

# **The effects of environmental and individual quality on reproductive performance**

A case study on blue tits

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# **The effects of environmental and individual quality on reproductive performance**

A case study on blue tits

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*To my wife, Aida. Her tender-loving care, patience and dedication have been a constant source of inspiration for me while writing this book*

*and*

*to my lovely son, Radin.*



# Contents

<b>Chapter 1</b>	General introduction	9
<b>Chapter 2</b>	Influence of fine-scale habitat structure on nest-site occupancy, laying date and clutch size in blue tits <i>Cyanistes caeruleus</i>	21
<b>Chapter 3</b>	Tree logging affects reproductive performance in blue tits <i>Cyanistes caeruleus</i> but tree type and tree age matter	49
<b>Chapter 4</b>	No effect of partner age and lifespan on female age-specific reproductive performance in a bird species with bi-parental care	59
<b>Chapter 5</b>	The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird	81
<b>Chapter 6</b>	The effect of male incubation feeding on female nest attendance and reproductive performance in a socially monogamous bird	101
<b>Chapter 7</b>	General discussion	119
	References	131
	Summary	154
	Samenvatting	156
	Acknowledgements	159
	Addresses of author and co-authors	165
	List of publications	167



Photos: Aida Ghahraman Poori



# Chapter 1

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**General introduction**

The investment of animals into energy-demanding activities, such as reproduction, may depend on environmental conditions and also on their individual potential or quality. As animals in a population differ in quality and occupy different environments based on reproductive requirements, the effects of environmental and individual quality on reproductive performance attract a great deal of attention from ecologists and have been extensively studied in animal populations.

For many species, there is a relatively brief period in the year where conditions are favourable for reproductive performance (Lack, 1968). This period of favourable conditions varies from year to year based on environmental conditions, such as ambient temperature and habitat quality. Hence, environmental quality affects reproductive performance in animals through its effects on habitat resources (e.g. food availability). In addition to environmental quality, within-population differences in individual quality lead to differences in reproductive performance (Stearns, 1992). In this thesis, I will focus only on habitat quality and ambient temperature as indices of environmental quality and individual age and/or lifespan as indices of individual quality. I will then explain the effects of these environmental and individual quality parameters on habitat preferences as expressed by nest-site occupancy and features of reproductive performance including laying date, clutch size and incubation patterns (female incubation and male incubation feeding). As environmental requirements (e.g. habitat requirements) for reproductive performance are varied in different animal species, I specifically focus on insectivorous birds in forest habitats as a study system.

## **1- Environmental quality and reproductive performance**

Environmental variables are important factors that exert considerable influence on reproductive performance. The environment comprises many different variables, but in this thesis I will focus only on two highly important indices of environmental quality: habitat quality and ambient temperature.

### **1-1- Habitat quality**

Habitat quality is a major determinant of reproductive performance for most bird species (Newton, 1989; Komdeur, 1992; Laaksonen et al., 2004). Different species and individuals have specific requirements for breeding in different habitats with different qualities and resources (e.g. food frequency; see Avery & Leslie, 1990; Jones, 2001; Mörtberg, 2001).

As a result of natural selection, individuals try to seek the best habitats for reproductive performance based on ideal choice (Fretwell & Lucas, 1970). Sometimes, non-ideal habitat selection occurs and individuals select lower-quality

habitats due to lower experience, greater competition and/or limitation of high-quality habitats (Lima & Zollner, 1996).

According to the theory of habitat selection, individuals of a breeding population which occupy high-quality habitats would achieve higher fitness than individuals occupying in low-quality habitats (Fretwell & Lucas, 1970; Bernstein et al., 1991). There are different indices to estimate habitat quality for birds (e.g. occupants' average survival, breeders density, number of fledglings per hectare, reproductive rates; for details see Chandler & King, 2011; Janiszewski et al., 2013). In all of these indices, food availability (which varies considerably between habitats (Tremblay et al., 2003)) is one of the main factors limiting habitat-related reproductive performance (Newton, 1998). In forest habitats, habitat quality for avian populations can be expressed and measured by vegetation structure and maturity surrounding the nesting sites, which have been correlated with insect abundance as food resources (Tye, 1992; Santos & Tellería, 1995; Bellamy et al., 2003). High-quality habitats with higher food availability have been shown to result in higher reproductive performance (Keller & van Noordwijk, 1994; Naef-Daenzer et al., 2000).

Habitat loss due to anthropogenic activities is increasing for many species in the recent years (Sih et al., 2000). Hence, knowledge of the influence of habitat quality on reproductive performance is important in birds (Lusk et al., 2003, Quevedo et al., 2006).

### **1-2- Ambient temperature**

One of the environmental variables that most clearly affects the variation in timing of reproductive performance is ambient temperature. Ambient temperature influences the forthcoming of favourable conditions (Wingfield et al., 1992), such as the period of maximal food abundance when young should be produced. Furthermore, at low temperature, energetic costs are higher and thus may constrain reproductive performance (Stevenson & Bryant, 2000). For example, individuals should intensify their investment in reproductive performance (e.g. incubation behaviour) in lower ambient temperature to meet their offspring's thermal requirements. Therefore, ambient temperature negatively affects the timing of breeding in insectivorous birds. With higher temperatures, the timing of bud burst of leaves will be started earlier which have an influence on abundance of foods such as insects (Kluyver, 1951; Perrins, 1965; van Balen, 1973; Slagsvold, 1976; Blondel et al., 1991; Belda et al., 1998; McCleery & Perrins, 1998; Sokolov, 2000; Both et al., 2004). Hence, ambient temperatures cause large annual variation in the

onset of reproductive performance and latter outcomes (e.g. clutch size, number of fledgling).

## **2- Individual quality and reproductive performance**

Life-history theory suggests that not all individuals in a population are of equal quality (Coulson, 1968). Reproductive performance is costly and individuals are limited in the degree to which they can invest time and resources to producing and raising their offspring (current investment) and also in their own future condition, survival, and further reproductive output (future investments). Hence, individual quality can have an influence on trade-off in individuals between current and future investments and ability to survive and reproduce (Darwin, 1859; Williams, 1966; Stearns, 1992).

Conceiving a universal method for measuring and defining individual quality is problematic, however, because individual quality can be measured by both phenotypic and genotypic traits. Since most variation between individuals is related to phenotypic characteristics (Schluter & Gustafsson, 1993; Svensson & Nilsson, 1995), phenotypic traits such as age, morphometric size, and body condition of individuals are often used as indices of individual quality (Kempnaers et al., 1992; Doutrelant et al., 2000; Kipper et al., 2006; Holt et al., 2013). The age of an individual is the most important predictor of phenotypic quality which usually correlates with individual quality (Kempnaers et al., 1992; Forslund & Pärt, 1995; Doutrelant et al., 2000, Kipper et al., 2006; Sergio et al., 2009). Hence, hereafter in the thesis I will focus on and describe age as a measure for individual quality in relation to reproductive performance.

### **2-1- Age of an individual**

Age often explains a large proportion of individual variation in reproductive performance (Clutton-Brock, 1988; Newton, 1989). Reproductive performance in birds generally improves and then declines with age (Clutton-Brock, 1988; Forslund & Pärt, 1995; Sanz & Moreno, 2000; Green, 2001; Pyle et al., 2001; Laaksonen et al., 2002). There are different hypotheses which explain the causes of age-specific reproduction: (1) The ‘selection’ or “individual heterogeneity” hypothesis proposes that age-related increases in reproductive performance are a consequence of the selective disappearance of individuals of lower quality or poor breeding ability. If high-quality individuals have survived longer, the disappearance of low-quality individuals changes age-related reproductive performance (Curio, 1983; Saether, 1990; Forslund & Pärt, 1995; Laaksonen et al., 2002), because low-quality individuals usually start their reproductive

performance later (Forslund & Pärt, 1995). (2) The ‘constraint’ hypothesis suggests that experienced individuals (e.g. with higher efficiency in foraging and breeding skills) should have a better reproductive performance than inexperienced individuals (Forslund & Pärt, 1995). (3) The ‘restraint’ hypothesis (Williams, 1966; Pianka, 1976) predicts that reproductive effort is dependent on an individual’s residual reproductive lifespan. It means that younger individuals should refrain or reduce their reproductive attempt, to improve their survival and be able to reproduce in the future, whereas older individuals should invest more in current reproduction due to terminal investment as a result of their diminished residual reproductive lifespan. (4) The ‘Senescence’ hypothesis suggests a within-individual decline in somatic or physiological function in reproductive performance with age (Williams, 1957; Hamilton, 1966), meaning that reproductive performance may decline in old individuals as a result of senescence.

Often for ageing studies, within- and between-individual changes in quality influence the relationship between age and reproductive performance. Within-individual studies on age-specific reproductive performance have higher reliability to biologists than population-level patterns, because population-level patterns do not consider within-individual processes such as improvement of reproduction with age or a reduction of reproduction as a consequence of senescence (e.g. Vaupel & Yashin, 1985; Forslund & Pärt, 1995; Cam et al., 2002; Van de Pol & Verhulst, 2006; Bouwhuis et al., 2009). Hence, within-individual studies in age-specific reproductive performance and survival are highly important. However, conducting within-individual studies on age-specific reproductive performance is difficult because it requires long-term monitoring of marked individuals from birth until death (Van de Pol & Verhulst, 2006; Bouwhuis et al., 2009).

## **2-2- Partner age**

Sexual selection theory predicts that investment in reproduction in most taxa depends on the partner’s characteristics (attractiveness or body quality; Trivers, 1972). For example, females mated with more attractive males (which likely transfer better genes to their offspring) display higher reproductive performance (Brooks & Kemp, 2001). Hence, males and females can interact in several ways throughout the reproductive process (Auld & Charmantier, 2011) and reproductive ageing trajectories of either partner may be influenced by the other. For example, females that invest more in female-specific traits such as lay date or clutch size may show faster senescence, dependent on partner quality (Bonduriansky et al., 2008; Auld & Charmantier, 2011; Auld et al., 2013).

In species with bi-parental care during some stages of reproductive cycle, such as chick rearing, conflicts between the sexes over parental investment can occur (Trivers, 1972). For example, the reduction of feeding effort by one partner should, in most cases, result in an increased effort by the other partner (Winkler, 1987). Each care-giver profits from more investment given by the other partner, which leads to a reduction in the amount of care given by the first partner (Parker, 1985). The importance of inter-sexual conflict over care has been recognized in recent years (e.g. Hurst et al., 1996; Pomiankowski, 1999; Royle et al., 2002) but still requires further study. For example, we do not know how individuals adjust their reproductive investment based on patterns of their own and their partner's age and/or quality. Hence, to gain a better understanding of ageing patterns in reproductive performance, the effect of an individual's age and quality in interaction with age and quality of the partner is likely to reveal further insights into inter-sexual conflict in reproductive investments.

### **3- Effects of environmental and individual quality on site occupancy and parameters of reproductive performance**

I will explain effects of environmental and individual quality on nest-site occupancy and features of reproductive performance as a case study including laying date, clutch size and incubation patterns (female incubation and male incubation feeding).

#### **3-1- Site occupancy**

The quality of the occupied habitats substantially influences fitness components. Nest-sites in poor quality habitats usually are occupied later the season compared to nest-sites in high quality habitats (Currie et al., 2000; Forstmeier, 2002; Sergio & Newton, 2003; Arriero et al., 2006). Hence, individuals should exhibit proportionally higher preference of high-quality habitats in comparison with low-quality habitats. Therefore, habitat occupancy would be expected to reflect a reliable measure of habitat quality or preference (Sergio & Newton, 2003; Janiszewski et al., 2013). Based on habitat selection theory, the nest sites with higher occupancy rate or preference should be associated with greater reproductive performance (Luck, 2002).

In addition to habitat quality, individual age or quality can explain some variation in site occupancy. Sometimes, age effect may be masked by environmental quality (Carrete et al., 2006). For example, in many populations, older or high-quality individuals may occupy the best habitats for breeding (e.g. Ulfstrand et al., 1981; Lemel, 1989; Sutherland, 1996) and younger or lower-

quality individuals probably will be forced to occupy lower quality sites (Fretwell, 1972; Rodenhouse et al., 1997). However, when we compare the performance abilities between individuals in habitats with similar quality, individual age differences in occupied habitat might be a major cause of the observed age-specific reproductive performance in the population (Pärt, 2001).

### **3-2- Laying date and clutch size**

In birds, laying date and clutch size are important predictors of reproductive performance and are closely related to fitness (Svensson, 1997, Tinbergen & Sanz, 2004, Visser et al., 2006, Garant et al., 2007). These traits can be influenced by environmental and individual quality, including habitat food availability and individual age, as well as and quality of the partner (Mousseau & Fox, 1998; Price, 1998; Cunningham & Russell, 2000). The proximate links between laying date, clutch size and habitat quality could be explained by temporal and spatial variation in food resource abundance (Maícas et al., 2012). In high-quality habitats with greater food availability, laying will be started earlier with larger clutch size than in low-quality habitats (Perrins, 1970; Zandt, 1994; Svensson & Nilsson, 1995; Nour et al., 1998; Blondel et al., 1999; Atiénzar et al., 2009, 2010; Redhead et al., 2013). Furthermore, laying date and clutch size are also typically considered female specific traits. Older females that begin breeding sooner may produce larger clutches (Sæther, 1990; Christians, 2002). As non-significant heritability in males for these traits is given, it is therefore assumed that males do not influence these traits (Van Der Jeugd & McCleery, 2002; Sheldon et al., 2003; Gienapp et al., 2006; Caro et al., 2009). However, the quality of male may have an indirect effect on female reproductive performance (e.g. Auld & Charmantier, 2011; Auld et al., 2013). For example, in species with bi-parental care, reproductive performance in females may improve with earlier laying and larger clutches when they are mated to older or high quality males (Horvathova et al., 2012).

### **3-3- Female incubation behaviour and male incubation feeding**

Incubation behaviour entails significant energetic costs that can vary depending on environment, individual characteristics and species (Reid et al., 2002; Tinbergen & Williams, 2002). Maintenance of proper temperatures during embryonic development is costly for the incubating parent, who is required to trade-off between self-maintenance to forage and meet their own energetic requirements and the thermal needs of the eggs and embryonic development (Webb, 1987; Williams, 1996; Thomson et al., 1998; Visser & Lessells, 2001).

In many species, but particularly those with female-only incubation, males sometimes feed the incubating female, which enables the female to increase nest attentiveness and in turn reproductive success (Lifjeld & Slagsvold, 1986; Nilsson & Smith, 1988; Martin & Ghalambor, 1999; Hatchwell et al., 1999; Tewksbury et al., 2002; Olson et al., 2006). The popular hypothesis for this male incubation feeding behaviour is the ‘female nutrition’ hypothesis, which states that male incubation feeding enables the female to increase the amount of time she can spend incubating (von Haartman, 1958; Royama, 1966). Variation in incubation behaviour and incubation feeding may be affected by environmental and individual characteristics. The most important factors that play fundamental roles on incubation patterns are environmental factors such as ambient temperature and food availability, related to habitat quality. These can have an influence on female incubation behaviour (Perrins, 1991; Conway & Martin 2000; Deeming, 2002; Weathers et al., 2002; Cresswell et al., 2003; Londono et al., 2008; Wang & Beissinger, 2009; Arnold, 2011) and male incubation feeding (Smith et al., 1989; Zanette et al., 2000; Pearse et al., 2004). In lower ambient temperatures, female nest attentiveness may increase to keep eggs within proper temperature ranges for successful embryo development (Webb, 1987; Sanz, 1997; Matysioková & Remeš, 2010). Furthermore, with decreasing ambient temperature, the intensity of male incubation feeding may decrease due to the decline in food availability as a result of a delay in vegetation bud burst (Zanette et al., 2000). The energetic cost of incubation probably will be lower in high-quality habitats with more food availability (Tinbergen & Dietz, 1994; Thomas et al., 2001).

In addition to environmental quality, individual quality such as age of an individual and experience can influence incubation parameters such as the onset of incubation (Bortolotti & Wiebe, 1993; Soler et al., 2001; Hanssen et al., 2002; Badyaev et al., 2003; Ardia et al., 2006; Ardia & Clotfelter, 2007; Kim et al., 2010) and male incubation feeding (Lifjeld et al., 1987; Siefferman & Hill, 2005). Older females may have higher foraging efficiency, allowing them to find food faster and return to the nest sooner. Furthermore, (due to similar reasons) older males may intensify the frequency of feeding the female during incubation (Lifjeld et al., 1987; Siefferman & Hill, 2005).

#### **4- Aim of the thesis**

In this thesis I investigated the effect of parameters associated with habitat quality and ambient temperature as indices of environmental quality and individual age and/or lifespan as indices of individual quality on predictors of reproductive



performance. In the thesis outline I will explain the specific aims for each chapter in more detail.

#### 4-1- Study system

Our study species, the blue tit *Cyanistes caeruleus*, is a small, socially monogamous passerine bird with bi-parental care. Blue tits are one of the species that produce the largest families of nidicolous birds in the world (Perrins & McCleery, 1989) and are widespread and common resident breeders throughout temperate deciduous or mixed woodlands. They are often considered oak forest specialists (e.g. Perrins, 1979; Blondel et al., 2006; Lambrechts et al., 2004). Blue tits usually adapt easily to nest-boxes and human-modified habitats (Hinsley et al., 2009) and can serve as a good model species for association between environmental and individual characteristics and reproductive performance.

Our study was carried out in the “De Vosbergen”, an estate in the north of the Netherlands near the city of Groningen (53°08’N, 06°35’E). The study area covers ca. 50 ha consisting of young and old mixed deciduous and coniferous forest interspersed by open grassland. The most dominant tree species in the area are deciduous trees: particularly English oak *Quercus robur* and European beech *Fagus sylvatica*. The common coniferous trees are douglas fir *Pseudotsuga menziesii*, Scots pine *Pinus sylvestris*, and Norway spruce *Picea abies*. In 2001 a nest box population of blue tits was established (Korsten, 2006) with 188 wooden nest-boxes (inner dimensions: ca. 9.0 × 12.5 × 25 cm, with a 2.6 cm entrance hole) designed especially for blue tits. Nest-boxes were dispersed at relatively regular intervals over the whole study area. In 2013, 21 more similar nest-boxes were added in the study area in new plot of the deciduous forest and in total 209 nest-boxes were available for blue tits from that year onwards. Blue tits breeding in nest-boxes were monitored following the protocols of the long-term programme established for the study population in 2001 (for details see Korsten, 2006). Hence, all the adult birds that were breeding in the population and their nestlings have been ringed. This makes a unique data set on blue tits in the “De Vosbergen” and also makes an ideal study population for ecological and behavioural research.

#### 4-2- Thesis outline

In **chapter 2** we used 13 years of breeding data of a population of blue tits to investigate the relationship between habitat quality and reproductive performance in an observational study. Most studies to date have investigated the relationship between vegetation and reproductive performance on a coarser scale between deciduous and coniferous forests and based on short-term data. We investigated

fine-scale vegetation characteristics, particularly the local densities and maturity of different tree species, and nest-site occupancy, laying date and clutch size. We also identified the main indices or predictors of habitat quality.

As this work was based on observational study, we also investigated patterns of habitat-related reproductive performance in **chapter 3**, with an experimental approach based on anthropogenic activity such as tree logging event in 2013. We investigated the manipulated effect of habitat on laying date and clutch size. We also discussed how habitat loss and fragmentation influence reproductive performance.

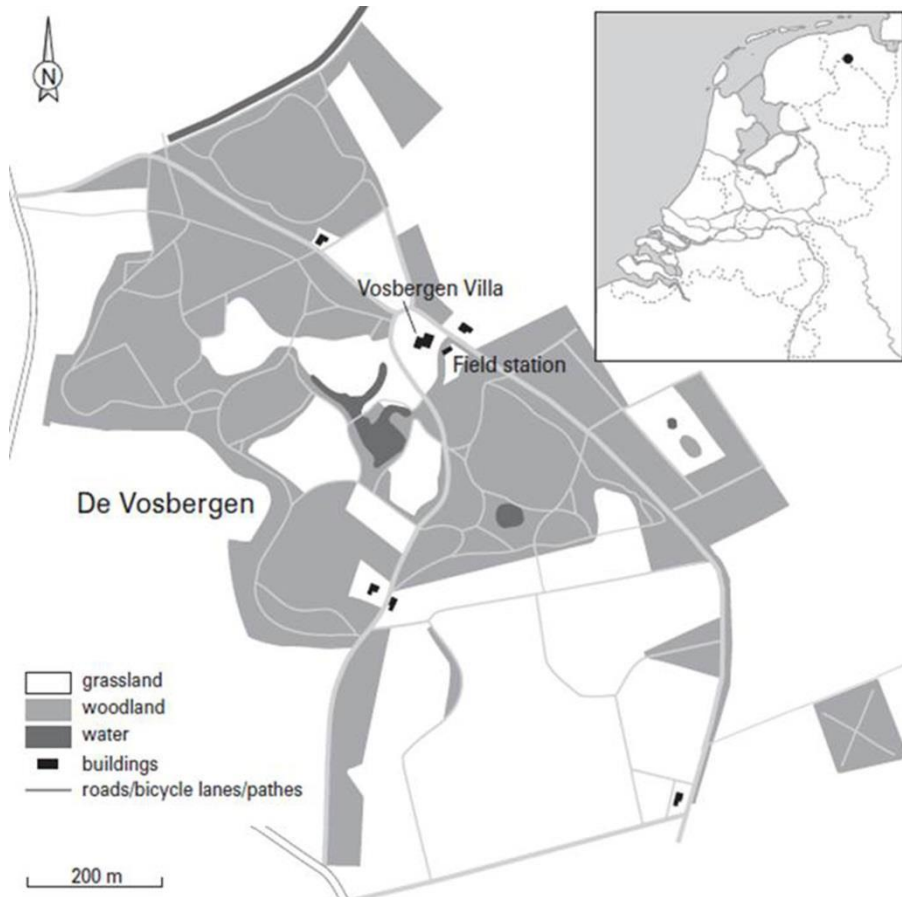
In **chapter 4** we investigated the relationship between ageing patterns as a parameters of individual quality on reproductive performance. We used 12 years of longitudinal breeding data on an individually marked blue tit population. We aimed to investigate whether female specific traits of reproductive performance (e.g. laying date and clutch size) are affected by individual ageing patterns and also the age and reproductive lifespan of the male partner, because little is known how age-specific reproductive performance is related to the age and reproductive lifespan of the partner.

In **chapter 5** we investigated the effects of environmental quality (i.e. ambient temperature and habitat quality) and age of an individual on incubation behaviour and incubation feeding, in blue tits during the breeding season in 2014. Incubation behaviour and incubation feeding are aspects of avian life history and include energetic costs that can vary depending on environmental characteristics and individual abilities or behaviours. We explained how incubation patterns vary in individuals and also in different environmental conditions.

In chapter 5, we uncovered some patterns of habitat and age specific incubation feeding in males, so in **chapter 6** we investigated the effect of male incubation feeding on female nest attentiveness and reproductive performance in blue tits. To date, there is little evidence for an effect of male incubation feeding on female nest attentiveness and reproductive outcomes in blue tits. We investigated how environmental factors (i.e. ambient temperature) and life-history traits (i.e. the date of incubation onset and clutch size) relate to male incubation feeding, and whether male incubation feeding leads to higher female nest attentiveness. Finally, we investigated whether female nest attentiveness can have an influence on parameters of reproductive performance such as duration of the incubation period, hatching success and nestling body mass.

In **chapter 7** I provided a synthesis in which the most important results of the thesis are summarized and placed in a broader context of other research findings to explain how environmental and individual characteristics influence reproductive

performance in bird populations. I also suggested some potentials and limitations for more studies on the population system in the future.



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**Figure 1** Study area ‘De Vosbergen’ (Korsten, 2006).



Photos: Seyed Mehdi Amininasab

# Chapter 2

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**Influence of fine-scale habitat  
structure on nest-site occupancy,  
laying date and clutch size in blue tits  
*Cyanistes caeruleus***

Seyed Mehdi Amininasab, Oscar Vedder, Elske Schut, Berber de Jong, Michael J. L. Magrath, Peter Korsten & Jan Komdeur

### **Abstract**

Most birds have specific habitat requirements for breeding. The vegetation structure surrounding nest-sites is an important component of habitat quality, and can have large effects on avian breeding performance. We studied 13 years of blue tit *Cyanistes caeruleus* population data to determine whether characteristics of vegetation structure predict site occupancy, laying date and number of eggs laid. Measurements of vegetation structure included the density of English oak *Quercus robur*, European beech *Fagus sylvatica*, and other deciduous, coniferous and non-coniferous evergreen trees, within a 20-m radius of nest-boxes used for breeding. Trees were further sub-divided into specific classes of trunk circumferences to determine the densities for different maturity levels. Based on Principal Component Analysis (PCA), we reduced the total number of 17 measured vegetation variables to 7 main categories, which we used for further analyses. We found that the occupancy rate of sites and the number of eggs laid correlated positively with the proportion of deciduous trees and negatively with the density of coniferous trees. Laying of the first egg was advanced with a greater proportion of deciduous trees. Among deciduous trees, the English oak appeared to be most important, as a higher density of more mature English oak trees was associated with more frequent nest-box occupancy, a larger number of eggs laid, and an earlier laying start. Furthermore, laying started earlier and more eggs were laid in nest-boxes with higher occupancy rates. Together, these findings highlight the role of deciduous trees, particularly more mature English oak, as important predictors of high-quality preferred habitat. These results aid in defining habitat quality and will facilitate future studies on the importance of environmental quality for breeding performance.

## 1- Introduction

In many birds, especially territorial species, one of the main determinants of fitness is the quality of the breeding habitat (e.g. Davenport et al., 2000; Langen & Vehrencamp, 1998; Pärt, 2001; Sergio et al., 2009). In the last few decades, measuring habitat quality–fitness relationships has posed a challenge of major importance for ecologists because of the need to consider biodiversity values for conservation of birds species, and also for landscape managers because of increasing anthropogenic influences and habitat loss (Sih et al., 2000). Ecologists have used different indices to estimate habitat quality for birds (see e.g. Chandler & King, 2011; Janiszewski et al., 2013), and one of these indices is the vegetation structure around nest-sites (e.g. Atiénzar et al., 2009, 2010; Bell et al., 2014; Wilkin et al., 2007, 2009). Both experimental and observational studies have demonstrated that the vegetation structure around nest-sites has an influence on breeding performance (e.g. Pärt, 2001; Arriero et al., 2006). Especially in insectivorous species of birds, the vegetation is one of the main environmental factors affecting food availability in forest habitats (van Balen, 1973; Blondel et al., 1991). Higher food availability during brood-rearing increases offspring growth and survival (Kroll & Haufler, 2007; Mägi et al., 2009). Thorough knowledge about these relationships can have implications for effective conservation of biodiversity, harvest management in forestry and also reforestation plans (Arriero et al., 2006).

In this study, we used 13 years of breeding data of a population of blue tits *Cyanistes caeruleus*, to evaluate the effect of vegetation structure on nest-site occupancy and two key parameters of breeding performance closely linked to fitness: laying date and clutch size. Blue tits are small, territorial passerines, typically breeding in pairs. While they breed in heterogeneous environments and in a variety of forest types, which differ in quality (e.g. Lambrechts et al., 2004), they are often considered Oak forest specialists (e.g. Perrins, 1979; Lambrechts et al., 2004; Blondel et al., 2006). Parents feed their chicks with invertebrates, particularly caterpillars, which are the main food item available during the brood-rearing phase (Perrins, 1991; Cholewa & Wesolowski, 2011). Availability of caterpillars and other arthropods depends on the timing of spring growth of leaves, which differs between tree species (Blondel et al., 1993). Tits (*Paridae* family) are sensitive to small differences in vegetation structure (Wilkin et al., 2007; Atiénzar et al., 2010) and also suffer reduced breeding performance in human-modified habitats (Hinsley et al., 2009). Hence, they can serve as a good model species to evaluate habitat quality effects on breeding performance (Blondel et al., 1993), and to guide landscape management.

Due to experiments performed in this population during the incubation and nestling stages, we were not able to incorporate other parameters of breeding performance (e.g. number of fledglings). Laying date and clutch size are often correlated with other parameters of breeding performance, such as number of fledged offspring, and subsequent offspring survival and recruitment (e.g. Perrins, 1965; Norris, 1993; Verboven & Visser, 1998; Both et al., 2000). Observational and experimental studies have also indicated that laying date and clutch size are influenced by food availability (Blondel et al., 1991; Nager et al., 1997; Bourgault et al., 2009; Smith et al., 2013). Site occupancy is one of the most important basic predictors that over the long-term reflects habitat quality (Sergio & Newton, 2003; Janiszewski et al., 2013).

To investigate the relationship between the habitat and these parameters of breeding performance (laying date and clutch size) as well as nest-site occupancy, we studied the characteristics of the trees, including their maturity, in the near vicinity of nest-boxes. Although previous studies have investigated the relationship between vegetation and various measures of breeding performance in blue tits and great tits *Parus major*, most of them have studied this on a coarser scale, for example by comparing parameters of breeding performance between deciduous and coniferous forests (e.g. Blondel et al., 1993; Mägi et al., 2009). Some more detailed and finer-scale studies have also investigated the relationship between parameters of breeding performance and the local densities of a single tree species, like food-rich oak trees (Wilkin et al., 2009; Bell et al., 2014). However, comprehensive fine-scale studies that simultaneously investigate several vegetation characteristics, including both the local densities and maturity levels of trees of different species surrounding the nest-sites, and relate these detailed vegetation characteristics to parameters of breeding performance are scarce (for exceptions see Arriero et al., 2006; Hinsley et al., 2009; Atiénzar et al., 2010). Specifically, the objectives of this paper are to examine the relationship between fine-scale vegetation characteristics, particularly the local densities and maturity of different tree species, and 1) nest-site occupancy, 2) laying date and 3) the number of eggs laid. Based on these analyses, we aim to identify the main vegetation indices as predictors of habitat quality.

## **2- Material and methods**

### **2-1- Study area and study population**

The study was conducted over 13 consecutive breeding seasons (2001-2013) on a nest-box breeding blue tit population at 'De Vosbergen' estate near Groningen in the North of The Netherlands (53°N, 06°E). The 54 ha study area consists of



mixed deciduous and coniferous forest interspersed with areas of open grassland. The study area contains about 188 wooden nest-boxes (inner dimensions: ca.  $9.0 \times 12.5 \times 25$  cm, with a 2.6 cm entrance hole) designed especially for blue tits. Nest-boxes have been installed in excess in the study area since 2001 and are dispersed at relatively regular intervals over the whole study area.

## 2-2- Breeding performance

Every breeding season (April–June), for each nest-box, breeding activities from the nest-building until the fledging phase were monitored. During the nest-building phase from the beginning of April all nest-boxes were checked regularly. For each blue tit breeding pair, we recorded the date of laying the first egg (hereafter referred to as ‘laying date’) and the number of eggs laid.

Various studies and experiments were carried out on this population during the years of monitoring, which may have influenced different parameters of breeding performance (see Korsten et al., 2006; Kingma et al., 2009; Vedder et al., 2010, 2012; de Jong, 2013; Schut et al., 2014). Some experiments were carried out during or before the onset of laying and some of them were carried out after the onset of incubation. Because of this, we did not use breeding performance parameters determined after clutch completion, and only selected data which were not influenced by experiments (see Supplementary material, Table S1). The selected parameters were: nest-box occupancy, laying date, and number of eggs laid. A nest-box was considered occupied in a particular year when it contained a nest with at least one egg. The occupancy rate was calculated for each nest-box on the basis of its availability (on rare occasions nest-boxes were occupied by other species such as great tits, and coal tits *Parus ater*, or nest-boxes were absent or damaged and could not be used for breeding that year) and number of years occupied during the 13-year period. Laying date was defined as the date of laying the first egg (1 April = day 1). Number of eggs was the total of all eggs laid. As a result of collection of eggs in some years without replacement with dummy eggs (see Supplementary material, Table S1), it was not possible to determine the originally intended clutch size, as females may, or may not, have compensated by laying additional eggs. For these years, the eggs were collected for most of the clutches in the population leaving the within-year comparisons meaningful. In recognition of this potential influence we use the term number of eggs laid instead of clutch size. We excluded second clutches, which occurred only rarely, as well as replacement clutches after failed first breeding attempts, from our analyses.

Experiments had an influence on the observed laying date and the number of eggs laid in 2006-2007 (unpublished results) and also on the number of eggs laid

in 2009 (Vedder et al., 2012; for details see Supplementary material, Table S1). As a result, for those years and breeding performance parameters, we only included control-treated nest-boxes in our analyses.

### **2-3- Measurements of habitat characteristics**

The vegetation structure of the habitat was measured by sampling the trees surrounding the nest-boxes. Tree sampling took place during two periods; the vegetation around 100 of the nest-boxes was sampled between 2002 and 2004, and around the remaining 88 nest-boxes in 2013. Because of the large time gap between the two sampling periods, we repeated the tree sampling for 20 randomly chosen nest-boxes in 2013 that had also been sampled between 2002 and 2004 and compared the vegetation values between the two sampling periods. All vegetation variables analysed were significantly correlated between sampling periods ( $0.51 \leq r \leq 0.92$ ,  $P \leq 0.02$ ; Pearson's correlations), which indicates relatively minor changes in vegetation structure between the two sampling periods. As a result, vegetation measurements of both periods were used in the analyses. We used the measurements taken during 2002-2004 for 80 nest-boxes, and measurements taken in 2013 for 108 nest-boxes.

In evaluating the radius around each nest-box in which vegetation structure may be relevant, we found different distance estimates in the literature on blue tits and great tits. For example, Stauss et al. (2005) reported average flight distances of blue tits between nest-boxes and foraging patches of about 22 m in preferred deciduous habitat. In other literature, the distance to foraging patches for great tits is given as limited to 45 m in 90% of the foraging trips (Naef-Daenzer & Keller, 1999). Another study in blue tits found average foraging distances during brood rearing of 25 m and 53 m in two different habitats with rich and poor food abundance, respectively. Remarkably, in one of the two areas, which had evergreen vegetation and hence poor caterpillar abundance, individual blue tits regularly flew more than 50 m, with even a few recordings of distances of >500 m (Tremblay et al., 2005). In some studies, researchers measured the habitat characteristics within 50 m from the nest-boxes for both great tits (Wilkin et al., 2009) and blue tits (Bell et al., 2014). The foraging distance may also vary during the different stages of the breeding cycle. For example, females may forage at much longer distances from the nest-box during the period of egg formation than during the incubation and the brood rearing stages, because during the latter stages they have to return frequently to the nest to incubate the eggs or feed the nestlings. In spite of this variation in distances, in this study a radius of 20 m was chosen, as a compromise between biological plausibility and practical feasibility given the

workload of counting and measuring trees. Furthermore, we assume that the vegetation structure estimates taken at a small spatial scale (a radius of 20 m) are representative for the vegetation at a somewhat larger scale surrounding the nest-boxes.

Within the 20 m radius, we sampled and identified the species of all living trees with a minimal circumference of 30 cm. Trees with thinner trunks were excluded as they were not considered to harbour a substantial amount of food for breeding blue tits. The trees' circumference (cm) was measured about 130 cm from the ground, using a measuring tape.

### 2-3-1- Classification of trees

We identified and measured 8442 trees surrounding 188 nest-boxes (including 80 nest-boxes sampled between 2002 and 2004 and 108 nest-boxes sampled in 2013; Table 1). The most dominant species surrounding the nest-boxes were English oak *Quercus robur* ( $n = 2168$ ) and European beech *Fagus sylvatica* ( $n = 2092$ ). Trees were divided into five main categories: 1) English oak, a deciduous species, the most dominant tree species in the area, and an important source of the main prey item, caterpillars, during the breeding season; 2) European beech, a deciduous species, and the second dominant species in the area; 3) Miscellaneous deciduous ( $n = 2129$ ): deciduous species other than English Oak and European Beech; for example European white birch *Betula pubescens* ( $n = 350$ ), Northern red oak *Quercus rubra* ( $n = 230$ ), and sycamore maple *Acer pseudoplatanus* ( $n = 202$ ) were included in this category. Deciduous trees are known as preferred breeding habitat for great tits and blue tits; 4) Coniferous trees ( $n = 1720$ ); for example Douglas fir *Pseudotsuga menziesii* ( $n = 444$ ), Scots pine *Pinus sylvestris* ( $n = 380$ ), and Norway spruce *Picea abies* ( $n = 300$ ); and 5) non-coniferous evergreen ( $n = 333$ ); for example holly *Ilex aquifolium*. Each of the five tree categories were further subdivided based upon trunk circumferences (Table 1), as an index of the maturity of the trees.

### 2-4- Statistical analyses

In the analyses, the vegetation variables were used as independent variables, and occupancy rate and breeding performance parameters (laying date, clutch size) were used as response variables. Similar to the approach by Wilkin et al. (2007), Atienzar et al. (2010), Maícas et al. (2012) and Bell et al. (2014), we used the counts (density) of trees in the different categories surrounding nest-boxes (Table 1) as vegetation variables. (In addition to the density of trees in the different categories, we separately used the proportion of deciduous trees, as broad-scale

index of habitat quality, defined as the number of all deciduous trees divided by the total number of all trees, in the 20-m radius around the nest-box).

Statistical models were implemented in R (version 3.1.0; R Development Core Team, 2014). Based on principal component analysis (PCA) we reduced the total number of vegetation variables (17 vegetation variables, see Table 1) to a smaller number of variables by merging different categories, while minimizing the loss of independent information. We used this reduced set of 7 variables as final vegetation variables in our further analyses.

Two types of models were used to analyse the relationships between vegetation variables and nest-box occupancy and breeding performance parameters. First, we applied generalized linear mixed models (GLMMs) with binomial error distribution and a logit link function using the lme4 package (version 1.1-7; Bates et al., 2014) to test the relationships between nest-box occupancy (response variable) and the vegetation variables (independent variables). Second, to determine whether vegetation variables and occupancy rate were related to laying date and number of eggs laid, we used linear mixed models (LMMs) with normally distributed errors and an identity link function, also using the package lme4. Given that the residuals of the models with the number of eggs laid (response variable) followed a normal distribution, and generalized linear mixed models with Poisson errors and a log link function failed to converge, we used models with normally distributed errors for fitting the number of eggs laid, instead of using Poisson errors, which are often used for count data. In both sets of models, we also included year and nest-box identity as random effects to statistically control for between-year variation and potential non-independence of multiple observations at the same nest-box. Maximal models (i.e. including all vegetation variables) with estimated coefficients (with associated standard errors, and *t* or *Z* and *P* values) are presented. *P* values < 0.05 were considered significant.

**Table 1** Frequency of trees and actual mean ( $\pm$  SD) circumference for the different tree categories.

Tree category	Tree circumference class (cm)	Number of trees	Actual circumference (cm, mean $\pm$ SD)
English oak		2168	122.7 $\pm$ 54.3
	30-50	217	39.4 $\pm$ 6.0
	50-100	477	74.0 $\pm$ 15.4
	100-200	1297	139.1 $\pm$ 25.0
	>200	177	235.9 $\pm$ 32.7
European beech		2092	94.2 $\pm$ 62.6
	30-50	627	38.6 $\pm$ 5.8
	50-100	711	71.2 $\pm$ 14.1
	100-200	607	141.3 $\pm$ 27.3
	>200	147	247.8 $\pm$ 49.5
Miscellaneous deciduous		2129	63.1 $\pm$ 43.0
	30-50	1160	38.1 $\pm$ 5.7
	50-100	687	66.7 $\pm$ 13.4
	100-200	235	142.3 $\pm$ 29.2
	>200	47	231.5 $\pm$ 26.2
Coniferous		1720	106.5 $\pm$ 46.1
	30-50	227	38.8 $\pm$ 5.7
	50-100	548	77.7 $\pm$ 14.6
	100-200	892	134.1 $\pm$ 24.0
	>200	53	228.7 $\pm$ 31.4
Non-coniferous evergreen		333	44.7 $\pm$ 14.7

### 3- Results

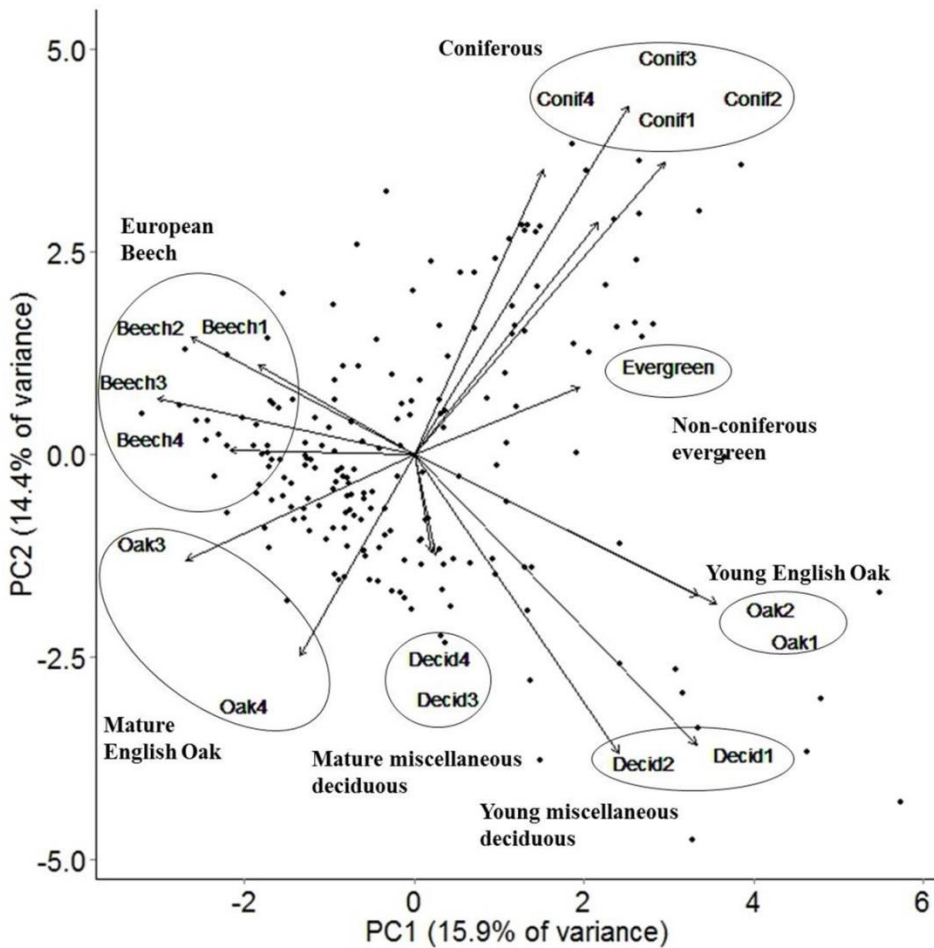
#### 3-1- Laying date and number of eggs laid

There were significant differences between years, both for the laying date (ANOVA,  $n = 1216$ ,  $F_{12,1203} = 97.27$ ,  $P < 0.001$ ), and for the number of eggs laid (ANOVA,  $n = 1144$ ,  $F_{12,1131} = 7.06$ ,  $P < 0.001$ ). During the 13 years of study, mean laying date was earliest in 2012 (around 12th April) and latest in 2013 (around 30th April). The (annual mean) minimum and maximum number of eggs

per clutch were laid in 2011 (10.4 eggs) and 2008 (12.6 eggs), respectively (Supplementary material, Fig. S1).

### **3-2- Reducing the number of vegetation variables based on principal component analysis**

Principal components analysis (PCA) was carried out on seventeen directly measured vegetation variables (Table 1) to find the main components summarizing the vegetation composition. The first ten principal components explained 83.3% of total variance in the measured vegetation variables, with a relatively small percentage of variance explained by the remaining components (Supplementary material, Table S2). According to these results and the relative importance of the different components (Supplementary material, Fig. S2), PC1 and PC2 were considered as the most important axes of vegetation variation, explaining 15.9% and 14.4% of the variance, respectively (30.3% of the total variance across all measured vegetation variables). Plotting the measured vegetation variables for each nest-box along these two axes (Fig. 1), allowed us to reduce the number of vegetation variables from 17 to 7, by merging different vegetation variables according to visual interpretation of Fig. 1. This left us with the following variables: (1) Young English oak trees (30-100 cm); (2) Mature English oak trees (> 100 cm); (3) European beech trees (> 30 cm); (4) Young miscellaneous deciduous trees (30-100 cm); (5) Mature miscellaneous deciduous trees (> 100 cm); (6) Coniferous trees (> 30 cm); and (7) Non-coniferous evergreen trees (> 30 cm). These seven variables were used as final vegetation variables in the models (see Table S3 for the correlations between the 7 vegetation variables and the first and second principle components resulting from the PCA analysis and Table S4 for the correlation matrix for these newly constructed variables).



**Figure 1** Biplot of the seventeen variables of tree density along the first and second principal component vectors. The number of vegetation variables was reduced from 17 to 7 final variables (shown in circles) on the basis of the multidimensional distribution of tree densities for the different categories. Code number represents the range of tree circumferences for each of the measured categories; 1: 30-50 cm, 2: 50-100 cm, 3: 100-200 cm, 4: > 200 cm.

### 3-3- Nest-box occupancy in relation to vegetation characteristics

Blue tits occupied nest-boxes significantly more frequently if deciduous trees made up a greater proportion of all trees surrounding the nest-box (Estimate  $\pm$  SE = 1.958  $\pm$  0.259,  $Z = 7.565$ ,  $P < 0.001$ ,  $n = 2405$ , random effects of nest-box and year: variance = 0.45, 0.35, respectively; Fig. 2a). Blue tits occupied nest-boxes less frequently with greater densities of surrounding coniferous and European

beech trees (Table 2). The density of young miscellaneous deciduous trees had a positive effect on the occupancy rate (Table 2). We found no significant relationships between nest-box occupancy and density for the other tree categories. However, there was a negative correlation between the density of coniferous and the density of mature English oak trees in the habitat surrounding nest-boxes (Supplementary material Table S4). Hence, in habitats with more coniferous trees, there were fewer mature oak trees. We therefore tested an alternative simpler model, which only included the densities of the two classes of English oaks (young and mature) as predictors. This yielded a positive association between nest-box occupancy rate and the density of mature English oaks (Estimate  $\pm$  SE =  $0.042 \pm 0.012$ ,  $Z = 3.578$ ,  $P < 0.001$ ,  $n = 2405$ , random effects of nest-box and year: variance = 0.64, 0.35, respectively), while there was no significant association between occupancy rate and the density of young English oaks (Estimate  $\pm$  SE =  $-0.007 \pm 0.011$ ,  $Z = -0.653$ ,  $P = 0.51$ ).

### **3-4- Laying date and number of eggs laid in relation to vegetation characteristics**

The laying date was advanced with a greater proportion of deciduous trees among all surrounding trees (Estimate  $\pm$  SE =  $-3.470 \pm 0.736$ ,  $t = -4.715$ ,  $P < 0.001$ ,  $n = 1216$ , random effects of nest-box and year: variance = 2.06, 27.87, respectively; Fig. 2b). Laying started earlier when the densities of mature English oak trees and young miscellaneous deciduous trees were higher (Table 3). Furthermore, laying started later when the density of coniferous trees was higher (Table 3).

More eggs were laid when the proportion of deciduous trees surrounding the occupied nest-boxes was higher (Estimate  $\pm$  SE =  $1.671 \pm 0.272$ ,  $t = 6.134$ ,  $P < 0.001$ ,  $n = 1144$ , random effects of nest-box and year: variance = 0.19, 0.26, respectively; Fig. 2c). The number of eggs laid was positively correlated with the density of mature English oak trees surrounding the nest-boxes (Table 4), and negatively correlated with the density of coniferous trees (Table 4).



**Table 2** Results of generalized linear mixed model (with binomial error distribution) for the relationships between nest-box occupancy and vegetation variables. Estimated coefficients (with associated standard errors, *Z* and *P* values) of significant variables are in bold.

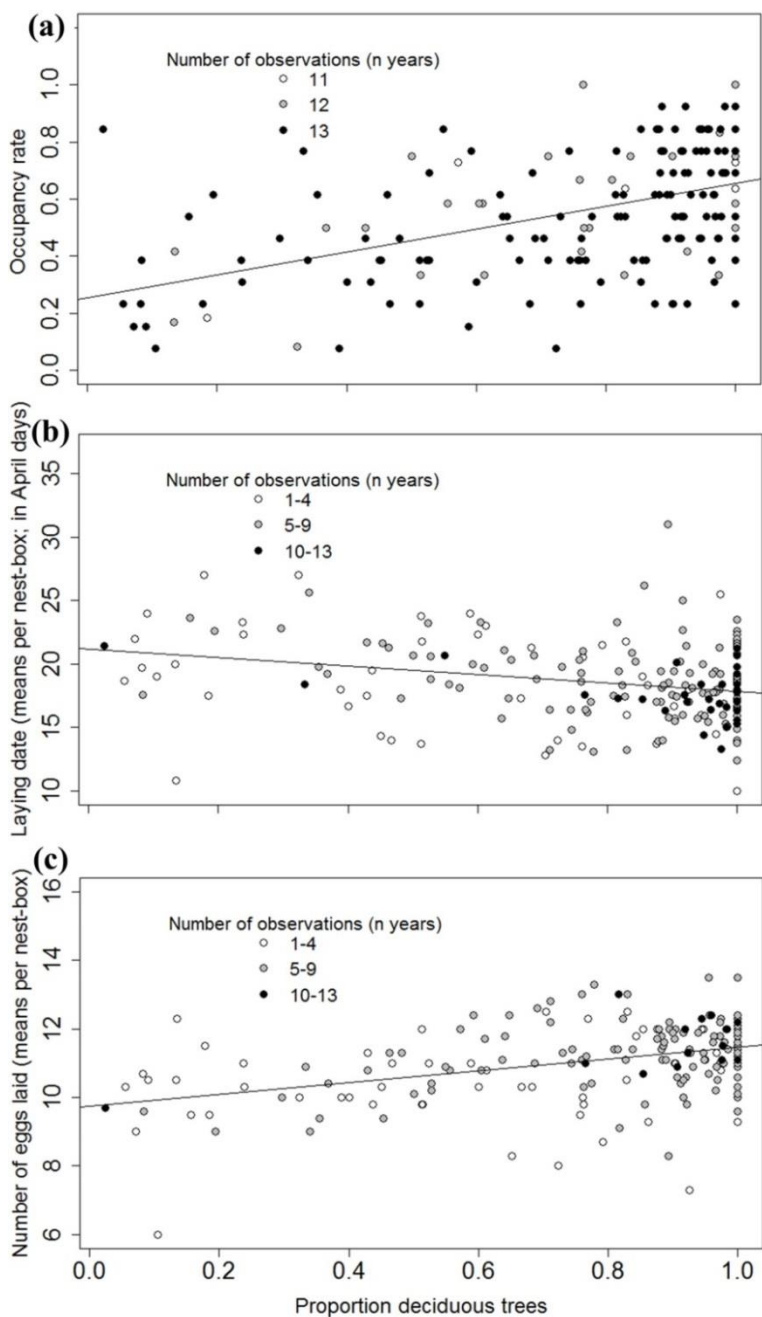
Vegetation variables	Estimate	Nest-box occupancy		
		SE	Z value	P value
Fixed effects				
(Intercept)	0.658	0.270	2.434	0.014
Young English oak	-0.019	0.011	-1.741	0.081
Mature English oak	0.015	0.012	1.256	0.21
European beech	<b>-0.013</b>	<b>0.007</b>	<b>-1.984</b>	<b>0.047</b>
Young miscellaneous deciduous	<b>0.012</b>	<b>0.006</b>	<b>2.010</b>	<b>0.044</b>
Mature miscellaneous deciduous	0.004	0.020	0.182	0.85
Coniferous	<b>-0.034</b>	<b>0.006</b>	<b>-5.419</b>	<b>&lt; 0.001</b>
Non-coniferous evergreen	-0.035	0.018	-1.904	0.056
Random effects		Variance		
Nest-box		0.41		
Year		0.35		
Sample sizes				
Years		13		
Nest-boxes		188		
Number of observations		2405		

**Table 3** Results of linear mixed model for the relationships between laying date and vegetation variables. Estimated coefficients (with associated standard errors, *t* and *P* values) of significant variables are in bold.

Vegetation variables	Estimate	SE	Laying date	
			<i>t</i> value	<i>P</i> value
Fixed effects				
(Intercept)	19.654	1.562	12.580	< 0.001
Young English oak	-0.003	0.029	-0.111	0.91
Mature English oak	<b>-0.120</b>	<b>0.030</b>	<b>-4.147</b>	<b>&lt; 0.001</b>
European beech	0.009	0.018	0.508	0.61
Young miscellaneous deciduous	<b>-0.036</b>	<b>0.014</b>	<b>-2.626</b>	<b>0.009</b>
Mature miscellaneous deciduous	0.061	0.051	1.202	0.23
Coniferous	<b>0.036</b>	<b>0.017</b>	<b>2.073</b>	<b>0.039</b>
Non-coniferous evergreen	0.032	0.050	0.634	0.53
Random effects		Variance		
Nest-box		1.53		
Year		27.82		
Residual		23.18		
Sample sizes				
Years		13		
Nest-boxes		188		
Number of observations		1216		

**Table 4** Results of linear mixed model for the relationships between number of eggs laid and vegetation variables. Estimated coefficients (with associated standard errors, *t* and *P* values) of significant variables are in bold.

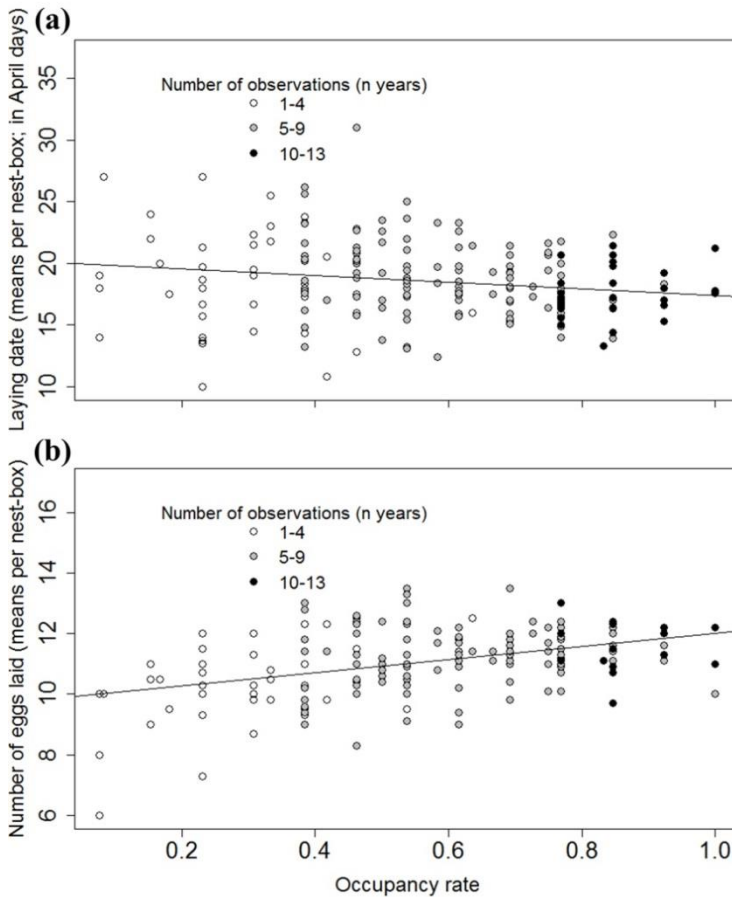
Vegetation variables	Estimate	Number of eggs laid		
		SE	<i>t</i> value	<i>P</i> value
Fixed effects				
(Intercept)	11.189	0.251	44.428	< 0.001
Young English oak	0.011	0.011	1.002	0.32
Mature English oak	<b>0.028</b>	<b>0.011</b>	<b>2.455</b>	<b>0.015</b>
European beech	-0.008	0.007	-1.130	0.26
Young miscellaneous deciduous	0.006	0.005	1.075	0.28
Mature miscellaneous deciduous	-0.003	0.019	-0.161	0.87
Coniferous	<b>-0.029</b>	<b>0.007</b>	<b>-4.303</b>	<b>&lt; 0.001</b>
Non-coniferous evergreen	0.005	0.020	0.269	0.79
Random effects		Variance		
Nest-box		0.19		
Year		0.25		
Residual		3.47		
Sample sizes				
Years		13		
Nest-boxes		188		
Number of observations		1144		



**Figure 2** The relationships between the proportion of deciduous trees and the (a) occupancy rates of nest-boxes (b) mean laying date; and (c) mean number of eggs laid during the period (2001-2013). The trend lines are least-squares regression lines added for visual purpose only, and do not represent the model estimates that are presented in the text.

### 3-5- Laying date and number of eggs laid in relation to occupancy rate of a nest-box

We found that laying date was negatively associated with occupancy rate (Estimate  $\pm$  SE =  $-3.665 \pm 0.906$ ,  $t = -4.046$ ,  $P < 0.001$ ,  $n = 1216$ , random effects of nest-box and year: variance = 2.20, 28.04, respectively; Fig. 3a). Furthermore, the number of eggs laid was positively associated with occupancy rate (Estimate  $\pm$  SE =  $1.754 \pm 0.343$ ,  $t = 5.109$ ,  $P < 0.001$ ,  $n = 1144$ , random effects of nest-box and year: variance = 0.26, 0.25, respectively; Fig. 3b). Hence, in nest-boxes that were more frequently occupied across years, laying started earlier and more eggs were laid.



**Figure 3** The relationships between the occupancy rates of nest-boxes and their mean values for (a) laying date; (b) number of eggs laid during the study period (2001-2013). The trend lines are least-squares regression lines added for visual purpose only, and do not represent the model predictions that are presented in the text.

## **4- Discussion**

### **4-1- Nest-box occupancy in relation to vegetation characteristics**

By linking nest-box occupancy to vegetation characteristics, we showed that nest-box occupancy can act as a good predictor for the quality of the habitat. The probability of nest-box occupancy was higher when the proportion of deciduous trees and young miscellaneous deciduous trees surrounding the nest-box increased. Conversely, negative correlations between the density of coniferous and European beech trees surrounding the nest-boxes and occupancy rate suggest that these tree species are indicators of poor-quality, non-preferred habitats. However, because there are negative correlations between the densities of different tree categories, we cannot exclude the importance of mature English oaks, which other studies have identified for great tits (Mänd et al., 2005; Wilkin et al., 2009). Indeed, an alternative model that only included young and mature English oaks as predictors, suggests that the density of mature English oaks can also act as a good predictor of preferred high quality habitat in blue tits. Yet, we cannot exclude the possibility that in blue tit and great tit populations are adapted to quite different vegetation types (e.g. see Tremblay et al., 2003; Mägi et al., 2009) and that different tree species may be better predictors of habitat quality for each of the two species. Overall our results are consistent with the findings of Sergio & Newton (2003) and Janiszewski et al. (2013), who suggest that nest-box occupancy rate in the long-term can be a simple and reliable indicator of habitat quality with relatively high potential for application to territorial species.

### **4-2- Laying date and number of eggs laid in relation to vegetation characteristics**

We found that laying date and number of eggs laid were associated with the local vegetation characteristics, and thus the distribution of a particular tree species. Laying started earlier and a larger number of eggs were laid in deciduous habitats and in particular in areas with a higher density of English oak trees. The finding of habitat-related laying date is consistent with other studies on blue tits (Blondel et al., 1993; Lambrechts et al., 2004; Arriero et al., 2006; Thorley & Lord, 2015) and great tits (Mänd et al., 2005; Wilkin et al., 2007; Mägi et al., 2009; Atienzar et al., 2010). Similarly, our finding that clutch size was related to vegetation variables has also been reported in other studies on blue tits (Blondel et al., 1993; Tremblay et al., 2003; Bell et al., 2014; but see Arriero et al. (2006) where no association was found) and great tits (Belda et al., 1998; Mänd et al., 2005; Mägi et al., 2009).

The proximate link of laying date and number of eggs laid with vegetation structure may be differences in food availability in trees of different species and

maturity surrounding breeding sites. For example, Svensson & Nilsson (1995) have shown in blue tits that experimental food supplementation prior to laying causes an advance in laying date. Although we have no data about food abundance in the trees surrounding the nest-boxes in our study area, other studies suggest that food availability varies between different vegetation types (van Balen, 1973; Perrins, 1991; Lambrechts et al., 1997). For example, deciduous trees, which produce new soft leaves each spring, support more caterpillars than coniferous trees (Blondel et al., 1993; Lambrechts et al., 2004; Mänd et al., 2005). Among deciduous trees, oaks are the most important food source, as they harbour more caterpillars and higher densities of other invertebrates than other deciduous tree species, which may enable birds in oak habitats to start breeding earlier (Blondel et al., 1991; Wilkin et al., 2007). Other studies have shown that leaves of coniferous trees are not edible by insects due to their hardness and biochemical compounds such as tannins (Feeny, 1970; Hatcher, 1990). The peak of insect abundance may also occur later in coniferous trees (Rytönen & Orell, 2001). Food availability can be an important constraint on energy expenditure for females, particularly early in the season (Tinbergen & Williams, 2002). Vegetation type-related variation in food availability may therefore have a greater influence on breeding parameters expressed at earlier stages of the reproductive cycle, such as laying date (Gienapp & Visser, 2006; Bourgault et al., 2009) and clutch size (Perrins, 1965; Marciniak et al., 2007).

In addition to the density of specific tree species surrounding the nest-boxes, their size and maturity also influence food availability within habitats (Arriero et al., 2006). We found that laying started earlier in nest-boxes surrounded by young miscellaneous deciduous trees. These findings did not agree with our expectation, because young miscellaneous deciduous trees should provide less foliage and associated food for blue tits. The density of young miscellaneous deciduous trees was positively correlated with the density of young English oaks (Supplementary material Table S4) surrounding the nest-boxes. Presumably, the high abundance of these young trees may provide enough food resources for blue tits. We also found that in habitats with more mature English oaks, egg laying started earlier and the number of eggs was greater. This suggests that, mature English oaks may provide greater food resources (e.g. caterpillars).

To assess the exact fitness consequences of the habitat structure around the nest-sites, complete measures of reproductive success would be required. Due to the experiments performed in this population (see Korsten et al., 2006; Kingma et al., 2009; Vedder et al., 2010, 2012; de Jong, 2013; Schut et al., 2014) we were not able to look at vegetation effects on breeding performance beyond the number of

eggs laid. However, in blue tits and great tits, clutch size is generally found to be positively correlated with other parameters of breeding performance such as hatching success (e.g. Arriero et al., 2006), number of fledglings (e.g. Lambrechts et al., 2004; Ahola et al., 2009) and local recruitment (e.g. Boyce & Perrins, 1987). But to ascertain that this is also the case in our study population, more research is needed on the relationship between habitat characteristics and other measures of breeding performance, like hatching and fledging success, and subsequent offspring survival and recruitment.

### **4-3- Laying date and number of eggs laid in relation to nest-box occupancy**

The relationships among nest-box occupancy, vegetation characteristics, and breeding parameters (laying date and number of eggs laid) were clearly congruent. We found earlier laying and a larger number of eggs laid in the nest-boxes that were more frequently occupied across the 13 years of research. Similarly, in great tits it was found that if a nest-box was more frequently occupied across years, clutches in that nest-box were laid earlier in the year and were larger (Mänd et al., 2005).

Occupancy rate has previously been suggested to indicate the quality and quantity of food resources surrounding nest-sites (Sergio & Newton, 2003; Janiszewski et al., 2013). Accordingly, we suggest that in our population nest-sites in higher-quality habitat with a higher proportion of deciduous vegetation and a relatively high density of mature English Oaks – which likely allows earlier breeding and larger clutches – are occupied before the nest-sites in lower-quality habitats (e.g. with coniferous vegetation). While this is also in line with predictions of theoretical studies (Bernstein et al., 1991), more empirical studies on the relationship between occupancy rate and measures of breeding success are required to investigate whether occupancy rate can serve as a simple and general predictor of habitat quality and breeding performance in blue tits and other bird species.

## **5- Conclusions**

We suggest that nest-box occupancy in the long-term can be a simple and reliable predictor of habitat preference and quality. As an immediate index, the proportion of deciduous trees surrounding the nest-site, and the density of English oak trees, particularly mature trees, appear to be good predictors of high quality habitats. Conversely, coniferous trees are indicators of poor-quality, non-preferred habitat. Our results indicate that blue tits preferentially occupy deciduous habitats with a high density of mature English oak trees (and conversely a low density of



coniferous trees), in which they start laying earlier and lay larger clutches. However, we cannot rule out that other blue tit populations may have adapted differently to habitat structure in areas with completely different vegetation.

### **Acknowledgements**

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## Supplementary material

**Table S1** Summary of experiments carried out in the study area between 2001-2013 with their possible influences on the laying date and the number of eggs laid.

Year	Experimental treatment <sup>a</sup>	Timing of the experimental treatment with regard to the breeding cycle	Effect on laying date?	Effect on number of eggs laid?	Reference <sup>b</sup>
2001	No experiments	-	-	-	
2002	UV manipulation of male crown plumage	Before egg laying	No	No	Korsten et al., 2006
2003	UV manipulation of male crown plumage	Before egg laying	No	No	Korsten et al., 2006
2004	Removal of nest material	During nest building	No	No	Unpublished results, ( $P = 0.15, 0.30$ )
2005	Egg collection; replacement with dummy eggs	During egg laying	No	No	Kingma et al., 2009
2006	Addition of nest-boxes near the focal nest-boxes; removal of nesting material; blocking of original nest-box; egg collection and replacement with dummy eggs	During nest building and egg laying	Yes	Yes	Unpublished results, ( $P = 0.029, 0.046$ )
2007	Addition of nest-boxes near the focal nest-boxes; removal of nesting material; blocking of original nest-box; egg collection and replacement with dummy eggs	During nest building and egg laying	Yes	Yes	Unpublished results, ( $P < 0.001, 0.003$ )
2008	Egg collection and egg addition	During egg laying	No	No	Vedder et al., 2010
2009	Egg collection; replacement with dummy eggs.	During egg laying	No	Yes	Vedder et al., 2012
2010	Testosterone implants in females and egg collection; replacement with dummy eggs	Before egg laying	No	No	de Jong, 2013
2011	Testosterone implants in females	Before egg laying	No	No	de Jong, 2013
2012	Egg collection	During egg laying	No	Possibly <sup>c</sup>	Personal communication
2013	Egg collection	During egg laying	No	Possibly <sup>c</sup>	Personal communication

<sup>a</sup> Only experimental treatments carried out before the incubation onset are presented.

<sup>b</sup> The first and second  $P$  values in the brackets are related to the effect of the experimental treatment on laying date and number of eggs laid, respectively.

<sup>c</sup> In 2012-2013, two eggs per nest were collected without replacement with dummy eggs. This was done for almost all observed breeding attempts. As breeding birds received the same treatment at almost all nest-boxes, we assumed the collection of eggs did not contribute to between-nest-box variation in the number of eggs laid within these years.

**Table S2** Loading factors, eigenvalues and variances explained for the first ten principal components resulting from a principal component analysis of vegetation variables.

Vegetation variables	Tree circumference class (cm)	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
<b>English oak</b>											
	30-50	0.36	-0.18	0.19	-0.20	0.27	-0.26	0.16	-0.08	0.10	-0.05
	50-100	0.33	-0.17	0.29	-0.20	0.18	-0.31	0.13	0.09	-0.02	-0.02
	100-200	-0.27	-0.13	0.36	0.25	-0.15	-0.05	0.09	0.31	-0.50	0.15
	>200	-0.13	-0.25	0.02	0.25	-0.46	0.04	0.17	-0.18	0.55	-0.32
<b>European beech</b>											
	30-50	-0.18	0.11	0.40	0.06	0.42	0.29	0.01	-0.20	0.18	-0.05
	50-100	-0.26	0.14	0.37	0.07	0.38	0.17	-0.05	0.04	0.26	-0.05
	100-200	-0.30	0.07	-0.14	-0.53	0.01	0.07	0.01	0.06	0.00	-0.07
	>200	-0.21	-0.00	-0.19	-0.58	0.00	0.18	0.13	0.03	0.05	0.02
<b>Miscellaneous deciduous</b>											
	30-50	0.33	-0.36	0.10	-0.10	-0.07	0.37	-0.13	-0.05	0.02	0.04
	50-100	0.24	-0.37	0.07	-0.08	-0.05	0.45	-0.23	-0.07	-0.09	0.07
	100-200	0.02	-0.12	-0.41	0.21	0.42	-0.01	-0.22	-0.00	-0.24	-0.63
	>200	0.02	-0.12	-0.45	0.27	0.35	0.01	0.09	0.01	0.26	0.63
<b>Coniferous</b>											
	30-50	0.22	0.28	-0.50	0.09	-0.03	0.50	-0.00	0.44	-0.00	-0.07
	50-100	0.29	0.36	0.06	-0.02	-0.09	-0.10	-0.28	0.38	0.27	0.01
	100-200	0.25	0.43	0.01	-0.02	-0.12	-0.11	-0.09	-0.22	0.06	-0.06
	>200	0.15	0.35	0.01	0.04	-0.06	0.19	0.11	-0.61	-0.33	0.11
<b>Non-coniferous evergreen</b>											
		0.19	0.08	-0.08	0.06	0.06	0.18	0.82	0.17	-0.05	-0.17
<b>Standard deviation</b>											
Eigenvalue		1.65	1.56	1.30	1.22	1.14	1.07	1.00	0.96	0.88	0.80
% variance explained		2.72	2.43	1.69	1.49	1.30	1.14	1.00	0.92	0.77	0.64
$\Sigma$ % variance explained		15.9	14.4	10.0	8.7	7.6	7.00	6.00	5.4	4.5	3.8
		15.9	30.03	40.3	49.0	56.6	63.6	69.6	75	79.5	83.3

**Table S3** Pearson's correlations between the first (PC1) and second (PC2) principal components with densities of trees of the reduced vegetation variables ( $n = 188$ ).

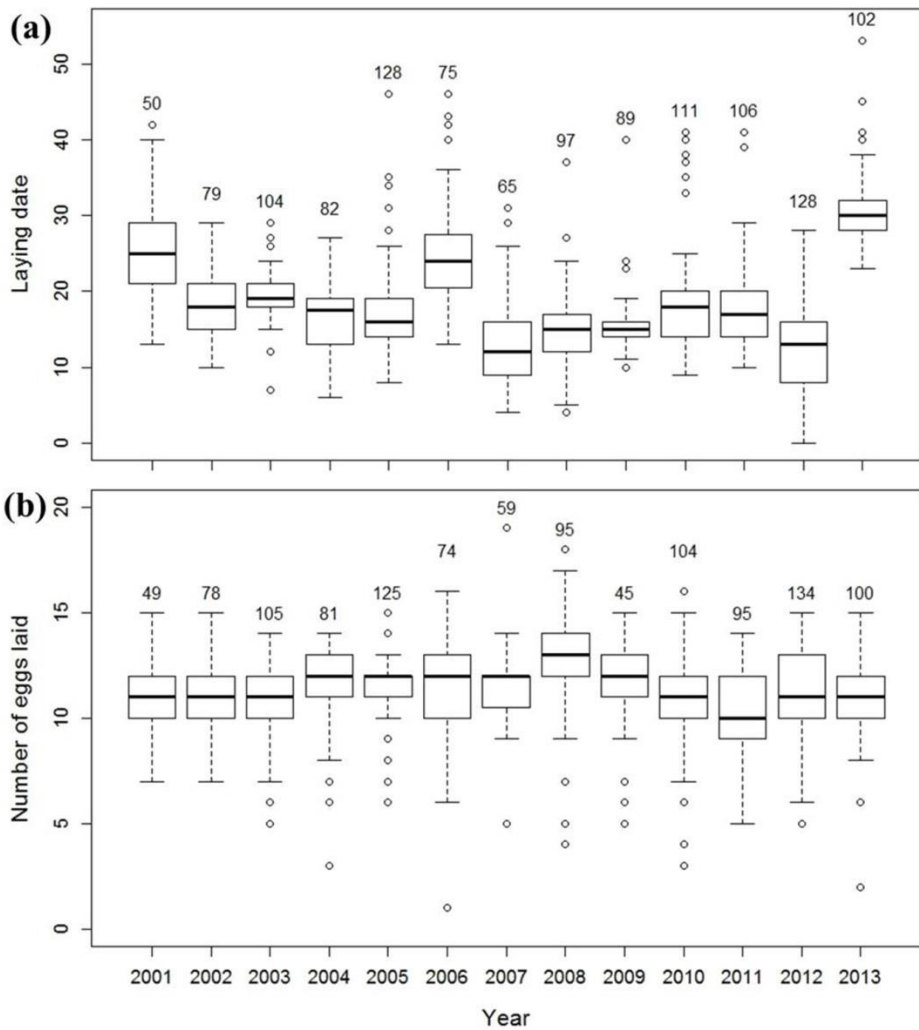
	Young English oak	Mature English oak	European beech	Young miscellaneous deciduous	Mature miscellaneous deciduous	Coniferous	Non-coniferous evergreen
PC1	0.62 ***	-0.47 ***	-0.62 ***	0.53 ***	0.04	0.54 ***	0.32 ***
PC2	-0.31 ***	-0.28 ***	0.23 ***	-0.62 ***	-0.22 **	0.76 ***	0.13

\*\*  $P \leq 0.01$ , \*\*\*  $\leq 0.001$

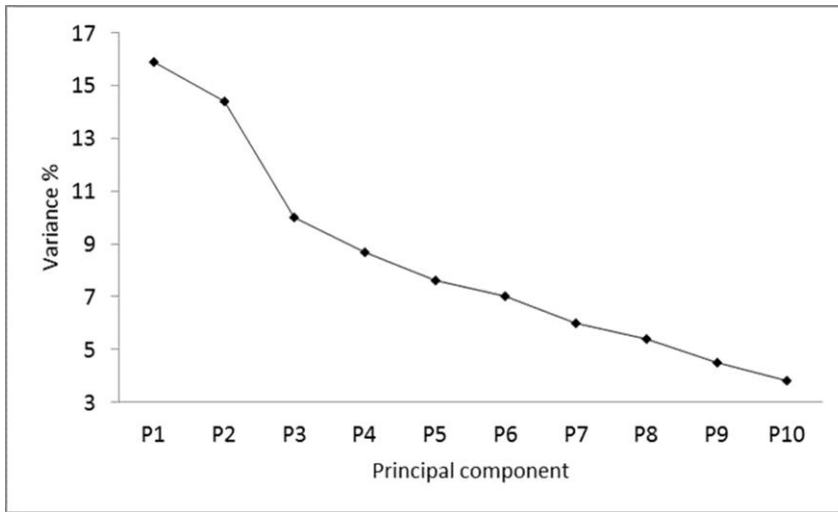
**Table S4** Pearson's correlations between the densities of trees for the reduced number of vegetation variables ( $n = 188$ ).

	Young English oak	Mature English oak	European beech	Young miscellaneous deciduous	Mature miscellaneous deciduous	Coniferous	Non-coniferous evergreen
Young English oak	1						
Mature English oak	-0.16 *	1					
European beech	-0.21 **	0.09	1				
Young miscellaneous deciduous	0.35 ***	-0.06	-0.27 ***	1			
Mature miscellaneous deciduous	-0.07	-0.21 **	-0.16 *	0.03	1		
Coniferous	0.03	-0.39 ***	-0.16 *	-0.11	-0.16 *	1	
Non-coniferous evergreen	0.13	-0.11	-0.13	0.02	0.01	0.17 *	1

\*  $P \leq 0.05$ , \*\*  $\leq 0.01$ , \*\*\*  $\leq 0.001$



**Figure S1** Boxplots of (a) laying date and (b) number of eggs laid in the study area from 2001-2013. Laying dates are given as April dates (1=1 April). Boxes indicate the median, and 25th and 75th percentiles; whiskers indicate the lowest and highest datum within 1.5 times the interquartile range (IQR) from the first and third quartile, respectively. Numbers above the boxes indicate the number of observations.



**Figure S2** Scree plot for the variance explained by the first ten principal components extracted from the principal component analysis of the vegetation variables.



Photos: Seyed Mehdi Amininasab



# Chapter 3

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## **Tree logging affects reproductive performance in blue tits *Cyanistes caeruleus* but tree type and tree age matter**

Seyed Mehdi Amininasab, Charles C.Y. Xu, Sjouke A. Kingma & Jan Komdeur

Journal of Ornithology (short note, provisionally accepted)

**Abstract**

For birds, habitat quality is largely determined by local vegetation and anthropogenic activities can negatively influence reproductive performance. A major logging event enabled us to examine the effect of tree removal on reproductive performance of blue tits *Cyanistes caeruleus*. Before and after logging, the maturity and type of trees around each nest-box were recorded and related to changes in reproductive performance. Logging of young coniferous, but not deciduous, trees significantly reduced the number of eggs laid. Differential logging has contrasting effects on blue tit reproductive performance and should be considered in forest management.

## 1- Introduction

Anthropogenic change in forests through activities such as logging often results in habitat loss and fragmentation, which is associated with reductions in biodiversity (Sih et al., 2000). For birds, local forest structure around nesting sites and territories is one of the main indices of breeding habitat quality as this is a major determinant of food availability and may therefore influence their reproductive performance (Blondel et al., 1991, 1993; Lambrechts et al., 2004; Mägi et al., 2009; Wilkin et al., 2009). Thus, a reduction of breeding habitat through logging may negatively affect avian reproductive performance.

While several studies have examined the effects of logging on reproduction in birds (e.g. Bourque & Villard, 2001; Gram et al., 2003), few have used fine-scale indices at the level of individual trees to directly investigate effects of habitat structure and logging on reproductive performance. By manipulating individual trees of different maturities and relating this to reproductive parameters of birds, it is possible to explore how logging may affect avian reproduction and to identify the proximate ecological factors that influence reproductive performance. As such, a deeper understanding of the relationship between forest structure and avian reproductive performance can help to develop more informed forest management plans.

In the winter of 2013, a substantial number of trees were logged in a field site inhabited by blue tits *Cyanistes caeruleus* subject to an ongoing long-term study. This created an ideal opportunity to investigate the effects of anthropogenic change in forest structure on reproductive parameters such as laying date and number of eggs laid. We hypothesized that logging of mature trees will negatively influence reproductive performance and this effect to be stronger in the case of cutting of deciduous trees are given their importance of food resources for Blue Tits (e.g. Amininasab et al. 2016).

## 2- Materials and methods

### 2-1- Study population and data collection

The nest-box population of blue tits was established in 2001 at 'De Vosbergen' estate near the city of Groningen in northern Netherlands (53°08'N, 06°35'E). 188 nest-boxes designed especially for blue tits were installed at regular intervals across an area of 54 ha consisting of mixed deciduous and coniferous forest interspersed with open grassland. Habitat quality was assessed following Amininasab et al. (2016) from 2001-2013. Briefly, deciduous and coniferous trees with a minimal circumference of 30 cm and within a 20 m radius of each nest-box

were considered. A radius of 20 m was chosen as a compromise between biological plausibility and practical feasibility given the workload of counting and measuring individual trees. Tree circumference was measured at breast height and used to categorize trees by size (small: 30-100 cm, medium: 100-200 cm, large: >200 cm). The logging occurred between November and December 2013, approximately 3-4 months before the breeding season. Trees selected for logging were marked and measured 2 weeks before the logging event. The local habitat around a nest-box was considered logged if at least one (coniferous or deciduous) tree was cut within a 20 m radius.

From April to June of each year, nest-boxes were checked daily to record the laying date (date at which the first egg is laid with April 1 representing day 1) and the number of eggs laid of each breeding pair. Due to the cold spring in 2013, the initiation of breeding was substantially delayed compared to previous years so averaging from 2001-2013 is a more reliable measure of pre-logging breeding parameters than values from 2013 alone (Amininasab et al., 2016). Thus, the mean laying date and number of eggs laid in 2001-2013 was calculated and used to represent breeding parameters in nest-boxes before the logging event while laying date and number of eggs laid in 2014 represented post-logging values. The change in laying date and number of eggs laid was obtained by subtracting post-logging from pre-logging values and used for longitudinal analyses.

## **2-2- Statistical analyses**

To control for year-to-year variation in laying date and number of eggs laid before logging (2001-2013), all breeding parameters were standardized to a mean of 0 and a standard deviation of 1 with the following equation:

Standardized  $x = \frac{x - \bar{x}_{year}}{sd\ x_{year}}$  (where  $x$  = laying date or number of eggs laid, and  $\bar{x}_{year}$  the average laying date or number of eggs laid in all nest-boxes in a given year)

R software was used to implement all statistical models (R Development Core Team, 2015). Linear models were used to test the effects of logging deciduous and coniferous trees of different size categories (small, medium and large; thus including six independent variables) on changes in laying date and number of eggs laid before (2001-2013) and after logging (2014). The models were ranked based on AICc, and we averaged the parameter estimates (with standard errors) over the estimates and weight of the best models (the model with lowest AICc and all other models where  $\Delta AICc < 2$ ), using the MuMIn package.  $P$ -values  $< 0.05$  were considered significant for each variable.

### 3- Results

During the logging event, coniferous and deciduous trees were removed in 25.7% and 27.5% of territories that were occupied the subsequent spring, respectively ( $n = 109$  territories). A total of 18 small (mean per territory = 1.55, range = 1–3), 22 medium (mean = 3.27, range = 1–11) and 9 large (mean = 1.44, range = 1–3) coniferous trees were cut and a total of 19 small (mean = 3.26, range = 1–17), 20 medium (mean = 2.4, range = 1–8) and 7 large (mean = 1.14, range = 1–2) deciduous trees were cut.

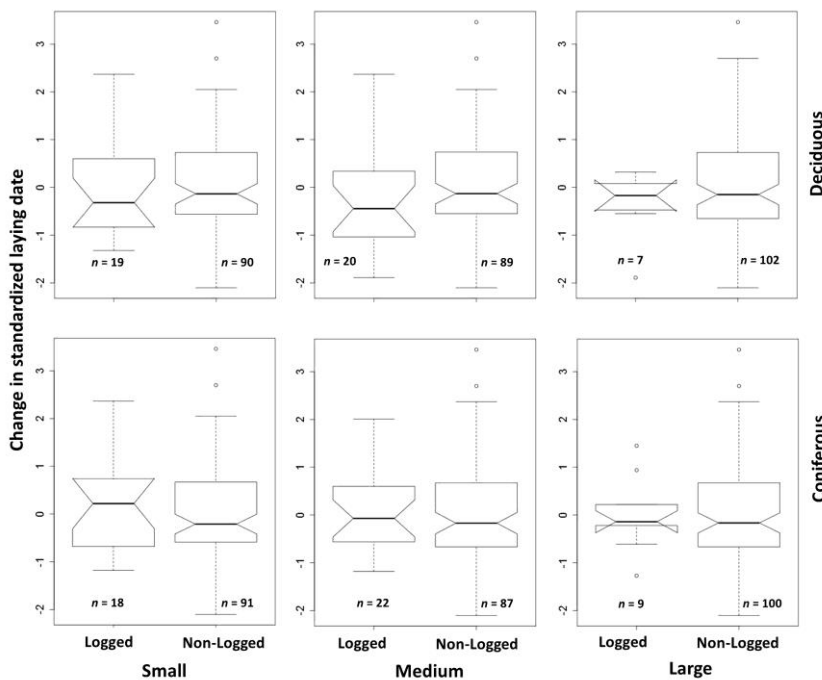
The analyses indicate that blue tits did not lay later in the year if deciduous or coniferous trees of any size were logged (Table 1, Figure 1). However, a significantly lower number of eggs was laid in nest-boxes situated in areas where small coniferous trees were cut (Table 2, Figure 2). There was no effect of logging deciduous or coniferous trees of any other size categories on the number of eggs laid.

**Table 1** Results of a linear model testing the relationships between change in standardized laying date of blue tits and logging of deciduous and coniferous trees of different sizes. The estimated coefficients (with associated standard errors,  $z$  and  $P$ -values) are based on averaging the models that gave the best fit (based on AICc). The order of variables is based on ranking by relative importance.

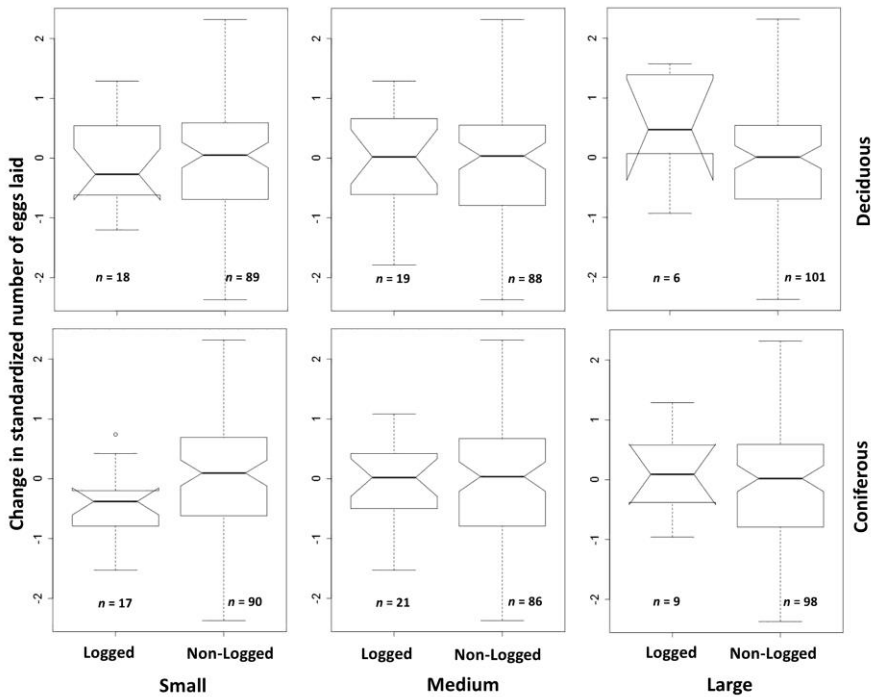
	Change in laying date			
	Estimate	SE	$z$ -value	$P$ -value
(Intercept)	0.107	0.109	0.98	0.33
Medium deciduous	-0.488	0.252	1.91	0.06
Small coniferous	0.323	0.253	1.26	0.21
Large deciduous	-0.362	0.380	0.94	0.34
Small deciduous	0.218	0.303	0.71	0.48
Medium coniferous	0.148	0.237	0.62	0.54

**Table 2** Results of a linear model testing the relationships between change in standardized number of eggs laid of blue tits and logging of deciduous and coniferous trees of different sizes. The estimated coefficients (with associated standard errors,  $z$  and  $P$ -values) are based on averaging the models that gave the best fit (based on AICc). The order of variables is based on ranking by relative importance and significant variables are in bold.

	Change in number of eggs laid			
	Estimate	SE	$z$ -value	$P$ -value
(Intercept)	-0.006	0.103	0.06	0.95
Small coniferous	<b>-0.534</b>	<b>0.265</b>	<b>1.99</b>	<b>0.046</b>
Large deciduous	0.539	0.384	1.38	0.17
Medium coniferous	0.294	0.267	1.09	0.27
Large coniferous	0.315	0.320	0.97	0.33
Medium deciduous	0.134	0.235	0.56	0.57
Small deciduous	0.101	0.246	0.41	0.68



**Figure 1** Notched box-plots showing the influence of logging deciduous and coniferous trees of different sizes on change in standardized laying date of blue tits. Notches represent confidence intervals around the median, which is based on the median  $\pm 1.57$  Interquartile Range/ $\sqrt{n}$ . Notches overlap in all plots indicating there is no strong evidence (95% confidence) that the medians differ.



**Figure 2** Notched box-plots showing the influence of logging deciduous and coniferous trees of different sizes on change in standardized number of eggs laid of blue tits. Notches represent confidence intervals around the median which is normally based on the median  $\pm 1.57 \times \text{Interquartile Range}/\sqrt{n}$ . Notches do not overlap when testing logging of small coniferous trees indicating that the medians differ (95% confidence).

#### 4- Discussion

Based on longitudinal analyses, we show that young (small) coniferous trees have an influence on blue tit reproductive performance. Specifically, we demonstrated that logging of local young coniferous trees around nest-boxes significantly reduces the number of eggs laid, but this had no effect on laying date.

Previous experimental studies on blue tits indicated that reproductive performance was influenced by food availability (e.g. Svensson & Nilsson, 1995). Compared to coniferous habitats, deciduous trees support more caterpillars and other insect communities as food sources during the brood rearing phase of blue tits due to leaf shape (tree buds) and branch surface phenotype (without glue produced by the trees) (e.g. Blondel et al., 1993; Lambrechts et al., 2004).

However, deciduous habitats may be occupied earlier leaving lower quality individuals to occupy coniferous habitats (Mägi et al., 2009; Amininasab et al., 2016). Thus, coniferous trees are also important because blue tit populations may adapt to coniferous habitats depending on the environmental context especially at lower latitudes (e.g. see Tremblay et al., 2003; Mägi et al., 2009). In addition, coniferous/evergreen trees may provide useful hiding spots for tits against predators outside or during the breeding season (Lambrechts et al., 2004). Hence, small changes in coniferous habitats can have significant effects on reproductive performance, especially when food supply is low.

Initially, logging of mature trees was suspected to have the greatest ecological impact on blue tit reproductive performance. Tree age is related to canopy size and larger canopies provide more food resources for blue tits. However, mature coniferous needles may be unappetizing to caterpillars and other insects because of their toughness and high levels of secondary components like tannins. In contrast, needles of small coniferous trees may contain less secondary metabolites and are generally less tough (Hatcher, 1990). Hence, young coniferous trees may provide better food resources for blue tits compared to mature trees, which could explain why only young coniferous trees had an effect on the number of eggs laid. In addition, the larger distance between the canopy of large trees and nest-boxes may cause the vertical flight between food resources and nest-boxes to be more energetically costly for blue tits. Lastly, small coniferous trees near nest-boxes might have served as hiding spots and removing them may have resulted in an increase in 'stress-related' hormones reducing clutch size (see e.g. Travers et al., 2010) since the logging event occurred approximately 3-4 months before the breeding season and individuals likely already adapted to the changes in habitat structure. Ultimately, however, separating the effects of stress due to logging disturbance and those of the food shortage due to tree logging is difficult and should be interpreted with caution.

Longitudinal analyses also indicated that logging deciduous trees of different sizes had no effect on laying date and number of eggs laid. In contrast, our earlier studies on this population showed that egg laying started earlier with greater number of eggs laid in habitats with more mature deciduous trees, possibly due to mature deciduous trees providing better food resources for blue tits (Amininasab et al. 2016). Thus, we expected that logging of mature deciduous trees should negatively influence reproductive performance parameters. Perhaps the small number of deciduous trees cut per territory did not significantly affect food supplies and most territories had sufficient food resources available despite



logging. Further experimental studies are needed to clarify these results and investigate the mechanisms in greater detail.

Although we could not incorporate other parameters of breeding performance (like fledging success) due to other experiments in this population (see Amininasab et al., 2016), laying date and the number of eggs laid are considered good predictors of reproductive fitness because they usually correlate with other traits including hatching success (e.g. Arriero et al., 2006), number of fledglings (e.g. Lambrechts et al., 2004), and recruitment (e.g. Boyce & Perrins, 1987).

Given the importance of young coniferous habitats for blue tit reproductive performance, the presence of these habitats should be incorporated in forest management plans for blue tits and other insectivorous forest birds.

### **Acknowledgments**

We thank Kraus-Groeneveld Stichting for permission to work on De Vosbergen estate as well as Peter Korsten, Oscar Vedder, Elske Schut, Berber de Jong, Michael Magrath, Reinaldo Marfull and several students who assisted with the field work. We also thank Peter Korsten and Han Olf for general advice. This study complies with the current laws of the Netherlands where it was conducted and permission for animal handling of birds was granted by the Animal Experiments Committee of the University of Groningen, the Netherlands. Research was supported by the Netherlands Organisation for Scientific Research (NWO-ALW 821.01.008) and other grants funded to Jan Komdeur between 2001 and 2014.



Photos: Seyed Mehdi Amininasab

# Chapter 4

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## **No effect of partner age and lifespan on female age-specific reproductive performance in a bird species with bi-parental care**

Seyed Mehdi Amininasab, Martijn Hammers, Oscar Vedder, Peter Korsten & Jan Komdeur

Journal of Avian Biology (Under review)

### **Abstract**

Studies of age-specific reproductive performance are fundamental to our understanding of population dynamics and the evolution of life-history strategies. In species with bi-parental care, reproductive ageing trajectories of either parent may be influenced by their partner's age, but this has rarely been investigated. We investigated within-individual age-specific performance (laying date and number of eggs laid) in wild female blue tits *Cyanistes caeruleus* and evaluated how the age and longevity of their male partner indirectly influenced the female's reproductive performance. Females showed clear age-dependence in both laying date and number of eggs laid. We found that female reproductive performance improved in early life, before showing a decline. Longer-lived females had an earlier laying date throughout their lives than shorter-lived females, but there was no difference in number of eggs laid between longer- and shorter-lived females. Within breeding pairs, the female's (age-specific) reproductive performance was not dependent on the age and longevity of the male partner. We conclude that the age and quality of the male partner may be of little importance for traits that are under direct female control.

## 1- Introduction

Studies of age-specific reproductive performance and reproductive lifespan are fundamental to our understanding of population dynamics and the evolution of life-history strategies (Stearns, 1992). In vertebrates, reproductive performance typically improves with age because of changes in physiology or reproductive allocation (Curio, 1983), or accumulation of breeding experience (Forslund & Pärt, 1995; Cichoń, 2003), before declining as a result of senescence (Clutton-Brock, 1988; Jones et al., 2008). To accurately describe and understand these within-individual processes, it is crucial to separate within-individual changes from changes in age composition that occur at the population level. For example, differences in intrinsic quality between individuals may be manifested by the occurrence of poor-quality individuals with low reproductive performance that die relatively early compared to high-quality individuals with high reproductive performance (e.g. Blas et al., 2009). Failure to correct for such selective disappearance may obscure within-individual patterns of senescence, or may even lead to wrong interpretation of the patterns of age-specific reproduction (see van de Pol & Verhulst, 2006; Bouwhuis et al., 2009). Longitudinal data – the monitoring of marked individuals throughout their lives – is required to separate these within- and between-individual effects (Nussey et al., 2008; Bouwhuis & Vedder, in press).

There is an increasing number of studies that have quantified patterns of reproductive ageing as a within-individual process in birds (see Nussey et al., 2013; Bouwhuis & Vedder, in press). Although most of those studies have focused on age-specific female reproductive performance, several recent studies have investigated age-specific reproductive performance as a within-individual process in both males and females. Generally, studies that considered both males and females have focused on traits that are directly influenced by the performance of both parents, such as the number of offspring that reach independence in species with bi-parental care (e.g. Millon et al., 2011; Torres et al., 2011; Balbontín et al., 2012), or focused on traits that are usually regarded as under mechanistic control by the female, such as clutch size (Schroeder et al., 2012; Zhang et al., 2015a). Studies which have investigated how ageing patterns of female reproductive traits are influenced by the age or lifespan of the male partner remain scarce (but see Balbontín et al., 2007; Brown & Roth, 2009; Auld & Charmantier, 2011; Auld et al., 2013). Given that mating patterns are often not random with respect to age (e.g. age-assortative mating; Black & Owen, 1995; Auld & Charmantier, 2011) and investment in reproduction may be influenced by (age-dependent) characteristics of the partner (e.g. attractiveness; Trivers, 1972; Burley, 1986), it is

important to also consider the effect of the partner when investigating patterns of age-specific reproduction. Male age or lifespan may potentially affect the age-specific expression of reproductive traits that are typically regarded as traits that are almost entirely determined by the female, such as laying date and clutch size (Sheldon et al., 2003; Caro et al., 2009). Hence, to gain a better understanding of ageing patterns in reproductive performance in females, the influence of their partner's age and lifespan should also be studied.

In a recent study on mute swans *Cygnus olor*, it was found that female reproductive performance was influenced by the age of the male breeding partner: females breeding with middle-aged male partners started laying earlier in the season and laid larger clutches compared to females breeding with young or old partners (Auld et al., 2013). Similarly, in barn swallows *Hirundo rustica* and wood thrushes *Hylocichla mustelina* females that were paired with middle-aged males started laying earlier in the season than those paired with either young or old partners (Balbontín et al., 2007; Brown & Roth, 2009). Finally, in a study on blue tits *Cyanistes caeruleus* females showed an improvement in reproductive performance (i.e. earlier laying and larger clutch size) and a reduced rate of reproductive senescence when they were mated with early-reproducing males, which were likely to be of higher quality than late-reproducing males (Auld & Charmantier, 2011).

In this study we aimed to investigate whether female age-specific reproductive performance is affected by the age and reproductive lifespan of the male partner, while accounting for selective disappearance of 'lower quality' individuals. We used 12 years of longitudinal breeding data on an individually marked blue tit population. Two measures of reproductive performance that are under direct female control were considered: laying date and clutch size; both of which are important predictors of fitness (e.g. Perrins, 1965; Norris, 1993; Verboven & Visser, 1998; Both et al., 2000). We tested the hypothesis that females improve their reproductive performance when they are paired with older males (which may also provide more resources), or longer-lived males (which may be of higher quality).

## **2- Materials and methods**

### **2-1- Study area and study population**

The blue tit is a widespread cavity-nesting bird that usually breeds in male-female pairs. Care for the chicks is shared between both pair members. The data presented here were collected between 2001 and 2014 as part of a long-term study on the blue tit population at 'De Vosbergen' estate near Groningen in the Netherlands

(53°08'N, 06°35'E). The study area covers 54 ha and is characterized by mixed deciduous and coniferous forest interspersed with areas of open grassland. In our study area, blue tits breed in nest-boxes of which a total of 188 have been available since 2001.

## **2-2- Data collection and definition of variables**

Blue tits breeding in nest-boxes were studied following the protocols of the long-term monitoring program established for the study population since 2001 (for details see Korsten, 2006). Each year, from early April onwards, the nest-boxes were checked regularly to determine the date of the first egg, clutch size and hatching date for each nest. We attempted catching the male and female breeding at each nest box when they were feeding their nestlings (mostly at 7-8 days of age; hatching = day 0) using a 'flap-trap' inside the nest-box. Individuals that were caught were aged in the field using plumage characters (classifying them into yearlings or older) according to Svensson (1992), and sexed according to the presence or absence of a brood patch (only females develop a brood patch). Each adult was marked with an individually numbered aluminum ring. All young were ringed, mostly at 7-8 days of age.

Various experiments have been carried out on this population during the years of its study (Korsten et al., 2006; Kingma et al., 2009; Vedder et al., 2010, 2012; de Jong, 2013; Schut et al., 2014; Supplementary material Chapter 2, Table S1). Some experiments were carried out before or during egg laying (before incubation started) and some of them were carried out after the incubation onset. Because these experiments may have influenced some aspects of reproductive performance, we focused on data on reproductive traits that were not influenced by experimentation (see Supplementary material Chapter 2, Table S1 for an overview of experiments for each year). We adopted a conservative approach and therefore selected only the laying date and the number of eggs laid as focal reproductive parameters. We acknowledge that there might be potential limitations associated with our study population being subjected to experiments. However, because we only focussed on traits that were not influenced by experimental manipulations, we have no reasons to assume that the experimental manipulations altered the conclusions of our study. The laying date was defined as the date the first egg was laid (1 April was taken as day 1). The number of eggs was the total number of eggs laid by a female during a reproductive attempt. As a result of the collection of eggs without replacement with dummy eggs (see Supplementary material Chapter 2, Table S1) in some years, it was not possible to determine the actual clutch size (i.e. the maximum number of eggs present in the nest during an unmanipulated

reproductive attempt), as females may have partly compensated for the removal of eggs by laying additional eggs. In recognition of this potential influence, we use the term number of eggs laid instead of clutch size for all years. We excluded second clutches, which occurred only rarely, as well as replacement clutches after failed first breeding attempts, from our analyses. Due to the experiments performed in the population during the incubation and nestling provisioning stages, we were not able to incorporate other relevant parameters of a pair's reproductive performance after the onset of incubation (e.g. number of fledglings, number of recruits).

The experimental manipulations influenced the laying date and the number of eggs laid in 2006-2007 (Amininasab et al., 2016), and the number of eggs laid in 2009 (Vedder et al., 2012; for details see Supplementary material Chapter 2, Table S1). As a result, for those years and breeding parameters, we excluded the experimental nests and only included unmanipulated control nests in our analyses.

The age of adults was estimated based on ringing records since 2001. In a number of cases, individuals (mostly unringed birds, presumably immigrants) were first caught with adult plumage (17.0% females and 15.9% males in our dataset). In these cases, we assigned them a minimum age of two years. Blue tits that were not caught during the breeding season for two consecutive years were assumed dead and their age of last reproduction (ALR) was defined as the age at which they were observed for the last time breeding in the population. Adult birds that were still alive in 2013 or 2014, and hence could not be assigned an ALR, were excluded from our dataset (following Bouwhuis et al., 2009). In total, following the above selection criteria, we recorded 989 breeding attempts: these included 932 breeding attempts of 633 females and 820 breeding attempts of 589 males. The percentage of breeding attempts where both female and male identity was recorded was 77.1%. Hereafter, the calculations are based on 763 breeding attempts where both female and male identity were recorded (541 females and 548 males). As the blue tit is a short-lived species (average lifespan of adults based on the individuals in our dataset is 1.86 years in females and 1.68 years in males), for the majority of individuals we only recorded a breeding attempt in a single year (381 females (70.4%) and 402 males (73.4%) were only recorded breeding in one year). However, a considerable number of individuals were recorded in multiple years, which allowed us to investigate longitudinal changes in reproductive performance. The number of females with repeated observations were: 2 times observed: 114, three times observed: 35, four times observed: 8, and five or more times observed: 3, and the number of males with repeated observations were: two times observed: 95, three times observed: 35, four times observed: 14, and five



times observed: 2. There was considerable variation in ALR in both female and males. The number of females with ALR 1 until ALR  $\geq 5$  were 250, 181, 67, 30, 13, respectively, and the number of males with ALR 1 until ALR  $\geq 5$  were 309, 153, 53, 21, 12, respectively.

### 2-3- Statistical analyses

A potential issue in separating female and male contributions to reproductive performance is that the ages of the partners are highly correlated (e.g. when partners are always the same age). Therefore, before investigating the impact of male age on female age-specific reproductive performance, we investigated the degree of age-assortative mating. For this primary test, in case a pair stayed together for multiple years, only one year was selected randomly. The age of male and female partners was significantly correlated in our dataset ( $t = 3.44$ ,  $df = 707$ ,  $r = 0.13$ ,  $P < 0.001$ ). However, the relatively small Pearson correlation coefficient of 0.13 between male and female age suggests that it should be possible to statistically separate the effects of the female and male partner's age using a multiple regression approach as described below.

We analyzed how egg laying onset and the number of eggs laid were predicted by female age and evaluated how the male partner's age affected the expression of these traits. We used linear mixed models (LMMs) with normally distributed errors and an identity link function using the package lme4 (version 1.1-7; Bates et al., 2014) in R (version 3.1.0; R Development Core Team, 2014). As the residuals of the model with the number of eggs laid as dependent variable approximated a normal distribution, and because an initial generalized linear mixed model with Poisson errors and a log link function failed to converge, we used normally distributed errors for fitting the number of eggs laid, instead of using Poisson errors, which are often used for count data.

The breeding parameters laying date and the number of eggs laid varied between years and also between different nest-boxes in each year (Amininasab et al., 2016). Therefore, we included year and nest-box identity as random effects to statistically control for differences between years and nest-sites. We only used breeding attempts in the model for which the identity and age of both pair members were known. Linear and quadratic effects of age were tested by including both age and its squared term (age<sup>2</sup>) as covariates. In the analyses of the number of eggs laid, a negative coefficient of the quadratic effect of age would suggest an initial increase in reproductive performance (i.e. increase in the number of eggs laid) followed by a decline. In the analyses of laying date, a positive coefficient of the quadratic effect of age would suggest an initial increase in

reproductive performance (i.e. an advanced laying date) followed by a decline. Furthermore, for the age effect to reflect an estimate of within-individual change, we also used female and male identity as random effects and the ALR for each individual as fixed effect in the models (see van de Pol & Verhulst, 2006 for a detailed explanation of this statistical method). The inclusion of individual identity as a random effect allows to control for the use of repeated, non-independent observations on the same individual in consecutive years, while ALR accounts for potential differential disappearance from the breeding population of birds of different intrinsic quality (van de Pol & Verhulst, 2006; Bouwhuis et al., 2009). We did not include the age of first reproduction in our models, because the majority of blue tits in our study population start their reproductive career at 1 year of age (81.3% of females and 84.1% of males). Two-way interactions between age, age<sup>2</sup> and ALR were included as fixed effects. Maximal models (i.e. including all explanatory variables and their two-way interactions) were simplified by backward stepwise removal of non-significant terms (starting with the least-significant interaction terms) to reach a minimal adequate model. Age, age<sup>2</sup>, ALR, and the random effects were always kept in the model, independent of their significance. Estimated coefficients for each term (with associated standard errors and *P*-values) are presented on the basis of the minimal adequate model. Following the terminology of Bouwhuis et al. (2009), Table 1 contains a brief description of all variables and interactions that are used in the models.

A significant quadratic effect of age does not necessarily provide evidence for senescence (Reid et al., 2003a; Keller et al., 2008), as it might also reflect improvement early in life only, with performance leveling off (but not declining) at later ages. We therefore also performed a ‘post-peak analysis’, using the minimal adequate model resulting from the analyses described above, but excluding the quadratic effect of age, and selecting only breeding attempts that occurred after the predicted peak in reproductive performance (cf. Bouwhuis et al., 2009; Hammers et al., 2012). If the age term in such a ‘post-peak model’ is significantly negative for clutch size, or positive for laying date, this provides support for performance showing a senescent decline with age. *P*-values <0.05 were considered significant.

**Table 1** Parameters used, and their interpretation, in models testing for a relation between age and female reproductive performance.

Fixed effect	interpretation
♀ or ♂ age	linear change in female reproductive performance with a direct effect of female age, or an indirect effect of male age
♀ or ♂ age <sup>2</sup>	quadratic change in female reproductive performance with a direct effect of female age, or an indirect effect of male age
♀ or ♂ ALR	linear change in female reproductive performance with female (direct effect) or male (indirect effect) reproductive lifespan
♀ age × ♀ ALR ♂ age × ♂ ALR	age effects on female reproductive performance differ for females (direct effect) or males (indirect effect) of different reproductive lifespan
♀ age <sup>2</sup> × ♀ ALR ♂ age <sup>2</sup> × ♂ ALR	age effects on female reproductive performance differ quadratically for females (direct effect) or males (indirect effect) of different reproductive lifespan
♀ age × ♂ age	age-dependent reproductive performance of females is dependent on the age of the male partner
♀ age × ♂ ALR ♂ age × ♀ ALR	age effects (direct for females and indirect for males) on female reproductive performance depend on the partner's reproductive lifespan
♀ age <sup>2</sup> × ♂ ALR ♂ age <sup>2</sup> × ♀ ALR	age effects (direct for females and indirect for males) on female reproductive performance differ quadratically depending on the partner's reproductive lifespan

### 3- Results

#### 3-1- Female reproductive performance: influence of own and partner age

Laying date and number of eggs laid showed clear age-dependence in relation to age of females, but not in relation the age of their male partners (Table 2, Fig. 1; Supplementary material, Table S1). Age of the male did also not explain variation in laying date and number of eggs laid when we repeated the model excluding the effects of female age (Supplementary material, Table S2, S3). In females, we found a clear pattern of improvement with age in both traits, until *ca.* three years of age (Fig. 1). Post-peak analyses (i.e. restricting the analyses to females  $\geq 3$  years old) of the reproductive attempts where the identity and age of both pair

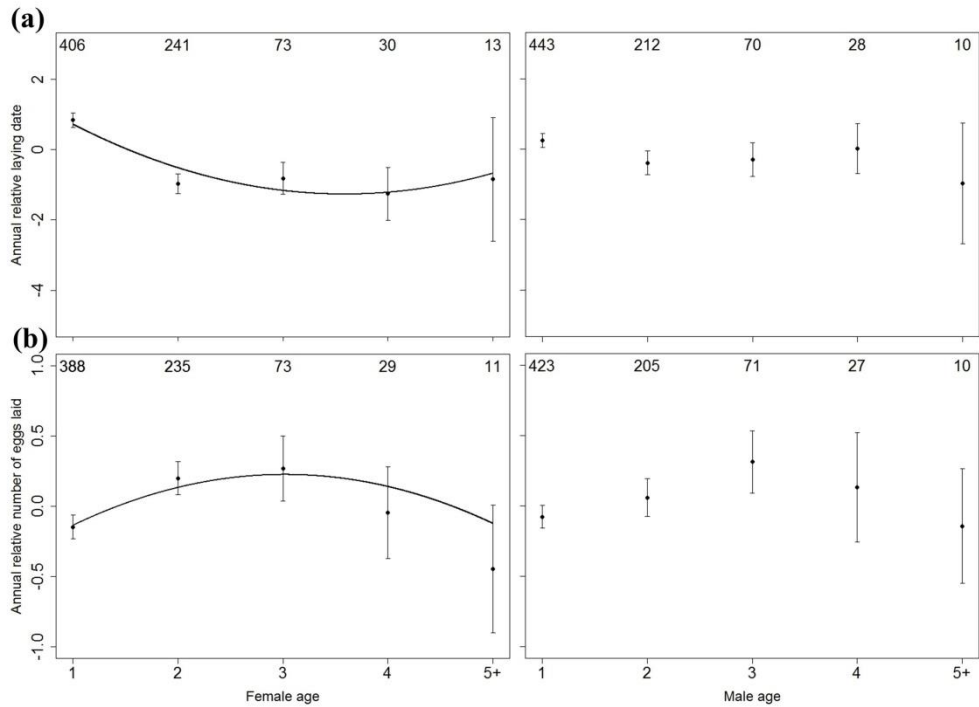
members were known provided no evidence for senescence in either of the two traits, but the sample sizes were rather small (Supplementary material, Table S4). Repeating these post-peak analyses using a larger dataset which included all females of known age (regardless of whether the identity of their partner was known) suggested that after three years of age the laying date delayed and the number of eggs laid decreased with age, but these effects were marginally non-significant ( $P = 0.051$  and  $P = 0.050$ , respectively; Supplementary material, Table S5). We found no significant interaction between female age and the age of the male partner (Table 2), indicating that the age of the male partner did not influence the female's pattern of age-dependent reproductive performance. Examination of the variances explained by the random effects in the final model (Table 2) corroborates our findings; female identity explains a considerable proportion of the variance in both laying date (27%) and number of eggs laid (39%), whereas male identity does not (6% and 7%, respectively).

### **3-2- Influence of male and female age-dependent selective disappearance on female reproductive performance**

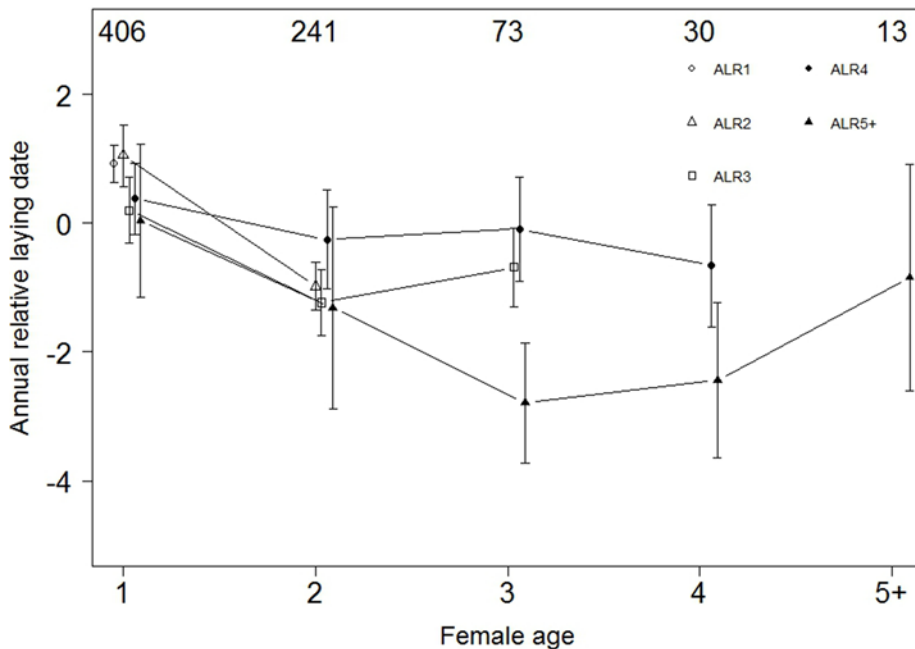
We found a clear pattern of age-dependent selective disappearance in females for laying date, but not for the number of eggs laid (Table 2; Supplementary material, Table S1). Specifically, we found that longer-lived females have an earlier age-specific laying date than shorter-lived females throughout their lives (Fig. 2). This analysis also suggests that the peak reproductive performance of longer-lived females occurred later in life than in shorter-lived females (Fig. 2). In males, there was no effect of life span on laying date or on the number of eggs laid (Table 2; Supplementary material, Table S2, S3). There was no relationship between female age-specific reproductive performance and the lifespan of the male partner (Table 2).

**Table 2** Linear mixed models investigating the effect of female age and the age of the male partner on laying date and number of eggs laid for breeding attempts in blue tits where the identity and age of both pair members are known. Estimated effects of each term (Est.) with associated standard errors (SE) and *P*-values are presented on the basis of the final model. ALR stands for age of last reproduction. Non-significant (ns) fixed effects, except the age, age<sup>2</sup> and ALR terms which were always retained in the model, were deleted by stepwise deletion, in order of least significance and starting with the interactions.

	Laying date			Number of eggs laid		
	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>
<b>Fixed effects</b>						
Intercept	22.50	1.73	<0.001	10.64	0.35	<0.001
♀ age	-5.30	1.23	<0.001	0.51	0.22	0.023
♀ age <sup>2</sup>	1.17	0.32	<0.001	-0.09	0.04	0.028
♀ ALR	-0.49	0.36	0.17	0.07	0.08	0.37
♀ age × ♀ ALR	0.49	0.27	0.07		ns	
♀ age <sup>2</sup> × ♀ ALR	-0.14	0.05	<0.01		ns	
♂ age	-0.36	0.61	0.56	-0.01	0.27	0.96
♂ age <sup>2</sup>	0.10	0.12	0.40	-0.01	0.05	0.82
♂ ALR	-0.03	0.17	0.85	0.11	0.07	0.14
♂ age × ♂ ALR		ns			ns	
♂ age <sup>2</sup> × ♂ ALR		ns			ns	
♀ age × ♂ age		ns			ns	
♀ age × ♂ ALR		ns			ns	
♀ age <sup>2</sup> × ♂ ALR		ns			ns	
♂ age × ♀ ALR		ns			ns	
♂ age <sup>2</sup> × ♀ ALR		ns			ns	
<b>Random effects</b>						
		Variance	Proportion variance explained		Variance	Proportion variance explained
♂ Identity		2.25	0.06		0.23	0.07
♀ Identity		10.12	0.27		1.38	0.39
Nest-box		1.72	0.05		0.13	0.04
Year		18.12	0.48		0.28	0.08
Residual		5.22	0.14		1.48	0.42
<b>Sample sizes</b>						
Individuals ♂		548			536	
Individuals ♀		541			532	
Years		12			12	
Breeding attempts		763			736	



**Figure 1** Overall pattern of (a) laying date and (b) number of eggs laid in relation to female age (direct effect) and the age of male (indirect effect) in blue tits. Relative reproductive performance is the observed value (of laying date or number of eggs) minus the mean value in a given year. Data are means and standard errors where the identity and age of both pair members are known. For each age class, sample sizes are given above the data points. The solid lines are the model predicted within-individual regression slopes from the final model (see Table 2).



**Figure 2** Age-specific laying date in female blue tits subdivided in groups of different age of last reproduction (ALR). Relative reproductive performance is the observed value of laying date minus the mean value in a given year. For each age class, sample sizes are given above the data points. The data points and error bars (connected with solid lines) represent means with standard errors at each age for individuals with different ALR.

4

#### 4- Discussion

In our study population, reproductive performance improved with female age in early life and tended to decline among older females. A similar pattern has been shown in many other bird species (see Nussey et al., 2013; Bouwhuis & Vedder, in press). While female performance in timing (laying date) and initial effort in reproduction (clutch size) was influenced by the female's own age, it was not influenced by her partner's age. This result, combined with the relatively small amount of variation in laying date and clutch size that was explained by male identity, suggests that these traits are predominantly determined by the female. This corroborates the findings of several quantitative genetic studies that indicated that these traits are mainly influenced by the genotype of the female (e.g. van der Jeugd & McCleery, 2002; Sheldon et al., 2003; Caro et al., 2009).

Males and females may allocate resources differently according to their different roles during the different stages of the reproductive cycle. Their different roles can cause differences in energetic investments between the sexes (Tavecchia et al., 2001; Bouwhuis & Vedder, in press). For example, the energetic and nutritional costs associated with egg production and optimizing egg laying onset are probably higher for females than for their male partner (see Monaghan & Nager, 1997; Monaghan et al., 1998). This, in turn, may explain why we observed clear age-dependence and improvement in these traits in females, but not in males. However, this is not always the case as other studies have found age-dependent improvements in both males and females for female-specific traits such as laying date and/or clutch size (barn swallow: Balbontín et al., 2007; blue-footed booby *Sula nebouxi*: Kim et al., 2011; mute swan: Auld et al., 2013). Conversely, the reproductive performance of males may improve with age for traits which are influenced by both male and female reproductive allocation (e.g. number of fledglings in species with bi-parental care; Brown & Roth, 2009; Millon et al., 2011).

For the two reproductive traits that we investigated, the model-predicted maximum female reproductive performance was reached around three years of age. Post-peak analyses on females partly suggested a delay in laying date and a decrease in clutch size in older females, but not in older males. These results are broadly consistent with some studies where reproductive senescence was only reported for females (barn swallow: Balbontín et al., 2012; collared flycatcher *Ficedula albicollis*: Evans et al., 2011), but differ from other studies where laying onset and/or clutch size were found to deteriorate both with female and the male partner's age (barn swallow: Balbontín et al., 2007; blue tit: Auld & Charmantier, 2011; blue-footed booby: Kim et al., 2011; house sparrow *Passer domesticus*: Schroeder et al., 2012). Hence, it is clear that sex-specific patterns of age-dependence in reproductive traits can differ between populations and species. However, currently there are too few studies that have assessed both sexes simultaneously to reach general conclusions regarding the causes of these differences.

For females, but not for males, we found a clear pattern of age-dependent selective disappearance with respect to laying date. Our analyses suggest that longer-lived females have an earlier age-specific laying date than shorter-lived females throughout their lives, and that the difference in age-specific laying date between individuals with different lifespans increases with age. An earlier laying onset in longer-lived females has also been shown in several other species (e.g. McCleery et al., 2008; Evans et al., 2011; Auld et al., 2013; but see Balbontín et



al., 2007, 2012; Kim et al., 2011). Potentially, shorter-lived females are in poorer condition throughout their lives, causing short-lived females to be more constrained than long-lived females to lay early (Torres et al., 2011).

Similar to our results, many other studies found no evidence for female selective disappearance with respect to clutch size (e.g. Bouwhuis et al., 2009; Balbontín et al., 2012; Potti et al., 2013), but exceptions occur (e.g. McCleery et al., 2008; Evans et al., 2011). Patterns of selective disappearance may vary between reproductive traits because some traits may be to a larger extent determined by the quality of the environment, instead of the quality of the bird (Zhang et al., 2015a,b).

In species with bi-parental care, reproductive performance in females may improve when they are mated to preferred (high quality) males (Horvathova et al., 2012). For example, in another study on blue tits, females that were paired with males that started their breeding career at a younger age (an indication of high quality) showed a slower rate of senescence in laying date and clutch size (Auld & Charmantier, 2011). Because most individuals in our population start breeding in their first year, we were not able to test whether male age of first reproduction explained female ageing trajectories in our population. However, we did not find a relationship between the female's age-specific reproductive performance and the lifespan (also a measure of quality) of the partner. Several studies found similar results as ours. For example, Kim et al. (2011) and Auld et al. (2013) found no association between male lifespan and female laying date in the blue-footed booby, and clutch size in the mute swan. In contrast to our study, mute swans started laying earlier when males were paired with relatively long-lived females (Auld et al., 2013). One explanation for why the patterns of covariation between male lifespan and the female partner's reproductive performance vary among species may be that males may invest more in maintaining a territory in longer-lived species (such as the mute swan), than in shorter-lived species (such as the blue tit). Therefore, males may exert a greater influence on female reproductive decisions early in the breeding cycle (e.g. laying date and clutch size) in longer-lived species (Auld et al., 2013).

In conclusion, our study suggests that the age and quality of the male may be of little importance for traits that are under direct female control. However, more studies are needed to seek for generality in between-trait and species differences in the role of male age and longevity in female reproductive performance.

### **Acknowledgements**

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## Supplementary Material

**Table S1** Linear mixed models investigating the effect of the age of female blue tits on laying date and number of eggs laid also including breeding attempts where the identity and age of only females are known. Estimated coefficients of each term (Est.) with associated standard errors and *P*-values are presented on the basis of final model. ALR means age of last reproduction. Non-significant (ns) fixed effects, except the age, age<sup>2</sup> and ALR terms, were deleted by stepwise deletion, in order of least significance and starting with the interactions.

	Laying date			Number of eggs laid		
	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>
<b>Fixed effects</b>						
Intercept	24.16	1.63	<0.001	10.39	0.27	<0.001
♀ age	-5.97	1.19	<0.001	0.66	0.20	0.001
♀ age <sup>2</sup>	1.25	0.30	<0.001	-0.12	0.03	<0.001
♀ ALR	-0.97	0.36	0.007	0.13	0.07	0.070
♀ age × ♀ ALR	0.61	0.27	0.025		ns	
♀ age <sup>2</sup> × ♀ ALR	-0.14	0.05	0.002		ns	
<b>Random effects</b>						
		Variance			Variance	
♀ Identity		14.05			1.29	
Nest-box		1.69			0.19	
Year		17.99			0.28	
Residual		9.00			1.90	
<b>Sample sizes</b>						
Individuals ♀		633			621	
Years		12			12	
Breeding attempts		932			893	

**Table S2** Linear mixed models investigating the effect of the age of the male partner on female specific reproductive traits for breeding attempts in blue tits where the identity and age of both pair members are known. Estimated coefficients of each term (Est.) with associated standard errors and *P*-values are presented on the basis of final model. ALR means age of last reproduction. Non-significant (ns) fixed effects, except the age, age<sup>2</sup> and ALR terms, were deleted by stepwise deletion, in order of least significance and starting with the interactions.

	Laying date			Number of eggs laid		
	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>
<b>Fixed effects</b>						
Intercept	17.33	1.36	<0.001	11.13	0.31	<0.001
♂ age	-0.23	0.68	0.73	0.08	0.28	0.78
♂ age <sup>2</sup>	-0.00	0.13	1	-0.03	0.05	0.62
♂ALR	-0.02	0.19	0.93	0.15	0.08	0.053
♂ age × ♂ ALR		ns			ns	
♂ age <sup>2</sup> × ♂ ALR		ns			ns	
<b>Random effects</b>						
		Variance			Variance	
♂ Identity		3.23			0.43	
Nest-box		2.31			0.20	
Year		17.20			0.27	
Residual		13.91			2.52	
<b>Sample sizes</b>						
Individuals ♂		548			536	
Years		12			12	
Breeding attempts		763			736	

**Table S3** Linear mixed models investigating the effect of the age of the male partner on female specific reproductive traits in blue tits (including breeding attempts where the identity and age of only males are known). Estimated coefficients of each term (Est.) with associated standard errors and *P*-values are presented on the basis of final model. ALR means age of last reproduction. Non-significant (ns) fixed effects, except the age, age<sup>2</sup> and ALR terms, were deleted by stepwise deletion, in order of least significance and starting with the interactions.

	Laying date			Number of eggs laid		
	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>
<b>Fixed effects</b>						
Intercept	17.62	1.34	<0.001	11.03	0.31	<0.001
♂ age	-0.43	0.68	0.52	0.16	0.28	0.57
♂ age <sup>2</sup>	0.02	0.13	0.90	-0.04	0.05	0.47
♂ALR	0.04	0.19	0.82	0.15	0.08	0.064
♂ age × ♂ ALR		ns			ns	
♂ age <sup>2</sup> × ♂ ALR		ns			ns	
<b>Random effects</b>						
		Variance			Variance	
♂ Identity		2.31			0.37	
Nest-box		2.82			0.25	
Year		16.46			0.34	
Residual		15.01			2.54	
<b>Sample sizes</b>						
Individuals ♂		589			573	
Years		12			12	
Breeding attempts		820			788	

**Table S4** Linear mixed models investigating age-specific laying date and number of eggs laid in female blue tits  $\geq 3$  years where the identity and age of both pair members are known. Estimated effects of each term (Est.) with associated standard errors and *P*-values are presented on the basis of final model. Non-significant fixed effects (ns) except single age and ALR terms were deleted by stepwise deletion, in order of least significance.

	Laying date			Number of eggs laid		
	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>
<b>Fixed effects</b>						
Intercept	16.15	2.41	<0.001	11.48	0.91	<0.001
♀ age	0.12	0.38	0.75	-0.27	0.21	0.22
♀ ALR	-0.30	0.51	0.56	0.29	0.22	0.19
♀ age × ♀ ALR		ns			ns	
<b>Random effects</b>						
		Variance			Variance	
♀ Identity		13.72			2.02	
Nest-box		2.75			0.52	
Year		15.96			0.31	
Residual		3.26			1.18	
<b>Sample sizes</b>						
Individuals ♀		85			87	
Years		11			11	
Breeding attempts		116			113	

**Table S5** Linear mixed models investigating age-specific laying date and number of eggs laid in female blue tits  $\geq 3$  years also including breeding attempts where the identity and age of only females are known. Estimated effects of each term (Est.) with associated standard errors and *P*-values are presented on the basis of final model. Non-significant fixed effects (ns) except single age and ALR terms were deleted by stepwise deletion, in order of least significance.

	Laying date			Number of eggs laid		
	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>
<b>Fixed effects</b>						
Intercept	13.76	2.16	<0.001	11.79	0.75	<0.001
♀ age	0.87	0.43	0.051	-0.42	0.21	0.050
♀ ALR	-0.27	0.50	0.59	0.32	0.20	0.10
♀ age × ♀ ALR		ns			ns	
<b>Random effects</b>						
		Variance			Variance	
♀ Identity		10.23			1.12	
Nest-box		2.08			0.46	
Year		13.82			0.13	
Residual		7.70			1.80	
<b>Sample sizes</b>						
Individuals ♀		101			101	
Years		11			11	
Breeding attempts		144			138	



Photos: Seyed Mehdi Amininasab



# Chapter 5

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## **The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird**

Seyed Mehdi Amininasab, Sjouke A. Kingma, Martje Birker, Hanno Hildenbrandt & Jan Komdeur

Behavioral Ecology and Sociobiology (provisionally accepted)

### **Abstract**

Incubation is an important aspect of avian life history. The behaviour is energetically costly and incubation strategies within species, like female nest attentiveness and the feeding by the non-incubating partner during incubation can, therefore vary depending on environmental and individual characteristics. However, little is known about their combined effect. We investigated the importance of ambient temperature, habitat quality and bird age on female incubation behaviour and male feeding of the female whilst incubating (incubation feeding) in blue tits *Cyanistes caeruleus*, a socially monogamous songbird. An increase in ambient temperature resulted in a higher nest temperature and this enabled females to increase the time off the nest for self-maintenance activities. Probably as a consequence of this, an increase in ambient temperature was associated with fewer incubation feedings by the male. Similarly, in areas with more deciduous trees, females had shorter recesses and males had a lower frequency of incubation feeding. Additionally, males increased the intensity of incubation feeding when their partners were young, although the lengths of recesses and female nest attentiveness were independent of female age. The temperature of nests of older females was, however, higher. Male age did not affect incubation feeding rate. In conclusion, the patterns of incubation behaviour were related to both environmental and individual characteristics, and male incubation was adjusted to females' need for food according these characteristics, which can facilitate new insights to the study of avian incubation energetics.

## 1- Introduction

Understanding why species differ in patterns of parental care is important in evolutionary ecology studies (Clutton-Brock, 1991). Incubation behaviour is an important aspect of avian parental care. Incubation is costly, and the magnitude of such costs can vary per species and depend on environmental and individual characteristics (Schultz, 1991; Tinbergen & Williams, 2002; Reid et al., 2002, 2003b).

Incubating females usually face a trade-off between spending time on the nest to incubate the eggs to promote embryo development and time off the nest for investment in self-maintenance (Ardia et al., 2009). As such, incubating females are often constrained in their nest attentiveness because of limited access to energy resources while incubating (White & Kinney, 1974; Martin, 1987), but females may adjust to this limitation by optimizing their incubation rhythm (Conway & Martin, 2000). The incubation rhythm constitutes of alternated periods, where females alternate leaving the clutch to obtain food (off-bouts) and returning to re-warm the eggs (on-bouts; Boulton et al., 2010). The incubation rhythm may therefore not only affect females' condition, but also the egg temperature and, hence, the embryo development (Lyon & Montgomerie, 1987; Williams, 1991).

In many species, particularly those with female-only incubation, males feed the incubating female, which may enable the female to increase nest attentiveness, and this may in turn affect the pair's reproductive success (Lifjeld & Slagsvold, 1986; Nilsson & Smith, 1988; Martin & Ghalambor, 1999; Hatchwell et al., 1999; Tewksbury et al., 2002; Olson et al., 2006). As such, the most important hypothesis for incubation feeding behaviour by males is the 'female nutrition' hypothesis (von Haartman, 1958; Royama, 1966), which states that incubation feeding enables the female to increase the time spent incubating (Camfield & Martin, 2009; Matysioková & Remeš, 2010; Matysioková et al., 2011; Ibáñez-Álamo & Soler, 2012). If so, male incubation feeding can be seen as an indirect form of parental care (Klatt et al., 2008; Matysioková et al., 2011). Hence, the study of male incubation feeding and understanding its variation within and between species is also important when studying incubation behaviour (Lyon & Montgomerie, 1987; Martin & Ghalambor, 1999).

Although incubation may be affected by incubation feeding, both variation in incubation behaviour and incubation feeding may also be affected by environmental characteristics. The most important factors shown to play a role in explaining variation in incubation and male incubation feeding are environmental factors such as ambient temperature and food availability related to habitat quality (e.g. Smith et al., 1989; Perrins, 1991; Zquette et al., 2000; Eikenaar et al., 2003;

Pearse et al., 2004; Arnold, 2011). Ambient temperature influences energy expenditure during incubation (Haftorn & Reinertsen, 1985; Reid et al., 1999; Conway & Martin, 2000; Tinbergen & Williams, 2002; Cresswell et al., 2004) because with lower ambient temperatures incubation time must be increased to keep eggs within temperature ranges for successful embryo development (Webb, 1987; Sanz, 1997; Matysioková & Remeš, 2010). The intensity of male incubation feeding may therefore increase (Amininasab et al., submitted) but can, at the same time, be predicted to decrease if decreasing ambient temperature leads to reduced food availability (Zanette et al., 2000). In addition to ambient temperature, habitat quality and food availability may have an effect on female nest attentiveness (Rauter & Reyer, 1997; Zimmerling & Ankney, 2005), recess length (off-bouts, Nilsson, 1994; Sanz, 1996; Cucco & Malacarne, 1997; Eikenaar et al., 2003; Duncan-Rastogi et al., 2006; Chalfoun & Martin, 2007), and male incubation feeding (Zanette et al., 2000; Matysioková & Remeš, 2010). Females in high-quality territories with higher food availability can spend more time incubating, potentially because their foraging efficiency is higher (Rauter & Reyer, 1997; Conway & Martin, 2000; Zanette et al., 2000; Zimmerling & Ankney, 2005). Thus, several studies have shown that environmental characteristics can be strong predictors of incubation and incubation feeding behaviour.

In addition to environmental characteristics, individual characteristics like age and quality can have an influence on female incubation behaviour (Soler et al., 2001; Hanssen et al., 2002; Badyaev et al., 2003; Ardia et al., 2006), and male incubation feeding (Lifjeld et al., 1987; Siefferman & Hill, 2005). Older or higher quality females may spend more time incubating the eggs (Ardia & Clotfelter, 2007). Similarly, older males may be more capable to increasing the frequency of feeding the female during incubation (Lifjeld et al., 1987; Siefferman & Hill, 2005). One potential explanation for age affecting incubation and incubation feeding may be that older individuals have a higher foraging efficiency (e.g. Pugsek & Diem, 1983; Sæther, 1990; Wunderle, 1991).

As the above-mentioned examples illustrate, incubation behaviour and incubation feeding can be affected by several components, but studies that simultaneously investigate the combined effects of ambient temperature, habitat quality, and individual age on both incubation behaviour and incubation feeding are scarce in songbirds (but see Matysioková & Remeš, 2010; Boulton et al., 2010 for exceptions). In this research we investigate the simultaneous effect of these factors on different measures of female incubation behaviour (nest attentiveness, recess length, and nest temperature) and male incubation feeding in blue tits *Cyanistes caeruleus*, a socially monogamous songbird with female-only

incubation and male incubation feeding behaviour. We predict a longer period of female nest attentiveness, a shorter recess length and a higher minimum nest temperature and a higher intensity of male incubation feeding when the ambient temperature is lower, when individuals are older, and when individuals occupy higher quality habitats.

## **2- Material and methods**

### **2-1- Study area and study population**

The study was conducted during the breeding season of 2014 (March-June) in a nest-box breeding blue tit population at ‘De Vosbergen’ estate near Groningen in the north of the Netherlands (53°N, 06°E). The 54 ha. study area consists of mixed deciduous and coniferous forest interspersed with areas of open grassland, and contains 209 nest-boxes (with a 26 mm entrance hole) designed especially for blue tits.

### **2-2- Breeding data collection**

Blue tits were studied following the protocols of the long-term monitoring program established for the study population since 2001 (for details see Korsten, 2006). From the end of March, all nest-boxes were checked at least once a week to determine laying date and clutch size. Laying date was estimated by counting back from the observed clutch size, assuming that one egg was laid per day (e.g. Kingma et al., 2009). The onset of incubation was determined by daily nest-box visits from the date the seventh egg was laid onwards. Onset of incubation was defined as the first day the female was found incubating or the first day the eggs were found uncovered and warm. A few days before the expected hatch dates (~day 11 of incubation onset), nest-boxes were visited daily to determine hatch date (hatching day 1 is the day of the hatching of the first egg).

We attempted to catch the male and female breeding at each nest box when they were feeding their nestlings (mostly 7-8 days old) using a “flap-trap” inside the nest-box. Each adult was marked with an individually numbered metal ring. Individuals were aged in the field using plumage characters (classifying them into yearlings or adults) according to Svensson (1992), and reliably sexed according to the presence or absence of a brood patch (only females develop a brood patch). The age of ringed adults was estimated based on ringing records since 2001. In a small number of cases, individuals (mostly unringed birds, presumably immigrants) were first caught with adult plumage (12.7% of 102 females and 8.0% of 87 males in our dataset). In these cases, we assigned them to two years old as older individuals were relatively rare (see below). Due to the low number of old

individuals (> 2years) in different age classes, the age classes were divided into 3 age group: one year old (56.9 % females and 57.5 % males), two years old (29.4 % females and 27.6 % males), and three or more years old (13.7 % females and 14.9 % males).

### **2-3- Measurements of female incubation behaviour**

Female incubation behaviour was recorded from day 5 of the incubation onset onwards. On day 4, temperature loggers (Thermochron iButtons, Maxim integrated products) were placed in each nest between the eggs. These temperature loggers were set to record temperature at 3 minute intervals. With this interval, it was possible to monitor the female incubation behaviour for circa 4 consecutive days. Other studies found no effect of temperature loggers on female incubation behaviour in songbirds (e.g. Weidinger, 2008). By using the fluctuations in temperatures recorded by the temperature loggers, it is possible to determine when a female left or returned to the nest. The Rhythm program (1.1; Cooper & Mills, 2005) was used to select incubation recesses from the temperature records, as defined when the temperature inside the nest dropped by more than 2 °C and the declining trend in temperature lasted more than 2 min. The Raven Pro program was used (1.5; Cooper & Mills, 2005) to visually inspect the time series. Furthermore, the recesses in the time series were manually selected if they had not been selected by Rhythm (for example, a sharp drop in temperature that lasted less than 2 min). From these data, it is possible to determine the time of onset and calculate the duration of each recess and female attentiveness bout. To validate the data on nest attentiveness derived from the temperature loggers, 10 nest-boxes were randomly selected and female nest attentiveness recorded by infra-red cameras in the nest-boxes calculated (mean total observation duration = 7.68 h). The female nest attentiveness data obtained by using the camera (using 'BirdBox'; see below for detailed procedures) were highly correlated with the data obtained by using temperature logger data ( $r = 0.74$ ,  $P = 0.014$ ).

As during the night females always incubate inside the nest-box, incubation behaviour patterns for this study were calculated from sunrise until sunset. For analyses, the total number of minutes the female was on the nest (on-bouts, female nest attentiveness), the mean length of recesses (off-bouts, mean time female spent off nest per bout) and minimum daily nest temperature were calculated.

### **2-4- Measurements of male incubation feeding**

The male incubation feeding behaviour inside the nest boxes was recorded with infra-red cameras which were placed directly under the lid of the nest box. In order

to let the birds grow accustomed to the presence of the camera, dummy cameras were placed in the nest boxes before egg laying. On day 5 after incubation onset, the dummy cameras were replaced by real cameras and on day 6 in the morning, recording was started and continued for circa~ 8 hours.

The video data were analysed with the program BirdBox (Hildebrandt, unpublished). The program calculates the picture moments  $M_{ij}$ ,  $i,j = \{0,1,2,3\}$ , and the luminance-histogram for each frame, the running average of frames and the total average of all frames in a video. The program then calculates the mean square errors of the moments of each frame with the moments of the previous frame, the running average and the total average. Similarly, the  $X^2$  distances of the histograms are calculated. From these signals, BirdBox generates a graph with time on the x-axis and 'activity' on the y-axis, with peaks most likely at entry/exit events. This time-line is displayed together with the actual video footage to guide the user finding relevant sequences in the footage. The user annotates events and sequences directly in the time-line. From this, BirdBox generates a summary of the outputs including; male incubation feeding (counts per hour), female nest attentiveness (minutes per hour) and female recess length (minutes). BirdBox uses the hardware accelerated H.264 video decoder of NVidia GPUs and CUDA for image analysis.

The duration the female is on the nest may affect the opportunity for the male to feed the female on the nest. Therefore, incubation feeding (number of times the male feed the female) was defined as the number of feeds while the female was inside the nest box. Note that we could not determine the number of male feedings that may have occurred away from the nest-box due to the dense vegetation surrounding the nest-boxes (see Nilsson & Smith, 1988; Pearse et al., 2004; Matysioková & Remeš, 2010).

## **2-5- Measurements of ambient temperature**

Ambient temperatures were obtained during the recording hours of incubation behaviour and incubation feeding from the metrological station located in Eelde Airport, Groningen, close (1.6 km) to the study area. The average daily temperature was calculated from sunrise until sunset for the days of incubation bahaviour recording (circa 4 consecutive days) per nest box. For the incubation feeding behaviour, the average daily temperature per nest box was used from the beginning until the end of recording (circa 8 hours).

### **2-6- Measurements of habitat quality**

Habitat quality was measured following an established protocol for the study area (for details see Amininasab et al., 2016) by measuring the tree sizes surrounding the nest-boxes in which female incubation behaviour and male incubation feeding were recorded ( $n = 92$ ). For evaluating the radius around each nest-box in which vegetation structure may be relevant, the radius of 20 m was chosen as a compromise between biological plausibility and practical feasibility (Amininasab et al., 2016). Furthermore, it was assumed that the vegetation structure estimates taken at a small spatial scale (the radius of 20 m) are representative for the vegetation at a wider scale surrounding the nest-boxes. Within the 20 m radius of nest-boxes, we sampled and identified the species of all living trees with a minimal circumference of 30 cm. Trees with thinner trunks were excluded as they were not considered to harbour a substantial amount of food for breeding blue tits. The trees' circumference (cm) was measured about 130 cm from the ground, using a measuring tape. We identified and measured 3727 trees surrounding the selected nest-boxes. We used the counts of trees including deciduous ( $n = 3209$ ) and coniferous species ( $n = 518$ ) surrounding the nest-boxes as habitat variables which represent food availability around the nest-sites. We also calculated the proportion of deciduous trees, defined as the number of all deciduous trees divided by the total number of all trees, in the 20 m radius around the nest-box as an index of habitat quality. The most dominant species surrounding the selected nest-boxes was English oak *Quercus robur* ( $n = 1047$ ), a deciduous species and an important source of the main prey item for blue tits, caterpillars, during the breeding season (Perrins, 1991; Blondel et al., 1991). Hence, the density of English oak trees was also defined as a separated index of habitat quality.

### **2-7- Ethical considerations**

This study conforms to the animal welfare standards and all experiments approved by the animal experimentation standards of the University of Groningen (DEC-6367). Data obtained from the temperature data loggers and red-vision cameras indicated that in most cases the birds returned to the nest. We used standard methods in capturing and handling adults in the nest-box. The duration of placing the temperature loggers, setting cameras and handling adults was kept to a minimum to minimize stress for the individuals.

### **2-8- Statistical analyses**

For the statistical analyses, we used the program R (version 3.1.0.; R Development Core Team, 2014). Two types of models were applied to analyze the relationships



between environmental and individual parameters (ambient temperature, habitat quality and age of each individual), and patterns of female incubation behaviour (female nest attentiveness, length of recess, and minimum nest temperature) or male incubation feeding frequency. Model residuals were always checked to confirm assumptions of normality. First, we applied linear models with normally distributed errors to test the relationships between patterns of female incubation behaviour (response variable) and environmental parameters and age of the female. Length of recesses was log transformed to ensure normality of the data. Second, for analyses of male incubation feeding, a generalized linear model with Poisson distribution (offset = total female incubating time) was used with male incubation feeding as response variable, and ambient temperature, habitat quality, age of male and age of female partner as predictors. In addition, Pearson correlations were used to explore singular correlations between variables, to detect collinearity between variables. As the density of English oak trees was positively correlated with proportion of deciduous trees surrounding the nest-boxes ( $r = 0.33$ ,  $P = 0.001$ ), the proportion of deciduous trees was included as an index of habitat quality in the models. Non-significant terms ( $P < 0.05$ ) were removed using stepwise deletion until the minimal model was produced. Statistical parameters of non-significant predictors were presented immediately before they were removed from the model.

### 3- Results

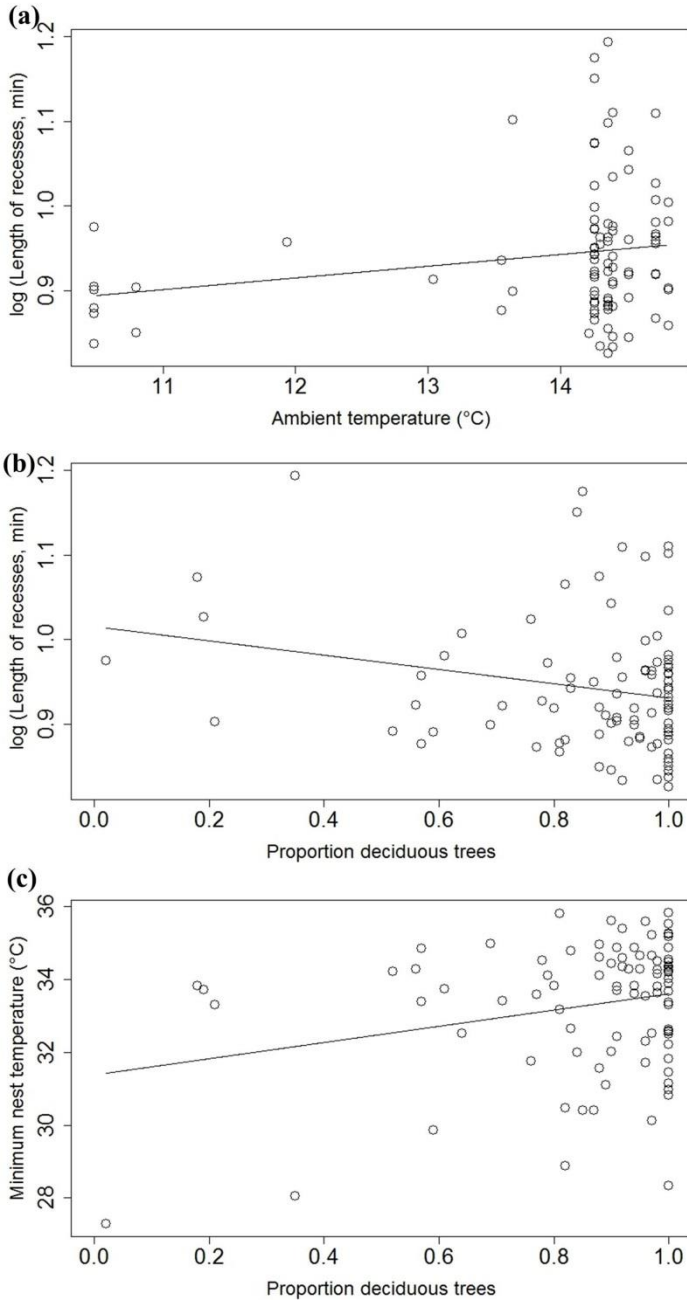
#### 3-1- Female incubation behaviour

Female blue tits left the nest-boxes with off-bouts averaging 8.91 min (SD = 1.80,  $n = 92$ ). The mean minimum nest temperature was 33.29 °C (SD = 1.80). The total mean female nest attentiveness was 42.15 (SD = 4.38) min. per hour. The average length of recesses per female was negatively correlated with the minimum nest temperature ( $r = -0.32$ ,  $P = 0.002$ ) and total nest attentiveness ( $r = -0.23$ ,  $P = 0.026$ ).

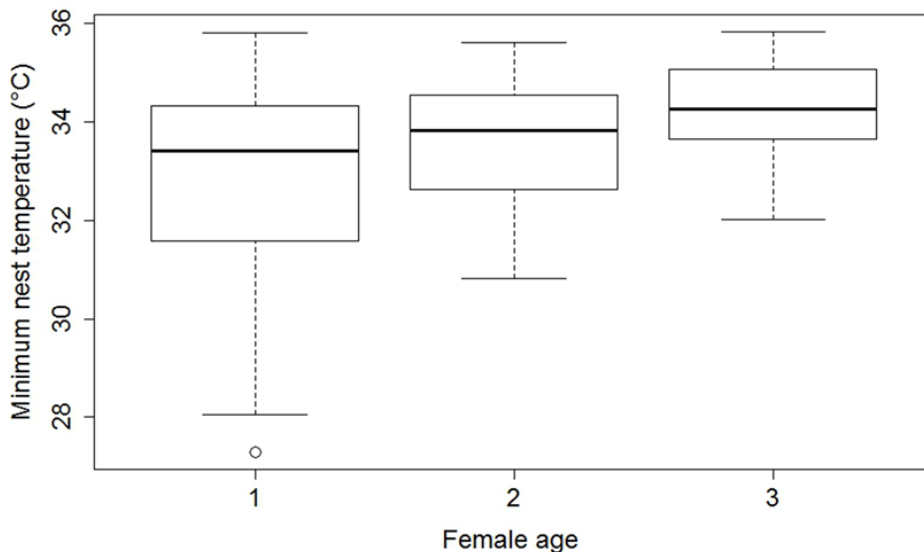
Females took significantly shorter recesses when the ambient temperature was lower and also when the proportion of deciduous trees surrounding the nest-boxes was higher (Table 1, Fig. 1a, b). There was no significant effect of female age on length of recesses. None of the variables investigated were associated with total female nest attentiveness (Table 1). The minimum nest temperature was higher when the ambient temperature and the proportion of deciduous trees surrounding the nest-boxes were higher (Table 1, Fig. 1c) and when females were older (Table 1, Fig. 2).

**Table 1** Linear model analyses of factors predicting length of recesses (min), female nest attentiveness (min/h) and minimum nest temperature (°C) over the incubation period ( $n = 88$ ) in blue tits.

Predictors	Length of recesses (min)			Female nest attentiveness (min/h)			Minimum nest temperature (°C)		
	Estimate ± SE	<i>t</i> value	<i>P</i> value	Estimate ± SE	<i>t</i> value	<i>P</i> value	Estimate ± SE	<i>t</i> value	<i>P</i> value
(Intercept)	0.813 ± 0.109	7.429	< 0.001	49.387 ± 6.368	7.756	< 0.001	25.072 ± 2.377	10.546	< 0.001
Ambient temperature (°C)	0.015 ± 0.007	1.990	0.049	-0.546 ± 0.447	-1.221	0.23	0.399 ± 0.167	2.388	0.019
Proportion deciduous trees	-0.095 ± 0.040	-2.335	0.021	1.680 ± 2.367	0.710	0.48	1.948 ± 0.884	2.204	0.030
Female age	0.000 ± 0.012	0.034	0.97	-0.629 ± 0.690	-0.910	0.36	0.585 ± 0.258	2.269	0.025



**Figure 1** The effect of ambient temperature and proportion of deciduous trees on patterns of female incubation behaviour. (a, b) the relationship between the length of female recess (min) with ambient temperature (°C) and proportion of deciduous trees surrounding the nest-boxes, respectively. (c) the relationship between the minimum nest temperature (°C) and proportion of deciduous trees surrounding the nest-boxes.



**Figure 2** Boxplots of minimum nest temperature (°C) in females with different age over the incubation period. Boxes indicate the median, and 25th and 75th percentiles; whiskers indicate the lowest and highest datum within 1.5 times the interquartile range (IQR) from the first and third quartile, respectively.

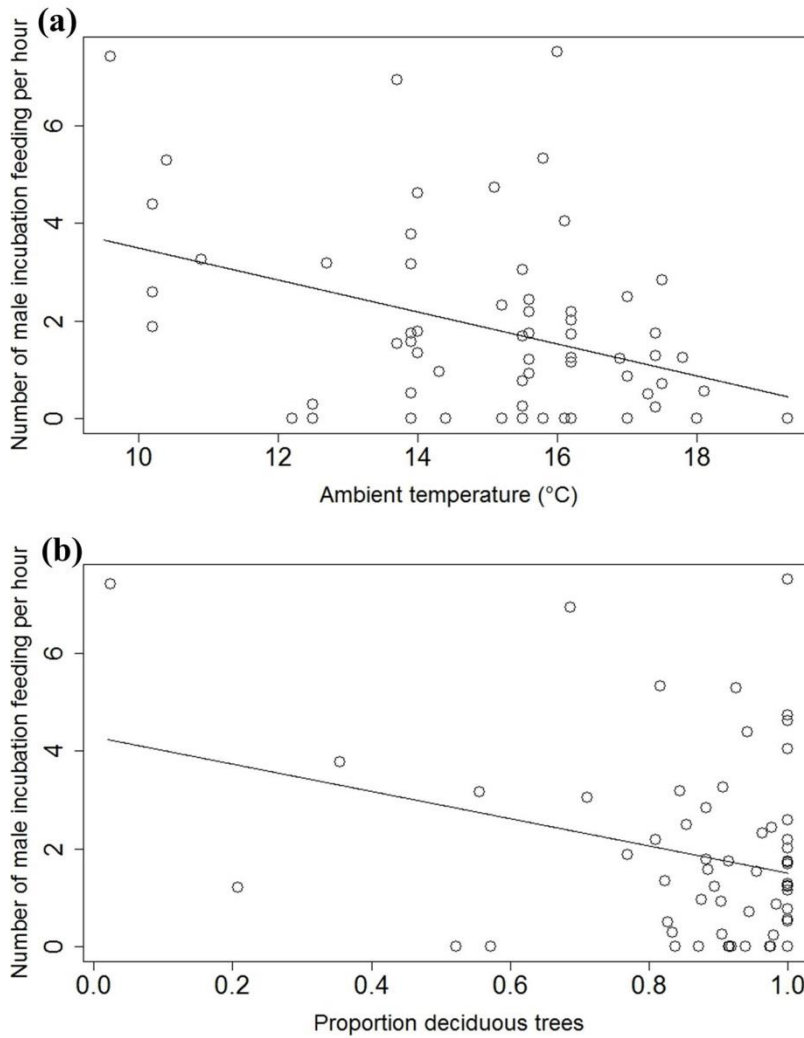
### 3-2- Male incubation feeding behaviour

Males fed the females on average 1.84 times per hour (SD = 1.89, range = 0 – 7.52,  $n = 63$ ). The frequency of male incubation feeding during the time the female was in the nest-box decreased with higher ambient temperatures and with a higher proportion of deciduous trees surrounding the nest-boxes (Table 2, Fig. 3a,b). There was no effect of male age and age of his female partner on intensity of male incubation feeding surrounding the nest-boxes with higher proportion of deciduous trees (Table 2).

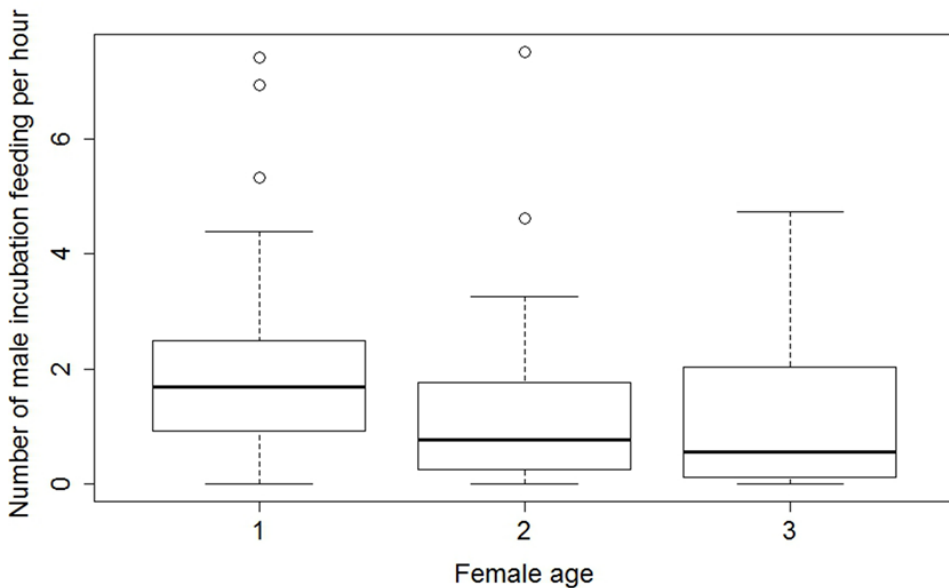
As female age was collinear with proportion of deciduous trees ( $r = 0.29$ ,  $P = 0.037$ ), we tested an alternative model only investigation the effect of female age on male incubation feeding which suggests that males increased the intensity of incubation feeding when their partners were younger (Fig. 4, Estimate  $\pm$  SE =  $-0.178 \pm 0.066$ ,  $z = -2.711$ ,  $n = 59$ ,  $P = 0.006$ ).

**Table 2** General linear model analysis with a Poisson distribution of factors predicting the intensity of male incubation feeding per female attentive hour ( $n = 53$ ).

Predictors	Number of male incubation feeding per female attentive hour		
	Estimate $\pm$ SE	$z$ value	$P$ value
(Intercept)	2.855 $\pm$ 0.278	10.262	< 0.001
Ambient temperature ( $^{\circ}$ C)	-0.120 $\pm$ 0.019	-6.323	< 0.001
Proportion deciduous trees	-0.550 $\pm$ 0.186	-2.956	0.003
Male age	-0.038 $\pm$ 0.082	-0.464	0.64
Partner (female) age	-0.071 $\pm$ 0.069	-1.026	0.30



**Figure 3** The relationships between the intensity of male incubation feeding per female attentive hour and the (a) ambient temperature (b) proportion of deciduous trees surrounding the nest-boxes over the incubation period.



**Figure 4** Boxplots of the intensity of male incubation feeding per female attentive hour in females with different age over the incubation period. Boxes indicate the median, and 25th and 75th percentiles; whiskers indicate the lowest and highest datum within 1.5 times the interquartile range (IQR) from the first and third quartile, respectively.

## 4- Discussion

### 4-1- Female incubation behaviour

Our results show that ambient temperature is one of important predictors of female incubation behaviour. Although total female nest attentiveness was not associated with ambient temperature, females modified the length of each recesses bout depending on the temperature. Lower temperatures caused females to spend less time off the nest per bout. It is found before that birds decrease the length of recesses when ambient temperatures are lower (Biebach, 1986; Conway & Martin, 2000; Boulton et al., 2010), most likely because of potentially harmful effects on the developing embryos when eggs are unincubated for prolonged amounts of time when it is cold (Boulton et al., 2010). In addition, prolonged recess would result in a net loss of female energy for re-warming the eggs (Camfield & Martin, 2009). However, there are studies which indicate no effect of ambient temperature on egg temperature (e.g. Bogdanova et al., 2007). Hence, these patterns can vary depending on species, populations, environment and also between different stages of the incubation cycle.

Habitat quality, another important parameter of environmental characteristics, may influence incubation behaviour (Henson & Cooper, 1993; Zicus et al., 1995; Rauter & Reyer, 1997, MacCluskie & Sedinger, 1999; Manlove & Hepp, 2000). For example, female nest attentiveness can increase in better quality habitats, because females using high-quality habitats are better able to satisfy food requirements (see Rauter & Reyer, 1997; Zanette et al., 2000; Eikenaar et al., 2003; Zimmerling & Ankney, 2005; Duncan-Rastogi et al., 2006; Chalfoun & Martin, 2007). Furthermore, higher food availability enables females to spend more time keeping eggs at optimal temperatures which may reduce the costs of incubation (Londoño et al., 2008). However, in our population, similar to Matysioková & Remeš's (2010) study on great tits, female nest attentiveness was not directly related to habitat quality. However, females took shorter off-bout length in high-quality habitats, suggesting that females presumably were able to find their food resources faster in these higher quality habitats.

In addition to environmental conditions, female age can influence on the incubation behaviour. In our study population, there was no effect of female age on length of recesses or female nest attentiveness. But, female age was positively associated with nest temperature. This result indicates that younger females may be physiologically limited in their energetic constraints and ability to incubate eggs (Aldrich et al., 1983; Yerkes, 1998), where older females may be more capable to insulate the eggs during the incubation. Additionally, in a study on glaucous-winged gull *Larus glaucescens*, Reid (1988) similar to us found that female age is not related to female nest attentiveness. In another study, Bogdanova et al. (2007) found no effect of female age on egg temperature in herring gull *Larus argentatus*. However, there are not enough studies to date to draw conclusions about age-specific patterns of incubation behaviour. Hence, more longitudinal studies are needed to unveil the mechanisms underlying the female age and patterns of incubation behaviour in birds.

#### **4-2- Male incubation feeding**

Our results show that the frequency of male incubation feeding during the time the female was in the nest-box decreased with higher ambient temperatures. Furthermore, the intensity of male incubation feeding was lower in nest-boxes around which the proportion of deciduous trees was higher. This shows that males lower their intensity of incubation feeding when environmental temperature and food conditions are favourable and under which females can reduce the duration of incubation bouts (Lifjeld & Slagsvold, 1986; Lifjeld et al., 1987; Smith et al., 1989; Kovařík et al., 2009). However, several studies showed opposite results. For



example, Zanette et al. (2000) found that male Eastern yellow robins *Eopsaltria australis* fed their incubating females more in high-quality habitats. In a study on great tits, Matysioková & Remeš (2010) indicated that male incubation feeding increased with habitat quality, but only in years with low food availability. The lower intensity of male incubation feeding in high quality habitats in our study indicate that likely, the area offered sufficient food resources to enable females to fulfill food requirements themselves. However, in agreement with Matysioková & Remeš (2010) study on great tits, our findings are based on male incubation feeding inside the nest-box and we were not able to measure the incubation feeding rate out of the nest-box which may obscure an habitat quality effect on overall incubation feeding. Furthermore, food availability usually covaries with ambient temperature (Londoño et al., 2008) and because of this, we cannot separate the effect of ambient temperature from habitat quality. However, it is also given that individuals that live in high-quality habitats with higher food availability may be able to compensate easier the temperature-induced stress (Dykstra & Karasov, 1992; McWilliams et al., 1999). Hence, we suggest that males feed the incubating females more in low-quality habitats (e.g. coniferous habitat) and when ambient temperature is lower. Thus, males feed females more often under circumstances when females need to incubate their eggs more, or at least when they can not afford to leave the nests for long at the time.

The intensity of incubation feeding in our study population was independent of male age, which was also found in great tits (Matysioková & Remeš, 2010). This was in contrast to our expectations, because we expected an increase in incubation feeding with male age due to improved experience and foraging efficiency. In spite of this, males only increased the intensity of incubation feeding when their partners were younger. This indicates that partners likely monitor each other's potential for parental care patterns (Houston et al., 2005). However, there are very few studies which indicate how incubation feeding varies with male age and the age and quality of female partner. Hence, more studies are needed to clarify the general effect of male and partner age on incubation feeding within and between species of birds.

## 5- Conclusion

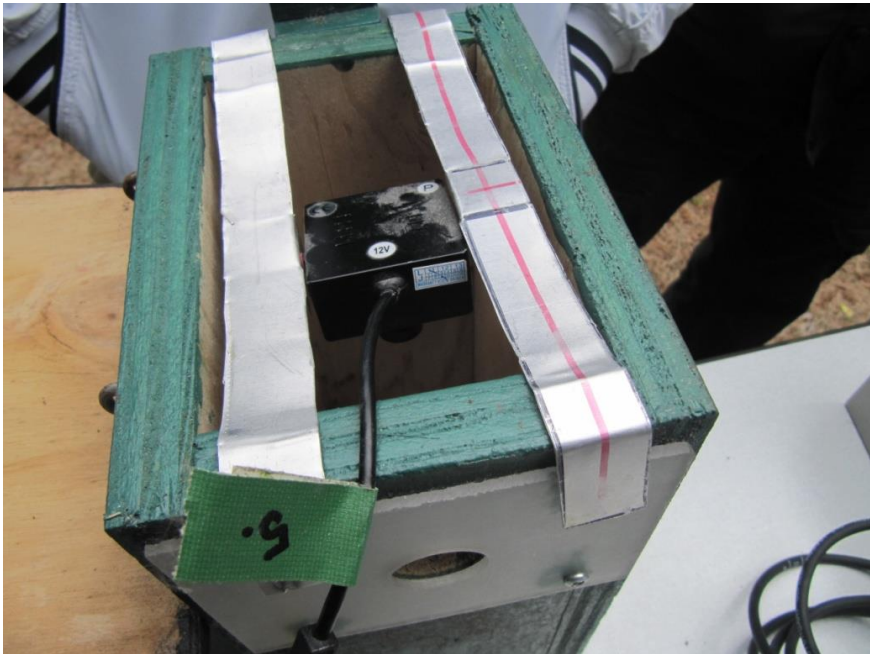
An increase in ambient temperature resulted in a higher nest temperature and this enabled females to increase self-maintenance activities off the nest. Probably as a consequence of this, an increase in ambient temperature was associated with fewer incubation feedings by the male. Similarly, in areas with more deciduous trees, females had shorter duration of recesses and males had a lower frequency of

incubation feeding. Males also increased the frequency of incubation feeding when their partners were young. The nest temperature of older females was higher. In conclusion, the patterns of incubation behaviour and incubation feeding were related to both environmental and individual characteristics, which can facilitate new insights to the study of avian incubation energetics and how species differ in patterns of parental care.

### **Acknowledgements**

We thank the Kraus-Groeneveld Stichting for permission to work on De Vosbergen estate. We thank Peter Korsten for general advice during the project and Roy Gommer and Paulien van der Werf for helpful analyses of temperature logger data. We also thank Bachelor and Master students for their indispensable help in the field in 2014. Permission for all procedures involving handling of blue tits was granted by the Animal Experiments Committee (DEC) of the University of Groningen, The Netherlands. The research was financially supported by a grant from The Netherlands Organisation for Scientific Research (NWO-ALW 821.01.008) and other grants funded to Jan Komdeur.





Photos: Seyed Mehdi Amininasab

# Chapter 6

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## **The effect of male incubation feeding on female nest attendance and reproductive performance in a socially monogamous bird**

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Journal of Ornithology (Submitted)

### **Abstract**

Incubation of eggs is a key factor of avian parental care. To ensure embryo development, incubating parents have to keep their eggs within appropriate temperature limits. To do so, incubating individuals allocate substantial energy to the thermal demands of their eggs, but they face a trade-off with self-maintenance (own metabolism) because they usually cannot forage during incubation. In species with female-only incubation, males can aid their partners by providing them with food on the nest. This may enable females to spend more time incubating and could, consequently, lead to improved reproductive performance. In this study, we investigated whether male incubation feeding affects female nest attendance in blue tits, *Cyanistes caeruleus*, and subsequently determined how this affects reproductive performance. We found that females incubated more when they were fed more by their male. Thus, males may enable females to incubate more when needed, as is in turn suggested by the fact that male incubation feeding was more frequent when the ambient temperature was lower and females incubated later in the season. Although male incubation feeding and female incubation behaviour did not result in a shorter time until the eggs hatched or higher hatching success, females that attended the nest more produced heavier nestlings. We suggest that the trade-off between self-maintenance and meeting eggs demands is lessened when females are assisted more by their partner during incubation.

## 1- Introduction

Incubation, being a key factor of avian parental care, requires a substantial energetic investment by incubating individuals (e.g. Camfield & Martin, 2009; Bulla et al., 2014). To ensure embryo development, eggs have to be kept within appropriate temperature limits (Yom-Tov et al., 1978; Reid et al., 1999, 2000; Stein et al., 2010). Thus, incubation is a crucial part of reproduction in almost all avian species (Matysioková & Remeš, 2010), but, as incubation is costly because individuals cannot incubate and forage at the same time, incubating individuals also face a trade-off with self-maintenance. A common system that has been adopted by most bird species, possibly as a resolution to this trade-off, is a uniparental incubation system in which only the female incubates while the male aids her by supplying food ('male incubation feeding'; Haľupka, 1994; Matysioková & Remeš, 2010; Stein et al., 2010). The 'female nutrition' hypothesis (Royama, 1966) is one of the most invoked theories in this context and states that male incubation feeding enables the female to increase the amount of time she can spend incubating (female nest attendance, Royama, 1966; Camfield & Martin, 2009; Matysioková et al., 2011; Stein et al., 2010; Ibáñez-Álamo & Soler, 2012). Hence, in order to understand avian reproductive strategies, it is important to understand the interplay between female incubation and male incubation feeding and the underlying factors that drive variation in these behaviours.

Previous research shows that the frequency of male incubation feeding often differs between individuals (Royama, 1966; Hatchwell et al., 1999; Matysioková et al., 2011; Stein et al., 2010). If male incubation feeding affects female incubation behaviour, this variation may be explained by variation in circumstances that affect the need for incubation. For example, environmental factors, such as (seasonal changes in) ambient temperature (Webb, 1987; Hatchwell et al., 1999; Camfield & Martin, 2009; Matysioková & Remeš, 2010) may affect the cooling down of eggs which may require females to incubate more. Furthermore, characteristics of the clutch, like number of eggs, may be correlated with male incubation feeding: females with a larger clutch may require more energy to incubate the eggs or may spend more time on incubating and less on foraging (de Heij et al., 2007), so that males might need to feed females who incubate larger clutches more frequently. Overall, females and males are expected to adjust respectively nest attendance and incubation feeding frequency to these factors in such a way that they shorten the incubation period (Haľupka, 1994; Hatchwell et al., 1999; Camfield & Martin, 2009; Stein et al., 2010), decrease developmental risks, and/or maximize hatching and reproductive success (Lyon & Montgomerie, 1985; Hatchwell et al., 1999; Martin & Ghalambor, 1999; Tulp &

Schekkerman, 2006; Stein et al., 2010). Therefore, it can be expected that the variation in incubation and incubation feeding affects individuals' reproduction depending on environmental circumstances and characteristics of the clutch.

In this research we investigate the effect of male incubation feeding on female nest attendance and pairs' reproductive performance in blue tits, *Cyanistes caeruleus*, a passerine species with female-only incubation and typical male incubation feeding behaviour. Little study has been done on the proximate and ultimate components of male incubation feeding in blue tits (see Nilsson & Smith, 1988) which stresses the necessity of additional research. Our study has the following aims (see also Fig. 1a): (i) to investigate whether environmental factors (i.e. ambient temperature) and life-history traits (i.e. the date of incubation onset and clutch size) relate to male incubation feeding and female nest attendance. (ii) to determine whether male incubation feeding leads to higher female nest attendance. (iii) to investigate the relation between female nest attendance and her reproductive performance, specifically the duration of the incubation period, hatching success and nestling body mass.

## **2- Materials and methods**

### **2-1- Study area and brood characteristics**

This study was conducted during the breeding season (March-June) of 2014 in 'De Vosbergen' which is located in northern Netherlands (53° 08'N, 06° 35'E). The area consists of 54 ha of mixed deciduous and coniferous forest, woodlands and spaces of grassland. In total 209 nest boxes designed for blue tits were present in the study population in 2014.

The first nest box check was performed at the end of March. Subsequently, occupied nest boxes with nesting material were regularly monitored to determine the date of first egg-laying, clutch size, date of incubation onset, duration of incubation period, hatching date and hatching success (proportion hatched eggs). After egg-laying started nest boxes were not approached for 6 additional days, to minimize disturbance of the nest (note that blue tits usually lay more than 7 eggs). After day 7, nest-checking was performed every day until incubation onset was observed. Incubation onset was either indicated by the female being present incubating the eggs or by the eggs being warm and uncovered during the nest check. When the date of incubation onset was determined, nest-checking was continued every day starting at day 11 of incubation to check for hatching (hatching day 1 is the day of the hatching of the first egg). Four days after hatching the nestlings were weighed using a Pesola spring balance. Nestling body mass was



not related to time of day when they were weighed ( $n = 59$ ;  $P = 0.19$ ), and therefore the original nestling body mass was used in the analyses.

## **2-2- Frequency of incubation feeding**

The incubation and incubation feeding behaviour inside the nest boxes were recorded with infra-red cameras which were placed directly under the lid of the nest box. In order to let the birds accustom to the presence of the camera, dummy cameras were placed in the nest boxes before egg laying. On day 5 after incubation onset, the dummy cameras were replaced by real cameras and on day 6 the recording was started between 8am and 11am and continued for on average ( $\pm$  SD)  $7.47 \pm 1.25$  hours ( $n = 63$  nest boxes).

The video recording were analysed with a specially designed program 'BirdBox' which enabled faster and more efficient video analyses (see Amininasab et al., submitted, Chapter 5 for detailed procedures). From this, BirdBox generates a summary of the outputs including (i) male incubation feeding (counts per hour), (ii) female nest attendance (minutes per hour). For male incubation feeding, we used similar data as in Amininasab et al. submitted (Chapter 5), in which we investigated the combined effects of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding. However, here we use incubation feeding behaviour in order to link this behaviour directly with female nest attendance and reproductive performance. From these data, male feeding per hour incubation was calculated as the number of feeds divided by the total time his female was incubating.

## **2-3- Ambient temperature**

To estimate the ambient temperature during the incubation period, hourly measurements of the online weather archive of Eelde Airport, Groningen (1.6 km from our study area), were used. The average temperature from the beginning until the end of recording was calculated per nest box.

## **2-4- Statistical analyses**

For the statistical analysis, the program R (version 3.1.0.; R Development Core Team, 2014) was used. We tested for several correlations as is indicated in Fig. 1a and Table 1. To test for correlations between male incubation feeding (response variable) and ambient temperature, clutch size and date of onset of incubation (independent variables), a generalized linear model with Poisson distribution (offset = total female incubating time) was used. To test whether male incubation feeding predicted female nest attendance, a linear model was used, with male

incubation feeding frequency as independent variable and female nest attendance as response variable, including ambient temperature, clutch size and date of onset of incubation as independent variables. The relationship between female nest attendance and incubation period (total number of days of incubation, response variable) was analysed with a generalized linear model with Poisson distribution while also including above-mentioned covariates. The correlation between female nest attendance and hatching success was tested with a generalized linear mixed model with a binominal distribution and logit link function (cbind) and the above-mentioned covariates. Male incubation feeding frequency was not included as a direct predictor for duration of incubation and hatching success, because incubation feeding could influence these variables through its effect on female nest attendance (Matysioková & Remeš, 2010). Finally, the relationships between male incubation feeding and female nest attendance, female nest attendance and nestling body mass, were analysed using linear models. The average nestling body mass per brood was used as the response variable. In all models, we started with the model including all independent variables and dropped the least significant variable in each step to find the minimal adequate model (where all variables had a significant effect;  $P < 0.05$ ). Due to the potential presence of collinearity between independent variables, we additionally tested for all singular correlations without other covariates, using spearman rank correlations (see Table 1).

### **2-5- Ethical note**

All procedures were performed according to the animal experimentation standards of the University of Groningen (DEC number 6367). Handling times and nest box visits were kept to a minimum in order to minimize disturbance of the birds.

### **3- Results**

The average clutch size was 11.06 eggs (SD = 1.71, range = 8 – 15,  $n = 63$ ) and the first and last date of onsets of incubation were 16 April and 02 May, respectively. The average ambient temperature during the recordings throughout the breeding season was 15.07°C (SD = 2.18, range = 9.57 – 19.30°C). On average, males fed the females 1.84 times  $\text{h}^{-1}$  of incubation (SD = 1.89, range = 0 – 7.52,  $n = 63$ ). In 14 of 63 (22%) observed nest boxes, females were never fed by males inside the nest box during the recording. Excluding those unattended nests resulted in an average male incubation feeding of 2.37 times  $\text{h}^{-1}$  of incubation (SD = 1.83, range = 0.22 – 7.52,  $n = 49$ ). On average, females incubated 43.93 min per hour (SD = 3.76, range = 35.13 – 51.36,  $n = 63$ ). Average hatching success (proportion hatched) was 0.88 (SD = 0.16, range = 0.33 – 1,

$n = 62$  ; one brood was abandoned before hatching) and incubation period was on average 13.45 days (SD = 1.30, range = 11 – 18,  $n = 62$ ). Average nestling body mass was 3.24 g per brood (SD = 0.52, range = 1.66 – 4.26,  $n = 59$ ; nestlings died before weighing in 3 nest boxes).

We show an overall overview of found relationships between environmental variables, life-history traits, incubation patterns and reproductive performance in Fig. 1b and explain each result separate in detail below.

### **3-1- Male incubation feeding in relation to incubation onset, ambient temperature and clutch size**

The frequency of male incubation feeding significantly increased throughout the breeding season (Table 2, Fig. 2). There was no significant effect of ambient temperature on male incubation feeding in the model with co-variates (Table 2). However, this might have been the effect of ambient temperature and incubation onset being correlated, as male incubation feeding was negatively correlated with ambient temperature (Table 1). Clutch size did not predict male incubation feeding (Table 2).

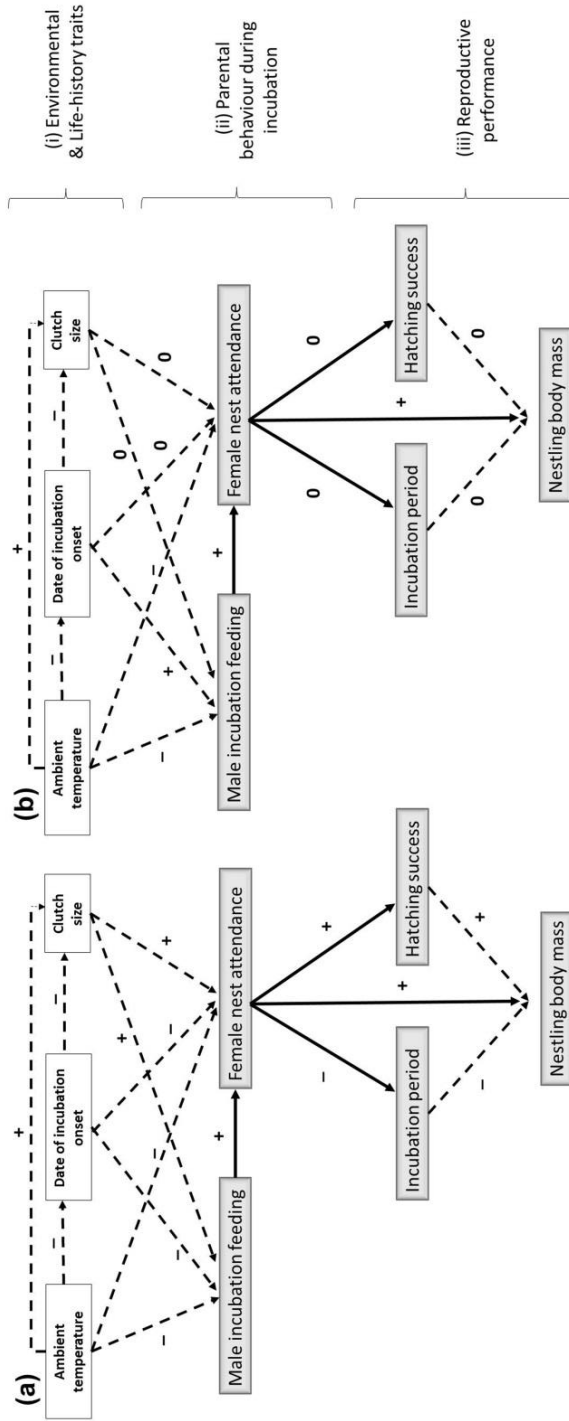
### **3-2- Female nest attendance in relation to male incubation feeding**

When including all co-variates, only ambient temperature negatively influenced female nest attendance (Table 3, Fig. 3b), but there was no effect of clutch size, date of incubation onset and frequency of male incubation feeding. However, in the model excluding the co-variates, a higher male incubation feeding frequency predicted higher female nest attendance (marginally significant ( $P = 0.051$ ), Fig. 3a). Again, this difference may be the result of male incubation feeding rate being significantly correlated with ambient temperature.

### **3-3- Reproductive performance in relation to female nest attendance**

Female nest attendance was not related to the incubation period (Estimate  $\pm$  SE =  $-0.006 \pm -0.009$ ,  $Z = -0.71$ ,  $P = 0.48$ ) and hatching success (Estimate  $\pm$  SE =  $0.003 \pm 0.05$ ,  $t = 0.06$ ,  $P = 0.95$ ) and these results were similar when including the co-variates in the model (Tables 4 and 5). We found, however, a positive correlation between female nest attendance and average nestling body mass (Fig. 4).

**Figure 1** An overall scheme of (a) our expectations and (b) results with presumed relationships (i-iii) between environmental variables, life-history traits, incubation patterns and reproductive performance in blue tits. Direction of arrows indicate correlation and effect (solid lines indicate the main story of the study and dashed lines indicate the covariances; no effect: 0, positive: + and negative: -).



**Table 1** Matrix showing Spearman correlation coefficient of pairwise comparison of various variables in blue tits.

	Clutch size	Date of incubation onset	Male incubation feeding	Female nest attendance	Incubation period	Hatching success	Number of nestling	Average nestling body mass
Ambient temperature	0.37 **	-0.62 ***	-0.29 *	-0.27 *	0.28 *	0.08	0.38 **	0.22
Clutch size		-0.34 **	-0.13	-0.15	0.04	-0.13	0.47 ***	0.04
Date of incubation onset			0.34 **	0.23	-0.31 **	0.03	-0.26 *	-0.22
Male incubation feeding				0.25 *	0.05	0.03	0.06	-0.12
Female nest attendance					-0.21	-0.17	-0.06	0.27 *
Incubation period						0.02	0.03	-0.17
Hatching success							0.46 ***	-0.14
Number of nestling								0.09

\*  $P \leq 0.05$ , \*\*  $\leq 0.01$ , \*\*\*  $\leq 0.001$

**Table 2** The effects of ambient temperature, clutch size and date of incubation onset on frequency of male incubation feeding in blue tits ( $n = 63$ ). Values for significant predictors included in the final model are in bold.

Frequency of male incubation feeding per hour				
Variables	Estimate	SE	<i>t</i> value	<i>P</i> - value
Intercept	-1.70	0.67	-2.54	0.01
Ambient temperature	-0.05	0.07	-0.70	0.48
Clutch size	0.05	0.07	0.66	0.51
Date of incubation onset	<b>0.11</b>	<b>0.03</b>	<b>3.57</b>	<b>&lt;0.001</b>

**Table 3** The effects of ambient temperature, clutch size, date of incubation onset and male incubation feeding on female nest attendance in blue tits ( $n = 63$ ). Values for significant predictors included in the final model are in bold.

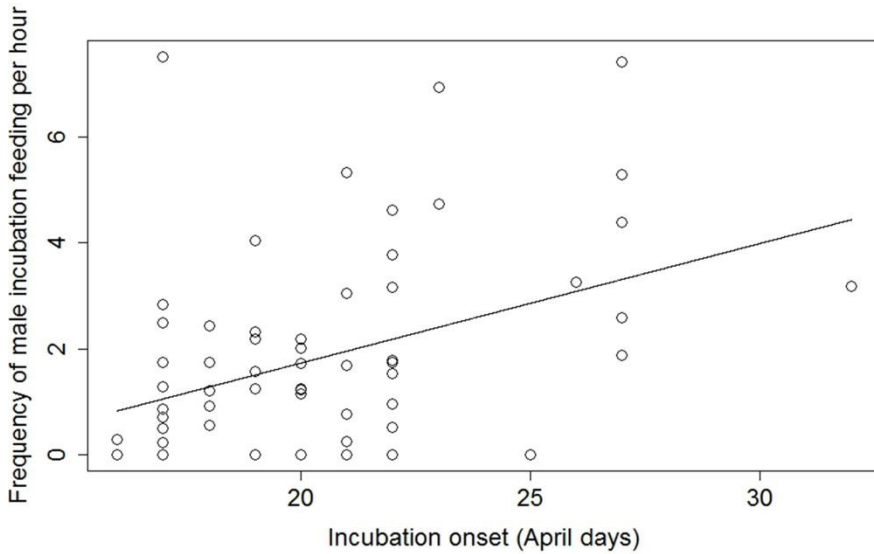
Female nest attendance (min/hour)				
Variables	Estimate	SE	<i>t</i> value	<i>P</i> - value
Intercept	52.82	3.16	16.69	<0.001
Ambient temperature	<b>-0.59</b>	<b>0.21</b>	<b>-2.84</b>	<b>0.006</b>
Clutch size	-0.03	0.31	-0.10	0.92
Date of incubation onset	-0.05	0.19	-0.27	0.79
Male incubation feeding	0.27	0.26	1.05	0.30

**Table 4** The effects of ambient temperature, clutch size, date of incubation onset and female nest attendance on incubation period in blue tits ( $n = 62$ ).

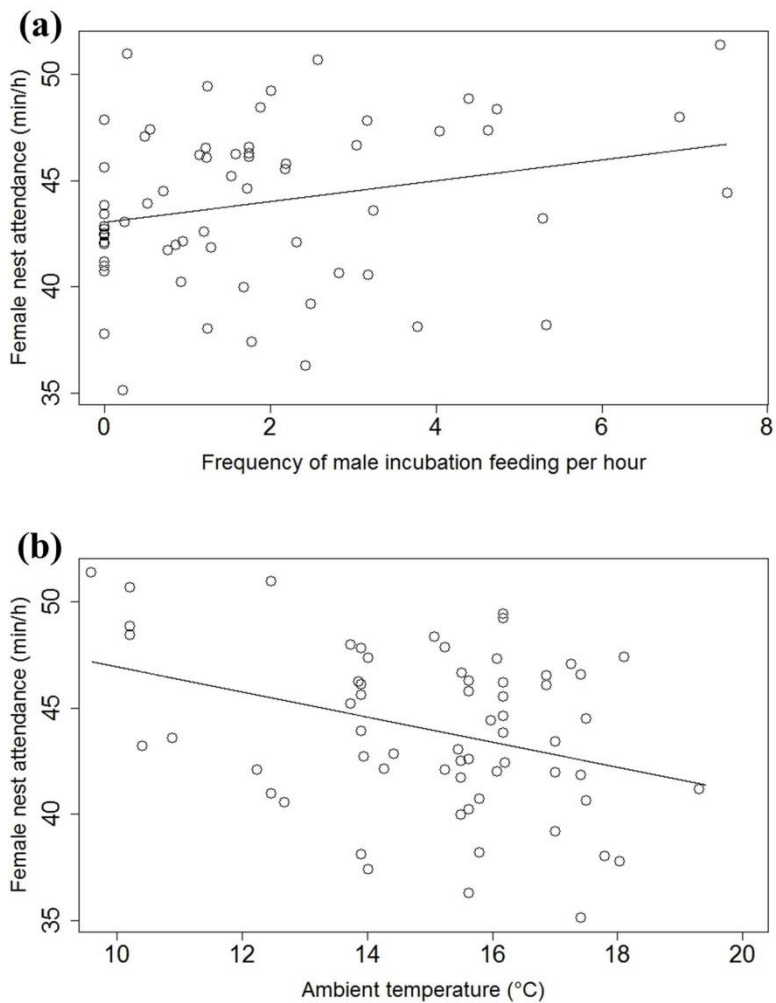
Incubation period (days)				
Variables	Estimate	SE	Z value	<i>P</i> - value
Intercept	2.89	0.80	3.61	<0.001
Ambient temperature	0.003	0.02	0.15	0.88
Clutch size	-0.001	0.02	-0.04	0.96
Date of incubation onset	-0.006	0.01	-0.42	0.67
Female nest attendance	-0.005	0.01	-0.48	0.63

**Table 5** The effects of ambient temperature, clutch size, date of incubation onset and female nest attendance on hatching success in blue tits ( $n = 62$ ).

Variables	Hatching success			
	Estimate	SE	<i>t</i> value	<i>P</i> - value
Intercept	-1.76	4.23	-0.42	0.68
Ambient temperature	0.18	0.12	1.55	0.13
Clutch size	-0.12	0.13	-0.91	0.36
Date of incubation onset	0.08	0.08	1.03	0.31
Female nest attendance	0.01	0.06	0.28	0.78

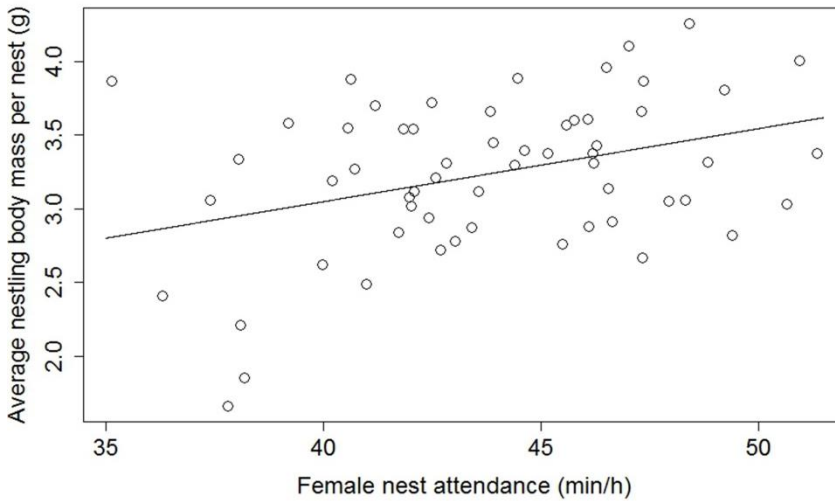


**Figure 2** The frequency of blue tit male incubation feeding is higher later in the season (incubation onset as day in April 2014,  $n = 63$ ).



**Figure 3** Blue tit female nest attendance (a) increases with increasing male incubation feeding frequency (Estimate  $\pm$  SE =  $0.49 \pm 0.24$ ,  $t = 1.99$ ,  $P = 0.051$ ,  $n = 63$ ) and (b) decreases with increasing ambient temperature (see Table 2).





**Figure 4** Average nestling body mass increases with higher female nest attendance in blue tits. (Estimate  $\pm$  SE =  $0.05 \pm 0.02$ ,  $t = 2.93$ ,  $P = 0.005$ ,  $n = 59$ ).

#### 4- Discussion

Our results suggest that the frequency of male incubation feeding increases throughout the breeding season and, in line with this, with lower ambient temperatures. Males do not change the intensity of incubation feeding based on clutch size. Our results therefore support the ‘female nutrition’ hypothesis, as males feed less with higher ambient temperatures when female nest attendance decreases. Female attendance did, however, not result in a shorter incubation period or higher hatching success, but females that exhibit higher nest attendance produced heavier nestlings. We discuss these results, their implications and potential complications below.

##### 4-1- Male incubation feeding in relation to ambient temperature, incubation onset and clutch size

Our results showed that male incubation feeding is significantly correlated with date of incubation onset, where females that incubated later in the season were fed more often. This result can be explained in several ways: (i) Earlier in the breeding season there might be more fertile females in the population (e.g. Vedder et al., 2012) so that males may spend more time visiting potential extra-pair partners instead of spending time on feeding their incubating female. However, the potential for gaining extra pair parentage may have an influence on the frequency

of male incubation feeding (Nisbet, 1973; Tobias & Seddon, 2002; Pearse et al., 2004; Tryjanowski & Hromada, 2005). (ii) Male incubation feeding may also increase over the season because females that incubate earlier in the season may have access to sufficient food in the territory, so that male feeding is less needed (Perrins, 1970; Martin, 1987). Indeed, if food availability is predicted by temperatures, this could explain our results, as males feed more when temperatures are lower. (iii) Food availability may actually be higher for later incubating females and this may also explain why males can feed their female more. Later incubating females may also be fed more as adaptive mechanisms to hatch their brood sooner by more nest attendance, in order to make sure hatching coincides with the food peak (Martin, 1987; Visser et al., 2006). Lifjeld et al. (1987) and Smith et al. (1989) studies on pied flycatchers, *Ficedula hypoleuca*, and Pearse et al. (2004) study on bewick's wrens, *Thryomanes bewickii*, resulted in similar outcomes. Therefore, we suggest that male incubation feeding may increase over the season depending on environmental situations.

We expected a higher incubation cost, such as more female nest attendance and higher frequency of incubation feeding, in larger clutches (Martin & Wiebe, 2000). However, male incubation feeding was not associated with clutch size in our study, which was also found in great tits, *Parus major* (Matysioková & Remeš, 2010). In an experimental study on great tits, clutch size enlargement had no effect on female energy expenditure (de Heij et al., 2008). However, no effect of clutch size on male incubation feeding may be also related to aspects of female behaviour or physiology (e.g. females in better condition laying larger clutches), a suggestion which requires more empirical study.

#### **4-2- Female nest attendance in relation to male incubation feeding**

The results of our study support the female nutrition hypothesis suggesting that male incubation feeding enabled the female to spend more time incubating. However, support for this came from the model that excluded other covariates and is based on a result bordering statistical significance ( $P = 0.051$ ). Including the ambient temperature, the date of incubation onset and clutch size in the model led to different results. Not male incubation feeding frequency, but ambient temperature, was associated with the incubation time spent by females. The different results of the excluding and including covariates might be because of the underlying correlations of ambient temperature and the date of incubation onset with male incubation feeding and these make it impossible to separate the relationships. Hałupka (1994) also found a similar pattern in meadow pipits, *Anthus pratensis*, where male incubation feeding frequency and female nest

attendance both co-varied with ambient temperature. These results suggest that males enable females to spend more time incubating, especially when eggs need to be incubated more. As such, this study adds to the support of the female nutrition hypothesis (Arcese & Smith, 1988; Moreno, 1989; Smith et al., 1989; Hatchwell et al., 1999; Klatt et al., 2008; but see Jawor & Breitwisch, 2006, Matysioková & Remeš, 2010, Boulton et al., 2010).

#### **4-3- Reproductive performance in relation to female nest attendance**

We predicted that an increase in female nest attendance associated with male feedings would shorten the overall incubation period and would increase hatching success due to the reduction of developmental risks. Our results do not support these predictions as there was no correlation of male incubation feeding with incubation period or hatching success. These results are similar as those by Hatchwell et al. (1999) and Pearse et al. (2004) who show no significant link between female nest attendance with incubation period or/and hatching success (e.g. Matysioková & Remeš, 2010; Stein et al., 2010). However, several other studies have documented that food supplementation can reduce incubation period or/and improve hatching success (Lyon & Montgomerie, 1985; Nilsson & Smith, 1988). The inconsistency between these studies and ours remains unexplained, but several potential reasons were put forward by Matysioková & Remeš (2010). First, female nest attendance and subsequent hatching success may be related to unmeasured differences in food quality brought by the male, or females may use food for self-maintenance than for incubation. These explanations seem unlikely to explain the results in our study, as females that were fed more frequently incubated longer. Second, and more likely, hatching success and incubation period may be effected by other factors than incubation, such as inbreeding (Hemmings et al., 2012; Kingma et al., 2013). Third, we could not record the incubation feeding outside the nest box due to the dense vegetation around the nest and monitoring limitations with binoculars (see Nilsson & Smith, 1988; Pearse et al., 2004; Matysioková & Remeš, 2010). However, incubation feeding off the nest may be important for a female's decision and subsequently may have an influence on incubation period length and hatching success. These potential explanations for the lack of correlation between male incubation feeding with incubation period or hatching success need to be considered in future work aimed to assess the potential evolutionary forces driving male incubation feeding.

Although we did not find an effect on hatching success and incubation duration, a higher female nest attendance resulted in higher average nestling body mass. The immediate link between these is not immediately clear and it has to be

noted that after hatching, other factors (e.g. parental feeding rates and ambient temperature during that period) may influence the growth of the nestlings, which may in turn correlate with male incubation feeding (Stein et al., 2010). However, there was no correlation between male incubation feeding and average nestling body mass, which may suggest that incubation, rather than male effort, explains our result. Alternatively, females who leave the nest less often and still find sufficient food, may be able to also feed their brood at a higher rate, as suggested by our finding that female nest attendance resulted in heavier nestlings. It seems that male incubation rate is adjusted to the needs of the incubating female, responding to temporal variation in environmental circumstances, rather than facilitating an overall improvement of reproduction.

Generally, demonstrating a causal effect of male incubation feeding on female nest attendance and other parameters of reproductive performance is difficult. Experimental studies should be conducted to separate the effects and avoid the underlying correlations of explanatory variables. For example, one should experimentally provision additional food to the female, while manipulating the ambient temperature to demonstrate a causal effect between male incubation feeding frequency, female nest attendance and outcomes of reproductive performance. Such an approach may reveal further insights into the patterns of avian incubation behaviour and reproductive performance.

## **5- Conclusions**

This research shows that females that incubate later in the breeding season get fed more by their partners than females that start incubating earlier, which is likely the effect of female nest attendance being higher in lower ambient temperature. The frequency of male incubation feeding increases the female nest attendance. Finally, female nest attendance is not correlated with the duration of the incubation period and hatching success, but may result in the production of heavier offspring. Generally, this research suggests that male incubation rate is adjusted to the needs of the incubating female, rather than facilitating an overall improvement of reproduction.

### **Acknowledgements**

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Photos: Seyed Mehdi Amininasab

# Chapter 7

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**General discussion**

Animal species have specific requirements based on environmental and individual characteristics which likely drive variation in reproductive performance. As parameters of environmental quality, habitat quality and ambient temperature affect reproductive performance in animals through their effects on food availability, particularly in forest birds (van Balen, 1973; Blondel et al., 1991; Holmes et al., 1996; Belda et al., 1998; Pärt, 2001). In addition to environmental quality, differences in individual quality (e.g. age and/or lifespan) lead to differences in reproductive performance (Stearns, 1992). Individual age is the most important predictor of individual quality based on phenotypic traits (Kempnaers et al., 1992; Forsland & Pärt, 1995; Doutrelant et al., 2000; Kipper et al., 2006; Sergio et al., 2009). In this chapter, I use short- and long-term monitoring to discuss the effects of these environmental and individual quality parameters on habitat preference (nest-site occupancy) and parameters of reproductive performance including laying date, clutch size and incubation patterns (female incubation and male incubation feeding). I then explain how these patterns, in association with other life-history traits (e.g. incubation onset and clutch size) influence outcomes of reproductive performance in insectivorous birds.

## **1- Environmental quality and reproductive performance**

### **1-1- Habitat quality effects on nest-site occupancy, laying date and clutch size**

By linking proxies of habitat quality (e.g. vegetation characteristics), occupancy rate and reproductive performance (e.g. laying date and clutch size) we were able to suggest indices of habitat quality. In chapter 2, we found that the proportion of deciduous trees surrounding nest-sites, and the density of English oak trees in particular, seem to be a key environmental index that determines habitat preference (as expressed by nest-site occupancy and reproductive performance) in blue tits. Conversely, coniferous trees were indicators of poor-quality, non-preferred habitat. We were also able to demonstrate that occupancy rate is a reliable, simple and ideal measure of habitat quality and low quality habitats were less frequently occupied over time than higher quality habitats (Chapter 2).

The proximate link between high-quality habitats and reproductive performance (e.g. earlier laying date and larger clutch size) will usually be explained by the availability of food resources (van Balen, 1973; Perrins, 1991; Lambrechts et al., 1997). However, measuring the food availability for birds before and during the breeding period is difficult and we had no data on the amount of food present in the different habitats. Nonetheless, both observational and experimental studies indicated that high-quality habitats would provide more



food than low-quality habitats (e.g. Svensson & Nilsson, 1995; Maícas et al., 2012). However, food directly influences the onset of reproductive performance by affecting the bird's energy (Perrins, 1970; Martin, 1987; Nager et al., 1997). Hence, birds on high-quality habitats are energetically less constrained in reproductive performance (Svensson & Nilsson, 1995).

In addition to habitat type (e.g. deciduous or coniferous), the maturity of trees present in the breeding habitat also plays an important role as a measure of food availability on reproductive performance (Blondel et al., 1987; Arriero et al., 2006). The relationship between tree maturity and food availability in the breeding habitat is different for deciduous and coniferous forests because mature deciduous trees provide more food resources than mature coniferous trees (Atiénzar et al., 2010). In our study, we found higher reproductive performance (e.g. earlier lay date and larger clutch size) in habitats with a higher density of mature English oaks than coniferous trees. In addition, probability of nest-box occupancy over time was higher in the habitats with higher proportion of deciduous trees and higher density of mature English oaks compared to coniferous trees. Accordingly, nest-sites in higher-quality habitats (with a higher proportion of deciduous vegetation and a relatively high density of mature English oaks) – which likely facilitate earlier breeding and larger clutches– become occupied earlier in the breeding season than nest-sites in lower-quality habitats (e.g. with coniferous vegetation, Chapter 2). Habitat selection theory predicts that individuals of a breeding population which occupy and prefer high-quality habitats with more food availability would achieve higher reproductive performance (Fretwell & Lucas, 1970; Bernstein et al., 1991). However, we can suggest that occupancy rate could also be used as a measure of reproductive performance. But, more studies on the relationship between occupancy rate and measures of breeding success (e.g. hatching or fledging success) can clarify this idea with more generality.

Usually the preferred and high-quality habitats are not always the best predictors of fitness. For example, preferred habitats (i.e. deciduous) may sometimes offer poorer reproductive performance than non-preferred (i.e. coniferous) due to the higher density of breeders and lower food availability per breeding pair (Mägi et al., 2009). Therefore, in populations with different vegetation (e.g. see Tremblay et al., 2003; Mägi et al., 2009), different tree species may be better predictors of habitat quality.

### **1-1-1- Does tree logging in habitats influence laying date and clutch size?**

We have correlational evidence that coniferous habitats are non-preferred and low-quality habitats compared to deciduous habitats (chapter 2), supporting less caterpillars and other insect communities as food sources for insectivorous birds (Blondel et al., 1993; Lambrechts et al., 2004). We also found that deciduous habitats were preferred by blue tits, as nest boxes present in deciduous habitats were occupied earlier than nest boxes present in coniferous vegetation (Chapter 2). Using experimental manipulation of individual deciduous and coniferous trees between breeding seasons, we were able to show that tree logging has a negative influence on blue tit reproductive performance. Specifically, we showed that logging of young coniferous trees significantly reduces the number of eggs laid by blue tits. Mature coniferous needles may be unappetizing to insects (Hatcher, 1990), while needles of small coniferous trees may contain less secondary metabolites like tannins and are generally less tough. Hence, young coniferous trees may provide better food resources for blue tits compared to mature trees in coniferous habitats. Thus, for blue tits in coniferous habitats, young coniferous trees may be a particularly important source of food. As food availability is an important constraint for individuals, particularly in degraded or manipulated habitats where food supply is low (Svensson & Nilsson, 1995; Arriero et al., 2006), small changes in coniferous habitats can have large effects on reproductive performance.

Longitudinal analysis also indicated that logging deciduous trees of different sizes had no effect on laying date and number of eggs laid. However, our earlier observational study on this population showed that in habitats with more mature deciduous trees egg laying started earlier with greater number of eggs laid (Chapter 2). That study also suggested that, mature deciduous trees likely provide higher foods for blue tits during the breeding season. Hence, we expected that logging of mature deciduous trees negatively influences the reproductive performance. Perhaps the small number of deciduous trees cut per territory did not significantly affect food supplies and most territories had sufficient food resources available despite logging. Therefore, more experimental studies are needed to investigate the effects of deciduous trees on reproductive performance in more detail.

However, young coniferous habitats should be considered in forest management plans for reproductive performance of blue tits and other insectivorous forest birds.

## **1-2- Environmental quality effects on incubation patterns**

Incubation is an energetically demanding period of the reproductive cycle and incubating individuals usually face a trade-off between spending time on the nest to incubate the eggs to promote embryo development and time off the nest to investment in self-maintenance (Ardia et al., 2009). As such, incubating females are often constrained in their nest attentiveness because of limited access to energy resources while incubating (White & Kinney, 1974; Martin, 1987), and behavioural patterns of incubating females should be a reflection of individual energy requirements (Aldrich et al., 1983). Hence, the role of the male during the incubation period may be essential to understand the energy budget of the female (de Heij et al., 2008). During the incubation stage, egg temperature may also be an important pathway for shaping interactions between female incubation and male incubation feeding (Ardia et al., 2009) because males sometimes feed the incubating female which enables the female to increase nest attentiveness to meet the thermal needs of the eggs and embryonic development. Therefore, habitat quality and ambient temperature as parameters of environmental quality via food availability may influence the pattern of avian incubation and incubation feeding.

In high-quality habitats with high food availability, females spend more time on the nest and shorter trips off the nest - either through faster acquisition of food (Folk & Hepp, 2003; Londoño et al., 2008) or through increased incubation feeding by male partners (Martin & Ghalambor, 1999; Tewksbury et al., 2002). This higher female nest attentiveness can increase incubation temperature. An increase in incubation temperature can increase the rate of embryo development and thus induce a shorter incubation period (Lyon & Montgomerie, 1985; Hatchwell et al., 1999; Stein et al., 2010). In spite of the positive effect of food and temperature on incubation behaviour, the effects of increased food and temperature on incubation behaviour usually offset each other (Londoño et al., 2008). Food frequency (e.g. caterpillars) in forest habitats increases with higher ambient temperature through its effect on an advancement in vegetation bud burst. In our study, higher ambient temperature caused females to spend more time on self-maintenance activities off the nest (e.g. foraging). Furthermore, females took shorter recesses when the proportion of deciduous trees surrounding the nest-boxes increased. We also found much higher nest temperature which indicates females adjust the egg temperature and the length of recesses on the basis of ambient temperature (Chapter 5).

The frequency of male incubation feeding during the time the female was in the nest-box decreased with higher ambient temperatures when the nest-box was situated in high-quality habitat (e.g. higher density of deciduous trees, Chapter 5).

However, the lower frequency of male incubation feeding in high quality habitats in our study indicates that food resources likely were enough during the incubation period and females were able to achieve their food requirements themselves.

## **2- Individual quality and reproductive performance**

### **2-1- Effects of female age and quality on laying date and clutch size**

Individuals in a population are not equal with respect to age and/or lifespan (as an index of individual quality). Therefore, individual quality based on ageing parameters is one of the most important factors which may lead to variation in reproductive performance (Ezard et al., 2007). In our study population, reproductive performance of females improved (earlier laying and larger clutch) with female age (Chapter 4). On average, females improve in reproductive performance up to the age of three years, due to improved skills (e.g. foraging ability and familiarity with the habitat; Forslund & Pärt, 1995). Post-peak analyses in our long-term study allowed us to quantify within-individual senescence. These analyses on females partly suggested a delay in laying date and a decrease in clutch size in older females. Patterns of senescence can differ between populations and species and also between reproductive traits and species may allocate resources differently to reproductive performance traits at old age (see Zhang et al., 2015b; Bouwhuis & Vedder, in press). Furthermore, females that invest more in sex-specific traits of reproductive performance (e.g. laying date and clutch size) may be expected to exhibit faster ageing in these traits (Bonduriansky et al., 2008).

Age of first reproduction (AFR) and age of last reproduction (ALR) particularly reflect the effects of underlying variation in individual quality. Age of first reproduction can be applied as an index of individual quality if higher-quality individuals are able to start reproductive performance earlier than lower-quality individuals (Auld & Charmantier, 2011). Similarly, age of last reproduction can also act as an index of individual quality in studies of age-specific mortality, and senescence (Vaupel & Yashin, 1985; Cam et al., 2002; McCleery et al., 2008). However, there is low variation in age of first reproduction in short-lived species such as blue tits and most individuals in our population started reproductive performance in their first year (Chapter 4). Therefore, the patterns of age-dependent reproductive performance are probably little affected by age of first reproduction (selective appearance) of individuals in our population. Conversely, the effects of age of last reproduction or life span (selective disappearance) may be more important on individual-quality related reproductive performance (van de Pol & Verhulst, 2006) because poor-quality individuals with low reproductive performance die relatively early compared to high-quality individuals with high

reproductive performance (e.g. Blas et al., 2009). Failure to correct for such selective disappearance may lead to wrong interpretation of the patterns of age-specific reproduction (see van de Pol & Verhulst, 2006; Bouwhuis et al., 2009).

Our analyses suggest that longer-lived females have an earlier age-specific laying date than shorter-lived females throughout their lives (Chapter 4). Short-lived individuals were probably more constrained in timing of reproductive performance (due to lower physiological condition or experience/skills) than long-lived individuals (Torres et al., 2011). We found no effect of female lifespan on clutch size (Chapter 4). This indicates that patterns of selective disappearance may vary between reproductive traits because some traits may be determined by the quality of the environment to a larger extent, instead of the quality of the bird (Zhang et al., 2015a, b). In general, we can conclude that effects of female age and lifespan (as an index of individual quality) are important for female reproductive performance.

### **2-1-1- Effect of partner ageing and quality on female laying date and clutch size**

Recent comparative studies showed that in species with bi-parental care, female birds classically increase their reproductive performance (e.g. clutch size) when mated to preferred males (high-quality or attractiveness males, Horvathova et al., 2012). This suggests that males indirectly influence reproductive performance by females. High-quality males are expected to survive better and, since such males are likely to have “good genes”, pass on more genetic benefits to offspring (Brooks & Kemp, 2001). In addition, these males may influence female ageing rate where change in genes expressed on a reproductive trait in one sex affect ageing rate in the other sex (Svensson & Sheldon, 1998; Maklakov et al., 2005; Promislow, 2003).

However, we did not find a relationship between the female’s age-specific reproductive performance with age and lifespan (a measure of quality) of the partner (Chapter 4). This suggests that reproductive performance can vary with either sex depending on species-specific reproductive roles of males and females (Balbontín et al., 2007). The energetic costs associated with egg production and optimizing egg laying onset are probably higher for females than for their male partner (see Monaghan & Nager, 1997; Monaghan et al., 1998). Hence, traits like laying date and clutch size are predominantly female-determined traits. This may explain why we observed age-dependence and improvement in these traits for females.

The patterns of covariation between male age and lifespan with the female partner's reproductive performance vary among species. One explanation for this may be that males may invest more in maintaining a territory in longer-lived species than in shorter-lived species. Therefore, males may exert a greater influence on female reproductive decisions early in the breeding cycle in longer-lived species (Auld et al., 2013). Furthermore, the effect of male age on female reproductive performance may be mediated through environmental conditions. Hence, the relative influence of environmental conditions needs to be considered when comparing the effects of patterns and processes of ageing in different stages of the reproductive cycle, and when comparing patterns in different populations (Nussey et al., 2013).

However, more studies are needed to investigate the generality in between-trait and species differences in the role of male age and lifespan in female reproductive performance.

## **2-2- Effects of age and quality on incubation patterns**

Individual quality usually influences incubation investment (Aldrich & Raveling, 1983; Gatti, 1983) and incubation feeding. Younger and inexperienced females may be physiologically limited in their energetic constraints and ability to incubate eggs (Aldrich et al., 1983; Yerkes, 1998). We found that older females maintain much higher incubation temperatures (Chapter 5). However, there was no effect of female age on average length of recesses and female nest attentiveness. In chapter 5, we showed that males increased the intensity of incubation feeding when their partners were younger. This indicates that breeding partners may monitor each other's behaviour, which in turn may influence their parental care patterns (McNamara et al., 1999; Houston et al., 2005;). When the quality of the females is good, the incubation feeding rate is lower (Lifjeld & Slagsvold, 1986; Lifjeld et al., 1987) and females may be able to meet the food requirements themselves. However, we used one year of data of age of an individual to determine the effect of age on incubation patterns. To our knowledge there are currently no other studies that have assessed the association between individual quality and avian incubation patterns. Hence, the longitudinal patterns of ageing are needed to reveal these associations with more reliability.

## **3- Do other life-history traits also influence incubation patterns?**

Both environmental quality (i.e. habitat quality) and individual quality (age of an individual) can explain variations in life-history traits such as laying date and clutch size, (Chapter 2 and 4) which in turn can have an influence on incubation

patterns. For example, the date of incubation onset usually positively correlates with laying date and both of these negatively correlate with ambient temperature (Chapter 6). Hence, female nest attentiveness decreases in higher ambient temperatures (Chapter 6). Furthermore, these associations may mask a direct relationship between ambient temperature and male incubation feeding, as date of incubation onset as well as ambient temperature determine male incubation feeding in singular correlations (Chapter 6). Together, this shows that males fed females more on the nest when ambient temperature is lower and when females laid their clutches later in the breeding season. This pattern may occur for the following reasons: (i) Earlier in the breeding season, there might be more fertile females in the population (e.g. Vedder et al., 2012) and males might spend more time to seek extra pair matings instead of feeding their incubating female. (ii) females that incubate earlier in the breeding season may have access to sufficient food in the territory (Perrins, 1970; Martin, 1987) and may get enough food independently of male support. (iii) food availability may actually be higher for later incubating females and these females may also be fed more as adaptive mechanisms to hatch their brood sooner by more nest attentiveness, in order to make sure there is a sufficient food available to feed the broods (Martin, 1987; Visser et al., 2006).

Environmental and individual characteristics (e.g. habitat quality and individual age) influenced clutch size variations (Chapter 2 and 4). Incubation costs of different clutches are varied based on a clutch's thermal needs (Reid et al., 2000, 2002). Hence, we expected a higher female nest attentiveness and higher rate of incubation feeding in larger clutches. However, incubation behaviour and incubation feeding were not correlated with clutch size in our study (Chapter 6). The absence of an effect of clutch size on incubation patterns in our study may be due to other aspects of female physiology. More empirical and longitudinal studies are needed to reveal the mechanisms underlying the association between clutch size and avian incubation patterns.

#### **4- Do incubation patterns influence outcomes of reproductive performance?**

The results of our study support the 'female nutrition' hypothesis, suggesting that male incubation feeding enable the female to spend more time incubating (Chapter 6). It has been postulated that an increase in female nest attentiveness associated with male feedings would shorten the overall incubation period, which in turn could increase hatching success due to the reduction of embryo developmental risks (Lyon & Montgomerie, 1985; Hatchwell et al., 1999; Tulp & Schekkerman,

2006; Camfield & Martin, 2009; Stein et al., 2010). Our results did not support these predictions, as we found no effect of female nest attentiveness on incubation period length and hatching success (Chapter 6). There was also no correlation between male incubation feeding frequency with incubation period and hatching success (Chapter 6). Hence, we cannot explain the lack of evidence for effects of female nest attentiveness on incubation period length and hatching success. Although we did not have the necessary data for more clarification, there are some ideas which may address these reproductive outcomes (in agreement with Matysioková and Remeš (2010)): (i) female nest attentiveness may be related to quality (type) not quantity of food brought by the male. (ii) female may use the food more into self-maintenance than incubating. (iii) incubation feeding outside the nest-box may be more important, which we have not measured. These reasons may influence female's final decision and subsequently have an effect on incubation period length and hatching success.

In spite of this, a higher female nest attentiveness resulted in higher average nestling body mass (Chapter 6). It is likely that females that breed in high-quality habitats were able to find their food faster with shorter recesses length, hatch their eggs with a higher probability and later provision nestlings with high-quality foods. However, there was no correlation between male incubation feeding and average nestling body mass (Chapter 6). Hence, we were not able to find a direct relationship between male incubation feeding and nestling body mass. This is in agreement with the fact that the rate of male incubation feeding is not a good predictor of parental care after hatching (e.g. Hatchwell et al., 1999; Stein et al., 2010). While the results of our study indicated that male incubation feeding enabled the female to spend more time incubating, demonstrating a causal effect of male incubation feeding on female nest attentiveness and its reproductive outcomes is difficult. Investigating supplementary feeding of females experimentally may demonstrate a causal effect and reveal further insights into the incubation strategies and outcomes of avian reproductive performance.

## **5- How do individuals respond to environment quality according to their own quality?**

We discussed that, in addition to habitat quality as an important parameter of environmental quality, individual quality also determines reproductive performance. Many studies have reported a positive association between individual and habitat quality (e.g. Korpimäki, 1990; Newton, 1991; Candolin & Voigt, 2001; Pärt, 2001). For example, older individuals generally have better access to high-quality resources because of age differences and experience in



finding the best resources (Danchin et al., 1998; Pärt, 2001) and younger and lower quality individuals are usually relegated to lower quality habitats (Newton, 1998). As a result, individual quality differences in reproductive performance may be confounded by environmental conditions (Carrete et al., 2006). Furthermore, high-quality or older individuals may be less sensitive to environmental conditions (e.g. Cam & Monnat, 2000; Hamel et al., 2009; O'Brien & Dawson, 2013) and birds living in high-quality habitats may also be able to compensate the temperature-induced stresses (Dykstra & Karasov, 1992; McWilliams et al., 1999). It is also possible that parental quality may play a significant but smaller role in the determination of reproductive performance than habitat quality (Przybylo et al., 2001). However, environmental and individual quality usually interact with each other and separating the effects of individual and environmental quality is often not easy (Krüger & Lindström, 2001; Sergio & Newton, 2003) and in agreement with Wilkin et al. (2009), more longitudinal and empirical studies are therefore necessary to separate the effects of environmental and individual quality to determine causal pathways between them and reproductive performance.



Photos: Peter Korsten

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Photo: Aida Ghahraman Poori



**Summary**

**Samenvatting**

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Bird species have specific energetic requirements which likely cause some variations in reproductive performance. The most important requirements are related to environmental and individual characteristics. Environmental quality affects reproductive performance through its effects on food availability, particularly in insectivorous birds. In addition to environmental quality, between-individual differences in quality lead to differences in reproductive performance. In this thesis, I investigated the effects of environmental quality (habitat quality and ambient temperature) and individual quality (age and/or lifespan) on nest-site occupancy and features of reproductive performance including laying date, clutch size and incubation patterns (female incubation and male incubation feeding) in blue tits (*Cyanistes caeruleus*). I used the findings to explain how these patterns associate with other life-history traits (e.g. incubation onset and clutch size) to influence outcomes of reproductive performance.

I showed that the proportion of deciduous trees surrounding the nest-sites, and especially the density of English oak trees (*Quercus robur*), seemed to be key environmental factors that determine reproductive performance in blue tits. Conversely, coniferous trees were indicators of poor-quality, non-preferred habitat. Nest-site occupancy rate is a reliable measure of habitat quality; I found a higher occupancy and reproductive performance in habitats with higher density of mature English oaks than coniferous trees.

Using experimental manipulation of individual trees, I demonstrated that logging of coniferous trees has negative effects on blue tit reproductive performance. Specifically, I showed that logging of young (small) coniferous trees in the proximity of nest sites significantly reduces the number of eggs laid.

The quality of the environment had a significant effect on incubation patterns. Controlling for the ambient temperature, females took shorter incubation recesses when the proportion of deciduous trees surrounding the nest-boxes increased. The frequency of male incubation feeding of the female in the nest-box was lower among pairs breeding in high-quality habitats.

Based on individual quality, female reproductive performance in our study population improved (earlier laying and larger clutch) with female age. Longer-lived females had an earlier age-specific laying date than shorter-lived females throughout their lives. Effects of female age and quality are evolutionarily important for female reproductive performance. However, I did not find a relationship between the female's age-specific reproductive performance and the age or lifespan (a measure of quality) of the partner. I conclude that traits like laying date and clutch size are predominantly female-determined traits.

Older females maintained higher incubation temperatures than younger females. Males increased the frequency of incubation feeding when their partners were younger, ambient temperature was lower and when females laid later clutches. The results of the study support the female nutrition hypothesis, suggesting that male incubation feeding enabled the female to spend more time incubating. There was no correlation between incubation patterns and incubation period and hatching success, but higher female nest attentiveness resulted in higher average nestling body mass.

To conclude, environmental and individual quality usually interact with each other and separating their effects can prove extremely difficult. More longitudinal and experimental studies are necessary to separate the effects of environmental quality and individual quality to determine causal pathways between them and avian reproductive performance.

## **De effecten van omgevings- en individuele kwaliteit op reproductief vermogen in pimpelmezen**

Vogels hebben specifieke energetische behoeften die variatie in reproductief vermogen – zoals life history kenmerken en incubatiegedrag – kunnen veroorzaken. De belangrijkste van deze behoeften zijn gerelateerd aan omgevings- en individuele eigenschappen. De kwaliteit van de omgeving beïnvloedt deze reproductieve kenmerken door effecten op voedselbeschikbaarheid, vooral in insectivore vogels. Aanvullend op de kwaliteit van de omgeving, zorgen ook verschillen in kwaliteit tussen individuen voor onderscheid in reproductief vermogen. In mijn proefschrift heb ik de effecten onderzocht van de omgeving (kwaliteit van het habitat en omgevingstemperatuur) en individuele kwaliteit (leeftijd en levensduur) op de bezettingsgraad van nestlocaties en aspecten van reproductief vermogen – waaronder legdatum, legselgrootte en incubatie patronen (incubatie door vrouwen en voer gedrag van de man tijdens de incubatie) – in pimpelmezen (*Cyanistes caeruleus*). Mijn bevindingen heb ik gebruikt om te verklaren hoe deze patronen samenvallen met eigenschappen van de levensloop (“life history kenmerken”; bijv. aanvang van incubatie and legselgrootte) en zo reproductief vermogen beïnvloeden.

In mijn proefschrift laat ik zien dat het aandeel loofbomen in de omgeving van het nest, en in het specifiek de dichtheid van Zomereiken (*Quercus robur*), een van de belangrijkste omgevingsfactoren is die reproductief vermogen bepaald in pimpelmezen. Naaldbomen daarentegen waren indicatoren van habitat van slechte kwaliteit, dat door de vogels werd vermeden. De bezettingsgraad van nestkasten is een betrouwbare maat voor de kwaliteit van het habitat: nestkasten met een hogere bezettingsgraad zijn geassocieerd met gunstigere reproductieve kenmerken en hangen in gebieden met een relatief hogere dichtheid van volwassen Zomereiken.

Door middel van experimentele manipulatie laat ik zien dat het kappen van naald- en loofbomen negatieve effecten heeft op reproductief vermogen in pimpelmezen. In het bijzonder laat ik zien dat het kappen van jonge (kleine) naaldbomen in de omgeving van het nest de legselgrootte negatief beïnvloedt.

De kwaliteit van de omgeving had een significant effect op incubatiepatronen. Onafhankelijk van de omgevingstemperatuur namen vrouwen kortere pauzes tijdens de incubatieperiode als de proportie loofbomen rond de nestkast toenam. Mannen voerden hun vrouwen minder vaak tijdens de incubatie in hogere kwaliteit habitat.

Oudere vrouwen hadden een hoger reproductief vermogen (vervroegde eileg en grotere legselgrootte). Ook hadden vrouwen met een langere levensduur een

vervroegde leeftijdsspecifieke legdatum over hun gehele leven in vergelijking met vrouwen met een kortere levensduur. De effecten van leeftijd en individuele kwaliteit zijn evolutionair belangrijk voor het reproductief vermogen van vrouwen. We hebben echter geen relatie gevonden tussen het leeftijdsspecifieke reproductief succes van de vrouw en de leeftijd of levensduur (een maat voor kwaliteit) van haar partner. Hieruit concludeer ik dat eigenschappen als legdatum en legselgrootte voornamelijk door vrouwen worden bepaald.

Oudere vrouwen hadden een hogere incubatietemperatuur dan jongere vrouwen. Verder verhoogden mannen de voerfrequentie tijdens de incubatie wanneer zij een jongere partner hadden, de omgevinstemperatuur lager was, en wanneer hun vrouw latere legsels had. De resultaten van deze studie ondersteunen de “female nutrition” hypothese, die erop wijst dat het voergedrag van de man de vrouw in staat stelt om langer te incuberen. Er was geen verband tussen incubatiepatronen, de duur van incubatie en broedsucces, maar meer nestbezoek door de vrouw leidde tot een hoger gemiddeld gewicht van de kuikens.

In conclusie, omgevings- en individuele kwaliteit spelen vaak een rol in wisselwerking, en het ontrafelen van deze effecten is daardoor ingewikkeld. Er zijn meer longitudinale en experimentele studies nodig om onderscheid te maken tussen de effecten van omgevings- en individuele kwaliteit en zo het oorzakelijke verband tussen deze effecten en reproductief succes bij vogels te bepalen.





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