Environmental effects on great tit life-histories

Teddy Wilkin
Linacre College

A thesis submitted for the degree of
Doctor of Philosophy
University of Oxford
Michaelmas term 2006

D.Phil. Environmental effects on great tit life-histories.

T.A. Wilkin. Linacre College. Michaelmas 2006

Abstract

Explaining variation between individuals is a central concept in ecology. Phenotypic variation is the product of genes, environments and their interactions. In contrast to genotypes which are fixed within individuals, environments vary considerably in time and space and have measurable effects on phenotypic quality between and within individuals. The aim of the current work was to identify environmental sources of life-history variation in a wild population of the great tit.

The size of Thiessen polygons formed around *c.* 8000 nestboxes occupied over a 41 year period was used to estimate breeding density at the level of the individual. Linear mixed modelling showed that birds breeding in large territories laid more eggs and produced heavier fledglings that were more likely to survive to breed, than those in smaller territories. Systematic capping of territory sizes revealed that birds breeding in territories more than 2ha in size were unconstrained by density. This method of measuring individual density identified important relationships between density and life-histories and allowed for the accurate separation of other environmental effects usually confounded by density.

For example, the life-histories and breeding density of woodland passerines often both vary with distance from the woodland edge. Using the Thiessen polygons to control for density we were able to independently examine edge effects on life-histories. Results confirmed higher density at edges and independently showed that birds near the woodland edge tended to lay smaller clutches of larger eggs later in the season, than birds away from the edge, probably due differences in habitat quality.

A further use of Thiessen polygons was to determine the scale at which to measure oak availability in the vicinity of each occupied nestbox. Birds breeding in oak rich polygons laid larger clutches, earlier in the season and had heavier nestlings than birds in oak poor polygons, independently of density and edge effects. What's more, including oaks in life-history models, reduced or eliminated the effect of the Thiessen polygons, suggesting that density dependent life-histories are to some extent explained by reduced oak availability at high density.

Clutch size, fledgling mass and recruitment were also found to correlate with local soil calcium. Analyses performed at several spatial scales found the greatest effect of calcium at scales of *c.*300m. This figure may indicate the average distance females were travelling to obtain calcium rich food during periods of high demands.

That breeding environments strongly affect life-histories has been demonstrated by the above work. However, no correlations were found between natal environment and the subsequent life-histories of recruited individuals, probably due to high mortality in great tits, which favours current condition over any character that conveys benefits later in life. This result shows that long-term effects of rearing environments cannot be assumed as it depends on the life-history conditions under which they are found.

The results of this study suggest a pervasive role of fine-scale environment variation in determining the life-histories of individual great tits. Moreover, the study demonstrates the efficacy of GIS to model such variation and applying it to explaining life-history variation in long-term databases.

To Mum and Dad
Semper fidelis

'It may metaphorically be said that natural selection is daily and hourly scrutinising, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life.'

Charles Darwin 1859

Acknowledgments

I am deeply indebted to my supervisor, Professor Ben Sheldon, for his astute guidance and unwavering support during course of my D.Phil. Thanks also to Dr Andrew Gosler for his companionship and advice and to Dr Robin McCleery for managing the Wytham database, around which this entire thesis is based. Many thanks also to Dr Dany Garant for being a statistics guru, Drs John Quinn and Matt Wood who commented upon several chapter drafts and to BBSRC who kindly provided funding.

In addition to the above colleagues, this thesis was completed with the help of others whose contributions span several decades; from data collection, to introducing me as a wide-eyed undergraduate to the compelling intricacies of ecology. For the former, thanks must go to all the workers on the great tit project at Wytham who have indefatigably collected data every year since 1947. Special recognition is made of Professor Christopher M. Perrins who, in the early 1960s, extended the great tit project to cover all of Wytham woods, thus encompassing the wide range of environments that are the focus of the current work. For the latter, warm thanks go to Drs John and Margaret Rostron and Mr Richard Lindsay of the University of East London, who were charged with the unenviable task of converting a zealous and ever-questioning undergraduate into a critically reasoning science graduate. Thanks also to my stoical Ewa for following me to three universities so that I could follow my dream, to Emilia for giving me a new reason to do so and to Mum for believing in me.

Dad, sorry you won't see this.

Contents

Appendices

Chapter 1: Introduction

Chapter 1: Introduction

That individuals vary in their ability to survive and reproduce is a fundamental concept in evolutionary ecology. When such variation is heritable across generations (Price & Schluter 1991), it represents the raw material from which natural selection shapes the form and distribution of characteristics in wild populations over time (Chesson 2000). Understanding the sources of individual variation is thus a primary aim for evolutionary ecologists for a number of reasons. First, variation in the degree to which individuals differ within population, determines it's ability adapt to environmental change (Caughley 1994). Second, identifying the sources of variation within a population can help us to understand the way different traits have evolved (Stearns 1992), and finally by examining the mechanisms that cause the differences we can begin to understand why particular groups of characters tend to occur together (Endler 1995).

Sources of biological variation include genetic differences between individuals, which are determined by an individual's ancestry and are usually fixed within individuals (Kashi et al 1997). In contrast, environments vary in time and can thus be a major source of variation among individuals. In addition, the environment may interact with genotypes in potentially complex ways to affect phenotypic variation between and within individuals (Gillespie& Turelli 1989; Wade & Kalisz 1990; Merila & Fry 1998). Thus, in the presence of directional selection, individuals of the same genotype are not necessarily equal in fitness, because the fitness of a genotype depends on the environments in which it is expressed (Scheiner 1993).

1.1 Aims

The aim of the current work was to identify environmental sources of life-history variation within a wild population of the great tit. This subject has received attention in the past (Boyce & Perrins 1987; Perrins & McCleery1989 Verhulst & Tinbergen 1991). However, most studies to date have related between-year changes in mean life-histories to environmental factors at the level of the population (e.g. Boyce & Perrins 1987); an approach that introduces several other potentially confounding sources of life-history variation. For example, populations are likely to vary demographically between years which will affect the population mean of a given trait. The population level approach also does not account for fine-scale environmental variation such as the availability of patchily distributed resource within a habitat area. The current study addresses both of these limitations by using a Geographical Information System (GIS) to model fine-scale environmental variation at the level of the individual territory, and by applying these data to models explaining the life-history variation associated with *c.*8000 great tit breeding attempts for which breeding locations were known. The aim was to model environmental variation in an attempt to explain consistent differences in reproductive performance between areas within a single study site. The first focus of the study will be to model environmental variation between breeding locations and to relate these data to the reproductive performance of focal individuals. Second, as the place of birth is also known for over half the breeding adults each year, this study offers the exciting and unique opportunity to accurately examine natal sources of life-history variation for a large sample size of individuals.

I hope that this study will offer some advances in our understanding of life-history variation in birds, and that these advances fall into two distinct categories. First, the thesis aims to provide a greater understanding of how fine-scale sources of habitat variation interact to determine individual fitness. At the population level, that individuals breeding in high quality habitat patches produce high quality offspring is well known. However, the current study offers the possibility to differentiate between areas that constitute good and bad quality habitats, in terms of both birth and breeding requirements, within a single habitat patch.

Second, performing analyses at several spatial scales will provide an important insight into the scale at which individuals perceive their environment and the resources within it, and the scale at which life history traits (and hence fitness) vary across individuals. Understanding the scale of an environmental effect is important for understanding how natural selection operates, and the extent to which local adaptation can occur. This subject has received little attention in the past as it requires detailed information on environmental and individual variation across scales within the context of a population study of marked individuals. Thus the current study is one of the first to accurately model the scale of individual resource acquisition and territorial behaviour in a wild population.

1.2 Environmental variation

According to evolutionary theory, an individual phenotype is the product of an individual's genotype, the environment it experiences before and during the development of that phenotype, and their interactions (Wade & Kalisz 1990; Merilä & Fry 1998). As genotypes are fixed, the environment (and the way it interacts with

genotypes) represents the only variable factor governing phenotypic variation between and within individuals (Boyce & Perrins 1987; Nager & Vannoordwijk 1995; Visser et al 1998). Environments vary in both spatial and temporal dimensions and the factors that constitute an environment depend on the focal species (Garant et al 2004). For example, for endoparasitic species the environment is biological in nature, whereas for most free-living organisms, the environment is predominantly physical and determined by processes working at and interacting between different scales (Levin 1992; Hanski 1994). At a continental scale, sources of environmental variation include climatic processes, whereas at smaller scales microgeological differences such as soil type and mineral availability are important determinants of environment quality. Different scales of environmental variation are likely to interact in complex ways to directly affect the character of a location at a specific point in time (Levin 1992). In addition, they also affect the environment indirectly by determining the distributions different vegetation communities which themselves constitute important environmental components (Guisan & Zimmermann 2000).

All organisms are in constant contact with their environment. However, the extent to which the environment affects an organism is likely to vary between taxa. For example, small terrestrial invertebrates are vulnerable to environmental change and depend on simple behavioural mechanisms such as kinesis to avoid excessive environmental exposure (Hughes 1985). On the other hand, vertebrates, such as birds (Aves) have evolved the ability to maintain a constant internal environment within a range of environmental conditions. This ability, called homeostasis, is energetically very expensive and so benefits are still available, in terms of cost reduction, for individuals in more favourable conditions (Hoar 1983; Carrascal et al 2001).

Environments are usually classified in terms of their physical characteristics. For example, topography, which determines microclimate variation (Bale et al 1998), is measured by relative changes in altitude, aspect orientation and slope gradient. These variables can be measured in the field or, as in the current work, can now be estimated by using 3D digital terrain models and satellite data (Maire & Datcu 2005). The physical qualities of an environment can also be estimated by describing the environment in terms of its location relative to a landscape feature such as a body of water, a source of pollution or a certain habitat type (Gilbert et al 2003). Using this technique one implicitly assumes that the substance (water, pollution) decreases in quantity with distance in equal directions from the source.

Environments may also be classified biologically, in terms of, for example, the abundance and distribution of conspecifics. This is called population density and is known to have a profound effect on many aspects of the lives of individuals, such that those breeding at low density are consistently observed to produce more surviving offspring than those at high density (Both et al 1999). Perhaps the most commonly considered biological environmental component is habitat type, which is usually, but not always, defined by the dominant vegetation community (Goldberg 2003). However, broad habitat classifications do not account for differences within habitats, and so their use is limited to comparisons made over large, landscape, scales. Biological environmental factors also include the availability and distributions of important food species, potential predators, parasites and pathogens. Describing environments in terms of their biological components is problematic as distributions vary in time and space and individuals of many species move freely within the environment. However, as the biological environment is a proximate predictor of

predation and starvation risks, it is nonetheless a critical component of environmental variation.

1.3 The problem of scale

Finding the most biologically meaningful scale at which to describe environmental variation is a persistent problem in ecology (Wiens 1989; Levin 1992) because the degree to which individuals vary with the environment differs depending on the scale at which they are observed (for example; Wiens *et al* 1986; Bohning-Gaese 1997; Thrush et al 2005) and because the prediction of an ecological response to environmental change requires the interfacing of processes operating at several spatial scales (Levin 1992).

There is no unifying scale at which ecological phenomena should be studied. However, commonly used scales include national, landscape and habitat, within which environments are thus assumed, implicitly, to be constant. Traditionally the most commonly adopted scale in ecological studies is the scale of the habitat type or study site. For example, several studies of avian reproductive ecology have contrasted the ecology of populations breeding in deciduous, compared with coniferous woodlands (e.g. Lambrechts *et al* 2004; Tremblay 2005). However, there is likely to be considerable environmental variation within such broad habitat classifications, and the characteristics that define a habitat type are unlikely to be randomly distributed within any such scale. Therefore, small scale within-habitat environmental variation is unaccounted for in analyses conducted at this scale. The current work addresses this limitation by conducting analyses over several spatial scales and by focusing on environmental variation within a single continuous woodland.

Study site

Wytham woods were bequeathed to the University of Oxford in the 1940s by Raymond ffennell and comprise (currently) 385 ha of a larger farm estate some 3 kilometres west of Oxford, UK. The donor stipulated that:

"every care should be taken to preserve the woods in their present state of natural beauty.... the University will take all reasonable steps to preserve and maintain the woodlands and will use them for the instruction of suitable students and will provide facilities for research it is in the hope and expectation of the grantor that the character of the lands included in this agreement and the buildings thereon will remain as far as possible as at present...".

The woodland has been used for a variety of long-term scientific studies since the 1950s and consequently is one of the best studied ecological sites in the world. Wytham is primarily mixed deciduous woodland although there are several open areas, marshes and some areas of scrub and mature conifers. Figure 1 shows Wytham's broad habitat classifications (from Gibson 1988), although most of the site is classified as oak woodland (NVC categories W8, W10 and W12; Whitbread & Kirby 1992). Dominant tree species include oak (*Quercus robur*), ash (*Fraxinus excelsior*), sycamore *(Acer pseudoplatanus)* and beech (*Fagus sylvatica*). The understory is mainly elder (*Sambucus nigra*), bramble (*Rubus fruticosa*), hawthorn (*Crataegus monogyna*), blackthorn *(Prunus spinosa)*, bracken *(Pteridium aquilinum)* and field maple (*Acer campestre*).

Figure 1. Wytham woods and their habitat classifications (from Gibson 1988)

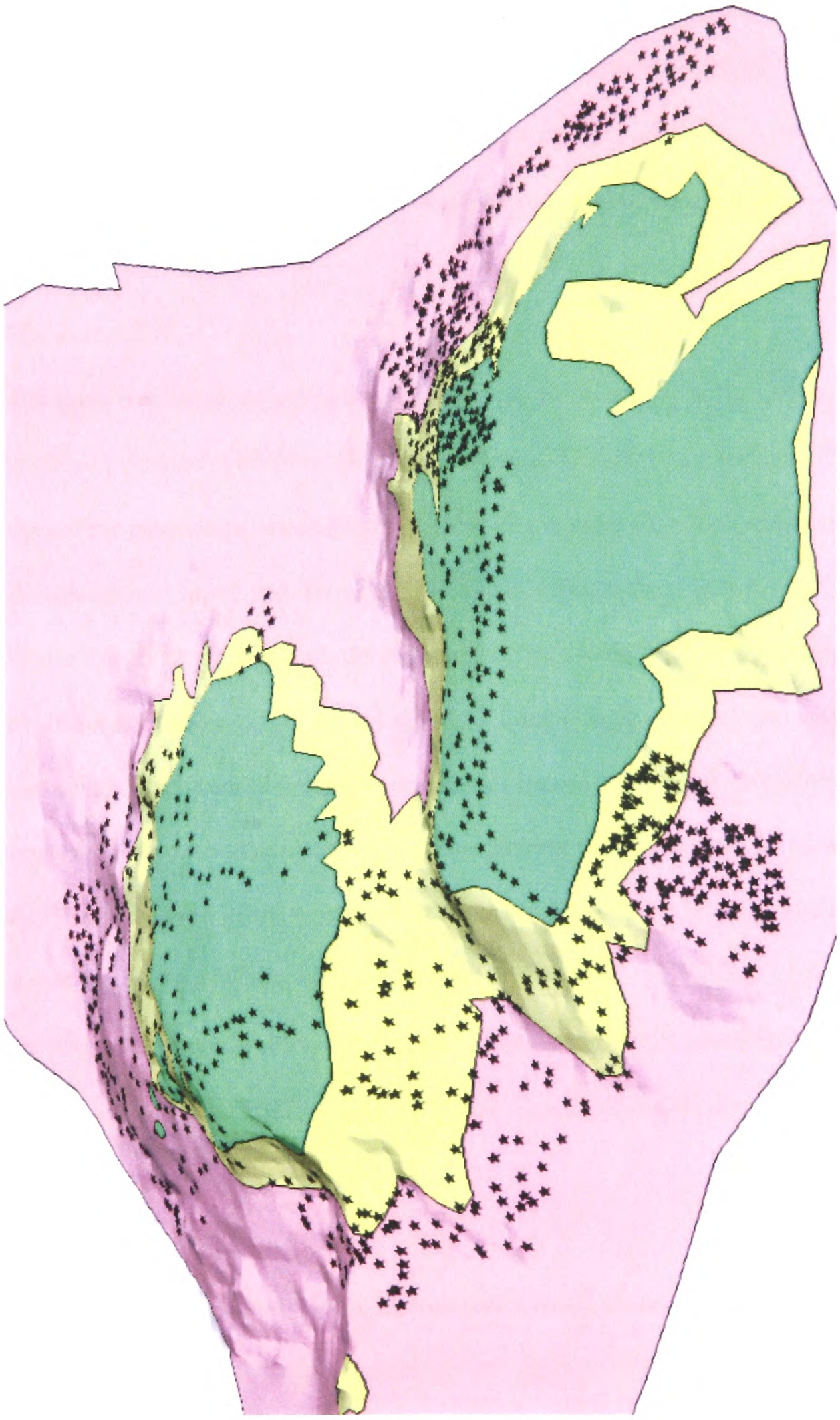


Figure 2. Soil types and nestboxes (asterisks) draped on a digital terrain model (DTM) of Wytham woods near Oxford, UK. Soil types begin at low altitude with Oxford clay (pink), rising through a band of sand (yellow) and finishing in two limestone caps (green).

Wytham varies markedly in geology and altitude (Fig 2), rising from Oxford Clay at 60m asl, through sand from the Lower Corallian at around 100m asl, to a limestone cap from the Upper Corallian, which forms the summit of the hill at 164m asl; I show in this thesis that this variation has considerable effects on a wide range of characters.

The Great Tit

The great tit (*Parus major*) is the largest of the British tits (family: Paridae). It is a territorial woodland bird that shows a preference for habitats dominated by deciduous trees. Few passerines have a larger range than the great tit, which extends from the British Isles to Japan and from the artic circle to South East Asia. Great tits have been invaluable in studying population dynamics (Lack 1964) and, more recently, evolutionary processes (Garant et al 2005). Lack (1966) suggests two virtues in particular which render great tits suitable for intensive study. Firstly, they prefer to breed in nestboxes than in natural cavities making their nests easy to locate in the field, and secondly, they winter in the same locality as they breed, enabling year round study. In addition, when researchers follow strict field-work protocols great tits are robust to scientific observations, allowing, for example, nestlings to be weighed and measured in the field by a competent and careful field worker.

Life-histories

The great tit at Wytham usually lays between 4 and 12 small whitish eggs (mean = 8.3, s.d. = 2.0), which weigh an average of 1.6g (s.d. = 0.14), at the rate of one per day. The young, which are naked and helpless, hatch synchronously after two weeks of incubation by the female (mean = 12.8 days, s.d. = 2.30). For the next three weeks

both of the parents provision the young primarily with caterpillars (Betts 1955; Perrins 1991) that are found at highest densities on oak trees (Gibb 1950; Gibb & Betts 1963), but also other invertebrates (Betts 1955; Gibb & Betts 1963). The average brood contains 7.4 nestlings (s.d. = 2.17) which weigh an average of 18.5g each (s.d. = 1.39) at day 15 (hatchday = 1).

After leaving the nest the mortality of fledglings is extremely high (Naef-Daenzer et al 2001); in the current dataset only 15% of nestlings observed at 15 days of age, survived to breed the following year. Heavy fledglings and those that fledged early in the season were more likely to survive to breeding age than lighter birds or those that fledged later (Verhulst et al 1995; Both et al 1999; Naef-Daenzer et al 2001). Post breeding adult mortality is also high (Payevsky 2006); at Wytham the average number of breeding attempts in the lifetime of a female is 1.6 (s.d. = 1.0) and 1.5 (s.d. = 0.9) times for males, such that 63% of breeding females and 67% of males only breed once. Factors governing adult survival include investment into reproduction, predation, inclement over winter conditions and the availability of beech mast as a winter food source (Tinbergen et al 1985; McCleery et al 1996; Perdeck et al 2000).

Despite high levels of mortality, the great tit population has increased in size from an average of 189 breeding attempts per year during the 1970s (s.d. = 38.3) to 308 attempts per year during the 1990's (s.d. = 81.3) (year vs. pop size, $r = 0.715$, d.f = 40). The proportion of breeding individuals in each year that were immigrant to the population i.e. individual born outside of Wytham nestboxes, has also risen from an average of 0.46 in the 1970s to 0.63 during the 1990s (year vs. prop, r = 0.639, d.f. = 40), while the age structure has remained similar with around half the birds breeding

each year being first year birds (mean proportion 0.52, s.d. = 0.09), which tend to produce fewer offspring than older birds. Immigrants tend to recruit fewer offspring than recruits (imm mean = 0.94, s.d. = 1.63 and recruits 1.08, s.d. = 1.72).

A brief history of the Wytham Great tit study

In the winters between 1946 and 1950 around 200 wooden nestboxes were erected by J.A. Gibb in the 26 ha area of Wytham called Marley wood (Gibb 1950; Fig. 3). Nestboxes have subsequently been occupied each spring by nesting great tits and its close relative the blue tit (*Cyanistes caeruleus*), both of which normally nest in natural cavities. Results from a survey showed that the whole great tit population had moved into the nestboxes (Gibb 1954), whereas a third of the blue tit population were still breeding in natural cavities. That all the great tits were found breeding in nestboxes is relevant for this thesis because it means that by checking nestboxes, all the breeding attempts made by individuals in the great tit population can potentially be monitored in each year. This has two important consequences for the current work. First, for a given individual it was possible to accurately measure its local breeding density, as the exact number and locations of neighbouring conspecifics were known. Secondly, it was possible to accurately estimate the population mean for a given trait such as clutch size, thus enabling the comparison of an individual's clutch size with an accurate estimation of the population mean in each year.

Figure 3. Wytham woods showing the location of nestboxes and the years in which they were installed. The shaded area with a dotted line represents a plantation that was included within the woodland perimeter in 1977. Most nestboxes are occupied by both great and blue tits with the exception of 147 blue tit-only boxes (with smaller diameter entrances) that were added in 2003 (half circles).

In the years between 1957 and 1965 the area containing the wooden nestboxes was expanded to include the majority of the woods (Fig. 3). The new total of a thousand or so nestboxes have remained in the same locations until the present day, unless a small move was necessitated by a tree fall. This is an important point as I was able to map the location of nestboxes and perform spatial analyses on individuals breeding in the nestboxes in prior years.

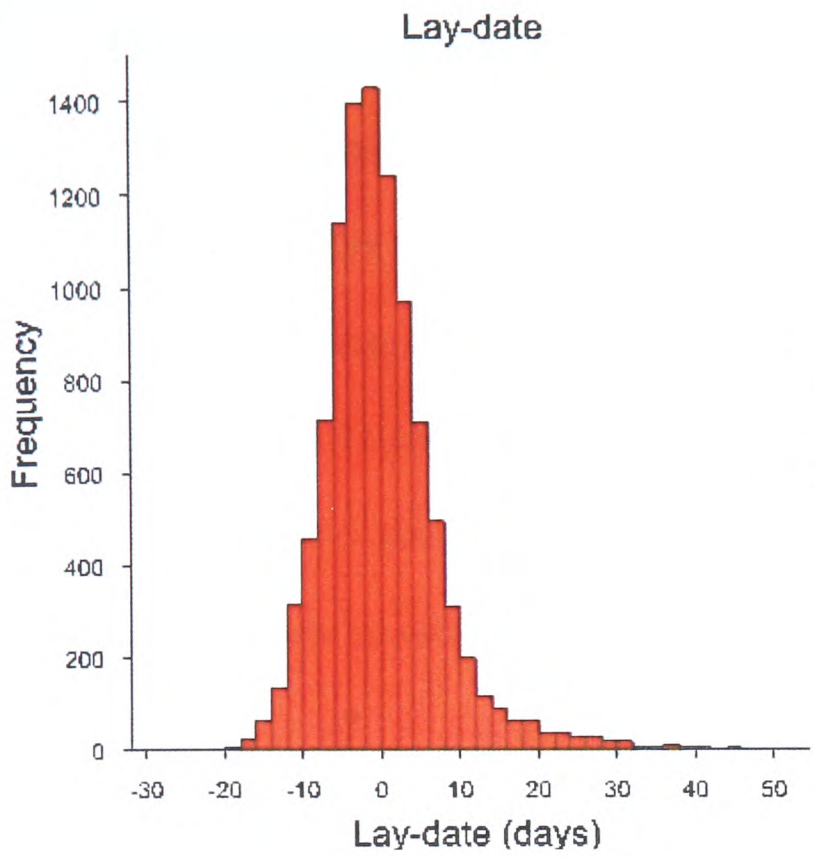
Birds breeding in the wooden nestboxes often suffered high levels of nest predation by woodpeckers and weasels (Dunn 1977; McCleery et al 1996). The former were able to peck holes into the boxes to gain access to the nestlings, and the latter were able to gain access directly through the entrance hole, as the boxes were attached directly onto the tree trunks. To address this problem, in the years between 1973 and 1975, the wooden nestboxes were replaced by woodcrete™ versions which were suspended from brackets attached to the trees (McCleery et al 1996). In this way the nestboxes were rendered almost predator-proof, which provided a unique opportunity to compare the breeding biology of birds breeding in the same territories but in the presence and absence of nest predation, which is exploited in Chapter 3 of the current thesis (see also McCleery et al 1996).

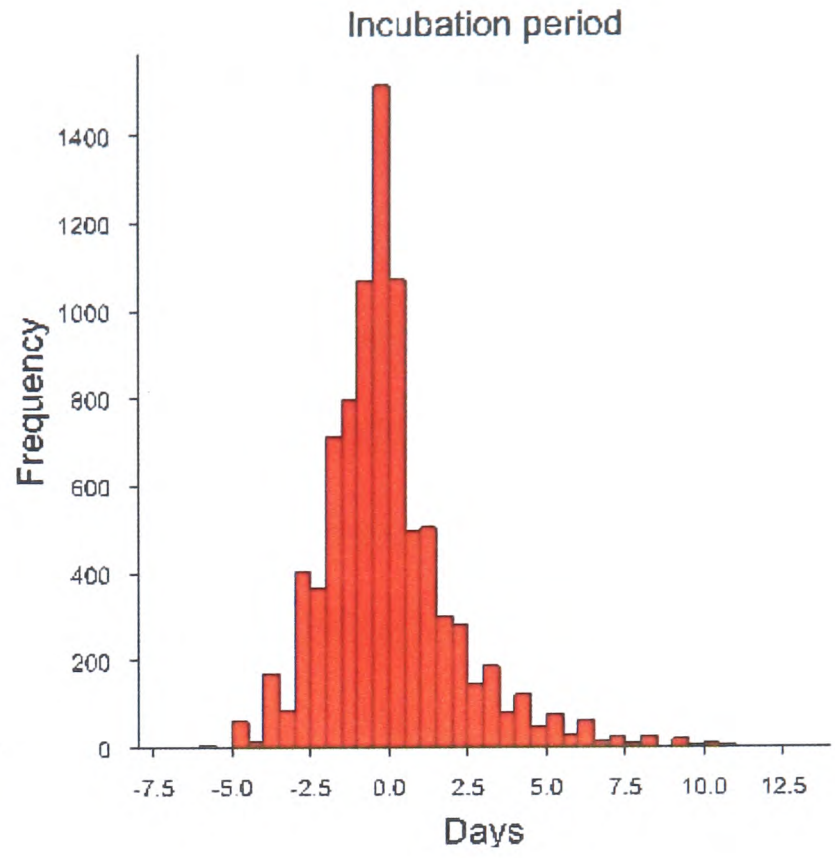
In 1977 a pine plantation of 24 ha (Pasticks) was furnished with 24 nestboxes and in 2003 147 blue tit only nestboxes were added in areas of low nestbox density (Fig. 3). The current thesis acknowledged these changes in nestbox number and configuration and their potential effects on the breeding biology of the birds by including only nestboxes and perimeters that were present in any given year.

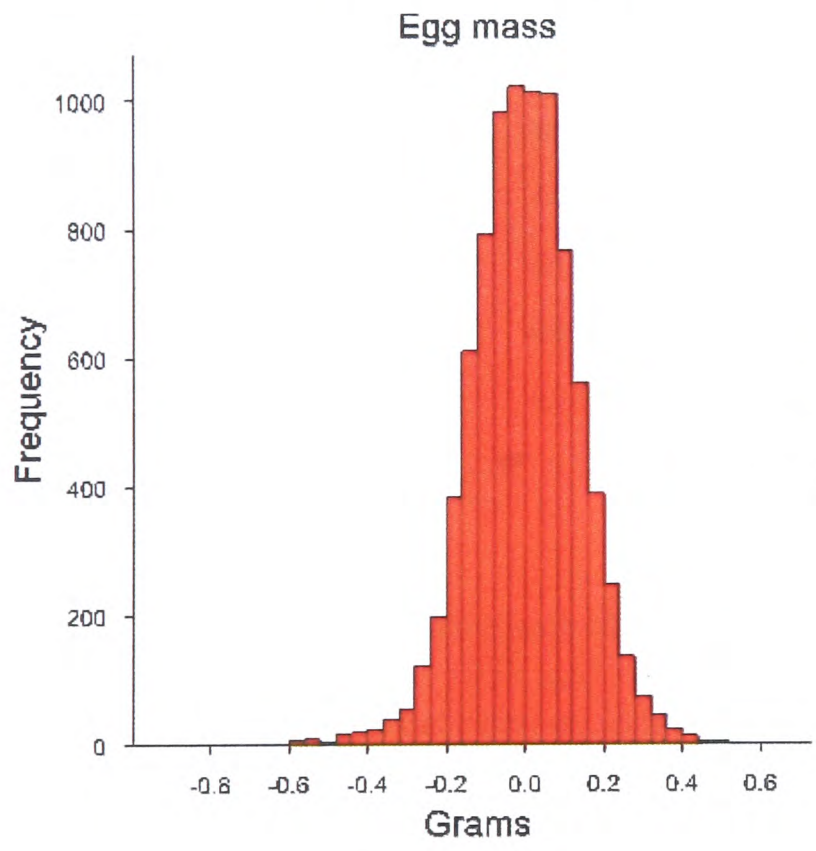
Life-history variation

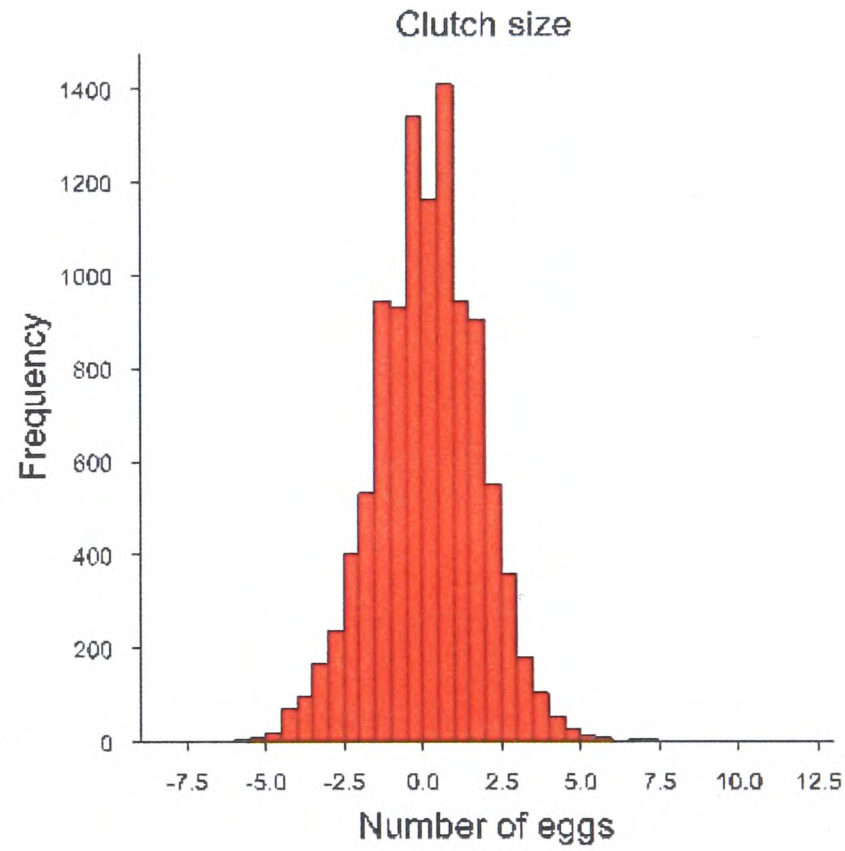
The life-history traits considered by the current work were lay-date, measured as the date on which the first egg of a clutch was laid (where 1st April = 1), clutch size, egg mass taken as the mean of between three and five unincubated eggs, incubation period (hatch-date minus clutch size and lay-date), mean fledgling mass per brood at day 15 (where hatch-date = day 1), and the number of recruits to the breeding population from each breeding attempt. The distributions of these traits are shown in Fig. 4. Large sample sizes, which ranged from 8568 for egg mass to 10115 for lay-date, meant that any departure from normality was likely to have negligible effects in models. Life-history variables were therefore treated as continuous variables and were analyzed in general linear models, or general linear mixed models, with normal error structures. The exception was that of the number of recruits per breeding attempt, which followed a Poisson distribution and so analyzed was in generalized models (or generalized linear mixed models) with Poisson error structure.

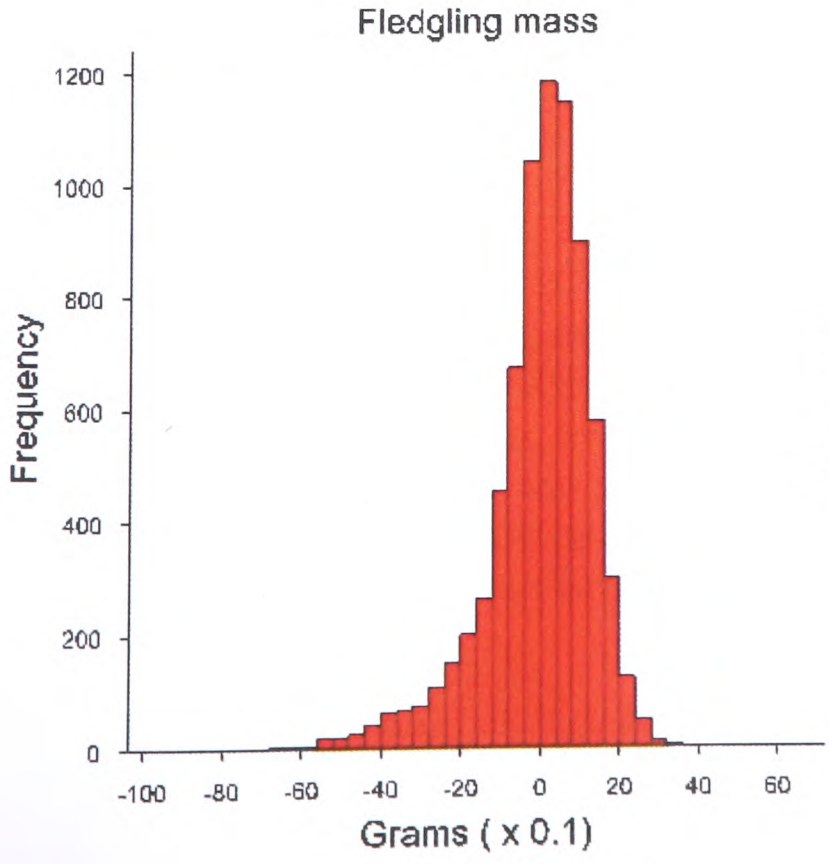
Figure 4. (Over leaf) The distributions of six great tit life-history traits. Data were collected from birds breeding in Wytham nestboxes between 1965 and 2005 and, with the exception of recruitment, which follows a Poisson distribution, are standardized for each year. Lay-date was measured in days after April 1st, incubation period (days) was estimated by subtracting lay-date and clutch size from the hatch-date, mean egg mass per brood measured as the mean mass of between 3 and 5 un-incubated eggs is displayed in grams, mean fledgling mass per brood is shown in units of 0.1 g and the number of recruits represents the number of offspring found breeding in Wytham nestboxes in subsequent years, per breeding attempt.

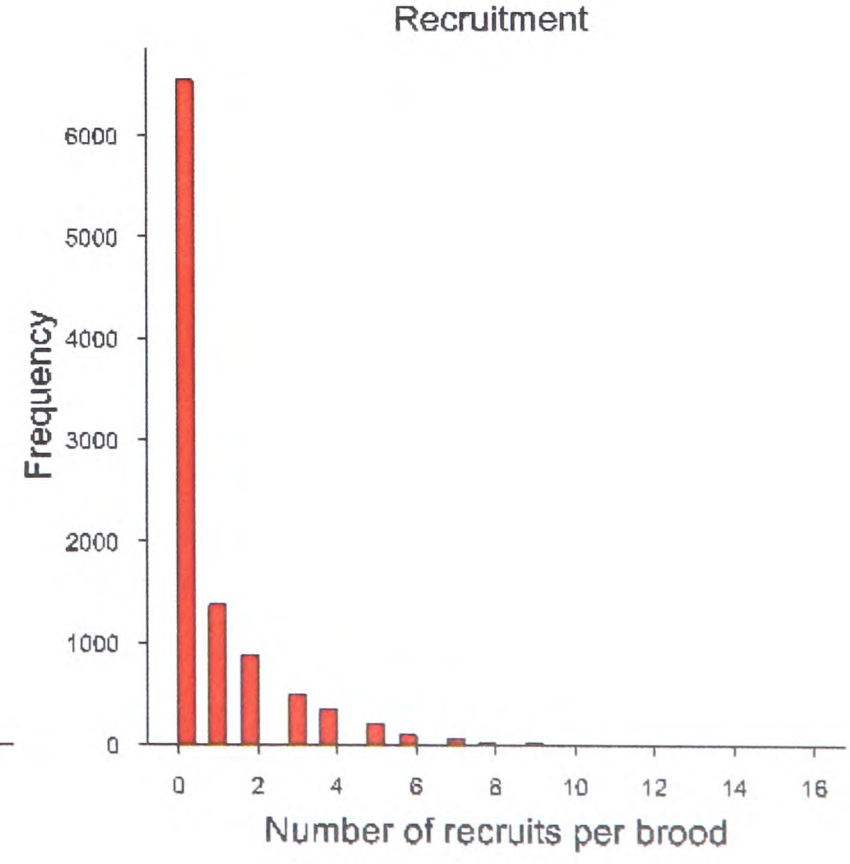

Lay-date
Frequency
Lay-date (days)


Incubation period
Frequency
Days


Egg mass
Frequency
Grams


Clutch size
Frequency
Number of eggs


Fledgling mass
Frequency
Grams (x 0.1)


Recruitment
Frequency
Number of recruits per brood

Life histories were also examined at the level of the individual, rather than at the level of the breeding attempt. Traits that were examined at this level included an individual's life span, measured as the number of years between year of birth and final year of breeding, the number of 'gap years' measured as the number of years between year of birth +1 and year of first breeding, and lifetime reproductive success. The distributions of theses traits, which were measured for individuals born and subsequently breeding in Wytham nestboxes, are shown in Figure 5.

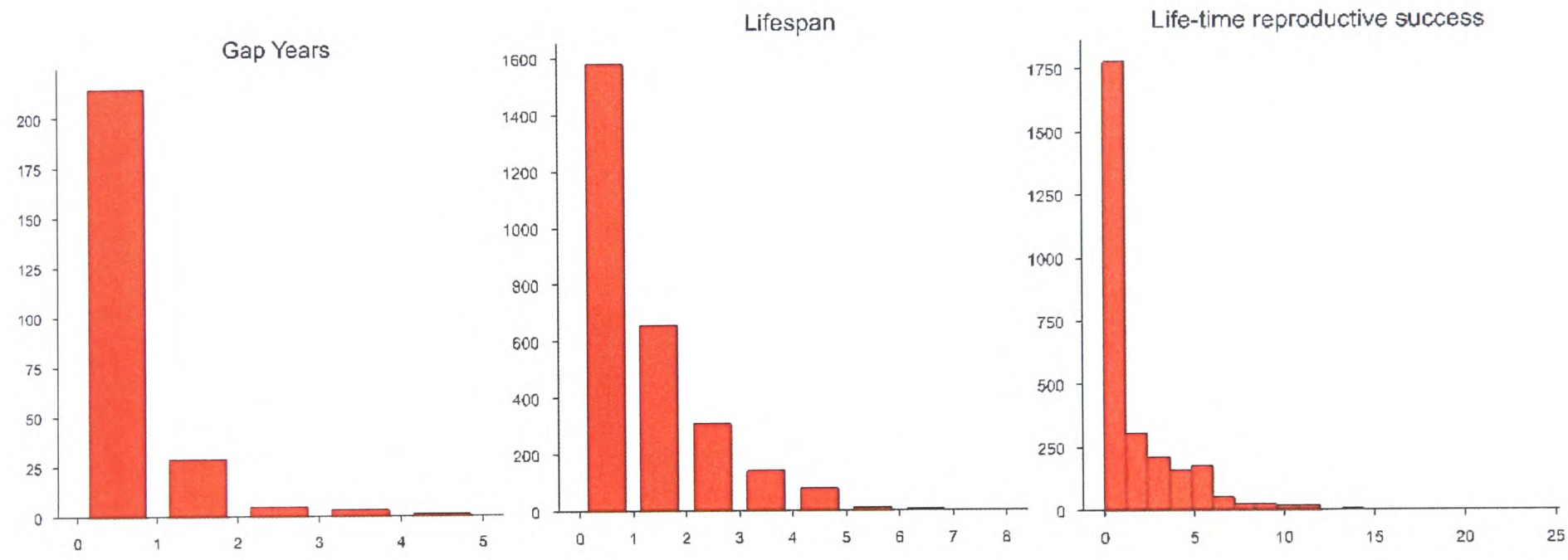
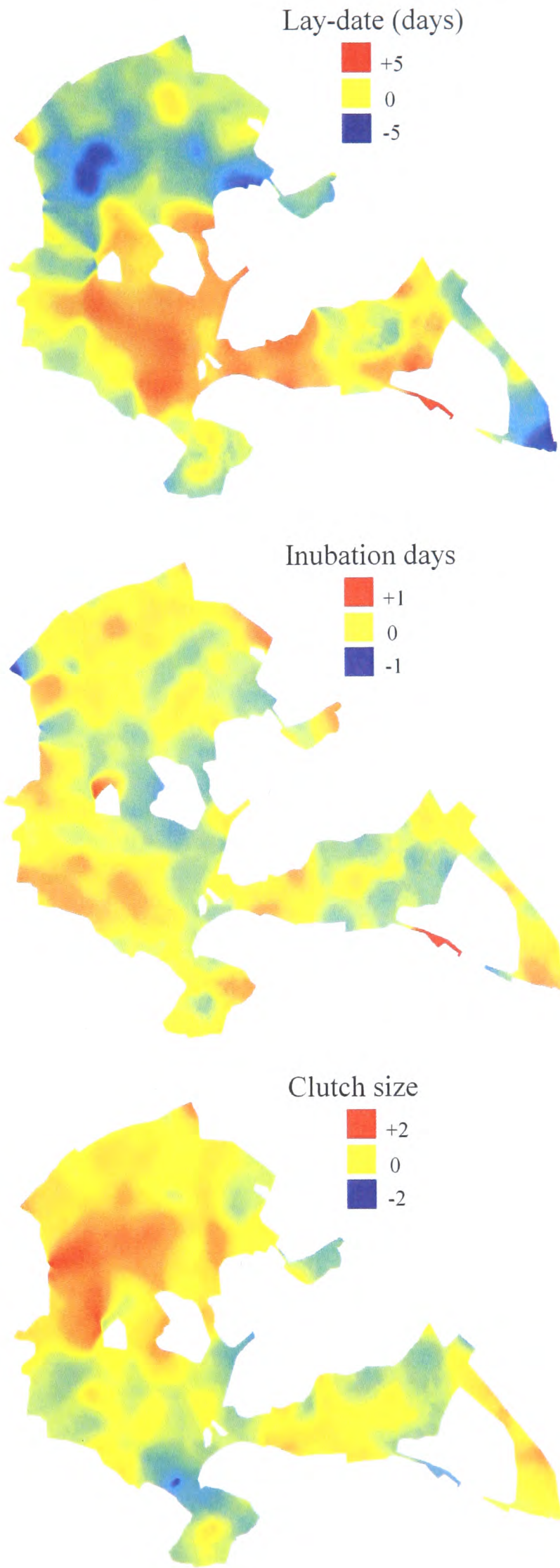
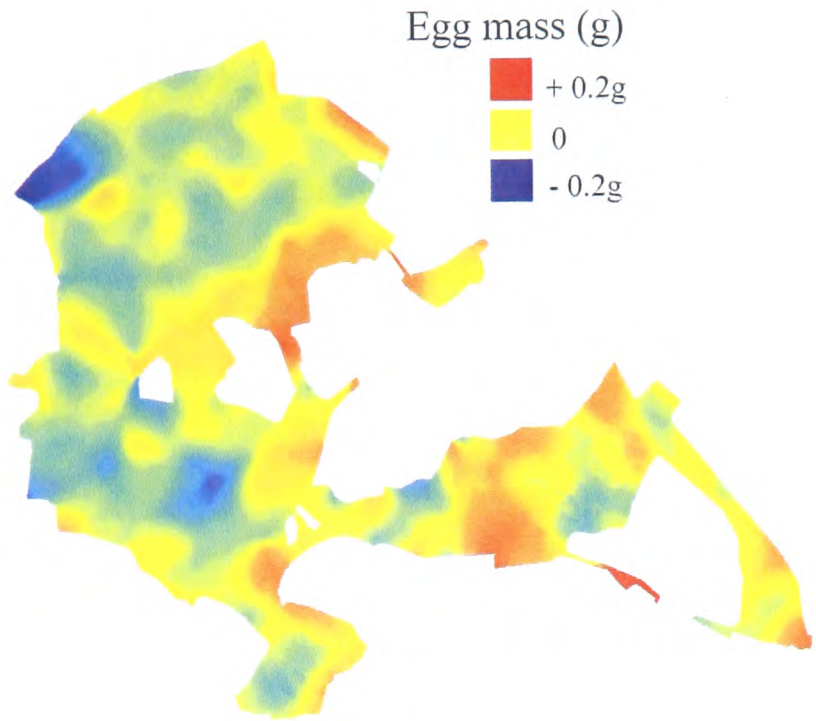
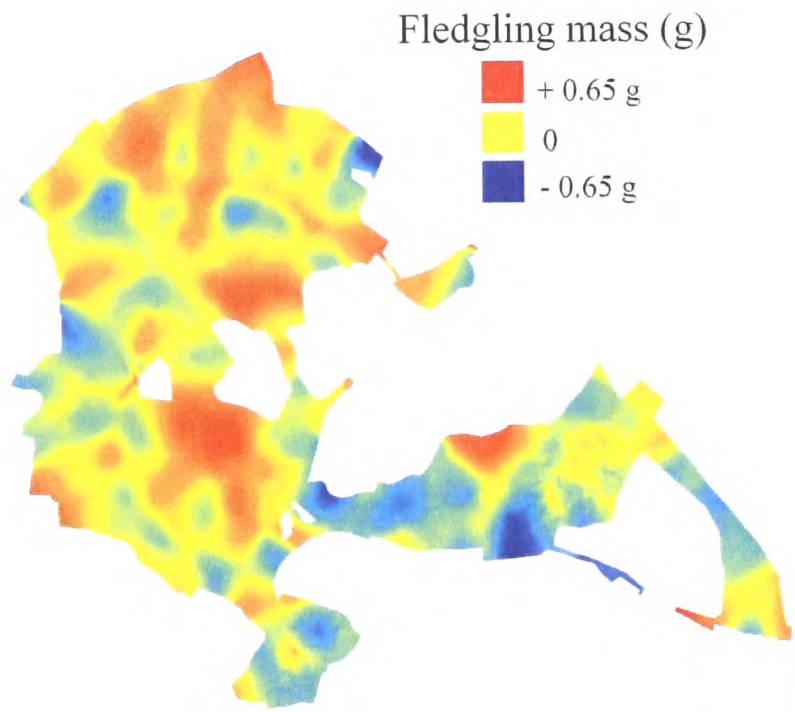


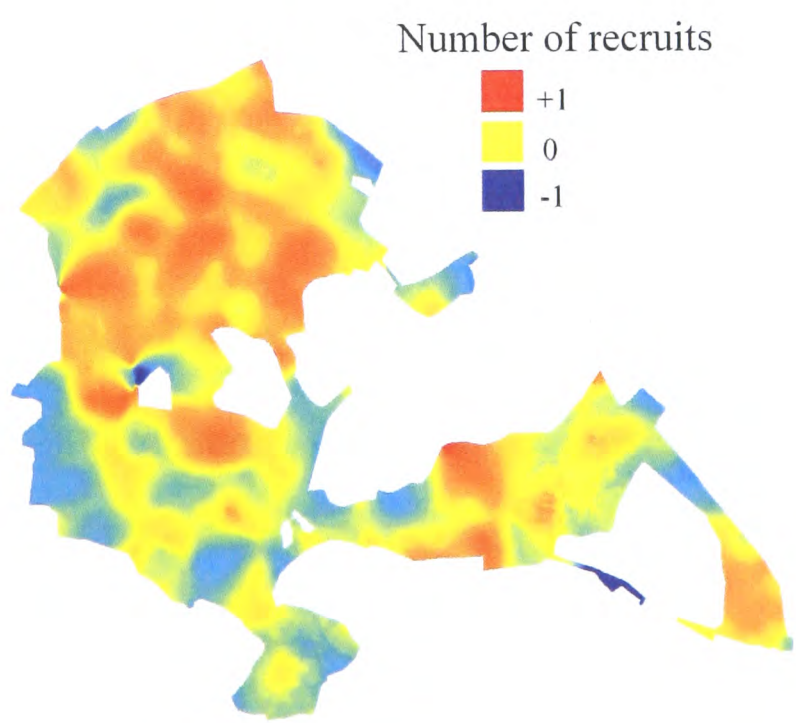
Figure 5. The distributions of three traits measured for 2164 female great tits born in Wytham nestboxes between 1959 and 2004 and breeding between 1965 and 2005. Gap years were the number of years between an individual's year of birth and year of first breeding. Individuals that did not have gap years (n = 1926) were excluded from the figure for illustrative purposes. Lifespan is the number of years between an individual's year of birth and year of final recorded breeding attempt. Lifespan and LRS are strongly positively correlated $r = 0.467$, $P < 0.001$.

Figure 6. (overleaf x 2) Interpolations of six great tits life-history traits measured for individuals breeding in Wytham nestboxes between 1965 and 2005. Variables, with the exception of recruitment, are standardized for year. An Inverse Distance Weighting interpolation technique was employed with search radii of 200m (half the average point density). Red areas indicate large values of the trait, for example, late lay-dates or heavy eggs, while blue areas are low values of the trait, yellow intermediate areas.


Lay-date (days)
+5
0
-5
Inubation days
+1
0
-1
Clutch size
+2
0
-2


Egg mass (g)
+ 0.2g
0
- 0.2g


Fledgling mass (g)
+ 0.65 g
0
- 0.65 g


Number of recruits
+1
0
-1

Thesis overview

This thesis consists of five manuscripts formatted for submission to peer-reviewed journals (one published, one submitted), followed by a general discussion and appendices. As a consequence, each chapter is a stand-alone study and contains a section detailing relevant methods. This approach inevitably leads to some degree of repetition but renders the work a more useful reference tool. In this section I outline the main focus of each chapter.

Density-dependent reproduction is a well documented phenomenon, whereby individuals breeding at high density do so at a reduced rate compared to those at low density (Both et al 2000; Both & Visser 2003). Most studies of density dependence in forest passerines compare densities at the population level and measure density as the number of individuals per unit area (Perrins 1965; Boyce & Perrins1987). This approach introduces several potentially confounding sources of life-history variation and does not account for spatial variation in density at the individual level. *Chapter 2* aimed to address these limitations by developing a new technique for measuring density at the level of the individual and by applying these data to explain individual life-history variation.

Habitats at the edge of a woodland differ from those in the interior due to increased exposure, temperatures fluctuations and concomitant changes in vegetation and invertebrate communities (Klaassen 1996; Davies-Colley et al 2000; Gehlhausen et al 200). At the level of the community, woodland edges are often more diverse than interior areas (Leopold 1933; Odum 1971), and at the population level woodland passerine life-histories (Huhtka et al.1999) and breeding density (Gates & Gysel

1978; Strelke & Dickson 1980) are often reported to vary with distance from the woodland edge. Previous studies of edge effects use the distance between the breeding location and the woodland edge as the measure of edge proximity (e.g. Murcia 1995). However, this method does not account for edges differing in layout or number. Also despite the number of studies on edge effects in woodland passerines, it remains unclear whether edges affect the reproductive performance of individuals directly or indirectly via changes in breeding density or in the proportion of poor quality individuals, which breed at a reduced rate, at edges. *Chapter 3* introduces a new method for describing a breeding location in terms of its edge proximity, which accounts for edges differing in layout and number. Moreover, the chapter compares first time, edge proximity with life-history variation while controlling for differences in density (*Chapter 2*) and between individuals.

Although a strong relationship is observed between variation in breeding density and many aspects of great tit life-histories (Krebs 1984; Both & Visser 2003), it is unlikely that the number of local conspecifics is directly responsible for determining life-history variation. More likely, increased competition reduces the proportion of some limited resource that is available per individual at high density. In the current study system, the preferred food for breeding great tits is the caterpillar of the winter moth (*Operophtera brumata*), which is found at highest densities on the foliage of oak trees (*Quercus spp.*)(Betts 1955 ;Gibb & Betts 1963). Therefore, it is likely that oak trees, which are presumably less available per individual at high density, are an important resource for breeding great tits. *Chapter 4* aims to investigate the relative importance of density and oak tree availability in determining life-history variation.

Calcium is a necessary micronutrient for breeding birds during egg formation and for nestlings forming skeletal structures (Perrins 1996; Klaising 1998). Several studies on forest passerines have reported reduced reproduction in low calcium areas (Graveland & Drent 1997). However, these studies often compare populations in different woodlands and thus are potentially confounded by other habitat differences. In addition, describing a breeding location in terms of its calcium availability is problematic as birds may, potentially, travel considerable distances to acquire calcium rich food items during periods of high demand. Soil calcium is patchily distributed over Wytham and varies 300-fold (Gosler et al 2005), making it the ideal location to study the spatial relationship between local soil calcium and reproductive output of great tits. *Chapter 5* performs spatial analyses to identify which life-history traits are reduced in low, compared to high calcium areas in Wytham and attempts to reveal the spatial scale at which great tits acquire calcium.

That individuals breeding in high quality breeding environments are more likely to produce high quality offspring, is well known (Boag 1987; Gustafsson et al 2005). However, there is a growing interest in the long-term effects of the rearing environments on the subsequent life-histories and fitness of surviving offspring (Lindström 1999). Recent studies have shown that offspring reared in high quality environments live longer and produce more offspring themselves, than offspring raised in poor quality environments (Reid et al 2003; Van de Pol et al 2006). *Chapter 6* of the current work examines the life-histories of over 5000 breeding great tits for which both breeding and natal environments are known, to compare the relevant importance of breeding environments, as detailed in the preceding chapters, and natal environments.

Appendices

I. Garant, D., Kruuk, L.E.B., **Wilkin, T.A.**, McCleery, R.H. and Sheldon, B.C. (2005) Evolution driven by differential dispersal within a wild bird population. *Nature*. **433** (7021): 60-65.

Evolutionary divergence depends on the balance between the diversifying effect of selection and the homogenizing effect of dispersal. However, if dispersal were non-random then it could act to reinforce, rather than dilute divergence. This paper shows for the first time that non-random dispersal has, over time, led to genetic divergence between two sub-populations in Wytham great tits, with respect to size.

II. Jubb, M., **Wilkin, T.A.** & Gosler, A.G. (2006) Eggshell-pigmentation, soil calcium and the local abundance, distribution and diversity of woodland snails (Mollusca). *Ardea*. **94** (1): 1-12

Calcium is an essential nutrient for breeding birds during egg production and for nestling developing skeletal structures. This field survey showed that within Wytham, abundance, size and diversity of snails, the main calcium source for great tits, was correlated with soil calcium at a fine-spatial scale.

III. Shapiro, J., Garant, D., **Wilkin, T.A**. & Sheldon, B.C. (2006) An experimental test of the causes of small-scale phenotypic differentiation in a population of great tits. *Journal of Evolutionary Biology.* **9**. 176-183

A cross fostering experimental test of the genotypic divergence of nestling mass reported in Appendix 1. Genetic effects on nestling condition and shape were found between areas separated by <3 km; nestlings born in areas of low breeding density areas were in better condition than nestlings born in high density areas, independently of where they were raised, thus confirming the genetic divergence of the trait over surprisingly small scale, despite extensive dispersal.

IV. **Wilkin, T.A.**, Perrins, C.M. & Sheldon, B.C. (2006). The use of GIS in estimating spatial variation in territory quality: a case study of lay-date in the Wytham Great Tit (*Parus major*). *Ibis In submission.*

This paper was presented to the 2006 British Ornithological Union Annual meeting entitled Woodland Birds: Their Ecology & Management at the University of Leicester, UK. It proposes several uses of GIS in predicting the lay date of great tits at Wytham, many of which are covered elsewhere in this thesis.

Author contributions

Author	Contribution to Chapters 2-6
Teddy A Wilkin	Conception and production of chapter text, figures and analyses. Digital mapping in the field.
Dany Garant	Several practical tutorials in mixed modelling over an extended period, and comments on some drafts.
Andrew G. Gosler	Collection of much long-term data. Discussion of great tit ecology, training in field techniques, and comments on some drafts.
Ben C. Sheldon	Overall guidance in research techniques, scientific practices and writing, great tit ecology, and comments on all drafts.

Appendix	Contribution of T.A.W.
I	Spatial analyses at the level of individual nestboxes, breeding density calculations and GIS map.
II	Experimental design, environmental investigation of sampling locations, student supervision and GIS maps.
III	Experimental design, fieldwork, student supervision, breeding density calculations and GIS map.
IV	Conception and production of analyses and manuscript.

References

Bale, C.L., Williams, J.B., & Charley, J.L. (1998) The impact of aspect on forest structure and floristics in some Eastern Australian sites. *Forest Ecology and Management*, **110**, 363-377.

Betts, M.M. (1955) Food of Titmice in Oak Woodland. *Journal of Animal Ecology*, **24**, 282-323.

Boag, P.T. (1987) Effects of nestling diet on growth and adult size of zebra finches (Poephila guttata). *The Auk*, **104**, 155-166.

Both, C., Tinbergen, J.M., & Visser, M.E. (2000) Adaptive density dependence of avian clutch size. *Ecology*, **81**, 3391-3403

Both, C., Visser, M.E., & Verboven, N. (1999) Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 465-469.

Both, C. & Visser, M.E. (2003) Density dependence, territoriality, and divisibility of resources: From optimality models to population processes. *American Naturalist*, **161**, 326-336.

Boyce, M.S. & Perrins, C.M. (1987) Optimizing Great Tit Clutch Size in a Fluctuating Environment. *Ecology*, **68**, 142-153.

Carrascal, L.M., Diaz, J.A., Huertas, D.L., & Mozetich, I. (2001) Behavioral thermoregulation by treecreepers: Trade-off between saving energy and reducing crypsis. *Ecology*, **82**, 1642-1654.

Caughley, G. (1994) Directions in Conservation Biology. *Journal of Animal Ecology*, **63**, 215-244.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343-

Davies-Colley, R.J., Payne, G.W., & van Elswijk, M. (2000) Microclimate gradients across a forest edge. *New Zealand Journal of Ecology*, **24**, 111-121.

Dunn, E. (1977) Predation by Weasels (Mustela nivalis) on Breeding Tits (Parus Spp) in relation to the density of Tits and Rodents. *Journal of Animal Ecology*, **46**, 633-652.

Endler, J.A. (1995) Multiple-Trait Coevolution and Environmental Gradients in Guppies. *Trends in Ecology & Evolution*, **10**, 22-29.

Flaspohler, D.J., Temple, S.A., & Rosenfield, R.N. (2001) Species-specific edge effects on nest success and breeding bird density in a forested landscape. *Ecological Applications*, **11**, 32-46.

Garant, D., Kruuk, L.E.B., McCleery, R.H., & Sheldon, B.C. (2004) Evolution in a changing environment: A case study with great tit fledging mass. *American Naturalist*, **164**, E115-E129.

Garant, D., Kruuk, L.E.B., Wilkin, T.A., McCleery, R.H., & Sheldon, B.C. (2005) Evolution driven by differential dispersal within a wild bird population. *Nature*, **433**, 60-65.

Gates, J.E. & Gysel, L.W. (1978) Avian nest dispersion and fledgling success in field-forest ecotones. *Ecology*, **59**, 871-883.

Gehlhausen, S.M., Schwartz, M.W., & Augspurger, C.K. (2000) Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology*, **147**, 21-35.

Gibb, J.A. (1950) The breeding biology of Great and Blue Titmice. *Ibis*, **92**, 507-539.

Gibb, J.A. (1954) Population changes of titmice. *Bird Study*, **1**, 40-48.

Gibb, J.A. & Betts, M.M. (1963) Food and Food Supply of Nestling Tits (Paridae) in Breckland Pine. *Journal of Animal Ecology*, **32**, 489-553.

Gibson, C. W. D. 1988. The distribution of ancient woodland plant species among areas of different history in Wytham Woods, Oxfordshire in Woodland Conservation and research in the caly vale of Oxfordshire and Buckingham. K. J. Kirky, Wright, F. J., Nature Conservancy Council.

Gilbert, N.L., Woodhouse, S., Stieb, D.M., & Brook, J.R. (2003) Ambient nitrogen dioxide and distance from a major highway. *Science of the Total Environment*, **312**, 43-46.

Gillespie, J.H. & Turelli, M. (1989) Genotype-Environment Interactions and the Maintenance of Polygenic Variation. *Genetics*, **121**, 129-138.

Goldberg, E. (ed.) (2003). National Vegetation Classification – ten years' experience using the woodland section. *JNCC Report*, No. **335**

Gosler, A.G. (1990) The Birds of Wytham- An Historical Survey. *Fritillary*, **1**, 29-74.

Gosler, A.G. (1993) *The Great Tit* Paul Hamlyn, London.

Gosler, A.G., Higham, J.P., & Reynolds, S.J. (2005) Why are birds' eggs speckled? *Ecology Letters*, **8**, 1105-1113.

Graveland, J. & Drent, R.H. (1997) Calcium availability limits breeding success of passerines on poor soils. *Journal of Animal Ecology*, **66**, 279-288.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147-186.

Gustafsson, L., Qvarnstrom, A., & Sheldon, B.C. (1995) Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature*, 311-313.

Hanski, I. (1994) Spatial Scale, Patchiness and Population-Dynamics on Land. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **343**, 19-25.

Hoar, W.S. (1983) *General and Comparative Physiology*. Prentice-Hall, 3rd edition.

Hughes, R.N. (1985) Mechanisms for Turn Alternation in Woodlice (Porcellio-Scaber) - the Role of Bilaterally Asymmetrical Leg Movements. *Animal Learning & Behavior*, **13**, 253-260.

Huhta, E., Jokimaki, J., & Rahko, P. (1999) Breeding success of pied flycatchers in artificical forest edges: The effect of a suboptimally shaped foraging area. *The Auk*, **116**, 528-535.

ICH. (2006). Interoperability Clearing House. *Glossary of Terms*. VA 22308

Kashi, Y., King, D., & Soller, M. (1997) Simple sequence repeats as a source of quantitative genetic variation. *Trends in Genetics*, **13**, 74-78.

Klaassen, W., Lankreijer, H.J.M., & Veen, A.W.L. (1996) Rainfall interception near a forest edge. *Journal of Hydrology*, **185**, 349-361.

Klasing, K.C. (1998) *Comparative Avian Nutrition.* CAB International, New York.

Krebs, J.R. (1984) Citation Classic - Territory and Breeding Density in the Great Tit, Parus-Major L. *Current Contents/Agriculture Biology & Environmental Sciences*, 14-14.

Lack, D. (1964) A Long-Term study of the Great Tit (Parus major). *Journal of Animal Ecology.* 33, 159-173

Lack, D. (1966). *Population Studies of Birds*. Oxford University Press, Oxford.

Leopold, A. (1933) *Game Management* Charles Scribner's Sons, New York.

Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, **14**, 343-348

McCleery, R.H., Clobert, J., Julliard, R., & Perrins, C.M. (1996) Nest predation and delayed cost of reproduction in the great tit. *Journal of Animal Ecology*, **65**, 96-104.

Maire, C. & Datcu, M. (2005) Earth observation image and DEM information aggregation for realistic 3-D visualization of natural landscapes. *Ieee Transactions on Geoscience and Remote Sensing*, **43**, 2676-2683.

Merilä, J. & Fry, J.D. (1998) Genetic Variation and Causes of Genotype-Environment Interaction in the Body Size of Blue Tit (Parus caeruleus). *Genetics*, **148**, 1233-1244.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58-62.

Naef-Daenzer, B., Widmer, F., & Nuber, M. (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, **70**, 730-738.

Nager, R.G. & Vannoordwijk, A.J. (1995) Proximate and Ultimate Aspects of Phenotypic Plasticity in Timing of Great Tit Breeding in a Heterogeneous Environment. *American Naturalist*, **146**, 454-474.

Perdeck, A.C., Visser, M.E., & Van Balen, J.H. (2000) Great Tit *Parus major* survival, and the beech-crop cycle. *Ardea*, **88**, 99-108.

Perrins, C.M. (1965) Population Fluctuations and Clutch-Size in the Great Tit, Parus major L. *The Journal of Animal Ecology*, **34**, 601-647.

Price, T. & Schluter, D. (1991) On the Low Heritability of Life-History Traits. *Evolution*, **45**, 853-861.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I., & Monaghan, P. (2003) Environmental variability, life-history covariation and cohort effects in the red-billed chough Pyrrhocorax pyrrhocorax. *Journal of Animal Ecology*, **72**, 36-46.

Scheiner, S.M. (1993) Genetics and Evolution of Phenotypic Plasticity. *Annual Review of Ecology and Systematics*, **24**, 35-68.

Stearns, S.C. (1992) *The Evolution of Life Histories* Oxford University Press, Oxford.

Strelke, W.K. & Dickson, J.G. (1980) Effect of forest clearcut edge on breeding birds in east Texas, USA. *Journal of Wildlife Management*, **44**, 559-567.

Tinbergen, J.M., Vanbalen, J.H., & Vaneck, H.M. (1985) Density Dependent Survival in an Isolated Great Tit Population - Kluyvers Data Reanalysed. *Ardea*, **73**, 38-48.

Van de Pol, M., Bruinzeel, L.W., Heg, D., van der Jeugd, H.P., & Verhulst, S. (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (Haematopus ostralegus). *Journal of Animal Ecology*, **25**, 616-626.

Thrush, S.F., Hewitt, J.E., Herman, P.M.J., & Ysebaert, T. (2005) Multi-scale analysis of species-environment relationships. *Marine Ecology-Progress Series*, **302**, 13-26.

Verhulst, S., Vanbalen, J.H., & Tinbergen, J.M. (1995) Seasonal Decline in Reproductive Success of the Great Tit - Variation in Time or Quality. *Ecology*, **76**, 2392-2403.

Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M., & Lessells, C.M. (1998) Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1867-1870.

Wade, M.J. & Kalisz, S. (1990) The Causes of Natural-Selection. *Evolution*, **44**, 1947-1955.

Whitbread, A. & Kirby, K. (1992) *Summary of National Vegetation Classification woodland descriptions (UK nature conservation, No. 4)* NCC.

Chapter 2: Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques

Journal of Animal Ecology 2006
75, 604–615

Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques

TEDDY A. WILKIN, DANY GARANT, ANDREW G. GOSLER and BEN C. SHELDON

Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, Oxford OX1 3PS, UK

Summary

1. Population density often has strong effects on the population dynamics and reproductive processes of territorial animals. However, most estimates of density-dependent effects use the number of breeding pairs per unit area in a given season and look for correlations across seasons, a technique that assigns the same density score to each breeding pair, irrespective of local spatial variation.

2. In this study, we employed GIS techniques to estimate individual breeding densities for great tits breeding in Wytham Woods UK, between 1965 and 1996. We then used linear mixed modelling to analyse the effect of density on reproductive processes.

3. The areas of Thiessen polygons formed around occupied nestboxes were used to approximate territory size (necessarily inverse of breeding density). There were significant, independent and positive relationships between clutch size, fledging mass and the number of offspring recruited to the population, and territory size (all $P < 0{\cdot}001$), but no effect of territory size on lay-date or egg mass.

4. Thiessen polygons are contiguous and cover all of the available area. Therefore, at low nest densities territory polygons were excessively oversized. Using a novel procedure to address this limitation, territory sizes were systematically capped through a range of maxima, with the greatest effect in the models when territories were capped at 0·9–2·3 ha. This figure approximates to the maximum effective territory size in our population and is in close agreement with several field-based studies. This capping refinement also revealed a significant negative relationship between lay-date and territory size capped at 0·9 ha ($P < 0{\cdot}001$).

5. These density-dependent effects were also detected when analyses were restricted to changes within individual females, suggesting that density effects do not merely result from either increased proportions of low-quality individuals, or increased occupation of poor sites, when population density is high.

6. Overall, these results suggest that, in the current population, great tits with territories smaller than *c.* 2 ha independently lay smaller and later clutches, have lighter fledglings, and recruit fewer offspring to the breeding population. These analyses thus suggest a pervasive and causal role of local population density in explaining individual reproductive processes.

Key-words: territory size, tessellation, Thiessen, Voronoi.

Journal of Animal Ecology (2006) **75**, 604–615
doi: 10.1111/j.1365-2656.2006.01078.x

Correspondence: Teddy A. Wilkin, Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, Oxford OX1 3PS, UK. E-mail: teddy.wilkin@zoo.ox.ac.uk

Introduction

Population density has a strong effect on the population dynamics and the reproductive processes of territorial animals (Newton 1992; Sutherland 1996). In many bird species, including the great tit *Parus major*, clutch size

(Kluijver 1951; Lack 1958; Perrins 1965), fledgling mass (Both 1998a; Garant *et al.* 2004) and recruitment of offspring (Both & Visser 2000) have been found to decline with increasing population density. High density has also been shown to reduce the chance of a territorial pair starting a second brood, the survival of territorial adults, the growth rate of chicks (Both & Visser 2000), and hatching and fledgling success (McCleery & Perrins 1985). Competition for limited resources is more intense at high density and is often cited as the likely cause of reduced fecundity under such conditions (Both 1998a; Both & Visser 2000). Reduced output at high density can result from several other concurrent processes such as mass starvation, the exclusion of a proportion of the population from reproduction (Newton 1992), or nest predation (Krebs 1971; Julliard *et al.* 1997; Sasvari & Hegyi 1998).

Most previous studies have analysed the effects of density at the population level, comparing mean reproductive output in a given year with the year-specific population density. However, numerous problems exist in between-year population-level analyses of density effects. For example, the efficiency of reproductive processes may decline with a rise in density due to proportionally more poor-quality sites being occupied during high-density years (Andrewartha & Birch 1954; Dhondt, Kempenaers & Adrianensen 1992). Also, in populations of small passerines, density is often determined by variation in overwinter survival during the previous winter. 'High-density' years usually occur after mild, food rich winters and are therefore often characterized by a high proportion of young and low-quality birds that produce few recruits. Between-year analyses do not adequately account for these sources of variation. Problems also arise with within-year analyses of the effects of density; as competition for nest sites is likely to increase with declining nest site availability, density dependence could result from better-quality individuals settling in areas with fewer nest sites and reproducing more successfully (Garant *et al.* 2005). Analyses of the effects of density should therefore aim to control for the characteristics of individual females as well as within-environment differences in habitat quality.

Density is most often measured as the number of breeding pairs per unit area (e.g. Perrins 1965; Orell & Ojanen 1983; Perrins & McCleery 1989; Both, Tinbergen & Visser 2000). Using this approach, all pairs of breeding birds in a given year are assigned the same breeding density value irrespective of spatial variation at the level of individual breeding events. However, variation in breeding density is likely to occur, usually due to variation in the availability of resources, such as suitable nest sites. For example, Brown, Mehlman & Stevens (1995) found that many bird distributions were characterized by large areas containing a few individuals, interspersed with 'hot spots' of high density. An alternative method for measuring breeding density at the level of the individual is based on the distance to the nearest breeding neighbour (e.g. Krebs 1971). Although this method has the advantage of assigning an individual measure of breeding density to each pair, it acknowledges no neighbours other than the nearest, and thus does not account for spatially variable breeding densities. For example, two pairs breeding close to each other, but a considerable distance from others, would be assigned the same nearest neighbour value as another similarly spaced pair in the centre of a densely packed cluster.

For a territorial species, territory size may provide a more accurate estimate of breeding density at the level of the individual where competition and reproductive decisions are thought to operate. However, the time spent in the field needed to assess territory sizes is considerable and often prohibitive. Furthermore, defensive behaviour does not necessarily relate to intraspecific breeding density or territory size, as the area defended may vary at different stages of the reproductive cycle. For these reasons, and because this method is not suitable for analysing historic, long-term data sets, there is a need to develop geometric territory models that estimate individual breeding density and take into account spatially variable breeding sites (see Adams 2001 for a review).

The aims of the current study were twofold. First, we examined the utility of a geometric tessellation technique for estimating territory size for 5007 pairs of great tits breeding over a 32-year period. We argue that the areas of the resulting territory polygons (necessarily inverse to local breeding density) serve as a simple model of local breeding density that operates at the level of the individual and accounts for spatial variation. Second, we use our measure of local breeding density to examine density dependence at different stages of the reproductive cycle and discuss possible causative processes.

Methods

FIELD DATA

Data were obtained during the Edward Grey Institute's long-term study of the great tit at Wytham Woods, near Oxford, UK. The data used in the present study were collected between 1965 and 1996, in accordance with methods described previously (e.g. Perrins 1965, 1979; Gosler 1993). Great tits breed almost exclusively in nestboxes in Wytham, the locations of which have remained more or less constant throughout the study, unless a minor move was necessitated by tree fall. Nestboxes were visited at least once a week to ascertain clutch initiation date (lay-date, where 1 April = 1), egg mass (the mean of three to five unincubated eggs) and clutch size, and chicks were weighed and ringed on day 15 after hatching (where hatch day = 1). For the purpose of this study, fledgling mass was averaged for each brood. Parents were trapped at nestboxes after the chicks reached 7 days of age (to reduce desertion risk), aged and sexed (Svensson 1994), and ringed, or their identities were established from (BTO) rings already fitted.

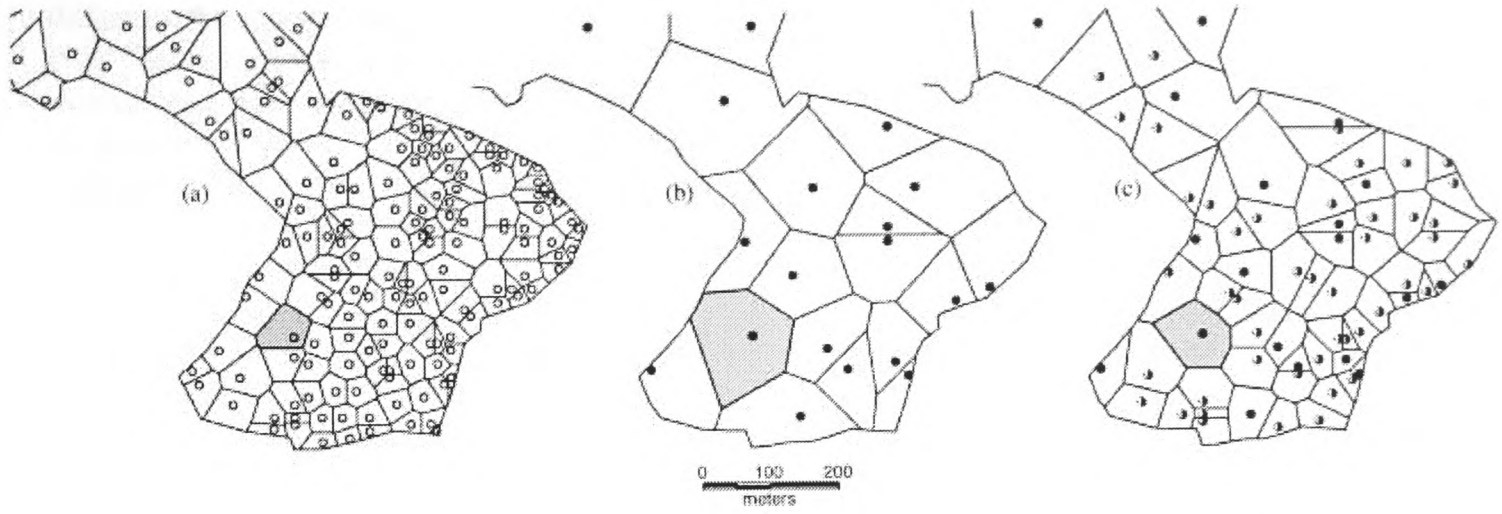


Fig. 1. Definitions of polygons and territories for breeding great tit density. An area of Wytham (Bean Wood) showing (a) all nest boxes with their tessellated polygons the areas of which provide an estimate of nest box spacing, (b) nest boxes occupied by great tits in 1972 and their tessellated polygons which provide a simple model for territory size, and (c) nest boxes occupied by great tit (solid circles) and blue tits (half solid circles) in the same year with their tessellated interspecific polygons. The nest box in the shaded area has a spacing polygon size of 0·4 ha. The great tit using the same nest box in 1972 had a tessellated territory size of 1·8 ha with five contiguous neighbours (b), and an interspecific polygon of 0·7 ha (c). The difference between the sizes of polygons (b) and (c), 1·1 ha, is used in the present study as a measure of local blue tit density for the focal pair of great tits.

We analysed first clutches (second clutches are very rare in Wytham), and only those in which more than four eggs were laid. Reproductive success was measured by the number of young from each brood that were recruited to the breeding population in subsequent years. This figure does not reflect the total numbers that survive to breed, as many leave Wytham and breed elsewhere (McCleery & Perrins 1985). However, the number of recruits remains an accurate measure of the relative success of nests within the context of this population study. Habitats were classified into the following four categories as in Gibson (1988), Gosler (1990) and Gosler, Higham & Reynolds (2005): (1) Ancient seminatural woodland; (2) eighteenth and nineteenth century plantations; (3) twentieth century plantations; and (4) secondary regenerated wood pasture (544, 223, 141 and 98 nestboxes, respectively). The spring temperature each year was recorded as the sum of the maximum temperatures for each day between 1 March and 20 April (the Warmth sum), as in McCleery & Perrins (1998).

DIGITAL MAPPING

Map Info Professional ver. 7 was used to produce yearly maps detailing the location of nestboxes in Wytham Woods that were occupied by great tits, or by great and blue tits during the breeding seasons of 1965–96. Altitude readings and the strength of the topographic slope for each nestbox were extracted from an Inverse Distance Weighting (IDW) interpolation of a 50-m resolution Land Form PROFILE Digital-Terrain-Model (DTM) data set provided by Ordnance Survey. The GIS software was also used to measure the distance between each nestbox and the woodland perimeter.

TERRITORY MODEL

The GIS software was used to generate quantitative predictions about the spacing of nestboxes and the size and shape of territories based on the relative location of nestboxes within the perimeter of the wood (20 km in length). By using a Dirichlet tessellation technique, we formed Thiessen polygons (Rhynsburger 1973; Tanemura & Hasegawa 1980; Stoyan, Kendall & Mecke 1987) around each nestbox at Wytham and used their sizes as a measure of nestbox spacing (Fig. 1a). A tessellated polygon is a geometric construct that contains all points closer to the generating point (in this case a nestbox) than to any other. This is achieved by placing boundaries exactly mid-way between all adjacent neighbours up to and including the woodland perimeter. The polygons are formed on a flat surface and therefore do not account for topographic variations in polygon size. For this reason, in all models we tested for an effect of gradient strength and an interaction with polygon size and found no effects. Polygons, hereafter called tessellated territories, were also formed around nestboxes occupied by great tits in each year (Fig. 1b) and used as a simple model for territory size. The model assumes that territoriality is strongest at the nestbox and declines with distance, as has been observed in many territorial animals (Giraldeau & Ydenberg 1987). The model also assumes that pairs maintain equal spacing, are of equal defensive ability and that territories are contiguous, mutually exclusive and cover all of the available habitat. Territories are assumed to be of equal quality. However, we might expect a negative relationship between habitat quality and territory size to reduce defensive costs and the risk of cuckoldry. Therefore we tested for an interaction between habitat type and territory size; we found no effect in these data. For each tessellated territory, the number of contiguous neighbours was also counted as a measure of crowding pressure (Fig. 1b). Great and blue tits compete for the same nestboxes and for food (Minot 1981; Minot & Perrins 1986). For this reason, Thiessen polygons were also formed around nestboxes occupied by either species (interspecific polygons Fig. 1c), and their areas calculated. In this study we use the

difference in size between the tessellated territory (Fig. 1b) and the interspecific polygon (Fig. 1c) to yield an estimate of the local density of blue tits for each pair of great tits. Using this method, a pair of great tits breeding in an area with no blue tits present would have an interspecific polygon equal in size to their tessellated territory, and therefore their local blue tit density would be zero. However, a pair of great tits breeding in close proximity to several blue tits would have an interspecific polygon considerably smaller than their tessellated territory and therefore would be assigned a higher score for local blue tit density.

To compensate for excessively large tessellated polygons in areas of low nestbox density, we systematically imposed a range of ceilings upon the size of territory polygons, and tested the effect of imposing a particular ceiling on the explanatory power of territory size in each model. For example, at a ceiling level of 1 ha, all polygons above this size were replaced with a value of 1 ha while polygons below 1 ha in size remained unaffected. This procedure was repeated with ceilings from 0·2 to 4·6 ha in increments of 0·1 ha (affecting 99% of the territory polygons at the 0·2 ha level and 4% at the 4·6 ha level). We hypothesized that ceilings at the high end of the range would reduce excessively large polygons to a more biologically reasonable level, with the result that using the capped territory data ought to explain more variation in reproductive traits than uncapped data. At the lower end of the range, the ceilings will reduce the area of realistically sized polygons, such that the capped data will explain less variation in reproductive traits. This combination of effects should be detected as a maximum in the effect size (test statistic) for the effect of territory size in the models. It was our aim to establish the ceiling level (i.e. maximum size) at which tessellated territory size explains the maximum amount of variation in reproductive traits. This method was employed rather than testing for a quadratic term because it yields more information regarding the scale at which the signals are maximized in the models.

STATISTICAL ANALYSES

Linear mixed models (LMM) with normal errors were performed with GENSTAT ver. 7·2 (VSN Intl 2003) to assess the effect of our measure of territory size on lay-date, clutch size, egg mass and fledgling mass. A Generalized Linear Mixed Model with a Poisson error structure was used to analyse the number of recruits to the breeding population with respect to territory size. In each model, year of reproduction and female identity were included as random effects and territory size was always included as a fixed effect. We also included terms for life-history stages occurring before the subject of analysis in each case (for example, clutch size in the case of number of recruited offspring). By including year as a random effect we control for between-year differences due to overall population density, and by including female as a random effect we control for systematic differences between females (due, for example, to differences in biometrics and condition). Our analyses, therefore, specifically and effectively consider variation within annual environments. The significance of factors in explaining variation was assessed from the Wald statistic, which is distributed asymptotically as χ^2 (VSN Intl 2003), and the amount of variation explained by each model was estimated as a percentage of the difference between the residual variance when only random effects were included and the residual variance of the final model. Five models were built using backward stepwise removal of nonsignificant factors depending on their Wald statistic: (1) the *lay-date* model controlled for the age of the female, spring temperature (warmth sum), altitude, female status (resident or immigrant, defined as whether hatched in a Wytham nestbox or not, respectively) and habitat type; (2) the resulting *clutch size* LMM included lay-date and the age of the female as fixed effects (as in Perrins 1965); (3) the *egg mass* model controlled for the age of the female, distance to the edge of the woodland and lay-date; (4) the *fledging mass* model controlled for clutch size, mean egg mass and lay-date as fixed effects (as in Garant *et al.* 2004) but also altitude (earlier phenology at lower altitudes; see Hopkins 1938); and finally (5) the *number of recruits* model controlled for lay-date, fledging mass and clutch size as fixed effects (as in Perrins & McCleery 1989). The models explain variation in a sequence of reproductive stages. Therefore, by including the previous stages as covariates, our analyses investigated the independent effect of density upon each stage. For ease of presentation, data are displayed graphically as residuals estimated by removing the polygon data from the model and rerunning the analysis.

To explore the effect of interspecific density on reproduction in great tits, models were also run using, as an alternative predictor, our measure of local blue tit density capped through a similar range of maxima to that used for the tessellated territories, and the results plotted in the same way. In this way we aimed to determine the level at which inter- and/or intraspecific density explained most variation in the dependent traits.

All subset regressions (GENSTAT, VSN Intl 2003) were used to select the combination of polygon data that explained most variation in the reproductive traits. Explanatory variables other than polygon data were forced in each model, while territory data and local blue tit density data capped at each level were included as possible explanatory variables. The combination of polygon data that returned the lowest Akaike value (see Burnham & Anderson 1998) was deemed to be the most suitable model. Thus, this is a formal statistical analysis of the graphical approach described above.

Density-dependent effects may occur partially because poor-quality birds are excluded from high-quality areas or those with low nest site availability (Dhondt *et al.* 1992). This could be termed an indirect effect of density upon the efficacy of reproduction. To investigate whether breeding density has a direct effect on great

Table 1. Results of mixed models assessing reproductive traits of great tits. Data used were from Wytham woods during 1965–96 (n = 4550). General linear models were used in each case, with the exception of the recruitment analysis where a generalized model with a Poisson error structure was used. Year of reproduction (n = 28) and female identity (n = 3484) were included as random effects. Percentages in parentheses indicate the amount of variation explained by the fixed component of each model

Dependent/independent factor	Wald χ^2	d.f.	Effect/(SE)	P
Lay-date (8%)				
Age	133·64	1	−0·8412/(0·07312)	< 0·001
Warmth sum	52·95	1	−0·09073/(0·012438)	< 0·001
Altitude	23·93	1	0·01807/(0·003580)	< 0·001
Female status (immigrant or resident)	16·7	1	R < I	< 0·001
Habitat type	14·82	3	2 < 3 < 1 < 4	< 0·001
Territory size (ha)	1·65	1	−0·08589/(0·068620)	0·199
Clutch size (13%)				
Lay-date	374·42	1	−0·06878/(0·003453)	< 0·001
Age of female	42·26	1	0·1167/(0·01781)	< 0·001
Territory size (ha)	14·68	1	0·05594/ (0·015376)	< 0·001
Mean egg mass (1%)				
Age	40·19	1	−0·01060/(0·001673)	< 0·001
Distance from woodland edge (m)	17·37	1	−0·00008172/(0·000019608)	< 0·001
Altitude (m)	8·35	1	0·0002575/(0·00008912)	0·004
Lay-date	3·79	1	0·0006508/(0·00033437)	0·052
Clutch size	4·24	1	−0·002752/(0·0013360)	0·039
Territory size (ha)	2·35	1	−0·002373/(0·0015492)	0·126
Mean fledgling mass (4%)				
Clutch size	92·31	1	−1·253/(0·1306)	< 0·001
Mean egg mass	51·31	1	10·14/(1·437)	< 0·001
Altitude	28·82	1	−0·04152/(0·007686)	< 0·001
Lay-date	19·75	1	−0·1510/(0·03461)	< 0·001
Territory size (ha)	11·73	1	0·5331/(0·15619)	< 0·001
Number of recruits (10%)				
Lay-date	109·52	1	−0·03655/(0·003493)	< 0·001
Mean fledgling mass	102·20	1	0·01769/(0·001750)	< 0·001
Clutch size	29·69	1	0·07020/(0·012883)	< 0·001
Territory size (ha)	12·33	1	0·04803/(0·013678)	< 0·001

tit reproduction, we repeated the models with a subset of repeat breeders. In this way, we were able to investigate the effect of territory size on reproductive parameters within individual females; this analysis thus assumes that 'quality' is relatively fixed for individuals, and thus it would not detect an effect due to individuals occupying poorer-quality territories in years in which their quality is reduced. However, as breeding-site fidelity is very high in this population (a mean of 112 m between successive breeding attempts in the current data, and see Harvey, Greenwood & Perrins 1979) we judge this process to be unlikely.

We also used Generalized Linear Models with Poisson errors to determine which factor(s) affected the lifetime reproductive success of a female, by testing for significance of the following parameters averaged over a female's lifetime: clutch size, lay-date, fledgling mass and territory size. By not controlling for the number of times she reproduced in her lifetime, this analysis contains an element of survival from one reproductive attempt to another.

Results

TERRITORY MODEL

Tessellated territory polygons were formed for 5007 occupied nestboxes over the 32 years of the study. The territories ranged from 0·06 to 14 ha in size with a mean of 1·6 ha (SD = 1·368). Clutch size, mean fledgling mass and the number of recruits from a breeding attempt were independently related both significantly and positively to territory size as estimated by the Thiessen tessellations (all P < 0·001; see Table 1). There was no suggestion of an effect of territory size on lay-date ($\chi^2_{(1)}$ = 1·65, P = 0·199) or egg mass ($\chi^2_{(1)}$ = 2·35, P = 0·126; Table 1). Mean residuals from the territory models were plotted against the area of the tessellated territories, expressed in increments of 0·2 ha (Fig. 2). Each significant variable shows an asymptotic function associated with territory size, with the asymptote about 2–3 ha, reflecting the minimum territory size unaffected by negative density effects. A negative relationship between territory size and lay-date is also apparent with a similar asymptote at 2–3 ha, but not significant in the model. Our measure of local blue tit density also explained significant variation in clutch size ($\chi^2_{(1)}$ = 5·01, P = 0·025), mean fledgling mass ($\chi^2_{(1)}$ = 7·13, P = 0·008) and the number of recruits ($\chi^2_{(1)}$ = 7·63, P = 0·006) when included in the models in place of territory size. Thus local breeding density, as measured by tessellated territories, strongly affected three of the five reproductive traits examined and a negative, but nonsignificant relationship was apparent between tessellated territory size and lay-date. Local blue tit density affected the same traits as intraspecific density but effects were weaker.

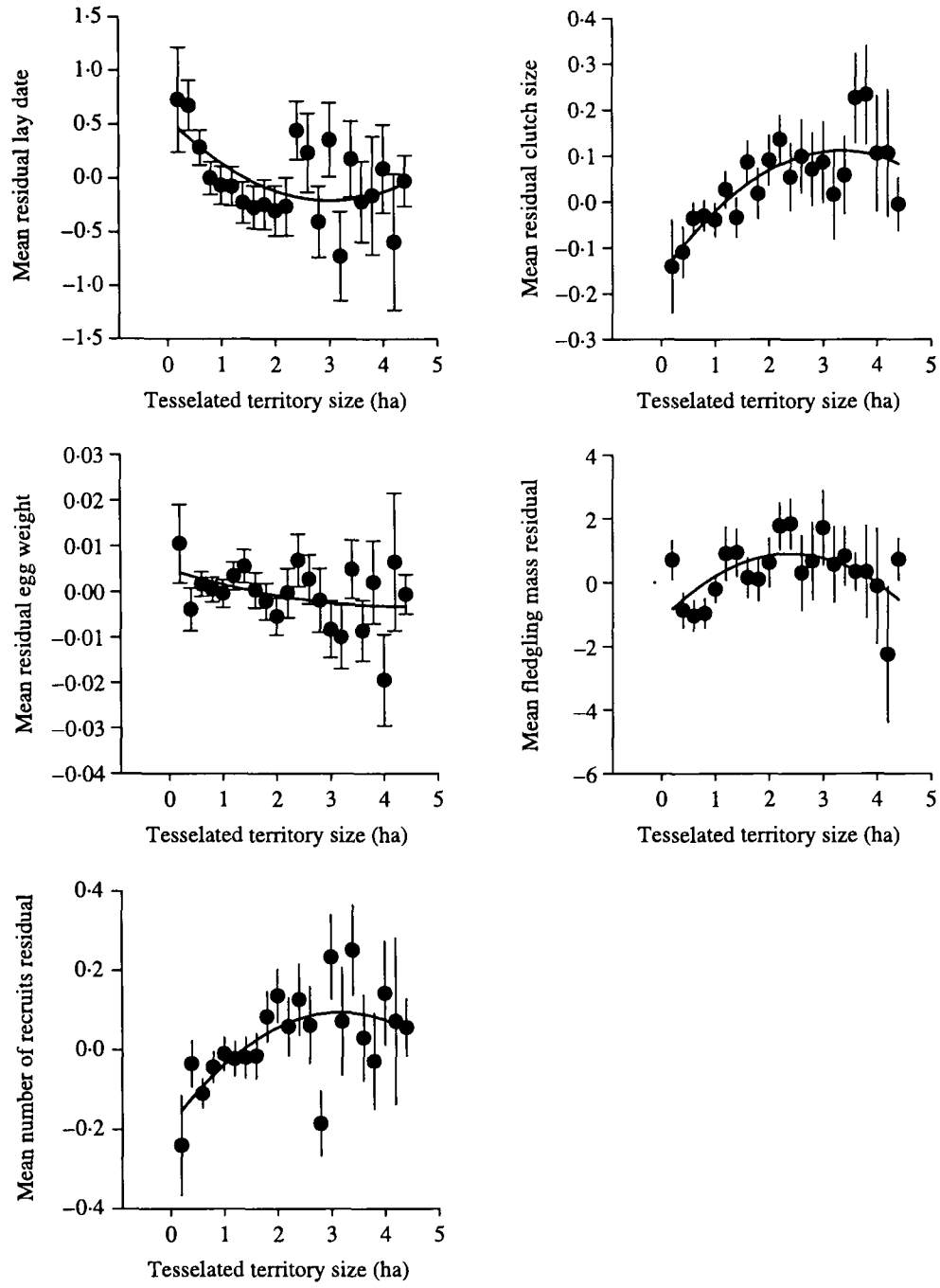


Fig. 2. Relationships between mean territory size classes and life history traits. Mean residual clutch sizeData used were from Wytham woods during 1965–96 (n = 4550). Year of reproduction and female identity were included as random effects, mean residual fledgling mass and mean residual number of recruits plotted against the area of the tessellated polygon containing the generating nest box. Data are displayed as residuals, estimated from full models without territory size (see text). Vertical bars are standard errors.

CAPPED TERRITORY SIZE

To explore the influence of variable ceilings on territory size, the models were rerun many times, on each occasion using territory data capped at a different level. The significance of the territory size measure in explaining reproductive traits was then plotted against the level at which it was capped (Fig. 3). All subset regressions showed that variation in lay-date was best explained by territory polygons capped at 0·9 ha ($\chi^2_{(1)} = 24{\cdot}64$, $P < 0{\cdot}001$), and variation in clutch size by polygons capped at 1·8 ha ($\chi^2_{(1)} = 28{\cdot}69$, $P < 0{\cdot}001$) (Table 2). The greatest amount of variation in mean fledgling mass was explained by territory polygons capped at 2·3 ha ($\chi^2_{(1)} = 17{\cdot}15$, $P = < 0{\cdot}001$), while in the number of recruits model territory polygons capped at 1·9 ha were selected ($\chi^2_{(1)} = 24{\cdot}14$, $P < 0{\cdot}001$) (Table 2). The lay-date and recruitment models explained more variation when capped, than when uncapped territory size was used, while the clutch size model explained less total variation. Ceilings of about 2 ha in size affected about 30% of the polygons, while the ceiling of 0·9 ha affected 59% of the polygons. It is striking that several of these analyses gave a consistent estimate of the territory size at which the effect is maximized (i.e. about 2 ha), and that in each case there is a clear maximum in the effect size. The exception is that of lay-date, which is maximized at 0·9 ha, suggesting that the commencement of breeding is affected by density on a smaller scale than are other traits. The maximum effect-size from the interspecific density analysis was lower than the average for intraspecific analyses (1–1·2 ha) and the overall effect size was smaller. This suggests that the scale over which blue tits affect great tits is smaller than the scale of intraspecific density.

WITHIN-FEMALE ANALYSIS

Within repeat breeding females, territory size capped at 0·9 ha was a significant predictor of lay-date ($\chi^2_{(1)} = 7{\cdot}92$, $P = 0{\cdot}005$), while territory size capped at 1·8 ha was a

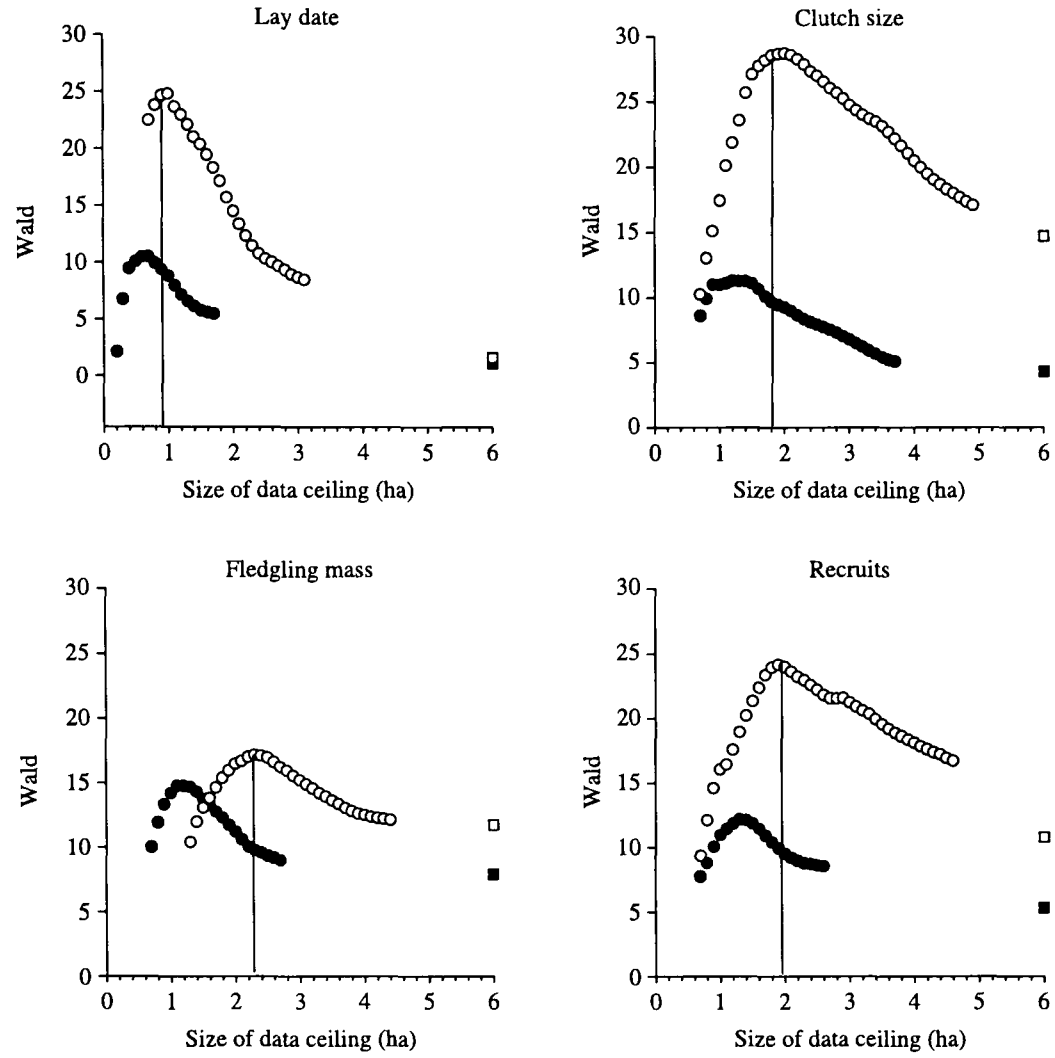


Fig. 3. Graphical estimation of the appropriate size at which to cap estimated territory size to account for over-estimation of size in low density areas. Figures show the Wald statistic (distributed as χ^2), from Linear mixed models analysing variation in lay-date, clutch size, fledgling mass and the number of offspring recruited to the breeding population, for a range of artificially imposed territory sizes (see text). All models include year of reproduction and female identity as random effects. Clutch size model controls for lay date and age of female; fledgling mass model controls for altitude, mean egg mass within the brood, lay date and clutch size; and the reproductive success model controls for lay date, clutch size and the mean fledgling mass within the brood. Open circles are data for great tits alone; solid circles represent the significance of ceilings imposed upon data indicative of local blue tit density (see text). Squares show the significance of the territory size (open) and blue tit density (solid) when no ceiling was imposed. In each model, territory size capped at between 0·9–2·3 ha was selected by all subsets regressions to explain the most amount of variation in the dependent variable, as indicated by the Akaike value (vertical lines).

Table 2. Refined mixed models using capped territory size as a measure of local density (see Table 1)

Dependent/independent factor	Wald χ^2	d.f.	Effect/(SE)	*P*
Lay-date (9%)				
Age	135·99	1	−0·8504/(0·07292)	< 0·001
Warmth sum	52·97	1	−0·09077/(0·012472)	< 0·001
Altitude	29·96	1	0·01935/(0·003536)	< 0·001
Female status (immigrant or resident)	16·7	1	*R* < I	< 0·001
Habitat type	12·61	3	2 < 3 < 1 < 4	< 0·001
Territory size (ha) capped at 0·9 ha	24·64	1	−2·272/(0·4577)	< 0·001
Clutch Size (13%)				
Lay-date	368·53	1	−0·06835/(0·003448)	< 0·001
Age of female	43·63	1	0·1185/(0·01782)	< 0·001
Territory size (ha) capped at 1·8 ha	28·69	1	0·1794/(0·03526)	< 0·001
Fledgling mass (4%)				
Clutch size	94·18	1	−1·271/(0·1307)	< 0·001
Mean egg mass	52·21	1	10·24/(1·436)	< 0·001
Altitude	32·19	1	−0·04437/(0·007778)	< 0·001
Lay-date	19·25	1	−0·1479/(0·03458)	< 0·001
Territory size (ha) capped at 2·3 ha	17·15	1	1·425/(0·3474)	< 0·001
Number of recruits (11%)				
Lay-date	109·80	1	−0·03656/(0·003489)	< 0·001
Mean fledgling mass	99·46	1	0·01746/(0·001751)	< 0·001
Clutch size	27·31	1	0·06731/(0·012879)	< 0·001
Territory size (ha) capped at 1·9 ha	24·62	1	0·1582/(0·03188)	< 0·001

Table 3. Results of mixed models used to assess significance of determinants of reproductive traits, using capped territory data and constructed within female using repeat breeders; 1094 individuals and 2761 breeding attempts (see Table 1)

Dependent/independent factor	Wald χ^2	d.f.	Effect/(SE)	*P*
Lay-date (8%)				
Age	64·03	1	−0·7015/(0·08766)	< 0·001
Warmth sum	56·53	1	−0·09117/(0·012127)	< 0·001
Altitude	12·22	1	0·01799/(0·005146)	< 0·001
Female status (immigrant or resident)	7·00	1	*R* < I	0·008
Habitat type	4·76	3	2 < 3 < 1 < 4	< 0·001
Territory size (ha) capped at 0·9 ha	7·92	1	−1·609/(0·5720)	0·005
Clutch size (12%)				
Lay-date	147·96	1	−0·05801/(0·004764)	< 0·001
Age of female	21·95	1	0·1021/(0·02181)	< 0·001
Territory size (ha) capped at 1·8 ha	7·06	1	0·1276/(0·04952)	0·008
Fledgling mass (4%)				
Clutch size	48·82	1	−1·227/(0·1749)	< 0·001
Mean egg mass	23·37	1	9·228/(1·9031)	< 0·001
Altitude	13·81	1	−0·03929/(0·010571)	0·001
Lay-date	14·92	1	−0·1732/(0·04517)	< 0·001
Territory size (ha) capped at 2·3 ha	20·89	1	2·151/(0·4613)	< 0·001
Number of recruits (8%)				
Lay-date	42·40	1	−0·03044/(0·004675)	< 0·001
Mean fledgling mass	57·05	1	0·01782/(0·002359)	< 0·001
Clutch size	14·90	1	0·06628/(0·0171730	< 0·001
Territory size (ha) capped at 1·9 ha	9·63	1	0·05543/(0·017864)	0·002

Table 4. The results of a log-linear model (Generalized Linear Model) with a Poisson error structure assessing the determinants of lifetime reproductive success (total number of offspring recruited to the breeding population) of 2935 female great tits, with respect to mean life-history traits and tessellated territory size

Dependent/independent factor	Estimate	SE	$t_{(2925)}$	*P*
Lifetime reproductive success				
Constant	−2·459	0·367	−6·7	< 0·001
Mean lay-date	−0·03187	0·00252	−12·64	< 0·001
Mean clutch size	0·1035	0·012	8·62	< 0·001
Mean fledgling mass	0·01334	0·0017	7·85	< 0·001
Mean territory size (ha)	0·0436	0·0133	3·28	0·001

significant predictor of clutch size ($\chi^2_{(1)} = 7{\cdot}06$, $P = 0{\cdot}008$; Table 3). Also within females, territory size capped at 2·3 ha was a significant predictor of fledgling mass ($\chi^2_{(1)} = 20{\cdot}89$, $P < 0{\cdot}001$) and territory size capped at 1·9 ha was significant in explaining variation of the number of recruits ($\chi^2_{(1)} = 9{\cdot}63$, $P = 0{\cdot}002$). Effects were weaker and models explained less variation than the between-female analyses, with the exception of the fledgling mass model. These results are important in suggesting a causal role of population density on reproductive output, as the output of an individual female can clearly be predicted by her territory size in different years.

LIFETIME REPRODUCTIVE SUCCESS AND SURVIVAL

For 2935 females, we found significant independent effects of mean lifetime clutch size ($t = 8{\cdot}62$, $P < 0{\cdot}001$), mean fledgling mass ($t = 7{\cdot}85$, $P < 0{\cdot}001$) and mean lay-date ($t = -12{\cdot}64$, $P < 0{\cdot}001$) on the lifetime number of offspring recruited to the breeding population. Our results also show an independent effect of mean lifetime territory size on the total number of lifetime recruits ($t = 3{\cdot}28$, $P < 0{\cdot}001$) (Table 4). We made no attempt to control for the number of times that a female in the data set reproduced and so these results contain an element of variance due to survival from one reproductive attempt to another. Residuals from the model were plotted against mean lifetime territory size (Fig. 4) showing a clear rise in lifetime reproductive success with mean territory size, until an asymptote at c.2·5 ha. In this case it seems that this relationship may be driven largely by the effect of very small territory sizes; above *c.* 1 ha the relationship appears flat.

Discussion

Our results demonstrate that Thiessen polygons represent a suitable model for estimating the territory size of great tits in historic data sets. Moreover, the model yields an individual measure of breeding density for each pair and accounts for variation in breeding density within environments. In this current study, territory sizes

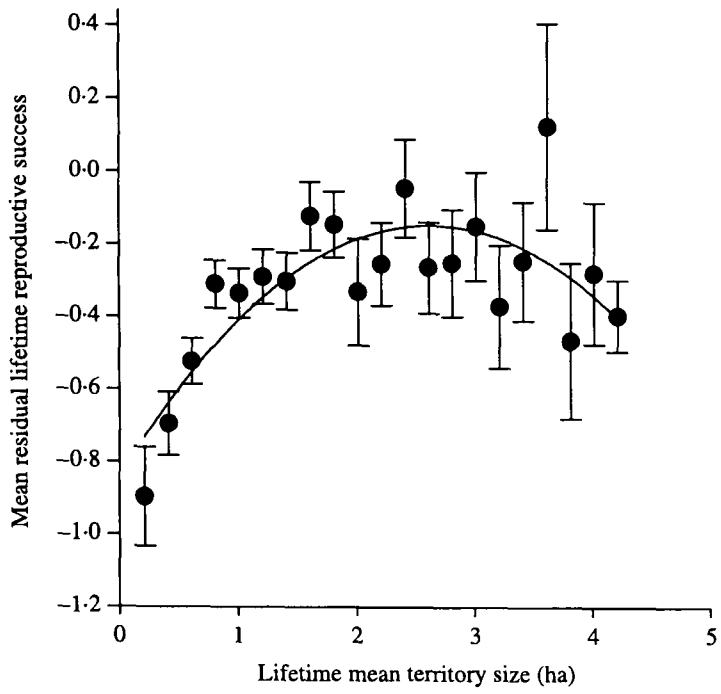


Fig. 4. Residual lifetime reproductive success as function of mean lifetime territory size. Model controls for clutch size, lay date and mean fledgling mass.

estimated by Thiessen polygons were highly significant independent predictors of clutch size, fledging mass and reproductive success. Further, we demonstrated a new capping method for refining the territory model by imitating interstices, which subsequently revealed a significant density effect on lay-date. This capping method also yielded an estimation of maximum territory size at different stages of the breeding season. All effects were apparent between and within females. No effect was found on egg mass, and we discuss some explanation for, and implications of, these results below.

TERRITORY MODEL TESTING

To test the territory model we compared the characteristics of the tessellated territories with those measured in the field in previous studies. In agreement with Krebs (1970), we found territories that included the edge of the woodland were larger than interior territories (t = 2·59, d.f. = 6474·27, P = 0·01) and that they had fewer contiguous neighbours (t = 52·24, d.f. = 6476, $P < 0·001$), although the latter is expected for simple geometric reasons. Note that the difference in size between edge and internal territories was not due to differences in nestbox spacing, as polygons based on this (Fig. 1a) showed no difference between those at the edge and those in the interior (t = 0·67, P = 0·504), suggesting that nestboxes were occupied less frequently at woodland edges. With regard to mean territory sizes, our mean uncapped territory size was 1·6 ha, which is somewhat larger than other field-based studies have found. For example, Krebs (1971) found a mean of 1·26 ha by drawing a perimeter around mapped observations and responses to song playback, and Both & Visser (2000) found a mean of 1·1 ha by enclosing observations with maximum convex polygons. Using an alternative measure, if we calculate density as the numbers of pairs per hectare, then our territory model gives an overall mean of 0·6 pairs per hectare. Perrins (1965) calculated 1·3 and 0·6 pairs per hectare in high- and low-density areas of Wytham (Marley and Great Wood, respectively) while Both *et al.* (2000) found between 0·3 and 1·1 pairs per hectare in another population. Our underestimate of density is probably due to our territory model using all of the available habitat, which leads to an overestimation of territory size in areas or years of low density. To account for this we capped territories systematically through a range of maxima and found that imposing a maximum territory size of 0·9–2·3 ha maximized the significance of the territory size effect in our models. This value probably represents the maximum territory size in our population, achieved by birds breeding in areas or years of low density. We consider it significant that, following a limitation of 2 ha, our mean territory size was reduced to 1·25 ha, a figure more in line with field-based studies (Krebs 1971; Both & Visser 2000). This is, to the best of our knowledge, the first time that this systematic capping method has been applied to refine a territory model, and we believe that there are many other applications of this technique with respect to spatial analyses where scale is uncertain.

LAY-DATE

As for many birds breeding in temperate climates, the timing of breeding is critical for great tits. Early fledglings have higher recruitment probabilities (Lack 1958; Perrins & McCleery 1989; Verboven & Visser 1998; Cresswell & McCleery 2003) probably due to a competitive advantage during the crucial 2 weeks after fledging. At the population level, we might expect mean lay-date to be delayed in high-density years due to a higher proportion of both poor-quality sites being occupied and young or poorer-quality birds being present, but we found no association between lay-date and the number of birds breeding in Wytham at the level of the population when controlling for spring temperature (t_{28} = 1·41, P = 0·169). Laying date is a highly plastic character, varying with respect to individual age, preceding spring temperature, altitude and habitat type in our analyses (Table 1). Earlier-breeding birds had larger clutches and independently produced heavier fledglings that were more likely to recruit to the breeding population but our analysis showed no effect of uncapped territory size on lay-date at the level of the individual despite a visible relationship between average residual lay-date and territory size (Fig. 2). However, our analyses show a clear density effect on laying date at the level of the individual subsequent to a territory size cap of 0·9 ha to control for oversized polygons. Explaining the maintenance of variation in laying date, despite it being subject to strong natural selection, has long been a challenge, and this trait is illustrative of many other characters that are under directional selection yet show substantial variation within populations (see Price, Kirkpatrick & Arnold 1988; Merilä, Sheldon & Kruuk 2001; Sheldon, Kruuk & Merilä 2003). One popular

explanation for the maintenance of variation in this character is that a large component of the variation in timing of breeding represents individual condition, and that selection acts on this component of variation (Price *et al.* 1988). Our results support this explanation, as we might reasonably expect local density to influence local condition, and hence timing of breeding. The capping of territory sizes also showed that territory size was smallest at the time of egg laying (0·9 ha). The number of tessellated territories affected by this ceiling level was 59%, which is also an approximation of the number of birds that are unaffected by density at the time of egg laying. This could be possibly explain why in the current data set no effect of density on lay-date is found at the level of the population; most birds are unconstrained by density at the time of egg laying. Møller (1990) concluded that territory sizes of many species were largest during the period of fertility, probably to reduce the likelihood of extra pair copulations and cuckoldry. However, Rodrigues (1998) conducted a field-based study on chaffinches *Fringilla coelebs* and reported a minimal territory size during the fertile period. Our analyses suggest that territory sizes increase through the breeding season, possibly because more resources are required when provisioning chicks later in the season. However, we believe this subject warrants further investigation.

CLUTCH SIZE

Density-dependent clutch size has often been demonstrated in great tits, both in correlational studies (Lack 1958; Perrins 1965; Orell, & Ojanen 1983), in which the mean number of eggs laid in a given year was negatively associated with the number of breeding pairs present, and in experimental studies (Both 1998b) in which changes in density resulted in changes in clutch size in the expected direction (but see Both & Visser 2000). When controlling for lay-date and clutch size, as earlier and older birds independently have larger clutches, we found a positive relationship between clutch size and territory size at the level of the individual. This result is in accordance with previous correlational studies. By examining the relationship between the clutch and territory sizes of repeat breeders, we found density-dependent clutch sizes within females, although this effect was weaker than between females. A similar analysis was performed by Both (1998b), who found that females breeding on the same territory in different years showed a negative correlation between the change in clutch size between years and the change in density. These within-female analyses imply a causal effect of density on clutch size, rather than a greater proportion of poor-quality sites being occupied, or poor-quality birds being present in high-density years. Whether the relationship between clutch size and density results from adaptive adjustment by females, or is instead caused by direct food limitation is unknown; distinguishing between these two explanations would require concurrent experimental manipulations of clutch size and breeding density. We are unaware of any such experimental work.

EGG MASS

When controlling for potentially confounding factors, our analyses showed no effect of territory size on egg mass at the level of the individual. This is contrary to the findings of Perrins & McCleery (1994) who, at the level of the population, found generally lighter eggs in years of high density. However, their analysis did not control for confounding factors such as age. For example, in our analysis the age of the female had a strong negative effect on the mass of the eggs ($\chi^2_{(1)} = 40{\cdot}19$, $P < 0{\cdot}001$). It is intriguing that birds breeding close to the woodland edge had heavier eggs than did birds within the wood, as did birds breeding at higher altitudes; these effects are currently under investigation. These last results, in addition to the age effect, suggest that egg size may be adjusted by individuals in relation to their breeding conditions: the larger eggs laid by younger birds, breeding closer to woodland edge and at higher altitudes suggest that larger eggs may be a response to poorer environmental conditions. If so, the lack of response to density is puzzling. It is also unexpected because clutch size and egg size show strong negative covariance at both phenotypic and genotypic levels in this population (D. Garant & B.C. Sheldon, unpublished analyses). Hence, an increased egg size in response to higher density would be expected as a correlated response to the change in clutch size. It is possible that one influence of increased density is to suppress the covariance between clutch size and egg size, although no interaction was found in these data.

FLEDGLING MASS

Density-dependent fledgling mass in the great tit has been shown previously at the level of the population (Garant *et al.* 2004). In an experimental study, Both & Visser (2000) found that an increase in territory size was followed by an increase in fledgling mass, independently of parent quality. Further, Both (1998a) found that an experimental increase in nestbox density was associated with a decline in nestling mass. The current study also found a strong positive effect of tessellated territory size on fledgling mass at the pair level, when controlling for differences in egg mass, lay-date and clutch size, showing that birds breeding in larger territories have heavier chicks than predicted by these factors alone. A territory effect on fledgling mass independent of clutch size may reflect an incomplete optimization of clutch size or may result from lower density birds being able to both lay more eggs and have heavier chicks. We also found an altitude effect such that birds at lower altitudes had heavier chicks independently of their earlier lay-date. A likely explanation of density-dependent fledgling mass is that nestling provisioning may be reduced in high-density areas, in terms of food quality and/or quantity, particularly if

parents also suffer from increased interference from other pairs.

RECRUITMENT AND LIFETIME REPRODUCTIVE SUCCESS

In the great tit breeding success declines seasonally (Perrins 1970; Perrins & McCleery 1989). This relationship is thought to be causal in both blue tits (Norris 1993) and great tits (Verhulst, van Balen & Tinbergen 1995); however, there is some evidence to suggest that differences in quality between early and late breeders also contribute to the seasonal decline (Verhulst *et al.* 1995). The current analyses also show a significant negative lay-date effect on the number of recruits to the breeding population. Furthermore, the lay-date effect on recruitment was also apparent within females, supporting the causal role of lay-date on reproductive success. Previous studies have shown that heavier fledglings are more likely to recruit to the breeding population (Both, Visser & Verboven 1999; Monros, Belda, & Barba 2002; Garant *et al.* 2004). The current analysis supports this result as, independent of their earlier lay-date, heavier chicks at Wytham were more likely to recruit. We also found a positive clutch-size effect on recruitment, which suggests that there may be an independent benefit of coming from a large brood. This effect has been shown before and may arise either from a genetic effect whereby fitter parents lay larger clutches (Both, Tinbergen, & van Nordwijk 1998), or from environmental covariance between parent and offspring characters.

In addition to the relationships described above, we found a strong positive effect of territory size on recruitment, independent of earlier lay-dates, larger clutches and heavier chicks. The same was true when we analysed the effect of mean lifetime territory size on lifetime reproductive success without controlling for the number of times an individual reproduced, indicating higher survival in larger territories. This suggests that there are additional fitness benefits of having a larger territory beyond that predicted by those factors controlled for above. For example, females are thought to adjust their clutch sizes to fit the number of offspring that they are able to raise in a given environment (Tinbergen & Daan 1990). If this adjustment were complete then we would not expect to see a strong environmental effect on reproductive success when controlling for clutch size. However, as our results show a strong effect of territory size on reproductive success independent of clutch size, we can conclude either that, in the current population, clutch size adjustment to population density is incomplete or that birds at low density are beyond some threshold in resource abundance and are thus able to produce both large clutches and have heavier chicks, which are more likely to recruit.

What causes this additional effect of territory size on lifetime reproductive output? There are several possibilities, among which are: (1) food limitation between fledging and independence from the parents; (2) increased predator activity during the same period due to attraction to higher density prey breeding areas; (3) an increased tendency for offspring to disperse further (i.e. outside Wytham) from high-density areas, which would appear as reduced recruitment in our data.

Conclusions

Thiessen polygons represent a suitable geometric model for estimating breeding density in great tits. The tessellation model provides an individual measure of breeding density for each pair and accounts for variations in breeding density within environments; estimated territory sizes agreed well with those estimated previously by more intensive methods. In the current study, lay-date, clutch size, fledging mass and reproductive success were strongly predicted by territory size, both between and within females, suggesting a pervasive role of local population density in explaining individual reproductive fitness. However, we found no effect of breeding density on egg mass, suggesting that resource limitation may not be an important determinant of this trait. We have also shown that capping territories imitated interstices effectively to overcome the problem of oversized polygons at low density. Our analyses suggest that mean maximum territory size increases from 0·9 during clutch initiation to 2·3 ha during nestling provisioning. We suggest that the model can be applied to other living systems at any scale in which conspecific environments are both spatially variable and influential.

Acknowledgements

We are grateful to the many people who collected data during the long-term tit study in Wytham, and to C. Both, C.M. Perrins, J.L. Quinn, M.J. Wood and an anonymous referee for their helpful comments on the manuscript. T.A.W. was funded by a studentship from the Biotechnology and Biological Sciences Research Council (BBSRC), D.G. was financially supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Postdoctoral Research Fellowship, and by a (BBSRC) grant to B.C.S; B.C.S. was funded by a Royal Society University Research Fellowship.

References

Adams, E.S. (2001) Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, **32**, 277–303.

Andrewartha, H.C. & Birch, I.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, IL.

Both, C. (1998a) Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology*, **67**, 667–674.

Both, C. (1998b) Density dependence of clutch size: habitat heterogeneity or individual adjustment? *Journal of Animal Ecology*, **67**, 659–666.

Both, C. & Visser, M.E. (2000) Breeding territory size affects fitness: an experimental study on competition at the individual level. *Journal of Animal Ecology*, **69**, 1021–1030.

Both, C., Tinbergen, J.M. & van Noordwijk, A.J. (1998) Offspring fitness and individual optimization of clutch

size. *Proceedings of the Royal Society of London, Series B Biological Sciences*, **265**, 2303–2307.

Both, C., Visser, M.E. & Verboven, N. (1999) Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society of London, Series B Biological Sciences*, **266**, 465–469.

Both, C., Tinbergen, J.M. & Visser, M.E. (2000) Adaptive density dependence of avian clutch size. *Ecology*, **81**, 3391–3403.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.

Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Cresswell, W. & McCleery, R. (2003) How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology*, **72**, 356–366.

Dhondt, A.A., Kempenaers, B. & Adrianensen, F. (1992) Density-dependent clutch size caused by habitat heterogeneity. *Journal of Animal Ecology*, **61**, 643–648.

Garant, D., Kruuk, L.E.B., McCleery, R.H. & Sheldon, B.C. (2004) Evolution in a changing environment: a case study with great tit fledging mass. *American Naturalist*, **164**, E115–E129.

Garant, D., Kruuk, L.E.B., Wilkin, T.A., McCleery, R.H. & Sheldon, B.C. (2005) Evolution driven by differential dispersal within a wild bird population. *Nature*, **433**, 60–65.

Gibson, C.W.D. (1988) The distribution of 'ancient woodland' plant species among areas of different history in Wytham Woods, Oxfordshire. *Woodland Conservation and Research in the Clay Vale of Oxfordshire and Buckinghamshire* (eds K.J. Kirby & F.J. Wright), pp. 32–40. Oxford Forestry Institute, Oxford, and Nature Conservancy Council, Peterborough.

Giraldeau, L.A. & Ydenberg, R. (1987) The centre-edge effect: the result of a war of attrition between territorial contestants? *Auk*, **104**, 535–538.

Gosler, A.G. (1990) The birds of Wytham: an historical survey. *Fritillary*, **1**, 29–74.

Gosler, A.G. (1993) *The Great Tit*. Paul Hamlyn, London.

Gosler, A.G., Higham, J.P. & Reynolds, S.J. (2005) Why are birds' eggs speckled? *Ecology Letters*, **8**, 1105–1113.

Harvey, P.H., Greenwood, P.J. & Perrins, C.M. (1979) Breeding area fidelity of great tits (*Parus major*). *Journal of Animal Ecology*, **48**, 305–313.

Hopkins, A.D. (1938) *Bioclimatics, a Science of Life and Climate Relations*. Miscellaneous Publication 280. US Department of Agriculture, Washington, DC.

Julliard, R., McCleery, R.H., Clobert, J. & Perrins, C.M. (1997) Phenotypic adjustment of clutch size due to nest predation in the Great tit. *Ecology*, **78**, 394–404.

Kluijver, H.N. (1951) The population ecology of the great tit, *Parus major* L. *Ardea*, **39**, 1–135.

Krebs, J.R. (1970) Regulation of numbers in the great tit (Aves: Passeriformes). *Journal of Zoology (London)*, **162**, 317–333.

Krebs, J.R. (1971) Territory and breeding density in the great tit, *Parus major*. *Ecology*, **52**, 1–22.

Lack, D. (1958) A quantitative breeding study of British tits. *Ardea*, **46**, 91–124.

McCleery, R.H. & Perrins, C.M. (1985) Territory size, reproductive success and population dynamics in the great tit, *Parus major*. *Behavioural Ecology: the Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibly & R.H. Smith), pp. 353–373. Blackwell Scientific Publications, Oxford.

McCleery, R.H. & Perrins, C.M. (1998) ... temperature and egg-laying trends. *Nature*, **391**, 30–31.

Merilä, J., Sheldon, B.C. & Kruuk, L.E.B. (2001) Explaining stasis: microevolutionary studies in natural populations. *Genetica*, **112**, 199–222.

Minot, E.O. (1981) Effects of interspecific competition for food in breeding blue and great tits. *Journal of Animal Ecology*, **50**, 375–385.

Minot, E.O. & Perrins, C.M. (1986) Interspecific interference competition – nest sites for blue and great tits. *Journal of Animal Ecology*, **55**, 331–350.

Møller, A.P. (1990) Changes in the size of avian breeding territories in relation to the nesting cycle. *Animal Behaviour*, **40**, 1070–1079.

Monros, J.S., Belda, E.J. & Barba, E. (2002) Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos*, **99**, 481–488.

Newton, I. (1992) Experiments on the limitation of bird numbers by territorial behaviour. *Biology Reviews*, **67**, 129–173.

Norris, K. (1993) Seasonal-variation in the reproductive success of blue tits – an experimental-study. *Journal of Animal Ecology*, **62**, 287–294.

Orell, M. & Ojanen, M. (1983) Effect of habitat, date of laying and density on clutch size of the great tit *Parus major* in Northern Finland. *Holarctic Ecology*, **6**, 413–423.

Perrins, C.M. (1965) Population fluctuations and clutch size in the great tit, *Parus major* L. *Journal of Animal Ecology*, **34**, 601–647.

Perrins, C.M. (1970) The timing of birds breeding seasons. *Ibis*, **112**, 242–255.

Perrins, C.M. (1979) *British Tits*. Collins, London.

Perrins, C.M. & McCleery, R.H. (1989) Laying dates and clutch size in the great tit. *Wilson Bulletin*, **101**, 236–253.

Perrins, C.M. & McCleery, R.H. (1994) Competition and egg-weight in the great tit *Parus major*. *Ibis*, **136**, 454–456.

Price, T., Kirkpatrick, M. & Arnold, S.J. (1988) Directional selection and the evolution of breeding date in birds. *Science*, **240**, 798–799.

Rhynsburger, D. (1973) Analytic delineation of Thiessen Polygons. *Geographyraphical Analysis*, **5**, 133–144.

Rodrigues, M. (1998) No relationship between territory size and the risk of cuckoldry in birds. *Animal Behaviour*, **55**, 915–923.

Sasvari, L. & Hegyi, Z. (1998) Bird predation by tawny owls (*Strix aluco* L.) and its effect on the reproductive performance of tits. *Acta Oecologica-International Journal of Ecologica*, **19**, 483–490.

Sheldon, B.C., Kruuk, L.E.B. & Merilä, J. (2003) Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution*, **57**, 406–420.

Stoyan, D., Kendall, W.S. & Mecke, J. (1987) *Stochastic Geometry and its Applications*. Wiley, New York.

Sutherland, W.J. (1996) *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford.

Svensson, L. (1994) *Identification Guide to European Passerines*. Svensson, Stockholm.

Tanemura, M. & Hasegawa, M. (1980) Geometrical models of territory. I. Models for synchronous and asynchronous settlement of territories. *Journal of Theoretical Biology*, **82**, 477–496.

Tinbergen, J.M. & Daan, S. (1990) Family-planning in the great tit (*Parus major*) – optimal clutch size as integration of parent and offspring fitness. *Behaviour*, **114**, 161–190.

Verboven, N. & Visser, M.E. (1998) Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos*, **81**, 511–524.

Verhulst, S., van Balen, J.H. & Tinbergen, J.M. (1995) Seasonal decline in reproductive success of the Great Tit: variation in time or quality. *Ecology*, **76**, 2392–2403.

VSN Intl (2003) *Genstat*, Version 7.2. VSN International Ltd, Oxford.

Received 18 July 2005; accepted 20 December 2005

Chapter 3: Edge effects in the Great Tit: Analyses of Long-term Data with GIS Techniques

Edge Effects in the Great Tit: Analyses of Long-term Data with GIS Techniques

TEDDY A. WILKIN,*‡ DANY GARANT,† ANDREW G. GOSLER,* AND BEN C. SHELDON*

*Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom
†Département de Biologie, Faculté des Sciences Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada

Abstract: *In contemporary fragmented landscapes, edges are commonplace, and understanding the effects of edge environments is thus essential for the conservation of forest communities. The reproductive output of forest passerines is often reduced close to forest edges. Possible explanations include overcrowding by conspecifics, elevated rates of predation, and the occurrence of lower-quality habitat and/or individuals at forest edges. We attempted to separate these processes by examining edge effects in the absence of nest predation and by effectively controlling for differences in breeding density and the quality of habitats and individuals. We used an edge distance index (EDI), which accounts for the number and distribution of edges in close proximity to a breeding location, to help explain variation in breeding density, nesting success, and reproductive traits of 8308 pairs of Great Tits (*Parus major*) breeding between 1965 and 2005, in Wytham, near Oxford, United Kingdom. Results from linear mixed modeling confirmed higher breeding density and a higher proportion of immigrant individuals at forest edges. Nevertheless, independently of these effects, we also found that birds laying later, with smaller clutches but larger eggs, were typical of edge environments. The number of offspring recruited to the breeding offspring per breeding attempt was also reduced at edges, both directly and mediated through changes in clutch size and laying date. Edge effects on life histories were detectable within individual females and up to 500 m from the woodland edge. Woodland edges are increasingly common in contemporary fragmented landscapes. Therefore these results, which suggest a pervasive effect of edges on reproduction, are of considerable importance to the management and conservation of forest communities.*

Keywords: breeding density, ecotone, habitat quality, nest predation, nesting success

Efectos de Borde sobre *Parus major*: Análisis de Datos de Largo Plazo con Técnicas de SIG

Resumen: *En los paisajes fragmentados contemporáneos, los bordes son frecuentes, y por lo tanto el entendimiento de los efectos de borde es esencial para la conservación de las comunidades forestales. A menudo, la productividad de paserinos se reduce cerca de los bordes de los bosques. Las explicaciones posibles incluyen hacinamiento, tasas de depredación elevadas y la ocurrencia de hábitat y/o individuos de menor calidad en los bordes del bosque. Intentamos separar estos procesos mediante el examen de los efectos de borde en ausencia de depredación de nidos y el control efectivo de las diferencias en la densidad reproductiva y de la calidad de los hábitats y de los individuos. Utilizamos un índice de distancia al borde (IDB), que incluye el número y distribución de bordes cercanos a una localidad de reproducción, para tratar de explicar la variación en la densidad reproductiva, el éxito de anidación y las características reproductivas de 8308 parejas de* Parus major *entre 1965 y 2005, en Wytham, cerca de Oxford, Reino Unido. Los resultados de la modelación lineal mixta confirmaron una mayor densidad reproductiva y una mayor proporción de individuos inmigrantes en los bordes de bosques. Sin embargo, independientemente de estos efectos, también encontramos que aves con nidadas menores, pero huevos más grandes, eran típicas de los ambientes de borde. El número de crías reclutadas por intento reproductivo también fue más reducido en los bordes, tanto directamente como por medio de cambios en el tamaño de nidada y de fecha de puesta. Los efectos de borde sobre las historias de*

‡*email teddy.wilkin@zoo.ox.ac.uk*
Paper submitted September 13, 2006; revised manuscript accepted March 1, 2007.

Conservation Biology Volume **, No. **, ***-***

DOI: 10.1111/j.1523-1739.2007.00767.x

vida fueron detectables entre hembras individuales y hasta 500 m del borde del bosque. Los bordes de bosques son cada vez más comunes en los paisajes fragmentados contemporáneos. Por lo tanto, estos resultados, que sugieren un fuerte efecto de los bordes sobre la reproducción, son de importancia considerable para el manejo y conservación de comunidades forestales.

Palabras Clave: calidad de hábitat, densidad reproductiva, depredación de nidos, ecotono, éxito de anidación

Introduction

A woodland edge or ecotone is the interface between the complex and relatively stable environment of the forest interior and the simple and highly variable external environment (Saunders et al. 1991). The results of many studies show that edge environments alter the distribution, abundance, and behavior of forest communities (Murcia 1995). Such edge effects may be direct, in terms of microclimate modification (Davies-Colley et al. 2000), or indirect, due to concomitant changes in vegetation composition, food supply, and the distribution of predators and conspecifics (Gates & Gysel 1978; Murcia 1995). Many extant woodland species probably evolved in continuous forests, where abrupt edges were rare, occurring only at riparian or geologic boundaries. In contrast, edges are commonplace in contemporary fragmented landscapes. For example, just 12% of the United Kingdom is covered in woodland and 8 of 10 wooded areas are <20 ha in size (Spenser & Kirby 1992). Organisms in such habitats will thus be within 250 m of an edge. Therefore, understanding the ecological effects of forest edges is imperative for efficient management and conservation of forest communities in current environments.

Edge environments are often more diverse than interior habitats at the level of the community, probably due to the presence of both internal and external species (Leopold 1933; Odum 1971). For example, woodland birds are often found at higher densities at woodland edges (Gates & Gysel 1978; Strelke & Dickson 1980). Nevertheless, avian nesting success (e.g., Paton 1993; Bátary & Báldi 2004; Deng & Gao 2005), fledgling mass (Huhta et al. 1999), and reproductive output are often, but not always (reviewed in Lahti 2001), reduced at forest edges. Possible explanations for altered bird reproduction at forest edges include overcrowding by conspecifics (Gates & Gysel 1978; Huhta et al. 1999), a concomitant rise in the level of predation (e.g., Paton 1993; Hartley & Hunter 1998; Bátary & Báldi 2004), and suboptimal habitat quality in terms of reduced foraging area (Huhta et al. 1999) and food availability. In addition, edge effects may result from a higher incidence of young, poorer-quality, or immigrant individuals at edges (Krauss et al. 2003). Despite the wealth of studies on edge effects, however, there are few examples where statistical or experimental separation of these factors has been preformed to determine causal relationships between altered reproduction and forest edges.

Most researchers who have examined edge effects have used the distance between the breeding location and the woodland edge (edge distance) to describe environments in terms of their edge proximity. Nevertheless, edge distance does not account for edges other than the nearest edge and it does not allow one to account for important differences in the geometric arrangement of edges. For example, consider four sites, each an equal distance from a woodland edge, that differ in their layout and number (Fig. 1). The first site is near a sharply acute edge that incises the woodland, the second is near a straight edge, the third is near two edges, and the fourth is circumvented by the edge (Figs. 1 a–d, respectively). Clearly the environment of the site in Fig. 1a is less influenced by the edge than the site in Fig. 1b, which in turn is less influenced by the edge than the sites in Figs. 1c and 1d. Nevertheless, on the basis of their edge distances, each of these four sites would be assigned the same measure of edge proximity. There is, therefore, a need to provide an edge proximity measure that accounts for edge distance and for the number and geometric arrangement of the edge relative to the breeding location.

We used a long-term data set, collected between 1965 and 2005 from a Great Tit (*Parus major*) population breeding in more than 1000 nest boxes at Wytham Woods, United Kingdom. This system offers an unusual opportunity to examine edge effects in the absence and presence of nest predation because in 1975 all the nest boxes, which remained in the same locations throughout the study, were replaced with near-predator-proof nest boxes. Thus, this system allowed us to examine edge effects on nesting success in the same territories in the presence and absence of nest predation. We devised an edge distance index (EDI) to account for both the edge distance and the number and layout of edges near breeding locations. We used a geographic information system (GIS) and linear mixed models to analyze the effect of EDI on the breeding density, nesting success, egg-laying date, clutch size, mean egg mass, mean fledgling mass, and recruitment for 8308 pairs of Great Tits.

Methods

Data

This study forms part of the Edward Grey Institute's long-term study of the Great Tit at Wytham Woods, near

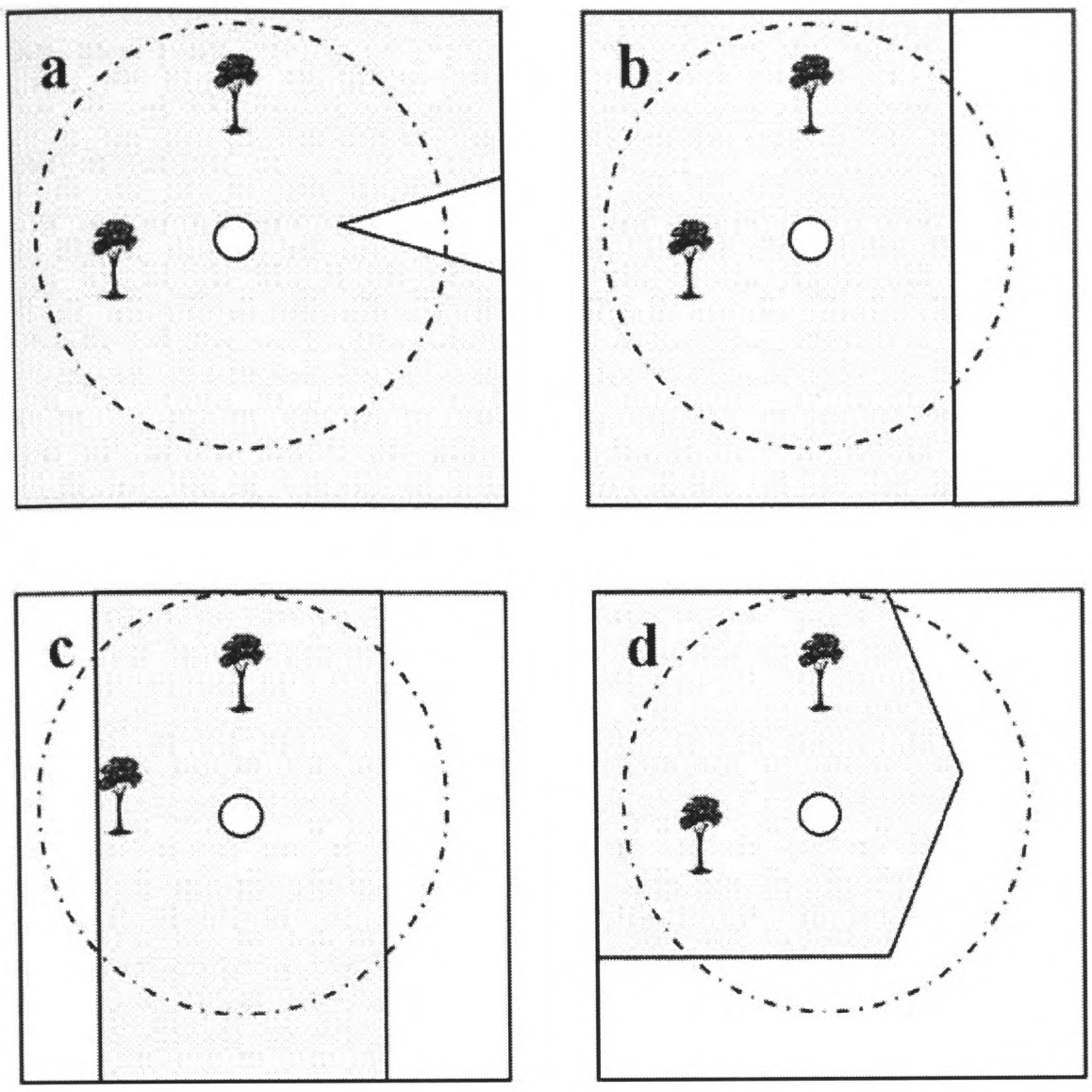


Figure 1. Representation of four sites (open circles) in a woodland (shaded area) contiguous to an area without woodland (unshaded area). Sites are adjacent to (a) a sharp incising edge, (b) a straight edge, (c) two straight edges, and (d) a circumventing edge. In each case the site is the same distance from the edge. According to the edge distance index we used, (a) is in the environment least effected by the edge, followed by, in order of increasing edge influence, (b), (c), and (d).

Oxford, United Kingdom. Data were collected between 1965 and 2005, in accordance with methods described previously (Perrins 1965, 1979; Gosler 1993). Great Tits breed almost exclusively in nest boxes in Wytham, the locations of which have remained constant throughout the study, unless a minor move was necessitated by tree fall. Nevertheless, between 1973 and 1975 the wooden nest boxes, which suffered from weasel predation rates as high as 50% in some years (McCleery et al. 1996), were replaced with woodcrete nest boxes (a mixture of sawdust, wood chips, and concrete), which were suspended away from the trunk of the tree and thus were almost predator proof. Nest boxes were visited at least once a week to ascertain clutch initiation date (lay date, where 1 April = 1), egg mass (mean of three to five unincubated eggs), and clutch size. Chicks were weighed and ringed on day 15 after hatching (hatch day was day 1), and for the purpose of this study, nestling masses at this age (fledging mass) were averaged for each brood. After the chicks reached 7 days of age, parents were trapped at the nest boxes and aged, sexed (Svensson 1994), and ringed or their identities were established from (BTO) rings that were already in place. An individual's status was either recruit or immigrant, defined as whether it hatched in a Wytham nest box or not, respectively. Immigrants to the population have come from variable, but unknown, distances outside the study area (Verhulst et al. 1997).

When analyzing life-history traits we used only first clutches (second clutches are rare at Wytham) and only those in which four or more eggs were laid to exclude clutches laid under atypical conditions such as disturbance or poor health (as in Wilkin et al. 2006). Reproductive success was measured as the number of young from each brood that were recruited to the breeding population in subsequent years (as in McCleery & Perrins 1985). This figure does not reflect the total number that survives to breed because many leave Wytham and breed elsewhere. Hence, we assumed that the number of recruits is an accurate measure of the relative success of nesting attempts (Verhulst et al. 1997 for some relevant data). For each wooden and woodcrete nest box, the percentage of successful breeding attempts (i.e., those that fledged at least one young) was used as a measure of total nesting success, whereas the fledgling success was measured as the proportion hatched clutches that fledged at least one nestling. The spring temperature each year was recorded as the sum of the maximum temperatures for each day between 1 March and 25 April (the warmth sum), as in McCleery and Perrins (1998). We used the habitat classification scheme proposed by Gibson (1988) in which there are five habitat categories: ancient, semi-natural woodland; 18th- and 19th-century broadleaf plantations; 20th-century plantations; secondary, regenerated wood pasture; and grasslands. There are three main soil

types at Wytham: Corallian limestone, sand, and Jurassic clay (Arkell 1947).

Digital Mapping

At Wytham we digitally mapped the locations of 1020 nest boxes and clearings exceeding 0.5 hectares (ha) with a Differential GPS system with submeter accuracy (Omnistar, Houston, Texas), a Laser range finder (LTI, Centennial, Colorado) and a Husky handheld rugged personal computer (Itronix, Coventry, United Kingdom) with PocketGIS software. We used Map Info Professional (version 7.8) and Vertical Mapper (version 3) to produce detailed maps of the location of the nest boxes within the woodland perimeter (20 km in length). An elevation reading for each nest box location was extracted from a land-form profile digital-terrain-model (DTM) data set provided by Ordnance Survey.

The shortest distance was measured between each nest box and (1) the perimeter of the woodland, (2) the perimeter or the woodland clearings, and (3) the perimeter, clearings, and an access road leading from the main entrance to the center of the woodland. To assess the distances we converted the perimeter into a series of points 10 m apart that were combined with the nest-box locations in a shortest-distance query in MapInfo (version 7.8). Circular buffers with 75-m radii were formed around each nest box and the area (square meters) of woodland that lay within each buffer was extracted. A radius of 75 m was chosen because the resulting buffer is 1.75 ha in size (πr^2). This area represents the maximum territory of a Great Tit most commonly found in the literature (Perrins 1965; Krebs 1971; Both et al. 2000) and exceeds in size two-thirds (67%) of the territories identified by tessellating space for the current population (Wilkin et al. 2006). In addition, results of studies of a closely related species, the Blue Tit (*Cyanistes caeruleus*), show that most provisioning trips are within 50 m of the nest box even in low-quality habitats (Stauss et al. 2005). Consequently, we expected that buffers stretching 75 m from each nest box in every direction would in all cases overlap the core of the territory, in most cases include all the foraging area, and in some cases contain the entire territory and represent a sensible measure of space for this species. We used the following equation to calculate the proportion of habitat to nonhabitat within the buffers:

$$P(r) = \frac{A(r)}{\pi r^2},$$

where P is the proportion of habitat within radius r and A is the area of habitat within radius r. We calculated an EDI value for each nest box by multiplying its edge distance (>0) by the proportion of habitat within its 1.75-ha buffer. Thus, nest boxes farther than 75 m from the woodland edge were assigned an EDI value equal to their edge distance, whereas nest boxes within 75 m of the woodland edge were assigned an EDI value in proportion to the incidence of woodland within their 1.75-ha buffers. For example, a nest box located close to an acute incising edge (Fig. 1a) would have a buffer dominated by woodland and would accordingly be assigned an EDI barely less than its edge distance. A nest box circumvented by an edge (Fig. 1d) would have a buffer with a smaller proportion of woodland and would therefore be assigned an EDI value considerably lower than its edge distance. The distribution of EDI was skewed in the current data set and so was square-root-transformed to achieve a normal distribution. Hereafter EDI refers to the transformed data.

In our models we controlled for differences in nest-box spacing by including the areas of Thiessen polygons (see Wilkin et al 2006) that were formed around all nest boxes and restricting the areas to within the perimeter of the woodland (nest-box spacing polygons). Differences in local breeding density were controlled for at the level of the individual pair by including the areas of Thiessen polygons, hereafter referred to as tessellated territories, formed around nest boxes that were occupied in each breeding season. A drawback of the tessellated territories is that extremely large territories are formed around nest boxes in low-density areas. Using a previously tested procedure to address this limitation, we capped territory sizes through a range of maxima, with the greatest effect in the lay-date model when territories were capped at 1 ha and in models when territories were capped at a mean of 2 ha (Wilkin et al. 2006).

Statistical Methods

We first assessed the degree of correlations at the level of the nest box to define the relationships between EDI and other environmental variables such as elevation, nest-box density (nest-box spacing polygons), and habitat type. The mean age and status scores (recruit = 1, immigrant = 0) were calculated for each nest box and were assessed, with respect to their EDI, in general linear models (GLM) with normal error structures.

We used a linear mixed model (LMM) in Genstat (version 8; VSN Intl 2005) to investigate the relationship between breeding density and EDI. Uncapped tessellated territory size was the dependent variable in the model (n = 8168), whereas EDI, nest-box elevation, habitat type, and nest-box spacing polygons were included as fixed effects. Nest box, female identities, and year were included as random effects to account for nonindependence within these subsamples.

For each nest box the proportion of successful nests was related to EDI in a GLM of binomial proportions by logits. We performed this analysis separately on data collected from wooden and woodcrete nest boxes. Similarly we analyzed fledging success with respect to EDI by using the proportion of broods in that nest box that fledged at least one young. We used a paired t test to test whether

nesting or fledging success differed between the two nestbox types.

We used linear mixed models (LMM) with normal errors to assess the effect of EDI on lay date, clutch size, egg mass, and fledgling mass. A generalized linear mixed model (GLMM) with a Poisson error structure was used to assess the effect of EDI on the number of recruits to the breeding population. We included female identity and year of reproduction in each model as random effects and EDI and environmental variables as fixed effects. By including year as a random effect we controlled for between-year differences in the environment. By including female identity as a random effect we controlled for systematic differences between females (due, e.g., to differences in biometrics and condition). Thus, our analyses tested whether during the lifetime of an individual, a change in EDI between years was mirrored by a change in the dependent variable. This analysis assumes that "quality" is relatively fixed within the lifetime of individuals; thus, it would not detect an effect due to individuals being excluded to edge environments in years in which their quality is reduced. Nevertheless, because breeding-site fidelity is high in this population (a median of 71 m between successive breeding attempts in the current data; see also Harvey et al. 1979 for additional studies), we judged this process to be unlikely. Our analyses therefore specifically and effectively considered variation within annual environments and within individuals.

The significance of factors in explaining variation was assessed from the Wald statistic, which is distributed asymptotically as chi square (VSN Intl 2005). We constructed models by backwards-stepwise removal of nonsignificant factors, depending on their Wald statistic. To test for quadratic effects we centered the EDI data by subtracting mean EDI from each EDI value and then ran the models with both the centered EDI data and centered EDI data squared. This approach renders the linear and quadratic terms uncorrelated, which results in the accurate separation of the two trends. For models in which the quadratic term was significant, we performed linear tests on data restricted to both above and below the centered EDI mean to illustrate directional trends within the nonlinear effect.

The lay-date model controlled for the age of the female, spring temperature (warmth sum), elevation, female status, habitat type, and restricted, tessellated territory size. The resulting clutch size LMM included lay date, the age of the female, and restricted territory size as fixed effects. The egg-mass model controlled for the age of the female, soil type, and lay date. The fledgling mass model controlled for clutch size, mean egg mass, elevation, lay date, and restricted territory size as fixed effects. The number-of-recruits model controlled for lay date, fledgling mass, restricted territory size, elevation, female status, and clutch size as fixed effects.

The models explained variation in a sequence of reproductive stages by including the previous stages as covariates (including, e.g., lay date in the clutch-size model). Thus our analyses investigated the independent effect of EDI on each stage. For ease of presentation, effects are displayed graphically as residuals formed by removing EDI from the model and rerunning the analysis. Models were run with, in turn, the EDI that acknowledged (1) the woodland perimeter; (2) the perimeter and the clearings; and (3) the perimeter, clearings, and the access road. The significance of the three types of EDI was determined in each model from the Wald statistic.

Results

Edge distances (m) were calculated for 1020 nest boxes at Wytham and ranged from 0.7 to 535.5 m (mean = 120.9, SD 104.0). The proportion of woodland to nonwoodland within 75 m of each nest box ($n = 1020$) ranged from 0.32 to 1.0 (mean = 0.9, SD 0.16) and 0.56 to 1.75 ha, respectively. The product of these two values, the EDI, ranged from 0.3 to 535.5 (mean = 118.9, SD 105.7). The EDI was positively associated with elevation (Pearson correlation, $r = 0.237, p < 0.001$) and with nest-box spacing polygon size (Pearson correlation, $r = 0.334$, $p < 0.001$); thus, edge nest boxes were at lower elevations and were closer together than interior nest boxes. The former is likely to be partly an effect of the geographical arrangement of the site, a forest cloaking a low hill. The distribution of EDI was right skewed, so we performed a square-root transformation for the following analyses; hereafter, EDI refers to the transformed data.

For a given nest box, EDI was a significant predictor of the average immigration status of both females ($t_{1001} = 3.19$, $p = 0.001$) and males ($t_{989} = 3.96$, $p < 0.001$), such that that there was a higher incidence of immigrants at the woodland edge when controlling for differences in elevation ($t_{1001} = 1.71$, $p = 0.087$; $t_{989} = 2.44$, $p = 0.015$). Therefore we controlled for status, and retained it when the values were significant, in life-history models. In contrast, EDI was not related to a higher incidence of first-year females ($t_{993} = -1.2, p = 0.232$) or first-year males ($t_{988} = 0.87, p = 0.386$) when controlling for differences in elevation ($t_{993} = 3.05$, $p = 0.002$; $t_{988} = 3.05$, $p = 0.002$) and size of the nest-box spacing polygon ($t_{993} = 3.43, p < 0.001$; $t_{988} = 2.22, p = 0.027$). Hence, although the breeding age of individuals was unrelated to edge proximity, a higher proportion of first-year birds were found at higher elevations and at lower densities.

We found a significant relationship between tessellated territory size and EDI ($t_{8618} = 41.98$, $p < 0.001$) when controlling for nest-box spacing ($t_{8618} = 576.12$, $p < 0.001$), elevation ($t_{(8618} = 86.59$, $p < 0.001$), and habitat

type ($t_{8618} = 48.99, p < 0.001$). Thus, breeding density was higher near the woodland edge, independent of the higher density at low elevation, in older habitats and in areas where nest boxes were closer together.

Mean nesting success was significantly lower in wooden compared with woodcrete nest boxes (means = 0.49 and 0.76, respectively; paired t test: $t_{737} = 17.25$, $p < 0.001$). Nevertheless, nesting success was unrelated to EDI in wooden ($t_{702} = 0.22, p = 0.826$) and woodcrete ($t_{994} = 0.59, p = 0.553$) nest boxes. Mean fledging success for those nests in which at least some eggs hatched was also significantly lower in wooden than in woodcrete nest boxes (means = 0.73 and 0.85, respectively; paired t test: $t_{695} = 8.77, p < 0.001$). Fledging success was positively associated with EDI in wooden ($t_{702} = 2.21, p = 0.027$) but not woodcrete ($t_{994} = 1.40, p = 0.162$) nest boxes (Fig. 2) when controlling for nest-box spacing. This means that broods from wooden nest boxes near the edge were less likely to fledge than broods in the interior. The differences between the total number of nest boxes ($n = 1020$) and the sample sizes in the preceding analyses represented the number of nest boxes that were not occupied by Great Tits during the separate phases of the study period (11 and 31 years, respectively).

Life-History Traits

Associations between EDI and lay date ($\chi^2_1 = 19.71, p < 0.001$), clutch size ($\chi^2_1 = 16.18, p < 0.001$), and egg mass size ($\chi^2_1 = 43.44$, $p < 0.001$; Table 1) were strong and independent when the whole data set (1965–2005) was included in the analyses. Birds breeding in environments closer to the edge laid smaller clutches of larger eggs later in the season. These analyses controlled for confounding factors such as immigrant status, elevation, and density. In contrast, EDI was only weakly related to fledgling mass ($\chi^2_1 = 3.07, p = 0.080$) and recruitment ($\chi^2_1 = 3.85, p = 0.050$) independent of the effects of EDI on previous life-history stages (Table 1). Removing clutch size and lay date increased the significance of EDI in explaining variation in recruitment ($\chi^2_1 = 6.87, p = 0.009$), which suggests an additional indirect effect of EDI on recruitment.

We tested for quadratic effects by including centered EDI and centered EDI squared in the above models. The linear and quadratic terms were strong predictors of lay date ($\chi^2_1 = 10.26$, $p = 0.001$; $\chi^2_1 = 26.52$, $p < 0.001$) and clutch size ($\chi^2_1 = 10.46, p = 0.001$; $\chi^2_1 = 13.45, p < 0.001$). In the lay-date model, a nonsignificant trend was detected below the EDI mean ($\chi^2_1 = 1.31, p = 0.252$), and a strong negative trend was returned for data falling above the EDI mean ($\chi^2_1 = 12.45, p < 0.001$). In the clutch size model, below the EDI mean ($\chi^2_1 = 3.71, p = 0.054$) the trend was nonsignificant and above the EDI mean ($\chi^2_1 = 10.67, p < 0.001$) the trend was strong and positive. The quadratic term was not associated with egg mass ($\chi^2_1 = 0.32, p = 0.573$) or fledging mass ($\chi^2_1 = 1.98, p = 0.182$). Recruitment was related to both the linear and quadratic terms ($\chi^2_1 = 6.41, p = 0.011$ and $\chi^2_1 = 5.8, p = 0.016$); a strong positive trend was detected below the EDI mean ($\chi^2_1 = 9.55, p = 0.002$), but no trend was detected above the EDI mean ($\chi^2_1 = 0.23, p = 0.633$).

Edge Type

Including woodland clearings of more than 1 ha in size in the EDI explained more variation in lay date ($\chi^2_1 = 27.05$, $p < 0.001$) than the standard EDI, based on comparison of the Wald statistic for the edge term in the two models. Nevertheless, including clearings made little difference to the effect size of EDI with respect to clutch size ($\chi^2_1 = 17.61$, $p < 0.001$), egg mass ($\chi^2_1 = 39.58$, $p < 0.001$), fledgling mass ($\chi^2_1 = 3.57$, $p = 0.059$), and recruitment ($\chi^2_1 = 3.62, p = 0.057$) models. Including the main access road and the clearings reduced the explanatory power of the EDI in the lay-date ($\chi^2_1 = 13.00, p < 0.001$) model but induced little or no change in other models.

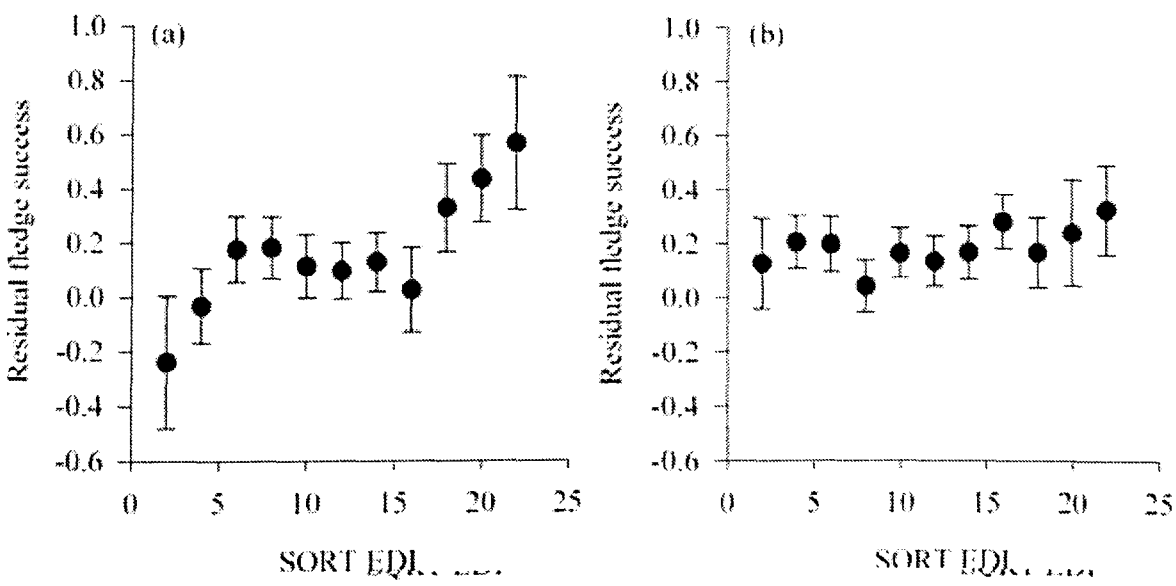


Figure 2. The residual fledging success of Great Tit broods in (a) wooden ($t_{702} = 2.23$, $p = 0.023$) and (b) woodcrete ($t_{994} = 1.40$, $p = 0.162$) nest boxes at Wytham woods, United Kingdom, with respect to the square-root-transformed edge distance index (SQRT EDI). Values of SQRT EDI increase with distance from the woodland edge.

Table 1. Results from linear mixed models explaining variation in the life-history traits of 8308 pairs of Great Tits breeding in Wytham nest boxes between 1965 and 2005.*

Dependent/independent factor	*Wald χ^2*	*df*	*Effect (SE)*		p
Lay date ($n = 8308$)					
elevation	100.3	1	0.03276	(0.003271)	<0.001
spring temperature	95.93	1	−0.08661	(0.008843)	<0.001
female age	83.9	1	−0.6509	(0.07106)	<0.001
habitat type	63.73	3			<0.001
female status	20.95	1	Rec < Imm		<0.001
edge distance index	19.71	1	−0.08228	(0.018532)	<0.001
territory size (max 1 ha)	11.04	1	−1.3	(0.3825)	<0.001
Clutch size ($n = 8308$)					
lay date	954.38	1	−0.06768	(0.002191)	<0.001
female age	40.61	1	0.09427	(0.014793)	<0.001
territory size (max 2 ha)	31.45	1	0.1809	(0.03225)	<0.001
edge distance index	16.18	1	0.01525	(0.003792)	<0.001
Egg mass ($n = 6994$)					
lay date	124.78	1	0.002319	(0.0002076)	<0.001
edge distance index	43.33	1	−0.002199	(0.0003341)	<0.001
female age	41.19	1	−0.008241	(0.0012841)	<0.001
soil type	12.29	2	1 >2 >3		0.002
Fledgling mass ($n = 5913$)					
lay date	157.13	1	−0.3498	(0.02791)	<0.001
clutch size	139.04	1	−1.309	(0.1110)	<0.001
elevation	50.69	1	−0.05012	(0.007040)	<0.001
egg mass	48.47	1	8.920	(1.2813)	<0.001
territory size (max 2 ha)	26.65	1	1.710	(0.3312)	<0.001
edge distance index	3.07	1	0.06224	(0.035521)	0.08
Recruitment ($n = 6671$)					
fledgling mass	167.44	1	0.01794	(0.001386)	<0.001
lay date	137.82	1	−0.03311	(0.002820)	<0.001
clutch size	33.37	1	0.06366	(0.011019)	<0.001
elevation	7.11	1	0.001858	(0.0006971)	0.008
territory size (max 2 ha)	5.32	1	0.07356	(0.031893)	0.021
edge distance index	3.85	1	0.006779	(0.0034535)	0.05
female status	3.84	1	Rec > Imm		0.05

**Sample sizes (n) reflect the availability of data. Edge distance index refers to the distance between a nest box and the woodland edge or edges (see text). Models include female identity (n = 5436) and year of reproduction (n = 41) as random effects and whether a female was a recruit or immigrant, defined as whether she hatched in a Wytham nest box or not, respectively.*

Discussion

Our results demonstrate that the EDI can be used effectively to describe a breeding environment in terms of its edge proximity. Edge environments were independently and significantly associated with higher breeding density and later, smaller clutches that consisted of larger eggs. All these terms are typically associated with poorer-quality breeding locations (e.g., the associations with breeding density are similar). The index also predicted the number of offspring recruited to the breeding population per breeding attempt, both directly and indirectly through changes in clutch size and lay date. Analyses restricted to a 9-year period of high nest predation showed no relationship between EDI and nesting success, although the effect was present in terms of fledging success. Our results suggest that edge effects may be surprisingly persistent because the relationship between EDI and the life-history variables was still detectable several hundred meters (perhaps up to 500 m) from the woodland edge. Hence, such effects may be present in all woodland fragments of <80 ha because this is the area necessary for the most interior of individuals to be more than 500 m from the edge. We believe that these results are therefore of importance for the conservation and management of fragmented forests.

Breeding Density at the Edge

Breeding density was higher at the woodland edge (Fig. 3a), a phenomenon that is supported extensively in the literature (e.g., Gates & Gysel 1978; Flaspohler et al. 2001). Woodland edges may be attractive habitats for some birds because of an increase in vegetation cover (Ratti & Reese 1988), which improves conditions for nesting (Yahner & Cypher 1987), foraging (Harris & Reed 2002), or singing (Strelke & Dickson 1980; Morgan & Gates 1982). Nevertheless, it is unclear why Great Tits breeding in nest boxes should do so at higher densities

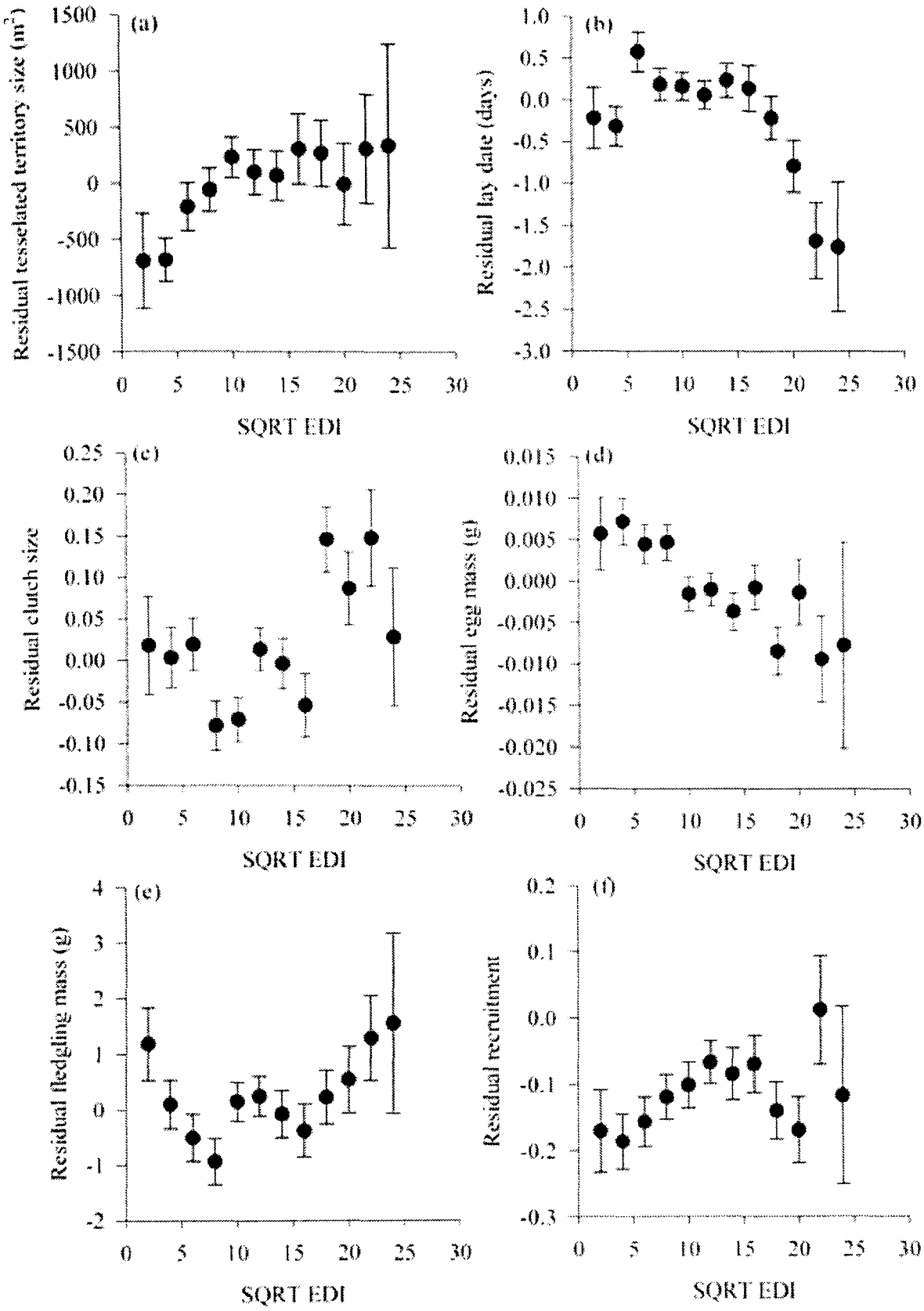


Figure 3. Relationships between the square-root-transformed edge distance index (SQRT EDI) and residual (a) tessellated territory size, (b) lay date, (c) clutch size, (d) mean egg mass, (e) mean fledgling mass, and (f) recruitment. Residuals were obtained from models including potentially confounding environmental variables and previous life-history traits (see Table 1 and text for details). Values of SQRT EDI increase with distance from the woodland edge.

at the woodland edge. A possible explanation is that for immigrating birds, high densities at the woodland edge represent a better option than breeding at lower densities in marginal habitats, such as hedgerows or small forests. Our results suggest an edge effect on breeding density that extends at least 100 m into the woodland (Fig. 3a).

Results of another study on forest passerines show an edge effect on the nest density of some species that extends over 300 m from the edge (Flaspohler et al. 2001). Several factors may influence the depth at which edge effects penetrate woodland. For example, edge effects will presumably vary in strength and/or depth between woodlands that adjoin agricultural areas and woodlands that are next to seminatural environments or urban developments (Morrison & Bolger 2002; Piper & Catterall 2004). In addition, the abruptness of an edge (e.g., whether it is sharply delineated or gradual) may also influence how far the edge effect penetrates the woodland (Suarez et al. 1997). For the most part, Wytham is surrounded by agricultural areas, although the River Thames and a highway pass within 20 m of the woodland to the northwest and southeast, respectively. The edges are abrupt in nature because the woodland perimeter is entirely fenced off from the surrounding areas. These features may have some influence in determining the strength and depth of the edge effects at Wytham.

Nesting Success

Nesting and fledging success was much poorer in wooden than in woodcrete nest boxes, probably due to higher predation by weasels and woodpeckers in the wooden boxes. In wooden nest boxes, fledging success was lower in edge environments, suggesting that broods near the edge were more likely to have suffered predation. Increased nest predation is a common, but not constantly (Keyser et al. 1998), reported edge effect for ground-nesting (Manolis et al. 2002) and cavity-nesting (Deng & Gao 2005) birds. Possible explanations include an increase in predator density and/or richness owing to the higher density of their prey and the incidence of both internal and external predators, respectively.

Life-History Traits

We found a higher incidence of immigrant birds at the woodland edge. This result is not particularly surprising because we expected immigrants to settle closer to their natal habitats, which are by definition outside of the main woodland. Nevertheless, our results also suggest that immigrants lay later and recruit fewer individuals to the breeding population than resident birds. Intuitively, one might assume that this effect is due to unfamiliarity with the environment. Nevertheless, these effects were persistent throughout the lifetime of an immigrant individual such that immigrants that survive to breed several times do so consistently later than resident birds, as shown by the absence of an interaction between female status and age on breeding date (status × age: $\chi^2_1 = 2.42, p = 0.120$). Therefore there must be some other processes at work. There are three possible processes. First, there may be a long-lasting effect of being born in poor environments (e.g., Reid et al. 2003), although there is little evidence for such effects in studies of short-lived passerine birds. Second, immigrants may differ genetically in their lay date. Nevertheless, given the relatively low heritability of this trait in the current population (McCleery et al. 2004), high rates of immigration, and that there was no effect of being born to an immigrant mother on lay date ($\chi^2_1 = 0.97$, $p = 0.326$; dam status added to lay-date model in Table 1), this mechanism is unlikely. Lastly, there may be some form of environmental or maternal priming of offspring that is related to their date of hatching, which would represent a process by which maternal effects induce a closer match in offspring phenotypes to the current environment, but we have no way to assess this at present.

Independent of a higher incidence of immigrant individuals at the edge, birds that bred close to the woodland edge bred significantly later than birds that bred away from the edge (Fig. 3b). This effect has not been seen before in the current population, possibly because it was concealed by the opposing and stronger effect of earlier breeding at low elevations, which happen to be nearer the edge. Birds at the edge also laid significantly fewer eggs than birds in the interior (Fig. 3c). Both effects were apparent when controlling for higher densities in edge environments and for the age of individuals. The latter affects lay date and clutch size, but was independent of distance from the edge.

Lay date and clutch size are determined by characteristics of the individual years (spring temperature), individual (genotype and phenotype), and territory (size, food availability) (Perrins 1965). Our analyses effectively controlled for differences between individuals and years, so we assumed that edge territories were of lower quality than interior territories. This assumption was, to some extent, confirmed by the somewhat unexpected finding that birds at the woodland edge laid heavier eggs than birds in the interior (Fig. 3d). This effect was independent of lay date (egg mass increased with seasonal advancement) and the age of individuals (older birds laid lighter eggs). Heavier eggs are sometimes associated with poor-quality habitats (see Christians 2002 and references therein). In addition, larger eggs may confer a fitness advantage in low-quality environments (Smith et al. 1995; Smith & Bruun 1998; Christians 2002) and some growth advantages to newly hatched nestlings (Williams 1994). Evidence of a poor habitat quality in edge environments was also provided for the current population by a video-camera study that showed fewer caterpillars (the preferred food for nestlings) being provided to nestlings in edge environments (GLM $t_{18} = 2.86, p = 0.011$) than in interior environments when controlling for elevation and brood size (L. King & T. Wilkin, unpublished data). Fewer caterpillars at the woodland edge, and therefore reduced territory quality, may be due to the more exposed environment that subjects invertebrates and the trees themselves to desiccation pressure (Laurance 2004).

In the current population smaller clutches have been linked recently with longer incubation periods, probably because they lose heat more readily than a large clutch (T.A.W., unpublished data). Recent analyses also show that, when controlling for clutch size, clutches with larger eggs are incubated for shorter periods than those with smaller eggs. This is probably because larger eggs are more thermally retentive than smaller eggs. Therefore, it is conceivable that birds breeding at the edge may be compensating for their smaller clutches and for a more exposed and presumably colder environment by producing larger eggs that retain more heat (Massaro et al. 2004).

The effect of edge environments on the number of offspring recruited to the breeding population was weak when controlling for edge effects on other life-history traits, which determine recruitment. This result is a little surprising, given that random dispersal would lead to those born on edges being more likely to disperse outside a patch and breed elsewhere than individuals born near the center, a process that would result in lower recruitment to the breeding population from edge nests. Nevertheless, in agreement with our findings, Matthysen (2002)

found that the likelihood of a bird recruiting outside of a woodland patch is unrelated to the distance between the natal nest and the woodland edge.

By including quadratic terms in our models, we found that the relationship between EDI and these life-history characters was often nonlinear and that this nonlinearity was not simply due to a difference between nests close to the edge versus all others. For example, in the case of lay date and clutch size, edge effects were not apparent between birds breeding within 200 m of the edge; rather, a linear trend was observed between birds breeding farther than 200 m from the edge. These results are important because they imply that edge effects may not be detectable as linear trends in smaller woodlands.

Edge Type and Scale

The EDI explained lay date better when small woodland clearings were designated as edges. Including woodland clearings, nevertheless, did not increase the explanatory power, based on the test statistic, of the EDI in models explaining variation in other, later life-history traits. If the effect is genuine, it is possible that the invertebrates are more prone to desiccation pressure or rely more heavily on sheltered habitats early in the season, which would explain edge effect on breeding time near woodland clearings. For example, the main food item of Great Tits in March is the Curculionid beetle *Strophosomus melanogrammus* (Betts 1955), which falls from vegetation and burrows into the ground on exposed or frosty days (Parry 1981). This could result in birds close to woodland edges, including small woodland clearings, suffering from poorer food availability and thus their being unable to reach breeding condition as early as interior birds. The main access road through the woodland did not affect Great Tit life histories, suggesting that long, narrow edges are insufficiently exposed to change habitat quality in adjacent areas. This result agrees with those of previous studies that show no effect of forest roads on nest predation levels (Ortega & Capen 2002), nesting success, clutch initiation date, clutch size, or fledgling success (King & DeGraaf 2002).

Edge effects were persistent over a distance of 500 m from the woodland edge. Edge effects on nest predation have been documented at distances of 600 and 200–500 m from the woodland edge (Wilcove 1985; Andrén & Angelstam 1988, respectively), whereas edge effects on nesting success (Manolis et al. 2002; Huhta et al. 2004; Deng & Gao 2005) and density (Flaspohler et al. 2001) have been documented at distances of 500 and 300 m, respectively. These findings are of considerable importance to the conservation of forest communities because if edge effects penetrate woodlands up to 500 m from the edge, effects would be omnipresent in woodlands of <80 ha. An unanswered question is the extent to which such effects are direct or indirect. For example, high densities at an edge, caused by high rates of immigration, may have cascading effects on the distribution of individuals over large distances. Our results suggest that further investigation into the causes of edge effects in other long-term studies for which large quantities of data are available may provide useful insight into the effect of habitat structure on productivity.

Acknowledgments

We are grateful to the many people who collected data during the long-term tit study at Wytham and to an anonymous referee for helpful comments on the manuscript. T.A.W. was funded by a studentship from the Biotechnology and Biological Sciences Research Council (BBSRC).

Literature Cited

Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology **69**:544–547.

Arkell, W. J. 1947. The geology of Oxford. Clarendon Press, Oxford, United Kingdom.

Bátary, P., and A. Baldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology **18**:389–400.

Betts, M. M. 1955. Food of Titmice in oak woodland. Journal of Animal Ecology **24**:282–323.

Both, C., J. M. Tinbergen, and M. E. Visser. 2000. Adaptive density dependence of avian clutch size. Ecology **81**:3391–3403.

Christians, J. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews **77**:1–26.

Davies-Colley, R. J., G. W. Payne, and M. van Elswijk. 2000. Microclimate gradients across a forest edge. New Zealand Journal of Ecology **24**:111–121.

Deng, W. H., and W. Gao. 2005. Edge effects on nesting success of cavity-nesting birds in fragmented forests. Biological Conservation **126**:363–370

Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecological Applications **11**:32–46.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology **59**:871–883.

Gibson, C. W. D. 1988. The distribution of ancient woodland plant species among areas of different history in Wytham Woods, Oxfordshire in Woodland Conservation and research in the caly vale of Oxfordshire and Buckingham. Nature Conservancy Council, Peterborough, United Kingdom.

Gosler, A. G. 1993. The Great Tit. Paul Hamlyn, London.

Harris, R. J., and J. M. Reed. 2002. Effects of forest-clearcut edges on a forest-breeding songbird. Canadian Journal of Zoology-Revue Canadienne De Zoologie **80**:1026–1037.

Hartley, M., and M. Hunter. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. Conservation Biology **12**:465–469.

Harvey, P. H., P. J. Greenwood, and C. M. Perrins. 1979. Breeding area fidelity of great Tits (*Parus major*). Journal of Animal Ecology **48**:305–313.

Huhta, E., J. Jokimaki, and P. Rahko. 1999. Breeding success of pied flycatchers in artificial forest edges: the effect of a suboptimally shaped foraging area. The Auk **116**:528–535.

Huhta, E., T. Aho, A. Jantti, P. Suorsa, M. Kuitunen, A. Nikula, and H. Hakkarainen. 2004. Forest fragmentation increases nest predation in the Eurasian Treecreeper. Conservation Biology **18**:148–155.

Keyser, A., G. Hill, and E. Soehren. 1998. Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passerine birds. Conservation Biology **12**:986-994.

King, D. I., and R. M. DeGraaf. 2002. The effect of forest roads on the reproductive success of forest-dwelling passerine birds. Forest Science **48**:391-396.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major*. Ecology **52**:1-22.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia **137**:591-602.

Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation **99**:365-374.

Laurance, W. F. 2004. Forest-climate interactions in fragmented tropical landscapes. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**:345-352.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.

Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2002. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. The Auk **119**:955-970.

Massaro, M., L. S. Davis, J. T. Darby, G. J. Robertson, and A. N. Setiawan. 2004. Intraspecific variation of incubation periods in Yellow-eyed Pengiuns *Megadyptes antipodes*: testing the influence of age, laying date and egg size. Ibis **146**:526-530.

Matthysen, E. 2002. Boundary effects on dispersal between habitat patches by forest birds (*Parus major*, P-caeruleus). Landscape Ecology **17**:509-515.

McCleery, R. H., and C. M. Perrins. 1985. Territory size, reproductive success and population dynamics in the Great Tit, *Parus major*. Pages 353-373 in R. M. Silby and R. H. Smith, editors. Behavioural Ecology: The ecological consequences of adaptive behaviour. Blackwell Scientific, Oxford, United Kingdom.

McCleery, R. H., and C. M. Perrins 1998. ". . . temperature and egg-laying trends." Nature **391**:30-31.

McCleery, R. H., J. Clobert, R. Julliard, and C. M. Perrins. 1996. Nest predation and delayed cost of reproduction in the Great Tit. Journal of Animal Ecology **65**:96-104.

McCleery, R. H., R. A. Pettifor, P. Armbruster, K. Meyer, B. C. Sheldon, and C. M. Perrins. 2004. Components of variance underlying fitness in a natural population of the Great Tit *Parus major*. The American Naturalist **164**:1-11.

Morgan, K. A., and J. E. Gates. 1982. Bird population patterns in forest edge and strip vegetation at Remington Farms, Maryland. Journal of Wildlife Management **46**:993-944.

Morrison, S. A., and D. T. Bolger. 2002. Lack of an urban edge effect on reproduction in a fragmentation-sensitive sparrow. Ecological Applications **12**:398-411.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution **10**:58-62.

Odum, E. 1971. Fundamentals in ecology. WB Saunders, London.

Ortega, Y. K., and D. E. Capen. 2002. Roads as edges: effects on birds in forested landscapes. Forest Science **48**:381-390.

Parry, W. H. 1981. Weevils (Coleoptera: Curculionidae) on foliage of Sitka spruce in north east Scotland. Scottish Forestry **35**:96-101.

Paton, P. W. C. 1993. The effect of edge of avian nest success: how strong is the evidence? Conservation Biology **8**:17-26.

Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit, L. Journal of Animal Ecology **34**:601-647.

Perrins, C. M. 1979. British Tits. Collins, London.

Piper, S. D., and C. P. Catterall. 2004. Effects of edge type and nest height on predation of artificial nests within subtropical Australian eucalypt forests. Forest Ecology and Management **203**:361-372.

Ratti, J. T., and K. P. Reese. 1998. Preliminary test of the ecological trap hypothesis. Journal of Wildlife Management **52**:448-491.

Reid, J. M., E. M. Bignal, S. Bignal, D. I. McCracken, and P. Monaghan. 2003. Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. Journal of Animal Ecology **72**:36-46

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation—a review. Conservation Biology **5**:18-32.

Smith, H. G., T. Ohlsson, and K.-J. Wettermark. 1995. Adaptive significance of egg size in the European Starling: experimental tests. Ecology **76**:1-7.

Smith, H. G., and M. Bruun. 1998. The effect of egg size and habitat on starling nestling growth and survival. Oecologia **115**:59-63.

Spenser, J. W., and K. J. Kirby. 1992. An inventory of ancient woodland for England and Wales. Biological Conservation **61**:77-93.

Strelke, W. K., and J. G. Dickson. 1980. Effect of forest clear-cut on breeding birds in East Texas. Journal of Wildlife Management **44**:559-567.

Stauss, M. J., J. F. Burkhardt, and J. Tomiuk. 2005. Foraging flight distances as a measure of parental effort in blue tits *Parus caeruleus* differ with environmental conditions. Journal of Avian Biology **36**:47-56.

Suarez, A. V., K. S. Pfennig, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conservation Biology **11**:928-935.

Svensson, L. 1994. Identification guide to European passerines. 4th edition. L. Svensson, Stockholm.

Verhulst, S., C. M. Perrins, and R. Riddington. 1997. Natal dispersal of Great Tits in a patchy environment. Ecology **78**:864-872.

Wilcove, D. S. 1985. Forest fragmentation and the decline of migratory songbirds. PhD thesis. Princeton University, Princeton, New Jersey.

Wilkin, T. A., D. Garant, A. Gosler, and B. C. Sheldon. 2006. Density effects on life-history traits in a wild population of the Great Tit *Parus major*: analyses of long-term data with GIS techniques. Journal of Animal Ecology **75**:604-615.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biological Reviews **68**:35-59.

Yahner, R. H., and B. L. Cypher. 1987. Effects of nest location on depredation or artificial arboreal nests. Journal of Wildlife Management **51**:178-181.

Chapter 4: Resource availability explains density-dependent reproduction in wild population of the great tit

Resource availability explains density-dependent reproduction in wild population of the great tit.

TEDDY A. WILKIN*[1], DANY GARANT[2], ANDREW G. GOSLER[1] & BEN C. SHELDON[1]

[1] Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Rd., Oxford OX1 3PS, UK

[2] *Département de Biologie, Faculté des Sciences Université de Sherbrooke, Sherbrooke, QC, J1K 2R1, Canada*

*Author for correspondence: teddy.wilkin@zoo.ox.ac.uk

Abstract

Density-dependent life-histories are commonly observed in wild populations. At the population level, a common explanation for life-history variation associated with breeding density is competition for limited resources. Here we test this hypothesis at the level of the individual in a long-term population study of great and blue tits (*Parus major* and *Cyanistes caeruleus*), in which density dependent effects on life-histories have been demonstrated. We used the size of Thiessen polygons, formed around nestboxes occupied by each species in each year, as individual measures of breeding density. The preferred food of tits, both prior to laying, and during the provisioning period, is found at highest densities on oak trees; therefore the number of oak trees in each polygon was used as a measure of food availability for the focal pair, independently of density. Both species bred earlier and laid larger clutches in oak-rich territories, and great tit fledglings were also heavier and more likely to recruit to the breeding population in such territories (all $P < 0.001$). Including oak availability and density simultaneously reduced, or eliminated, the effect of density in the models, suggesting that in the current population, density dependent life-histories are largely due to reduced oak availability at high density. Thus this study demonstrates the efficacy of using the distribution of specific vegetation type as a surrogate for a patchily distributed food source and suggests that limited access to food at high density contributes towards density dependent reproduction in a wild population.

Keywords: winter moths, caterpillars, oaks, density, competition, life-histories, resource availability, Wytham, *Parus major*

Introduction

Density-dependent processes are responsible for the negative feedback loops which regulate many populations (Hornfeldt 1994; Murdoch 1994). Haldane (1953) was one of the first ecologists to suggest that, as no population increases in size indefinitely, every population must have at least one process that results in an increase in numbers when it is relaxed and a decrease when active. Regulation is achieved either through changes in the birth or death rates, emigration or immigration rates, or both (Krebs 1995; Albon et al 2000). In wild populations accurately measuring and distinguishing between mortality and immigration can be problematic (Waser et al 1994). Birth rates and reproductive strategies are, however, much easier to measure and consequently examples of density dependent reproduction are common (e.g. Both & Visser 2000; Wilkin et al 2006). For example, a negative relationship between density and reproductive output has been observed in several taxa including plants (Kirchner et al 2005), insects (Wardhaugh & Didham 2005; Hildrew et al 2004), mammals (Stewart et al 2005), fish (Jones & Coulson 2006) and birds (Sillett et al 2004; Armstrong et al 2005; Wilkin et al 2006).

Despite widespread evidence for density-dependent reproduction, few studies have been able to establish the exact mechanisms that cause reduced reproductive output at high density. In most cases it is unlikely that density *per se* is responsible, but more likely an increase in density causes a change in some other process that affects reproduction. The most common explanation for reduced output at high density is more competition for limited resource, such as food, at high densities (Seki & Takano 1998; Both & Visser 2003). However, at the level of the population, other possible explanations include increased predation (Schmidt & Whelan 1999) or parasitism

(Lessells 1985), the occupation of lower quality territories (Dhondt et al 1992), a higher proportion of lower quality individuals and higher incidence of conspecific disputes (Lopez-Sepulcre & Kokko 2005), at high densities (Sinclair 1989). In addition, other indirect processes may also be important. For example, if the predation of offspring is more likely at high density, then selection may favour a smaller number of offspring that are less conspicuous and presumably quicker to raise (Dunn 1977; Krebs 1970).

At present, studies have been unable to quantify the relative importance of such processes, primarily because of difficulties in simultaneously measuring breeding density of the focal and other species, resource availability and behavioural responses at biologically meaningful scales (Ray & Hastings 1996). For example, most studies measure density as the number of individuals per unit area (e.g. Both et al 2000) and resource availability is either compared between habitats (Beldal et al 1998; Tremblay et al 2005) or expressed in terms of yearly (Verboven et al 2001) or seasonal (Naef-Daenzer et al 2000) changes in the availability of prey species. In this way the allocation of specific food patches to individuals within a unit area is impossible. Therefore, if we are to understand the mechanisms that determine density dependent life-histories, it is necessary to measure the density, resource availability and behaviour processes at the level of the individual territories.

In forest passerines, such as the great tit (*Parus major*) and the blue tit (*Cyanistes caeruleus*) several life-history traits have been shown to be density-dependent, including the timing of breeding (Wilkin et al 2006), clutch size (Both et al 2000), nestling mass (Both et al 1999) and reproductive success (Wilkin et al 2006). Limited

food supply at high density has been suggested as an important factor determining density-dependent reproduction in great tits (Both & Visser 2003). Caterpillars, such as the larvae of the winter moth (*Operophtera brumata*) and the green tortrix (*Tortrix viridana*) are the preferred food items for great and blue tits (Blondel et al 1991; Perrins 1991; Banbura et al. 1999); studies at the level of the population have shown that differences in the timing and size of the caterpillar peak are responsible for broad scale differences in reproductive success (van Noordwijk et al 1993; Seki & Takano 1998; Naef-Daenzer et al 2000). At the landscape scale, the distribution, and presumably abundance, of caterpillar larvae is strongly predicted by the availability of deciduous, compared with evergreen trees (Bondel et al 1993). As a result tits breeding in broadleaved forests (high food availability) do so at a higher rate that those in mixed or coniferous forests (medium and low food availability, respectively). Differences between such populations include higher reproductive effort (Catalan & Haeger 1996; Stauss et al 2005b; Tremblay et al 2005), lower quality males (Lambrechts et al 2004), later lay dates (Massa et al 2004), smaller clutches and broods (Lack 1956; Massa et al. 2004), lower quality nestlings (Lambrechts et al. 2004) and lower reproductive success (Catalan & Haeger 1996) in pine or mixed, compared to broadleaf, forests. Other effects reported for such comparisons include female biased sex ratio (Stauss at al 2005a), lower nestling survival (Perrins 1979), larger home ranges (Naefdaenzer 1994) and lower recruitment (Catalan & Haeger 1999) in pine forests. However, many of these studies did not control for differences in breeding density between these habitats, which may mitigate food availability per pair and thus lead to an underestimation of habitat effects (Catalan & Haeger 1996).

At a finer scale, many species of caterpillar display a preference for oak (*Quercus* sp.) over other deciduous trees (Wint 1983; Foss & Rieske 2003). For example, Summerville et al (2003) found a higher caterpillar richness and abundance on oak leaves, compared with those of other deciduous species. As well as oak feeding caterpillars, about a third of the great tit diet prior to egg laying (Feb – March), is adult Cynipid gall-wasps such as *Andricus sp.* and *Neuroterus sp* which are found ovipositing exclusively on oak buds during this time (Betts 1955). Consequently, oak trees are likely to play a very important role in the life-history of individual tits (Hartley 1953; Perrins & Birkhead 1983) with substantial effects on individual fitness (Catalan & Haeger 1996). Furthermore, as the number of oak trees that are available per pair will, all else being equal, be reduced at high breeding density, oak availability presents a possible mechanism by which food availability, and consequently reproductive output is reduced at high density. However, to date no studies have been performed at an individual level to establish the relationship, if any, between density, oak availability and life history variation.

Alternative explanations for density dependent reproduction include an increase in the duration and frequency of aggressive encounters at high density, which would result in less time available for foraging, provisioning nestlings and other essential maintenance behaviour (Kempenaers & Dhondt 1992). The incidence of aggression in this context takes two forms. Firstly, territorial defence, which in tits is the responsibility of the male, is likely to be more intense at high density, where competition for space is more intense, and also with an increase in the number of neighbouring territories. A male that spends more time in defensive behaviour is likely to provide fewer nuptial feeds to the female, providing a possible mechanism

for female life-history changes at high density. Secondly, in many systems an increase in density by one species is often mirrored by increases in other species affected by the same regulatory processes (Minot & Perrins 1986). One such example occurs in woodland bird communities, in which different species often show similar population fluctuations between years (Minot 1981). In this case it is likely that interspecific competition will also increase with density, either in terms of exploitation or interference competition, or both. Therefore, concomitant changes in heterospecific density also provides a possible mechanism for density dependent life-history variation.

The aim of the current study was to test the mechanisms of reduced food availability and increased aggression in determining density dependent reproduction in a long-term population study of great and blue tits. We use a GIS territory model to accurately measure individual breeding density. We assume that our measure of breeding density, like any other, is ultimately a surrogate for the density dependent processes that determine life-history variation. Therefore at the individual level we use the number of oaks trees in a territory as a measure of individual resource availability and we use geometric estimations of territorial defence and interspecific interactions. The rationale behind these analyses was that any process contributing to density-dependent reproduction would account for a significant proportion of the variance in life-history traits while simultaneously reducing the explanatory power of density in life-history models.

Methods

Data

This study was conducted as part of a long--term population study of the great and blue tits at Wytham Woods, near Oxford, UK. Data were collected between 1965 and 2005, in accordance with methods described elsewhere (Perrins 1965, 1979; Gosler 1993). In Wytham, great tits breed almost exclusively in nestboxes, the locations of which have remained constant throughout the study, unless a minor move was necessitated by tree fall. All nestboxes were visited at least weekly to ascertain the first egg lay-date (where 1 April =1), egg mass (the mean of three to five unincubated eggs) and clutch size. Chicks were weighed and ringed on day 15 after hatching (where hatch day = 1); fledgling mass was averaged for each brood in the current study. Parents were trapped at nestboxes after the chicks reached seven days of age (to reduce desertion-risk), aged, sexed (Svensson 1994) and ringed or their identities were established from (BTO) rings already fitted. In the current study, an individual's status was either recruit or immigrant, defined as whether hatched in a Wytham nestbox or not, respectively.

We only analyze first clutches (genuine second clutches are rare in this population) and only those in which four or more eggs were laid. We also restricted the analyses to broods for which the identity of the mother was known so that we could control for differences between females. Reproductive success was measured as the number of young from each brood that were recruited to the breeding population in subsequent years. This figure does not reflect the total numbers that survive to breed, as many leave Wytham and breed elsewhere (McCleery & Perrins 1985; Verhulst et al 1997). However, the number of recruits remains an accurate measure of the relative success of nests. The spring temperature each year was recorded as the sum of the maximum

temperatures for each day between 1 March and 25 April (the Warmth Sum), as in McCleery and Perrins (1998). The habitat classification proposed by Gibson (1988) is used here and identifies five habitat categories; ancient semi-natural woodland; 18th and 19th century broadleaf plantations; 20th century plantations; secondary regenerated wood pasture; and grasslands.

Digital Mapping

The locations of oak trees (N = 3580) and nestboxes (N = 1168) at Wytham Woods, UK were digitally mapped to an accuracy of ±3m in the field using an OmniSTAR 3000 LR12 Differential GPS system with a Criterion 400 Laser range finder. A Handheld rugged PC (Husky Fex21) with PocketGIS software was used for data processing in the field and to transfer coordinates onto a standard desktop PC. MapInfo Professional ver. 7.8 and Vertical Mapper ver. 3 were then used to produce maps detailing the location of the oak trees and nestboxes within the woodland perimeter (20km in length). At the time of mapping, oak trees were assigned into three size classes based on the volume and completeness of their crown and therefore the potential size of their caterpillar population. Immature trees and mature trees with over 50% dieback were assigned size category 1, mature trees with complete crowns or partial dieback, and very large trees with 50% dieback were size category 2. Very large mature trees with either partial or no dieback were size category 3. An altitude reading for each nestbox location was the extracted from an Inverse Distance Weighting (IDW) interpolation of a Land Form PROFILE Digital-Terrain-Model (DTM) dataset provided by Ordnance Survey. The GIS was also used to calculate the distance between each nestbox and the perimeter of the woodland (edge distance).

By using a Dirichlet tessellation technique, we formed Theissen polygons (Rhynsburger 1973; Tanemura & Hasegawa 1980; Stoyan *et al.* 1987) around each great and blue tit nest in each year. A tessellated polygon is a geometric construct that contains all points closer to the generating point than to any other. The size of the polygons is therefore necessarily inverse to the density of the focal points, in this case nestboxes (McCleery & Perrins 1985; Wilkin et al 2006), and they provide an individual measure of breeding density, which accounts for the locations of several breeding neighbours. A drawback of the tessellation technique is that in areas of low density, large and biologically meaningless polygons are formed. This limitation was addressed by Wilkin *et al* (2006) who systematically capped the polygon sizes through a range of maxima and ran models aiming to explain life-history variation at each ceiling. In the case of the great tit, they found that polygon sizes best explained variation in lay-date when capped at around 1ha, and variation in other traits when capped at around 2 ha. Using the same technique we have found that blue tit territory polygons best explain life-history variation when capped at 1ha (T. Wilkin unpublished data). These sizes agree with the average territory size estimated by response to playback or minimum convex polygons in several different populations (see Wilkin et al 2006 and references therein).

The GIS software was used to extract the number of oak trees within each (full size) tessellated polygon as a measure of food availability for the focal pair of tits. This approach was employed because it uses individual-specific, and density dependent, scales at which to count oak trees and also because it results in the mutual exclusivity of oak trees between nests. This is in contrast to counting the number of oaks within a given radius of each nestbox, an approach which uses the same scale for nests at

different densities and would potentially allocate the same oak trees to more than one nest. An oak index was also calculated for each territory by summing the size scores of all the oak trees within the territory. This figure (Oaksum) thus accounts for the total oak canopy within the territory rather than the number of trees. The number of intraspecific territories contiguous to each focal territory was used as a measure of the incidence of territorial defence (see Sillett et al 2004), as individuals with several neighbours may be expected to spend more time in disputes than those with few neighbours. As great and blue tits compete for food (Betts, 1955) and nest sites (Minot & Perrins 1986), we also extracted the number of heterospecific tit nests within each territory as a measure of interspecific competition.

Statistical Methods

Linear mixed models (LMM) with normal errors were performed to assess the effects of our variables on the lay-date, clutch size, egg mass, and fledgling mass of great tits breeding in the focal nestboxes. A generalized linear mixed model (GLMM) with a Poisson error structure was used to explain variation in recruitment. Female identity and year were included as random effects in models explaining life history traits; by including year as a random effect we control for between year-differences in the environment, and by including female as a random effect we control for systematic differences between females due, for example, to differences in biometrics, or genetics or condition. These analyses therefore specifically consider variation within annual environments and within individuals. In this way, we were able to investigate the effect of oak trees on reproductive parameters within individual females; this analysis thus assumes that 'quality' is relatively fixed for individuals, and thus it would not detect an effect due to individuals being displaced to oak poor areas in

years in which their quality is reduced. However, as breeding-site fidelity is very high in this population (a median of 70m between successive great tit breeding attempts in the current data, and see Harvey *et al.* 1979) we judge this process to be unlikely. Environmental variables were included in models as fixed effects. The significance of factors in explaining variation was assessed from the Wald statistic, which is distributed asymptotically as χ^2 (VSN Intl 2003). Models were constructed by backwards-stepwise removal of non-significant factors depending on their Wald statistic.

Statistical Models

Statistical models were first run with the size of Thiessen polygons to estimate the effects of density on life-history variation (Model 1). Models were then run again, but this time including the number of oaks, neighbours and heterospecific nests for each territory (Model 2).

(1) The *lay-date* models controlled for the age of the female, spring temperature (warmth sum), altitude, female status (resident or immigrant, defined as whether hatched in a Wytham nestbox or not, respectively), habitat type, tessellated territory restricted to a maximum size of 1ha (see Wilkin et al 2006) and the edge distance. (2) The resulting *clutch size* LMMs included lay-date, the age of the female, edge distance, territory size capped at 2 ha and spring temperature as fixed effects. (3) The *fledgling mass* models controlled for clutch size, mean egg mass, altitude, lay-date and territory size capped at 2ha as fixed effects and finally, (4) the *number of recruits* models controlled for lay-date, fledgling mass, territory size capped at 2 ha, altitude and clutch size as fixed effects. The models explain variation in a sequence of

reproductive stages. Therefore, by including the previous stages as covariates, for example including lay-date in the clutch size model, our analyses investigated the independent effect of local oak trees upon each stage. Analysing recruitment in this way does not give a good estimate of the overall effects of a variable, as models only show which environmental factor affects recruitment independently of its affects on previous life history traits. For this reason a GLM with Poisson errors was used to estimate the overall effect of oak availability on recruitment. For ease of presentation, data are displayed graphically as residuals estimated by removing the number of local oak trees from the mixed model and rerunning the analysis.

The blue tit lay-date models included the spring temperature, the age of the female and territory size restricted to a maximum size of 1 ha (see Wilkin et al 2006). The blue tit clutch size models controlled for lay-date, the age of the female and territory size capped at 1.5 ha. It was not possible to analyze fledging mass for blue tits due to lack of data.

Results

Tessellated territories were formed around 10665 great tit and 12527 blue tit occupied nestboxes over 41 and 40 years of the study, respectively. These sample sizes are larger than those subsequently analysed because breeding attempts for which the female was not identified and others that failed were included in the density estimate, because their presence were biologically relevant, but not in the statistical analyses because of the inability to control for the identity of the female. The size of great tit territories estimated by this method ranged from 0.022 (220m^2) to 15.14 ha (median = 1.09 ha) and blue tit territories from 0.039 (390 m^2) to 12.9 ha (median = 0.79 ha).

The number of oaks within each great tit territory ranged from 0 to 139 (median = 8), and within blue tit territories from 0 to 134 (median = 6). The number of contiguous neighbours ranged from 2 to 12 (median = 6) for great tit territories and from 1 to 12 for blue tits (median = 6). Our measure of great and blue tit densities, (the size of the tessellated territory), were correlated with the number of oak trees (r_{GT}= 0.566; r_{BT} = 0.638, both $P < 0.001$) and the number of heterospecific tits within the territories (r_{GT} = 0.347; r_{BT} = 0.415, both $P < 0.001$), and the number of contiguous neighbours to each territory (r_{GT}= 0.223, $P < 0.001$; r_{BT} = 0.310, both $P < 0.001$). These correlations confirm that the occurrence of oaks trees, heterospecific nests and the number of neighbouring territories were correlated with density and could therefore potentially act as mechanisms responsible for density dependent reproduction.

Life-histories

Great tit life-histories varied considerably with demographic and environmental factors, previously demonstrated by the current work (Chapters 2 & 3). For example, older great tits and those breeding in the interior of the woodland laid larger clutches earlier in the season than younger or birds breeding at the woodland edge (Table 1), and clutches laid early in the season tended to be larger and give rise to heavier fledglings that were more likely to survive to breed than later clutches. These results have been documented and discussed elsewhere and will not be covered further here.

Model 1: Including the size of Thiessen polygons as an individual estimate of density.

The restricted size of tessellated territories was a significant predictor of great tit lay-date ($\chi^2_{(1)}$ = 10.21, P = 0.001), clutch size ($\chi^2_{(1)}$ = 28.53, $P < 0.001$), fledgling mass ($\chi^2_{(1)}$ = 36.81, $P < 0.001$) and recruitment ($\chi^2_{(1)}$ = 9.51, P = 0.002) (Table 1). The

restricted size of tessellated territories was also a significant predictor of blue tit lay-date ($\chi^2_{(1)} = 17.32$, $P < 0.001$) and clutch size ($\chi^2_{(1)} = 30.69$, $P = 0.001$) (Table 2). Sample sizes for these analyses ranged from 5359 to 8456 depending on the factor in each analysis which had least available data. For example, only broods that survived until day 15 were available for use in any model which included fledgling mass.

Model 2: Including the number of oaks, neighbours and heterospecific nests for each territory. We found that the number of oak trees in a territory was significantly associated with early lay-dates in great tits ($\chi^2_{(1)} = 41.67$, $P < 0.001$; Fig 2a) and blue tits ($\chi^2_{(1)} = 36.36$, $P < 0.001$; Fig 2b). Oak trees density within territories was also significant in explaining clutch size variation in great tits ($\chi^2_{(1)} = 28.18$, $P = 0.001$; Fig 2c) and blue tits ($\chi^2_{(1)} = 26.8$, $P < 0.001$; Fig 2d) and fledging mass variation in great tits ($\chi^2_{(1)} = 19.41$, $P < 0.001$; Fig 2e). Independent of the effects of oaks trees on these life-history traits, we found no relationship between the number of oak trees in each territory and great tit recruitment rates ($\chi^2_{(1)} = 0.5$, $P = 0.48$; Table 1). However, the number of oaks in each territory was a significant predictor of great tit recruitment in a simple GLM ($t_{(8618)} = 9.46$, $P < 0.001$; Fig 2f).

An increased number of heterospecific nests in a territory delayed lay-date in the blue tit ($\chi^2_{(1)} = 5.46$, $P = 0.019$), though the effect was weak, and not apparent at all in the great tit ($\chi^2_{(1)} = 1.25$, $P = 0.263$); it was also weakly associated with reduced clutch size in the great tit ($\chi^2_{(1)} = 3.64$, $P = 0.057$) but not the blue tit ($\chi^2_{(1)} = 2.31$, $P = 0.129$). The number of blue tits nests in a great tit territory was positively associated with great tit fledgling mass ($\chi^2_{(1)} = 7.57$, $P = 0.006$) but was unrelated to recruitment

($\chi^2_{(1)} = 0.77$, $P = 0.380$). These results indicate that some life-history traits are weakly associated with the presence of another, closely related species.

Great tit clutch size was slightly reduced in territories with more conspecific neighbours ($\chi^2_{(1)} = 6.19$, $P = 0.013$; Table 1). The number of neighbours was unrelated to other great and blue tit life-history traits (Tables 1, 2), suggesting that the incidence of conspecific disputes is not an important source of life-history variation in tits.

Following the addition of oak trees to the life-history models, restricted territory size no longer explained lay-date variation in great tits ($\chi^2_{(1)} = 1.92$, $P = 0.166$) or blue tits ($\chi^2_{(1)} = 3.21$, $P = 0.073$) (Tables 1, 2). Similarly, the effect of density was reduced in models explaining great tit ($\chi^2_{(1)} = 11.24$, $P = 0.001$) and blue tit ($\chi^2_{(1)} = 7.32$, $P = 0.007$) clutch size, and great tit fledgling mass ($\chi^2_{(1)} = 14.35$, $P < 0.001$) and recruitment ($\chi^2_{(1)} = 5.99$, $P = 0.014$)(Tables 1, 2).

Oak tree size classes

Models that used the sum of the oak sizes within each territory, rather than just their number, were slightly more effective than the number of oaks in explaining lay-date variation in great tits ($\chi^2_{(1)} = 52.80$, $P < 0.001$) and blue tits ($\chi^2_{(1)} = 40.42$, $P < 0.001$). Clutch size was less related to the sum of oaks in great tits ($\chi^2_{(1)} = 16.94$, $P = 0.019$) and blue tits ($\chi^2_{(1)} = 21.34$, $P = 0.019$) than the number of oaks. Also less related to sum of oaks was great tit fledgling mass ($\chi^2_{(1)} = 14.36$, $P = 0.019$) and recruitment ($\chi^2_{(1)} = 0.09$, $P = 0.768$). These results suggest that the size of oak trees in a territory is important in determining great and blue tit lay-dates but not other life history traits.

Discussion

Tessellated territory size, as a measure of breeding density, was strongly associated with great and blue tit lay-date and clutch size, and great tit fledgling mass and recruitment. We found that the number of oak trees within each territory 1) explained a significant amount of life-history variation for both species and 2) greatly reduced or eliminated the effect of density in our models. These results strongly suggest that density dependent reproduction in the current system is due in part to reduced oak availability at high densities.

Great and blue tits at low breeding density laid larger clutches earlier in the season than birds at high density; great tits at low densities also had heavier nestlings which were more likely to recruit to the breeding population (Model 1). These effects were independent of each other and were apparent within individual females, such that within the lifetime of a female any change in her breeding density was mirrored by a change in her life-history. These effects have been shown before for the current population (Wilkin et al 2006) and elsewhere (Both & Visser 2003) and confirm a pervasive role of density in determining life-history variation.

Independently of the effects of density, we also found that food availability, measured by the number of oak trees in each territory, significantly advanced great and blue tit breeding (Fig. 2 a, b) and was significantly and positively related to great and blue tit clutch size (Fig. 2 c, d) and great tit fledgling mass (Fig. 2 e). Furthermore the effect of density was greatly reduced or eliminated in models including oak tree availability (Tables 1 & 2). For example, following the inclusion of oaks in the lay-date and

clutch size models, the effect of density, which was previously strongly associated with both life-history traits, dropped out of the lay-date models and was reduced by more than half for great tit and by more than two-thirds for blue tit clutch sizes. Similarly, a reduction in the significance of density was seen in the great tit fledgling mass model following the inclusion of oaks. These results suggest that a considerable proportion of life-history variation normally attributed to density can be explained by fewer oaks and therefore less food available per pair breeding at high density.

We found no effect of oak availability on the recruitment rates of great tits, independently of the strong effects that oaks had on fitness related life-history traits, such as lay-date and fledgling mass. However, there is a clear relationship between the number of oaks within a territory and recruitment rates in a simple linear regression (Fig 2f). This suggests that there is an effect of oak availability on reproductive success but it is mediated through life-history traits already accounted for in the recruitment model, such as clutch size and lay-date.

Independently of the effects of density and oak availability, great tit clutch size was slightly reduced in territories with more contiguous neighbouring territories. This suggests that female great tits are constrained in the number of eggs they lay by the presence of neighbouring pairs, possibly because males spend more time in territorial defence and less time in nuptial feeding, thereby reducing her ability to lay more eggs (Krebs 1970; but see Kempenaers & Dhondt 1992). In support of this hypothesis we found no effect of the number of neighbouring territories on great tit life-histories later in the season (e.g. nestling mass) when the function and frequency of courtship

feeding is thought to be reduced (Krebs 1970). Great tit clutch size was also reduced in territories containing a higher number of blue tit nests, probably because blue tits reduced the food availability in a territory (Minot 1981). However, later in the season great tit fledgling mass was increased in territories containing more blue tits. This effect may conceivably have been due to great tits benefiting from nearby blue tits in terms of vigilance behaviour and alarm calls, leaving more time available for great tits to provisioning their nestlings (Carrascal & Moreno 1992).

Elucidating the extent to which density dependent processes effect reproduction in wild populations is problematic, due to difficulties in measuring density, resource availability and conspecific interactions and intraspecific competition at the level of the individual. Using novel GIS techniques at the level of the individual we were able to measure breeding density, food availability and the incidence of territory defence and interspecific interactions. These analyses suggest that limited access to food at high density contributes towards density dependent reproduction in a wild population.

References

Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, J. M. Pemberton, and T. H. Clutton-Brock. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. Journal of Animal Ecology **69**:1099-1110.

Armstrong, D., Davidson, R., Perrott, J., Roygard, J. & Buchanan, L. 2005. Density-dependent population growth in a reintroduced population of North Island saddlebacks. Journal of Animal Ecology **74**: 160-170.

Banbura, J., Lambrechts, M. M., Blondel, J., Perret, P. & Cartan-Son, M. 1999. Food handling time of Blue Tit chicks: constraints and adaptation to different prey types. Journal of Avian Biology **30**: 263-270.

Beldal, E. J., E. Barba, J. A. Gil-delgado, D. J. Iglesias, G. M. Lopez, and J. S. Monros. 1998. Laying date and clutch size of Great Tits (Parus major) in the Mediterranean region: a comparison of four habitat types. Journal Fur Ornithologie **139**:269-276.

Betts, M. M. 1955. Food of Titmice in Oak Woodland. Journal of Animal Ecology **24**: 282-323.

Blondel, J., A. Dervieux, M. Maistre, and P. Perret. 1991. Feeding Ecology and Life-History Variation of the Blue Tit in Mediterranean Deciduous and Sclerophyllous Habitats. Oecologia **88**:9-14.

Blondel, J., Dias, P. C., Maistre, M. & Perret, P. 1993. Habitat Heterogeneity and Life-History Variation of Mediterranean Blue Tits Parus-Caeruleus). Auk **110**: 511-520.

Both, C., and M. E. Visser. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. Journal of Animal Ecology **69**:1021-1030.

Both, C., Visser, M.E., & Verboven, N. (1999) Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 465-469.

Both, C., Tinbergen, J.M., & Visser, M.E. (2000) Adaptive density dependence of avian clutch size. *Ecology*, **81**, 3391-3403.

Both, C. & Visser, M. E. 2003. Density dependence, territoriality, and divisibility of resources: From optimality models to population processes. American Naturalist **161**: 326-336.

Carrascal, L. M., and E. Moreno. 1992. Proximal Costs and Benefits of Heterospecific Social Foraging in the Great Tit, Parus-Major. Canadian Journal of Zoology-Revue Canadienne De Zoologie **70**:1947-1952.

Catalan, R. M. & Haeger, J. F. 1996. Breeding patterns of the Great Tit (Parus major) in a pine plantation and a holm oak forest in a Mediterranean region (southern Spain). Revue D Ecologie-La Terre Et La Vie **51**: 341-357.

Crawley, M.J. & M. Akhteruzzaman. 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. Functional Ecology **2:** 409-415.

Dhondt, A. A., B. Kempenaers, and F. Adriaensen. 1992. Density-Dependent Clutch Size Caused by Habitat Heterogeneity. Journal of Animal Ecology **61**:643-648.

Foss, L. K.& Rieske, L. K. 2003. Species-specific differences in oak foliage affect preference and performance of gypsy moth caterpillars. Entomologia Experimentalis Et Applicata **108**: 87-93.

Haldane, J. B. S. 1953. Animal populations and their regulation. New Biology **15**: 19-21.

Hartley, P. H. T. 1953. An Ecological Study of the Feeding Habits of the English Titmice. Journal of Animal Ecology **22**:261-288.

Hildrew, A., Woodward, G., Winterbottom, J. & Orton, S. 2004. Strong density dependence in a predatory insect: larg

Hornfeldt, B. (1994) Delayed Density-Dependence as a Determinant of Vole Cycles. *Ecology*, **75**, 791-806.

Jones, J. & Coulson, T. 2006. Population regulation and demography in a harvested freshwater crayfish from Madagascar. Oikos **112**: 602-611.

Kempenaers, B., and A. A. Dhondt. 1992. Experimental Test of a Hypothesis Explaining Density Dependent Clutch-Size in Tits Parus-Spp. Ibis **134**:192-194.

Keyser, A., Hill, G. & Soehren, E. 1998. Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passerine birds. Conservation Biology **12**: 986-994.

Kirchner, F., Luijten, S., Imbert, E., Riba, M., Mayol, M., Gonzalez-Martinez, S., Mignot, A. & Colas, B. 2005. Effects of local density on insect visitation and fertilization success in the narrow-endemic Centaurea corymbosa (Asteraceae). Oikos **111**: 130-142.

Krebs, J. R. 1970. Efficiency of Courtship Feeding in Blue Tit Parus-Caeruleus. Ibis **112**:108-110.

Krebs, C. J. 1995. 2 Paradigms of Population Regulation. Wildlife Research **22**:1-10.

Lack, D. 1956. Variations in the Reproductive Rate of Birds. Proceedings of the Royal Society of London. Series B, Biological Sciences **145**: 329-333.

Lessells, C. M. 1985. Parasitoid Foraging - Should Parasitism Be Density Dependent. Journal of Animal Ecology **54**:27-41.

Lopez-Sepulcre, A., and H. Kokko. 2005. Territorial defense, territory size, and population regulation. American Naturalist **166**:317-329.

Minot, E. O. 1981. Effects of interspecific competition for food in breeding blue and great tits. Journal of Animal Ecology **50**:375-385.

Minot, E. O. & Perrins, C. M. 1986. Interspecific interference competition - nest sites for Blue and Great tits Journal of Animal Ecology, **55**: 331-350.

Massa, B., Lo Valvo, F., Margagliotta, B. & Lo Valvo, M. 2004. Adaptive plasticity of blue tits (Parus caeruleus) and great tits (Parus major) breeding in natural and semi-natural insular habitats. Italian Journal of Zoology **71**: 209-217.

Naef-Daenzer, L., B. Naef-Daenzer, and R. G. Nager. 2000. Prey selection and foraging performance of breeding Great Tits Parus major in relation to food availability. Journal of Avian Biology **31**: 206-214.

Noordwijk, A. J. V., McCleery, R. H. & Perrins, C. M. 1995. Selection for the Timing of Great Tit Breeding in Relation to Caterpillar Growth and Temperature. Journal of Animal Ecology **64**: 451-458.

Perrins, C. M. 1979. British Tits, Collins, London.

Perrins, C. M., and T. R. Birkhead. 1983. Avian Ecology. Blackie, Glasgow.

Ray, C., and A. Hastings. 1996. Density dependence: Are we searching at the wrong spatial scale? Journal of Animal Ecology **65**:556-566.

Seki, S. I. & Takano, H. 1998. Caterpillar abundance in the territory affects the breeding performance of great tit Parus major minor. Oecologia **114**: 514-521.

Schmidt, K. & Whelan, C. 1999. Nest predation on woodland songbirds: when is nest predation density dependent? Oikos **87**: 65-67.

Sillett, T., Rodenhouse, N. & Holmes, R. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. Ecology **85**: 2467-2477.

Sinclair, A. R. E. 1989. In Ecological Concepts (Ed, Cherrett, J.) Blackwell Scientific, Oxford 197-241.

Stauss, M. J., Burkhardt, J. F. & Tomiuk, J. 2005a. Foraging flight distances as a measure of parental effort in blue tits *Parus caeruleus* differ with environmental conditions. Journal of Avian Biology **36**: 47-56.

Stauss, M., Segelbacher, G., Tomiuk, J.& Bachmann, L. 2005b. Sex ratio of *Parus major* and *P-caeruleus* broods depends on parental condition and habitat quality. Oikos **109**: 367-373.

Stewart, K., Bowyer, R., Dick, B., Johnson, B. & Kie, J. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia **143**: 85-93.

Summerville, K. S., Crist, T. O., Kahn, J. K. & Gering, J. C. 2003. Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. Ecological Entomology **28**: 747-757.

Svensson, L. 1994. Identification guide to European Passerines, fourth edition. Svensson, Stockholm.

Tremblay, I., Thomas, D., Blondel, J., Perret, P. & Lambrechts, M. M. 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits Parus caeruleus. Ibis **147**: 17-24.

Verboven, N., J. M. Tinbergen, and S. Verhulst. 2001. Food, reproductive success and multiple breeding in the Great Tit Parus major. Ardea **89**:387-406.

Verhulst, S., C. M. Perrins, and R. Riddington. 1997. Natal dispersal of Great Tits in a patchy environment. Ecology **78**:864-872.

Wardhaugh, C. W. & Didham, R. K. 2005. Density-dependent effects on the reproductive fitness of the New Zealand beech scale insect (Ultracoelostoma assimile) across multiple spatial scales. Ecological Entomology **30**: 733-738.

Waser, P. M., S. R. Creel, and J. R. Lucas. 1994. Death and Disappearance - Estimating Mortality Risks Associated with Philopatry and Dispersal. Behavioral Ecology **5**:135-141.

Wint, W. 1983. The Role of Alternative Host-Plant Species in the life of a Polyphagous Moth, Operophtera brumata (Lepidoptera: Geometridae). Journal of Animal Ecology **52**:439-450.

Tables

Table 1. Results of Linear Mixed Models explaining variation in the life-history traits of 5913 - 8456 pairs of great tits breeding in Wytham Woods, UK, between 1965 and 2005. Model 1 shows relationships between life-history traits and factors shown previously to be important, including density estimated by the size of tessellated territories formed around occupied nestboxes in each year. Model 2 differs from model 1 by also including the number of contiguous neighbours to each territory and the number of oaks trees and blue tits within each territory.

Dependent/Independent factor	**Model 1**		**Model 2**			
Lay-date (3.9 / 4.1%)	Wald 1	P 1	Wald 2	P 2	Effect 2	s.e 2
Altitude (m)	106.12	<0.001	105.55	<0.001	0.03371	0.003281
Spring temperature	96.03	<0.001	95.79	<0.001	-0.08722	0.008912
Female age	83.87	<0.001	85.82	<0.001	-0.6559	0.07080
Habitat type	23.69	<0.001	24.44	<0.001		
Edge distance (m)	33.63	<0.001	22.29	<0.001	-0.004121	0.0008728
Female status (Imm / Res)	20.92	<0.001	22.01	<0.001	R < I	
Restricted territory size(ha)	*10.21*	*0.001*	*1.92*	*0.166*	*-0.5601*	*0.40423*
Oaks in territory	-	-	*41.67*	*<0.001*	*-0.04121*	*0.006384*
Blue tits in territory	-	-	1.25	0.263	0.07103	0.063446
Number of neighbors	-	-	0	0.978	0.001700	0.0603059
Clutch Size (20.3 / 20.5%)						
Lay-date	950.28	<0.001	931.68	<0.001	-0.06696	0.002194
Female age	35.9	<0.001	36.71	<0.001	0.08952	0.014775
Edge distance (m)	23.82	<0.001	23.92	<0.001	0.0009052	0.0001850
Restricted territory size (ha)	*28.53*	*<0.001*	*11.24*	*<0.001*	*0.1204*	*0.0000035*
Oaks in territory	-	-	*28.19*	*<0.001*	*0.007759*	*0.0014612*
Blue tits in territory	-	-	*3.64*	*0.057*	*-0.02486*	*0.013038*
Number of neighbors	-	-	*6.19*	*0.013*	*-0.03132*	*0.012592*
Fledgling mass (12.4 / 12.3%)						
Clutch size	149.68	<0.001	156.64	<0.001	-1.390	0.1111
Lay-date	160.49	<0.001	155.09	<0.001	-0.3469	0.02786
Altitude (m)	48.48	<0.001	49.57	<0.001	-0.04980	0.007073
Egg mass (g)	46.19	<0.001	47.57	<0.001	8.793	1.2748
Restricted territory size (ha)	*36.81*	*<0.001*	*14.35*	*<0.001*	*1.368*	*0.3612*
Oaks in territory	-	-	*19.41*	*<0.001*	*0.06230*	*0.014142*
Blue tits in territory	-	-	*7.57*	*0.006*	*0.1017*	*0.11217*
Number of neighbors	-	-	0.82	0.365	-0.3652	0.13269
Recruitment (14.8 / 14.8%)						
Fledgling mass (g)	170.7	<0.001	170.83	<0.001	0.01820	0.001392
Lay-date	140.18	<0.001	140.06	<0.001	-0.03343	0.002824
Clutch size	38.51	<0.001	38.73	<0.001	0.06913	0.011107
Altitude (m)	9.09	0.003	9.16	0.002	0.002118	0.0006997
Restricted territory size (ha)	*9.51*	*0.002*	*5.99*	*0.014*	*0.08549*	*0.034931*
Oaks in territory	-	-	0.5	0.48	-0.0009437	0.0013360
Blue tits in territory	-	-	0.77	0.38	0.01071	0.012207
Number of neighbors	-	-	*1.63*	*0.201*	*0.01367*	*0.010695*

Table 2 Results of Linear Mixed Models explaining variation in the life-history traits of 5359 pairs of blue tits breeding in Wytham Woods, UK, between 1965 and 2004. Model 1 shows relationships between life-history traits and factors shown previously to be important, including density estimated by the size of tessellated territories formed around occupied nestboxes in each year. Model 2 differs from model 1 by including and the number of oaks trees and great tits within, and the number of contiguous neighbours to, each territory.

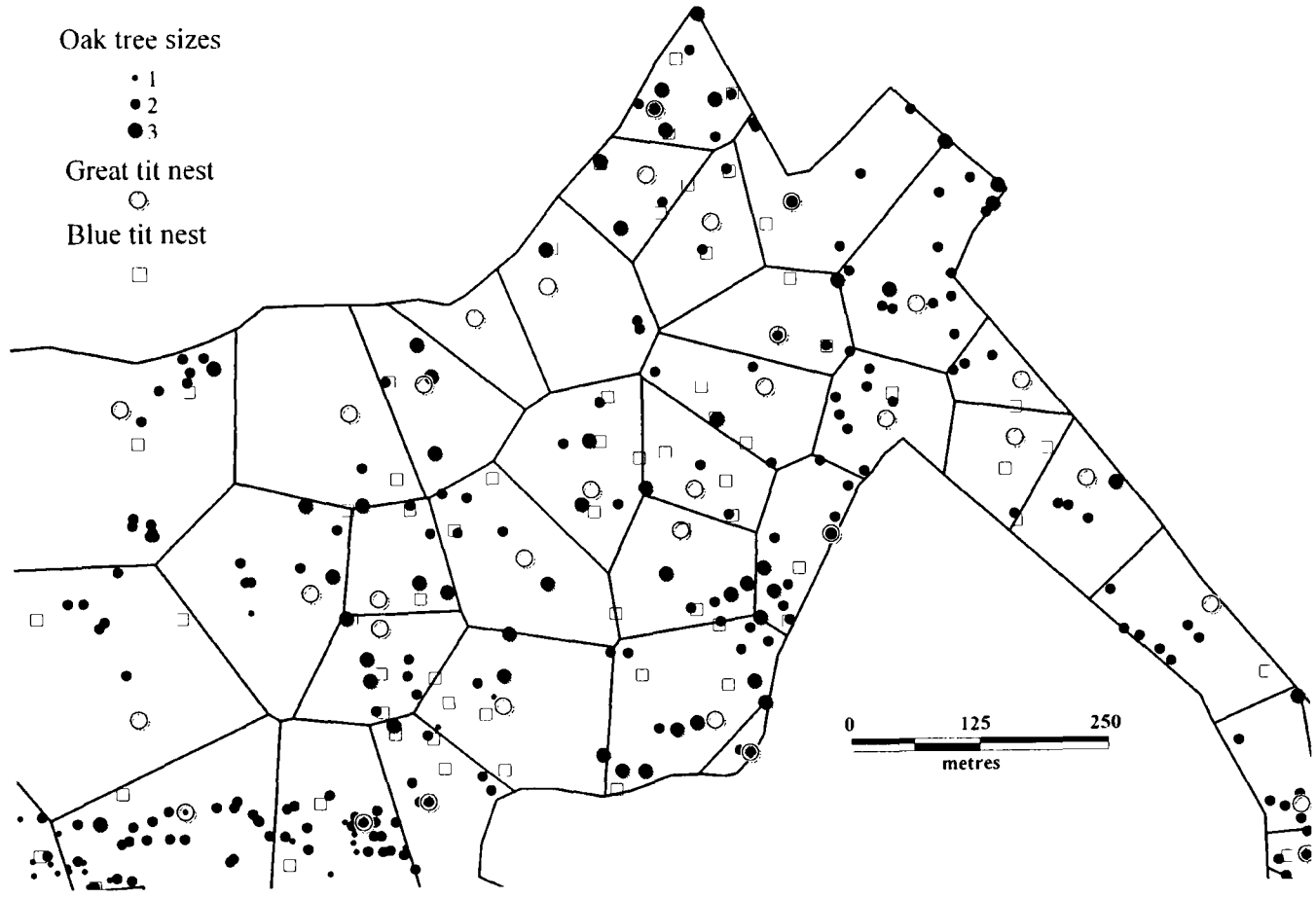
Dependent/Independent factor	**Model 1**		**Model 2**			
Lay-date (7.4 / 7.5 %)	Wald 1	P 1	Wald 2	P 2	Effect	s.e
Spring temperature	51.07	<0.001	51.7	<0.001	-0.08097	0.011261
Female age	19.09	<0.001	19.53	<0.001	-0.4704	0.10647
Restricted territory size(ha)	*17.32*	*<0.001*	*3.21*	*0.073*	*-0.9278*	*0.22294*
Oaks in territory	-	-	*36.36*	*<0.001*	*-0.04969*	*0.008241*
Great tits in territory	-	-	*5.46*	*0.019*	*0.2458*	*0.10524*
Number of neighbors	-	-	*2.38*	*0.123*	*-0.1009*	*0.06536*
Clutch Size (33.7 / 34.1%)						
Lay-date	1560.5	<0.001	1524.16	<0.001	-0.1423	0.00365
Female age	6.29	0.012	6.56	0.01	0.07192	0.028419
Restricted territory size (ha)	*7.32*	*0.007*	*30.69*	*<0.001*	*0.03492*	*0.028018*
Oaks in territory	-	-	*26.8*	*<0.001*	*0.01250*	*0.002469*
Great tits in territory	-	-	*2.31*	*0.129*	*-0.04043*	*0.028791*
Number of neighbors	-	-	*0.03*	*0.86*	*0.002915*	*0.0174177*

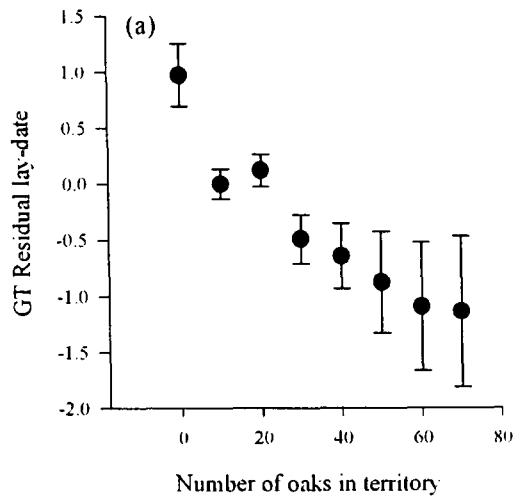
Figures

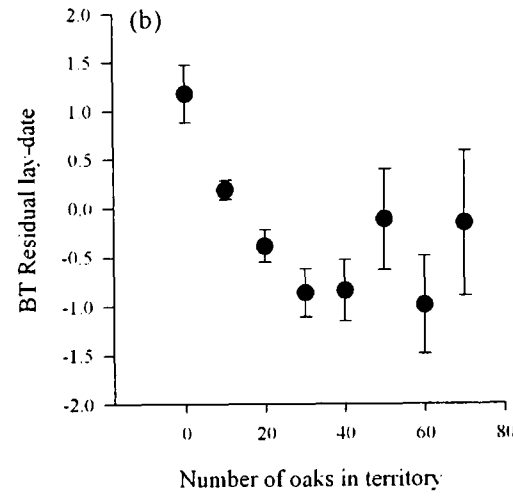
Figure 1. A section of Wytham Woods (Marley Wood) showing the locations of nest boxes occupied by great tits in 1992 (open circles) and their tessellated territories. Caterpillars, which are the preferred food item of tits, are found at highest densities on oak trees, which are shown here by solid dots of differing sizes representing trees with varying sizes of crowns. Blue tit nests are shown as open squares. The current study uses the size of each territory as a measure of breeding density, the number of oaks trees in each territory as a measure of food availability, the number of contiguous neighbours as an estimate of intraspecific interactions and the number of blue tits within each territory as a measure of interspecific competition.

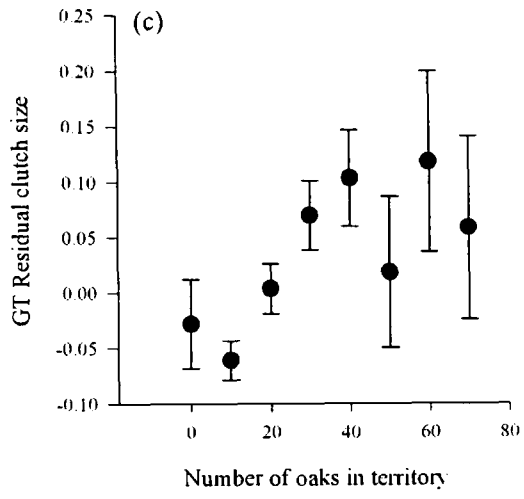
Figure 2. Residual great and blue tit (a, b) lay-date, (c, d) clutch size and great tit (e) fledgling mass plotted against the number of oaks within a tessellated territory. Models control for the size of the territory, other environmental factors and previous life-history traits (see text), and include year and female identity as random effects. Also shows the number of great tit recruits per breeding attempt plotted against the number of oaks within each territory (f). Bars indicate standard errors. Data were collected from birds breeding in Wytham nestboxes between 1965 and 2005 and sample sizes ranged from 5913 to 8456 depending on the availability of data.

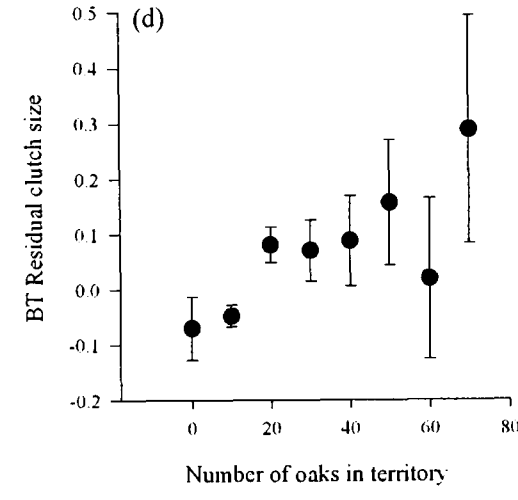
.

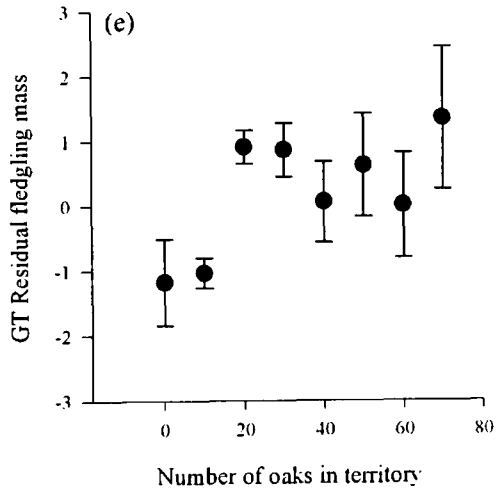

Oak tree sizes
1
2
3
Great tit nest
Blue tit nest
0
125
250
metres

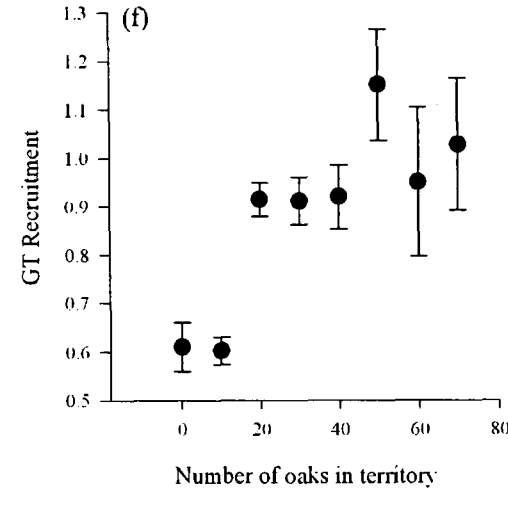

(a)
GT Residual lay-date
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0
20
40
60
80
Number of oaks in territory


(b)
BT Residual lay-date
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0
20
40
60
80
Number of oaks in territory


(c)
GT Residual clutch size
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
0
20
40
60
80
Number of oaks in territory


(d)
BT Residual clutch size
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
0
20
40
60
80
Number of oaks in territory


(e)
GT Residual fledgling mass
3
2
1
0
-1
-2
-3
0
20
40
60
80
Number of oaks in territory


(f)
GT Recruitment
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0
20
40
60
80
Number of oaks in territory

Chapter 5: Calcium effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data at several spatial scales

Chapter 5: Effects of soil calcium on life-history traits in a wild population of the great tit (*Parus major*): analysis of long-term data at several spatial scales

Effects of soil calcium on life-history traits in a wild population of the great tit (*Parus major*): analysis of long-term data at several spatial scales

TEDDY A. WILKIN*[1], DANY GARANT[2], ANDREW G. GOSLER[1] & BEN C. SHELDON[1]

[1] *Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Rd., Oxford OX1 3PS, UK*

[2] *Département de Biologie, Faculté des Sciences Université de Sherbrooke, Sherbrooke, QC, J1K 2R1, Canada*

*Author for correspondence: teddy.wilkin@zoo.ox.ac.uk

Keywords: birds, clutch size, environmental scale, fledgling mass, GIS,

Running header: Calcium and great tit reproduction

Summary

1. Calcium is essential for breeding birds during egg formation, and for skeletal development in nestlings. Small woodland birds are unable to store calcium in sufficient quantity, so they target calcium rich food such as snails, the distribution of which is determined by local soil calcium and by vegetation type.

2. Studies have suggested that birds breeding in woodlands with low soil calcium may be limited in the size or number of eggs they lay and in the quality of their nestlings. However, these studies are usually confounded by different factors and as birds forage non-randomly and may travel considerable distances to acquire calcium, describing different breeding environments in terms of their calcium availability is problematic.

3. Here we address these problems by exploring the spatial relationships between soil calcium and the life-history traits of *c.*6000 pairs of great tits breeding in a single continuous woodland over 41 years.

4. Soil calcium was sampled in a 200m grid over the study site and varied 300 fold from 63-21000 $mg.100g^{-1}$. The maximum soil calcium within a range of distances from each nestbox was extracted to reveal the distance at which the calcium signal was maximized in models explaining life-history traits.

5. We found strong associations between soil calcium and clutch size, fledgling mass and recruitment rate, at scales of 260 - 340m (all $P < 0.001$). These results suggest that females were travelling inter-territorially to acquire calcium. However, the soil calcium of the nearest sampling site to each breeding pair was the strongest predictor of mean fledgling mass ($P < 0.001$) suggesting that local calcium is more important during nestling stages. There was no effect of soil calcium on lay-date, egg mass or the length of the incubation period.

6. These results suggest that small woodland passerines may be constrained by calcium availability, but that the constraint may only become apparent over quite long distances. This is the first study to have demonstrated a spatial relationship between soil calcium and life-history traits within a single continuous woodland.

Introduction

Calcium is an essential micronutrient for breeding birds during egg formation and for nestlings developing skeletal structures (Graveland, Sandee & Drent 1995; Perrins 1996; Klaising 1998). Eggshells and the skeletons of nestling birds contain approximately 35% and 22% calcium respectively, and the demand for calcium during egg formation is 10-15 times that of a similar sized gravid mammal (Graveland & Van Gijzen 1994; Carey 1996). Some birds, such as chickens and pigeons, are able to store calcium within special leg bone medulla prior to egg-laying and then rapidly mobilize large quantities during egg production (Clunies, Emslie, & Leeson 1992; Carey 1996). However, smaller birds, such as tits (Paridae), are restricted in this ability, and as a consequence their endogenous stores are insufficient to meet the calcium demand during egg-laying (Graveland & Van Gijzen 1994; Pahl et al 1997). For example, the blue tit (*Cyanistes caeruleus*) has a skeleton that contains 0.175g of calcium and a clutch that requires a total of 0.25g of calcium (Graveland *et al* 1995). The normal diets of most small woodland passerines also contain insufficient calcium to provide for egg or skeletal formation. For example, the normal diet of a great tit (*Parus major*) in spring consists mainly of Coleoptera, Hymenoptera and Diptera imagines (Betts 1955) and is thought to provide only 10% of the calcium required by egg laying females, and only 15% of that required by nestlings (Simkiss 1967; Graveland and Van Gijzen 1994). Therefore, to meet calcium demand, small passerines forage specifically for calcareous rich substances during egg production and when provisioning nestlings (Creutz 1953; Graveland 1996).

The preferred source of calcium for great tits during the breeding season is small woodland snails (Graveland 1990; Gosler 1993; Perrins 1996), the abundance and

distributions of which are determined by local soil calcium and vegetation type (Mänd, Tilgar & Leivitis 2000b; Jubb, Wilkin & Gosler 2006). Females consume 90% of the calcium required for egg production during the 10 (or so) day egg-laying period. To meet this requirement, birds in snail-poor areas may spend twice the time, 43 percent of daylight hours, searching for calcium rich substances (Graveland & Berends 1997), severely restricting their normal foraging time budget even when snails are readily available. Thus acquiring extraneous calcium may lead to a reduction in protein intake and condition, which may result in a reduction in clutch size or egg size. For example, Gosler et al (2006) showed that females on low calcium soils have reduced muscle scores after laying their clutches. Such an indirect effect of poor calcium availability on avian reproduction may be widespread but would be difficult to detect without experimental manipulation.

During the last decade there have been several calcium supplementation experiments designed to examine the role of calcium in limiting avian reproduction (for example, Graveland & Drent 1997). Results have been equivocal, with no clear effect of calcium in some cases, probably due to a lack of calcium limitation in some populations, or to deficient supplementation protocols (Reynolds, Mänd & Tilgar 2004), or to the confounding effects of metabolic calcium limitation mediated through, for example, metal toxicity (Eeva & Lehikoinen 1995). Studies of the effect of calcium limitation on breeding birds also suffer from practical difficulties associated with measuring calcium availability in the wild, and in tracking birds to ascertain where, and from which items, they obtain their calcium. For example, Ramsay and Houston (1999) found very low snail densities in the leaf litter at their study site in Scotland, but the gizzard contents of female blue tits during egg laying

was found to contain large numbers of small snails. This indicates that birds are better able to find calcium sources in the wild than are researchers.

In many cases supplementation experiments have left distances of as little as 100m between experimental and control plots, and assumed that control birds would not move such a distance to reach the calcium supplementation (for example Graveland & Drent 1997; Mänd, Tilgar & Leivits 2000; Tilgar, Mänd & Magi 2002; Tilgar et al 2004). However, there is little evidence to support this assumption, which may have led to an underestimation of calcium limitation had control birds obtained calcium from outside the control area. For example, nests in calcium poor areas have been known to contain calcareous grit from nearby anthropogenic sources (Graveland & Drent 1997), but little is known about the scale or the importance of such acquisition. Furthermore, supplementing an area with calcium and comparing life-histories with those in a control area introduces confounding factors between the sites (Weimer & Schmidt 1998). Alternating the supplementation between areas and years would address this limitation but we are unaware of any such study. Yet, despite these limitations, calcium supplementation has been linked in some cases to fewer nest desertions and fewer defective eggs (Graveland & Drent 1997), earlier breeding, larger broods and heavier nestlings (Mänd, Tilgar & Leivits 2000a), larger clutches, broods, and fledglings (Tilgar, Mand & Magi 2002) and larger and thicker-shelled eggs (Mänd et al 2000b) in calcium-supplemented great tit nests. Despite these clear experimental effects, these studies may have underestimated the magnitude of calcium limitation if birds were traveling further than expected to acquire calcium, or due to the confounding effects of habitat differences. Therefore, there is the need to

examine the effects of calcium limitation and acquisition at several spatial scales while controlling for differences between habitats.

The aim of the current study was to use GIS techniques to describe breeding environments in terms of their local soil calcium for a wild population of the great tit at Wytham woods, UK. We then examined the spatial relationship between soil calcium, and the life-history traits obtained from a long term dataset in this population, to establish the importance of different calcium estimates on these traits. We also aimed to determine the scale at which supplementation experiment should be conducted.

Methods

Field data

This research was carried out as part of the Edward Grey Institute's long-term study of the Wytham great tit population, the general methods of which have been described many times (e.g. Perrins 1979; Gosler 1993). The (currently) 1168 nestboxes at Wytham were visited on a weekly basis from early April each year, to monitor the progress of reproductive attempts. For example, egg mass is taken as the mean of three or four unincubated eggs and lay-date is counted backwards from the visit date assuming females lay one egg per day. The parents are trapped after day 7 (hatch = day 1) to decrease the risk of desertion, aged and sexed (as per Svensson 1994), weighed and ringed or their identities established from existing (BTO) rings. On day 15 the brood is ringed and weighed; for the purpose of the current study, fledgling mass was averaged for each brood. The nest is visited once more to establish how many of the nestlings fledged. Recruitment is measured as the number of fledglings that are found breeding in nestboxes in subsequent years. This figure does not represent the total success of the brood, as many individuals leave Wytham to breed (McCleery & Perrins 1985), but it remains a useful relative measure of success between broods. The spring temperature each year was recorded as the sum of the maximum temperatures for each day between 1 March and 25 April (the Warmth sum), as in McCleery and Perrins (1998). The habitat classification proposed by Gibson (1988) is used here and identifies five habitat categories; ancient semi-natural woodland; 18^{th} and 19^{th} century broadleaf plantations; 20^{th} century plantations; secondary regenerated wood pasture; and grass lands.

Soil Calcium Sampling

At Wytham, intersections of the 100m Ordnance Survey grid are marked on the ground by numbered posts. In 1974 the Commonwealth Forestry Institute of Oxford University took 163 soil samples from alternate posts in a chess-board pattern (Dawkins & Field 1978; Horsfall & Kirby 1992; see Fig. 1a). Results from this survey showed that Wytham varied strikingly in its soil calcium concentration, from 63 to 21000 $mg.100g^{-1}$. This variation results from its varied geology; Wytham is a hilltop woodland that rises from Oxford clay at around 60-70m asl, up through a band of Lower Corallian sand at between 90—130m asl, to a cap of Upper Corallian limestone which forms the hill's summit at 164m asl.. A small resample of 50 plots in 1991 showed that the original data were still reliable (Farmer 1995): soil calcium values within plots from 1991 were highly correlated with those from 1974 (r_{48} = 0.936, $P < 0.001$).

GIS techniques

The locations of 1020 nestboxes at Wytham Woods were digitally mapped in the field using a Differential GPS system (sub-meter accuracy). GIS software MapInfo 7.8 and Vertical Mapper 3.0 were then used to combine nestbox locations with calcium data from the soil survey to estimate the soil calcium environment for breeding great tits. We focused on three approaches:

Nearest calcium sampling site. The GIS software was used to select the nearest soil sampling site to every nestbox at Wytham. The calcium value of this plot was then used as a measure of local calcium availability for the focal nestbox (as in Gosler, Higham, & Reynolds 2005).

Mean and maximum within territory calcium availability.

Calcium values were interpolated between the sampling plots in order to create a continuous soil calcium profile covering all of the study area (Fig. 1a). We used an Inverse Distance Weighting (IDW) interpolation technique because it can estimate local trends between spatially discontinuous and highly variable data. The technique uses a moving point average to interpolate cell values by averaging the weighted sums of all data points within a user-defined search area, such that points farther away influence the cell value less than those that are close (decay exponent = 2). In this case, the radii of the search and the display areas were set at the average point density (200 m). The actual calcium values at the sampling locations were significantly correlated with the interpolated values at the sampling locations (*coeff* = 0.944, $P < 0.001$), showing that the interpolation was a valid technique for estimating soil calcium over the whole study site. Calcium values were allocated to nestboxes by using a Dirichlet tessellation technique; we formed Thiessen polygons (Rhynsburger 1973; Tanemura & Hasegawa 1980; Stoyan, Kendall & Mecke 1987) around occupied nestboxes at Wytham and used the polygons as a simple territory model. A tessellated polygon is a geometric construct that contains all points closer to the generating point, in this case a nestbox, than to any other. This is achieved by placing boundaries exactly mid-way between all adjacent neighbours up to and including the woodland perimeter. The model assumes that pairs maintain equal spacing, are of equal defensive ability and that territories are contiguous, mutually exclusive and cover all of the available habitat. The territory model and the calcium interpolation model were then run concurrently and a region inspection query was used to extract predictions of calcium environment inside each territory. We extracted the mean and the maximum within territory calcium values and used them as measures of calcium

availability. Our prediction was that if individuals forage non-randomly within their territory to acquire specific calcium rich foods during periods of high demand, then the maximum calcium value within their territory will be the more biologically meaningful measure of calcium availability.

Maximum calcium value within a given distance of each nestbox.

Search buffers were formed around every nestbox at Wytham and the maximum calcium value found within each buffer was assigned to the generating nestbox as a measure of its local calcium value (Fig. 1b). The maximum calcium value was used as it was predicted that birds would forage non-randomly in order to obtain calcium rich food items. This process was performed repeatedly with buffers ranging from 50 to 500m in order to find the scale at which the effect of calcium was maximized in models explaining life history traits. Our reasoning was that by searching systematically for the maximum effect size, we perform an unbiased assessment of the scale over which an environmental effect is maximised. Buffers formed around nestboxes close to the woodland edge reached beyond the perimeter of the woodland, and so we can be less certain about the soil calcium environment surrounding these nestboxes. For this reason in all models we tested for an interaction between soil calcium and distance to the woodland edge. We found no effect, suggesting that these buffers did not bias our estimation of calcium environments around edge nestboxes. The distance between the maximum calcium plot within each buffer and the focal nestbox was also extracted.

Statistical methods

Linear mixed models (LMM) with normal errors were performed with Genstat ver. 8 (VSN Intl 2005) to assess the effect of our measures of local soil calcium on lay-date, clutch size, egg mass and fledgling mass. A generalized linear mixed model (GLMM), with a Poisson error structure, was used to analyse the number of recruits to the breeding population with respect to local soil calcium. In each model, we included year as a random effect to control for between-year differences. We also included female identity as an additional random effect to control for systematic differences between females (due, for example, to differences in biometrics and condition) and repeated measurements on individuals. Our analyses therefore specifically and effectively consider variation within annual environments and within individual females. Local soil calcium was always included as a fixed effect. Five models were built using backward stepwise removal of non-significant fixed factors depending on their Wald statistic. The fixed effects were chosen based on previous work on the determinants of individual variation in this species and population. (1) The *lay-date* model controlled for the age of the female, spring temperature, altitude, habitat type and restricted tessellated territory size (2) The *clutch size* LMM included lay-date, the age of the female and restricted tessellated territory size as fixed effects (3) The *egg mass* model controlled for the age of the female, distance to the edge of the woodland and lay-date. (4) The *fledging mass* model controlled for lay-date, clutch size, mean egg mass, altitude and restricted tessellated territory size as fixed effects, and finally, (5) the *recruitment* model controlled for lay-date, fledging mass, clutch size and restricted territory size as fixed effects (see Table 1). The models explain variation in a sequence of reproductive stages. By including the previous stages as covariates (e.g. laying date in the clutch size model), our analyses investigated the independent effect of calcium upon each stage. Models were run repeatedly, with different

measures and scales of local soil calcium availability, and the effect size of calcium with respect to the dependent variable was assessed from its Wald statistic, which is distributed asymptotically as χ^2 (VSN Intl 2005). The amount of variation explained by each model was estimated as a percentage of the difference between the residual variance when only random effects were included and the residual variance of the final model. Results from selected models are displayed graphically, as residuals estimated by removing the calcium data from the models and rerunning the analyses.

The Wald statistic returned for the maximum calcium value within a given distance was plotted against that radius to illustrate the relationship between search areas and the effect of the calcium in the model. For those models in which a clear effect of variable scale was apparent (e.g. a monotonic or curvilinear relationship), all sub-set regressions (VSN Intl 2005) were used to select the radius at which the maximum calcium value explained most variation in the reproductive traits, depending on the Akaike scores. Explanatory variables other than the maximum calcium value were forced in each model, while maximum calcium values within each radius were included as possible explanatory variables. The calcium data that returned the lowest Akaike value (see Burnham & Anderson 1998) was deemed to be the most suitable model. Thus, this is a formal statistical application of the graphical approach described above (see Wilkin et al 2006 for another example).

For life-history traits that were significantly influenced by more than one measure of calcium, for example mean and maximum within-territory soil calcium in separate models, all sub-set regressions were used to select the calcium measure(s) that best

explained variation in the trait. In these regressions all other factors were forced into the model.

Condition was defined as a female's mass when controlling for her wing length (as a measure of body size) and the time of day and the age of her brood when she was weighed. The latter two variables account for daily variation in mass and the gradual reduction in size of the female's reproductive organs, respectively. The condition of 3887 females in 5887 reproductive attempts was analyzed with respect to soil calcium, altitude and life-history traits in a LMM which included year and female identity as random effects. This analysis does not of course infer causation as females may be in good condition because they are in a high calcium environment, or in a high calcium environment because they are in good condition (c.f. Garant et al. 2005). However, this remains a suitable approach to compare the quality of females between high and low soil calcium environments, irrespective of causation.

Results

Variation in Calcium Concentration

Calcium was sampled at 163 locations across Wytham and ranged from 63 to 21000 $mg.100g^{-1}$ (Fig. 2a). The maximum soil calcium value within a given radius of each nestbox was calculated for between 8576 (150m radius) and 9824 (500m radius) breeding attempts and captured the full range of calcium values (e.g. Fig 2b). Different sample sizes occurred between these analyses as more nestboxes were included within larger distances from soil plots. Tessellated territories were formed around 8961 occupied nestboxes (mean per year = 218) and the maximum and mean

interpolated calcium values, which ranged from 146.51 to 15742.63 mg.100g^{-1} and from 125.17 to 14758.62 mg.100g^{-1} (Fig 2c) respectively, were extracted from each territory.

Nearest Calcium Value

As not all areas of Wytham were included in the soil sampling program, the distances between nestboxes and the nearest soil sampling sites ranged from 4.32 m in the sampled area, to 1010m for nestboxes in the non-sampled area. Therefore, we restricted this analysis to nestboxes within 165m of a soil sampling plot (this distance was chosen as it separated the nestboxes between two distinct areas across a natural boundary), thus utilizing 8751 reproductive attempts (Fig. 2d). The soil calcium level of the nearest soil sampling site to each nestbox was related significantly to fledgling mass ($\chi^2_{(1)} = 12.68$, $P < 0.001$; Fig 3a) but not lay-date ($\chi^2_{(1)} = 0.25$, $P = 0.62$), clutch size ($\chi^2_{(1)} = 1.69$, $P = 0.193$), egg mass ($\chi^2_{(1)} = 0.18$, $P = 0.667$), incubation period ($\chi^2_{(1)} = 1.29$, $P = 0.256$) or recruitment ($\chi^2_{(1)} = 0.14$, $P = 0.705$). Following this result we might predict that the calcium levels at locations close to the nestboxes would be better predictors of fledgling mass than soil sampling locations further away. However, in the fledgling mass model we found no interaction between soil calcium and the distance between the nestbox and the soil sampling site ($\chi^2_{(1)} = 1.90$, $P = 0.169$). The quadratic effect of nearest calcium value was also significant in explaining fledgling mass variation ($\chi^2_{(1)} = 9.59$, $P = 0.002$) suggesting that the effect may also be non-linear. These results suggest that the mean fledging mass within a brood is strongly and positively associated with soil calcium equally through a spatial scale of between 4.32 and 165m from each nestbox. Other life-history traits were unaffected by soil calcium variation at these scales.

Within territory calcium availability

The maximum and mean within territory soil calcium, as estimated by an IDW interpolation between calcium sampling sites, were used to explain life history variation for 8961 pairs of breeding great tits. The maximum within tessellated-territory calcium availability was a significant predictor of fledgling mass ($\chi^2_{(1)}$ = 6.38, P = 0.012) and clutch size ($\chi^2_{(1)}$ = 7.17, P = 0.007) but not lay-date ($\chi^2_{(1)}$ = 1.62, P = 0.203), egg mass ($\chi^2_{(1)}$ = 0.96, P = 0.326), incubation period ($\chi^2_{(1)}$ = 0.01, P = 0.909) or recruitment ($\chi^2_{(1)}$ = 3.45, P = 0.063). The mean within territory calcium availability was significantly and positively related to fledgling mass ($\chi^2_{(1)}$ = 11.42, P < 0.001) but not lay-date ($\chi^2_{(1)}$ = 2.83, P = 0.093), clutch size ($\chi^2_{(1)}$ = 3.79, P = 0.052), egg mass ($\chi^2_{(1)}$ = 0.06, P = 0.801), incubation period ($\chi^2_{(1)}$ = 0.38, P = 0.539) or recruitment ($\chi^2_{(1)}$ = 1.62, P = 0.203). These results show that the average within territory soil calcium levels were positively related to fledgling mass but not other life-history traits. The maximum within territory calcium level was positively associated with both fledgling mass and clutch size. However, these effects are generally rather weak, and statistical significance is achieved through the large sample size.

Maximum calcium within radii of nestboxes

Models were run with the maximum calcium value within a given distance from each nestbox included as a fixed effect. Models were run several times, on each occasion including maximum calcium measured at a different scale; Fig. 3 shows the Wald statistic for calcium in the models, plotted against the radius of the search area for each trait. There were no clear patterns relating maximum soil calcium level at any

scale, and incubation period, lay date and egg mass (Figs 2a, b & d). According to all sub-sets regression analyses the scale that best explained variation in clutch size was 310m ($\chi^2_{(1)} = 33.10$, $P < 0.001$; Fig 2c), that for fledgling mass was 260m ($\chi^2_{(1)} = 13.83$, $P < 0.001$; Fig 2e), and recruitment was around 340m ($\chi^2_{(1)} = 14.36$, $P < 0.001$; Fig 2f) from each nestbox. These results may be indicative of the scale at which soil calcium is important for great tit clutch size, fledgling mass and recruitment at Wytham.

Fledgling mass was significantly predicted in different models by mean and maximum within-territory interpolated calcium, by maximum calcium at a scale of 260m and by the calcium level of the nearest soil sampling location. However, an all sub-sets regression, which could have selected more than one calcium predictor, selected the nearest calcium value on its own as the most suitable calcium measure to explain variation in this trait (Akaike scores: Mean Territory Ca = 4910.4, Maximum Territory Ca = 4913.4, 260m Ca = 4910.0 & Nearest Ca = 4908.7).

Female condition

Larger females, as assessed by wing length, were heavier than smaller females ($\chi^2_{(1)} = 253.96$, $P < 0.001$), and female mass increased throughout the day ($\chi^2_{(1)} = 318.08$, $P < 0.001$) and declined with the age of the brood ($\chi^2_{(1)} = 424.34$, $P < 0.001$). Independently of these effects, older females ($\chi^2_{(1)} = 15.57$, $P < 0.001$) and those breeding at higher altitudes ($\chi^2_{(1)} = 4.76$, $P = 0.029$) tended to be heavier for their size, probably indicating better condition. Condition was also negatively associated with brood size ($\chi^2_{(1)} = 42.01$, $P < 0.001$) and positively with fledgling mass ($\chi^2_{(1)} = 140.78$, $P < 0.001$). Lay-date was a significant negative predictor of female condition

($\chi^2_{(1)} = 22.1$, $P < 0.001$), suggesting that females heavier for their size laid earlier in the season than lighter females. Birds were heavier for their size in colder years ($\chi^2_{(1)} = 10.87$, $P < 0.001$). Independently of these effects, neither the maximum soil calcium value within 300m of each nestbox, nor the nearest calcium value to each nestbox were associated with female condition ($\chi^2_{(1)} = 1.36$, $P = 0.244$; ($\chi^2_{(1)} = 0.83$, $P = 0.361$), suggesting that birds breeding in high calcium areas were not in better condition than those breeding in low calcium areas.

Discussion

We examined the spatial relationship between soil calcium and the life-history traits of a wild population of birds. We found that within a single continuous piece of woodland, soil calcium was significantly and independently associated with the clutch size of breeding females and the mass and recruitment probability of nestling great tits, while lay-date, egg mass and incubation period were unaffected by soil calcium. The effect size of calcium on those traits that it most strongly affected was maximised at distances between 260-340m. We also found that mean fledgling mass was most strongly associated with soil calcium on a within-territory scale. Our results suggest that females may travel some distance, certainly across adjacent territories, to locate calcium rich food items.

Calcium predictors of life history traits

We found no effect of soil calcium at any scale on the laying-date of great tits at Wytham. Studies that report earlier laying-dates in calcium supplemented compared to control areas (e.g. Mänd et al 2000) provided calcium prior to the egg laying period. It is not clear whether such provision may have caused good quality birds,

who are likely both to breed earlier and be of higher competitive ability, to settle in calcium supplemented areas, thus producing earlier mean lay-dates in supplemented areas. Other studies that began to provide calcium either after settlement or at the nest building stage found no difference in lay-date between supplemented and control areas (Graveland & Drent 1997; Bidwell & Dawson 2005). Tilgar et al (1999) found that calcium supplementation advanced lay-dates only in years when laying was late relative to other years. To test whether calcium was a predictor of lay-date in late years, we restricted our analyses to years that returned positive residuals from a regression on mean lay-date by year, and found a weak negative relationship between calcium availability at a scale of 300m and lay-date ($\chi^2_{(1)} = 4.33$, $P = 0.037$). Reversing the exclusion revealed an insignificant effect of calcium $\chi^2_{(1)} = 0.05$, $P = 0.826$). To some extent this confirms the findings of Tilgar et al (1999) but in the current population the effect soil calcium on the timing of breeding was very weak, at best.

Fledgling mass was strongly and positively associated with all of our estimates of soil calcium availability. However the strongest predictor of mean fledgling mass, and the variable selected by an all sub-set regression, was the calcium value of the soil sampling location closest to the nestbox (Fig. 4a). Therefore, from the current analyses and from previous observations we can assume that nestlings acquire the calcium they need to form their skeletal structures primarily from parental provisioning trips made close to the nestbox. Given that parents are presumably most constrained in their foraging behaviour when feeding nestlings, this effect is not unexpected. A relationship between nestling mass and calcium concentration has been reported several times in the literature (Blancher & McNicol 1991; Ormerod, et al

1991; Dawson & Bidwell 2005) and is probably largely due to reduced calcification of skeletal structures. For example, by measuring the plasma activity of the bone alkaline phosphatase, Tilgar et al (2004) showed that the bone formation of nestlings with a poor calcium diet was delayed compared with calcium supplemented nestlings, although they found no difference in nestling mass between the groups.

Clutch size and recruitment are reduced in areas with low calcium concentration within Wytham (Fig 4b, c). Increases in clutch size have been reported in several (Tilar et al 2002; Mänd et al 2000b), but not all, supplementation studies (Graveland and Drent 1997), while increases in recruitment, independently of changes in other life-history traits, are rare, perhaps due to lack of data. However, several studies imply increased reproductive success following calcium supplementation via changes in life-history traits that are linked with fitness, such as raising more fledglings (Tilgar et al 2002) that were in better condition (Dawson & Bidwell 2005). That small passerines need more calcium to lay a clutch than they can store, leads to the prediction that avian reproduction is not possible in areas devoid of calcium. Similarly we would expect reduced clutches in low calcium areas, given the increased search time per unit of calcium. Our results confirm this prediction and show that soil calcium can be used as a measure of calcium availability for breeding birds, despite it being a surrogate for calcium rich food items such as snails (Jubb et al 2006). Figs 4a and 4b show asymptotes at around 14000 mg. $100g^{-1}$ which may represent a threshold level of soil calcium required for reproduction unconstrained by calcium for great tits at Wytham.

We found no effect of calcium availability on egg mass, when controlling for heavier eggs being laid both later in the season and by younger individuals. Equal egg sizes between high and low calcium areas has been seen previously in the current population (Gosler et al 2006) while studies elsewhere have shown increases in egg mass with calcium supplementation (Mänd & Tilar 2003; Bidwell & Dawson 2005). In studies that provided calcium during the period of territory formation (e.g. Mänd & Tilar 2003), increased egg mass and other perceived changes in supplemented areas may result from non-random settlement. For example, high quality individuals, who lay heavier eggs, may have settled in supplemented, rather than in control areas. Egg mass is also a commonly reported difference between birds breeding on calcium rich and calcium poor soil types (e.g. Weimer & Schmidt 1998), but such studies are often confounded by habitat, due to the geological differences. The relationship between calcium availability and egg mass is further complicated by the fact that larger eggs are often associated with, and may confer growth advantages to nestlings in, poorer habitats (Smith et al 1995; Smith & Bruun 1998; Christians 2002). Our results partially confirm this, as birds at Wytham laid larger eggs at the edge of the woodland, where habitat quality may be reduced due to edge effects, than they did in the interior. Following a removal of edge distance as a predictor from the egg mass model, calcium at the scale of 310m was significant ($\chi^2_{(1)} = 6.99$, $P = 0.008$), suggesting that, at Wytham, habitat quality may be confounding factor with calcium availability, when analysing egg mass. We also found an increase in egg mass with altitude. This may be because larger eggs are more thermally retentive and so are more suitable at higher altitudes where it is colder. Thus, in our analyses, which controlled for both edge and altitudinal effects, we found no effect of soil calcium on egg mass.

Calcium analyses vs population biology

Clutch size and recruitment were predicted by the maximum soil calcium level within 310 and 340m of the nestbox respectively. These results may be indicative of the distances that females are prepared to travel to locate calcium rich food items. If this is so, then females may have been travelling between territories to acquire calcium. In the current population it is estimated that the average territory is just over 1 ha in size (Wilkin et al. 2006). A foraging range of c. 300m therefore suggests that females may be foraging up to three territories away in order to obtain sufficient calcium for egg production. These long-distance foraging visits need not be particularly frequent but may explain the small percentage of provisioning trips in which parents disappear from view. For example, Stauss et al (2005) report that they were unable to ascertain the destination of 10% the foraging trips made by blue tits. Such requirement for inter-territorial foraging behaviour by females breeding in calcium poor areas may have a wide range of consequences at the population and individual levels. For example, at the population level, the incidence of extra pair copulations may increase with calcium limitation, both because females that have left the territory may encounter other males, but also as the male who is left behind might seek copulations from neighbouring females (Griffith et al 2002). At the individual level, certain personalities of birds may be more inclined to travel inter-territorially than other personality types, thus interacting with the effect of calcium limitation. Furthermore, individuals who have previously dispersed long distances as juveniles and also immigrants to the population may, or may not be more likely to embark on long distance foraging trips (Dingemanse *et al* 2003).

Female Condition

Older birds tended to be heavier for their size, i.e. in better condition, than younger birds. This is probably due to older birds having more experience and knowledge of the local area and therefore possessing the ability to maintain higher condition. Birds with larger broods tended to be in poorer condition than those with smaller broods probably due to the increased energetic expenditure involved in provisioning a higher number of nestlings. Female condition declined seasonally, either because birds in poor condition bred later or because breeding later was more costly, due to, for example less food availability, thus resulting in reduced condition. Heavier birds had heavier fledglings, probably reflecting the heritable component of this trait (Garant et al 2004), and birds were in better condition, or at least heavier, in colder years, reflecting the higher energetic costs of surviving colder nights (Gosler 2002). In contrast to these strong predictors, soil calcium was not associated with female condition, which suggests an absence of indirect effects of calcium availability in life-history traits. This result is somewhat surprising as birds that spend more time looking for or travelling further to obtain calcium rich food items would be expected to be in poorer condition. However, as birds in calcium poor areas provision smaller broods of lighter fledglings, this may partially compensate for their own lowered condition.

Conclusion

The results presented here have a number of implications. Firstly we have shown a spatial correlation which suggests that female great tits are prepared to travel over 300m to acquire calcium for egg formation. Therefore, this scale might be more appropriate when assessing calcium limitation in the wild and when designing

calcium supplementation experiments. Most supplementation experiments conducted on great tit populations leave 100m between calcium supplemented and control nests in (Graveland & Drent 1997; Tilgar et al 2002; Mänd et al 200; Tilgar et al 2004). Our results suggest that in these studies control birds might have been able to acquire calcium from supplemented areas, thus leading to an underestimation of the effects of calcium limitation in the wild. For example, Graveland and Drent (1997) reported that feeders placed directly below occupied nestboxes were visited by other birds. Second, it changes the typical view of individual birds remaining within their territories for the duration of the breeding season, as our correlation suggests that females may be foraging inter-territorially during egg formation. We have also shown that within a single woodland, clutch size and fledgling mass, which are major determinants of survival to reproduce (Tinbergen & Boerlijst 1990), are reduced in areas of low calcium.

We have shown that by repeating analyses at several spatial scales, and by modelling environmental data with GIS, it is possible to establish the scales at which individuals move within a landscape during different periods of the breeding season to find essential nutrients. We believe that the current approaches have a wide range of applications in landscape ecology. For example, the formation of different sized search buffers around breeding locations can be used to establish the scale on which any resource is important to breeding individuals.

References

Bidwell, M. T. & Dawson, R. D. (2005) Calcium availability limits reproductive output of tree swallows (*Tachyinceta bicolor*) in a nonacidified landscape. *The Auk,* **122,** 246-254.

Betts, M.M. (1955) Food of Titmice in Oak Woodland. *Journal of Animal Ecology*, **24**, 282-323.

Blancher, P.& McNicol, D. (1991) Tree swallow diet in relation to wetland acidity. *Canadian Journal of Zoology,* **69**.

Burnham, K.P. & Anderson, D.R. (1998) *Model selection and inference: a practical information-theoretic approach* Springer-Verlag, New York.

Carey, C. (1996) In *Avian energetics and nutritional ecology* (Ed, Carey, C.) Chapman and Hall, New York, pp. 324-374.

Clunies, K., Emslie, J., & Leeson, S. (1992) Effect of dietary calcium level on medullary bone calcium reserves and shell weight of leghorn hens. *Poultry Science*, **71**, 1348-1356.

Christians, J. (2002) Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews*, **77**, 1-26.

Creutz, G. (1953) Schnecken als Nahrung von Singvogeln. *Vogelwelt,* **74,** 52-54.

Dingemanse, N.J., Both, C., van Noordwijk, A.J., Rutten, A.L., & Drent, P.J. (2003) Natal dispersal and personalities in great tits (Parus major). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 741-747.

Dawkins, H. C. and D. R. B. Field (1978). C.F.I. Occasional Paper No. 1. *A Long-term suveillance system for British woodland vegetation*. Oxford, Commonwealth Forestry Institute, University of Oxford.

Dawson, R. D.& Bidwell, M. T. (2005) Dietary calcium limits size and growth of nestling tree swallows Tachycineta bicolor in a non-acidified landscape. *Journal of Avian Biology,* **36,** 127-134.

Eeva, T.& Lehikoinen, E. (1995) Egg shell quality, clutch size and hatching success of the great tit (Parus major) and the pied flycatcher (Ficedula hypoleuca) in an air pollution gradient. *Oecologia,* **102,** 312-323.

Farmer, A.M. (1995) Soil chemistry change in a lowland English deciduous woodland. *Water, Air and Soil Pollution*, **85**, 677-682.

Garant, D., L. E. B. Kruuk, R. H. McCleery, and B. C. Sheldon. (2004). Evolution in a changing environment: A case study with great tit fledging mass. *American Naturalist* **164**: 115-129.

Gibson, C. W. D. 1988. The distribution of ancient woodland plant species among areas of different history in Wytham Woods, Oxfordshire in Woodland Conservation and research in the caly vale of Oxfordshire and Buckingham. K. J. Kirky, Wright, F. J., Nature Conservancy Council.

Gosler, A.G. (1993) *The Great Tit* Paul Hamlyn, London.

Gosler, A.G. (2002) Strategy and constraint in the winter fattening response to temperature in the great tit Parus major. *Journal of Animal Ecology*, **71**, 771-779.

Gosler, A.G., Higham, J.P., & Reynolds, S.J. (2005) Why are birds' eggs speckled? *Ecology Letters*, **8**, 1105-1113.

Gosler, A. G., Higham, J. P. & Reynolds, J., Wilkin, T. A. (2006) Soil calcium availability and reproduction in the great tit *Parus major* Part 1: fecundity and condition of the female. *Journal of Animal Ecology*. In revision.

Graveland, J. (1990) Effect of acid precipitation on reproduction in birds. *Experientia,* **46,** 962-970.

Graveland, J. (1996) Avian eggshell formation in calcium-rich and calcium-poor habitats: Importance of snail shells and anthropogenic calcium sources. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **74**, 1035-1044.

Graveland, J.& Berends, A. E. (1997) Timing of the calcium intake and effect of calcium deficiency on behaviour and egg laying in captive great tits, Parus major. *Physiological Zoology,* **70,** 74-84.

Graveland, J. & Drent, R.H. (1997) Calcium availability limits breeding success of passerines on poor soils. *Journal of Animal Ecology*, **66**, 279-288.

Graveland, J.& vanderWal, R. (1996) Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. *Oecologia,* **105,** 351-360.

Graveland, J.& Van Gijzen, T. (1994) Arthropods and Seeds Are Not Sufficient as Calcium Sources for Shell Formation and Skeletal Growth in Passerines. *Ardea,* **82,** 299-314.

Graveland, J., Sandee, H.& Drent, R. (1995) In *The Quest for Calcium*(Ed, Graveland, J.) Ponsen & Looyen, Wageningen, pp. 81-100.

Graveland, J.& Berends, A. E. (1997) Timing of the calcium intake and effect of calcium deficiency on behaviour and egg laying in captive great tits, Parus major. *Physiological Zoology,* **70,** 74-84.

Griffith, S.C., Owens, I.P.F., & Thuman, K.A. (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195-2212.

Horsfall, A.S. & Kirby, K.J. (1992) *The use of permanent quadrats to record changes in the structure and composition of Wytham Woods, Oxfordshire.* Research and survey in nature conservation no. 1. JNCC, Peterborough.

Jubb, R.M., Wilkin, T.A. & Gosler, A.G. (2006) Eggshell-pigmentation, soil calcium and the local abundance, distribution and diversity of woodland snails (Mollusca). *Ardea*, **94**, 59-70.

Klasing, K.C. (1998) *Comparative Avian Nutrition.* CAB International, New York.

Mänd, R., Tilgar, V.& Leivits, A. (2000a) Reproductive response of Great Tits, Parus major, in a naturally base-poor forest habitat to calcium supplementation. *Canadian Journal of Zoology,* **78,** 689-695.

Mänd, R., Tilgar, V.& Leivits, A. (2000b) Calcium, snails and birds: a case study. *Web Ecology,* **1,** 63-69.

Månd, R.& Tilgar, V. (2003) Does supplementary calcium reduce the cost of reproduction in the Pied Flycatcher Ficedula hypoleuca ? *Ibis,* **145,** 67-77.

McCleery R.H. & Perrins C.M. (1985) Territory size, reproductive success and population dynamics in the great tit, Parus major. *Behavioural Ecology: The Ecological Consequences of Adaptive Behaviour.* (eds R.M. Sibly & R.H Smith), pp. 353–373. Blackwell Scientific Publications, Oxford.

Ormerod, S.J., O'Halloran, J., Gribbin, S.D., & Tyler, S.J. (1991) The ecology of dippers Cinclus cinclus in relation to stream acidity in upland Wales: breeding performance, clacium physiology and nestling growth. *Journal of Applied Ecology*, **28**, 419-433.

Pahl, R., Winkler, D.W., Graveland, J., & Batterman, B.W. (1997) Songbirds do not create long-term stores of calcium in their legs prior to laying: Results from high-resolution radiography. *Proceedings of the Royal Society of London, Series B*, **264**, 239-244.

Perrins, C.M. (1979) *British Tits* Collins, London.

Perrins, C. M. (1996) Eggs, egg formation and the timing of breeding. *Ibis,* **138,** 2-15.

Ramsay, S.L. & Houston, D.C. (1999) Do acid rain and calcium supply limit eggshell formation for blue tits (Parus caeruleus) in the UK? *Journal of Zoology*, **247**, 121-125.

Reynolds, S. J., Mând, R.& Tilgar, V. (2004) Calcium supplementation of breeding birds: directions for future research. *Ibis,* **146,** 601-614.

Rhynsburger, D. (1973) Analytic delineation of Theissen Polygons. *Geographical Analysis*, **5**, 133-144.

Simkiss, K. (1967) *Calcium in reproductive physiology,* Chapman and Hall, London and New York.

Smith, H.G. & Bruun, M. (1998) The effect of egg size and habitat on starling nestling growth and survival. *Oecologia*, **115**, 59-63.

Smith, H.G., Ohlsson, T., & Wettermark, K.-J. (1995) Adaptive Significance of Egg Size in the European Starling: Experimental Tests. *Ecology*, **76**, 1-7.

St. Louis, V., Breebaart, L.& Barlow, J. (1990) Foraging behaviour of tree swallows over acidified and nonacidic lakes. *Canadian Journal of Zoology,* **68**.

St. Louis, V. L.& Barlow, J. C. (1993) The reproductive success of Tree Swallows nesting near experimentally acidified lakes in northwestern Ontario. *Canadian Journal of Zoology,* **71,** 1090-1097.

Stauss, M.J., Burkhardt, J.F., & Tomiuk, J. (2005) Foraging flight distances as a measure of parental effort in blue tits Parus caeruleus differ with environmental conditions. *Journal of Avian Biology*, **36**, 47-56.

Stoyan, D., Kendall, W.S., & Mecke, J. (1987) *Stochastic Geometry and its Applications.* Wiley, New York.

Svensson, L. (1994.) *Identification guide to European Passerines*, fourth edn. Svensson, Stockholm.

Tanemura, M. & Hasegawa, M. (1980) Geometrical models of territory. I. Models for synchronous and asynchronous settlement of territories. *Journal of Theoretical Biology,* **82**, 477-496.

Tilgar, V., Mänd, R., & Leivits, A. (1999) Effect of calcium availability and habitat quality on reproduction in Pied Flycatcher *Ficedula hypoleuca* and Great Tit *Parus major*. *Journal of Avian Biology*, **30**, 383-391.

Tilgar, V., Mand, R., & Magi, M. (2002) Calcium shortage as a constraint on reproduction in great tits Parus major: a field experiment. *Journal of Avian Biology*, **33**, 407-413.

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

Tilgar, V., Månd, R., Kilgas, P.& Reynolds, S. J. (2005) Chick development in free-living great tits Parus major in relation to calcium availability and egg composition. *Physiological and Biochemical Zoology,* **78,** 590-598.

Tinbergen, J.M. & Boerlijst, M.C. (1990) Nestling Weight and Survival in Individual Great Tits (*Parus Major*). *Journal of Animal Ecology*, **59**, 1113-1127.

VSN Intl. (2005) *Genstat, Version 7.2.* VSN International Ltd, Oxford.

Weimer, V., and K. H. Schmidt. (1998). Studies on the egg quality of the Great Tit (*Parus major*) in relation to soil-condition. Journal Fur Ornithologie **139**:3-9.

Wilkin, T.A., Garant, D., Gosler, A., & Sheldon, B.C. (2006) Density effects on life-history traits in a wild population of the great tit Parus major: analyses of long-term data with GIS techniques. *Journal of Animal Ecology*, **75**, 604-615.

Tables

Table 1. Results from linear mixed models explaining variation in the life-history traits of great tits breeding in Wytham nestboxes between 1965 and 2005. Soil calcium was measured in a 200m grid across the study site. Methods of assigning calcium values to nestboxes were selected by Akaike values in all subset regressions. The maximum soil calcium value within 310 and 340m of each nestbox were the most significant positive predictors of clutch size and recruitment respectively. The nearest soil calcium value to each nestbox was the most significant predictor of fledgling mass. The amount of variation explained by each model is shown in parentheses.

Dependent/Independent Factor	**Wald χ^2**	**d.f**	**Effect / (s.e.)**		**P**
Incubation Period(30.1%)					
Lay-date	861.29	1	-0.1491	0.00508	<0.001
Clutch size	339.41	1	-0.3427	0.01860	<0.001
Egg mass (g)	79.22	1	-1.956	0.2197	<0.001
Female age	31.45	1	0.1486	0.02650	<0.001
Female mass (g)	15.86	1	-0.01251	0.003142	<0.001
Max Ca 220m (g)	*0.12*	*1*	*-0.001628*	*0.0047337*	*0.731*
Lay-date (9.9%)					
Spring temperature	89.4	1	-0.08544	0.009036	<0.001
Female age	72	1	-0.6402	0.07545	<0.001
Territory size (max 1ha)	28.87	1	-2.337	0.4350	<0.001
Habitat type	65.81	3			<0.001
Altitude (m asl)	21.23	1	0.02016	0.004376	<0.001
Max Ca 340m (g)	*1.65*	*1*	*-0.02267*	*0.017635*	*0.199*
Clutch size (26.1%)					
Lay-date	881.28	1	-0.07285	0.002457	<0.001
Female age	37.34	1	0.09849	0.016051	<0.001
Max Ca 310m (g)	33.11	*1*	*0.01936*	*0.003378*	*<0.001*
Territory size (max 2ha)	14.18	1	0.1357	0.03554	<0.001
Egg mass (15.1%)					
Lay-date	91.9	1	0.002197	0.0002292	<0.001
Female age	32.43	1	-0.007972	0.0014000	<0.001
Edge distance (m)	21.88	1	-0.00007748	0.000016564	<0.001
Altitude (m asl)	10.02	1	0.0002967	0.00009372	0.002
Max Ca 340m (g)	*0.74*	*1*	*0.*	*0.0*	*0.391*
Fledgling mass (12.7%)					
Lay-date	129.5	1	-0.3687	0.03240	<0.001
Clutch size	100.45	1	-1.258	0.1255	<0.001
Altitude (m asl)	73.83	1	-0.07251	0.008439	<0.001
Egg mass (g)	30.73	1	8.043	1.4509	<0.001
Territory size (max 2ha)	26.98	1	1.866	0.3593	<0.001
Nearest Ca value (g)	*12.68*	*1*	*0.2146*	*0.06026*	*<0.001*
Recruitment (29.7%)					
Fledgling mass (g)	137.22	1	0.01806	0.001564	<0.001
Lay-date	112.83	1	-0.03249	0.003102	<0.001
Clutch size	25.71	1	0.06109	0.012007	<0.001
Max Ca 340m (g)	14.36	*1*	*0.01048*	*0.003030*	*<0.001*
Territory size (max 2ha)	4.76	1	0.07918	0.034120	0.029

Figures

Figure 1. Map of Wytham Woods showing a) the location of the 163 soil sampling plots from 1974 shown as filled circles. The crosses represent 6 example nestboxes with 330m radius buffers form around them. The maximum calcium value within these buffers was used, in models explaining life-history traits, to describe the calcium availability for birds breeding in the focal nestbox. This procedure was repeated over several spatial scales (radii). b) Soil calcium, which ranged from 63 (white) to 21000 (dark) mg.100g^{-1}, interpolated between the sampling plots. Also shown, for illustrative purposes, are tessellated territories formed around occupied great tit nestboxes in a given year (19xx). The maximum and mean interpolated calcium values were also extracted and used here to describe the calcium availability for the focal nestbox.

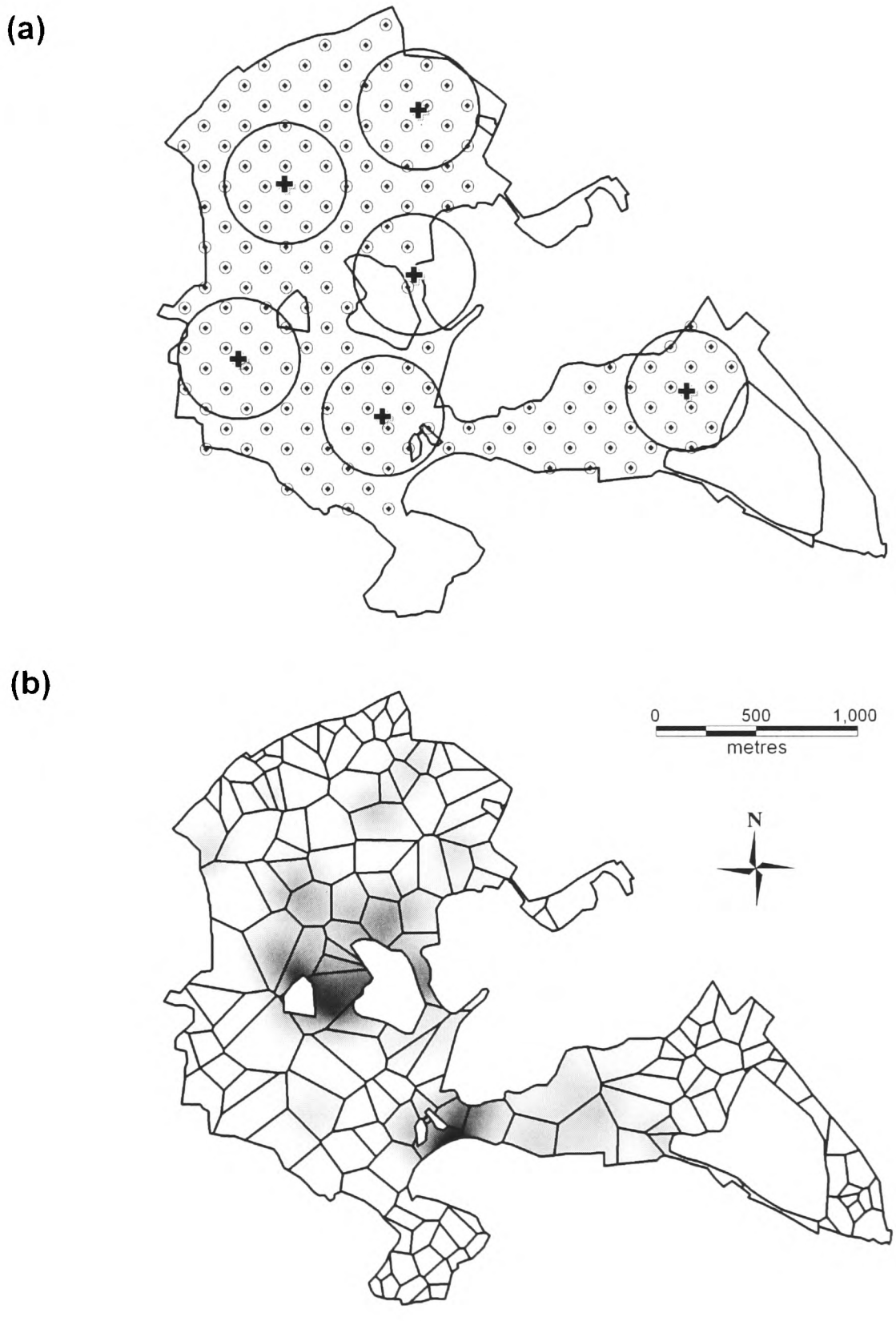


Figure 2 (a) The distribution of soil calcium sampled at 163 locations in 200 a metre grid which covered *c.* 85% of Wytham Woods, UK. Soil calcium was used to explain variation in life-history traits for great tits breeding in nestboxes between 1965 and 2005. Also shown are distributions of (b) the maximum soil calcium value sampled within 310 meters of 8960 breeding pairs, and (c) the mean within tessellated territory soil calcium for 8961 breeding attempts, and (d) the soil calcium of the nearest sampling location to 8570 breeding attempts.

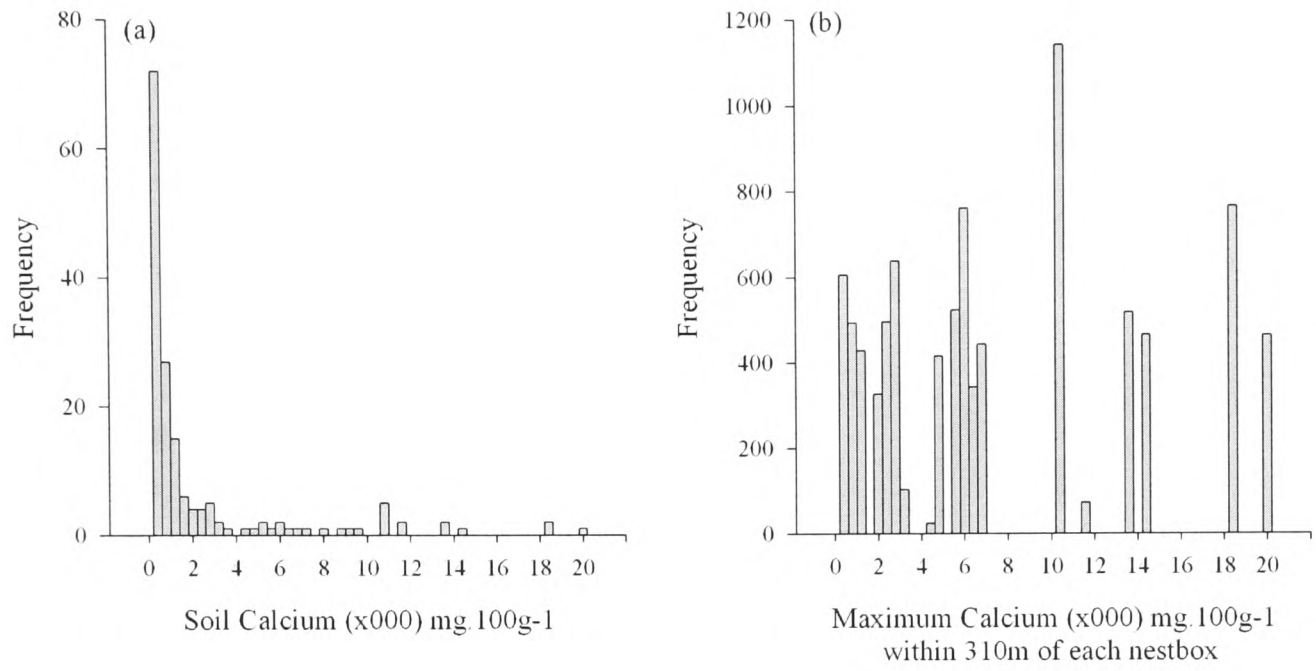


Figure 3. Graphical estimation of the appropriate radius (from a great tit nestbox) within which to extract the maximum soil calcium reading. Figures show the Wald statistic distributed as a χ^2 and obtained from linear mixed models analyses of (a) incubation period, (b) lay-date, (c) clutch size, (d) egg mass, (e) fledgling mass and (f) the number of offspring recruited to the breeding population, for a range of search radii (see text). All models include year of reproduction and female identity as random effects.

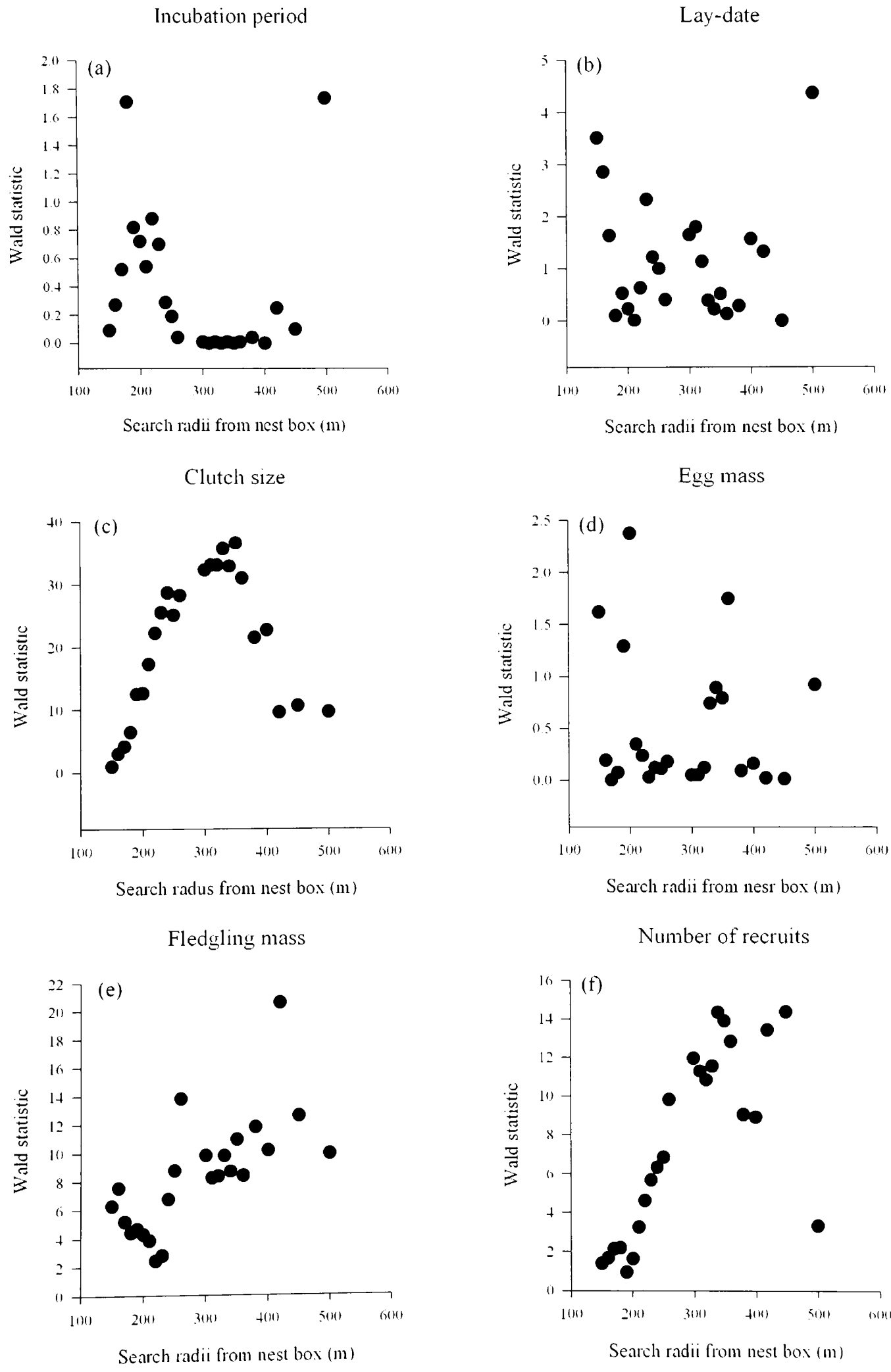
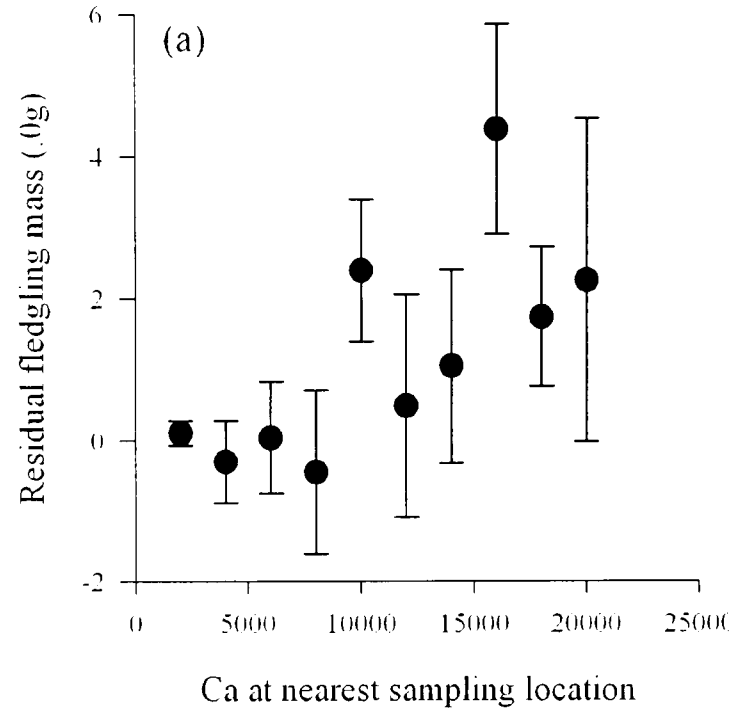
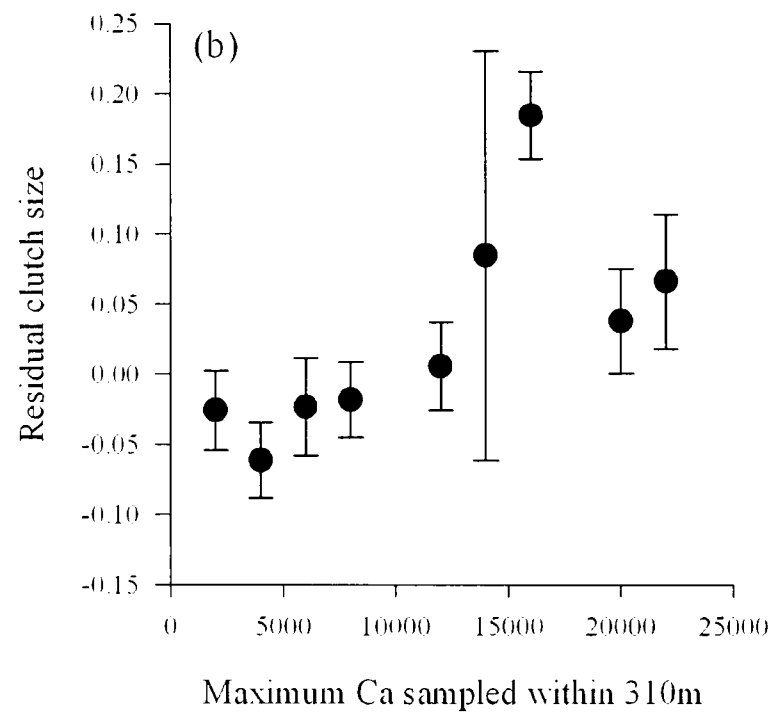
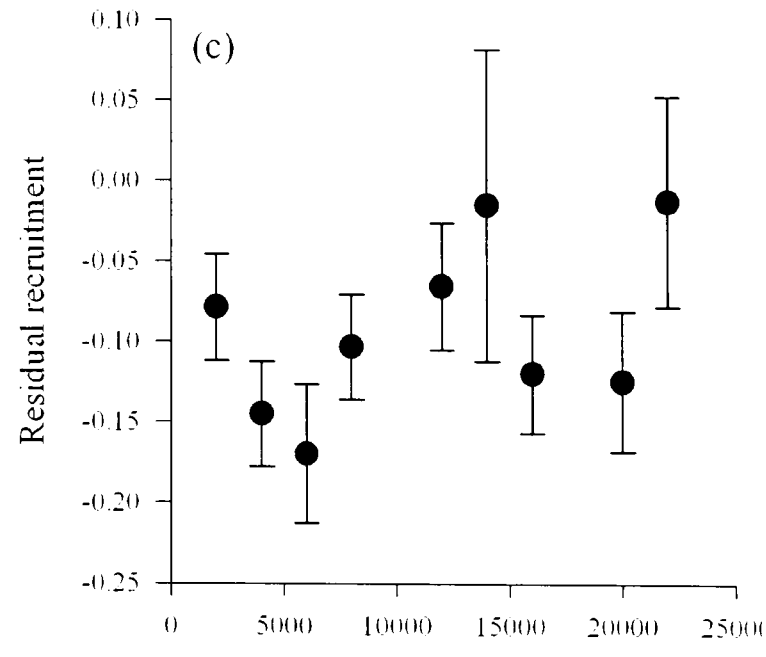


Figure 4. Significant relationships between soil calcium and residual (a) fledgling mass, (b) clutch size and (c) recruitment. Model (a) uses the soil calcium level at the nearest sampling location to each nestbox (4-165m). In models (b) and (c) calcium was estimated by the maximum calcium level sampled within 310m and 340m of each nestbox, respectively.







Chapter 6: Natal environment is unrelated to great tit life-history traits.

Natal environment is unrelated to great tit life-history traits

TEDDY A. WILKIN*, & BEN C. SHELDON

Edward Grey Institute, Department of Zoology, South Parks Rd., Oxford OX1 3PS, UK

Running head: Natal environment in the Great tit.

*Author for correspondence: teddy.wilkin@zoo.ox.ac.uk

Summary

Conditions experienced early in life have been shown to have marked long-term effects on subsequent life-history traits in many organisms. Persistent effects of the early environment are of considerable importance for several ecological and evolutionary processes, because they are likely to shift selection on life-histories towards fewer offspring of higher quality, have major implications for our understanding of the causes of individual variation, and suggest that habitat choice can have cascading trans-generational effects. In addition, early environments may affect entire cohorts, therefore acting as a delayed population-regulation mechanism. At the level of the individual, long-term effects of early conditions have recently been reported for several long-lived bird and mammal species. Here, we report analysis of variation in the life-histories of over 5000 wild great tits (*Parus major*) for which natal and breeding environments were known. While we found marked effects of current (breeding) environments on a wide range of life-history traits at the individual level, we found very little evidence of any influence of natal environment on these characters. We found weak cohort effects due to variation in the natal environmental, but these were again weaker than the effect of the current environment. The absence of detectable long-term natal effects may be a consequence of high rates of mortality in great tits favouring investment in current conditions, respectively, rather than investment in characteristics that confer long-lasting advantages realised later in life. Our results suggest that persistent effects of the natal environment are not all-pervasive, and that further work should try to understand the life-history conditions under which they are found.

Introduction

A central goal of evolutionary ecology is to try to understand the processes that contribute to causing individuals to vary in their phenotypes. According to evolutionary theory phenotypic variation is determined by genes, the environment and their interactions [1-4]. However, in contrast to genotypes, which are fixed within individuals, the environments experienced by individuals usually vary in time and space and their effects on phenotypic variation may not be immediately apparent, instead manifesting themselves in complex ways later in life [5]. However, a special case of an environmental effect that has attracted considerable recent interest is the existence of persistent effects of the early environment on subsequent life history trajectories. For example, in addition to having short-term effects on offspring quality [6-8] conditions experienced early in life have recently also been shown to have long-term effects on the life-histories and reproductive success of offspring [5,9].

Persistent natal environmental effects are of considerable current interest as they may have important implications for population dynamics and for our understanding of several ecological and evolutionary processes. For example, annual variation in environmental quality can influence the subsequent reproductive success of entire cohorts and may therefore act as a delayed population regulatory process [10,11]. Such cohort effects may be difficult to observe in the wild, as individuals born in 'good quality' years may later be reproductively constrained by higher numbers of breeding conspecifics [12,13]. The condition of offspring may also influence their dispersal abilities [14,15]. For example, offspring condition has been linked with the quality of the habitats in which great tits eventually settle to breed [16], and with dispersal success in barnacle geese [14]. If high quality individuals are more likely to

settle in high quality habitats then such non-random dispersal, mediated through the quality of early conditions, may also act to influence the genetic structure of populations [17,18] and may amplify source-sink relationships between cohorts, or groups of individuals, born in optimal and suboptimal habitats [19].

Long-term effects of early conditions may also to magnify life-history trade offs [20]. Life-history theory predicts that parents should prioritize their own survival over reproductive effort when the environment is unpredictable, assuming that juveniles are more vulnerable to inclement conditions than parents [20,21]. Therefore, if surviving offspring raised in poor conditions are likely to reproduce at a lower than average rate throughout their lives, theory predicts a further reduction in reproductive effort in poor quality environments. Likewise, if offspring from good quality environments are likely to display increased fecundity and survival, then parental investment should be maximised in high quality conditions. In more general terms, long-term effects of early conditions are also likely to shift the optimum parental investment strategy towards fewer offspring of higher quality, regardless of environmental quality.

Rearing conditions are primarily determined by the attributes and abilities of the parents [22] and by the quality of the natal environment [23,24], the latter being partially controlled by the former. These factors influence offspring development principally, but not exclusively (see [25,26]), by determining the quality of neonatal nutrition; the number, sex and relative rank of competing siblings can also affect the development of an individual offspring [9,27].

That offspring reared in high quality environments develop more quickly [28], are in better condition at independence [29], and are more likely to survive to breeding age [30,31] than offspring raised in poor environments is well known. However, early environmental conditions have also been linked to adult morphology [28], size [23,32] and attractiveness [27], as well as territory quality [16,31] and some pre-breeding fitness components such as recruitment probability [23,30] and age at first breeding [9]. Early conditions have also been shown to affect the life-histories of breeding adults; heavy female nestlings have been associated with larger clutches [23,32,33] and heavier eggs [34], and offspring on poor quality diets have bred at a slower rate than controls [35]. Long-term effects of early conditions on lifetime reproductive success have also been reported [9,30,31,36].

The aim of the current study was to investigate life-history variation in a large sample of great tits for which details of the natal and breeding environments were known. First, we explore the extent to which natal and breeding environments are similar, then we partition life-history variation into that attributable to the independent effects of birth year and location, breeding year and location, differences between breeding females and the unexplained residual variation between observations. Then we test the effect of a range of biologically relevant specific environmental factors on life-history variation in males and females, an approach that allowed us to simultaneously compare the effects of breeding and natal environments in determining individual life-histories. The choice of the environmental effects was governed by previous work (Chapters 2-5) which has identified environmental correlates of life-history variation. We also examined the effects of annual variation in rearing conditions on the life

histories of entire cohorts, while accurately controlling for individual differences in the subsequent breeding density of recruited individuals.

Results

1. Natal and breeding environments

Natal and breeding environments were known for 2703 female and 2722 male great tit recruits born between 1959 and 2004 and recorded as breeding between 1965 and 2005. Dispersal distances ranged from zero, when an individual bred in its natal nestbox (n = 2 females, n = 8 males), to 3530m (median = 793 m females, 528 m males; Figure 1). Altitudes a.s.l. ranged from 61 m to 163 m, and edge distances ranged from 0.3 m to 535 m. Breeding and natal territory sizes ranged from 694 m^2 and 1081 m^2, to the imposed maximum territory size of 2 ha, respectively. The number of oaks in breeding and natal territories varied from 0, to 102 and 106, respectively.

2. Inter relationships between natal and breeding environments

Many of the specific environmental measures used to describe natal and breeding sites were correlated (Table 1; unshaded boxes). For example, as the study site at Wytham is a hilltop woodland, edge distance was correlated with altitude ($r = 0.199$, $P < 0.001$), and, as birds breed at higher density at the woodland edge (Chapter 3), territory size was also correlated with edge distance ($r = 0.293$, $P < 0.001$). The strongest environmental correlation was between territory size and the number of oak trees within each territory, as large territories are likely to contain more oak trees ($r = 0.509$, $P < 0.001$). However, these correlations, although statistically significant, were weak enough to allow the separation of their effects in mixed models. Each specific measure of the natal environment was weakly (r between 0.144 - 0.213) but significantly (all $P < 0.001$) correlated with the same measure of the subsequent breeding environment of the same individual (Table 1; bold). Correlations between

natal and breeding environments are unsurprising for two reasons. First, the restricted natal dispersal (Fig 1) will inevitably lead to a resemblance between natal and breeding habitat, as environmental variables are spatially autocorrelated. Second, offspring from good quality environments may be more likely to settle in higher quality breeding areas [16,18,31]. However, weak non-random settlement does not compromise the current approach, as it simultaneously considers breeding and natal environments for a large sample of individuals.

3. Partitioning life-history variation

Using linear mixed models, we were able to partition the total phenotypic variance in four life history characters to different sources; total phenotypic variances attributable to each source are given in Table 2, while Fig. 2 illustrates the estimates as percentages of the overall variance for each trait. The contribution of different sources of variance to each trait differed across traits; for example breeding time was strongly influenced by differences among years, whereas egg mass was strongly influenced by differences among females. For three traits (laying date, clutch size, offspring mass), the effect of the current, breeding, environment was substantially larger than that of the natal environment (ratio of variance components: 2.4-7.9). In addition, the year of observation explained at least 10% of the variance for each trait. The exception to this rule was egg mass, for which the effect of the natal environment exceeded that of the current environment, differences between years were relatively unimportant, but differences among females explained a large proportion of the variance.. Hence, in general, these analyses suggest that current environments are more important than natal environments in explaining life history trait variation in this species.

4. Specific effects of breeding environment

In linear mixed models, all measured great tit life-history traits were strongly and significantly predicted by variation in current breeding environments (Fig. 3; Table 3). For example, independently of the effects of female age and spring temperature (Table 3), lay date was earlier in oak-rich territories, at low altitudes and in nestboxes further from the woodland edge (Fig. 3. a, b, c) and in more mature habitat types (all $P > 0.001$). Clutch size increased with territory size, with the distance from the woodland edge and with oak tree availability (all, $P < 0.003$; Fig. 3 d, e, f). Eggs were lighter later in the season (Table 3) and at low altitude but heavier close to the woodland edge (Fig. 3. g, h). Fledglings in large or late clutches were lighter than those in small or early clutches, and fledging mass was significantly correlated with egg mass (Table 3). Independently of these effects, fledging mass was increased at lower altitudes, in larger territories and in those territories containing more oak trees (Fig. 3 i, j, k). These results show that many aspects of the current breeding environments of these birds have substantial and independent effects on variation in life-history traits.

The lifespan of female great tits recruited from local nests ranged from one to nine years, with 65% of recruited individuals having just one year between their year of birth and final when recorded breeding. Males were recorded breeding up to seven years after their year of birth, with 69% of recruits disappearing after a breeding attempt in their first year. There was no difference between the average number of times that recruits and immigrants bred in the full dataset (t- test, $t_{(4290)} = 1.23$, $P = 0.220$). Female longevity increased with mean lifetime territory size as a linear ($\chi^2_{(1)} = 11.78$, $P < 0.001$) but more so as a quadratic term ($\chi^2_{(1)} = 24.14$, $P < 0.001$; Fig. 4a).

Male longevity increased with mean lifetime territory size ($\chi^2_{(1)} = 7.06$, $P = 0.008$; Fig. 4c) and the mean number of oaks in the territory ($\chi^2_{(1)} = 6.12$, $P = 0.013$; Fig. 4d) as quadratic terms in the same model.

Lifetime reproductive success of breeding individuals in the current dataset ranged from zero to 24 for females (median = 1, UQ = 2), and 23 for males (median = 1, UQ = 2), with 53% of breeding females and 51% of males recruiting no offspring to the breeding population. For females, LRS increased with mean lifetime territory size as a quadratic term ($\chi^2_{(1)} = 4.30$, $P = 0.038$), while male LRS increased with mean lifetime territory size ($\chi^2_{(1)} = 3.82$, $P = 0.050$) and mean lifetime oak availability ($\chi^2_{(1)} = 5.09$, $P = 0.024$) as quadratic terms in the same model. Figure 4 shows male and female lifespan and LRS as functions of breeding and natal environments, and functions fitted to mean values.

5. Specific effects of natal environments

In contrast to breeding year and location the year of and location of birth were weakly or unrelated to life-history variation in a variance component analysis (Table 2; Fig. 2). The only substantial effect of natal environment was found for egg mass, where, while year of birth was accounted for little variation, location of birth accounted for a significant proportion of variation (3.7%, $P < 0.05$). This was the only example of a natal factor which accounted for more variation than a breeding factor.

When we analysed the influence of the specific natal environment on life-history trait variation for 2703 individual females, we found almost no evidence of relationships between life-histories variation and the natal environments (Table 3), even though

these specific environmental characters had marked effects in the current breeding environment. For example, laying date was unrelated to oak availability, altitude, edge distance (Fig. 3 a, b, c) or the habitat type of the natal nestbox (all $P > 0.05$). Clutch size was not associated with natal oak availability, territory size or edge distance (all $P > 0.098$; Fig. 3 d, e, f). Egg mass was unrelated to natal altitude, though weakly related to natal edge distance (Fig. 3 g, h). Fledgling mass was not associated with natal altitude, natal territory size and the number of oaks in the natal territory (Fig. 3 i, j, k).

When life-histories were analysed over the entire lifespan of individuals, we again found no evidence that the natal environment was responsible for variation among individuals. Female longevity and LRS were unrelated to natal territory size (Fig. 4 a, b) and all other environmental factors. Male longevity and LRS were unrelated to natal territory size (Fig. 4 c, d), natal oaks (Fig. 4 e, f) and all other environmental factors.

6. Cohort effects

Annual variation in the quality of the rearing environment was a significant predictor of subsequent male ($\chi^2_{(1)} = 5.41$, $P = 0.020$) and female ($\chi^2_{(1)} = 9.13$ $P = 0.003$; Fig. 5a) breeding territory size, suggesting that individuals reared in a 'good' year bred at higher density when recruited to the breeding population. Variation in the quality of the rearing environment was also significantly related to the number of years between an individual's year of birth and year of first breeding both for males ($\chi^2_{(1)} = 33.63$, $P < 0.001$) and females ($\chi^2_{(1)} = 161.11$, $P < 0.001$; Fig. 5b), indicating that offspring born in a 'good' year took longer to recruit to the breeding population, presumably

because of increased competition for breeding sites. To separate the effects of annual variation in rearing environments from the effect of subsequently higher breeding density on life-histories we included breeding territory size as a covariate in the following models. Annual variation in the rearing environment was a weak but significant positive predictor of female cutch size ($\chi^2_{(1)} = 7.51$, $P = 0.006$; Fig. 5c), when controlling for territory size ($\chi^2_{(1)} = 10.71$, $P = 0.001$), the number of oak trees in the territory ($\chi^2_{(1)} = 9.36$, $P = 0.002$), lay-date ($\chi^2_{(1)} = 450.35$, $P < 0.001$), female age ($\chi^2_{(1)} = 29.27$, $P < 0.001$) and the distance to the woodland perimeter ($\chi^2_{(1)} = 18.76$, $P < 0.001$). However, rearing environments had no effect on female lay-date ($\chi^2_{(1)} = 1.15$, $P = 0.284$), egg mass ($\chi^2_{(1)} = 0.38$, $P = 0.539$) or fledgling mass ($\chi^2_{(1)} = 0.82$, $P = 0.366$).

Discussion

We used a long-term study of free-living great tits for which the natal and breeding environment were known for more than 5000 individuals to assess the relative importance of natal environments in causing long-term, persistent environmental effects. Life-history variation was strongly related to the year and specific characteristics of the environment in which those traits were measured. In contrast we found very little evidence of an influence of natal environments on life history variation of breeding great tits, which strongly suggests that long-term effects of early conditions are absent in this species.

Breeding Environments: That breeding environments affect breeding parameters is well known [37,38] and at Wytham environmental and life-history variation were correlated. For example, a multivariate variance component analyses showed that both the year and location of breeding accounted for significant proportions of all measured life-history traits, when controlling for differences between individuals. These results strongly indicate that, in the current system, specific aspects of the breeding location are likely to be important sources of life-history variation. Indeed, mixed modelling of specific environmental effects confirmed that several different aspects of the breeding environment were strong predictors of life-history variation. For example, life-histories varied with altitude, probably due to differences in temperature and concurrent phenology, and density due to increased competition for food at high density (Chapters 2 & 4). However, current results also suggest a cost associated with individuals breeding at very low density (Fig. 4a, b, c, e) i.e. in larger territories. This cost is possibly due to an increased territory defence for males at low density [39,40] and a consequent decrease in nuptial feeding and provisioning

received by the female and nestlings, respectively (although see [41]). Also, males in larger territories sing more frequently [40] and will therefore be more exposed to predation by sparrow hawks [42] which would explain the reduction in longevity at low density. These results also indicate a strikingly consistent estimation of optimal territory size of around 1.5 ha and also confirm the efficacy of capping tessellated territories at a maximum of 2ha (Fig. 4a, b, c, e).

Independent of the effects of density, life-histories varied with the distance between the nestbox and the woodland edge (Chapter 3). Note that edge distance and altitude are correlated but their effects lay-date and egg mass are opposed, confirming the effective statistical separation of correlated environmental factors. Oak availability also influenced life-history variation due to reduced food availability in oak poor territories (Chapter 4). The current analyses also show decline in LRS and lifespan in very oak rich territories (Fig. d, f) probably due to an increase in territorial defence caused by more frequent territory invasions by individuals from oak poor territories [43,44]. This explanation is supported by the absence of an effect of oak availability on female lifespan or LRS.

Natal Environments: Despite strong and consistent effects of breeding environments on life-history variation, we found no similar effects of natal environment on the life-histories of recruited individuals. For example, a variance component analyses showed that natal location was unrelated to clutch size and fledgling mass and only weakly related to lay-date and egg mass. Similarly year of birth was unrelated to lay-date, egg mass and fledging mass and only weakly related to clutch size. In each case the year of breeding explained more variation than the year or birth, and the breeding

location accounted for more variation in traits than the birth location, strongly suggesting that the breeding environment was a more important source of life-history variation than the natal environment. This was confirmed by linear mixed modelling of biologically meaningful environmental factors which showed that life-history variation was unrelated to the specific environmental factors measured at the natal nestbox.

The exception was that of variation in egg mass, which in the variance component analysis, was more associated with the natal than with the breeding location. . However we did not detect a strong effect of natal environment in our model (Table 2) apart from a weak association with natal edge proximity. That egg mass may be influenced by early conditions has been suggested by previous work [33,34]. Therefore we further investigated the relationship between natal environment and egg mass variation by including other environmental factors in the egg mass model in Table 2 and found a significant relationship between natal oak tree density and egg mass ($\chi^2_{(1)} = 8.80$, $P = 0.003$). However, as nestlings in oak rich areas are heavier at fledging, it is likely that they are also heavier, and lay larger eggs as breeding adults. In this case the quality of nestling diet would be regarded as a predictor of adult mass and an indirect influence on egg mass. To test this we included the mass of the female when she was breeding (and controlled for the time of day, wing length and the age of the brood to control for diurnal mass increase, body size and seasonal gonad reduction, respectively), which confirmed that females that were heavier for their size laid larger eggs($\chi^2_{(1)} = 57.99$, $P < 0.001$)(as in [45]). However, natal oak availability remained significant in the model following the inclusion of adult female mass ($\chi^2_{(1)} = 8.82$, $P = 0.003$) suggesting that early nutrition effects egg mass

independently of the mass of the adult bird. These results confirm another study which have linked early nutrition to egg mass [33,34] and are probably due to the quality of the diet determining gonad size.

Cohort Effects: We found that male and female offspring from years of high reproductive success took longer to recruit to the breeding population. There are four mechanisms that might influence time to recruitment in our study. Firstly, a gap year may be when an individual breeds outside of the woodland perimeter. However, as adults rarely disperse far between breeding attempts (median = 60m) we judge it unlikely that many individuals will alternate between internal and external habitats. Secondly, a gap year may result from an individual breeding in a natural cavity rather than a nestbox, although alternate between cavity types is rare in the current [46]. Thirdly, a gap year may occur in our data due to a failed nesting attempt, or due to an individual's inability to obtain a territory or a mate in that year. The two later hypotheses are similar in the fact that they both result in the individual not breeding in that year. In support of this hypothesis, recruits from 'good' years subsequently bred at higher density, where it is more difficult to secure a territory and mate, than offspring from poor quality years. We found that female recruits from 'good' years laid slightly more eggs than offspring from poor years. This effect, which has been suggested previously [32,33] provides some evidence of a long-term effect of rearing conditions on great tit reproduction. However, the effect was weak and only apparent when controlling for subsequent breeding density and so is, in effect, a hidden trend; females from 'good' years actually lay smaller clutches as they invariably breed at high density.

The general trend of an absence of long-term effects is somewhat surprising in the light of several recent studies reporting long-lasting effects of natal environments life-histories [9,30,31]. However, studies that have linked life-histories with natal conditions have mostly been conducted on long-lived, iteroparous species with high recruitment, or on captive populations where many sources of mortality are removed. For example, Oystercatchers, which live for up to 17 years, breed up to 10 times and have recruitment rates of 31-41%, show significant variation in adult pre-breeding survival and LRS with natal territory quality [31] and the long-term fitness of female red deer, which are also long lived, has been linked with the spring temperature and breeding density in their year of birth [36].

In the Wytham great tit population, a fledged individual only has a 15% probability of surviving to breed and of those that do breed, females and males do so an average of just 1.6 and 1.5 times, respectively. The absence of long-term effects of rearing environments may be explained by these higher levels of post-fledging and post-breeding mortality, which will result in strong selection for qualities that increase current and breeding condition rather than any quality that may convey a smaller but longer lasting advantage later in life. Our analyses confirm the importance of the breeding environment as a source of life-history variation and show that long-term effects of early conditions cannot be assumed found in wild populations. Further work should aim to understand under what conditions such effects are to be expected.

Methods

Data

This study forms part of the Edward Grey Institute's long-term study of the great and blue tits at Wytham Woods, near Oxford, UK. Data used in the present study were colleted between 1959 and 2005, in accordance with methods described previously [37,47,48]. Great tits breed almost exclusively in nestboxes in Wytham, the locations of which have remained constant throughout the study, unless a minor move was necessitated by tree fall. Nestboxes were visited at least weekly to ascertain clutch initiation date (lay-date, where 1st April =1), egg mass (the mean of three to five unincubated eggs) and clutch size. Chicks were weighed and ringed on day 15 after hatching (where hatch day = 1) and for the purpose of this study, fledgling mass was averaged for each brood. Parents were trapped at nestboxes after the chicks reached seven days of age (to reduce desertion-risk), aged, sexed [49] and ringed or their identities were established from (BTO) rings already fitted.

We only used the first clutches (genuine second clutches are very rare at Wytham) and only those in which four or more eggs were laid. Unless stated otherwise, we only used breeding attempts made during the first year of reproduction, as the effects of natal environments are expected to be most pronounced early in life [5,50]. The spring temperature each year was recorded as the sum of the maximum temperatures for each day between 1 March and 25 April (the Warmth sum), as in [51]. The habitat classification proposed by [52] is used here and identifies four habitat categories; semi ancient natural woodland; 18th and 19th century broadleaf plantations; 20th century plantations, and secondary regenerated wood pasture. Natal environments were not measured for individuals born before 1965, as not all nestboxes were in place and so estimating density and other factors was not possible.

The lifetime reproductive success (LRS) of an individual was measured by the total number of young produced by that individual that were recruited to the breeding population in subsequent years. This figure does not reflect the total numbers that survive to breed, as many leave Wytham and breed elsewhere [16,53]. However, we believe the total number of recruits remains an accurate measure of the relative success of individuals. The mean number of recruits per nest in a given year was used a measure of environmental quality in that year (as in [30]). This measure thus summarized the large scale breeding conditions of that year which, in the current population, are determined by a combination of breeding density, spring temperature, the timing and duration of the caterpillar peak, relative to when birds bred, and the size of the beech crop in the following winter [37,48]. The longevity of an individual was measured as the number of years between year of birth and final year when recorded breeding, and 'gap' years were the number of years between year of birth and the first year when recorded breeding.

Digital Mapping

The locations oak trees and nestboxes at Wytham Woods, UK were digitally mapped in the field to submeter accuracy. MapInfo Professional ver. 7 and Vertical Mapper ver. 3 were then used to produce maps detailing the location of the oak trees and nestboxes within the woodland perimeter (20km in length). The areas of tessellated (Thiessen) polygons formed around occupied nestboxes in each year were used as individual measures of breeding density, hereafter referred to as territories. A drawback of this method is that in areas of low density, extremely large and biologically meaningless territories are formed. This limitation has been addressed by

capping territory sizes through a range of maxima with the greatest effect in life-history models when capped at a maximum of 2ha [54]. In the current study territory size is thus capped at 2ha. As the preferred food for the adults and their nestlings is found at highest densities on oak trees [55,56], the number of oak trees within each tessellated territory was used as a measure of oak, and therefore food availability for the birds in the focal nestbox. Using this method the scales at which oak trees were counted were variable between nests and determined by locations of competing neighbours, and results in the mutual exclusivity of oak trees between nestboxes The altitude of each nestbox location was estimated from a 3D interpolated model of Wytham [54] and the GIS was used to measure the distance between each nestbox and the woodland perimeter.

Statistical methods

Linear mixed models with normal errors were performed to analyze the life-histories of female great tits born, and later breeding in the nestboxes with respect to environmental variation. Female identity and year were included as random effects in models explaining life history traits; by including year as a random effect we control for between year-differences in the environment, and by including female as a random effect we control for systematic differences between females due, for example, to differences in biometrics and condition. These analyses therefore specifically consider variation within annual environments and within individuals. Environmental variables were included in models as fixed effects and the significance of factors in explaining variation was assessed from the Wald statistic, which is distributed asymptotically as χ^2 [57]. Models were constructed by backwards-stepwise removal of non-significant breeding environment factors depending on their Wald statistic.

Once the environmental variables that influenced life-histories during the breeding attempt were established, the same environmental factors were included for the individuals' natal nestbox. In this way it was possible to separate the effects of current breeding environment on life-histories, from the effects of their natal environments.

Models

1. Lay-date is well known to vary with spring temperature and the age of the female. In the current population we also see lay-date varying independently with altitude, proximity to the woodland edge, between oak rich and oak poor areas and habitat types. Therefore these environmental factors the female's breeding and natal nestbox were included in the lay-date LMM for.
2. Clutch size declines seasonally and increases with the age of the female. Environmental effects on clutch size were an increase with territory size, distance from the woodland edge and oak availability. The clutch size model thus included these factors measured for both the breeding and the natal nestboxes.
3. Egg mass increases seasonally and declines with the age of the female. However in the current dataset of recruits in their first year of breeding, we found no relationship between female age and egg mass and so age was not included in the final LMM. Egg mass varies in the current population with altitude and edge proximity and so these variables, for the natal and breeding locations, were included in the LMM.

4. Fledgling mass correlates with egg mass, and decreases seasonally and with clutch size. Environmental factors, which were included for breeding and natal locations, were altitude, territory size and oak availability.

Longevity and LRS of males and females were assessed with respect to linear and quadratic territory size, altitude, edge distance and the number of oaks in the territory. Each environmental factor was included in the analyses in two forms, firstly averaged over the life of the individual and secondly as measured at the natal location. In this way it was possible to simultaneously consider the effects mean breeding and natal environments on the dependent variable. These analyses were performed in Linear mixed models which included year of birth as a random effect. Birds still alive in 2005 were excluded from the longevity analysis.

Natal conditions at the level of the cohort were estimated by the mean reproductive success per nest in the year of birth. A full dataset was employed for analyses at the level of the cohort such that several reproductive attempts were included for individuals in different years. For this reason mixed models were used with either male or female identity, and year of birth included as random effects to control for non independence within these subgroups. Natal conditions at the level of the cohort were compared with the number of gap years and the subsequent territory sizes for males and females, in Linear mixed models (LMM). Natal conditions were then compared with female lay-date, clutch size, egg mass and fledgling mass. Other covariates were included in these life-history models as in Table 2.

Acknowledgments

TAW was funded by BBSRC; we gratefully acknowledge the huge amount of work that has gone into the collection of the data analysed in this paper by a very large number of fieldworkers.

References

1. Gillespie JH, Turelli M (1989) Genotype-Environment Interactions and the Maintenance of Polygenic Variation. Genetics 121: 129-138.
2. Scheiner SM (1993) Genetics and Evolution of Phenotypic Plasticity. Annual Review of Ecology and Systematics 24: 35-68.
3. Qvarnstrom A (1999) Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (Ficedula albicollis). Evolution 53: 1564-1572.
4. Merila J (1997) Expression of genetic variation in body size of the collared flycatcher under different environmental conditions. Evolution 51: 526-536.
5. Lindström J (1999) Early development and fitness in birds and mammals. Trends in Ecology & Evolution 14: 343-348.
6. Merila J (1996) Genetic variation in offspring condition: An experiment. Functional Ecology 10: 465-474.
7. Garant D, Dodson JJ, Bernatchez L (2003) Differential reproductive success and heritability of alternative reproductive tactics in wild Atlantic salmon (Salmo salar L.). Evolution 57: 1133-1141.
8. Van de Pol M, Bakker T, Saaltink D-J, Verhulst S (2006) Rearing conditions determined offspring survival independent of egg quality: a cross foster experiment with Oystercatchers Haematopus ostralegus. Ibis 148: 203-210.

9. Cam E, Monnat JY, Hines JE (2003) Long-term fitness consequences of early conditions in the kittiwake. Journal of Animal Ecology 72: 411-424.

10. Turchin P (1990) Rarity of density dependence or population regulation with lags? 344: 660-663.

11. Saether B-E (1997) Environmental stochasticity and population dynamics of large herbivores: a search for meachnisms. Trends in Ecology & Evolution 12: 143-149.

12. Hornfeldt B (1994) Delayed Density-Dependence as a Determinant of Vole Cycles. Ecology 75: 791-806.

13. Rose KE, Clutton-Brock TH, Guinness FE (1998) Cohort Variation in Male Survival and Lifetime Breeding Success in Red Deer. Journal of Animal Ecology 67: 979-986.

14. van der Jeugd HP (2001) Large barnacle goose males can overcome the social costs of natal dispersal. Behavioral Ecology 12: 275-282.

15. Imms RA, Hjermann DO (2001) Condition-dependent dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. Oxford: Oxford University Press. pp. 203-216.

16. Verhulst S, Perrins CM, Riddington R (1997) Natal dispersal of Great Tits in a patchy environment. Ecology 78: 864-872.

17. Delestrade A, McCleery RH, Perrins CM (1996) Natal dispersal in a heterogeneous environment: The case of the Great tit in Wytham. Acta Oecologica-International Journal of Ecology 17: 519-529.

18. Garant D, Kruuk LEB, Wilkin TA, McCleery RH, Sheldon BC (2005) Evolution driven by differential dispersal within a wild bird population. Nature 433: 60-65.

19. Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65: 169-175.

20. Stearns SC (1992) The Evolution of Life Histories. Oxford: Oxford University Press.

21. Hirshfield MF, Tinkle DW (1975) Natural selection and the evolution of reproductive effort. Proceedings of the National Academy of Sciences of the United States of America 72: 2227-2231.

22. Schluter D, Gustafsson L (1993) Maternal Inheritance of Condition and Clutch Size in the Collared Flycatcher. Evolution 47: 658-667.

23. Sedinger JS, Flint PL, Lindberg MS (1995) Environmental Influence on Life-History Traits: Growth, Survival, and Fecundity in Black Brant (Branta Bernicla). Ecology 76: 2404-2414.

24. Przybylo R, Wiggins DA, Merila J (2001) Breeding success in Blue Tits: good territories or good parents? Journal of Avian Biology 32: 214-218.

25. Leung B, Forbes MR (1997) Modelling fluctuating asymmetry in relation to stress and fitness. Oikos 78: 397-405.

26. Anand KJS, Coskun V, Thrivikraman KV, Nemeroff CB, Plotksy PM (1999) Long-term behavioral effects of repetitive pain in neonatal rat pups. Physiology & Behavior 66: 627-637.

27. Gustafsson L, Qvarnstrom A, Sheldon BC (1995) Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. Nature: 311-313.

28. Boag PT (1987) Effects of nestling diet on growth and adult size of zebra finches (Poephila guttata). The Auk 104: 155-166.

29. Sheldon BC, Merila J, Lindgren G, Ellegren H (1998) Gender and environmental sensitivity in nestling collared flycatchers. Ecology 79: 1939-1948.

30. Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P (2003) Environmental variability, life-history covariation and cohort effects in the red-billed chough Pyrrhocorax pyrrhocorax. Journal of Animal Ecology 72: 36-46.

31. Van de Pol M, Bruinzeel LW, Heg D, van der Jeugd HP, Verhulst S (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (Haematopus ostralegus). Journal of Animal Ecology 75: 616-626.

32. Perrins CM, McCleery RH (2001) The effect of fledging mass on the lives of Great Tits Parus major. Ardea 89: 135-142.

33. Haywood S, Perrins CM (1992) Is Clutch Size in Birds Affected by Environmental-Conditions During Growth. Proceedings of the Royal Society of London Series B-Biological Sciences 249: 195-197.

34. Potti J (1999) Maternal effects and the pervasive impact of nestling history on egg size in a passerine bird. Evolution 53: 279-285.

35. Blount JD, Metcalfe NB, Arnold KE, Surai PF, Monaghan P (2006) Effects of neonatal nutrition on adult reproduction in a passerine bird. Ibis 148: 509-514.

36. Kruuk LEB, Clutton-Brock TH, Rose KE, Guinness FE (1999) Early determinants of lifetime reproductive success differ between the sexes in red deer. Proceedings of the Royal Society of London Series B-Biological Sciences 266: 1655-1661.

37. Perrins CM (1965) Population Fluctuations and Clutch-Size in the Great Tit, Parus major L. The Journal of Animal Ecology 34: 601-647.

38. Perrins CM, McCleery RH (1989) Laying Dates and Clutch Size in the Great Tit. Wilson Bulletin 101: 236-253.

39. Ewald PW, Hunt GL, Jr., Warner M (1980) Territory Size in Western Gulls: Importance of Intrusion Pressure, Defense Investments, and Vegetation Structure. Ecology 61: 80-87.

40. Sasvari L (1991) Territoriality in the Great Tit Parus-Major at Low and High-Densities. Bird Behaviour 9: 88-93.

41. Kempenaers B, Dhondt AA (1992) Experimental Test of a Hypothesis Explaining Density Dependent Clutch-Size in Tits Parus-Spp. Ibis 134: 192-194.

42. Gotmark F, Andersson M (2005) Predation by sparrowhawks decreases with increased breeding density in a songbird, the great tit. Oecologia 142: 177-183.

43. Eberhard JR, Ewald PW (1994) Food Availability, Intrusion Pressure and Territory Size - an Experimental-Study of Annas Hummingbirds (Calypte Anna). Behavioral Ecology and Sociobiology 34: 11-18.

44. Camfield AF (2006) Resource value affects territorial defense by Broad-tailed and Rufous hummingbirds. Journal of Field Ornithology 77: 120-125.

45. Perrins CM, McCleery RH (1994) Competition and Egg-Weight in the Great Tit Parus-Major. Ibis 136: 454-456.

46. East ML, Perrins CM (1988) The Effect of Nestboxes on Breeding Populations of Birds in Broadleaved Temperate Woodlands. Ibis 130: 393-401.

47. Perrins CM (1979) British Tits. London: Collins.

48. Gosler AG (1993) The Great Tit. London: Paul Hamlyn.

49. Svensson L (1994.) Identification guide to European Passerines. Stockholm: Svensson.

50. Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends in Ecology & Evolution 16: 254-260.

51. McCleery RH, Perrins CM (1998)... temperature and egg-laying trends. Nature 391: 30-31.

52. Gibson CWD (1988) The distribution of ancient woodland plant species among areas of different history in Wytham Woods, Oxfordshire. In: Kirky KJ, Wright, F. J., editor. Woodland Conservation and research in the caly vale of Oxfordshire and Buckingham. No. 15 ed: Nature Conservancy Council.

53. Riddington R, Gosler AG (1995) Differences in Reproductive Success and Parental Qualities between Habitats in the Great Tit Parus-Major. Ibis 137: 371-378.

54. Wilkin TA, Garant D, Gosler A, Sheldon BC (2006) Density effects on life-history traits in a wild population of the great tit Parus major: analyses of long-term data with GIS techniques. Journal of Animal Ecology 75: 604-615.

55. Gibb JA (1950) The breeding biology of Great and Blue Titmice. Ibis 92: 507-539.

56. Gibb JA, Betts MM (1963) Food and Food Supply of Nestling Tits (Paridae) in Breckland Pine. Journal of Animal Ecology 32: 489-553.

57. VSN Intl (2005) Genstat, Version 7.2. Oxford: VSN International Ltd.

Tables

Table 1. Correlation matrix of environmental factors between (shaded) and within (open) natal and breeding locations of great tits at Wytham woods (n = 2146). Figures in bold indicate correlation coefficients between the same variables measured at nestbox of birth and nestbox of first breeding. Significance is indicated by $*P <$ 0.05, $**P > 0.01$ and $***P < 0.001$. See text for definitions of variables.

	Altitude	Edge	Oaks	Habitat	Territory	Natal Altitude	Natal Edge	Natal Oaks	Natal Habitat	Natal Territory
Altitude	1.00									
Edge	0.199 ***	1.00								
Oaks	0.070 **	0.219 ***	1.00							
Habitat	-0.206 ***	-0.014 N.S.	0.042 *	1.00						
Territory	0.343 ***	0.293 ***	0.509 ***	-0.271 ***	1.00					
Natal Altitude	**0.175 *** **	0.046 *	0.041 *	-0.066 ***	0.073 ***	1.00				
Natal Edge	0.074 **	**0.114 *** **	0.112 ***	0.001 N.S.	0.099 ***	0.236 ***	1.00			
Natal Oaks	0.052 *	0.073 ***	**0.169 *** **	0.010 N.S.	0.166 ***	0.087 ***	0.243 ***	1.00		
Natal Habitat	-0.079 ***	0.032 N.S.	-0.004 N.S.	**0.111 *** **	-0.026 N.S.	-0.162 ***	-0.008 N.S.	0.055 *	1.00	
Natal territory	0.140 ***	0.100 ***	0.154 ***	-0.042 *	**0.213 *** **	0.364 ***	0.327 ***	0.503 ***	-0.265 ***	1.00

Table 2. Variance component estimates (± standard errors) for four great tit life-history traits, obtained from Linear Mixed Models performed on a long-term (41 year) dataset. Asterisks denote significance at *** <0.001, ** < 0.01, * <0.05.

	Random effects					
Trait	Year	Natal year	Nestbox	Natal nestbox	Female i.d.	Residual
Lay-date	44.18 (±10.03) ***	0.49 (±0.31) N.S.	2.76 (±0.59) ***	1.15 (±0.51) *	2.92 (±1.02) **	39.64 (±1.23) ***
Clutch size	0.374 (±0.093) ***	0.065 (±0.029) *	0.135 (±0.029) ***	0.024 (±0.029) N.S.	0.934 (±0.071) ***	1.558 (±0.054) ***
Egg mass	0.000495 (±0.000153) **	-0.000029 (±0.000062) N.S.	0.000366 (±0.000178) *	0.000629 (±0.00025) *	0.007828 (±0.000504) ***	0.0078 (±0.000335) ***
Fledgling mass	19.9 (±10.03) ***	0.4 (±0.31) N.S.	7.9 (±0.59) ***	1 (±0.51) N.S.	24.2 (±1.02) ***	137.6 (±5.1) ***

Table 3. Results from linear mixed models explaining variation in great tit lay-date, clutch size, egg mass and fledgling mass. Data were restricted to the first year in which females was recorded breeding, models included female identity, year of breeding and year of birth as random effects and were constructed in two stages. First, models were formed by backward stepwise removal of variables relating to breeding environments (non bold factors). Then, any environmental variable retained in the model was measured at the natal nestbox and included in the same model (bold). This approach allowed the simultaneous analyses of the effects of breeding and natal environments on the life-histories of 2703 female great tits breeding over a 41 year period.

Dependent/Independent Factor	**Wald χ^2**	**d.f.**	**Effect / (s.e.)**		**P**
Lay-date					
Spring temperature	71.26	1	*-0.08486*	*0.010053*	<0.001
Altitude (m)	45.38	1	0.03290	0.004884	<0.001
Edge proximity	20.49	1	-0.005490	0.0012127	<0.001
Oaks	17.48	1	-0.03926	0.009392	<0.001
Female age	17.31	1	-0.9884	0.23758	<0.001
Habitat type	36.13	3			<0.001
Natal habitat type	**5.05**	**3**			**0.168**
Natal altitude	**1.04**	**1**	**-0.004936**	**0.0048294**	**0.307**
Natal oaks	**0.77**	**1**	**-0.007625**	**0.0086757**	**0.379**
Natal edge proximity	**0.11**	**1**	**-0.0003930**	**0.00119367**	**0.742**
Clutch size					
Lay-date	446.62	1	*-0.06681*	*0.003161*	<0.001
Female age	28.76	1	0.1189	0.02216	<0.001
Edge proximity	17.73	1	0.0009651	0.00022917	<0.001
Territory size (max 2 ha)	9.09	1	0.1470	0.04875	0.003
Oaks	7.47	1	0.005617	0.0020551	0.006
Natal territory size (max 2 ha)	**2.74**	**1**	**0.09244**	**0.055888**	**0.098**
Natal oaks	**1.84**	**1**	**0.002784**	**0.0020548**	**0.175**
Natal edge proximity	**0.17**	**1**	**-0.0001010**	**0.00024260**	**0.677**
Egg mass					
Lay-date	28.67	1	0.002115	0.0003949	<0.001
Edge proximity	16.17	1	-0.00009810	0.000024396	<0.001
Altitude (m)	4.69	1	0.0002360	0.00010897	0.03
Natal edge proximity	**4.04**	**1**	-0.00004810	0.000023938	**0.044**
Natal altitude	**0.33**	**1**	*0.00006130*	*0.000107213*	**0.567**
Fledgling mass					
Clutch size	72.73	1	-1.310	0.1536	<0.001
Lay-date	60.26	1	-0.2982	0.03841	<0.001
Altitude (m)	38	1	-0.05957	0.009664	<0.001
Egg mass	24.05	1	*8.670*	*1.7678*	<0.001
Oaks	12.13	1	0.06794	0.019510	<0.001
Territory size (max 2 ha)	5.84	1	1.168	0.4837	0.016
Natal Oaks	**2.18**	**1**	-0.02639	0.017896	**0.14**
Natal Altitude	**2.05**	**1**	0.01351	0.009435	**0.152**
Natal territory size (max 2 ha)	**0.25**	**1**	0.2528	0.50152	**0.614**

Table 4. Results from a Linear mixed model explaining clutch size variation for 4336 great tit breeding attempts monitored between 1965 and 2005. Clutch size decreases seasonally but increases with age, and several environmental predictors. Also, for a given female, clutch size increases with the quality of her rearing conditions, measured here by the mean reproductive success in her year of birth. Female identity (n = 2757) and year of breeding (n = 41) were included as random effects.

Dependent/Independent Factor	**Wald χ^2**	**d.f.**	**Effect / (s.e.)**		**P**
Clutch size					
Lay-date	450.35	*1*	*-0.06636*	*0.003127*	<0.001
Female age	29.27	1	0.1181	0.02182	<0.001
Edge proximity	18.76	1	0.0009723	0.00022451	<0.001
Territory size (ha)	10.72	1	0.00001575	0.000004812	0.001
Oaks	9.36	1	0.006172	0.0020176	0.002
Mean recruitment in birth year	*7.51*	*1*	*0.2930*	*0.10695*	*0.006*

Figures

Figure 1. The distribution of natal dispersal distances, measured as the distance between a nestbox of birth and the first breeding nestbox, for 2722 male (median = 538 m) and 2703 female (median = 793 m) wild great tits born between 1959 and 2004 and breeding between 1965 and 2005.

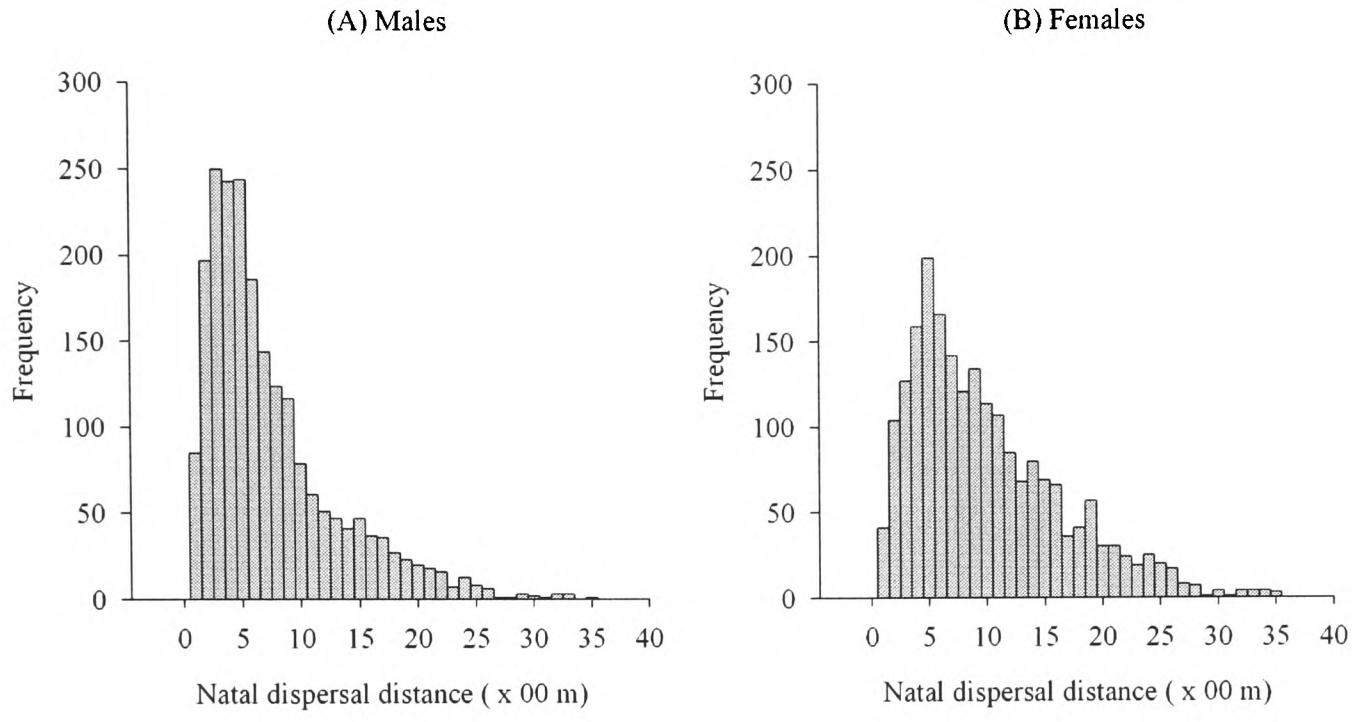


Figure 2 The percentage of variation in four great tit life-history traits explained by 5 random effects and the unexplained variation between observations. Asterisks denote significance at *** <0.001, ** < 0.01, * <0.05.

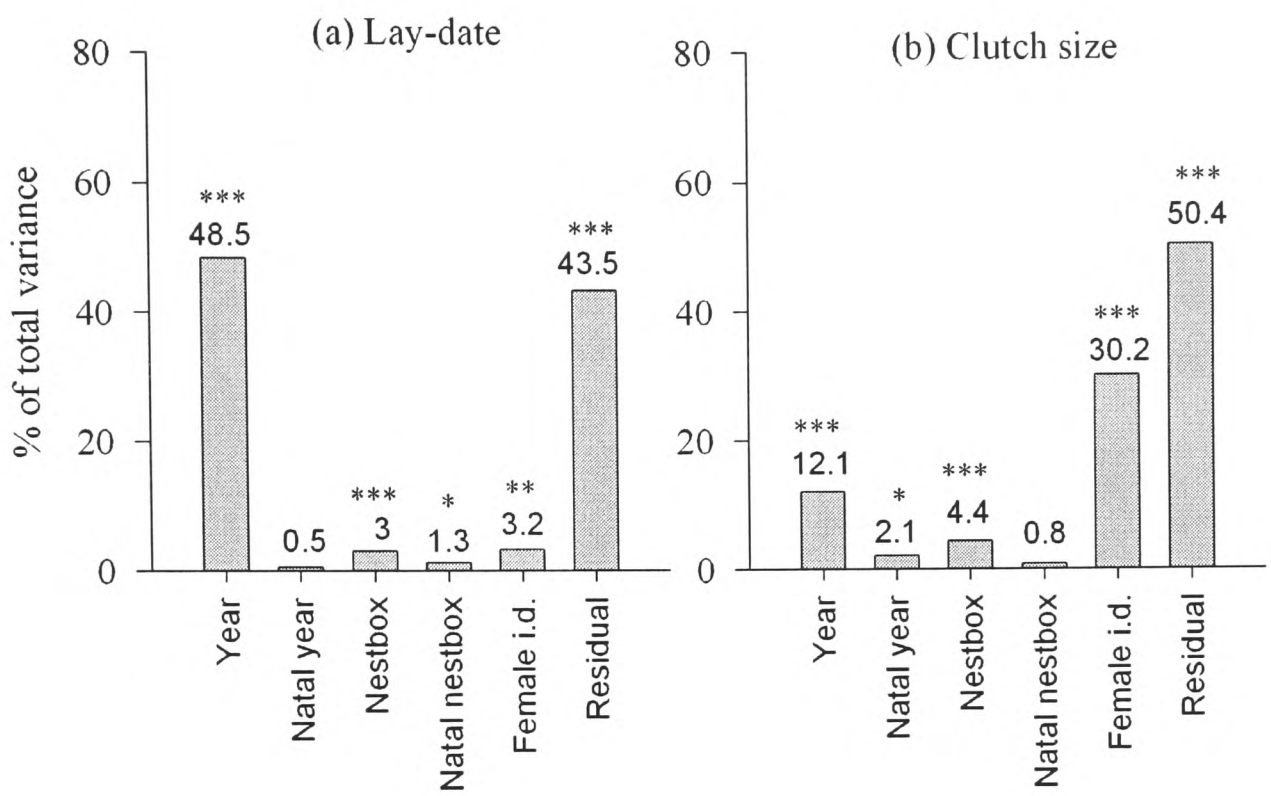


Figure 3. Results from four linear mixed models explaining variation in great tit lay-date (a-c), clutch size (d-f), egg mass (g, h), fledgling mass (i, k). Closed circles and bold lines, indicate strong relationships between the life-history trait and the breeding environment where it was measured. Open circles and dotted lines, however show little, if any association between the life-history trait and individual's natal environment. Functions are fitted to mean values, data are restricted to first breeding attempts and models control for the female's year of birth and the year of breeding as random effects (Table 3).

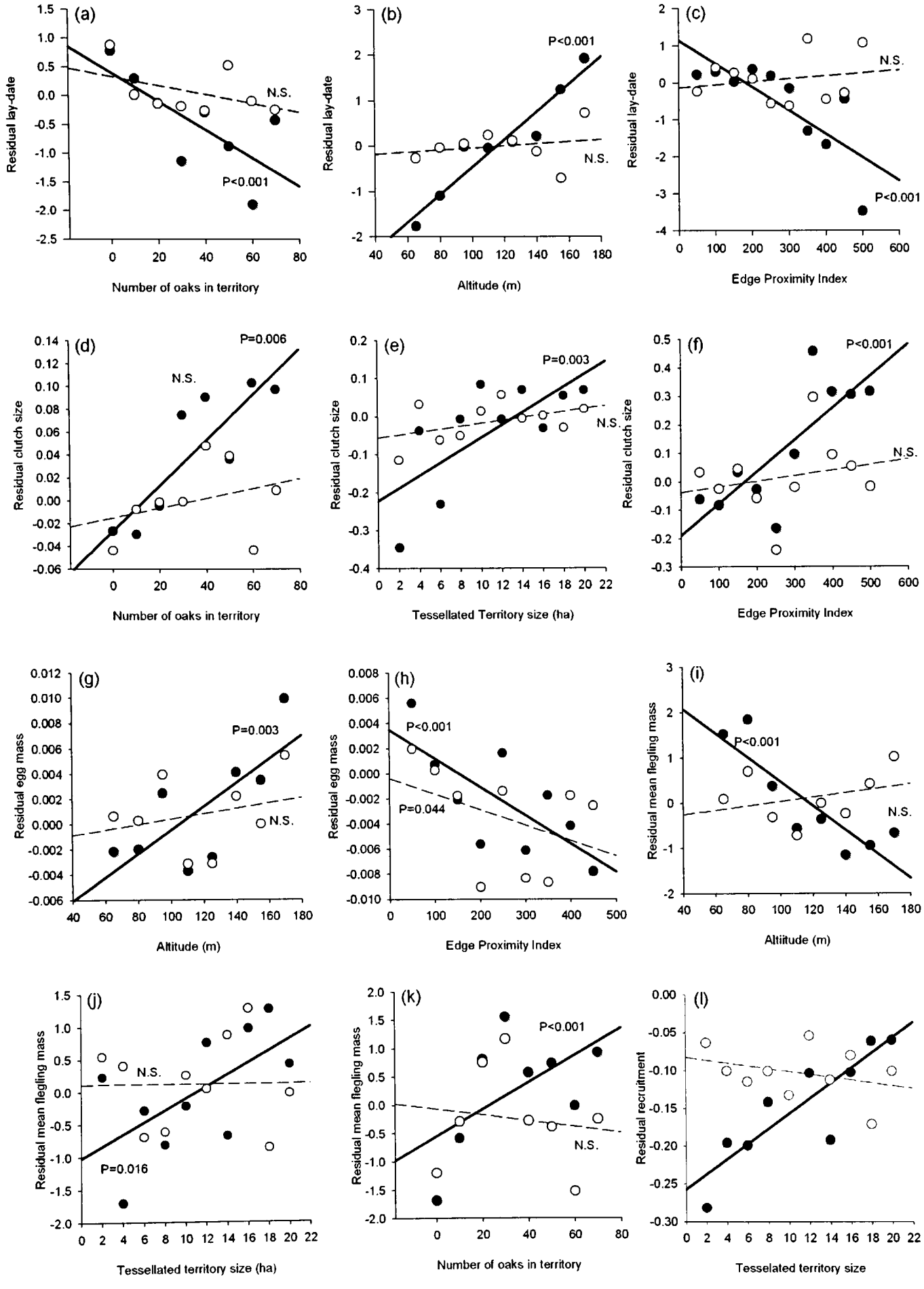
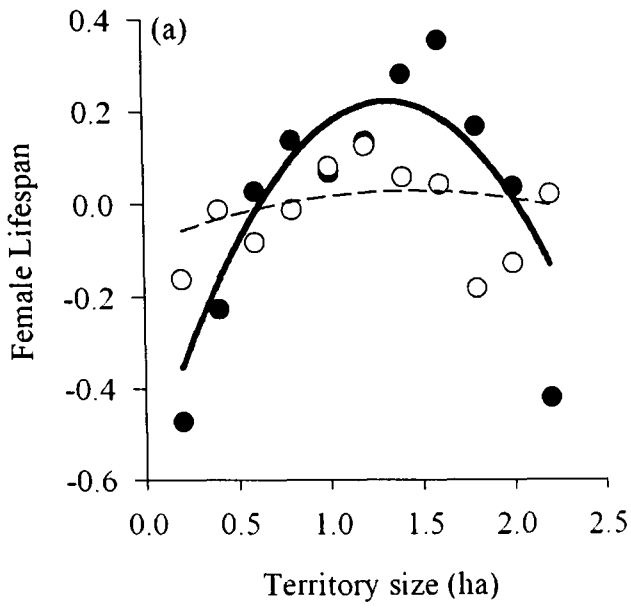
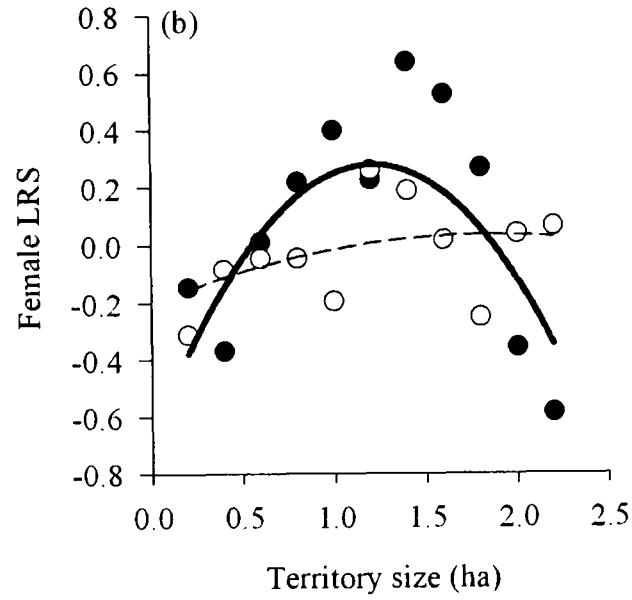
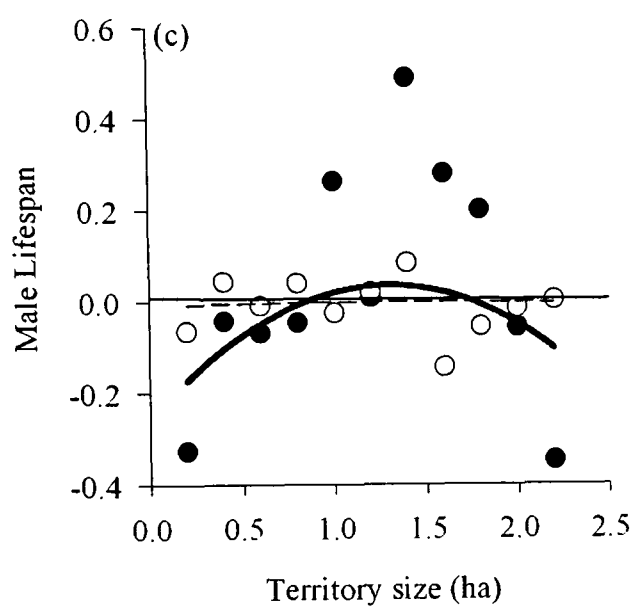
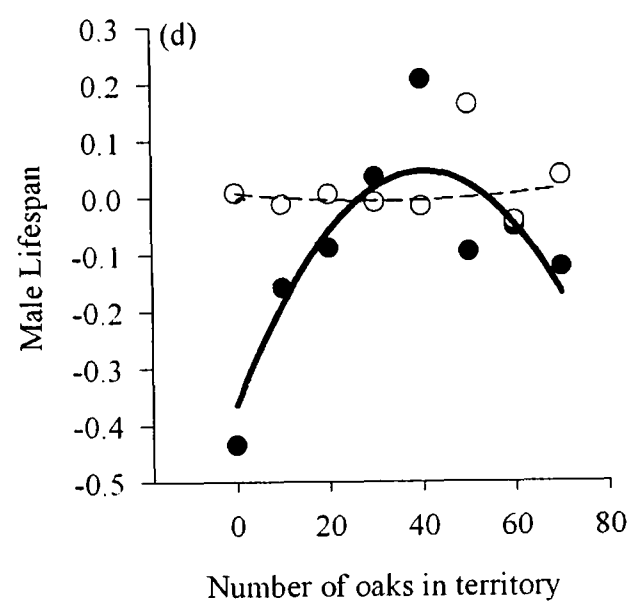

(a)
Residual lay-date
N.S.
P<0.001
Number of oaks in territory
(b)
Residual lay-date
P<0.001
N.S.
Altitude (m)
(c)
Residual lay-date
N.S.
P<0.001
Edge Proximity Index
(d)
Residual clutch size
P=0.006
N.S.
Number of oaks in territory
(e)
Residual clutch size
P=0.003
N.S.
Tessellated Territory size (ha)
(f)
Residual clutch size
P<0.001
N.S.
Edge Proximity Index
(g)
Residual egg mass
P=0.003
N.S.
Altitude (m)
(h)
Residual egg mass
P<0.001
P=0.044
Edge Proximity Index
(i)
Residual mean flegling mass
P<0.001
N.S.
Altiitude (m)
(j)
Residual mean flegling mass
N.S.
P=0.016
Tessellated territory size (ha)
(k)
Residual mean flegling mass
P<0.001
N.S.
Number of oaks in territory
(l)
Residual recruitment
Tesselated territory size

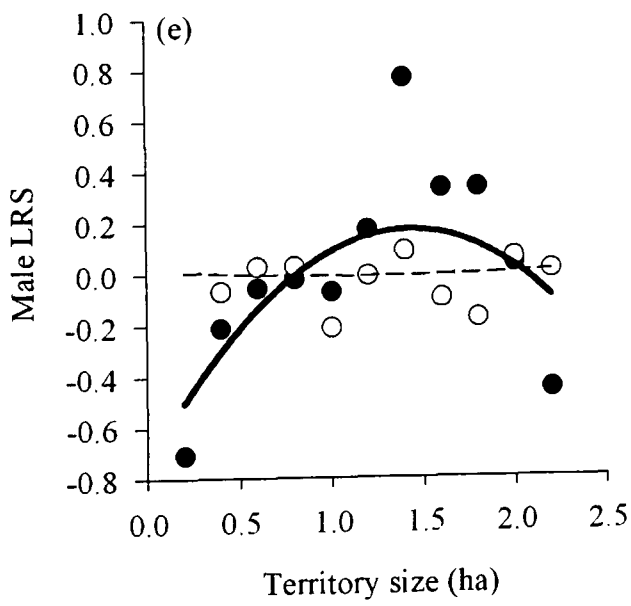
Figure 4. Results from four linear nixed models explaining variation in female lifespan (a) and LRS (b), and male lifespan (c, d) and LRS (e, f). Closed circles and bold lines indicate strong quadratic relationships between the life-history trait and the breeding environment where it was measured. Open circles and dotted lines, however, show little, if any association between the life-history trait and individual's natal environment. Functions are fitted to mean values and models control for female identity, year of breeding and year of birth as random effects. Note the costs associated with very low density and very oak rich territories, see text for explanations.


(a)
Female Lifespan
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.0
0.5
1.0
1.5
2.0
2.5
Territory size (ha)


(b)
Female LRS
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
0.0
0.5
1.0
1.5
2.0
2.5
Territory size (ha)


(c)
Male Lifespan
0.6
0.4
0.2
0.0
-0.2
-0.4
0.0
0.5
1.0
1.5
2.0
2.5
Territory size (ha)


(d)
Male Lifespan
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
0
20
40
60
80
Number of oaks in territory


(e)
Male LRS
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
0.0
0.5
1.0
1.5
2.0
2.5
Territory size (ha)

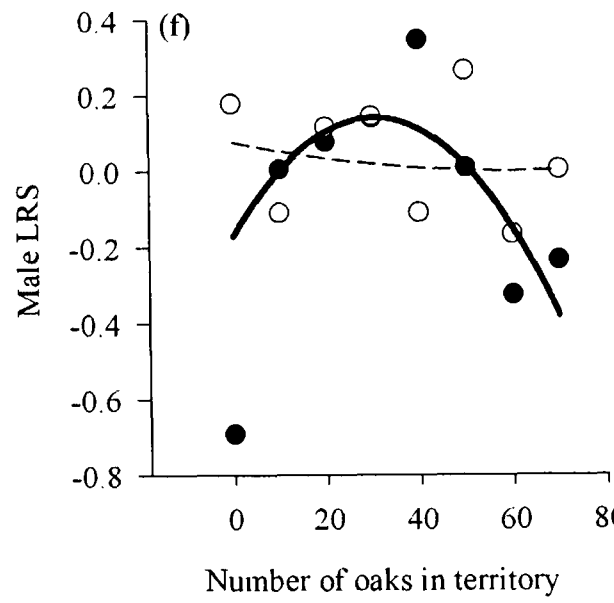
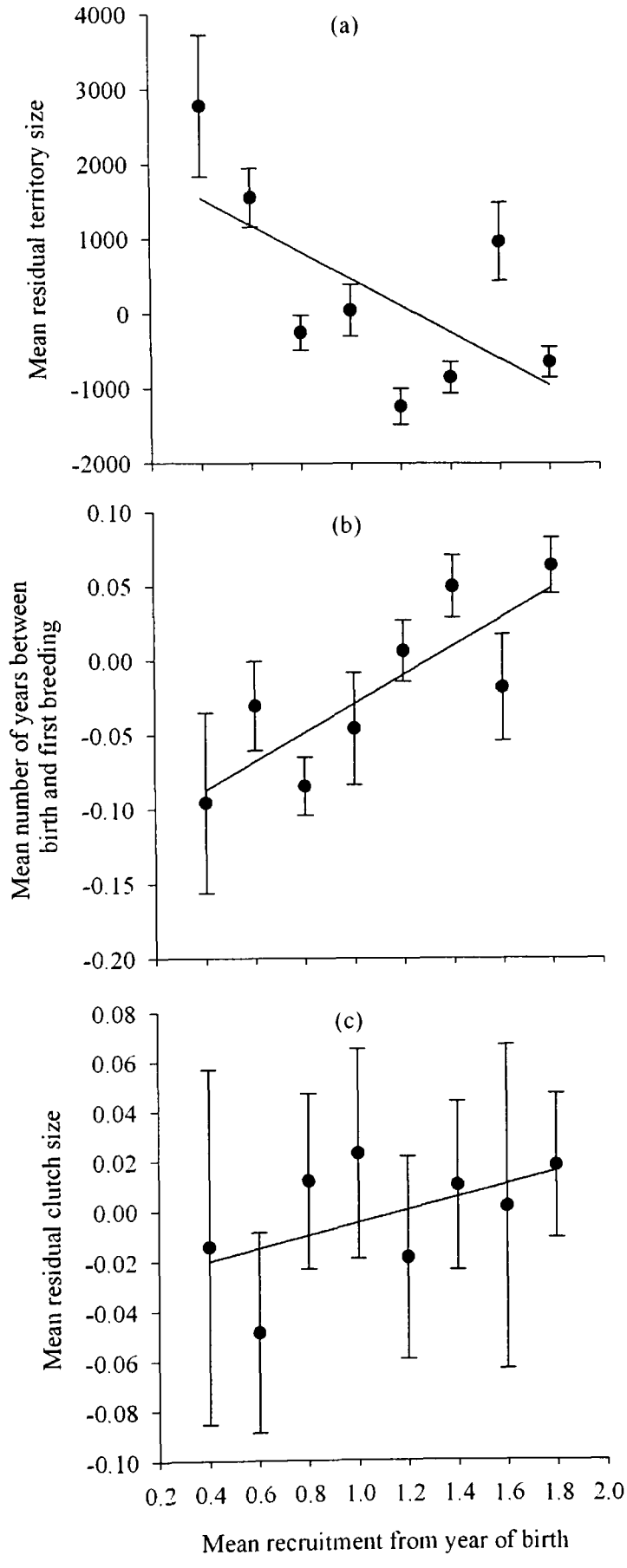

(f)
Male LRS
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
0
20
40
60
80
Number of oaks in territory

Figure 5. Relationships between the mean reproductive success in an female's year of birth and (a) her subsequent tessellated territory size as an inverse measure of breeding density and (b) the number of years between her year of birth and year of first breeding. These suggest that females born in 'good' years may suffer from density dependent constraints later in life. However, a weak but significant positive relationship exists between the mean reproductive success in an individual's year of birth, and her subsequent clutch size (c), when controlling for density.



Chapter 7: Discussion

7.1 Aims

The aim of the current work was identify environmental sources of life-history variation within a wild population of the great tit at Wytham Woods, UK. Most previous work on the life-history variation of woodland passerines has failed to account for potentially confounding sources of life-history variation and fine-scale environmental heterogeneity. The current work aimed to model environmental variation at the scale of individual territories within a single patch of woodland and to apply these data to explain life-history variation in a long-term (41 year) dataset. This approach, combined with detailed information on marked individuals, allows the separation of environmental sources of individual variation from intrinsic differences between individuals and examination of variation within the lifetime of individuals. Such analyses, although correlational, can be used to infer causation between environmental and life-history variation, as they determine whether, within the life-time of an individual, changes in the environment are mirrored by changes life-histories, in the expected direction. I also aimed to exploit the unique opportunity to simultaneously analyse the effects of breeding and natal environments on life-history variation for a large sample of individuals. Thus, the combination of within-habitat and within-individual analyses renders the current approach a useful tool for explaining life-history variation.

7.2 Outcomes

The current work shows that fine-scale variation in breeding density, altitude, woodland edge proximity, soil calcium, oak tree availability and habitat type had consistent and pervasive effects on life-history variation between and within individual great tits. In contrast, we found no long-lasting effects of natal

environments on the subsequent life-histories of recruited individuals. I will discuss some of the interesting points arising from these findings, some of the limitations, and some further directions in the work, below.

Breeding density

Density-dependent reproduction is a commonly observed phenomenon in wild populations. At the population level, possible explanations include increased predation and a higher proportion of low quality territories and/or individuals in high density years. To separate these effects it is necessary to measure density at the level of the individual and control for differences between individuals and habitats. The size of Thiessen polygons formed around occupied nestboxes was used as an individual measure of density and was a strong predictor of breeding date, clutch size, fledgling mass and reproductive success, independently of differences between individuals and habitats (Chapter 2). Moreover, by analysing changes within females, we showed that within the lifetime of an individual female, any change in her local density was mirrored by a change in the life-history variables in the expected direction. Hence, this work supports the hypothesis of a causal link between breeding density and great tit reproduction.

Despite the close relationship between the size of Thiessen polygons and great tit life-histories, no test has yet been made of the extent to which the tessellated territories accurately represent real great tit territories. However, I have made preliminary arrangements to collaborate with Dr. Christiaan Both of the University of Groningen who is in possession of a large number of great tit territory maps. These territories were obtained by forming minimum convex polygons which enclosed all the locations

at which a given pair were observed in territorial disputes, singing or foraging with chattering. My plan at the time of writing is to digitize the locations of the Dutch nestboxes, the outline of their mapped territories and the perimeter of the woodlands into a GIS layer and to extract the exact size of the mapped territories. It will then be possible to form Thiessen polygons around the nestboxes and to compare their size with the size of the actual territories mapped by Dr.Both. By using a program such as Ranges 6.0 (), I also hope that it will be possible to also compare the degree of overlap between the Thiessen polygons and the actual territories, with that expected by chance. It will also be an interesting exercise to employ the capping technique to the Dutch Thiessen polygons to establish whether a proportion of their population is also unconstrained by density (as is the case in Wytham; see Chapter 2) and if so, at what polygon size do the constraints become apparent.

Effects confounded with density

An additional benefit of accurately measuring density at the level of the individual is that it allows the independent analysis of other environmental sources of life-history variation that are usually confounded by density. For example the life-histories and the breeding density of woodland passerines often both vary with distance to woodland edges. Therefore, reduced reproduction at woodland edges may be due to higher breeding density rather than edge proximity *per se*. Observed edge effects may also be due to a higher proportion of immigrants, (which breed later than residents), young or low quality individuals at edges. In Chapter 3, I used the Thiessen polygons formed in Chapter 2 to control for density and used field data to control for potential 'quality' differences between individuals, thus allowing the independent analysis of life-history variation with edge distance. Results confirmed higher breeding density

and a higher proportion of immigrant individuals near the woodland edge. Independently of the potential effects of density and immigration great tit life-histories were also found to vary with edge distance; 'edge' birds laid smaller clutches of larger eggs later in the season, compared with 'interior' birds. This is the first time that edge effects have been documented for the Wytham population of great tits, probably because of the opposing and stronger effect of altitude on reproduction; edge areas at Wytham are at predominantly low altitude, where birds breed earlier and at a higher rate. It was therefore necessary to accurately control for differences in density, altitude and between individuals before it was possible to identify independent and direct edge effects.

The direct effect of edges on great tit reproduction suggests that there was some property of edge habitats that rendered them less favourable places to breed. One possibility is that edges may be more exposed to the wind and the sun, making them microclimatically more variable and less suitable as breeding habitats than interior areas. This hypothesis is consistent with the finding of larger eggs at the edge, which are less prone to temperature fluctuations than smaller eggs due to a lower surface to volume ratio. Previous studies have reported a positive correlation between ambient temperature and egg size (Magrath 1992; Barkowska et al 2003); however it may be the variation in temperature that induces an increase in egg mass. An experimental approach is necessary to test this hypothesis. One approach would be to alternate between heating and cooling a nestbox for short periods throughout the breeding season. This may imitate the temperature fluctuations associated with edge environments and may invoke a change in life-histories comparable to those observed at edges.

Another explanation for edge effects on great tit reproduction is that, due to the more exposed environment, invertebrates populations may be at lower densities, and therefore less available as food, at the woodland edge. Preliminary data from a recent masters project which I supervised suggests that prey availability may vary with distance from the edge, as 1st year great tits breeding at the woodland edge provisioned a lower proportion of caterpillars to their nestlings than those in the interior (Fig. 1; L. King & T. Wilkin, unpublished data). It may therefore follow that other invertebrates, including those that are important during egg laying, may also persist at lower densities at woodland edges which would result in variation in great tit lay-date and clutch size with edge distance.

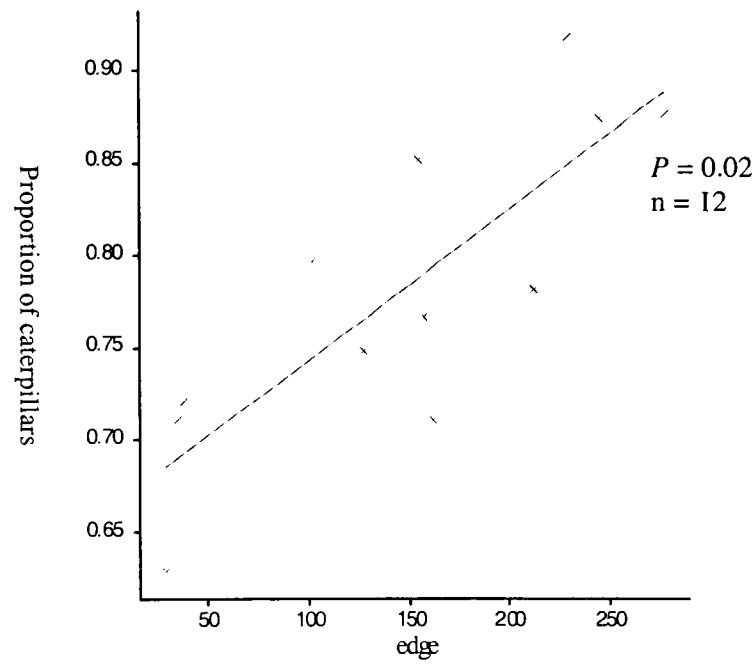


Figure 1. The proportion of caterpillars provisioned to nestlings by first year birds, as a function of the distance between the nest and woodland edge. That young birds provision less caterpillars at the woodland edge provides some evidence of reduced food availability at edges which would explain the correlation between variation in great tit life histories with edge distance. (L. King & T. Wilkin, unpublished data)

Resource availability

As well as measuring density, the Thiessen polygons formed in Chapter 2 also provided a means of describing environmental variation at individual and biologically meaningful scales. For example, the preferred food of the great tit is found at highest densities on oak trees (Foss & Rieske 2003; Summerville et al 2003), which leads to the prediction that great tit reproduction may improve with oak availability local to the nest site. However, selecting the most appropriate scale at which to measure local oak availability is problematic. One approach is to use a certain radius from each breeding location. However, this leads to the oak trees being shared between territories, as each tree could potentially be counted for several nestboxes; further, the suitability of the radius will vary between areas and with density. Thus, the Thiessen polygons that were used to measure density throughout this thesis were also used to measure oak tree availability at the scale of the individual territory. Using this approach oak trees were mutually exclusive between nestboxes and were counted at individual scales determined by the location of neighbouring conspecifics; oaks were counted close to, and far from, nests at high and low density, respectively. Results showed that birds breeding in oak rich territories laid larger clutches earlier in the season and produced heavier nestlings than birds in oak poor territories, reflecting higher quality habitats due to more food availability (Chapter 4). Moreover, including oak availability in life-history models greatly reduced or eliminated the effect of density in explaining life-history variation, suggesting that a proportion of the life-history variation attributed to density effects in this species is probably due to reduced oak, or food, availability at high densities. Thus, this chapter demonstrates the efficacy of using the distribution of a specific vegetation type as a surrogate for a patchily distributed food source, and that resource availability explains a proportion of

density dependent reproduction in a wild population. Further work to test the effects of oak availability on great tit reproduction could include comparing variation in nestling diet with oak availability. A recent masters project that I supervised used nestbox cameras to observe the proportion of caterpillars provisioned to nestlings and showed that birds breeding in nestboxes with an oak tree nearby provisioned a higher proportion of caterpillars than birds breeding far from an oak tree ($t_{(19)} = -3.07$, $P = 0.007$), when controlling for the distance between the nestbox and the woodland edge (Fig. 2). However, we found no effect of the number of oak trees within Thiessen polygons formed around each occupied nestbox on the proportion of caterpillar brought to the nest ($t_{(19)} = 1.28$, $P = 0.215$). The small sample size and unusually wet conditions during the observation period renders the study inconclusive but a useful preliminary indication of the possible effects of oak availability on nestling and presumably also adult nutrition.

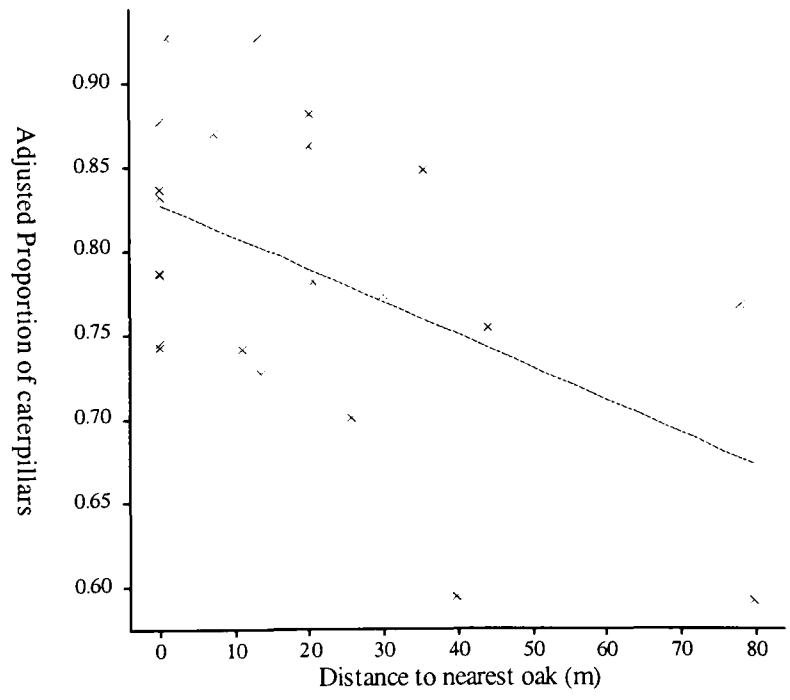


Figure 2 The proportion of caterpillars provisioned to nestlings as a function of the distance between the nest and the nearest oak tree. Where distance = 0 the nestbox was on an oak tree. This model also controls for the distance between the nestbox and the woodland edge.

Chapters 2 and 4 provide correlational evidence to suggest that conspecific density and oak tree abundance independently affect great tit life-histories. However, as with any correlational study, there exists the possibility that there is another unmeasured and confounding difference contributing to effects. Hence, although analyses in this thesis have controlled for broad scale habitat types and differences between individuals there remains the possibility that another force is at work which results in the observed correlations between density and oak availability, and great tit life-histories. An experimental test, with *a priori* predictions, is therefore needed to complement the correlational observations described above.

Possible directions for future research include observing life-history changes while simultaneously manipulating of breeding density and oak availability. As previous work has shown that breeding density is easily controlled by the density of the nestboxes provided, manipulations could be achieved by placing nestboxes in blocks differing in density in a factorial design with oak tree distribution. This approach should enable the separation of the effects of density from the effects of oak availability, as high and low density breeding attempts will be monitored in areas of both high and low oak tree densities. Funding has been secured for myself and other members of the EGI to conduct such a study in Bagley wood near Oxford during 2007-09, where I hope that some of these questions will be addressed.

Chapter 4 also ignores an additional level of complexity in the relationship between oak tree availability and great tit life-histories. To successfully raise a brood of nestlings, great tits must synchronise their period of maximum food demand with a brief window of peak caterpillar abundance each year (Noordwijk et al 1995). Results from the current work show that great tit reproductive success is highest in

oak rich areas (Chapter 4), but output is likely to be considerably reduced if the nestling period, specifically when the brood are at day 10 (hatchday=1), does not coincide with the caterpillar peak (Seki & Takano 1998). That the most successful individuals in a population are those that best time their breeding, is a commonly observed phenomenon among woodland passerines (Nager & Van noordwijk 1995; Tremblay et al 2003). However, it remains unclear which cues are important for the timing of breeding, particularly as the decision of when to breed is, in the case of great tits, made around 30 days before the period of maximum demand (8-10 days of egg laying, 13-15 days of incubation, 10 days of nestling growth), not including the time it takes for a female to reach breeding condition prior to egg-laying (Perrins 1991). As there is considerable variation in the mean lay-date between years, it is unlikely that day length is an important cue. However, temperature is often found to be a strong predictor of oak leaf bud burst, the caterpillar peak and the mean lay-date of woodland birds. Clearly a pervasive role of temperature in the temporal ecology of woodland communities is of considerable interest, especially in light of global climate change, as there is the potential for severe temporal disruption between trophic levels depending on their response temperature changes (Buse et al 1999; Visser & Holleman 2001). For example, Cresswell & McCleery (2003) found that Wytham great tits are now breeding earlier relative to the food peak, compared with previous years and that they maintain synchronicity by significantly increasing their incubation period. However, several important questions remain unanswered. For example, anecdotal evidence suggests that oak trees at the bottom of Wytham hill, where it is warmer, leaf around one week before those at the summit (altitudinal difference = 100m). However, little is known about the scale at which bud burst and presumably caterpillar peaks vary spatially, or the scale at which such variation is apparent. It

is also not known to what extent the caterpillar peak can be predicted from the bud-burst of the oak tress, and to what degree the bud burst can be predicted from environmental factors such as altitude or topography. Life-history traits, particularly fledgling mass are likely to vary with caterpillar abundance at low levels of abundance, but at high abundance we might expect the effect to disappear as a saturation point is reached (Tremblay et al 2003). Little is known about the threshold level, the scale at which it operates or the way in which it might interact with synchrony. Other ecological questions relate to the effects of, and the way in which individual great tits may compensate for, lack of synchrony. Presumably, it will result in a decline in the quality of the nestling's diet. However, we do not know how or at which spatial scale individuals perceive synchrony or at what point in the decline of nestling diet, adults are prepared to switch from local asynchronous foraging to inter-territorial foraging trips to seek more synchronous food patches (Tremblay et al 2005).

I hope that the oak model presented in Chapter 4 will provide a firm foundation on which to base future investigations in this area. Possible approaches include an intensive monitoring of caterpillars and oak bud burst in a given area of Wytham, which would enable spatial and temporal variation in these variables to be related to similar variation in the lay-date of local birds. Data collected over a number of years would improve our understanding of the repeatability and predictability of oak tree bud burst and the implications of its spatial and temporal variation for caterpillars and for the life-histories of great tits. It would also be possible to conduct a study on foraging ecology by using nestbox cameras to identify the proportion of caterpillars brought to the nestlings, and PiT tags to measure provisioning rate for males and

females. This would provide a better understanding of the way in which individuals compensate for asynchronicity and the consequences for nestling diet, growth and recruitment probability. In 2006 a DPhil student joined the EGI with the view to looking at some of these questions.

Natal environments

That breeding success varies among environments has been shown by the current work. However, several recent studies on long-lived birds and mammals have observed persistent long-term effects of natal environments on the life-histories of recruited offspring (Reid et al 2003; Van de Pol et al 2006). To establish if similar effects exist in populations of great tits, Chapter 6 simultaneously analysed the effects of breeding and natal environments on the life-histories of 2703 female and 2722 male great tits for which both natal and breeding environments were known. As predicted from analyses in previous chapters, life-histories were strongly influenced by several components of the breeding environment. However, independently of these effects, no relationship was found between an individual's natal environment and any life-history trait. The exception was that of egg mass which was weakly related to the number of oak trees local to the natal nest. However, this effect, which was presumably due to high quality early nutrition, was weaker than the effects of the current (breeding) environment on egg mass. A possible explanation for the general absence of long-term effects of rearing environments is that the great tit is a short lived species with high post-fledgling and post-breeding mortally. Thus any character that improves short term survival or breeding success is likely to be selected for, over any character that conveys a smaller, long lasting benefit later in life. Therefore long-term effects of natal environments cannot be assumed as it depends on the life-history

of the species. For example, a study of Oystercatchers, which are long lived (13 – 17 years) with high recruitment (31-41%), showed that the adult pre-breeding survival of individuals raised in high quality territories was 1.6 times higher, and their life-time reproductive success was 2.2 times higher than individuals reared in low quality territories (Van de Pol et al 2006). Also a study on red deer showed that high density and cold springs in the year of birth reduced the several components of long-term fitness in females (Kruuk et al 1999). The current work is the first to examine life-history variation with rearing conditions in a short-lived passerine with high mortality and shows that the presence of long-terms effects depends on the life-history stages of the species.

The natal environment may, however, have long-term *indirect* effects on the life-histories of offspring that were undetected in the current analyses. For example, natal environments have been shown in the current work to affect the mass, or condition of fledglings (Chapter 3; Appendix 3), which is in turn associated with recruitment probability. It is therefore conceivable that nestlings in better condition at fledging are more fecund later in life. To test this, a Linear mixed model was performed to investigate the relationship between a female's mass as a nestling at day 15 (hatchday=1) and her subsequent clutch size. The identity of the female, the year of breeding and the year of birth were included as random effects to control for non-independence within these subgroups. The mass of the female when breeding was also included as a covariate so that the effect of her mass as a nestling on clutch size could be separated from the effect of her mass as an adult. Adult mass varies with the size of the bird (here estimated from wing length), with the time of day and with the age of the brood so these factors were also included as covariates. Results from the

model are shown in Table 1, which suggest that the mass of a female nestling is a significant and positive predictor of her subsequent clutch size independently of her adult mass (Fig. 3). This finding agrees with that of Haywood & Perrins (1992) who performed a similar analysis but did not control for the weight of the female when she was an adult, and Potti (1999) who reported a relationship between the volume of eggs produced by a female and her body condition when she was a nestling. The negative effect of adult mass on clutch-size may be due to the fact that adults are trapped at nestboxes after day 7, so females that laid a large clutch may be lighter as they are using more energy reserves to provision a large brood. This result suggests that early environments may have an indirect effect on the life-histories of great tits by determining nestling mass which in turn influences life-histories. It is my intention to complete a full set of analyses, first detailing the relationship between the mass of an individual as a nestling and as an adult. This relationship is of interest to me as some recent studies have reported negative effects of poor early nutrition followed by period of compensatory growth (Alvarez & Metcalfe 2005; Fisher et al 2006; Johnsson & Bohlin 2006). A cost associated with compensatory growth may mean that females of similar mass for their size, will not have similar life-histories as it will depend on the difference between their mass as an adult and as a nestling. Secondly, I hope to analyse the effects of nestling mass on subsequent life-history variation, including longevity and lifetime reproductive success for females and males. I also hope to gain an understanding of the causal pathway between natal habitat quality, nestling mass and subsequent life-history variation by using analytical techniques such as path analyses.

Table 1. Results from a Linear mixed model explaining variation in clutch size for 3247 great tit breeding attempts. Model contains environmental effects discussed elsewhere, and also the mass of each female when provisioning her brood (BS) and when a nestling at day 15 (NS). The positive relationship between nestling mass and subsequent clutch size **(bold)** shows that females that are heavy as nestlings go on to lay larger clutches. Conversely, females that have laid large clutches weigh less than females with smaller clutches, but this is probably due to the extra energy invested in egg production and provisioning a larger brood. Model contains female identity, year of breeding and year of birth as random effects.

Fixed effect	**Wald**	**P**	**effect**
Lay-date	300.84	<0.001	-
Female age	32.8	<0.001	+
Female breeding mass (BS)	32.34	<0.001	-
Female nestling mass (NS)	**23.85**	**<0.001**	**+**
Age of brood when weighed (BS)	12.35	<0.001	-
Edge distance	11.19	<0.001	+
Territory size	10.39	0.001	+
Number of oaks in territory	4	0.045	+
Time of day when weighed (BS)	1.83	0.176	+
Wing length when weighed (BS)	0.39	0.531	+

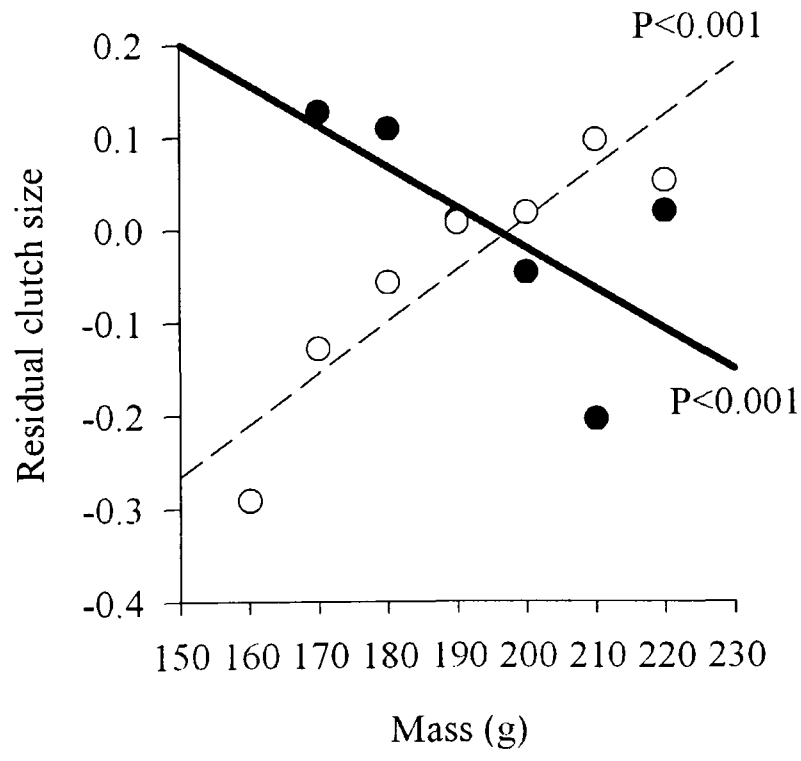


Figure 3. The mass of breeding female great tits plotted against their mean residual clutch size (closed circles), showing that lighter females are associated with larger clutches. Also shows the mass of females as nestlings, plotted against their subsequent clutch sizes (open circles). This result suggests that heavy female nestlings lay larger clutches once recruited to the breeding population. See Table 1.

Soil calcium

Calcium is a necessary nutrient for birds during egg production and for nestlings forming skeletal structures (Graveland & Drent 1997; Dawson & Bidwell 2005). Several studies have shown that birds in woodlands with calcium poor soils breed at a lesser rate than those on calcium rich soils (Tilgar et al 1999). However, studies between geologically distinct areas are invariably confounded by habitat. Supplementation experiments also show variation in life-histories between supplemented and control areas (Mand & Tilgar 2003). However, measuring calcium availability in the wild is problematic, as it is unclear how far birds travel to acquire calcium (Reynolds et al 2004). Chapter 5 was the first attempt to link fine-scale variation in soil calcium with life-history variation in a wild passerine population. Several methods of assigning calcium availability to a given nestbox were explored and results showed that soil calcium local to each nestbox was a strong predictor of clutch size, fledgling mass and recruitment, independent of the density (Chapter 2) and edge effects (Chapter 3). This is of considerable interest as it shows a direct link between soil calcium and avian reproduction and contributes towards our understanding of life-history variation. Furthermore, the relationship is of considerable interest for the conservation of forest passerines, as studies have shown that soil acidification renders calcium less available in the environment (Graveland et al 1994; Ramsay & Houston 1999). If calcium has been gradually leeched from the soil in Wytham over the last 40 years, as it has at other sites (Graveland & vanderWal 1996), we would expect a negative correlation between soil calcium sampled in the same locations in both 1974 and 1991 and we would expect the effect of soil calcium on life-histories to have increased over time. To test the former I correlated the two soil surveys and found that although highly correlated ($r_{148} = 0.891$, $P < 0.0001$),

calcium availability had declined, and especially in the most calcium-rich soils. I tested the latter prediction by performing a Linear mixed model to explain variation in great tit clutch size. As in Chapter 3, female identity was included as a random effect, while year, in this case, was included as continuous and fixed effect. I tested for an interaction between year and calcium in effecting clutch size, as a significant result would suggest that the effect of calcium on clutch size depends on the year of breeding. The interaction was indeed significant and the strength of the effect of local soil calcium on the clutch-size is indeed increasing (Ca * year $\chi^2_{(1)} = 17.14$, $P < 0.001$), while clutch-size itself is declining ($\chi^2_{(1)} = 121.12$, $P < 0.001$). These results suggest that the soil calcium at Wytham is reducing and that relationship between soil calcium and clutch size is stronger now than it has been in the past. This result is the first evidence of calcium limitation on in a highly calcic, as opposed to a base poor environment and shows how acid rain can leech essential micronutrients from the environment with important consequences for forest communities.

Scale

Chapter 2 introduced a novel method for conducting analyses over a range of spatial scales. Thiessen polygons formed around nestboxes occupied by great tits were used as an individual measure of breeding density. However, as the polygons covered all the available habitat, in areas of low density extremely large and biologically meaningless polygons were formed. This led to the prediction that there existed a threshold level of polygon size below which polygons resembled natural territories. In an attempt to identify the threshold level that separated biologically meaningful from meaningless polygons, territory polygons were capped through a range of maxima and used in separate models explaining life-history variation. Results showed that

applying a maximum territory size of 2ha maximized the density signal in life-history models, suggesting that birds breeding in polygons larger than 2ha in size were unconstrained by density. This figure is thus an estimation of the maximum territory size in the current population and agrees with several field based studies of territory size (Krebs 1971; Both et al 2000). The result suggests that Thiessem polygons of more than 2ha in size are not entirely contiguous with all their neighbours, rather there are interstices between the territories; no man's land that is not in the territory of any bird. This could be tested by placing a caged male great tit in different locations between birds breeding at low density and observing which males, if man, respond aggressively towards the intruder. This approach would establish the territory boundaries between, what our results suggest are, biologically meaningless polygons.

This result is important for several reasons. Firstly, it sheds light on the way in which individuals use space within the environment. Secondly, it shows that the systematic capping of Thiessen polygons in life-history models can help to identify which individuals within a population are unconstrained by density. This level of understanding could not have been achieved by using traditional methods of measuring density, such as the number of pairs per hectare. Finally, the method has applications beyond the current system as the focal points could also be, for example, the locations of mice in an experimental maze or even cultures of bacteria in a Petri dish.

Chapter 5 also conducted analyses at several spatial scales. First, buffers were formed around each nestbox and the highest soil calcium level within each buffer was used as a life-history predictor for birds that bred in the focal nestbox. Buffers of different

sizes were formed through a range of radii and the maximum soil calcium level at each scale was used as a predictor in separate life-history models. The scale at which the correlation between soil calcium and life-histories was maximised was *c.*300m of each nestbox. This scale may be indicative of the average distance that females were travelling to acquire calcium during periods of high demand. This novel technique highlights the way in which buffers of differing radius can be used to quantify the scale at which individuals are affected by resources within their environment. At Wytham the average territory is just over one hectare in size (Chapter 2) and so if females are travelling 300m to acquire calcium this suggests that they are crossing at least two territories during these foraging trips. This interpretation may seem unlikely. However several studies have have observed great tits travelling similar distances to acquire food. For example, Gibbs & Betts (1965) frequently recorded great tits that were breeding in pine plantations travelling 350-500m from the nest to acquire food for the nestlings, Kluijver (1951) reported similar distances travelled by great tits to reach feeding platforms, and several studies have concluded that great tits are not confined to their territories while provisioning young (Gibb 1956).

The scale of calcium acquisition in the wild could be tested by combining a calcium supplementation program with the use of PiT tag loggers. The design could be as follows. A sample of female great tits could be caught in mist nests in later winter and fitted with PiT tags rings. Then a grid of calcium feeders equipped with PiT tag loggers could be placed around Wytham immediately prior to, and for the duration of the breeding season, such that they record the identity of any individual visiting the feeder. When adults are trapped at nestboxes towards the end of the breeding season the distance between nestboxes and calcium feeders visited by females will be

calculated. My prediction is that birds breeding in areas of high soil calcium will travel only short distances, if at all, to obtain calcium supplements, while birds breeding in calcium poor areas will be prepared to travel further to meet their calcium demands.

Conclusion

Overall, this study demonstrates the efficacy of GIS approaches to modelling environmental variation and applying it to explaining life-history variation in long-term databases. The work has introduced several new methods of measuring environmental variation The results of this study suggest a pervasive role of fine-scale variation in breeding, but not natal environments in determining the life-histories of individual great tits.

References

Barkowska, M., J. Pinowski, and B. Pinowska. 2003. The effect of trends in ambient temperature on egg volume in the Tree Sparrow Passer montanus. Acta Ornithologica **38**:5-13.

Both, C., Tinbergen, J.M., & Visser, M.E. (2000) Adaptive density dependence of avian clutch size. *Ecology*, **81**, 3391-3403.

Buse, A., Dury, S.J., Woodburn, R.J.W., Perrins, C.M., & Good, J.E.G. (1999) Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology*, **13**, 74-82.

Dawson, R.D. & Bidwell, M.T. (2005) Dietary calcium limits size and growth of nestling tree swallows Tachycineta bicolor in a non-acidified landscape. *Journal of Avian Biology*, **36**, 127-134.

Foss, L.K. & Rieske, L.K. (2003) Species-specific differences in oak foliage affect preference and performance of gypsy moth caterpillars. *Entomologia Experimentalis Et Applicata*, **108**, 87-93.

Fisher, M.O., Nager, R.G., & Monaghan, P. (2006) Compensatory growth impairs adult cognitive performance. *Plos Biology*, **4**, 1462-14

Gibb, J.A. (1956) Territory in the genus Parus. *Ibis*, **98**, 420-429.

Gibb, J.A. & Betts, M.M. (1963) Food and Food Supply of Nestling Tits (Paridae) in Breckland Pine. *Journal of Animal Ecology*, **32**, 489-553.

Graveland, J., Vanderwal, R., Vanbalen, J.H., & Vannoordwijk, A.J. (1994) Poor Reproduction in Forest Passerines from Decline of Snail Abundance on Acidified Soils. *Nature*, **368**, 446-448.

Graveland, J. & vander Wal, R. (1996) Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. *Oecologia*, **105**, 351-360

Graveland, J. & Drent, R.H. (1997) Calcium availability limits breeding success of passerines on poor soils. *Journal of Animal Ecology*, **66**, 279-288.

Haywood, S. & Perrins, C.M. (1992) Is Clutch Size in Birds Affected by Environmental-Conditions During Growth. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **249**, 195-197.

Johnsson, J.I. & Bohlin, T. (2006) The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1281-1286.

Krebs, J.R. (1971) Territory and breeding density in the great tit, Parus major. *Ecology*, **52**, 1-22.

Kruuk, L.E.B., Clutton-Brock, T.H., Rose, K.E., & Guinness, F.E. (1999) Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1655-1661.

Magrath, R. D. 1992. Seasonal-Changes in Egg-Mass within and among Cluthes of Birds - General Explanations and a Field-Study of the Blackbird Turdus-Merula. Ibis **134**:171-179.

Mand, R. & Tilgar, V. (2003) Does supplementary calcium reduce the cost of reproduction in the Pied Flycatcher Ficedula hypoleuca ? *Ibis*, **145**, 67-77.

Noordwijk, A. J. V., R. H. McCleery, and C. M. Perrins. 1995. Selection for the Timing of Great Tit Breeding in Relation to Caterpillar Growth and Temperature. Journal of Animal Ecology **64**:451-458.

Perrins, C.M. (1991) Tits and their caterpillar food supply. *Ibis*, **133**, 49-54.

Potti, J. (1999) Maternal effects and the pervasive impact of nestling history on egg size in a passerine bird. *Evolution*, **53**, 279-285.

Ramsay, S.L. & Houston, D.C. (1999) Do acid rain and calcium supply limit eggshell formation for blue tits (Parus caeruleus) in the UK? *Journal of Zoology*, **247**, 121-125.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I., & Monaghan, P. (2003) Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, **72**, 36-46.

Reynolds, S.J., Mand, R., & Tilgar, V. (2004) Calcium supplementation of breeding birds: directions for future research. *Ibis*, **146**, 601-614.

Summerville, K.S., Crist, T.O., Kahn, J.K., & Gering, J.C. (2003) Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. *Ecological Entomology* **28**, 747-757

Tilgar, V., Mand, R., & Leivits, A. (1999) Effect of calcium availability and habitat quality on reproduction in Pied Flycatcher Ficedula hypoleuca and Great Tit Paras major. *Journal of Avian Biology*, **30**, 383-3

Tremblay, I., Thomas, D.W., Lambrechts, M.M., Blondel, J., & Perret, P. (2003) Variation in Blue Tit breeding performance across gradients in habitat richness. *Ecology*, **84**, 3033-3043.

Tremblay, I., Thomas, D., Blondel, J., Perret, P., & Lambrechts, M.M. (2005) The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits Parus caeruleus. *Ibis*, **147**, 17-24.

Van de Pol, M., Bruinzeel, L.W., Heg, D., van der Jeugd, H.P., & Verhulst, S. (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **75**, 616-626.

Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 289-294.