SPATIAL VARIATION IN GREAT TIT LAYING DATE

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Preface

This internship report is the result of a decision I made at the beginning of 2007. At that time I had to choose a final internship subject for my Biology Master at Wageningen University. I found out that at the Animal Population Biology department of the NIOO was working on spatial analysis of bird’s timing of reproduction. I already had experience with spatial analysis and Geo Information Systems, but never worked with birds before. Therefore I chose this topic to get to know a new group of animals as well as a new group of ecologists in Heteren.

After almost four months I’m happy that I chose for this subject. I’ve learned a lot about the biology of great tits, blue tits and pied flycatchers and I’ve tried to understand the complicated process of timing of their reproduction. The fieldwork was wonderful; I’ve spent a great time in the forest jumping over tree logs while being scratched by blackberry-thorns and blood-sucked by ticks... After many hot, dry and thirsty weeks I’ve seen the other side of the meteorological spectrum during the end of my fieldwork. However, writing in your notebook, which is laying on your knee, with a bird in the hand, sitting on a ladder, while water is dripping from your head on the notebook pages, is also something one has to experience in a life-time to call himself a graduate biologist! It was also nice to learn how to trap the parental birds and how to ring the chicks. All in all, I had a nice time at the Buunderkamp during the nest box checks, thinking about why the birds are laying their eggs there at that point in time.

The start of my work was not at the ideal time with regard to the great tit reproduction season, therefore I think time to prepare and think over everything well, was a bit too short. Also, combining my research project together with the rest of the fieldwork that had to be done at the Buunderkamp was not always easy.

My work could never have been done without the help and support of the people around me. First of all I would like to thank Marcel Visser and Leonard Holleman. Thanks for the time we could discuss my fieldwork and your comments on the report. Marcel, I appreciate it very much, you were always available when I had a question. Leonard, thank you for the tips and the field-knowledge you wanted to share with me. I want to thank Gustavo Gutierrez Tomás for allowing me to use the data of the supplementary food experiment. I want to thank Christine Janse and Melina de Koning for their help with the vegetation survey at the Buunderkamp. Finally I want to thank Marcel Dicke for reading the report and being my supervisor from university side.

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Abstract
The seasonally reproducing forest bird great tit (*Parus major*) is known to use several environmental cues to regulate the onset of egg-laying. In this study it was attempted to investigate the spatial and temporal variation of cues and see whether they could be related to laying dates. Therefore several cues; such as light, temperature and food availability were mapped in a population of great tits in a mixed coniferous – broad-leaved forest in the Netherlands.

Not in all cues clear spatial and temporal differences were found. This is probably caused by the extreme high spring temperatures in 2007. It was characterized as the warmest in 300 years. Given that temperature is a factor that influences all other cues that were investigated, except photoperiod, and usually increases the speed of processes, the high temperature probably caused that little to no variation was present in the collected data.

**Key words:** *Parus major* – spatial variation – timing of reproduction – cues
Introduction

The timing of seasonal activity, also named phenology, is a trait that can have major fitness consequences in habitats with strong seasonality (e.g. Daan et al., 1990). When there is only a limited period each year in which conditions for growth and reproduction are optimal, it is important for an organism that it is synchronized with the organism(s) of which it depends. The variation in phenology that is accordingly shown within individuals and between years, is caused by phenotypic plasticity, that is; the same genotype forms different phenotypes in different environments (Nager & Vannoordwijk, 1995).

Phenology is well-studied in birds, probably because of their public popularity and wide distribution. A trait that is often used in bird phenology studies is laying date. The current study focuses on the timing of breeding of the great tit (Parus major). This is a small European forest bird that breeds in natural cavities and also accepts nest boxes. During egg formation, incubation and the raising of the chicks, the bird requires large amounts of food, which is available only during a short period of the year. Caterpillars (mainly winter moths, Opheroptera brumata) are the main food source for nestlings of great tits. And since caterpillars feed on newly emerged leaves, food for the chicks is thus not available until budburst (Nilsson & Källander, 2006).

Therefore great tits have evolved proximate responses to environmental cues to regulate reproductive function so that chicks can be raised during an optimal breeding time. Cues that are used by birds to regulate the start of egg laying can be categorized as photoperiodic and non-photoperiodic. Photoperiod is the most important long term predictive cue that is spatially constant and is used to initiate the required physiological processes in advance to the breeding season (Partecke et al., 2004). Non-photoperiodic cues such as weather conditions, budburst, food availability and energy intake rate may vary considerably both temporally and spatially. Therefore these factors are used to fine-tune the timing of reproduction within the ‘reproductive window’ created by photoperiod (Lambr echts & Perret, 2000; Nilsson & Källander, 2006; Partecke et al., 2004; Visser et al., 2006).

Timing of egg laying has important consequences for the number of nestlings, nestling growth and fledging weight (Visser et al., 2006). And since fledging weight has been shown to be a determinant of subsequent survival, it does affect fitness (Naef-Daenzer & Keller, 1999).

Although birds can use cues in their environment, the studies of Visser et al. (1998; 2006) indicated that the great tit is not changing its timing of reproduction while the peak in food availability is advancing. The reason that is suggested for this is that great tits do not respond in the same rate to increasing spring temperatures as vegetation and caterpillars do. In this way a mismatch between the food demand and the food availability does occur.

The evolution of the birds’ breeding season is not yet fully understood. To get a better understanding of it, proximate questions about the causal relations, and ultimate questions about functional significance need to be answered.

Two main explanations are currently suggested. The breeding season might be adapted to the time of caterpillar appearance needed later for the chicks. Or it might be constrained by the lack of energy to produce eggs (Nager & Vannoordwijk, 1995 and references therein). Therefore this study investigates spatial and temporal variation of factors in a forest to see to what extent they may explain the pattern in laying dates in heterogeneous forest in the Netherlands.
Research question and hypotheses

The NIOO has collected data on breeding of great tits at the Buunderkamp study area from 1983. At the start of the internship, there was the idea that laying date at the Buunderkamp may show spatial structuring, possibly caused by photo pollution of a gas station adjacent to the area. Therefore the average deviation from the annual average laying date was calculated per nest box for the years 1983-2006. The pattern of these deviations is shown in Figure 2A. The area shows variation in laying deviations, and nearby nest boxes show more resemblance than with nest boxes further away, suggesting spatial autocorrelation.

When the average laying dates of the period are categorized as ‘early years’ and ‘late years’ based on the sign (- or +) of the residuals (see Figure 1) and mapped again, it seems that the patterns of ‘early years’ and ‘late years’ differ. In Figure 2B, the area in which the laying date is categorized as ‘early’ is larger and stretches more to the southeast compared to Figure 2C.

To analyze the phenomenon of spatial structuring of laying dates at the Buunderkamp and the differences between ‘late years’ and ‘early years’, the following research question was formulated:

*Can the spatial pattern in great tit laying date at the Buunderkamp be explained by the spatial and temporal variation in biotic and abiotic factors?*

In this article variation in factors that possibly influence the timing of great tits are investigated. In the study area, measurements are done on light intensity and temperature. Furthermore a vegetation survey is done, and characteristics of the vegetation and caterpillar phenology are recorded. Also a feeding experiment is performed on great tits in the laying phase, and activity pattern was recorded for some birds.
Figure 2. Average annual deviation of great tit laying date (April days) per nest box at the Buunderkamp for ‘all years’ (A), ‘early years’ (B) and ‘late years’ (C). After IDW interpolation, the terrain between nest boxes was classified in three classes (early, intermediate and late) based on Jenks’ natural breaks on the data of ‘all years’ (A) to make the patterns comparable. N per nest box varies between 2 and 13 (A), 2 and 7 (B), 2 and 8 (C).
With respect to photoperiod, temperature and food availability, the following seven hypotheses were formulated:

**Photoperiod**
Since photoperiod is setting the boundaries for the period in which egg laying can take place, artificial light from a gas station terrain adjacent to the northern side of the area may affect the birds, physiologically and / or behaviourally.

1. Breeding close to the gas station is affecting great tits perception of photoperiod.
2. Birds close to the gas station can forage longer during the egg laying phase, because they can increase their day length due to the photo pollution of the gas station.

**Temperature**
Also temperature to which great tits, as well as other levels of the trophic interaction, are exposed to may affect laying date. Temperature might have direct effect on the birds, but also vegetation or caterpillars may develop faster at sites that are warmer than others and birds may locally respond to that. The ambient temperature may differ in the area because of local differences in openness of the vegetation cover. But possibly also due to the highway, which may act as a warmth reservoir and wind may transport the heat into the forest causing a temperature gradient.

3. Local ambient temperature in April varies at the Buunderkamp and influences laying date.

**Food availability**
Since broad leaved trees are known to support ten times as much food as coniferous trees (Keller & Vannoordwijk, 1994) and since the Buunderkamp is a heterogeneous forest, food availability in the area may differ, both temporally and spatially which also may influence timing of reproduction.

Since great tits forage within close vicinity of their nest box during breeding, it is likely that great tits try to match their breeding moment with the availability of food around the nest box, both during egg laying and raising of the chicks. And because great tits are known to forage on birch and larch trees during egg laying (Visser et al., 1998), they may be less constrained in egg production when they are breeding in or close to plots with high density of birch or larch.

~ in the (pre-)laying phase

4. When great tits are experimentally provided with supplementary food during nest building, they will advance their laying date.
5. Great tits breeding in or close to plots with high birch density will lays eggs earlier because these plot provide in food earlier than other plots.

~ during chick rearing

6. The earliness of the red oak budburst influences the laying date of great tits close to those plots.
7. The earliness of the caterpillar biomass peak influences the laying date of great tits close to those plots.
Material & Methods

Study area
The study was conducted at the Buunderkamp, a poor mixed coniferous - broad-leaved forest between Ede and Arnhem, (52° 1'1.95"N, 5°45'23.60"E) in the period March to May 2007. The forest canopy consists of pine (*Pinus nigra* and *Pinus sylvestris*), fir (*Abies* spp. and *Pseudotsuga menziesii*), oak (*Quercus rubra* and *Quercus robur*), birch (*Betula verrucosa*), larch (*Larix kaempferi*) and beech (*Fagus sylvatica*). Within-stand variation in tree species and density is rather low, while stands of different species are dispersed in a mosaic-like pattern over the whole area (see Figure 3). The northern side of the forest borders on the highway A12. This highway has a gas station and a parking terrain adjacent to the forest, which are illuminated in the evening and night. The northwestern part of the forest which is surrounding the gas station (henceforth termed: sub-study area) consists mainly of pine trees with some small stands or lanes with red oak trees.

Figure 3. Main tree species per stand at the Buunderkamp. Yellow to orange stands refers to broad-leaved trees, other colours are coniferous trees.

GIS techniques
All the maps in this study were made with ArcGIS 9.1 (ESRI, Redland, CA). The interpolation maps of laying date were made using inverse distance weighting (IDW) interpolation. Temperature and light interpolation maps were made using Spline interpolation.
Light intensity (1)
The illumination caused by the lights on the terrain of the gas station was measured on two
evenings ± 1.5 hours after sunset using a LX-93 lux measuring device (Nieuwkoop BV,
Aalsmeer, the Netherlands). Measurements were done at nest boxes close to the gas station.
The device was held at 2 m. height with the sensor directed to the gas station. When the
device indicated that light intensity was 0 lux, no new measurements further away from the
gas station in that direction were performed.

Activity pattern (2)
In a few nest boxes occupied by blue tits in the egg laying phase, ‘passing sensors’ were
placed to record day-night rhythms. Therefore a PVC ring with a small LED opposite to a
light-sensitive sensor was placed in the nest box opening. When a bird entered or left the nest
box a signal was sent to a recording device. At the time of installation of the passing sensor, a
battery and the recording device were put on top of the nest box in a black plastic bag.
For this measurement, blue tits were used instead of great tits because the latter were already
part of another experiment (see 4). The activity patterns of the blue tits were recorded from
the 20th to the 24th of April.

Temperature (3)
Air temperature in the sub-study area was recorded during the egg laying period. Therefore
eight Hobo temperature dataloggers (Onset CC, Bourne, USA) were equally distributed over
the study area. Five loggers were placed at the 5th of April and three were added on the 18th of
April. The temperature sensors were placed at the northern side of a tree at ± 1.5 m. height
and recorded temperature every 15 minutes. Average temperatures were calculated for two
periods in April; 5-18 April and 18-30 April.
To exclude intrinsic differences between dataloggers, the dataloggers were also exposed to
equal temperature circumstances for 36 hours. The temperature range within this period was
10-25 °C. Subsequently datalogger 8 was expressed as a function of each of the other
dataloggers using linear regression. These functions were then applied to the measured values
for each particular datalogger, resulting in comparable temperatures between dataloggers.

Food provision experiment (4)
One experiment was done by Gustavo Gutierrez Tomás at the Buunderkamp with great tits
during the pre-laying phase. The nest boxes in the whole study area were visited daily and
provided with 9 g. of mealworms in a tray within the nest box. This treatment was started
from the moment the nest was ‘half completed’ and ended when the 1st egg was laid. A
control treatment consisted of an empty food tray. Application of food treatment boxes were
interchanged with control treatments each time a ‘half completed nest’ was discovered.
Vegetation composition (5)
The vegetation map (Figure 3) was made by dividing the whole study area in stands based on the majority of a certain tree species. If necessary, the estimated tree density was used as a second criterion for dividing them in different stands. For each stand, several characteristics were visually recorded as shown in Table 1. The overall tree density per stand was recorded according to the methods of Jonsson et al (1992).

Table 1. Vegetation parameters recorded in each stand. Trees are defined as stems with a height > than 5 m, undergrowth is defined as trees and shrubs >0.5 and <5 m.

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
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<tbody>
<tr>
<td>Stand surface</td>
<td>Surface area (ha) of stand (calculated with ArcGIS)</td>
</tr>
<tr>
<td>Percentage oak trees</td>
<td>Percentage of oak trees relative to all trees</td>
</tr>
<tr>
<td>Percentage birch trees</td>
<td>Percentage of birch trees relative to all trees</td>
</tr>
<tr>
<td>Percentage broad-leaved trees</td>
<td>Percentage of broad-leaved trees relative to all trees</td>
</tr>
<tr>
<td>Percentage coniferous trees</td>
<td>100 - Percentage broad-leaved trees</td>
</tr>
<tr>
<td>Percentage undergrowth</td>
<td>Percentage of ground surface covered by undergrowth</td>
</tr>
<tr>
<td>Main tree species</td>
<td>Tree species having the highest number of stems</td>
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<tr>
<td>Tree density</td>
<td>Number of trees per ha</td>
</tr>
<tr>
<td>Density birch trees</td>
<td>Number of birch trees per ha</td>
</tr>
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</table>

Oak budburst (6)
In five oak plots in the sub-study area, 10 to 12 oak trees of the same species were scored for bud burst with a 4-day interval according to the Chene index. This index describes the budburst from stage 0 (not green, un-swollen bud) to stage 3 (leafs unfolded, with 90° angle between leaf and leafstalk) and is a measure for when caterpillars can access the plant material for feeding.

Caterpillar frass (7)
Beneath eight red oak trees in the sub-study area two caterpillar frass-nets were placed to indirectly measure the peak in caterpillar biomass. The droppings were collected from the nets with a four to six day interval. After collection the droppings were dried in a stove and weighted and average per tree. Detailed methods are described in Visser et al (2006) and references therein.
Results

Light intensity (1)
The recorded light intensity 1.5 hours after sunset, ranged between 0 - 0.7 lux at the 20th of March and between 0 - 0.6 lux at 24th of April. The recorded values for one of the evenings are shown in Figure 4. The maximum distance over which light was detectable with the measuring device was about 75 m. from the gas station. However, with my own eyes, the light was visible at a distance > 300 m.

Figure 4. Light intensity (lux) at the Buunderkamp caused by artificial lighting of the gas station terrain, measured on 24 April ± 1.5 hours after sunset.
Activity pattern (2)
No observations on foraging birds at the illuminated terrain were done during dusk. However, the activity pattern of four blue tit females during the egg laying phase was recorded. In Figure 5 it can be seen that nest box 18 was closest to the light source and 299 the furthest away. In Figure 6 the wake up- and sleep times of the blue tits is shown. The number of observations per bird was rather low and varied between nest boxes because of differences in clutch size. Due to the low number of observations, no tests of significance were performed. From the observations, it seems that the blue tit female occupying nest box 299 is active the longest (13:48 h.), whereas the female in nest box 306 seems to be active the shortest (13:03 h.).
Temperature (3)
The ambient temperature at different locations in the sub-study area seemed to differ considerably within both periods. These local differences are spatially consistent during the measured period. In the first part of April, the temperature difference between the highest and the lowest average was 3°C (Figure 7). In the second period the overall temperature was higher, and the maximum difference was 1.7°C (Figure 8). It seems that the northwestern part of the area is generally cooler than the rest. The highest temperature in both periods was measured in a relatively open stand with pine trees.

Figure 7. Average temperature at the Buunderkamp for the period 5-18 April.

Figure 8. Average temperature at the Buunderkamp for the period 18-30 April.
Food provision (4)
The start of egg-laying of great tits that were provided with supplementary food during nest building was not significantly different from the control group (14.2 ± 1.2 vs. 13.5 ± 0.6 respectively; ANOVA, F = 0.46; P = 0.50).

![Figure 9](image)

Figure 9. Great tit laying date at the Buunderkamp 2007. Birds were provided with mealworms during nest building. Food: 14.2 ± 1.2; control 13.5 ± 0.6; NS (ANOVA; F = 0.46; P = 0.50)

Vegetation composition (5)
When the average density of birch trees per stand was compared between early, intermediate and late parts (see Figure 2 and Figure 10) no significant differences were found between the three terrain timing classes (ANOVA, F = 2.01; P = 0.16).

![Figure 10](image)

Figure 10. Stands were assigned a class; early, intermediate or late when >50% of the stand was overlapping with one of the three (similarly named) laying date deviation classes as shown in Figure 2A. Numbers within stands indicate average density of birch trees / ha (± SE) of all stands of the same class.
Oak budburst (6)

According to the Chene index, when stage 1 is reached, caterpillars can reach the leaves. Therefore the date on which stage 1 was reached was compared between the five oak plots. The four red oak plots CCC, JJJ, KKK, LLL as shown in Figure 11 were all significantly earlier in budburst than the common oak plot OOO (ANOVA; $F = 19.6$, $P < 0.01$; $F = 42.3$, $P < 0.01$; $F = 12.4$, $P < 0.01$; $F = 16.6$, $P < 0.01$ respectively). Within red oaks, only plot JJJ was significantly different from plot CCC and KKK (ANOVA; $F = 42.3$, $P < 0.01$; $F = 10.7$, $P < 0.01$ respectively).

In the overall budburst phenology (see Figure 13), plot CCC seemed to be developing somewhat faster than the three other red oak plots. The foliating of plot OOO, consisting of common oak however, seemed to develop considerably slower ($\pm$ 10 days) than the red oak plots.

Figure 11. Location of the oak plots that were scored for timing of bud burst.
Figure 12. Budburst date (defined as date on which stage 1 of Chene budburst index was reached) per plot. All bars represent red oak plots, except the dashed bar which is common oak. Bars that share no letters above are significantly different at P < 0.05.

Figure 13. Average budburst score for five oak plots according Chene index (0 = not green, un-swollen bud, stage 3 = leaves unfolded, with 90° angle between leaf and leafstalk). All plots consist of red oak, except ‘OOO’, which is common oak.
Caterpillar frass (7)
The mass of the droppings collected in the nets was weighted for five of the eight red oak trees that were sampled; the other three were not weighted and were assumed not to deviate from the others. Although there were quite big differences between trees in overall caterpillar frass (almost factor 4), no differences are shown in the timing of the peak in biomass (Figure 15).

![Figure 14. Location of red oaks that were sampled for timing of the peak in the caterpillar biomass.](image)

![Figure 15. Average caterpillar frass per sampled tree.](image)
Discussion

Effect of light (1,2)
The illumination of the gas station terrain was measured on two evenings after sunset. As none of the measurements did exceed 0.7 lux and regarding that light intensity of full moon on a clear night is about 0.25 lux (source: website Petzl, 2007), it can be assumed that the effect on the perception of day and night in the birds can be neglected. It is unlikely that the low light intensity that enters the small part of the forest would have direct effect on the endocrinology of the birds and in that way the onset of egg laying. Therefore direct effect of light seems an unlikely explanation for the pattern as shown in Figure 2.

The activity pattern however, may still be affected by the light because birds may extend their diurnal behaviour. Light during nighttime improves an animal’s ability to orient itself and it is known that many usually diurnal birds and reptiles, forage under artificial lights (Longcore & Rich, 2004).

The illuminated terrain does contain oak and pine trees, providing possibilities for birds to forage with the use of the light, although predation risk may increase. Because the study area was not visited during dusk, it cannot be confirmed whether birds indeed use the light for foraging.

But the four blue tits that were followed during egg laying show small differences in activity pattern, although there seems to be no reason to think that this is related to the distance from the gas station. Unfortunately no activity pattern of a bird in a nest box directly bordering to the gas station terrain could be recorded.

In another bird; the blacktailed godwit (Limosa l. limosa) it has been shown that light affects the choice of nest site. De Molenaar et al. (2000) showed that the density of nests in the illuminated area was lower than the control area. Also birds nesting earlier in the year, chose sites farther away from the lighting, while those nesting later filled in sites closer to the lights. This is contrary with the pattern in laying dates of great tits at the Buunderkamp (see Figure 2), but this is probably because in great tits other factors such as territory quality are more important in the choice of nest site than light. The question is whether this would still be the case in a homogeneous forest.

Effect of temperature (3)
Temperature is an important cue for great tits, because it is the underlying factor influencing other potential cues, indicated by the strong correlation between temperature and budburst, as well as emergence of caterpillars and the start of egg laying (Buse et al., 1999; Nilsson & Källander, 2006). Therefore the extremely warm spring of 2007 (source: website KNMI, 2007) with an average of 11.7°C may have resulted in little or no contrast in all temperature dependent processes that were measured. Rates of chemical reactions are temperature dependent and generally increase with increasing temperature. High temperatures may therefore cause a higher development speed in plants.

But the temperature did spatially vary at the Buunderkamp in the period that the measurements were done. Vegetation characteristics and thus the openness of the terrain are the most likely explanation for the observed differences. The highway did not show to positively affect the temperature in the part of the forest that is close to it.

A direct effect of temperature on laying date is unlikely since Nager & Vannoordwijk (1992) showed that heating or cooling nest boxes in the pre-laying and laying phase and did not affect laying date in great tits.
However, the relation in Figure 16 shows an interesting pattern. To see indirect effects of temperature in one of the periods on laying date, one could multiply the maximum temperature difference with the x-variable of the equation. For 5-18 April a difference of 3°C then indicates advancement in laying date of 6 days. The effect of a temperature difference in the period 18-30 April at the other hand seems to have hardly any effect on annual average laying date.

The contrast between the effects of temperature in early and late spring is corresponding with the study of Visser et al. (2006). But this long-term relation between temperature and laying date should be applied with care on temperature differences within one year in one study area. Besides it is hard to say whether the observed spatial differences are reflecting what the birds and their environment are exposed to. Tree crowns and caterpillar development at the Buunderkamp may be exposed to temperature differences that are smaller than what is measured at 1.5 m height. Therefore the temperature differences that were recorded at the Buunderkamp do probably not match the pattern in laying dates as shown in Figure 2.

![Figure 16. Average annual laying date of great tits at the Buunderkamp as a function of the average temperature in the April period for the years 1983-2006. Regression equation for 5-18 April: y = -2.0387x + 40.512; 18-30 April: y = 0.005x + 24.233.](image)

**Effect of food availability in the (pre-)laying phase (4,5)**

Food availability in the pre-laying and the laying phase is mainly determining when the birds can start with egg laying, because this is energetically costly (Nager & Vannoordwijk, 1992). The provision of supplementary food in the pre-laying phase did not significantly influence laying date in the fed group compared to the control group. Based on the idea that supplementary food may neutralize the inhibiting effect of lack of food, this is contrary to what is expected. Moreover, previous studies did show that supplementary feeding advances laying date (Nilsson & Källander, 2006 and references therein). However, the aforementioned study also indicated that it only may have an effect when food is indeed a constraint, such as in cold springs or habitats of low quality. It is quite likely that the supplementary feeding was not of much meaning because the warm spring may have already provided in enough food for the birds. This is also in correspondence with the observation that not all birds that got a feeding treatment were eating all the mealworms every day.
Birch density in a stand was not different between laying date class. This is also contrary to the expectations, because birch (and larch) are known to provide food for great tits in the pre-laying phase (Visser *et al.*, 2006) and birds breeding close to high birch density may be less constrained in egg formation. Here again the effect of the warm spring may have caused that food was not a constraint, so that birds breeding close to high birch densities were not experiencing an advantage. However, the used method may also be the reason for this result, because it is a relatively coarse approach. Although great tits do not forage in a clear circular radius around their nest box, investigating vegetation in a radius around the nest box may be a better approximation of habitat quality than pooling nest boxes of the same laying date and comparing this with underlying vegetation characteristics.

**Food availability during the chick rearing phase (6,7)**

Food availability during the chick rearing phase is considerably affecting the survival of chicks (Naef-Daenzer & Keller, 1999; Visser *et al.*, 2006). Since budburst and caterpillar biomass are both cues for the amount of food that is available during chick rearing, and because great tits are restricted to an area close to their nest box, they are expected to adapt their laying date in correspondence with the timing of the food peak in their territory. In timing of budburst, differences were found between red oak and common oak, but also within red oak. It is known that between individual trees of common oak consistent differences occur of several weeks (Nilsson & Källander, 2006; Visser *et al.*, 2006). The observed differences in some of the red oaks in the current study were not bigger than a few days, but significant. This may be caused by genetic difference as well as soil characteristics, therefore differences in the trees should be carefully applied to larger zones in the forest. In caterpillar biomass peak no differences in timing were found. This may be due to the relatively large time-span between the frass collections. In addition the aforementioned high spring temperature could also have caused that there is no variation in timing, because caterpillar development is also temperature dependent (van Asch & Visser, 2007 and references therein). Since there is considerable variation in height of the peak there is also variation in time that food availability is above a critical threshold. (Verboven *et al.*, 2001). This means that peak height is also an indication of the ‘food stock’ of that particular tree.

**General discussion and recommendations**

The current study has investigated many factors that can influence the timing of reproduction in great tits. Since only light from the gas station and vegetation composition can be assumed spatially constant, only these factors could be related to breeding data of previous years. All other factors could have been related to this year breeding data if not at the same time an experiment was performed by another researcher which possibly has disturbed the timing of breeding of the birds. But based on this study it was possible to determine the probability of the hypotheses and suggest new experiments to increase the understanding of the complicated process of timing of breeding in birds.

It would be interesting to test the effect of light on foraging by placing lights in a homogeneous forest and compare this with a similar forest without lights. Great tits can in this way be enabled to use the light for foraging during the egg-laying phase, but it may also have an effect on choice of nest site and predation. This can also be combined with the application of the ‘passing sensors’ in nest boxes at different distances from the light source, to monitor the activity pattern of the birds in relation to the light.
It would also be interesting to apply the supplementary food experiment to nest boxes surrounded by high birch density, and compare them with nest boxes with low birch density. In that way the relative importance of birch tree density in the pre-laying phase can be assessed.

A last suggestion is about relating nest box parameters with environmental factors, especially vegetation. It would be very valuable if standardized ways can be developed to describe the habitat quality or characteristics per nest box in order to do proper and structured spatial analysis. The current method for vegetation is quite coarse and does not have the nest box as focal site. Probably vegetation characteristics in a circle around the nest box provide a good method as already was done for pied flycatchers (Janse - ten Klooster, 2007).
References


