of parents also involved (Mägi and Mänd 2004). Food availability is one of the main environmental factors limiting avian reproduction (Newton 1998). Earlier investigations have pointed to the probable link between multiple breeding and dynamics of food availability within different habitats. For example, the reason for overall greater frequency of second clutches in great tits breeding in conifers has been suggested to lie in a relatively low but a steady food availability during the breeding season, compared to deciduous forests where food peaks occur at the beginning of the breeding season followed by a significant declines (Van Balen 1973, Gosler 1993).

In this study, we explored whether the above-described habitat and seasonal differences in reproductive parameters in great tits can be explained by habitat-specific dynamics of food availability. Both correlative and experimental approach was applied. First, in order to explore whether the habitat-related and seasonal patterns of these variables correspond to each other, we compared basic reproductive parameters, caterpillar abundance and parental provisioning rates in the deciduous and coniferous habitats during two successive breeding attempts. Second, we experimentally increased the hunger level of the nestlings using temporal deprivation of food, and recorded the parental feeding behavior before and after food deprivation. We expected that hungrier chicks beg more intensely, that forces parents to increase their feeding effort. We assumed that the chances of parents to compensate for the increased food demand of the nestlings by increasing provisioning rate is less limited within habitats of high food abundance than in habitats of low food abundance, where the feeding rate of parents is close to the upper limit of their capability (as found, e.g., by Sanz et al. 2002, Stauss et al. 2005).

MATERIALS AND METHODS

Study area

Data was collected in the surroundings of Kilingi-Nõmme (58° 7'N, 25° 5'E) in SW Estonia in 2004. The size of the study area is approximately 50 km^2 and it contains a mosaic of two forest types – coniferous and deciduous (see map of study area in Mägi and Mänd 2004 or Mänd et al. 2005). Deciduous forests either occur as isolated patches within agricultural landscape or as 250 – 500 m wide riparian stripes along stream valleys. These are mostly unmanaged forests growing on fertile soils and have a rich deciduous understorey. The most common species are grey alder *Alnus incana* and silver birch *Betula pendula*. Coniferous forests are typically managed and grow on nutrient poor sandy or peat soils where the dominant tree species is Scots pine *Pinus sylvestris*, that sometimes forms mixed stands together with Norway spruce *Picea abies* or downy birch *Betula pubescens*.

Great tits bred in wooden nest boxes with a cavity of 11 x 11x 30 cm and an entrance diameter of 3.5–4.0 cm. Nest boxes were mounted on tree trunks at height of 1.5–2.0 m and were arranged in lines, so that each line generally consisted of some tens of nest boxes within homogeneous (either in coniferous of deciduous) habitat. Distances between neighboring nest boxes were 50–60 m.

Nest boxes were annually cleaned of old nest material before the beginning of the breeding season.

Basic reproductive parameters

Nest boxes were checked as often as necessary to record laying date for the first egg, clutch size, hatching date and number of fledglings. First and second breeding attempts were clearly distinguishable since there was no overlap between dates of laying the first and second clutches (see also Mägi and Mänd 2004). Adults were captured during the second half of the nestling period, and sex determined by brood patch. Birds were weighed with a Pesola spring balance to a precision of 0.1 g, tarsus was measured using sliding caliper to the nearest 0.1 mm and wing length to the nearest 1 mm. The same parameters in fledglings were measured on day 15 post-hatch. In case of fledglings' parameters, brood means were used as independent data points. Each adult and fledgling was marked with an individual aluminum ring. When calculating fledging success, depredated and deserted nests were omitted from the analysis.

Feeding rate

We recorded adult provisioning rates to the offspring by filming nest-boxes with video cameras placed on tripods 5–7 m away from nest-boxes, and hidden in the bushes as good as possible. All recordings were conducted only in dry weather between 08:00 a.m. – 15:00 p.m. According to Gibb (1955), during this time-span feeding frequency remains relatively stable. Each nest was filmed 65 min on two sequential days and exactly at the same time of day. In both days, camera was placed in the same location. First filming took place when nestlings were nine days old, since in this developmental stage the energy requirement of great tit nestlings has been demonstrated to be the highest (Perrins 1965, van Balen 1973). The aim of the first filming was to record the normal feeding activity of adults at this stage. The next day, nest box entrance was closed for two hours with a piece of cardboard and reopened when filming started. We assumed this manipulation to increase the hunger level and accordingly the begging rate of the chicks, forcing thereby parents to increase their feeding effort (Grieco 2002b, Wright et al. 2002, Rosivall et al. 2005). According to Kölliker et al. (1998), a two-hour food deprivation period is enough to increase the hunger level of the nestlings whereas at the same time does neither induce any remarkable stress nor long-term effects on the condition and survival of the nestlings. When calculating feeding frequency for an individual, only the time interval between the first nest visit and the end of filming was taken into account. For each visit, the sex of the parent was determined using plumage characteristics. Nests that included filmings where sexes could not always distinguished due to a poor location of the camera, were omitted from the analysis. In order to achieve normal distribution of data, feeding frequencies were log-transformed before statistical analyses. The effect of manipulation was studied using repeated measures ANOVA, with adult's feeding frequency before and after manipulation as repeated factor and habitat (coniferous and deciduous) and breeding attempt (first and second) as discrete factors. Given that the feeding frequency correlated positively with brood size (see results), the number of nestlings during filming was always kept in models.

Food abundance

Caterpillars usually make up the majority of the diet of great tit nestlings (Gibb and Betts 1963, Royama 1970, Van Balen 1973, Cramp et al. 1993, Rytkönen and Krams 2003). Changes in caterpillar abundance throughout the breeding season were monitored by frass-fall method (e.g., Seki and Takano 1998, Visser et al. 2006). Five collecting sites in each habitat were randomly selected each site containing four collectors (round plastic funnels with 30 cm diameter) placed beneath trees or bushes about 40 cm above the ground. At the end of the funnels there was a 1 x 4 paper coffee machine filter, where the frass accumulated during the collection period. Filters were collected and replaced every five days from May 4th till June 23rd. Filter contents was dried at 35–40ºC and stored in plastic bags. Later frass was separated from litter, kept at 60ºC for 48 hours and weighed to the precision of 0.1 mg. For one data-point, the mean of four funnel frass samples collected during five days in the same collecting place was calculated. This data together with the daily variation in temperature was used to calculate caterpillar biomass, as shown in Tinbergen and Dietz (1994).

RESULTS

Basic reproductive parameters

Second broods occurred more frequently in coniferous habitat than in deciduous habitat (66% and 37%, respectively), however the difference was not statistically significant (χ^2=3.55, df=1, P=0.06). Laying of first clutches started on average 2.4 days earlier in deciduous forest compared to coniferous forest (T-test, $t_{21,19}$=2.29, P=0.03), however the time of laying second clutches did not differ among habitats ($t_{9,16}$=0.12, P=0.9). Second clutches were on average much smaller than first clutches in both habitats (Fig. 1A; GLM, $F_{1,67}$=42,79, P<0,0001; Tukey HSD post hoc P<0.001 for deciduous habitat and P=0.006 for coniferous habitat). However, the fact that habitat as the main effect did not appear to be significant but instead the breeding attempt*habitat interaction was significant ($F_{1,67}$=4.30, P=0.04) indicates that the decline in clutch size between successive breeding attempts was steeper in deciduous than in coniferous habitat (Fig. 1A). Overall, more offspring fledged per nest in coniferous than in deciduous forest (Fig. 1E; Table 1). Even though post hoc test showed that latter difference was significant only during the first breeding attempt (Tukey P=0.01) and not during the second (Tukey P=0.63), the interaction of breeding attempt*habitat was not significant (Table 1).

Habitat had a significant main effect on the body weight as well as on tarsus and wing length of the fledglings (Table 1). However, the breeding attempt*habitat interaction term was also significant. Post hoc test revealed that differences in the body measurements of the fledglings appeared only during the first breeding attempt: all studied parameters had significantly higher values in the coniferous compared to the deciduous forests (Fig. 1B-D; Tukey P<0.001 for all parameters). No habitat difference in offspring parameters was found during the second breeding attempt (Tukey HSD, all P values above 0.8). Further investigation revealed a significant increase in fledgling parameters among successive breeding attempts within the deciduous habitat (Fig. 1; Tukey P=0.07 for weight, P<0.001 for tarsus and P=0.003 for wing), whereas no such change occurred in coniferous habitat (Tukey P=0.26, 0.98 and 0.98, respectively).

Parental feeding rate

Breeding attempt as the main effect did not affect parental feeding frequency significantly when controlled for brood size, but feeding frequency was significantly higher in deciduous compared to coniferous habitat (Tables 2–3; Fig. 2). However, a significant breeding attempt*habitat interaction indicates on differences between habitats only during first broods (Tukey P<0.001) but not second broods (Tukey P=0.99). Latter is due to the fact that feeding frequency per nestling in deciduous habitat tended to decrease between two successive breeding attempts whereas increased in coniferous habitat (Fig. 2). However, these changes were neither significant in deciduous (Tukey P=0.10) nor in coniferous habitat (Tukey P=0.18) when analyzed separately. Feeding rates of different sexes did not differ significantly from each other (Table 3).

After experimental food deprivation, parents significantly increased their provisioning frequency, compared with that in previous day (GLM [repeated measures design], Tables 2–3). When different sexes were analysed separately, the increase (1.7 x) was significant in females ($F_{1,36}$=5.76, P=0.022), but not in males ($F_{1,35}$=0.28, P=0.6). However, the sex*experiment interaction was not significant. The effect of manipulation did neither differ between habitats nor breeding attempts, since the interactions between these factors and the experiment were not significant.

Provisioning rate was not related to body parameters of parents, when both sexes were included in the same model. However, when different sexes were analysed separately, provisioning rate was negatively related to male's body weight (GLM; $F_{1,21}$=5.32, P=0.03, β= –0.42). Body parameters of 15-day-old nestlings were all significantly and negatively related to male's provisioning frequency, when controlled for habitat type and breeding attempt (GLM; weight: $F_{1,39}$=9.7, P=0.003, β= –0.37; tarsus length: $F_{1,39}$=5.5, P=0.024, β= –0.31; wing length: $F_{1,38}$=9.1, P=0.004, β= –0.38; both parents in the same model). At the same time, fledglings' weight and tarsus length were not related to female's provisioning frequency (weight: $F_{1,39}$=0.2, P=0.66; tarsus length: $F_{1,39}$=0.3, P=0.57). Exceptionally, there was a significant positive relationship between female's feeding frequency and fledglings' wing length ($F_{1,38}$=4.5, P=0.04, β=0.28).

Caterpillar abundance

In general, caterpillar biomass in the forest was higher during the second broods compared to the first broods (Fig. 3; GLM; $F_{1,8}$=110.0, P<0.0001). However, a significant breeding attempt*habitat interaction ($F_{1,8}$=14.0, P=0.006) indicates that seasonal increase in caterpillar abundance was relatively low and non-significant within deciduous habitat (Tukey P=0.08), but caterpillars in the coniferous habitat were remarkably more abundant during second broods compared to first broods (Tukey P<0.001; Fig.3).

DISCUSSION

Basic reproductive parameters

The pattern of basic reproductive parameters of great tits, in the current study, corresponded very well to the one described earlier by Mägi and Mänd (2004) and Mänd et al. (2005). Pairs breeding in coniferous forests tended to have second broods more often than those in deciduous forests, however the difference was neither significant in this study year nor in a longer run (Mägi and Mänd 2004). During the first breeding attempt, great tits started egg-laying earlier in deciduous than in coniferous forests, and also clutch size tended to be slightly larger within the deciduous forests. Even though the latter tendency was not statistically significant in this particular year, it was proved to be a rule in a longer run (Mänd et al. 2005). Despite this relatively better start in the deciduous forest, both the fledging success and the body condition of fledglings were significantly lower in deciduous compared to coniferous habitat. During the second breeding attempt, in contrast, tits breeding in deciduous forests laid on average fewer eggs than those in coniferous forests, whereas body condition of the chicks was significantly better than it was measured during first broods within the same habitat and similar to chicks in coniferous forests. Also, fledging success of the second broods did not differ between the two habitats, as it was proved to be among the first broods. Hence, this study year almost perfectly resembles an average breeding year of this study system, when compared to the long-term data (Mägi and Mänd 2004, Mänd et al. 2005).

What did the food deprivation experiment tell us?

What lies behind the patterns above? It has been hypothesized that providing nest-boxes within the deciduous habitat that is preferred by birds may raise the density of great tits to a supra-optimal level, causing relative food shortage (Rodenhouse et al. 1997, Sanz 2001, Mänd et al. 2005). This is probably not the case in non-preferred coniferous habitat where the density remains relatively low despite erecting the same amount of nest-boxes (Mänd et al. 2005). Thus such a "density trap" (named after Rodenhouse et al. 2006) may lie behind the relatively poor breeding performance of tits in the deciduous habitat during the first breeding attempt. If this is the case, one should expect the ability of parents to increase their provisioning rate as a response to the experimental food deprivation of broods is more limited in the deciduous than in the coniferous habitat.

However, the results of our manipulation were not consistent with the suggestion above. Even though parents significantly increased their feeding frequency after the temporary food deprivation of the chicks (Tables 2–3), the effect of manipulation did neither differ between the compared habitats nor between successive breeding attempts. However, it is possible that the duration of the food deprivation was too short to cause a sufficient increase in the begging intensity of the nestlings and therefore parental response remained too weak to reveal any habitat or seasonal differences in food limitation. An alternative explanation would be that food shortage during brood rearing is not responsible for the relatively poor breeding performance in deciduous habitat, and other factors should be considered. Note that our recent data, suggesting an inferior physiological condition of females within deciduous habitat during early incubation stage (V Tilgar et al. unpublished data) is consistent with this second assumption.

Parental provisioning and offspring size

On the other hand, habitat and seasonal patterns of the parental provision rate and body parameters of the offspring seem to be in a remarkably clear correspondence with each other, although in a somewhat unexpected way (Figs. 1–2). The relatively high feeding rate of parents within the deciduous habitat during the first breeding attempt resulted in a relatively low weight of the offspring together with a shorter tarsus and wing length measured within the same habitat and during the same period of time. In deciduous habitat, an increase in the average body size of the offspring among successive broods was accompanied by a slight decline in parental provisioning frequency, whereas in coniferous habitat these trends were the opposite. As a result, neither parental feeding rate nor offspring size differed significantly between two habitats during the second breeding attempt. To put it briefly, among great tits it seems that the lower the parental feeding rate, the better the growth of the nestlings.

We propose two possible and non-exclusive explanations for such an inverse relationship between parental provisioning frequency and offspring size. First, even though many authors have used feeding frequency as a direct measure of the parental provisioning effort (e.g., Conrad and Robertson 1992, Christe et al. 1996, Hurtrez-Bousses et al. 1998, Radford et al. 2001, McCarty 2002, Tripet et al. 2002, Biard et al. 2005), have other researchers shown that this is not always a reliable indicator (e.g., Nour et al. 1998, Grieco 2001, 2002a, Tremblay et al. 2005). Lower feeding frequency does not necessarily indicate to a lower food supply and/or a lower provisioning level of chicks. In certain circumstances, parents may spend more time in looking for energetically more payable food items (Betts 1955, Royama 1970, Nour et al. 1998, Grieco 2001, 2002a, Stauss et al. 2005), which ensures better growth as well as a higher survival of the offspring (Tremblay et al. 2005). For example, it has been found that the average prey size brought to the nest by great tits is significantly larger than the average prey size available in the environment (Cramp et al. 1993). In other words, a relatively low feeding frequency may actually mean a higher selectivity and, therefore, a relatively higher amount of food brought to chicks per unit of time. It is also possible that if the food items are on average smaller, parents need to feed nestlings more frequently than in the case of larger food items. The existence of clear correlations between habitat type, size of the food item and parental feeding frequency among passerines has been demonstrated, e.g., by Stauss et al. (2005) and Tremblay et al. (2005). Schwagmeyer and Mock (2003) found that house sparrows reduced their per-chick delivery rates as the season progressed, since very large lepidopteran larvae became a more common prey item later in summer. Perhaps the same pattern could explain seasonal decline in the feeding frequency of great tits within deciduous forests of our study area?

According to the second explanation, parents may adjust their feeding effort with respect to the current condition of the nestlings. When chicks are in a good condition and grow well, they presumably are less hungry and therefore begging intensity is lower (Kölliker et al. 1998, Grieco 2001). Parents may correspondingly decrease provisioning of such high-quality offspring (Kölliker et al. 1998, Grieco 2001). Our finding where the feeding frequency of the males was negatively correlated with the body parameters of the fledglings even when controlled for habitat type and breeding attempt, is consistent with the suggestion above. A negative relationship between feeding rate and nestling growth has recently been observed in blue tits by Stauss et al. (2005, but see Moreno et al. 2004). In Corsica, blue tit nestlings that were experimentally infected with ectoparasites were being fed more frequently by their parents but grew slower than parasite-free nestlings (Blondel et al. 2002, Banbura et al. 2004, Simon et al. 2004). Thus the observed habitat-related and seasonal differences in parental feeding rates and offspring parameters may reflect, for instance, some corresponding differences in the number of ectoparasites in the nests. Moreover, it is not excluded that differences may be due to variations in egg quality, since recent studies have revealed that nestlings' growth as well as condition may result from several maternal effects obtained via eggs (e.g., Dzialowski and Sotherland 2004, Veiga et al. 2004, Verboven et al. 2005, Szigeti et al. 2007).

Again, our finding that during the first breeding attempt females within the deciduous habitat are in a relatively worse physiological condition during early incubation stage (V Tilgar et al. unpublished data) is consistent with the second explanation, suggesting that the reasons for the described patterns of reproductive performance may indeed lie in a much earlier stage than the brood rearing period. To address this problem, an experimental approach is needed, including manipulation of the overall condition of chicks and swapping broods between different habitats, accompanied by recording not only the feeding frequency of parents, but also the size and quality of food items brought to the chicks in different habitats during different breeding attempts.

Seasonal trends in caterpillar abundance

Previous studies have shown that food availability within deciduous forests notably declines after the first breeding attempt, whereas remains fairly stable in coniferous forests during the entire breeding season (Van Balen 1973, Gosler 1993, Slagsvold and Lifjeld 1985) or peaks later during the breeding season (Eeva et al. 2000, Rytkönen and Orell 2001). The analysis of our frass fall data revealed a substantially different food dynamics in our study system, compared to what has been described previously. In the deciduous habitat, caterpillar abundance remained relatively stable throughout the breeding season, with the exception of only a slight and insignificant increase towards the end of the season. At the same time, there was a remarkable increase in caterpillar abundance during the second breeding attempt within the coniferous habitat.

Interestingly, this pattern does not show any consistency with the observations of feeding frequency of the adults and offspring measurements, which differed significantly between habitats during the first breeding attempt, but not during the second. At the moment, one can only speculate about the reasons for such apparent controversy. First, the current frass fall method is not very suitable for comparing absolute values of caterpillar supply between habitats, since the estimates may be biased due to differences in the canopy structure of different forest types. Therefore we cannot be sure whether food availability during the first broods indeed is at about the same level within the two habitats as it appears on the graph (Fig. 3). Note that earlier studies of Mänd et al. (2005) carried out in the same study area by using a different method have demonstrated that during first broods there is a higher caterpillar abundance in deciduous habitat compared to coniferous habitat. Thus, it is possible that during first broods food abundance is still lower in coniferous forests compared to deciduous forests, and that latter disparity finds compensation through an increase in food abundance in the conifers later in the season whereas in deciduous forests it appears to be almost no change in food abundance. Second, it is possible that the estimated abundance of caterpillars does not reflect the actual food availability for birds. There may exist, for example, a seasonal decline either in the nutritional value or palatability of caterpillars (e.g., an increase in the content of some poisonous or distasteful compounds or development of special defensive morphological structures later in summer) or in the effectiveness of finding or consumption of caterpillars (e.g. due to foliage development, increased interference, parasites, heath stress etc.). Note that although the habitat-specific food dynamics in our study area differed from that in other areas studied, it still seems to benefit second broods in coniferous habitat.

However, one cannot exclude the possibility that caterpillar abundance is not a limiting factor during brood rearing in this study system while seasonal patterns in feeding frequency and offspring measurements are related to some factors other than food abundance. For example, Mägi and Mänd (2004) have suggested that having relatively small broods of well-attended young during the second breeding attempt in deciduous habitat may be a tactical decision of females who had performed poorly during the first breeding attempt, while having relatively large broods. The importance of a good body condition of the offspring has been demonstrated to significantly increase towards the end of the breeding season, due to an increased predation risk at that period of time (Naef-Daenzer et al. 2001, Götmark 2002). Also, Pimentel and Nilsson (2007) have recently suggested that different allocation of reproductive investment between successive breeding attempts may play an important role in optimizing breeding tactics in different environments. Again, only a more thorough investigation of foraging behavior of adults during brood rearing period, accompanied by a detailed study of seasonal dynamics in food quality, could help to unravel this puzzle.

Conclusions

This study demonstrates an inverse relationship between seasonal patterns of offspring growth and parental feeding rates in great tits within different habitat types. The results of the food deprivation experiment were not consistent with our idea that parental ability to feed nestlings may be limited to a different extent within different habitats. Moreover, the habitat-related variation in seasonal dynamics of caterpillar abundance was not consistent with the respective patterns in offspring growth and parental feeding rates. These findings suggest that habitat-related differences in nestling growth in birds cannot be explained merely by the variation in food abundance during brood rearing, and the possibility that true reasons for such differences lie at an earlier stage of the breeding season, should be considered. To shed light on these questions, a more detailed study including experimental approach together with thorough investigation of the size as well as quality of food items brought to the nestlings within different habitats during different breeding attempts is necessary.

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Table 1. The effect of habitat type (HT) and breeding attempt (BA) on body parameters and number of fledglings in great tits (ANOVA).

	Weight			**Tarsus length**			**Wing length**			**No of fledglings**		
	df	**F**	**P**	**df**	**F**	**P**	**df**	**F**	**P**	**df**	**F**	**P**
BA	1	0.65	0.42	1	8.67	**0.005**	1	6.72	**0.01**	1	25.24	**<0.001**
HT	1	16.60	**0.0001**	1	5.30	**0.02**	1	8.83	**0.004**	1	8.88	**0.004**
BA x HT	1	9.79	**0.003**	1	11.70	**0.001**	1	9.57	**0.003**	1	1.38	0.25
Error	62			62			61			63		

Table 2. Feeding frequency (visits per hour per nestling) of 9–10-day-old nestlings by great tit parents within different habitats during successive breeding attempts. Dec – deciduous habitat, Con – coniferous habitat, Control – day before experimental food deprivation of the brood, Deprived – immediately after experimental food deprivation of the brood.

			Female			**Male**		
			Mean	**SD**	**n**	**Mean**	**SD**	**n**
First broods	Dec	Control	2.17	1.01	11	1.65	0.81	12
		Deprived	3.62	2.62	11	3.32	2.72	12
	Con	Control	0.73	0.30	12	1.07	0.45	13
		Deprived	1.47	0.99	12	1.80	0.80	13
Second broods	Dec	Control	1.12	0.41	9	1.48	0.88	9
		Deprived	2.01	1.58	9	1.32	0.88	9
	Con	Control	1.10	0.62	9	1.43	0.64	6
		Deprived	1.53	1.52	9	1.65	0.99	6

Table 3. The effects of habitat type, breeding attempt, sex of parent and food deprivation experiment on parental feeding frequency in great tits (GLM, repeated measures design). Brood size was included in the model as covariate. Only significant interaction is given.

	df	**F**	**P**
Brood size	1	13.3	**0.0005**
Breeding attempt	1	0.5	0.46
Habitat type	1	11.0	**0.001**
Sex of parent	1	0.0	0.94
Breeding attempt x Habitat type	1	8.7	**0.004**
Error	72		
Food deprivation experiment	1	4.5	**0.038**
Error	72		

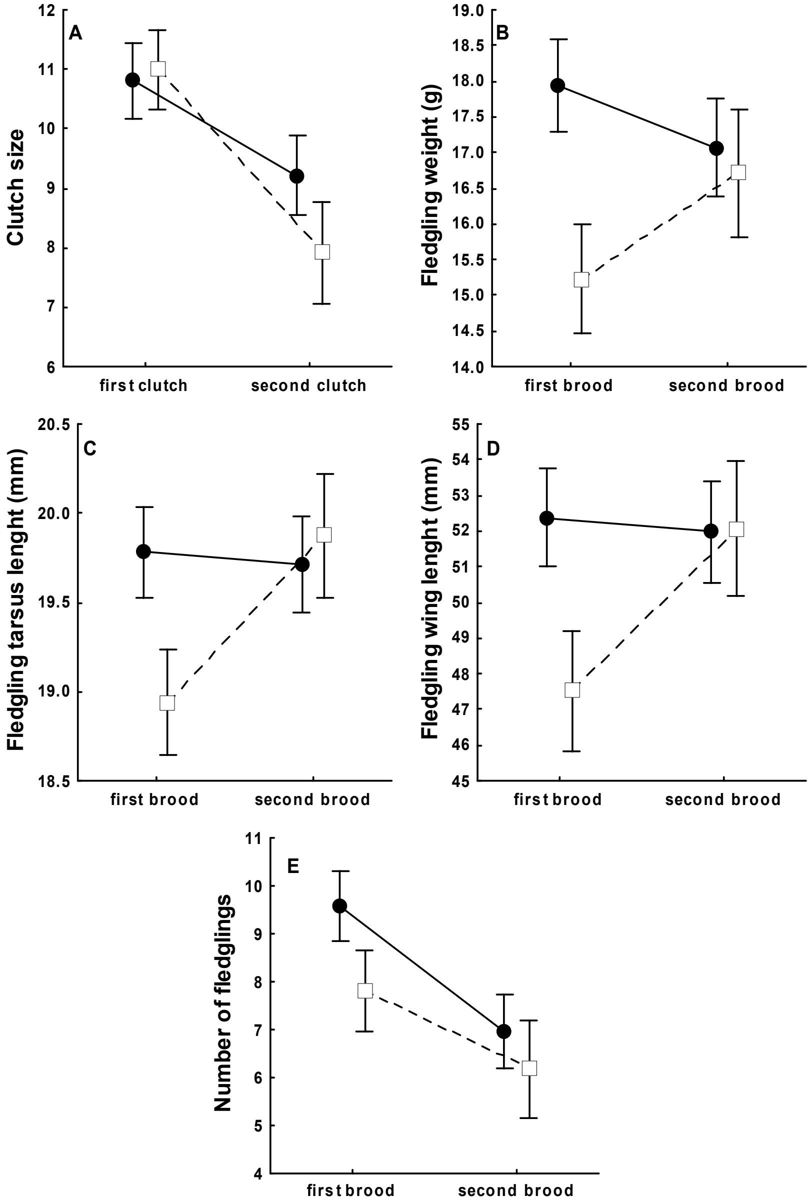

Fig. 1. Basic reproductive parameters (mean ± 95% confidence interval) in great tits breeding in deciduous (empty square) and coniferous (black dot) habitats, during successive breeding attempts.

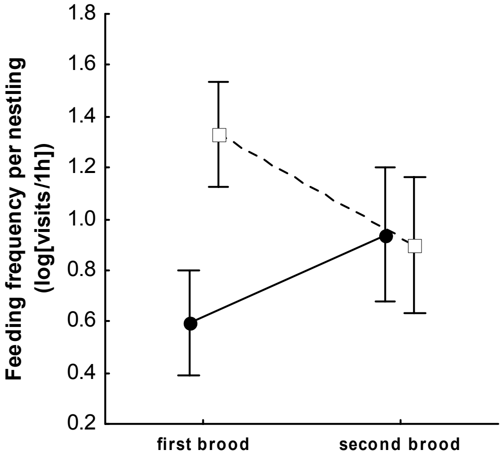

Fig. 2. Parental feeding frequency (mean ± 95% confidence interval) in great tits breeding in deciduous (empty square) and coniferous (black dot) habitats, during successive breeding attempts.

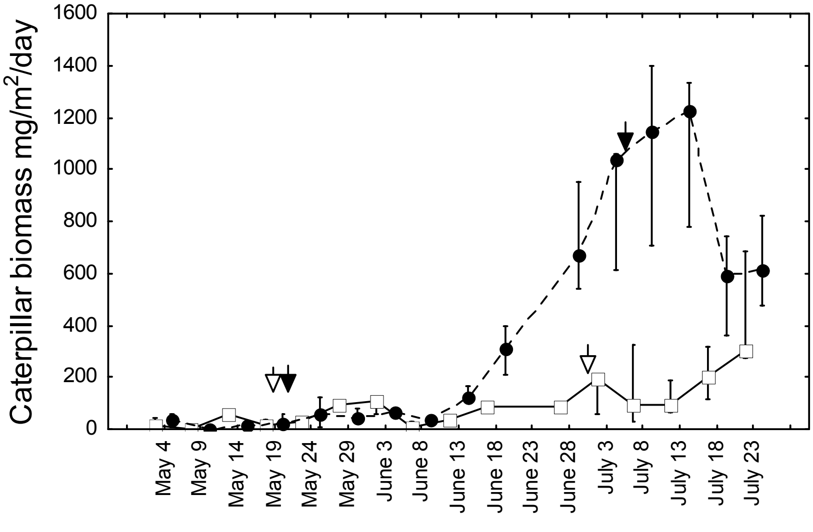

Fig. 3. Dynamics of caterpillar biomass (median ± 25% quartiles) in deciduous (empty square) and coniferous (black dot) habitat throughout the breeding season of great tits. Arrowheads denote median hatching dates in deciduous (empty) and in coniferous (black) habitats during the first and the second breeding attempts.

CURRICULUM VITAE

I. General

Name	Marko Mägi
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Languages spoken	Estonian (mother-tongue), English, German, Russian.
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II Research history

Research interests	Multiple breeding and its spatial and temporal changes in heterogeneous habitat system.

Publications

Tilgar, V., Mänd, R. & Mägi, M. 2002. Calcium shortage as a constraint on reproduction in Great Tits *Parus major*: a field experiment. *Journal of Avian Biology* 33: 407– 413.

Mägi, M. & Mänd, R. 2004. Habitat differences in allocation of eggs between successive breeding attempts in great tits (Parus major). *Ecoscience* 11: 361–369.

Tilgar, V., Mänd, R., Ots, I., Mägi, M., Kilgas, P. & Reynolds, S. J. 2004. Calcium availability affects bone growth in nestlings of free-living great tits Parus major, as detected by plasma alkaline phosphatase. *Journal of Zoology, London (J.Zool., Lond.)*263: 269–274.

Kilgas, P., Mänd, R., Mägi, M. & Tilgar, V. 2006. Hematological parameters in brood-rearing great tits in relation to habitat, multiple breeding and sex. *Comparative Biochemistry and Physiology A*: *Molecular & Integrative Physiology* 144: 224–231.

Tummeleht, L., Mägi, M., Kilgas, P., Mänd, R. & Hõrak, P. 2006. Antioxidant protection and plasma carotenoids of incubating great tits (*Parus major* L.) in relation to health state and breeding conditions. *Comparative Biochemistry and Physiology C: Toxicology & Pharmacology* 144: 166–172.

Mänd, R., Tilgar, V., Kilgas, P. & Mägi, M. 2007. Manipulation of laying effort reveals habitat-specific variation in egg production constraints in great tits (*Parus major*). *Journal of Ornithology* 148: 91–97.

Conference theses

Mägi, M., Mänd, R. & Tilgar, V. 2001. What happens to conclusions when second broods are involved: a study on Great Tits *Parus major.* 3^{rd} Meeting of the European Ornithologist Union. Groningen, The Nederlands, 21-25 August. Suuline ettekanne.

Tilgar, V., Mänd, R., Leivits, A. & Mägi, M. 2001. All that glitters is not gold: fragments of rich habitat function like "ecological trap" for Great Tits *Parus major.* 3^{rd} Meeting of the European Ornithologist Union. Groningen, The Nederlands, 21–25 August.

Mägi, M. & Mänd, R. 2003 "Habitat-specific differences in the level of intraseasonal iteroparity in Great Tits breeding in heterogeneous environment." IV Euroopa Ornitoloogiaühingu konverents 2003 Chemnitzis (Saksamaa): Links and Perspectives in European Ornithology. Suuline ettekanne.

Mägi, M. & Mänd, R. Role Of Intraseasonal Iteroparity In Optimising Breeding Tactics Of Animals In Heterogeneous Environments. 10th Jubilee Congress of the International Society for Behavioral Ecology 10–15 July 2004, University of Jyväskylä, Finland. Stendiettekanne.

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II Teaduslik ja arendustegevus

Peamised uurimisvaldkonnad	
	Lindude korduvpesitsus ja sigimisnäitajate ajalis-ruumiline muutlikkus heterogeenses elupaigas.

Publikatsioonide loetelu

Tilgar, V., Mänd, R. & Mägi, M. 2002. Calcium shortage as a constraint on reproduction in Great Tits *Parus major*: a field experiment. *Journal of Avian Biology* 33: 407– 413.

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Tummeleht, L., Mägi, M., Kilgas, P., Mänd, R. & Hõrak, P. 2006. Antioxidant protection and plasma carotenoids of incubating great tits (*Parus major* L.) in relation to health state and breeding conditions. *Comparative Biochemistry and Physiology C: Toxicology & Pharmacology* 144: 166–172.

Mänd, R., Tilgar, V., Kilgas, P. & Mägi, M. 2007. Manipulation of laying effort reveals habitat-specific variation in egg production constraints in great tits (*Parus major*). *Journal of Ornithology* 148: 91–97.

Konverentside teesid

Mägi, M., Mänd, R. & Tilgar, V. 2001. What happens to conclusions when second broods are involved: a study on Great Tits *Parus major.* 3rd Meeting of the European Ornithologist Union. Groningen, The Nederlands, 21–25 August. Suuline ettekanne.

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Mägi, M. & Mänd, R. 2003 "Habitat-specific differences in the level of intraseasonal iteroparity in Great Tits breeding in heterogeneous environment." IV Euroopa Ornitoloogiaühingu konverents 2003 Chemnitzis (Saksamaa): Links and Perspectives in European Ornithology. Suuline ettekanne.

Mägi, M. & Mänd, R. Role Of Intraseasonal Iteroparity In Optimising Breeding Tactics Of Animals In Heterogeneous Environments. 10th Jubilee Congress of the International Society for Behavioral Ecology 10–15 July 2004, University of Jyväskylä, Finland. Stendiettekanne.

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