Quantifying biases in a long-term field study: finding Wytham's missing tits



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"At times our own light goes out and is rekindled by a spark from another person"

-Albert Schweitzer

I would like to express deep gratitude to the following people, all of whom helped light the flame within me. First, my Supervisor Ben Sheldon for having faith in me for many years both as an employee and as a student, for his steady guidance and for always encouraging me to reach my full potential. My hero Colin, my adopted mentor Tobias, and my comrades in the social network team: Damien, Lucy, Ross, Antica, Brecht, Camilla, Reinder, Josh, and Bernhard. And of course, the EGI entourage: Andy, Chrissy P, Stu, Shelly, Cam, Amy, Corentin, John Quinn, Irem. Great geologist Kathleen. My favourite companions for helping me keep perspective; Matilda, the Australian associates Shannon and Cam; USA counterparts Rurik and Lynn, and Magnificent Mariners Jack, Charles, Dickie, Grif and Zoe. My officemate/housemate/bestie all-rounder extraordinaire Nicole Milligan. Finally Mum, Dad and my amazing co supervisor Ella Cole, without whom this undoubtedly would not have been possible. Words truly cannot express how grateful I am to you, for your unwavering support and for being more like flame throwers.

This thesis is dedicated to my fantastic husband Danny Price, who knows more about the Wytham tit population than any astrophysicist should; for leading me to, and leading me out of Oxford.

Abstract

Quantifying biases in a long-term field study: finding Wytham's missing tits

Inferences drawn from long-term field studies of animals are vulnerable to biases in observability of different classes of individuals, which may lead to biases affecting ecological and evolutionary conclusions. Advancing statistical techniques are providing increasing evidence that individuals missing from population samples show consistent individual differences, although any resulting biases remain poorly understood. In this thesis, I investigate how biases can occur in estimating individual variation in reproductive success and residence behaviour within a natural great tit (*Parus major*) population. The primary objective of this thesis is to investigate whether individuals that are detected using standard sampling techniques are representative of the entire population. To do so, I use RFID technology to sample more completely across seasons, investigating individual detectability throughout the year.

I show that females that fail early in their breeding attempt, before they are identified under standard sampling protocols, are more likely to be young and immigrants from outside the study population and breeding in poorer quality habitats. As a consequence, estimates of the fitness of immigrants versus residents, age effects on fitness, and the age and immigration-specific effects of habitat quality derived from standard survey methods are likely to be underestimates. I show that the high failure rate amongst immigrant females may be a result of late arrival time to the breeding grounds. These findings imply that costs of dispersal might impact on reproductive success. Moreover, I show that the exclusion of early nest failures from analyses can lead to underestimates in the effects of dispersal on reproductive success; as a consequence, current work concluding that immigrants have lower fitness than residents is likely to underestimate the size of this effect.

This thesis also provides some of the first baseline data tracking the presence or absence of passerines within a population across seasons. Our findings suggest that certain individuals are less likely to be detected as a function of their phenotype. We identify sex as a predictor of failure to be detected breeding, with males less likely to be detected. We also find that the likelihood of detection during successive breeding and winter surveys is repeatable across years. This adds to a gathering body of knowledge suggesting that sampling at certain times of the year selects for specific phenotypes. This thesis represents the first large-scale investigation of individuals that remain undetected in a long-term great tit population study, demonstrating that more attention should be given to the question of whether methods for surveying natural populations introduce systematic biases that influence conclusions about ecological and evolutionary processes.

Author Contributions

Main contributors

Lindall R. Kidd had independent intellectual input into all aspects of the thesis, collected night scanning field data, and assisted in collecting two years of breeding and winter field data. Also analysed data, wrote drafts and incorporated co-authors comments to produce final versions of all chapters.

Ben C. Sheldon (Supervisor and co-author of all data chapters) had intellectual input, gave guidance in research techniques, and advice on analysis methods and writing. Conceived overall project and secured funding and gave detailed comments on all drafts.

Ella F. Cole (Co-supervisor and co-author of all data chapters) had intellectual input, gave guidance in research techniques and advice on analysis methods, contributed toward the collection of night scanning data for Chapter 2 and gave detailed comments on all drafts.

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CHAPTER 1

GENERAL INTRODUCTION



"Variations, however slight and from whatever cause proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to other organic beings and to their physical conditions of life, will tend to the preservation of such individuals"

-Darwin

General Introduction

1.1 Long-term datasets in ecology and evolution

The biological field of ecology deals with the multitude of ways in which organisms interact with and in turn influence their surroundings. The field is barely a century old: the first scientific society dealing with ecology, The British Ecological Society, was founded in 1913; this was followed by the first ecological textbook in 1927 (Elton 1927). Evolutionary ecology lies at the intersection of ecology and evolutionary biology, and approaches the study of ecology in a way that explicitly considers the evolutionary histories of species and the interactions between them (Pianka 2011). This evolutionary approach to ecological questions resulted in a major revolution in biology during the last half century; we now have a strong understanding of biological mechanisms and how they control and constrain the adaptive response of individuals. Direct experimentation is often impractical as many ecological phenomena cannot be manipulated. As such, evolutionary ecologists rely heavily on comparative approaches. The development of evolutionary ecology as a discipline is linked to the accumulation of data on the distribution and abundance of species in space and time (Magurran et al. 2010). For example, through studies of bird populations, Lack (1954; 1966; 1968) showed that reproductive rates are subject to natural selection.

Early ecologists showed great foresight when they began systematic data collection; without these data sets we would have a more limited understanding of the long-term ecological and evolutionary processes that affect populations. Processes affecting populations, such as the demographic processes controlling animal numbers and the evolutionary processes generating adaptation, are difficult to simulate under laboratory conditions because they may act over many years or decades. Furthermore, laboratory or captive conditions can rarely replicate the range of environmental

variation in nature. The need for data extending over adequate periods of time to investigate these processes highlights the importance of long-term datasets of populations, some of which are as old as the field of ecology itself. Long-term population studies accumulate data on the distribution and abundance of species in space and time. The oldest study, the Park Grass Experiment, begun in 1856 in Hertfordshire England and is the longest running ecological experiment in the world (Tilman et al. 1994). Long-term monitoring was extended to other taxa with the Continuous Plankton Recorder beginning in 1925 (Richardson et al. 2006). These data collections were initiated to answer applied questions; however, it was realised that they were useful for investigating temporal patterns not only at the population level, but at other hierarchical levels including genes, communities and ecosystems. For example, data from the Park Grass Experiment have been used to tackle problems ranging from the evolution of adaptation at a local scale, to the link between community composition and climatic perturbation (Silvertown et al. 2006). The ecological value of long term data became clear through these pioneering studies, which are part of a growing number of temporally extended studies forming the basis of a large body of knowledge pertaining to organismal biology.

Currently, there are two main groups of studies of wild animals that track the same population over time: those that focus on population-level description of change, and those that mark, identify, and follow individual animals. Studies at the population level are important for answering questions about the demographic processes that control animal numbers (Lack 1966; Sinclair 1977; Newton 1998). Such studies provide detailed records of population dynamics and are useful for monitoring factors that affect changes in geographical distribution, density and growth. For example, population studies have provided important insights into the effects of human activities on animal populations (Ratcliffe 1970; Darimont et al. 2009; Oro, Jiménez & Curcó 2012) and the effects of climate change on density and reproduction in dif-

ferent organisms (Pounds et al. 2006; Kausrud et al. 2008; Pateman et al. 2012). Nevertheless, longitudinal population studies are limited in their ability to identify the proximate causes of changes in population size. Such proximate causes are better quantified by studies that mark, identify, and follow individual animals.

1.2 Long term data and individual variation

Individual differences are of crucial importance to biology as they afford materials for natural selection to act on (Darwin 1872) and identifying individual variation within natural populations remains a fundamental aim of evolutionary ecology. Data from long-term individual-based studies are able to monitor the development and life history of individually recognisable animals, enabling assessment of the fitness costs and benefits of different traits or breeding strategies. As such, these data offer unique insights into the operation of natural selection and the causes of fluctuations in population size and structure. Long-term studies of individuals extending over three or more decades are available for many populations of vertebrates, including red deer, great tits and chimpanzees (Clutton-Brock & Sheldon 2010b) and provide data that are crucial for exploring evolutionary and ecological hypotheses. There are a multitude of studies that could be used to illustrate this importance. A good example is the examination of the survival costs of reproduction in red deer (*Cervus elaphus*). The red deer population on the Isle of Rum, Scotland, has been studied intensively since 1972 and data from this study now comprise the complete life histories of over 95% of individuals. Calves are caught, weighed, measured and uniquely marked with ear tags for both sexes and collars for females shortly after birth (see Clutton-Brock, Guinness & Albon 1982 for further details). Current reproductive effort of red deer has been shown to reduce survival probability over the coming year, especially in young and old individuals. In contrast, an increase in cumulative reproductive effort, defined as the proportion of year in which a female has bred since sexual maturity, increases

the probability of survival (Moyes et al. 2006). This positive effect on survival of cumulative reproduction is assumed to be generated by differences in individual fitness (Moyes et al. 2006), emphasising the need to account for reproductive history when estimating survival probabilities of animals.

Long-term data not only allow for investigation into population level patterns through cross-sectional analyses, but also allow investigation into within individual processes through longitudinal analyses. For example, age-related declines in breeding success have been shown for a wide range of species through population level analyses (Clutton-Brock 1988; Newton 1989) and long-term studies continue to provide further insight into individual processes such as senescence (see examples within Nussey et al. 2013). We continue to make progress toward a theoretical understanding of population processes through studies of the genetic basis of quantitative traits. These studies provide valuable insights into the evolutionary trade-offs that may contribute to the maintenance of genetic diversity, for example, via sexually-antagonistic effects and maternal effects (see review by Kruuk, Slate & Wilson 2008). Furthermore, individual-based studies provide data that can be used to examine kinship and social relationships, age-related changes in life history parameters and estimates of selection. For a full overview of the uses of such data in ecological and evolutionary studies see reviews by Clutton-Brock and Sheldon (2010a) and Magurran and colleagues (2010).

One of the most fundamental contributions of individual-based studies has been to reveal the extent and causes of variation in breeding success (Clutton-Brock & Sheldon 2010a). For example, studies have shown large differences in individual breeding success, where the majority of recruits to the population are produced by a small proportion of the population; this has implications for population dynamics and the genetic structure of populations (Clutton brock 1988; Newton 1989). The collection of data on individual fitness variation underpins all contributions that long-term population studies have made to the field of ecology and evolution. It is invariably either

the direct aim of monitoring programmes (eg. reproductive rates), or an implicit aim (e.g. in a selection analysis). A key aim of this thesis is to investigate the biases that can occur in estimating individual detectability within natural populations.

1.3 How and when individuals are monitored

Over the years, a huge variety of methods have been developed to monitor wild animal populations (Seber 1982, 1986; Lancia, Nichols & Pollock 1994; Thompson, White & Gowan 1998; Schwartz & Seber 1999; Williams, Nichols & Conroy 2002) with the specific sampling techniques used depending on the biology of the species and the aims of the monitoring programme. Direct observations and indirect methods are two classes of commonly used techniques for sampling wild animal populations. Direct observation is based on counts of observed individuals using techniques such as re-sightings, removal experiments, and transects or plot surveys (see examples presented in Thompson, White & Gowan 1998). Capture-Mark-Recapture (CMR) is a technique used to make inferences from observations of individuals where animals are captured, marked, released, and re-captured many times, resulting in a set of capture histories for every observed animal (Williams, Nichols & Conroy 2002).

In contrast, indirect sampling methods infer reliable estimates of population size through measures where individuals are not detected or counted directly, but through a sign showing that the animal has been in the area. Indirect methods are often referred to as population or abundance indices (Thompson & Fleming 1994) and are particularly useful for rare or elusive species (Mills et al. 2000). Examples of indirect methods include photographic 'capture' (Mace et al. 1994; Karanth et al 2006), ingestion of biomarkers (Garshelis & Visser 1997), responses to audio calls (Smith, Thompson & Perrins 2001; Dorcas et. al 2009) and faecal (Mondol et al. 2009) and track counts (Stephens et al. 2006). Recent advances in genetic profiling allows indirect sampling of populations through the acquisition of samples via hair snags,

faeces, regurgitated pellets, or other tissue (see reviews by Morin & Woodruff 1996 and Mills et al. 2000). Both direct and indirect sampling methods are capable of distinguishing between individuals within a population. In some instances, after an initial capture, an individual can be fitted with a tracking device and 'recaptured' through the transmission of a radio telemetry signal (Millspaugh & Marzluff 2001). Furthermore, individuals can be recognised through indirect techniques such as photographic 'capture' or genetic profiling of tissue samples.

In addition to choosing which sampling method to use, researchers must also decide when to sample populations. Long-term monitoring involves multiple measurements over time, resulting in a collection of site visits (or replicates). This replication is important for addressing temporal variability in the ecological processes of interest, such as population trends (Westcott et al. 2012). Sampling large numbers of individuals throughout the year can be logistically difficult. For example, for many bird and mammal species, outside of the breeding season territoriality breaks down, making it harder to track individuals. Monitoring individuals during the breeding season is the most widely used method in wild animal population studies (see Clutton-Brock & Sheldon 2010a for examples within). In addition to deciding when to sample within years, researchers must consider the aims of the monitoring programme at a broader spatial scale. Many ecological processes fluctuate between years; consequently there may be a need to sample over multiple years. For example, the costs and benefits of different reproductive strategies can be strongly influenced by rare events like droughts or epidemics, so it could be misleading to use data from only one or two seasons to compare their advantages (Clutton-Brock & Sheldon 2010b).

1.4 Incomplete sampling and sampling biases

Broadly, a population consists of a group of organisms of the same species occupying a particular space at a particular time (Krebs 2001). The first step in any monitoring

programme is defining the population to sample. This can be difficult as populations are not closed systems (individuals may leave or enter a given group or area), and may be highly dependent on time and/or spatial scale (for example, flocking behaviour in winter versus territorial behaviour during breeding). Usually measuring the complete population is too expensive or logistically impossible, so the aim of most monitoring programmes must be estimated from a sample (i.e. a subset selected for measurement) of the population of interest (Gitzen et al. 2012). Sample estimates are subject to biases and uncertainty. For instance, sampling individuals at any specific time of year can result in a non-random subset of individuals from the whole population. For instance, consider samples collected during the breeding season, the time at which the majority of long term population studies are undertaken. There are three main reasons why individuals may go undetected in breeding surveys. First, the monitoring scheme (e.g., timing of capture) can result in some breeding attempts being undetected. For example, during nest surveys of birds, individuals associated with these nests are often identified after they have reached a certain stage in their reproductive effort. In many species, some individuals may therefore fail before they can be identified (Heisy & Nordheim 1995). Moreover, early identification of breeders can result in premature desertion of the nest (Kania 1992) which may lead to a trade-off between data collection and interference with the outcome of the breeding attempt. Secondly, some breeding individuals may not be found. For instance, in long-term seabird monitoring surveys, breeding individuals are typically re-sighted at the breeding colony from fixed observation towers (e.g., see Frederiksen & Bregnballe 2000; Tavecchia et al. 2001). Individuals that consistently nest on the side of the colony furthest from the observation tower have a lower likelihood of re-sighting (Prévot-Julliard, Lebreton & Pradel 1998). Finally, some individuals may not attempt to breed at all; many vertebrates may skip breeding in some years to manage their energy budget and trade-off between growth and reproduction. This is a common phenomenon in fish (Brännäs,

Jonsson & Lundqvist 2002), mammals (Solomon & Jaquot 2002; Voight & Streich 2003), reptiles (Bull & Shine 1979) and birds (Newton & Rothery 2001).

The non-breeding component of any population can be hard to quantify. For example, much of the data on the composition of non-breeders within bird populations come from indirect experimental removal of territorial individuals that are replaced by known non-breeders. These experimental removals have now been done on more than 50 species of birds (see review by Newton 1992). Although highly useful, a potential problem with this method is that it only detects individuals that are non-breeding because of competition for territories and not individuals that attempted to breed but fail before they were identified, or those that voluntarily forego reproduction. Furthermore, take-over of territories requires non-breeding individuals to be sufficiently close by to detect recent residencies of breeding sites.

Just as sampling during the breeding season can introduce biases, data collected during the winter may result in biased samples of individuals. The breeding population may not be equivalent to the wintering population. Samples collected in the winter have been shown to differ from those sampled breeding (Bauchau & Van Noordwijk 1995). Furthermore, many studies have shown that monitoring populations during any stage of the annual cycle can result in sampling bias as events during one stage of the annual cycle are likely to influence populations in subsequent stages (Drent 1984; Marra, Hobson & Holmes 1998; Sillet, Holmes & Sherry 2000; Gill et al. 2001).

1.5 Consequences of incomplete sampling and sampling bias

Incomplete detection of individuals is inherent to any wild animal population study and leads to the problem of biased detectability (Royle & Nichols 2003). This problem has long been acknowledged in conservation biology (Manel, Williams & Ormerod 2002), and although it was highlighted by Grafen (1988), the implications of imperfect

detectability for inference in ecological and evolutionary studies have only recently started to receive attention (see review by Nakagawa & Freckleton 2008). This is of particular concern because significant patterns in missing data are often due to underlying biological causes which can lead to systematic biases in data sets. For example, recent studies of behavioural syndromes have revealed that behavioural observations are likely to be missing for shy and inactive individuals (Biro & Digemanse 2009; Garamszegi, Eens & Török 2009). Other biologically significant patterns of missing data arise in detection surveys, where different life history strategies within a species can cause differential capture/observation rates of individuals (Lebreton et al. 1992). For example, detection probabilities of birds are known to vary with sex (Pradel et al. 1997; Tavecchia et al. 2001), age (Pradel et al. 1997; Tavecchia et al. 2001) and breeding status (Cam et al. 2002; Grosbois & Thompson 2005).

The consequences of sampling biases have been highlighted by recent studies showing that the assumption of perfect detectability can lead to flawed inferences. Individual differences in detection rates has been shown to bias survival estimates downwards if not accounted for (Pradel et al. 1997; Prévot-Julliard et al. 1998). Gimenez and colleagues (2008) reanalysed the findings of two long-term datasets and found that the assumption of perfect detectability led to flawed inferences. The authors investigated the relationship between body mass and survival of weavers (see Covas et al. 2002) and the rate of senescence of roe deer (see Gaillard et al. 1993). They first conducted 'naïve' analyses which assumed that all individuals were detected equally. After this, they adopted a mark-recapture modelling approach that explicitly accounted for the detection process, ensuring unbiased demographic parameter estimates (Lebreton et al. 1992). By comparing the results of the naive and the mark-recapture modelling analyses, they showed that sampling biases affect previous conclusions, altering estimates of the form of natural selection acting on the body mass of birds and underestimating the rate of senescence in roe deer (Gimenez et al. 2008). Similarly,

Hadfield (2008) found that estimates of evolutionary parameters such as heritability and selection are biased if estimated without accounting for observations missing due to premature death in relation to the trait of interest.

1.6 Overcoming sampling biases

Both methodological and statistical approaches have been developed to minimise sampling biases. Much attention has been given to improving sampling methods and the experimental design used to obtain data (Gitzen et al. 2012). In an attempt to overcome biases, researchers try to use spatially and temporally random sampling regimes and minimize selectivity for individuals with certain behavioural or physical characteristics (MacKenzie & Kendall 2002). Additionally, there is increasing emphasis on using multiple sampling techniques simultaneously, in order to account for heterogeneity in catchability in order to decrease biased samples (Crespin et al. 2008). For example, in one study investigating the behaviour of Palearctic migrant passerines in West Africa, birds were mist netted and marked with colour rings. The colour rings were re-sighted and these data were combined with mark-recapture data from mist netting for analyses (Salewski, Thoma & Schaub 2007).

Increasingly, the importance of handling missing data is beginning to be addressed in ecology and evolutionary biology with an emphasis on statistical methods to account for data that may be missing from samples (Hadfield 2008; Nakagawa & Freckleton 2011). The most commonly used of these are multi-state CMR models which account for the proportion of the marked individuals that are alive but may not be recaptured at a particular sampling occasion. These models account for variation in recapture probabilities and the possibility that recapture and survival rates differ for individuals in different states. They have been extensively used for the study of survival, recruitment and population growth (Williams, Nichols & Conroy 2002). For a full review of the contribution of CMR techniques to studies of evolution and ecology

see Cam (2009). Despite the best efforts to obtain random samples, the extent to which results are influenced by missing data through non-random sampling is still an area of uncertainty (Little & Rubin 2002; Horton & Kleinman 2007; McKnight, McKnight & Figueredo 2007). It is suggested that researchers should, at the very least, investigate whether missing data represent a non-random sample of their full data (Nakagawa & Freckleton 2008).

1.7 Great tits as a model species for population monitoring

The first studies which monitored the development and life histories of individually recognisable animals were of great tits (*Parus major*) established in the Netherlands in 1912, and the UK in 1947 (see Kluijver 1951; Perrins 1965). To this day, the great tit remains one of the world's best studied avian species and nestbox populations of these species are still a widely used study system in evolutionary and behavioural ecology (e.g. Charmantier et al. 2008; Korsten et al. 2013; Reed et al. 2013). These small songbirds have a broad geographic range, extending from Europe through to Asia and Northern Africa (Gosler 1993). They are secondary cavity nesters which readily take to nest boxes, preferentially selecting them over natural cavities as breeding sites (Perrins 1965). Therefore, when an excess of nest boxes are provided, almost the entire breeding population can easily be monitored (Perrins 1979). This allows detailed collection of data on reproductive strategies for large numbers of recognisable individuals. Furthermore, it is also possible to follow individuals over their entire reproductive lifespan because they are territorial and have limited breeding dispersal (Harvey, Greenwood & Perrins 1979). Due to their general tolerance of nest-monitoring disturbances, they have become a model species for studies of life history variation in the wild.

As with any study species, recapture probabilities may differ for different classes of individuals. For example, recapture probabilities for female great tits have been

shown to decline with age (Bouwhuis et al. 2012). Many inferences based on population studies of great tits are formed from censuring only the breeding population and there is the unstated assumption that other populations are equivalent. Moreover, the censusing of nest boxes means that these study systems are prone to the aforementioned problems in detectability associated with monitoring only breeding individuals. Although experimental removal has been done in breeding great tit populations (see Krebs 1982), the non-breeding component of the population remains hard to quantify. This is of particular concern as previous studies have shown that non-breeding populations consist of different samples of birds than those detected during the breeding season. For example, some individuals leave the study site in winter to return the next spring for breeding (Drent 1984). Moreover, winter transients may also be over represented in data collected during the non-breeding period (Bauchau & Van Noordwijk 1995). As such, there is reason to believe that population censuses carried out either during the breeding or non-breeding season systematically miss particular classes of individuals. Despite great tits being a model species for evolutionary and ecological studies, little work addressing detectability biases in these populations exists. It is this examination of detectability biases that forms the major concern of this thesis.

1.8 Main aim and study system

Although the general statistical problem of missing data has been well studied, issues associated with this problem in field monitoring programs have not (Gitzen et al. 2012). It is this knowledge gap that I am aiming to address in this thesis which explores detectability biases in a great tit population. The body of work contained in this thesis is based on data collected as part of a long-term study of breeding great tits in Wytham woods, a mixed deciduous 388ha woodland in Oxfordshire, UK (51 ° 46', 1 ° 19'W). Since 2007, as part of studies into the social ecology in this

population (Aplin et al. 2012; Farine, Garroway & Sheldon 2012), individuals have been fitted with a Passive Integrated Transponder (PIT) and it is estimated that 90% of the total population is now tagged (see Aplin et al. 2013) (Fig 1.1). PIT tags are a form of Radio Frequency Identification (RFID) transponder, which allow automatic identification through the contactless transfer of data and an increasing number of ornithological studies are utilising them (see review by Bonter & Bridge 2011). This RFID technology provides us the unique opportunity to more completely sample individuals throughout the year: we can now detect if an individual is present at higher resolutions than previously possible. The Wytham population is sampled in the breeding season and winter, using a range of different methods, all of which may potentially lead to biases in sampling. In this thesis, I use RFID technology to complement traditional mark-recapture methods to look directly at recapture detection rates without reliance on detectability models.

The Wytham study of breeding great tits was founded by David Lack in 1947, and is one of the longest running studies of individually recognisable animals in the world. Breeding birds have undergone continuous nest monitoring since the study was initiated in the east part of the woods. By 1965, over 1000 nest boxes were erected throughout the remainder of the woods. Typically, between 300-450 of these are used annually by breeding great tits during the spring (April – June). Great tits begin laying in April and May and breeding is timed so that the nestling period coincides with the brief peak in caterpillar abundance (Perrins 1991). After hatching, both parents provision the chicks until they fledge approximately 20 days later. Typically, one brood is attempted per season; second broods are usually attempted only after an initial failure (Perrins 1979). All chicks are ringed with individually numbered metal rings when they are 15 days old, in accordance with the British Trust for Ornithology's (BTO) ringing scheme. Parents are trapped at the nest using spring traps and identified by their ring number, or fitted with a new ring if they are an immigrant

to the study site. Individuals are aged and sexed based on plumage characteristics (Svensson 1992). The Wytham population is characterized by high levels of connectivity with the surrounding areas resulting in relatively high immigration rates. About half of the breeding birds originate from outside the woods (Bouwhuis et al. 2010). All unringed birds trapped in Wytham are assumed to be immigrants to the woods (i.e not fledged from a Wytham nest box) because the proportion of chicks born in natural cavities is documented to be low (Harvey, Greenwood & Perrins 1979; Perrins 1979). More recently, recapture histories of breeding females between 1960-2009 show similar recapture probabilities (83%) to those estimated using mark-recapture modelling methods (Bouwhuis et al. 2012). This suggests either that there are very few birds in natural cavities, or that if there are birds in natural cavities, very few of them switch between nest boxes and natural cavities to breed.

In this population, PIT tags were used to identify breeding individuals in one of two ways. Nest boxes were visited at night and scanned with a hand-held PIT tag reader whilst the female was roosting inside; great tits roost on the nest during the laying and incubating period (Gosler 1993). Additionally, customized faceplates with an antenna embedded within (Manufactured by Dorset Identification, Netherlands) were used in place of the original faceplate on nest boxes to identify adults provisioning their chicks in the 2012 breeding season.

Over the winter, juveniles and adults aggregate into flocks. During this period, individuals are monitored by mist netting or remote identification using PIT tag-based data logging systems. An intensive period of mist netting occurs over winter, targeting individuals immigrating into the study site. In addition to this, seed feeders are fitted with RFID antennae in place of the perch for both access holes (manufactured by Francis Scientific Instruments Ltd, UK). When an individual takes seed from the feeder, its identity is transmitted by the tag and stored with a timestamp by the attached data logger. Therefore, each datum consists of identity, location, date and

time of detection. Between 2007- 2009, 16 feeders were randomly rotated between 65 sites every four days (Fig 1.2). Feeders were constantly open and logged continuously during this period. In the winter of 2010/11 the logging system was extended so that a feeder remained in place at each of the 65 sites for the duration of the winter (Fig 1.2).

1.9 Thesis aims and overview

The main objective of this work is to quantify and explore detectability biases in the monitoring of the great tit population at Wytham woods. This work aims to identify and describe individuals that are undetected through the traditional sampling protocol. It is particularly important to identify any patterns amongst individuals that are currently undetected; finding these "missing tits" will provide more complete data on population demographics. The Wytham tit study is representative of other longitudinal studies of tit populations; it follows that the findings reported here will have implications for other studies throughout the Northern hemisphere. In addition, any findings relating to biases in estimates of dispersal and age effects will be more widely relevant to many wild animal populations across taxa.

This thesis consists of two data chapters:

In Chapter 2 I investigate sampling bias associated with monitoring the breeding population in Wytham. Failed identification of breeding individuals caused by early reproductive failure has been estimated to account for 6% of all breeding attempts (Bouwhuis et al. 2010), but it is currently unknown whether this sample represents a random subset of the total population. To date, the only empirical work that has investigated which birds fail early briefly describes the age categories of early failures by following colour ringed individuals in the early stages of breeding (Dhondt 1985). I describe previously unknown patterns of early nest failure rates and explore some of the mechanisms underlying them. To do this, I focus on factors known to influence

reproductive success such as age, residency status and habitat. Furthermore, I investigate some of the biological mechanisms that may potentially drive rates of early nest failure. I then explore any consequences that these missing individuals will have on estimates of fitness within this population and discuss the broader implications of these.

In Chapter 3, I aim to expand on findings from Chapter 2 by exploring whether population sampling carried out either during the winter or during the breeding season represents a biased sample of the entire population. It is difficult to target the movement of animals between seasons and systematic biases can be introduced as a result of the sampling period used during monitoring. Traditionally within Wytham, inferences based on the breeding population are extrapolated to the wintering population. In this chapter I aim to discuss the overlap between these two populations. In order to do this I use a combination of breeding data and data collected during the winter via mist netting and RFID detection systems to identify whether different classes of individuals behave in different ways with respect to their movements in and out of the study area. There also exists a fundamental gap in the literature regarding why small passerines might not be detected breeding (Orell et al. 1994); I aim to address this by identifying predictors of winter residency and failure to be detected breeding locally within this population. My main objectives are to investigate (i) the effects of sampling technique on estimates of population structure; (ii) the demography of wintering and breeding populations in order to predict which birds may go undetected at certain times of the year based on age, sex, residency status, or habitat characteristics, and (iii) how winter detection patterns are influenced by demographic characteristics. In doing so, I aimed to learn more about which individuals are detected at different times of the year and their movements throughout the year. Such interactions are likely to influence patterns of gene flow and responses to selection.

1.10 Tables and figures



Figure 1.1: A great tit pullus showing the metal BTO ring and plastic PIT. The PIT tags have the glass PIT fully encased in plastic, moulded to a plastic ring of the same length (Manufactured by IB Technology, UK).

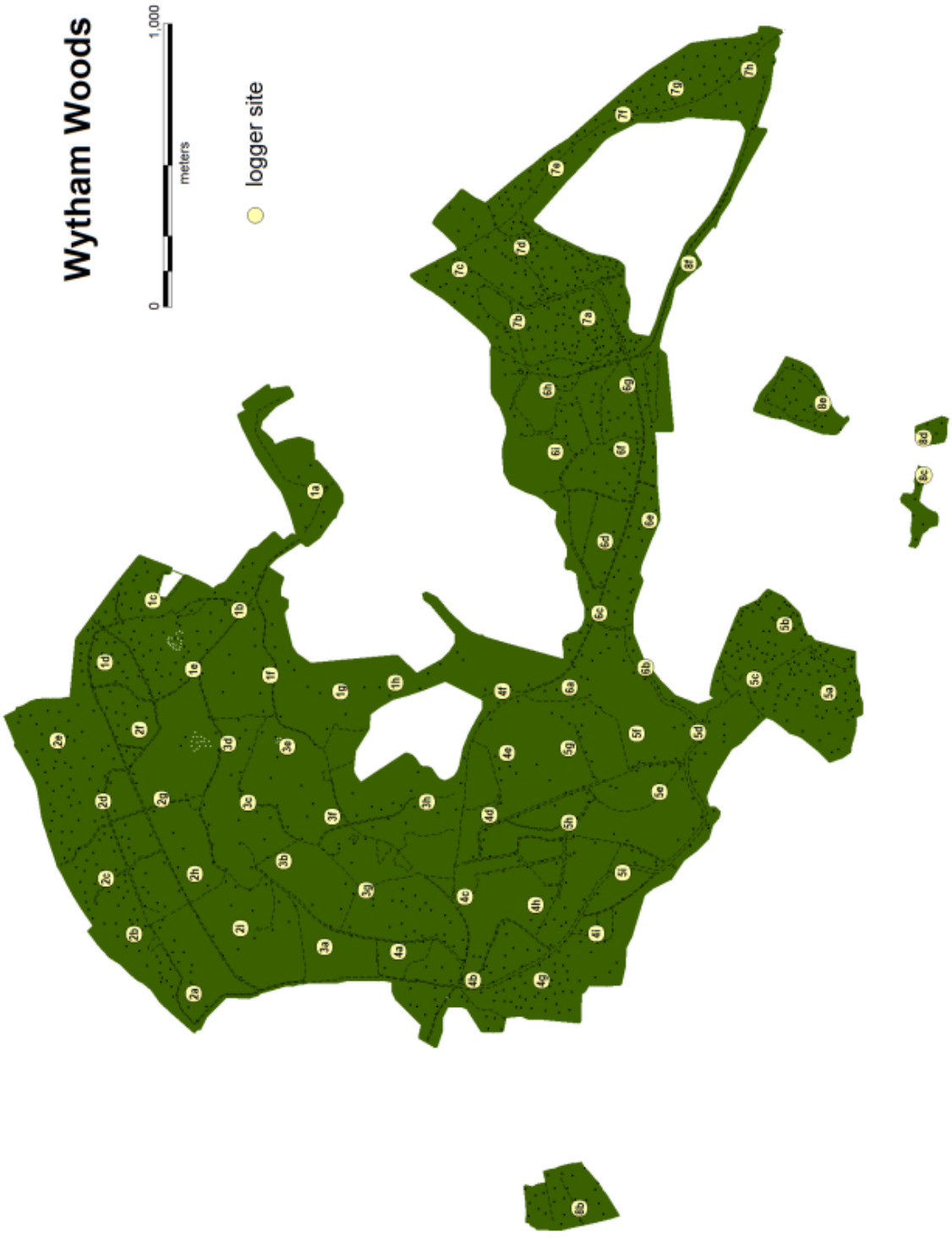


Figure 1.2: Map of the study site, of Wytham Woods, showing the 65 sites of RFID detection feeding stations.

CHAPTER 2

WHO ESCAPES DETECTION? QUANTIFYING SAMPLING BIASES IN A LONG-TERM FIELD STUDY



Image Credit: Nicole Milligan

"Great is the power of steady misrepresentation"

- Darwin

Who escapes detection? Quantifying sampling biases in a long-term field study

Abstract

Inferences drawn from long-term field studies are vulnerable to biases in observability of different classes of individuals, which may lead to biases in the estimates of selection, or fitness. Population surveys that monitor breeding individuals can introduce such biases by not identifying individuals that fail early in their reproductive attempts. Here, we quantify biases in detectability of breeding females in a long-term population study of the great tit, *Parus major*, by sampling more completely throughout the breeding season. We identify females whose breeding attempts fail before they would normally be censused, and explore whether this early failure can be predicted by a number of intrinsic and extrinsic factors. We also investigate the effect of these biases on estimates of reproductive performance. We show that females that fail early in their breeding attempt are more likely to be young and immigrant from outside the study population, and breeding in poorer quality habitats. As a consequence, estimates of the fitness of immigrants versus residents, age effects on fitness, and the age and immigration-specific effects of habitat quality are likely to be underestimates. Moreover, the exclusion of early nest failures from analyses underestimates the effects of dispersal on reproductive success; as a consequence, current fitness estimates that show reduced fitness of immigrants versus residents are likely to be underestimates. We suggest that, while these conclusions are specific to this study, such effects are quite likely to be widespread, and that more attention should be given to the question of whether methods for surveying natural populations introduce systematic bias that will influence conclusions about ecological and evolutionary processes.

Keywords: detectability bias, great tits, natural populations, *Parus major*, sampling.

2.1 Introduction

Long-term field based studies of marked individuals have contributed in many ways to our understanding of ecological and evolutionary processes operating within populations (Clutton-Brock & Sheldon 2010a). These processes are difficult to simulate under laboratory conditions because they may act over many years or decades, and

because laboratory or captive conditions can rarely replicate the full range of environmental variation in nature. Studies that mark, identify, and follow individual animals are particularly useful for quantifying the proximate causes of changes in population size. Furthermore, data from individual-based studies can be used to monitor the development and life history of individually recognisable animals, enabling assessment of the fitness costs and benefits of different traits or breeding strategies. Such data thus allows researchers to take an evolutionary perspective, providing repeated measures of the direction and strength of overall selection (Siepielski, DiBattista & Carlson 2009). Further, such data allow accurate measures of age-related changes in life history parameters, and can be used to examine kinship and social relationships (Clutton-Brock & Sheldon 2010a).

A major assumption of individual-based studies is that detected individuals are a representative sample of the population. Despite researchers' best efforts to obtain random samples of animals, biases are likely to exist. For example, recent studies of behavioural syndromes revealed that behavioural observations are likely to be missing for shy and inactive individuals (Biro & Dingemanse 2009; Garamszegi, Eens & Török 2009) and recapture probabilities can differ for different classes of individuals (Tavecchia et al. 2001; Crespin et al. 2002; Sluydts et al. 2007), leading to the problem of biased detectability (Royle & Nichols 2003). This problem has long been acknowledged in conservation biology (Manel, Williams & Ormerod 2002), and although it was highlighted by Grafen (1988), the implications of imperfect detectability for inferences in ecological and evolutionary studies have only recently started to receive attention (reviewed in Nakagawa and Freckleton, 2008). If undetected individuals represent a biased sample of the population, their exclusion from empirical studies may significantly alter overall inferences. For example, Hadfield (2008) showed that estimates of heritability and selection are biased if estimated without accounting for missing observations due to premature death in relation to the trait of interest. Ad-

ditionally, Gimenez et al. (2008) reanalysed the findings of two long-term datasets and found that the assumption of perfect detectability led to flawed inferences, altering estimates of the form of natural selection acting on the body mass of weavers (see Covas et al. 2002) and underestimating the rate of senescence in roe deer (see Gaillard et al. 1993).

Understanding the extent and causes of variation in reproductive success remains both one of the fundamental contributions of longitudinal field based studies (Clutton-Brock & Sheldon 2010a), as well as an on-going aim for current work. However, obtaining accurate data to quantify reproductive success in wild populations remains a challenge. Imperfect detection rates are of particular concern in surveys of breeding populations, where detection rates may be imperfect because a subset of breeding attempts fail before breeders are identified, leaving data truncated (Heisey & Nordheim 1995). Consequently, observed breeding attempts form a non-random subset of the breeding population, under-representing individuals with poor reproductive performance.

Variation in reproductive success has been found to be caused by a range of intrinsic and extrinsic factors. One frequent intrinsic predictor of reproductive success is age; reproductive success generally increases with age, reaching a plateau, before declining in old age as a reflection of reproductive senescence (Clutton-Brock 1988; Sharp & Clutton-Brock 2009; Nussey et al. 2012). A second intrinsic factor that has been linked to reproductive success is dispersal status. Many studies have shown that immigrants have lower reproductive success compared to residents, despite no difference in survival rates between the two classes (Wiggett & Boag 1993; Bensch et al. 1998; Orell et al. 1999). Although the underlying causes of this effect are not well understood, there are a number of possible mechanisms. First, arrival time at a breeding site may drive differences in reproductive performance between local and immigrant individuals, as late arrival may limit access to high quality territories

(Oring et al. 1991) or delay mate acquisition (Lozano, Perreault & Lemon 1996; Dickerson, Quinn & Willson 2002). A second possibility is that varying exposure to human disturbance drives differences in reproductive success between immigrants and locally-born individuals. Capture and handling as part of population monitoring can cause individuals to abandon their nests (Kania 1989, 1992), therefore also potentially biasing estimates of reproductive success. Furthermore, studies of birds have shown that individuals become habituated to human disturbance (Burger & Gochfeld 1999; Walker, Dee Boersma & Wingfield 2006), suggesting that naïve birds entering into study populations may be more adversely affected by disturbance than resident individuals. In addition to these intrinsic factors, extrinsic factors can influence an individual's reproductive success; reproductive success has been linked to local habitat quality and territory size in a wide variety of species (Vehrencamp, Koford & Bowen 1988; Högstedt 1980). Individuals with low reproductive success that abandon their reproductive attempt before they can be identified may represent a biased sample of the total phenotypic variation within populations, with respect to both intrinsic and extrinsic factors.

Among the first long-term individual-based field studies of animals were those of tits (Paridae; Kluijver 1951; Lack 1954) and nestbox populations of these species are still a widely used study system in evolutionary and behavioural ecology (e.g. Charmantier et al. 2008; Korsten et al. 2013; Reed et al. 2013). Typically, the breeding population is surveyed (and hence survival and recruitment inferred) by trapping parents after a certain stage in the breeding cycle; similar procedures are followed for long-term studies of many other bird populations (Perrins, Lebreton & Hirons 1991). Clearly, censusing at a given point in the breeding cycle has the potential to yield incomplete fitness estimates when some breeding attempts fail before the census point. This has the potential to generate biased inference if the probability of failure is higher for certain types of individuals. In the present study, we employ RFID tech-

nology to census the population of breeding females early in reproduction. As a result we are able to identify females that fail early in their breeding attempt that would otherwise have remained unidentified under the standard sampling protocol for the study population. This paper has three main objectives: (i) to investigate intrinsic and extrinsic predictors of early nest failure, with an aim to quantify biases in current population sampling techniques; (ii) to explore the underlying mechanisms linking residency status and early nest failure; (iii) to assess the consequences of sampling biases for estimates of fitness.

2.2 Methods

2.2.1 Study population

The great tit is a small hole-nesting passerine, abundant in a wide range of wooded habitats throughout much of Europe, which readily breeds in artificial nest boxes (Perrins 1979). This study was undertaken on a population at Wytham Woods, a 388ha mixed deciduous woodland in Oxfordshire. There are 1020 nest boxes which have remained at fixed locations throughout the study since the early 1960s. Typically, between 300-450 of these are used annually by breeding great tits during the spring (April – June). Nests are monitored regularly as part of a long-term population study, further details of which are given elsewhere (Perrins 1965; Gosler 1993). Great tits lay one egg a day and, in most cases, nests are first distinguished from those of other tit species (C*yanistes caeruleus, Periparus ater, Poecile palustris*) based on an average egg weight of 1.3g or greater (determined by weighing three or more eggs). After hatching, both parents provision the chicks at the nest until they fledge approximately 20 days later. Breeding individuals are identified by trapping at the nestbox using spring traps when their chicks are at least 7 days old, and aged and sexed based on plumage characteristics (Svensson 1992, see below). All chicks and

unringed breeding adults are ringed at nest boxes in accordance with the BTO's ringing scheme. Since 2007, in addition to a BTO ring, almost every trapped adult and fledged nestling has been fitted with a uniquely numbered PIT tag moulded into a plastic leg ring (IB technology, Aylesbury, UK). The fledging success of each breeding attempt is established by visiting nests at the end of the season, and recording numbers of dead chicks.

In addition to monitoring during the breeding season, throughout the winter, great tits are trapped using mist nests at a seed feeder, and immigrants to the woods are ringed and fitted with a PIT tag. Across all winters, from November to February, one 18 m net was set at a fixed centrally located site on a weekly basis. In addition to this, for the duration of the study period, teams of people operated two-three nets simultaneously in close proximity to one another and moved every week to cover the entire study area. In the winter leading to the breeding season of 2009, a total of 56 days were spent catching at multiple sites per day between late August and late February. In the winter before the 2010 breeding season, mist netting procedures were similar to those used in the previous winter, a total of 56 days were spent catching at multiple sites between August and early March. In the winter leading up to the 2012 breeding season, mist netting efforts increased and were more standardised. In addition to the centrally located feeder, teams of ringers would consecutively operate three-four nets at regularly spaced intervals throughout the study site. A total of 68 days were spent ringing between multiple sites from mid-August to early March 2012.

2.2.2 Assigning immigration status and age to captured birds

The proportion of chicks born in natural cavities in Wytham has previously been documented as very low (Greenwood, Harvey & Perrins 1979; Perrins 1979), and therefore all unringed birds trapped in Wytham are assumed to be immigrants to the study site. While there are no more recent data that have repeated that reported by

these earlier studies, there are three lines of evidence that suggest that the assumption remains reliable enough for the analyses presented here. First, the proportion of nests at which a female was identified between 1960-2009 (10233/12281 = 0.83) is very similar to the overall estimated recapture probability using mark-recapture modelling methods over the same time period (0.83±0.07: Bouwhuis et al. 2012). This suggests either that there are very few birds in natural cavities, or that if there are birds in natural cavities, very few of them switch between nest boxes and natural cavities to breed. Second, the proportion of immigrant birds in the breeding population (median proportion immigrant females = 0.49; IQR 0.41-0.57; N = 45 years between 1965-2009) has not increased over time, which would be expected to be the case if there were an increased number of birds breeding in natural cavities in the study population, unless these birds' offspring were less likely to breed in artificial nest boxes. In fact, excluding the years 1960-1964 when the proportion of immigrants was artificially high as the study was being established, the proportion of locally-ringed nestlings among the population of identified breeding females each year has increased weakly (GLM, binomial errors, N = 45 years from 1965-2009: $\chi^2_1 = 5.52$, $P = 0.02$); there is no consistent change over time for the proportion of identified breeding males that were locally born ($\chi^2_1 = 0.27$, $P = 0.06$). Third, while we cannot rule out the possibility that there exists a class of birds that avoid artificial nest sites and whose offspring also avoid such nests sites, we are confident that this class of birds cannot be very large, as in each year of this study >1000 person-hours are spent in the field between April-June, and at most only a small handful of natural cavity nests of great tits found (in contrast, natural cavity nests of blue tits are regularly encountered during standard fieldwork). Hence, even if some of the class of birds termed 'immigrant' in the following analyses were in fact born in natural cavities on the study site, they will at most make up a small fraction of the total class of immigrants. Hence, we believe that the category 'immigrant' represents, with a high degree of confidence, birds born

outside the study area.

The age (in years) of birds born in nest boxes within Wytham is known precisely, and can be assigned for immigrants to the study site using plumage characteristics (Svensson 1992). Immigrants with juvenile plumage were identified as yearlings (in their first year of life) and individuals first caught in Wytham with adult plumage were assigned a minimal age of two years (Bouwhuis et al. 2009; Bouwhuis et al. 2010; Bouwhuis et al. 2012).

2.2.3 Remote identification of breeders early in reproduction

The PIT tags fitted to great tits allow automatic identification through the contactless transfer of data. An external antenna is used to induce current in the electric circuit of the PIT tag via varying magnetic fields. In turn, the PIT tag circuit emits an electromagnetic signal with an encoding of its unique ID; this is received by the external antenna and decoded by an attached PIT tag reader. The PIT tags can be read by an antenna at a distance of up to 15 cm. Recapture histories show that the proportion of individuals captured in 2009, 2010 and 2012 in which a female great tit has a leg ring but no PIT tag were low (10%, 5% and 0% respectively). The proportion of the total population that is PIT-tagged is estimated at over 90%, (see Aplin et al. 2013).

During the breeding season, all nest boxes were checked weekly to ascertain the date of the first egg (hereafter lay date). Once a nest had been identified as a great tit nest (see above), it was visited at night and scanned with a hand-held PIT tag reader (manufactured by Dorset Identification, Netherlands), in order to identify the female roosting inside without causing disturbance. All females were assumed to be in the box at the time of scanning as females roost on the nest during the laying and incubating period (Gosler 1993). Data collected during this study support this assumption; all females later caught at the nest corresponded to the female identified

through earlier scans. Of course, it is possible that some females did roost outside the box and were subsequently assumed to have no pit, but data collected during this study showed no evidence of this, and often females could be heard hissing inside the box when the scanner did not return a PIT. A total of 844 nests were scanned during the 2009, 2010 and 2012 breeding seasons and the proportion of the known nesting attempts in next boxes scanned in each year was 75%, 92% and 100% respectively. The majority of nests (85%) were scanned while the female was still laying; however, it should be noted that 15% of nests were scanned after the onset of incubation. Hence, this methodology allowed us to identify females whose breeding attempts failed between egg laying and the time when adults are normally identified, when nestlings were approximately one week old. We note that we were unable to identify females that failed in the very early stages of egg laying (less than three eggs), however this comprised less than 3% of all breeding attempts.

Assessment of the accuracy of the records obtained by scanning was based on comparisons of identities of scanning records with the identities of females later caught at nest boxes (i.e. scanner failure was inferred if no PIT tag was read, but the female was found, on subsequent trapping, to be carrying a functional PIT tag). There were no instances where the scanner returned a PIT tag that did not later match the female subsequently caught at the box (n=702 captures). During the 2009 and 2010 breeding seasons an older model of scanner was used; this was found to be 93% and 91% accurate respectively. In 2012 we used an improved scanner which was 100% accurate and successfully detected all PIT-tagged females that were subsequently captured (n=342). Due to the low overall detection error (95% across the entire sample) we did not correct this classification for scanner error.

2.2.4 Assigning immigration status and age to birds without PIT tags

If the scanner did not detect a PIT tag during the night-time scans, we assumed that the great tit roosting inside was not carrying a PIT. As over 90% of the population is pit tagged (Aplin et al. 2013), very few birds are ringed but not tagged, and the rate of nesting in natural cavities is low, we assumed that these individuals had not previously been caught, and were therefore unringed immigrants to the study site. The age of these unringed females is unknown. However because 91% of immigrants into Wytham are first caught as yearlings (Greenwood, Harvey & Perrins 1979), and it is unlikely that a female would be resident for multiple years without being captured, it is likely that the great majority of roosting females without PIT tags were in their first year of life. For the purpose of our analysis we therefore assumed that all scanned nests that did not register a PIT code were nests associated with a yearling immigrant female (but see statistical methods).

2.3 Data analysis

2.3.1 Intrinsic and extrinsic predictors of early nest failure

We compared individuals that had failed early in reproduction to those that successfully reared young to at least seven days old, the age at which breeding adults are caught and identified under standard protocol. An early nest failure was therefore defined as a breeding attempt that failed before chicks were reared to seven days old. Our first objective was to explore intrinsic and extrinsic determinants of early nest failure, which was done using a generalized linear mixed model (GLMM) with a binomial error structure. Our full model included the continuous fixed effects lay date (date of first egg), female age (in years), the quadratic effect of female age, and local oak tree density (as a proxy for territory quality), and the discrete fixed effect

female immigration status (ringed immigrant, unringed immigrant, or locally born). Breeding season territory quality is partly dependent upon the density of oak trees (Wilkin, King & Sheldon 2009) as oak trees (largely *Quercus robur* at this site) support high densities of insects, particularly caterpillars of the winter moth (*Operophtera brumata*) which form a key element of the food of great tit nestlings. We used the number of oak trees with a diameter at breast height of 50cm or greater within a 75m radius of the nestbox as a surrogate for habitat quality. Habitat quality, defined in this way, is highly variable in Wytham; on average each territory has 8 oak trees, ranging from 0-72. So that both the linear and the quadratic effects of age could be interpreted in the same model the age term was centred (following Schielzeth 2010). Year of reproduction and nestbox were included as random effects in the model. If a bird bred multiple times across years, we randomly selected a single breeding attempt for analysis; this was done because our models would not converge with female identity included as a random effect, probably due to too few repeat observations of females between years. Known second breeding attempts by females within the same year (n = 28) were also excluded. All statistical tests were performed in the R environment, version 2.12.2 (R Core Team 2012).

The full model described above contains a sample of birds for which age was estimated (see methods). Therefore to further explore the effect of age, a separate GLMM was run containing only locally born birds (for which exact age is known). Random and fixed effects were the same as those included in the full model (with the exception of immigration status which was omitted because all birds were locally born). If a locally born bird had bred multiple times across years, we randomly selected a single breeding attempt for analysis.

2.3.2 Immigration status and early nest failure

Our second objective was to explore the mechanisms underlying the relationship between immigration status and early nest failure. We aimed to test two hypotheses: (a) early nest failure rates would be higher amongst individuals that arrive late into the study site, and (b) individuals that have not experienced previous human disturbance (e.g., handling) would have higher rates of early nest failure. In order to do this, two GLMMs were run on subsets of the full data set. These analyses were restricted to individuals observed breeding in their first year of life; this allowed us to be certain of each individual's immigration status, removing any potential bias that could result from including unidentified adult immigrants that may have bred in previous years before being caught and identified.

The first GLMM investigated the importance of ringing date in explaining early nest failure. As there was a period of intensive mist netting which occurred at regular intervals throughout the study site for the duration of this study (see above for further details), we assumed that immigrants were caught and ringed soon after they arrived into the woods. As such, we subsequently refer to ringing date as a proxy for arrival time. Immigrants were split into either winter arrivals (those caught during winter mist netting) or unringed individuals (those that arrived just prior to the breeding season and were subsequently not caught during winter mist netting sessions – see above). Locally born individuals were born in nest boxes on the study site. The model included the fixed effect ringing date (locally born, winter arrivals, unringed immigrants (late arrivals)), and random effects year of reproduction and nest box. During the winter of 2011/2012, the frequency of mist netting sessions was particularly high and also more standardized (see methods), meaning that we had increased resolution of arrival time for a subset of birds. Therefore, in addition to the model described above, a separate logistic regression was carried out on this subset of immigrants, using capture date (days from the start of September 2011) as a proxy for

arrival date, and early nest failure at the binary response variable (n=63).

A further GLMM was used to explore the effect of exposure to human handling on early failure rates. Individuals were assigned to categories based on their previous exposure to human disturbance through handling. Locally born birds were classified as 'unhandled' (if they had not been handled since they were ringed as nestlings) or 'handled' (if they had been captured and handled as an adult). We thus assume that being handled after leaving the nest is categorically different from being handled as a nestling. Immigrants that had previously been ringed were classified as 'handled' and unringed immigrants which have never been caught were classified as 'unhandled'. If early nest failure is influenced by previous exposure to disturbance we expect that the handled locals will be the least affected by disturbance, followed by the handled immigrants, then unhandled locals (handled as nestlings only) and the unhandled immigrants. The model included the fixed effect handling category (unhandled local, handled local, unhandled immigrant, handled immigrant) and the random effects year of reproduction and nest box.

2.3.3 Estimating fitness differentials

Our final objective was to investigate any consequences of sampling biases for estimates of fitness. In order to do this, GLMMs were run on two data sets, one included only nests where the female was trapped at the nest after chicks had reached 7 days old (the standard sampling protocol). The other also included all early nest failures, where females had been identified through night scanning. The models investigated the binary variable fledgling success (0/1), where 1 represents a nest where any chicks fledged successfully. Fixed effects included lay date (date of first egg), female age (in years), the quadratic effect of female age, female immigration status (immigrant or locally born) and oak tree density (see description of full model above for more details). Year of reproduction and nest box were included as random effects.

2.4 Results

2.4.1 Patterns of nest failure

Over three breeding seasons there were 844 breeding attempts by great tits that were scanned at night, 146 (17.2%) of which failed early (i.e. before reaching the stage where nestlings were 7 days old). Locally-born birds accounted for 359 (42%) of breeding attempts and had an early nest failure rate of 12%. A total of 339 ringed immigrants attempted to breed, with an early nest failure rate of 15%. Only 150 unringed immigrants attempted to breed and rates of early nest failure were higher, at 33%. Almost half of the nests that failed early deserted after chicks hatched, during the chick rearing stage (49%). Failure during the egg laying and incubating stages were lower, at 30% and 21% of total failures respectively. There was no significant effect of immigration status on the stage at which nests failed (χ^2=2.153, df=2, P=0.34). There was also no effect of age on the stage at which early nest failure occurred (χ^2=0.934, df=2, P=0.14). Early nest failure rates were similar in 2009 and 2010 at 13% and 12% respectively; however nest failure rates in 2012 were almost twice as high, at 22%.

2.4.2 Female age-related patterns of early nest failure

In the main model, there was an effect of age, but no indication for a quadratic effect (β=0.135, P=0.12); with younger birds more likely to fail early (β=-0.914, P=0.047; Table 2.1, Fig 2.3); this suggests that age may be a predictor of early nest failure. However, early nest failure rate was unrelated to both the linear and quadratic age effect within a subsample of locally born birds (β=2.54, P=0.364, β=-0.545, P=0.327 respectively, see Table 2.2).

2.4.3 Female immigration status and early nest failure

Our measure of immigration status explained significant variation in nest failure rates of breeding great tits (Table 2.1); unringed immigrant females were 3.7 times more likely to fail early than locally born birds (β=1.299, P<0.001). There was no significant difference between nest failure rates of ringed immigrants and locally born individuals (β=0.292, P=0.262). We found a significant effect of ringing date on nest failure rates within the subset of first year breeders (Table 2.3; Fig 2.1). There was no significant difference between early nest failure rates between earlier arriving immigrants and locally born indivuals (β=0.292, P=0.26; Fig 2.1), but later-ringed individuals (unringed immigrants) were significantly more likely to fail early than earlier ringed individuals (locally born individuals) (β=1.319, P<0.001; Fig 2.1). Further support for this effect was obtained from the separate analysis of a subsample of immigrants caught and ringed in the winter of 2011/2012, which revealed a significant negative effect of ringing date (here taken to be a proxy for arrival date) on early nest failure (arrival date: β= -0.012, SE= 0.005, P= 0.046).

The nests of unhandled immigrants were more likely to fail early than those of unhandled locally-born birds (β=1.398, P<0.001; Table 2.3; Fig 2.2). However there was no difference in nest failure rates between unhandled locally born birds and handled locally born and handled immigrants (β=0.233, P= 0.681; β=0.175, P=0.650, respectively; see Table 2.3; Fig 2.2). These results provide little support that previous experience of human disturbance influences early nest failure rate.

2.4.4 Timing of breeding, territory and nest failure

There was a significant negative relationship between early nest failure rate and lay date (β=-0.054 P=0.002; Table 2.1). This suggests that laying late in the season increases chances of early nest failure. Oak tree density was also a significant indicator

of early nest failure rates (β=-0.019, P=0.027; Table 2.1): the number of oaks trees within a 75m radius of breeding territories is negatively associated with early failure rates.

2.4.5 Biases in reproductive success estimates

Our results show no effect of immigrant status on fledgling success when analyses do not include early nest failure data (β=0.138, P=0.521; Table 2.4). However, once early failures were included in analyses, immigrants were significantly less likely to fledge young than locally born birds (β=-4.19, P=0.004; Table 2.4). This suggests that the inclusion of early nest failure data can significantly alter previous estimates of reproductive success.

2.5 Discussion

In this paper we identify whether standard sampling techniques exclude a biased sample in a population of great tits. We show that early nest failures are a biased sample of the population, with respect to immigrant status and age. Young birds and unringed immigrants were more likely to fail before being caught and identified at nests under the standard protocol. In addition, we identify some of the possible mechanisms driving difference in early nest failure rates between immigrants and locally born individuals, with failure in the early phase depending on habitat characteristics and ringing date for birds that were ringed during the non-breeding season. These results have implications for previous estimates of fitness in this population, leading to biased estimates of reproductive success for immigrants to the study site.

Younger females had higher rates of early nest failure; this is consistent with previous studies from Wytham and other bird populations where reproductive performance is strongly affected by age (Perrins 1965; Perrins & Moss 1974; Clutton-Brock 1988; Newton 1989; Sæther 1990). The age effect was only present when unringed immi-

grants were included in the analysis, which could result from the increased power of the larger sample size; although it may indicate that age alone is not an important predictor of early nesting failure. Instead, there may be an interaction between age and immigration status, with young immigrants being more likely to fail early than any other class. However, we are unable to test this interaction using our dataset because we assumed all unringed immigrants were first year breeders, based on the knowledge that 91% of immigrants into Wytham are yearlings (Greenwood, Harvey & Perrins 1979).

A key finding from this study is that unringed individuals, assumed to be immigrant to the study site, have higher rates of early nest failure than locally born birds; suggesting that there is potentially a large reproductive cost associated with dispersal. Several other studies of individually marked bird populations have also found that immigrants have reduced reproductive success than residents (Part 1994; Julliard, Perret & Blondel 1996; Verhulst & Van Eck 1996; Bensch et al. 1998; Wheelright & Mauck 1998; Orrell et al. 1999). Specifically, within Wytham, immigrants perform less well than locally born birds independent of survival rates (Clobert et al. 1988; Bouwhuis et al. 2010). Individual quality may drive these differences; immigrants often originate from low quality areas surrounding Wytham woods (Riddington & Gosler 1995; Verhulst, Perrins & Riddington 1997) and can suffer from long-term natal effects (Bouwhuis et al. 2010).

Individuals that are caught and ringed later during the winter had higher rates of early nest failure than those that were caught early. In this study, ringing date is likely to be closely linked to arrival time at the breeding grounds which has been shown to be a major contributor to reproductive success in several bird species, such as warblers and swallows (Francis & Cooke 1986; Møller 1994). After the breeding season, great tits spend the winter in loose aggregations or flocks (Ekman 1989). Some studies suggest that later arriving individuals incur higher reproductive costs

through delays in finding mates or nesting sites (Lozano & Lemon 1999) and that birds arriving late will have to settle in low quality habitat. Although the quality of the local habitat (estimated by the number of oak trees within the vicinity of the nest) had a significant effect on early breeding failure, a post hoc analysis revealed that residents and early-arriving birds did not occupy higher quality territories than late-ringed birds (number of oaks: β= -0.009, SE= 0.001, T value= -0.72). Therefore, any difference in reproductive success due to ringing date and the subsequent inferred arrival time cannot be due to this aspect of habitat quality. Several other underlying mechanisms might drive differences in nest failure rates between early ringed and later ringed individuals. For instance, it is difficult to separate the effects of age, breeding experience and local familiarity on reproductive success. Numerous studies show that birds arriving earlier are older or in better condition than later arrivals (Arvidsson & Neergaard 1991; Stolt & Fransson 1995; Lozano, Perrault & Lemon 1996). In great tits, clear dominance hierarchies arise in any group situations (Gosler 1993); early arrival could enable individuals to become more established in the dominance hierarchy in winter flocks (Sandell & Smith 1991). Additionally, it has been shown that familiarity with neighbours increases reproductive success, suggesting that there are socially mediated costs of immigration. For example, a recent study found that great tits with more familiar neighbours had a greater chance of successfully fledging offspring (Grabowska-Zhang, Wilkin & Sheldon 2012). However, investigating these mechanisms was beyond the scope of this study.

We found little evidence to support the hypothesis that immigrants may be more likely than locally born birds to suffer early nest failure in monitored populations because they have previously received less exposure to human disturbance. Previous experience of disturbance can reduce an individual's sensitivity to human presence (Burger & Gochfeld 1999; Walker, Dee Boersma & Wingfield 2006; Ellenberg, Mattern & Seddon 2009), suggesting that naïve birds entering into study populations

may be more adversely affected by disturbance than resident individuals. Therefore if early nest failure is caused by population monitoring, we would expect that the nests of individuals that had prior experience of disturbance through being handled were less likely to fail than naïve birds. In our study, it may be that the exposure to disturbance experienced by repeatedly-handled birds was not sufficient to reduce disturbance-induced failure. Alternatively, birds may not generalise the experience of being handled to disturbance by humans during nest monitoring. We therefore cannot rule out the possibility that early nest failure may be caused by individual differences in responsiveness to the disturbance caused by nest-monitoring.

We have shown that the exclusion of early nest failures from analyses can underestimate the effects of dispersal on reproductive success. As a consequence, current fitness estimates that show reduced fitness of immigrants versus residents are likely to be underestimates. This may have implications for other findings from populations of marked animals. For example, age structure has been shown to underestimate or mask the effects of senescence at the population level (Vaupel & Yashin 1985; Gimenez et al. 2008). If there are two classes of individuals with low and high survival probabilities, the overall survival rate will be increasingly influenced by the individuals with the highest survival over ages (Gimenez et al. 2008). A similar effect may exist on age related estimates of reproductive success from nest surveys, where the overall rate of reproductive success will be increasingly influenced by the individuals with the highest rate of success. In Wytham, there is a decline in female recapture probability with age (Bouwhuis et al. 2012). If early failures contribute to this decline, age-specific reproductive values and subsequent reproductive senescence estimates may be biased. As more immigrants are missing from the sampled population than previously thought, our understanding of the effects of early life conditions for reproductive success and senescence may be altered. For example, in Wytham, immigrating females achieve similar reproductive success to locally born females in

the first two years of life but subsequently suffer from elevated rates of reproductive senescence (Bouwhuis et al. 2010). However, if immigrants perform worse than previously thought in early years, as our results suggest, there may not be any accelerated senescence.

Additional investigation into the effects of individual variation on reproductive success would be beneficial in further quantifying any biases that may result from imperfect detectability. For example, several studies have shown that individuals vary in their propensity to desert a nest, based on traits such as body condition (Dubiec 2011) and cognitive abilities (Cole et al. 2012). Whether factors such as these explain early nest failure remains to be established. However, we demonstrate that methods for surveying natural populations introduce systematic bias that will influence conclusions about ecological and evolutionary processes. Given the current and future advancement of technologies available to monitor wild populations, researchers should re-assess conventional survey methods to enhance the accuracy and completeness of biological data, in order to increase the robustness of conclusions that are drawn from them.

By remotely identifying breeding females during laying and incubation, we have shown that missing breeding attempts due to early nest failure represent a biased sample of the population. Our analysis suggests that these individuals likely represent a biased sample in terms of age class and immigration status. In particular, we have shown that previous estimates of the effect of age and immigration status on reproductive success are likely to have been underestimated. This has implications for other nest surveys and longitudinal breeding studies. The ability to more accurately quantify missing data with new technologies, such as RFID, offers unique opportunities to further assess biases that occur from exclusion of individuals in analyses.

2.6 Tables and figures

Table 2.1: Results of a GLMM assessing early nest failure rates of great tits within Wytham woods. Data used were from a single attempt per individual over three breeding seasons (n=711). The response is binary (0/1), where 1 represents an early nest failure. Reference category for female status is locally born individuals, immigrants to the study site are those that were not born within Wytham but had previously been caught and ringed, unringed immigrants were identified by scanning nest boxes with a PIT tag scanner but had never been caught. Year of reproduction (variance=0.033) and nestbox (variance<0.001) were included as random effects in the model.

Fixed Term Full model	β ± SE	z value	P
Female residency status, Immigrant	0.292 ± 0.261	1.120	0.262
Female residency status, Unringed immigrant	1.299 ± 0.283	4.587	<0.001
Oak density	-0.019 ± 0.008	-2.202	0.027
Lay date	-0.054 ± 0.018	-3.026	0.002
Age^2	0.135 ± 0.086	1.570	0.116
Age in Years	-0.914 ± 0.462	-1.978	0.047

Table 2.2: Results of a GLMM assessing early nest failure rates of locally-born great tits within Wytham woods. The response is binary (0/1), where 1 represents an early nest failure. Data used were from a single attempt per individual over three breeding seasons (n = 344). Year of reproduction (variance<0.001) and nestbox (variance=39.39) were included as random effects.

Fixed Term Locally born only	β ± SE	z value	P
Oak density	0.038 ± 0.087	0.434	0.664
Territory size	-0.263 ± 0.601	-0.438	0.661
Lay date	0.087 ± 0.104	0.833	0.405
Age^2	0.066 ± 0.392	0.169	0.866
Age in years	-0.139 ± 2.044	-0.068	0.946

Table 2.3: Results of two GLMMs assessing early nest failure rates of immigrant and locally-born great tits. 421 female great tits were assigned to categories based on ringing date, a proxy for arrival time (a.) and previous exposure to handling (b.) The response is binary (0/1), where 1 represents an early nest failure. Year of reproduction (variance<0.001) and nestbox (variance<0.001) were included as random effects. Reference categories were locally born individuals.

a.	Fixed Term Ringing date	β ± SE	z value	*P*
	Locally born	-1.988 ± 0.297		
	Unringed	1.319 ± 0.293	4.499	<0.001
	Ringed during winter	0.151 ± 0.363	0.415	0.678
b.	Fixed Term Handling	β ± SE	z value	*P*
	Unhandled local	-2.259 ± 0.401		
	Handled local	0.233 ± 0.567	0.411	0.681
	Unhandled immigrant	1.398 ± 0.317	4.403	<0.001
	Handled immigrant	0.175 ± 0.386	0.454	0.650

Table 2.4: Results of GLMMs assessing biases in estimates of reproductive success (measured here as whether or not any young fledged successfully from a nest). Data on the left include all breeding attempts where the females was known, including those that failed early in their reproductive attempt and were identified through RFID scanning. Data on the right do not include early failures and represent samples collected under the standard protocol. The response is binary (0/1), where 1 represents a nest where chicks fledged. Data used were from a single attempt per individual over three breeding seasons (n = 690). Year of reproduction (variance=0.033) and nestbox (variance=0.065) were included as random effects.

	Data including early nest failures			Data without early nest failures		
Fixed Term Fledged chicks	β ± SE	z value	*P*	β ± SE	z value	*P*
Age in Years	0.491 ± 0.313	1.571	0.117	0.098 ± 0.341	0.289	0.772
Age^2	-0.073 ± 0.059	-1.233	0.217	-0.052 ± 0.059	-0.869	0.385
Number of oaks	-0.007 ± 0.006	1.053	0.292	-0.004 ± 0.007	-0.516	0.606
Residency status, Local	-0.491 ± 0.172	2.838	0.004*	0.138 ± 0.216	0.642	0.521
Lay date	0.012 ± 0.012	0.964	0.335	-0.017 ± 0.015	-1.130	0.259

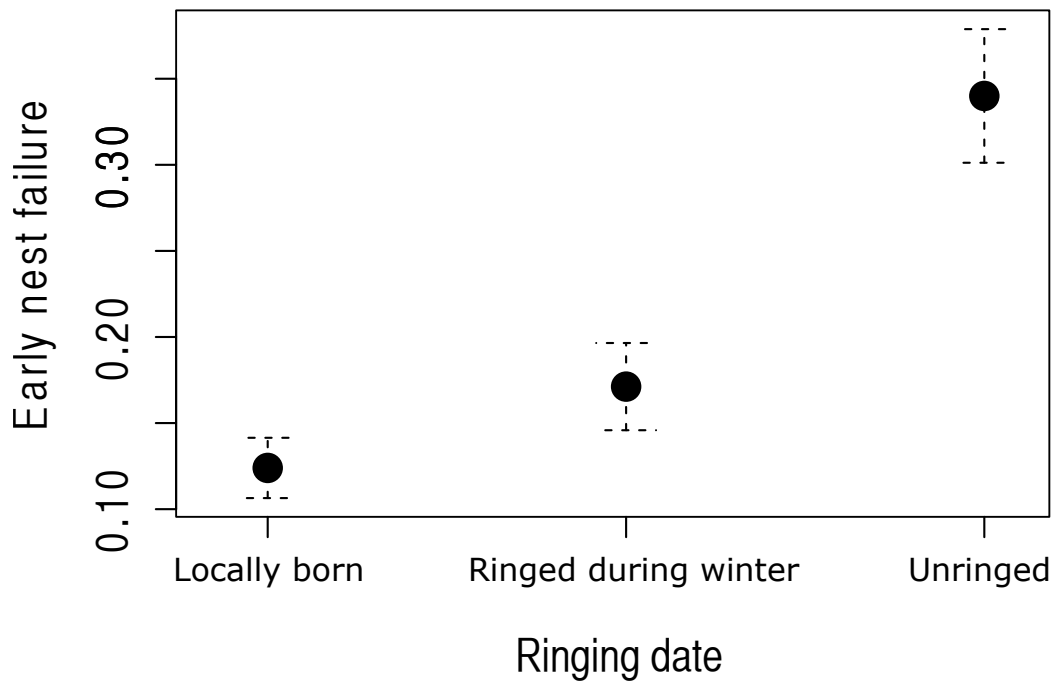


Figure 2.1: Proportion of female great tits that fail early in their breeding attempt, before successfully rearing chicks to 7 days old, the stage at which they are identified in Wytham woods, for different ringing date categories (n=421). Ringing date is used as a proxy for arrival time. Locally born birds were present in the woods since birth the previous summer, immigrants ringed during the winter proceeding the breeding season were known to have been present in the woods during the winter, and unringed birds were assumed to have arrived late, towards the end of winter (see methods).

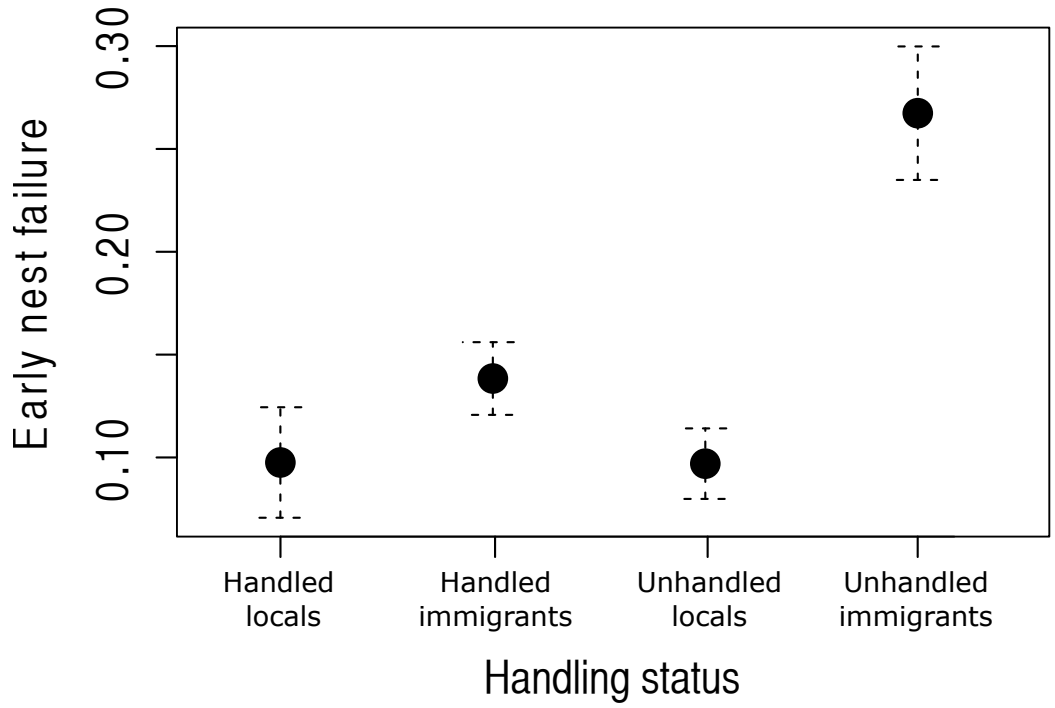


Figure 2.2: Proportion of female first year great tits that fail early in their breeding attempt, before successfully rearing chicks to 7 days old, the stage at which they are identified in Wytham woods, for different human-disturbance categories (n=421). Individuals were grouped into categories based on previous exposure to human handling; handled locally born birds have been handled the most both as chicks and adults, handled immigrants have been handled as adults, unhandled locally born birds had not been handled as adults and unringed immigrants had never been exposed to human disturbance through handling.

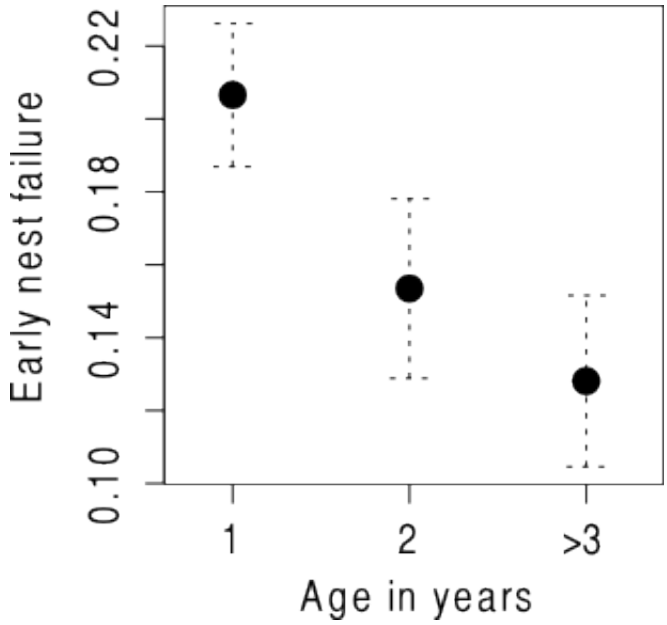


Figure 2.3: Proportion of female great tits that fail early in their breeding attempt, before successfully rearing chicks to 7 days old, the stage at which they are identified in Wytham woods, in relation to age in years (n=711).

CHAPTER 3

INVESTIGATING PREDICTORS OF DETECTABILITY BY TRACKING INDIVIDUALS ACROSS SEASONS: A CASE STUDY OF GREAT TITS (*PARUS MAJOR*)



Catching winter in their carved nostrils,
the traitor birds have deserted us,
leaving only the hardy tits
for spring negotiations.

- Adapted from 'The Sparrows' by Leonard Cohen

Investigating predictors of detectability by tracking individuals across seasons: a case study of great tits (*Parus major*)

Abstract

Long-term monitoring of naturally regulated populations is important for providing data that extend over adequate periods of time to identify the temporal and spatial dynamics of populations. The breeding season is the main focus of many studies in evolutionary and behavioural ecology, and it is often assumed that inferences based on the breeding population apply throughout the year, such as during non-breeding and wintering periods. However sampling during the breeding season excludes individuals that do not breed, fail before they can be identified, or breed outside the study area. In this study, we use RFID technology to track individuals across seasons and investigate intrinsic predictors of detectability rates within a wild great tit (*Parus major*) population. We describe previously undocumented samples collected using varying sampling techniques and show that different techniques vary in their ability to capture different parts of an overall population's structure. In addition, our results suggest that certain individuals are less likely to be detected as a function of their phenotype. We identify sex as a predictor of failure to be detected breeding, with males less likely to be detected. Our results suggest that this is not due to males being harder to catch at the nest. We also find that the likelihood of detection during successive breeding and winter surveys is repeatable across years. We found no evidence that individual characteristics such as age, sex and residency status were significant predictors of winter residency. Nonetheless, they do affect patterns of movement throughout the winter, with younger immigrants being more transient. Distance from the breeding site to the edge of the study site has a significant effect on an individual's detectability the following winter; birds that breed close to the edge of the woods are less likely to be detected the following winter, suggesting that they are more likely to disperse for winter. We show that the complex interactions between individuals during one stage of the annual cycle influence their detectability in subsequent stages. The sex and habitat-specific seasonal effects on detectability shown here illustrate the importance of sampling individuals within populations during different stages of their life history and may serve as an important model for further work.

Keywords: great tits, detectability, natural populations, non-breeding, *Parus major*, RFID, sampling period.

3.1 Introduction

Ecologists and evolutionary biologists are interested in the dynamics of populations in time and space. These include changes in the composition of individuals, for example with respect to age and sex. However, populations are rarely discrete units; animals are moving in the landscape and those movements dictate the extent to which breeding and non-breeding communities of individuals are connected. This suggests the need to define populations and the relationships between them more clearly. These movements can promote or limit interactions between individuals of different phenotypes, thereby influencing patterns of gene flow and responses to selection. Long-term monitoring of naturally regulated populations allows us to do so by providing data that extend over adequate periods of time to identify factors underlying population dynamics and evolutionary processes (Clutton-Brock & Sheldon 2010a). Long-term monitoring involves multiple measurements over time, resulting in a collection of site visits (or replicates). This replication is important for addressing temporal variability in the ecological processes of interest, such as population trends (Westcott et al. 2012). Yet, temporal patterns in sampled populations are only directly descriptive of corresponding patterns in populations if the proportion sampled is constant through time (Link & Sauer 1998). The time that passes between sampling determines what processes can be detected, with processes that occur on timescales shorter than the temporal resolution of the sampling period not being detectable. Likewise, processes that occur on longer timescales than the survey length cannot be detected.

Many long-term population studies focus on the breeding season as a sample period (see Clutton-Brock & Sheldon 2010a, for examples within) and inferences based on breeding data are often extended to other populations such as non-breeding

or wintering populations. Yet, the structure of populations outside of the breeding season can have strong effects on populations; studies have shown that events during one stage of the annual cycle are likely to influence populations in subsequent stages (Drent 1984; Marra, Hobson & Holmes 1998; Sillet, Sherry & Holmes 2000; Gill et al. 2001). For example, migratory bird populations are limited year round by habitat-mediated processes that are limiting or regulatory in both winter and summer, as well as along migratory routes (Holmes 2007). In addition, carry over effects can occur when processes in one season influence the success of an individual in the following season. This phenomenon has the potential to explain a large amount of variation in individual fitness (Harrison et al. 2011). For example, adult Brent Geese with offspring are limited in habitat choice due to the low foraging efficiency of their juveniles; this leads to a carry-over effect where parents are less likely than expected to breed again the following year (Inger et al. 2010). The non-breeding period can be a time of substantial exploratory movement, which informs decisions on where to settle or breed, and whom to breed with. Understanding how animals move between breeding attempts and the underlying mechanisms that drive these movements has important and far reaching applications. An example of this is investigating declines in animal abundance (Sherry & Holmes 1995; Sillet, Holmes & Sherry 2000).

Sampling only breeding animals is also problematic because it detects only a fraction of the population, excluding individuals that do not breed (e.g. Smith & Arcese 1989; Mönkkönen 1990; Newton 1992), fail before they can be identified (Chapter 2; Heisy & Nordheim 1995), or breed but are not found (Prévot-Julliard, Lebreton & Pradel 1998). Unfortunately, it is difficult to quantify the non-breeding component of populations (Newton & Rothey 2001; Vogeli et al. 2008). Nonetheless, individuals that are not detected breeding are a well-defined component of animal populations and theory shows that the presence of these individuals can have substantial effects on populations. For instance, the presence of non-breeders alters the stability of pop-

ulation size (see review by Gordon 1997). Furthermore, declines in population rates can be underestimated when non-breeders are not taken into account during censuses (Kokko & Sutherland 1998; Kenward et al. 2000). It is therefore important to try and determine what categories of individuals are not detected breeding, whether those individuals exhibit different behaviours outside of the breeding season, and what the consequences are for the structure and connectivity of populations throughout the year.

There are a number of reasons why some individuals may not be sampled during certain times of the year. For example, several studies of individually marked birds have shown that sampling breeding birds can underestimate the number of males in the population due to an excess of non-breeding male individuals (Ekman & Askenmo 1986; Mönkkönen 1990; Orell et al. 1994). This excess of is often attributed to a lack of a breeding partner due to sex biased mortality rates (e.g. Lack 1954; Bulmer & Perrins 1973; Ekman 1984). Age also influences an individual's detectability (Pradel et al. 1997; Tavecchia et al. 2001; Bouwhuis et al. 2012) and younger birds are less likely to be detected breeding (Newton 1992; Orell et al. 1994). Residency status can influence detectability at certain times of the year; winter transients have been shown to be over represented in data collected during the non-breeding period (Bauchau & Van Noordwijk 1995). In addition, by identifying early nest failures, we have previously shown that immigrants are less likely to be detected during the breeding season than residents (Chapter 2). This may be due to deferred costs of dispersal (Stamps, Krishnan & Reid 2005) such as delays in mate acquisition (Pärt 1994; Lozano, Perreault & Lemon 1996). Differences in habitat can also influence an individual's detection probability during certain times of the year. Non-breeders have been shown to occur in poorer quality areas that have higher levels of anthropogenic disturbance (Penteriani, Ferrer & Delgado 2011). Previous work has also shown that an individual may delay reproduction in order to gain a higher quality territory in a

later reproductive attempt (Zack & Stuckbury 1992; Ens et al. 1995).

Investigating the detectability of individuals within populations across seasons has traditionally been difficult; this is largely due to difficulties associated with tracking individuals between periods of the annual cycle (Harrison et al. 2011). However the development of cheap RFID technology allows us the opportunity to follow large numbers of individually recognisable animals at a scale that was previously not possible. In this study, we use a large dataset collected through extensive sampling of individuals fitted with PIT tags to investigate (i) the effects of sampling technique on estimates of population structure; (ii) the demography of wintering and breeding populations in order to predict which birds may go undetected at certain times of the year based on age, sex, residency status, or habitat characteristics, and (iii) how winter detection patterns are influenced by demographic characteristics. In doing so, we aim to learn more about individual detectability and movements throughout the year. Such interactions will thereby influence patterns of gene flow and responses to selection.

3.2 Methods

3.2.1 Study population and data collection

This study was conducted on a population of great tits in Wytham woods, a mixed deciduous woodland in Oxfordshire, UK (51 ° 46', 1 ° 19'W). The study site consists of a discrete 388 ha area of contiguous mixed woodland that is isolated from other woodlands by agricultural landscapes. The great tit is a monogamous hole-nesting species that is territorial during the breeding season and flock-living during the winter (reviews in Perrins 1979; Ekman 1989). Great tits within Wytham have been fitted with a PIT tag moulded into a plastic leg ring in order to investigate the social ecology in this population (Aplin et al. 2012; Farine, Garroway & Sheldon 2012).

PIT tagging commenced in the spring of 2007 when all breeding great tits and pulli were tagged at nest boxes (Table 3.1). The tags consisted of a 12mm glass PIT which operated at a frequency of 125KHZ (supplied by Francis Scientific Instruments Ltd, UK) and were glued to a plastic colour ring. These tags continued to be fitted on all captured tits through to the winter of 2008/09. They were replaced in the spring of 2009 by a second generation of tag design, with the glass PIT encased in white plastic attached to a ring. This negated the chance of the PIT becoming unglued, which was a possibility with the first tag type. The second generation tags were manufactured by CORERFID, UK and used on all great tits until the spring of 2010. It was later discovered that this design potentially led to a small number of leg injuries in 3% of the PIT tagged population, so no adults or pulli were tagged at nests in 2010. In the winter of 2010, a third generation of tag was designed that continues to be used currently. These designs have the PIT fully encased in plastic, moulded to a plastic ring of the same length (Manufactured by IB Technology, UK). The proportion of the total population that is PIT tagged is estimated at over 90%, (see Aplin et al. 2013). The number of great tits tagged in consecutive years and a breakdown of PIT tag designs is shown in Table 3.1. Great tits residing in Wytham are subject to year round monitoring, both through the trapping of breeding adults, and trapping throughout the winter.

(a) Breeding season sampling

The great tit population in Wytham has undergone long-term nest monitoring surveys since 1947. There are currently 1020 nest boxes distributed throughout the woods which are used by breeding great tits in the early summer (April-June). Every breeding season, nests are checked weekly to obtain records of breeding parameters in accordance with the protocol followed by the long term population study; further details of which are described elsewhere (Perrins 1965; Gosler 1993). All Wytham

hatched individuals are fitted with a uniquely identifiable metal ring at the nest when they are 14 days old. In addition, Breeding individuals are trapped at the nest using spring traps whilst feeding 7-12 day old nestlings and fitted with a ring and PIT tag (unless already ringed). Any unringed individuals caught as adults are assumed to be immigrants to the population (i.e., not fledged from a nest box within Wytham woods) – see Chapter 2 for further discussion of this assumption.

(b) Winter sampling

Juveniles and adults aggregate into loosely formed flocks over autumn and winter (September–March). During this time, individuals are detected using two methods; mist netting and automated RFID logging detection systems. Across all years, at varying intensities, great tits have been trapped using mist nests at a seed feeder. For the duration of the study period, from November to February, one 18m net was set at fixed centrally located site within the woods on a weekly basis. In addition to this, teams of people operated two-three nets simultaneously in close proximity to one another and moved every week to cover the entire study area. Between September 2007 - February 2008, unstandardized mist netting efforts took place throughout the woods, with ~50 days spent catching. In the winter of 2008/09, a total of 56 days were spent catching at multiple sites per day from late August to late February. In the winter of 2009/10, mist netting procedures were similar to those used in the previous winter, a total of 56 days were spent catching at multiple sites between August and early March. In the winter of 2010/11, mist netting efforts were more frequent and catching occurred 6 days per week, across multiple sites consecutively for a 3 month period. In the winter of 2011/12 and 2012/13, in addition to the centrally located feeder, teams of ringers would consecutively operate three-four nets at regularly spaced intervals throughout the study site. On average, 68 days were spent ringing between multiple sites from mid-August to early March in these years.

In addition to trapping with mist nets, the winter population was monitored remotely using a PIT tag based logging system. We installed automated feeding stations in a stratified grid at 65 locations throughout the woods (See map in Chapter 1); these feeders were fitted with RFID antennae in place of the perch for both access holes (manufactured by Francis Scientific Instruments Ltd, UK). When an individual visited the feeder, its identity was transmitted by the tag and stored with a timestamp by the attached data logger. The specific RFID sampling regime varied across years throughout this study (Table 3.1). From 2007- 2009, 16 feeders were randomly rotated between 65 sites every four days. Feeders were constantly open and logged continuously during this period. In the winter of 2010/11 the logging system was extended so that a feeder remained in place at each of the 65 sites for the duration of the winter. These feeders opened and closed automatically at dawn and dusk and recorded visits every three seconds, alternating between access holes (Manufactured by Dorset Identification, Netherlands). This interval was chosen based on video footage of individual visits to a feeder. Feeders logged for two consecutive days each week, with the feeders closed at other times and not recording visits. Logger sites provide reliable coverage throughout the study site and because feeders are only open on two consecutive days, they do not provide a stable food source which prevents individuals from becoming reliant on them. By only supplying food for two days per week, natural population regulation processes were likely to have been in operation when food was not available; great tits do not store food, and therefore the benefits of utilising supplementary food are likely only to be felt during the periods when it is available. Feeders were in place for a two week period in February of the winter of 2010/11. In the winter of 2011/12 and 2012/13 the feeders were in place and logging from Sept-March. Only logging sites that were within the boundaries of the main woods were included in analyses; the four logging sites in external areas surrounding the woods were excluded. For a full breakdown of automated winter logging details

see Table 3.1.

3.3 Statistical analyses

3.3.1 Comparisons of recapture methods

Our first objective was to determine whether varying recapture methods resulted in similar demographic estimates within samples of birds collected during (i) breeding nest surveys, (ii) RFID detection systems and (iii) mist netting. Simple contingency tables were used to examine the relationship between each sampling technique and age, sex and residency status. For all analyses, individual characteristics were binary such that age was categorised as either 'first year' or 'adult'. Residency status was defined as resident or immigrant depending on whether the individual was born in a Wytham nestbox or not, respectively. Only pulli that had been detected since being ringed at nest boxes (i.e., first years) were included in these analyses. All Statistical tests were performed in the R environment, version 2.12.2 (R Core Team 2012).

3.3.2 Detections across consecutive seasons

a. Breeding detectability

Our second objective was to explore intrinsic and extrinsic determinants of an individual's detectability across seasons. We aimed to test the following hypotheses:

1. Young and old individuals are less likely to be detected breeding
2. Males are less likely to be detected breeding than females
3. Immigrants are less likely to be detected breeding than residents

In order to do this, generalized linear mixed models (GLMMs) with a binomial error structure were run on subsets of the full data set. The first GLMM investigated

whether individuals that were detected in consecutive winter seasons were also detected in the intervening breeding season. These data included any individual that had been seen in two consecutive winters (between 2007/2008 and 2011/2012, n=2184 individuals). In such a case, when an individual had been detected in successive winters, the individual was considered to be present in terms of the Wytham breeding population. The status of individuals in the intervening breeding season was recorded as undetected or detected. Within a matrix, individuals that were not detected breeding were assigned a "0" and those that were detected breeding were assigned a "1". For the analysis, fixed effects included age (in years during the intervening breeding season), the quadratic effect of age, sex, the interaction between age and sex (age*sex interaction), and residency status (immigrant or locally born). For a full breakdown and justification of each effect included in analyses see Table 3.2. In the model, age is based on year of birth for locally born birds, or plumage characteristics (Svensson 1992) for immigrants. In Wytham, 91% of immigrants enter the population as yearlings (Perrins 1979), so exact age is known for these birds. For immigrants that were first caught with adult plumage, a minimal age of two years was assigned (Bouwhuis et al. 2012). So that both the linear and the quadratic effects of age could be interpreted in the same model the age term was centred (following Schielzeth 2010). Year of detection (n=5) and ring number (n= 1310) were included as random effects in the model.

A second GLMM was run on this subset of data (including any individual that has been seen in two consecutive winters) to investigate any possible effects of the RFID logger distance to the edge of the woods on detectability. This was done in order to determine if an individual's location in relation to the edge of the woods during the winter, affected its detectability the next season. Only individuals detected during the winters of 2011/12 and 2012/13 were included in this analysis because loggers were only in place continually at all 65 sites within the woods during these winters

(Table 3.1). RFID logger distance to the edge of the woods was assigned to individuals based on the distance to the edge of the woodland in metres from the site where an individual was most frequently detected across the winter. Fixed and random effects were included as in the full model above.

Finally, because males are harder to catch at the nest than females (McCleery et al. 1996), a third GLMM was run on this subset of data in order to investigate if any sex effects were influenced by successful breeding attempts within the study area for which the male was not caught. In order to account for any males that bred but were not caught in the data set, we determined the breeding attempts where no male was caught and removed the corresponding females (n=171 individuals). In doing so, we aimed to test if any shortfall of males detected breeding was due, in part, to males being harder to catch at the nest. For the analysis, fixed effects included age (in years during the intervening breeding season), age^2, sex, age-sex interaction, and residency status. Age was assigned and centred as described in the model above. Year of detection (n=5) and ring number (n= 1193) were included as random effects in the model. This analysis indicates if sex biases in detection rates are influenced by the sample of males that are not caught at the nest each year. Once these males were accounted for (i.e. corresponding females removed from our analysis), we expected the ratio of males to females detected breeding to become more balanced.

We also investigated the repeatability of the likelihood of detection during breeding surveys for this subset of individuals where presence was (1) and absence (0). We calculated repeatability and its associated standard error and 95% confidence interval using GLMM-based repeatability estimation (rptR package in R, Nakagawa & Schielzeth 2010) with a binomial distribution and logit-link. These data consisted of any individual that was resident in Wytham over two breeding seasons (n=487).

b. Winter detectability

In order to further explore intrinsic and extrinsic determinants of an individual's detectability across seasons. Another GLMM was used to investigate whether individuals that were detected in consecutive breeding seasons were also detected in the intervening winter.

We aimed to test the following hypotheses:

1. Young individuals are more likely to be detected in the winter than older individuals

2. Immigrants are more likely to be detected in the winter than residents

3. Males are more likely to be detected in the winter than females

Data used in this analysis included any individual that was seen in two consecutive breeding seasons (between 2007 and 2012, n=1484). Individuals were considered to be present (assigned a binomial value "1") in the Wytham winter population if they were detected in successive breeding seasons. Any individual not detected in the intervening winter was considered to have not been present ("0") in the woods during winter. Only first year and adult individuals were included in this model; pulli that were ringed at nest boxes and detected breeding the subsequent year were not included. Fixed effects included age (in years during the intervening winter season), age^2, sex, age-sex interaction, residency status and nestbox distance to the edge of the woods. For a full breakdown and justification of each effect included in analyses see Table 3.2. Age was assigned and centred as in the model above. The distance to the edge of the woods of the nestbox where an individual was detected breeding was based on the number and distribution of edges in close proximity to each breeding location. Edge distances were calculated by Wilkin et al. (2007) and the average distance of nest boxes to the edge of the woods was 120.9m, ranging from 0.7m to

535.5m. Year of detection (n=5) and ring number (n=1063) were included as random effects in the model.

As above, we investigated the repeatability of the likelihood of detection during winter for this subset of individuals, where presence was (1) and absence (0). We once again used GLMM-based repeatability estimation (rptR package in R, Nakagawa & Schielzeth 2010) with a binomial distribution and logit-link. These data consisted of any individual that was resident in Wytham over two winters (n=210). Pulli that were ringed at nest boxes and detected breeding the subsequent year were not included in this analysis.

3.3.3 Winter RFID detection patterns

Our final objective was to investigate how winter detection patterns are influenced by demographic characteristics. Only individuals that were ringed prior to the start of collection of RFID data were included in these analyses; excluding any immigrants to the study site that were tagged during the focal winters. Our first model evaluated the relationship between individual characteristics and the distance to the edge of the woods of the site that an individual frequented the most. In order to do this we used a GLMM with a gaussian error structure. For a full breakdown and justification of each effect included in analyses see Table 3.2. Fixed effects included age, age^2, age-sex interaction, the year of detection (winter) and residency status. Distances to the edge of the woods data were transformed (square root) to meet the assumption of normality. Ring number (n=990) were included as random effects. Only data collected during the winter of 2011/12 and 2012/13 were used in these analyses as RFID detection systems were in place across the entire study site during this time (Table 3.1).

A second GLMM investigated the relationship between how often each individual was detected at logger sites and whether it correlated with demographic character-

istics. We calculated the number of days that every individual was detected across all sites for the duration of the winter logging period. We expected that less dominant, immigrant and younger individuals would be detected at feeders more often. For a full breakdown and justification of effects included in analyses see Table 3.2. Fixed effects included age, age^2, age-sex interaction, the year of detection (winter), residency status, the interaction between age and residency status, and distance from the RFID logger site to the edge of the woods. RFID logger site (n = 61) and ring number (n=990) were included as random effects.

3.4 Results

3.4.1 Comparisons of recapture methods

A total of 13,125 individual great tits were fitted with both metal rings and PIT tags throughout the study (Table 3.1). Of these, 1314 (10 %) were ringed and PIT tagged as adults breeding at nest boxes and 9801 (75 %) were ringed at nest boxes as pulli. During the autumn and winter, 2010 (15%) adults were ringed and PIT tagged during mist netting (Table 3.1). Over the duration of the study, of the 1314 individuals that were first PIT tagged as adults at nest boxes, 404 (31%) were subsequently detected by mist netting and 635 (48%) by RFID detection systems. Of the 9801 individuals that were tagged as pulli at nestboxes, 1187 (12%) were subsequently detected by mist netting and 1689 (17%) via RFID detection systems. 738 (37%) of the 2010 individuals that were initially pitted at mist nets during the winter were detected at RFID detection loggers. Over the study period, a total of 1825 individuals that were already carrying PIT tags were re-trapped at mist nets. The number of individuals from each breeding and winter cohort that were seen across the study period are presented in Table 3.3. Around half of the adults detected breeding in any given year were detected in the following winter of the same year (Table 3.3); a third of

these were subsequently detected breeding the following year. The proportions of individuals detected from one year to another are similar across the study period (Table 3.3).

The sex ratio differed significantly within samples collected by varying techniques (χ^2=46.52 df=2 P<0.001); samples collected during the breeding season had a higher proportion of females than those collected in the winter using RFID and mist netting (χ^2=23.64 df=1 P<0.001, χ^2=42.21 df=1 P<0.001, respectively; Table 3.4). Sex ratios within samples collected in the winter were similar regardless of the sampling technique (χ^2=1.476 df=1 P=0.22; Table 3.4).

The proportion of immigrants to the study site also differed significantly across samples (χ^2= 201.44 df=2 P<0.001; Table 3.4). Significantly fewer immigrants were detected using RFID compared to those detected breeding (χ^2=110.99 df=1 P<0.001; Table 3.4) and in the winter via mist netting (χ^2=181.34 df=1 P<0.001; Table 3.4). The proportion of immigrants detected breeding did not differ from those detected via mistnetting (χ^2=3.5 df=1 P=0.06; Table 3.4). Since immigrants cannot be detected by RFID methods until they have been either mist netted, or caught breeding, this difference is unsurprising.

Differing sampling techniques also detected significantly different numbers of first years and adults within samples (χ^2= 594.51 df=2 P<0.001; Table 3.4). Adults were significantly more likely to be detected breeding than in the winter via RFID and mist netting (χ^2= 321.28 df=1 P<0.001, χ^2=546.25 df=1 P<0.001, respectively; Table 3.4). Winter sampling techniques detected significantly more first years, although proportions significantly differed between the two techniques (χ^2= 42.061 df=1 P<0.001), with mist netting detecting less adults and more first year individuals than RFID loggers (Table 3.4).

3.4.2 Detections across consecutive seasons

There was no significant relationship between detection probabilities of adults during the breeding season and either the linear or quadratic components of age (β=0.351 P=0.278, β=-0.051 P=0.220, respectively; Table 3.5). Our results show that males are less likely to be detected breeding than females (β=-1.108 P<0.001; Table 3.5; Fig 3.1). Our results suggest that this is unlikely to be because males are harder to catch at the nest as we determined the breeding attempts where no male was caught and removed the corresponding females from the data. After the subsample of females were removed, the effect was still significant suggesting that sex differences in detectability do not result from males being more difficult to catch at the nest (β=-0.73±0.317 z value= 2.304 P=0.021; Fig 3.1).

We found no significant interaction between age and sex (β=0.083 P=0.558; Table 3.5). Our measure of residency status does not explain significant variation in detectability during the breeding season (β=-0.211 P=0.278; Table 3.5), with immigrants to the study site and locally born individuals having similar detectability. There was no relationship between detectability during the breeding season and the location of the site where an individual spent the majority of its time in the winter; individuals that frequented sites closer to the edge of the woods had the same likelihood of being detected breeding as those that frequented more centrally located sites (β=-0.003±0.002 z value=1.359 P=0.174). Hence, to summarise, detection likelihood in the breeding season was not strongly influenced by age, residency status or the location that an individual most frequented during the previous winter season.

There was no significant relationship between detection probabilities of adults during the winter season and either the linear or quadratic components of age (β=-0.123 P=0.148, β=0.016 P=0.692, respectively; Table 3.6). We also found no significant relationship between sex and the likelihood of detection during the winter (β=0.113 P=0.370; Table 3.6), and the interaction between age and sex was not significant

(β=0.092 P=0.462; Table 3.6). Additionally, there was no effect of an individual's residency status on detectability during winter (β=0.006 P=0.961; Table 3.6). There was a slight significant positive relationship between detectability in the winter and the location of an individual's territory during the breeding season. Nest box distance from the edge of the woods in the breeding season was a significant indicator of detection probability the following winter (β=0.002 P=0.047; Table 3.6); an individual that bred closer to the edge of the woods was less likely to be detected in the winter.

Our results show that the likelihood of detection during breeding nest surveys is repeatable across years (R=0.884 CI= 0.83-0.93 P<0.001; Table 3.7; Table 3.8). This suggests that not being detected breeding one year can predict the likelihood of being detected the next year. Similarly we found that the likelihood of detection during winter is repeatable across years (R=0.67 CI=0.60-0.79 P<0.001; Table 3.7; Table 3.8). Hence, individuals are consistent in their detectability across sampling periods.

3.4.3 Winter detection patterns and demographic characteristics

We found no significant relationship between the linear and quadratic components of age and the location of the RFID site where an individual spent the majority of time in relation to the distance to the edge of the woods (β=0.075±0.199, β=-0.023±0.029, respectively; Table 3.9). There was also no relationship between sex and RFID site preference (β=-0.099±0.182; Table 3.9). Additionally, the interaction between age and sex was not significant (β=0.023±0.118; Table 3.9). Our results show no significant relationship between residency status and the distance from the edge of the woods of the site where an individual is detected the most during the winter (β=0.215±0.192; Table 3.9). The year of detection had an effect on whether individuals were more likely to spend their time at sites located closer to the boundaries of the woods (β=-0.251±0.107; Table 3.9).

Our results show a significant relationship between the linear and quadratic components of age and the number of days that an individual was detected by RFID loggers during the winter; with middle aged birds being detected more often (β=9.681±1.160, β=-1.189± 0.169, respectively; Table 3.10; Fig 3.2). We found that males used the feeders significantly more often than females (β=4.439±0.813; Table 3.10; Fig 3.3), although the interaction between age and sex was not significant (β=-0.669±0.640; Table 3.10). There was a significant effect of residency on the number of days that an individual was detected at RFID feeders; residents visited feeders more often than immigrants (β=2.545±0.868; Table 3.10). The distance of the RFID logger site to the edge of the woods did not explain variation in the number of days that individuals visited feeders (β=0.137±0.168; Table 3.10). There was an effect of year on an individual's propensity to visit the feeders (β=7.958±5.454; Table 3.10; Fig 3.4).

3.5 Discussion

We use a large data set collected through extensive sampling of individuals fitted with PIT tags, to follow individuals across seasons and investigate some of the mechanisms underlying these movements. We quantify the proportion of individuals sampled using varying recapture techniques, and show that different techniques vary in their ability to capture different parts of an overall population's structure. The sex ratio was equal during the winter regardless of the sampling technique used, and skewed during the breeding season; this may suggest that we are not sampling males as efficiently as females during breeding censuses. We identify sex as a predictor of failure to breed locally, with males less likely to be detected breeding. After removing the equivalent sample of females from analyses, our results suggest that differences in breeding detectability between sexes are not due to males being harder to catch at the nest. Nest box distance from the edge of the woods during the breeding season had a significant effect on an individual's detectability the following winter; a bird that bred closer

to the edge of the woods was less likely to be detected the following winter. These results suggest that the complex interactions between individuals during the breeding season may influence their detectability in subsequent stages. During the winter, our results indicate that individual characteristics are not significant predictors of winter residency, although they do affect patterns of movement, with younger immigrants being more transient.

A key finding from this study is that males are less likely to be detected breeding than females. This excess of non-breeding males has previously been shown in Wytham (Krebs 1970; Perrins 1979) and other populations (Ekman and Askenmo 1986; Mönkkönen 1990; Orell et al. 1994). We were able to show that this variation is unlikely to be because males are harder to catch at the nest. Furthermore, we found no difference in detectability between males and females during the winter. Although we cannot be sure that undetected males failed to breed altogether, as they may have bred outside of the woods, it is possible that they did not manage to establish a territory.

During the winter, we found that individual characteristics were not significant indicators of winter residency. However, they do affect patterns of movement throughout the season. Older birds are more dominant than juveniles (Sandell & Smith 1991), so have more to gain by being resident in the winter. Although we did not find any effect of age on winter residency, our results show that older birds are less transient than younger individuals. This may be due to dominance effects, since older birds are generally higher in the dominance hierarchy and are therefore more likely to monopolise supplementary food at RFID loggers by excluding or usurping younger subordinates (Krebs, MacRoberts & Cullen 1972; Laet 1985). In addition males may need to stay close to breeding sites to defend territories and become familiar with conspecifics, whereas females can move outside of the woods into better feeding sites, such as in nearby gardens. Conversely, males may potentially force females out of the

woods through competition for limited resources. Data collected during the winter via RFID suggest that this may be the case, as males use the feeders more often than females.

These dominance interactions may also drive the effects of habitat on detection rates. We show that an individual that bred closer to the edge of the woods is less likely to be detected in the winter. This may be a result of spatial partitioning where more dominant birds exclude less dominant individuals from core zones, leaving them to associate in bordering areas. Within Wytham, birds that occupy territories closer to the centre of the woods during the breeding season have higher reproductive success (Wilkin et al. 2007). Similarly, it may follow that individuals that breed closer to the centre of the woods are more dominant and have more to gain by being resident in the winter. During the winter, dominant birds may drive the less dominant individuals out of the woods for competition over resources, to return the next spring for breeding (Drent 1984).

We found that the likelihood of detection during breeding nest surveys is repeatable across years; not being detected breeding one year indicates whether an individual is likely to be detected the next. This may suggest that certain individuals are less likely to be detected as a function of their phenotype other than the intrinsic factors we investigated such as age and residency status. For example, variation in individual quality such as body condition (Dubiec 2011) and cognitive abilities (Cole et al. 2012) has been shown to influence fitness, which may affect detectability during nest surveys (Chapter 2).

We show that individuals have different detectability as a function of their phenotypes. As a consequence sampling individuals at a specific time of year, i.e. breeding, will result in a non-random subset of individuals from the whole population, excluding non-breeding birds that are more likely be male. These biased samples have consequences for ecological conclusions. For example, survival estimates have been

shown to differ due to sampling period, independently of the sampling technique used (Bauchau & Van Noordwijk 1995). Moreover, previous work has found a strong relationship between breeders and non-breeders of the same population, suggesting that non-breeder dynamics may affect breeding population mechanisms, including density dependence (Kokko & Sutherland 1998; Penteriani et al. 2005). Density dependence affects life-history traits and is one of the key processes regulating bird population dynamics (Lack 1954). However, most density dependence studies have focused primarily on breeding populations, and have generally ignored the possibility that non-breeder mortality has the potential to affect demographic rates (Penteriani, Ferrer & Delgado 2011). Additional estimates that rely solely on data collected on breeding individuals may also be compromised. For example, previous studies suggest that there is sex biased mortality within Wytham based on samples of individuals detected breeding (Clobert et al. 1988; Bouwhius et al. 2012). As the non-breeding component is missing from these estimates, this may not be due to increased mortality of either sex and could in part be due to an absence of one sex during sampling.

Other ecological consequences of any potential sex bias during the breeding season require further investigation. For example, surplus males are supposed to be responsible for an apparent lack of impact of sparrowhawk presence on breeding tit density (Newton, Dale & Rothery 1997); during the incubation period females have a lower predation risk. Furthermore, unpaired males might father extra pair offspring (Ewen, Armstrong & Lambert 1999; Kempenaers et al. 2001), which can result in biased estimates of reproductive success if only paired males are known. Rates of extra pair paternity in chicks within Wytham are currently estimated at 12.7% (Patrick et al. 2012) and unpaired males may father some of these offspring. Failure to detect males that breed can arise from multiple sources. Firstly, males are harder to catch at the nest than females (Mcleery et al. 1996), although our results suggest that this does not account for a significant amount of undetected breeding males in this study.

Second, there is no way of identifying males that fail early before they are caught on the nest with older chicks and we have no way to assess the frequency of this cause. Although we suggest that failure to establish a territory and attract a female seems likely to underlie the excess of resident males that are non-breeders in Wytham.

Birds are among the most intensively studied group of animals with respect to life history evolution (Lessells 1991) and although a large array of methods have been developed to monitor populations, most studies focus on the breeding season as a sampling period. In this study, we provide empirical data involving more diversified life histories to compare the demographics of wintering and breeding populations within Wytham. We show that the sampling period for surveying natural populations can introduce systematic bias that will influence conclusions on population demography. The age, residency status, habitat and sex-specific seasonal correlations shown here illustrate the importance of sampling individuals within populations during different stages of their life history. We suggest that more attention should be given to the sampling period, particularly when sampling during breeding seasons, and that future population level studies should attempt to account for classes of individuals that will be routinely missed.

3.6 Tables and figures

Table 3.1: A breakdown of methods of PIT tagging and RFID recapture techniques used to monitor a population of great tits within Wytham woodland from the summer of 2007 to the winter of 2012/13. Individuals were either PIT tagged breeding (BR) as adults or pullus at nest boxes, or as adults during the winter (WI) in consecutive years.

Cohort	No. of newly PIT tagged adults	No. of pulli PIT tagged at the nest	Type of PIT tag used	RFID Logging regime	RFID Logging dates	RFID Logger schedule
BR 2007	768	2878	blue glued			
WI 2007	207		blue glued	16 logger rotation	Aug-Mar	3-4 days until seed empty
BR 2008	215	2076	blue glued			
WI 2008	140		blue glued	16 logger rotation	Sep-Feb	3-4 days until seed empty
BR 2009	120	1873	white tube			
WI 2009	149		white tube	16 logger rotation	Sep-Feb	3-4 days until seed empty
BR 2010	10	0	white tube			
WI 2010	776		new model	one at every site (65)	Two weeks in February	1 day per week
BR 2011	145	1773	new model			
WI 2011	502		new model	one at every site (65)	Sep-March	2 consecutive days per week
BR 2012	56	1201	new model			
WI 2012	236		new model	one at every site (65)	Sep-March	2 consecutive days per week

Table 3.2: Fixed effects included in GLMMS investigating detectability of individual great tits within Wytham woods. Each effect and its justification for inclusion in a model is shown in the table. Model abbreviations include: BD, Breeding detectability; WD, Winter detectability; DI, Distance to the edge of the woods from RFID site; ND, Number of days detected at RFID sites.

Fixed predictors	**Description/levels**	**Justification**	**Models incl. as a variable**
Age in years*	Continuous, range 1-9	Age has been shown to influence detectability (Newton 1992; Orell et al. 1994; Pradel et al. 1997; Tavecchia et al. 2001; Bouwhuis et al. 2012)	BD, WD, DI, ND
Age^2	Continuous, range 1-81	In this population individuals have been shown to undergo reproductive senescence (Bouwhuis et al. 2012) which may affect detectability.	BD, WD, DI, ND
Sex	2-level factor, male or female	Sex has been shown to influence detectability (Ekman and Askenmo 1986; Mönkkönen 1990; Orell et al. 1994; Pradel et al. 1997; Tavecchia et al. 2001).	BD, WD, DI, ND
Residency status	2-level factor, immigrant or locally born	Residency status has been shown to influence detectability (Chapter 2)	BD, WD, DI, ND
RFID distance to woodland edge	Linear distance from the RFID site most used by each individual to the woodland edge. Continuous, range 12.6-392 m (mean 119.8 m)	Detectability has been shown to be influenced by habitat edge effects (Penteriani, Ferrer & Delgado 2011).	BD,ND,
Nest box distance to edge of woods	Linear distance from the breeding site (nest box) to the woodland edge. Continuous, range 0.7-535.5 m (mean 120.9 m)	Within Wytham, birds that occupy territories closer to the centre of the woods during the breeding season have higher reproductive success (Wilkin et al. 2007) which may influence detectability (Chapter 2)	WD, ND
Age*Sex interaction	Interaction between age and sex	Parids form strong dominance hierarchies in which males are dominant over females and younger individuals (Smith 1989; Sandell & Smith 1991; Lahti, Orell & Rytkönen 1996). This may influence detectability.	WD, DI, ND
Winter	The winters in which RFID data were collected	The specific sampling regime during the winter varied between the winters of 2011/12 and 2012/13.	DI, ND
Residency status * Age in years	Interaction between residency status and age in years	Parids form strong dominance hierarchies in which residents may be dominant over older immigrants (Smith 1989; Sandell & Smith 1991; Lahti, Orell & Rytkönen 1996). This may influence detectability.	ND

* So that both the linear and the quadratic effects of age could be interpreted in the same model the age term was centred (following Schielzeth 2010).

Table 3.3: Matrix showing the numbers of adult great tits detected breeding through nest surveys (BR) and during the winter (WI) through RFID detection systems and mist netting at seed feeders. Data shown are from the summer of 2007 to the winter of 2012/13. In each case the summer runs from April-June and the winter season runs from 2007/08 to 2012/13 from September through to March. Numbers in the same row represent a cohort of individuals, where the first value in each line gives the number of birds that were recorded for the first time in a given season. The proportion of individuals from each cohort recorded in subsequent sampling seasons is shown in parentheses below the raw values.

		2007		**2008**		**2009**		**2010**		**2011**		**2012**	
		BR	**WI**	**BR**	**WI**	**BR**	**WI**	**BR**	**WI**	**BR**	**WI**	**BR**	**WI**
2007	**BR**	768	419 (0.55)	301 (0.39)	219 (0.28)	112 (0.14)	67 (0.09)	45 (0.06)	16 (0.02)	5 (0.006)	4 (0.005)	3 (0.004)	3 (0.004)
	WI		898	397 (0.44)	354 (0.39)	157 (0.17)	112 (0.12)	77 (0.09)	34 (0.04)	15 (0.02)	15 (0.02)	8 (0.01)	7 (0.01)
2008	**BR**			688	408 (0.59)	206 (0.30)	128 (0.19)	90 (0.13)	42 (0.06)	11 (0.02)	20 (0.03)	16 (0.02)	10 (0.01)
	WI				954	366 (0.38)	266 (0.28)	143 (0.15)	84 (0.09)	37 (0.04)	52 (0.05)	26 (0.03)	23 (0.04)
2009	**BR**					514	278 (0.54)	189 (0.37)	88 (0.17)	44 (0.09)	47 (0.09)	31 (0.06)	23 (0.07)
	WI						1005	363 (0.36)	244 (0.24)	93 (0.09)	146 (0.15)	65 (0.06)	73 (0.07)
2010	**BR**							589	234 (0.40)	139 (0.24)	151 (0.26)	92 (0.16)	83 (0.14)
	WI								1094	262 (0.24)	369 (0.23)	196 (0.18)	228 (0.12)
2011	**BR**									445	284 (0.64)	183 (0.41)	164 (0.37)
	WI										1261	499 (0.40)	578 (0.46)
2012	**BR**											586	385 (0.66)
	WI												919

Table 3.4: The proportion of different categories of great tits detected during nest surveys (breeding), using automated Radio Frequency Identification (RFID) detection systems and mist netting during the winter between the summer of 2007 and the winter of 2012/13.

		Breeding	RFID detection	Mist netting
Sex				
	Female	0.56	0.49	0.48
	Male	0.44	0.51	0.52
Residency status				
	Immigrant	0.52	0.4	0.53
	Locally born	0.48	0.6	0.47
Age				
	First year	0.47	0.72	0.67
	Adult (older than first winter)	0.53	0.28	0.33

Table 3.5: Results of mixed models assessing whether adult great tits that are resident in winter (detected in two consecutive winters), are detected in the intervening breeding season within Wytham woods between 2007 and 2012. 1344 great tits were assigned to categories based on presence (1) or absence (0) during surveys of breeding birds between two consecutive winter detections. Year of detection (n=5, variance=1.03) and ring number (n=1310, variance=6.40) were included as random effects.

Fixed Term Probability detected breeding	$\beta \pm$ SE	z value	P
Age in years	0.351 ± 0.323	1.086	0.278
Age^2	-0.051 ± 0.323	-1.227	0.220
Sex, male	-1.108 ± 0.192	-5.773	<0.001
Age*sex interaction	0.083 ± 0.155	0.542	0.558
Residency status, locally born	-0.211 ± 0.194	-1.084	0.278

Table 3.6: Results of mixed models assessing whether great tits that breed within Wytham woods in two consecutive years, are detected in the intervening winter between 2007 and 2012. 1484 adult and juvenile great tits were assigned to categories based on presence (1) or absence (0) during surveys of non-breeding birds (during the winter), between two consecutive breeding detections. Year of detection (n=5, variance=0.094) and ring number (n=1063, variance=0.223) were included as random effects.

Fixed Term Probability detected in winter	β ± SE	z value	*P*
Age in years	-0.123 ± 0.085	-1.445	0.148
Age^2	0.016 ± 0.041	0.397	0.692
Sex, male	0.113 ± 0.126	0.896	0.370
Age*sex interaction	0.092 ± 0.125	0.735	0.462
Residency status, locally born	0.006 ± 0.125	0.049	0.961
Breeding (nextbox) distance to edge of woods	0.002 ± 0.001	1.930	0.047

Table 3.7: Repeatability (R) of the likelihood of detection for great tits during breeding nest surveys (a) and winter sampling (b). Great tits that were resident over either two breeding seasons, or two winters, were assigned to categories based on presence (1) or absence (0) in Wytham woods between 2007-2012.

Data	Model	Link scale		
		R	SE	95% CI
(a.) breeding detectability	GLMM with logit-link and additive overdispersion	0.884	0.027	0.83-0.93
(b.) winter detectability	GLMM with logit-link and additive overdispersion	0.670	0.055	0.61-0.79

Table 3.8: Count data of the detection combinations for great tits across two breeding seasons (a), and two winters (b). Great tits that were resident over either two breeding seasons or winters were assigned to categories based on presence (y) or absence (n) in Wytham woods between 2007-2012.

a.		Present in 1st breeding season	
		Y	N
Present in 2nd breeding season	Y	243	49
	N	52	143

b.		Present in 1st winter season	
		Y	N
Present in 2nd winter season	Y	123	37
	N	33	17

Table 3.9: Results of mixed models assessing whether great tits that visited automated RFID feeding sites within Wytham woods spent more time at sites located closer to the edge of the woods. A total of 1480 detections were collected over two winters (2011/2012, 2012/2013). Ring number (n=990, variance=7.298) were included as random effects. Parameter estimates in bold are deemed important in explaining variation in respective effect, as in each case 2xSE ± Estimate does not overlap zero.

Fixed Term	Estimate	SE	t value
Age in years	0.075	0.199	0.376
Age^2	-0.023	0.029	-0.778
Sex, male	-0.099	0.182	-0.548
Age*sex interaction	0.023	0.118	0.192
Residency status, locally born	0.215	0.192	1.115
Winter	**-0.251**	0.107	-2.333

Table 3.10: Results of mixed models assessing the number of days that individual great tits visited automated RFID feeding sites within Wytham woods. A total of 1480 detections were collected over two winters (2011/2012, 2012/2013). Ring number (n=990, variance=78.291) and the RFID site where each individual spent the majority of their time (n=61, variance=6.513) were included as random effects. Parameter estimates in bold are deemed important in explaining variation in respective effect, as in each case 2xSE ± Estimate does not overlap zero.

Fixed Term Number of days detected	Estimate	SE	t value
Age in years	**9.681**	1.16	8.345
Age^2	**-1.189**	0.169	-7.000
Sex, male	**4.439**	0.813	5.458
Age*sex interaction	-0.669	0.6403	-1.045
Residency status, locally born	**2.545**	0.868	2.93
Residency status, locally born* Age in years	**2.370**	0.66	3.592
RFID site distance to the edge of the woods	0.137	0.168	0.81
Winter	**9.343**	0.598	15.605

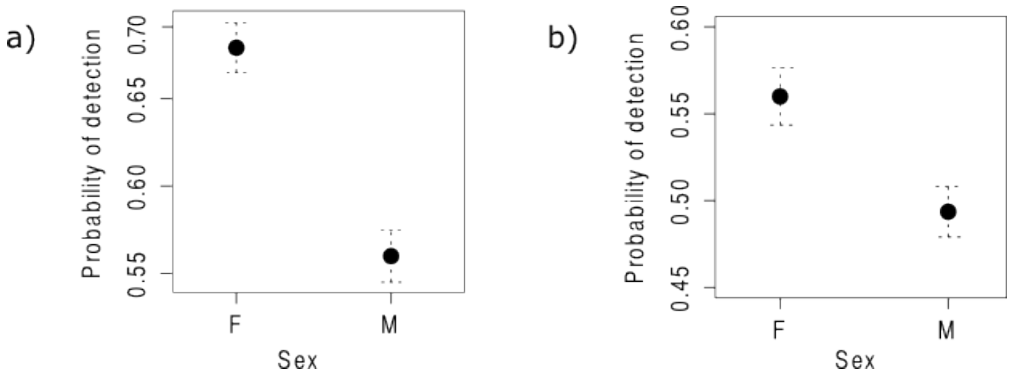


Figure 3.1: The proportion of male and female great tits detected during breeding nest surveys in Wytham woods between 2007-2012. All individuals were resident in the woods at the time of the surveys and were assigned to categories based on presence (1) or absence (0) during surveys of breeding birds between two consecutive winter detections (a). As males are harder to catch at the nest, we determined the breeding attempts where no male was caught and removed the corresponding females from the data set (b).

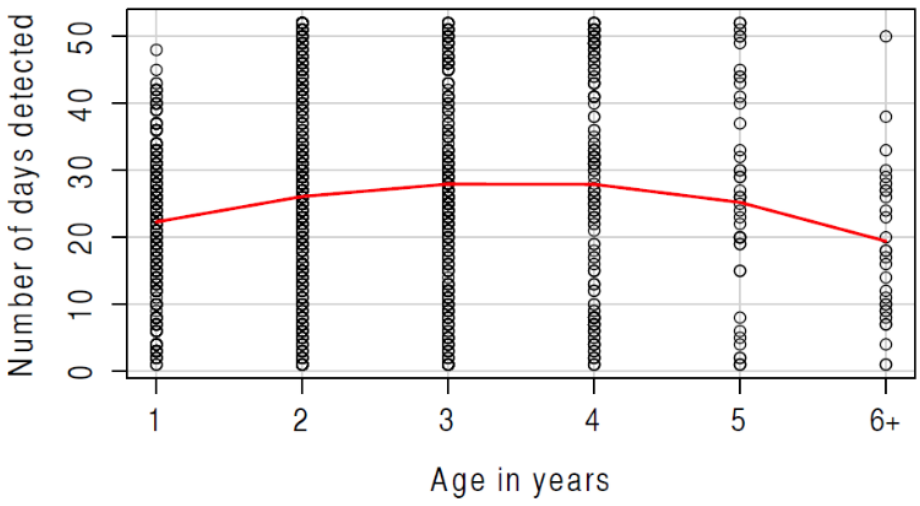


Figure 3.2: The number of days that individual great tits of different ages spent at RFID detection feeders within Wytham woods during the winters of 2011/12 and 2012/13.

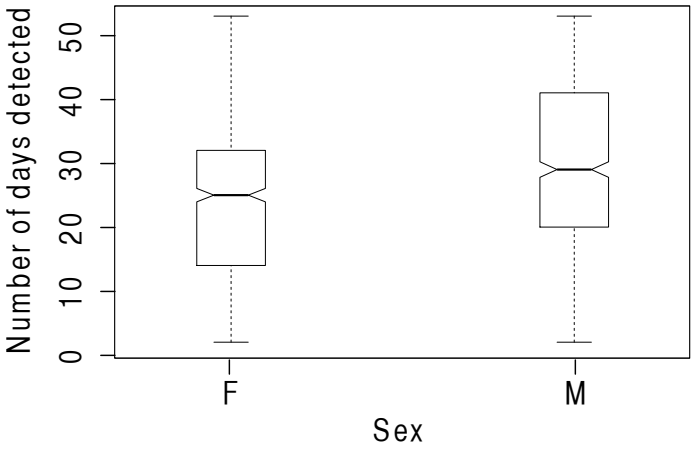


Figure 3.3: The number days that male and female great tits spent at RFID detection feeders within Wytham woods during the winters of 2011/12 and 2012/13.

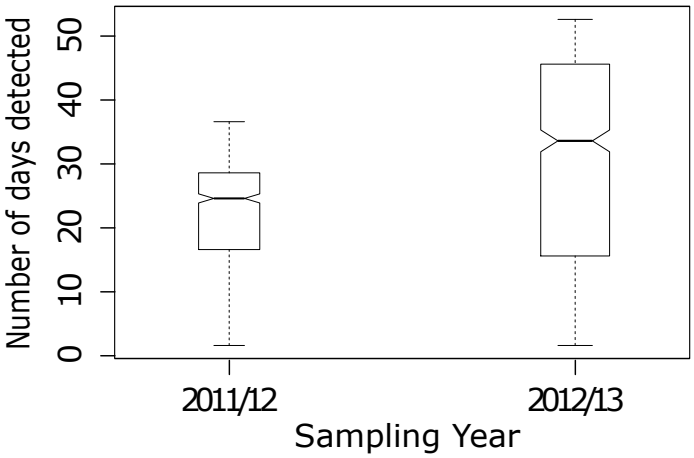


Figure 3.4: The effect of sampling year on the number of days that individual great tits spent at RFID detection feeders within Wytham woods over two winter seasons (2011/12 and 2012/13).

CHAPTER 4

GENERAL DISCUSSION



"The best solution to handle missing data is to have none"

-R.A Fisher

General Discussion

4.1 Discussion

In this thesis, I investigated how biases can arise in estimating individual variation in reproductive success and residence behaviour within a natural bird population. In this final chapter, I briefly review the aims and motivation for this study and summarise its main findings, before evaluating the robustness of the conclusions drawn and the implications they have for studies of natural populations.

4.2 Aims and motivation

The primary aim of this thesis was to investigate whether individuals that are detected using standard sampling techniques are representative of the entire population within a study site and how any bias may affect conclusions from ecological and evolutionary studies. Long-term monitoring of wild animal populations during the breeding season is one of the most powerful ways to study ecology and evolution and some key studies are responsible for a disproportionate number of publications in organismal biology (Clutton-Brock & Sheldon 2010a). Among the first long-term individual-based field studies of animals were those of tits (Paridae; Kluijver 1951; Lack 1954) and the Wytham study of great tits remains a key study system in evolutionary and behavioural ecology. The present work was motivated by the knowledge gap regarding individuals that remain undetected during standard surveys. Although the general statistical problem of missing samples has been well studied, issues associated with biased detection rates in the field within long-term population monitoring programs have received limited attention (Gitzen et al. 2012).

This thesis addressed two main reasons why individuals can go undetected using standard sampling techniques in wild animal populations. Firstly, the monitoring

scheme (e.g., timing of capture) can result in some individuals being undetected. For example, during nest surveys, breeding individuals are identified after they have reached a certain stage in their reproductive effort. In many species, some reproductive attempts may fail before individuals can be identified (Heisy & Nordheim 1995). Early identification of breeders can itself result in premature desertion of the nest (Kania 1992); for researchers, this leads to a trade-off between data collection and interference with the outcome of the breeding attempt. At present, little empirical data exists on individuals within populations that fail early in their reproductive attempt, before they can be identified. Currently, only one such study provides data on early reproductive failure in parids, but sample sizes were small (see Dhondt 1985). As such, there is little evidence for the expectation that individuals that fail early in their reproductive attempt represent a biased sample of the breeding population; observed breeding attempts form a non-random subset of the breeding population, under-representing individuals with poor reproductive performance. Individuals with low reproductive success may represent a biased sample of the total phenotypic variation within populations, with respect to both intrinsic and extrinsic factors. For example, reproductive success has been shown to vary with age (Clutton-Brock 1988; Sharp & Clutton-Brock 2009; Nussey et al. 2012), residency status (Wiggett & Boag 1993; Bensch et al. 1998; Orell et al. 1999) and local habitat quality (Högstedt 1980; Vehrencamp, Koford & Bowen 1988) in a wide range of species. Thus, while the sources of variation in reproductive success have been studied for decades, the causes and consequences of early reproductive failure are poorly understood. In this thesis, I used a non-invasive approach which allowed me to establish key intrinsic factors for large numbers of individuals early on in their breeding attempt with minimal effect on the breeding outcome.

A second reason why individuals can go undetected relates to the sampling season. Sampling during the breeding season may miss particular classes of individuals

that do not breed. Skipping breeding (the absence of breeding between years) is a widespread phenomenon for many species of birds (see Cam et al. 2008 for references within). However, most studies focus on long-lived species, such as seabirds and raptors (Newton & Rothery 2001; Sergio, Blas & Hiraldo 2009; Goutte et al. 2011; Danchin & Cam 2012; Tartu et al. 2013). As such, there is little information available on why passerines might not breed (Orrell et al. 1994). Furthermore, it is often assumed that conclusions based on breeding data also apply to non-breeding and wintering populations. For example, conclusions about the age structure of populations have been drawn from sampling breeders (Rebke et al. 2010; Sharp & Clutton-Brock 2010). The second key aim of this thesis was therefore to determine whether sampling during the breeding season results in accurate estimates of population composition and dynamics throughout the year. Specifically, I made use of different sources of data collected during the non-breeding period to better understand how age, dispersal and sex influence the likelihood of local breeding or winter residency. It can be difficult to follow large numbers of identifiable individuals during the non-breeding period because territoriality often breaks down and free roaming flocks form (Ekman 1989). There is reason to believe that population censuses carried out either during the breeding or non-breeding season systematically miss particular classes of individuals. Individuals may differ in how the move in and out of the population over time which has implications for detectability. For example, winter transients may be over represented in data collected during the non-breeding period (Bauchau & Van Noordwijk 1995). In this thesis, I therefore use RFID technology to track large numbers of individually marked great tits through the winter and compare these data to data collected during the breeding season.

4.3 Detectability and phenotypic variation within Wytham

The key finding from this thesis is that there are consistent differences amongst individuals that are routinely missed under the current sampling regime within Wytham woods. I show that different classes of individuals are missed from routine sampling in this population, as a result of early reproductive failures, failure to breed locally and non-winter residency. These individuals represent a non-random subset of the total phenotypic variation within the population with respect to age, sex and residency status (Table 4.1).

The results suggest that certain intrinsic and extrinsic characteristics predict under what survey method certain types of individuals may go undetected. For example, I show age and sex specific biases in detection rates in this population. First-year breeders are more likely to have higher rates of early nest failure than older females, and therefore are less likely to be detected during the breeding season (Chapter 2; Table 4.1). Males detected in the winter, which are considered to be resident in Wytham, are less likely to be detected breeding compared to females (Chapter 3; Table 4.1). Our findings therefore indicate that an excess of males remain undetected through current nest surveys. I showed that this is unlikely to be due to males being harder to catch at the nest than females: after accounting for males that bred but were not caught in our analyses, I still found an excess of non-breeding males (Chapter 3). Such an excess of non-breeding males has several potential implications for population dynamics. For example, unpaired males might father extra pair offspring (Ewen, Armstrong & Lambert 1999; Kempenaers et al. 2001), which can result in biased estimates of reproductive success if only paired males are known. Rates of extra pair paternity in chicks within Wytham are currently estimated at 12.7% (Patrick et al. 2012) and unpaired males may father some of these offspring. There is evidence in other studies that non-breeding males affect paternity estimates. Previous paternity

studies from natural populations of birds have shown that there is often a fraction of unassigned extra pair young to which paternity is unknown (Yezerinac, Weatherhead & Boag 1995; Foerster et al. 2003; Charmantier & Perret 2004; Li et al. 2009; Stewart, Westneat & Ritchison 2010). For instance, in one study 28% of all extra-pair young were sired by unknown males not found breeding in the study area; these extra-pair young accounted for the main difference in heterozygosity (Foerster et al. 2003). The unknown nature of these individuals makes it difficult to draw inferences about males that engage in extra-pair copulations within populations. Previous studies of identified individuals have shown that extra-pair males were larger and sing longer strophes than the cuckolded males in a Belgian population (Kempenaers et al. 1992; Kempenaers, Verheyen & Dhondt 1997).

I found that an individual's residency status strongly influenced its detectability within Wytham. Female immigrants to the study site had higher rates of early nest failure and were subsequently more likely to be missing from breeding surveys (Chapter 2; Table 4.1). Breeding detectability has previously been shown to vary with residency status in this population since the recapture probability of immigrants is lower than that of locally born females (Clobert et al. 1988; Bouwhuis et al. 2010). It is unclear what causes this difference in reproductive success and subsequent detectability, but I identified late arrival of immigrants to the breeding site as a reason for higher rates of early nest failure (Chapter 2). Some studies suggest that later arriving individuals incur higher reproductive costs through delays in finding mates or nesting sites (Lozano & Lemon 1999), and show that later arriving birds have a reduced likelihood of acquiring a breeding territory (Sergio, Blas & Hiraldo 2009).

Indeed, I showed that the quality of breeding habitat had a significant effect on early nest failure rates (Chapter 2; Fig 4.1). Site quality differences were also evident in the winter as individuals that bred in sites closer to the edge of the woods, which are likely to be of poorer quality (Wilkin et al. 2007) were less likely to be detected

in the winter (Chapter 3). I suggest that these habitat effects on detection rates are driven by the higher dominance of resident birds; in parids, resident birds that hold or have previously held a territory are more dominant than immigrants (Sandell & Smith 1991; Lahti et al. 1996). This may result in spatial partitioning where more dominant birds exclude less dominant individuals from core zones, leaving them to associate in bordering areas. Such spatial partitioning may directly affect rates of reproductive success and subsequent detection rates during breeding surveys. For example, within Wytham, birds that occupy territories closer to the centre of the woods during the breeding season have higher reproductive success (Wilkin et al. 2007). Previous studies have shown that higher proportions of immigrants were found at the woods edges during the breeding season and that laying later was typical of edge environments (Wilkin et al. 2007). Similarly, I found that birds laying late in the season increased rates of early nest failure (Chapter 2). The results in this thesis demonstrate that factors of ecological origin (e.g. reduced access to high quality sites and social subordination to older resident birds) may mediate differences in individual detectability throughout the year. For a full summary of the main findings in this thesis, refer to Table 4.1 and Fig 4.1.

4.4 Implications for understanding population dynamics

If a portion of the population remains unsampled in long-term studies of individually marked animals, this can have consequences for direct estimates of population growth, connectivity and for estimates of variation in key individual variables such as reproductive success (Gimenez et al 2008; Hadfield at al 2008). Above I discussed how detection bias may affect inference on population connectivity through immigration and emigration. Here, I will focus on biases in previous estimates of reproductive success which I quantified in Chapter 2. The effect of these missing individuals on estimates of population growth or decline was not specifically investigated in this

thesis but is briefly discussed below.

Our results showed that individuals missing from current sampling do not represent a random sample of the population in relation to age, sex and residency status. As a consequence, current fitness estimates that show reduced fitness of immigrants versus residents and reduced reproductive success for young individuals are likely to be underestimates. It is difficult to evaluate the extent to which failure to account for missing individuals' compromises estimates that rely solely on breeding data, but our results show that estimates of immigrant versus residents for fledging success are significantly altered once missing individuals are included in analyses (Chapter 2). There was no effect of residency status on fledgling success when analyses did not include early nest failure data. However, once early failures were included in analyses, immigrants were significantly less likely to fledge young than locally born birds. Differences in reproductive success between locally born and immigrant individuals have been identified within Wytham before (Clobert et al. 1988; Bouwhuis et al. 2010), but this study suggests that such differences may be greater and occur in more years than previously believed. Furthermore, residency status also contributes to the patterns of age specific reproductive performance in Wytham (Bouwhuis et al. 2009). Our results suggest that both the direct effect, and the age specific reproductive performance which they influence, may have been underestimated by the exclusion of the early nest failures, who are more likely to be immigrants.

The current literature reveals mixed results for the extent to which reproductive success of immigrants and locally born individuals differ. Some studies show that immigrants have lower rates of reproductive success (Part 1994; Julliard, Perret & Blondel 1996; Verhulst & Van Eck 1996; Orrell et al. 1999; Bensch et al. 1998; Wheelright & Mauck 1998), whereas others have shown that immigrants have equal or higher reproductive success than more established residents (Berger 1987; Krohne & Burgin 1987; Hoover 2003). This disparity between studies may in part be explained

by the incorrect estimation of differences between immigrants and residents. For example, the exclusion of undetected immigrants that fail early in their reproductive attempt. It would be interesting to test for the effect of sampling protocol on the strength and direction of the results using meta-analysis. If the Wytham woods great tits are representative, it may be that monitoring schemes that estimate reproductive failure late in the reproductive cycle are less likely to pick up differences between residents and immigrants. Regardless, the bias that current protocols induce may have implications for conclusions regarding the causes of variation in reproductive success, and the consequences of that variation for ecological and evolutionary processes in this and potentially other long-term study populations.

As well as the aforementioned consequences for previous estimates of reproductive success, the missing individuals that we identified in this study have broader implications for understanding population dynamics and conservation strategies. Much attention has been given to sexually mature individuals without breeding territories, often referred to as 'floaters' (Smith 1978). The term floaters can have different definitions depending on the ecological and behavioural context in which animal populations are considered (see review by Penteriani et al. 2011). For the purpose of this thesis, I consider them to be the non-breeding component of the Wytham population, identified in (Chapter 3).Traditionally, quantifying the floater component of populations has been difficult; most data arise from experimental removal of territorial birds which are replaced by known non-breeders. These experimental removals have now been done on more than 50 species of birds (see review by Newton, 1992), including the great tit within Wytham (Krebs 1970). A potential problem with this method is that it can be difficult to determine if replacement birds had no territory at all, or moved from a lower quality to a higher quality territory. Following the studies by Krebs, little empirical work has been done in Wytham that aims to document and quantify floaters. Our results suggest that doing so may provide important insights,

especially from a perspective that puts Wytham woods in a broader context as one of many interlinked breeding locations scattered throughout the landscape.

Floaters have gained increased attention in ecological literature as they are recognised as an essential element in the regulation of population structures, trajectories, spatial temporal distributions and stability (Jamieson & Zwickel 1983). In particular, they have been shown to act as an important buffering pool, with the floater to breeder ratio being a key variable when assessing the potential for the population to act as a source of recruits to other populations (Newton 1988; Kokko & Sutherland 1998). For example, monitoring the composition of recruits from the floating population can allow the early prediction of a future population decline at the time when it might still be possible to prevent (Kenward et al. 2000; Ferer et al. 2003). Despite this, floaters are still an unknown quantity in many populations and most research focuses on the population dynamics of breeders. This is of particular concern as breeding based censuses often do not detect decreases in floater populations (Wilcove & Terborgh 1984; Rhoner 1996) which can lead to delays in detecting population declines (Kokko & Sutherland 1998; Kenward et al. 2000).

By adding to the knowledge of the links between breeding and non-breeding communities, I contribute towards a more reliable method for forecasting changes in population viability that may be applicable to threatened species (Penteriani et al. 2011). Our results may also have implications for studies of density-dependence within populations. Density-dependence affects many life-history traits and is one of the key processes regulating bird population stability and dynamics (Lack 1954). Previously, potential mechanisms underlying density dependence have been related to the breeding portion of a population and consequently have generally ignored the possibility that non-breeder (floater) mortality has the potential to affect demographic rates (Penteriani et al. 2011). More recent research has found that floater dynamics may affect density dependence. For example, an increase in floater mortality within settle-

ment areas can both explain puzzling declines or extinctions of breeding populations (Penteriani et al. 2005) and patterns of density-dependence fecundity (Penteriani et al. 2006). A further study has demonstrated that Allee effects can be the result of high mortality of floaters in settlement areas, which makes pair formation more difficult due to the lack of new individuals potentially available to replace a lost mate, starting the extinction process (Penteriani, Otalora & Ferrer 2008). An Allee effect is a causal positive relationship between the number of individuals in a population and their fitness, arising through a variety of possible mechanisms, one example being an increasing lack of mating encounters as a population becomes scarce (Courchamp, Berec & Gascoigne 2008). In Wytham, such Allee effects are unlikely because of the high population density and male-biased population. Nevertheless, although great tits are of little conservation concern, by assessing the link between the breeding and non-breeding components within Wytham, the results from this thesis have broader applications to conservation strategies.

4.5 Limitations and future directions

There are some limitations of the work presented in this thesis and that are important to discuss. Perhaps the most important limitation of this study was that we were unable to quantify missing samples of males as effectively as those of females. Not only was this the case for the night scanning method (Chapter 2) where early nest failure estimates could only be obtained for females, but also in the study of yearly variation in population composition where differences in the rates of trapping at the nest between males and females could potentially have confounded results (Chapter 3). Similarly, previous research on this population has failed to quantify estimates of population dynamics as effectively for males as females, for instance, estimates of reproductive success are often missing for males (Bouwhuis et al. 2009; Bouwhuis et al. 2010). As yet, it remains difficult to quantify whether males are attempting

to breed but failing early in their reproductive attempt, which no doubt accounts for some of the excess of non-breeding males during the breeding season. However, it is particularly important to try and quantify the age and immigration status of males that are missing from current breeding samples, as the results from this thesis (Chapter 3), suggest that they are in excess amongst the floater population. The sex and age composition of these floaters has broad implications for population dynamics and conservation strategies as discussed above.

Another limitation of this research was the differing sampling regimes used throughout the winter over the duration of the study. Data were collected by either mist netting or RFID detection systems in the winter, but the exact methodology varied between years. Mist netting efforts were less frequent in the winter of 2007/08 and 2008/09 and sampling across the study site was not fully standardized. Following the winter of 2010/11 mist netting efforts became more standardised, although the efforts of 2010/11 were much greater than in later years. In part, this was due to variation in RFID detection systems; during the winter of 2010/11 only two weeks of RFID data were collected late in the season (i.e., February). In contrast, in 2011/12 and 2012/2013, data were collected at 65 sites across the woods continually from September through to March. Less RFID data were collected between 2007 and 2009, with only 16 loggers being used on rotation across the 65 sites. Further details of the specific sampling regimes for each winter can be found in Chapter 3. It is reasonable to assume that differences in sampling regimes could affect the results and therefore need to be considered when drawing conclusions. For example, in Chapter 3, we showed that year significantly influenced the site and number of days that individuals visited RFID feeders. This may be due to variation in the extent of RFID data, although it may also be due to underlying ecological and environmental differences between winters, for example, yearly natural food availability. The abundance of natural food resources such as beech mast during winter is widely understood to affect winter sur-

vival and subsequent breeding density in tits (Perrins, 1966; Perdeck, Visser & Van Balen 2000), and is also likely to moderate the extent of feeder exploitation across years. Although the beech mast crop was low in both the winter of 2011/12 and 2012/13 (pers obs) and unlikely to confound the effects of RFID feeder use, it is impossible to tease apart the effect of food availability in our data due to the different sampling regimes between years. In addition, the mist netting data were not used in any spatial analyses in Chapter 3 (i.e., detectability and distance to the edge of the woods). This is because only the approximate location where each individual was caught was recorded during mist netting sessions. As mist netting was repeated throughout the winter and covered the entire study site, it could have been beneficial to record the specific site that each individual was caught at in more detail. Such data could later have been of use in further spatial investigations into movements of individuals throughout the woods during the winter. The aforementioned limitations highlight the more general issue of non-standardized methods, which may potentially affect conclusions in natural study populations. Magurran and colleagues (2010) have suggested that changes in methodology is one of the biggest problems confronting users of long-term datasets. Changes can arise for multiple reasons, ranging from substantial uncontrollable ecological variation, to the development of new statistical or sampling technologies. As illustrated in this thesis, non-standard methods are particularly problematic when the number of years is small.

As well as creating a better understanding of the types of samples missing from breeding surveys, this thesis has inevitably raised several questions. Firstly, we found that immigrants had higher rates of early nest failure than residents. Individual quality may drive differences in reproductive success between immigrants and residents within Wytham; immigrants often originate from low quality areas surrounding the woods (Riddington & Gosler 1995; Verhulst, Perrins & Riddington 1997) and can suffer from long-term natal effects (Bouwhuis et al. 2010). Furthermore, other stud-

ies have shown that individuals born in good quality territories have a head start on early life, with repercussions on subsequent long-term performance (Sergio et al. 2009); leading to a complex relationship between individual quality and habitat quality. Indeed, previous studies have shown the two traits co-vary with one another and our results suggest that the effect of lower lifetime reproductive success in immigrants in this population may be inextricably linked to environmental effects such as habitat quality. The relative importance of individual quality and habitat quality as mechanisms underlying differences in reproductive success remains to be established for this population. I propose that this could be investigated as an extension to the work in this thesis. Data for early nest failures of Wytham born birds could be used to investigate whether natal habitat quality influence early failure rates within this population.

In avian species, environmental variability affects nest desertion rates resulting in early nest failure (Carlisle 1982; Breuner 2011). In contrast, I also show that individuals are consistent in their detectability across sampling periods: the likelihood of detection during both winter and breeding is repeatable across years (Chapter 3). So why are individuals consistent in their detectability, despite yearly environmental variability? This may be influenced by consistent individual variation in traits which could be constant across years. For example behavioral syndromes, which may be consistent across years, have been shown to influence individual detectability (Biro & Digemanse 2009; Garamszegi, Eens & Török 2009). Furthermore, the probability of nest desertion (and hence early nest failure) has been shown to depend on individual body condition for many species (Newton, Marquiss & Village 1983; Chastel et al 1995; Groscolas et al. 2008), including great tits (Dubeic 2011). Variation in corticosterone concentration is also a factor affecting nest desertion in Parids (Ouyang, Quetting & Hau 2012). If some individuals are of inherently poorer quality, and consistently in lower condition across breeding seasons, this may influence early nest

failure rates and subsequent detectability. There were not enough early failing females across multiple years to investigate the repeatability of early nest failure in this thesis (n=16 individuals). Nevertheless, our results suggest that consistent individual traits may underlie detectability across seasons.

A key finding from this study is that samples of individuals' remain undetected during breeding surveys within the Wytham population, but the behaviour and location of these individuals during the breeding season remains a mystery. If floaters remain within the woods throughout the breeding season, there would be ecological implications for breeding pairs. For instance, an excess of non-breeding males (Chapter 3), could potentially lead to more intra and inter-sexual interactions, including extra pair copulations, and increased territorial disputes. However, previous studies have shown that the floater component of populations may occupy areas outside of the main breeding site (Penteriani et al. 2011). Whilst Wytham is isolated from other woodlands by surrounding agricultural and urban landscapes, it is characterised by high connectivity with the surrounding areas (Verhulst, Perrins & Riddington 1997; McCleery et al. 2004). Some great tits undoubtedly breed around Wytham in gardens, hedgerows and small woodlots and previous estimates suggest that they constitute only a small fraction (6%) of all immigrant birds coming into Wytham to breed (Verhulst et al. 1997). Our results suggest that this rate may be higher as these individuals are also likely to be undetected breeders with the current monitoring scheme. Furthermore, previous studies have suggested that a considerable proportion of Wytham birds disperse over much larger distances than would be expected on the basis of dispersal within Wytham (Verhulst et al.1997). Thus, areas surrounding the study site may sustain a portion of the Wytham population, potentially acting as a source or a sink. However, little is known about the role of Wytham within the broader matrix of breeding habitats within the landscape which could form the basis of further investigation.

4.6 Concluding remarks

Ecologists and evolutionary biologists are interested in the dynamics of populations in time and space. These include changes in the composition of individuals, for example with respect to age and sex. Birds have been the most intensively studied group of animals with respect to life history evolution (Lessells 1991) and a large array of methods have been developed to sample them (Bibby et. al. 2000). Although much attention has been given to improving the design used to obtain data on wild animal populations (Gitzen et al. 2012), it is often difficult to sample them thoroughly. The assertion that population samples are representative of the entire population has long been questioned (Thompson et al. 1998). We show that different classes of individuals are missed from routine sampling in this population, as a result of early reproductive failures, failure to breed locally and non-winter residency. These individuals represent a non-random subset of the total phenotypic variation within the population with respect to age, sex and residency status. We show that the exclusion of unsampled individuals significantly biases estimates of reproductive success in this population. The findings from this thesis underscore the importance of monitoring not just the breeding component of populations, but also their links to the non-breeding component. These complex interactions between age, sex and residency status in this population lead to differences in detectability of individuals throughout the year. By identifying factors that result in an individual remaining undetected, we can better understand how to census more completely.

4.7 Tables and figures

Table 4.1: Summary of intrinsic factors investigated in this thesis for their effect on detectability within a wild great tit population.

Intrinsic factors	Influence on winter detectability	Influence on breeding detectability	Direction of effect
Age in years	✗	✓	Younger birds were more likely to fail early in their breeding attempt.
Age^2	✗	✗	Detectability was unrelated to the quadratic effect of age in both seasons.
Sex	✗	✓	Males were less likely to be detected breeding than females.
Residency status	✗	✓	Immigrants to the study site were more likely to fail early in their breeding attempt than locally born individuals.

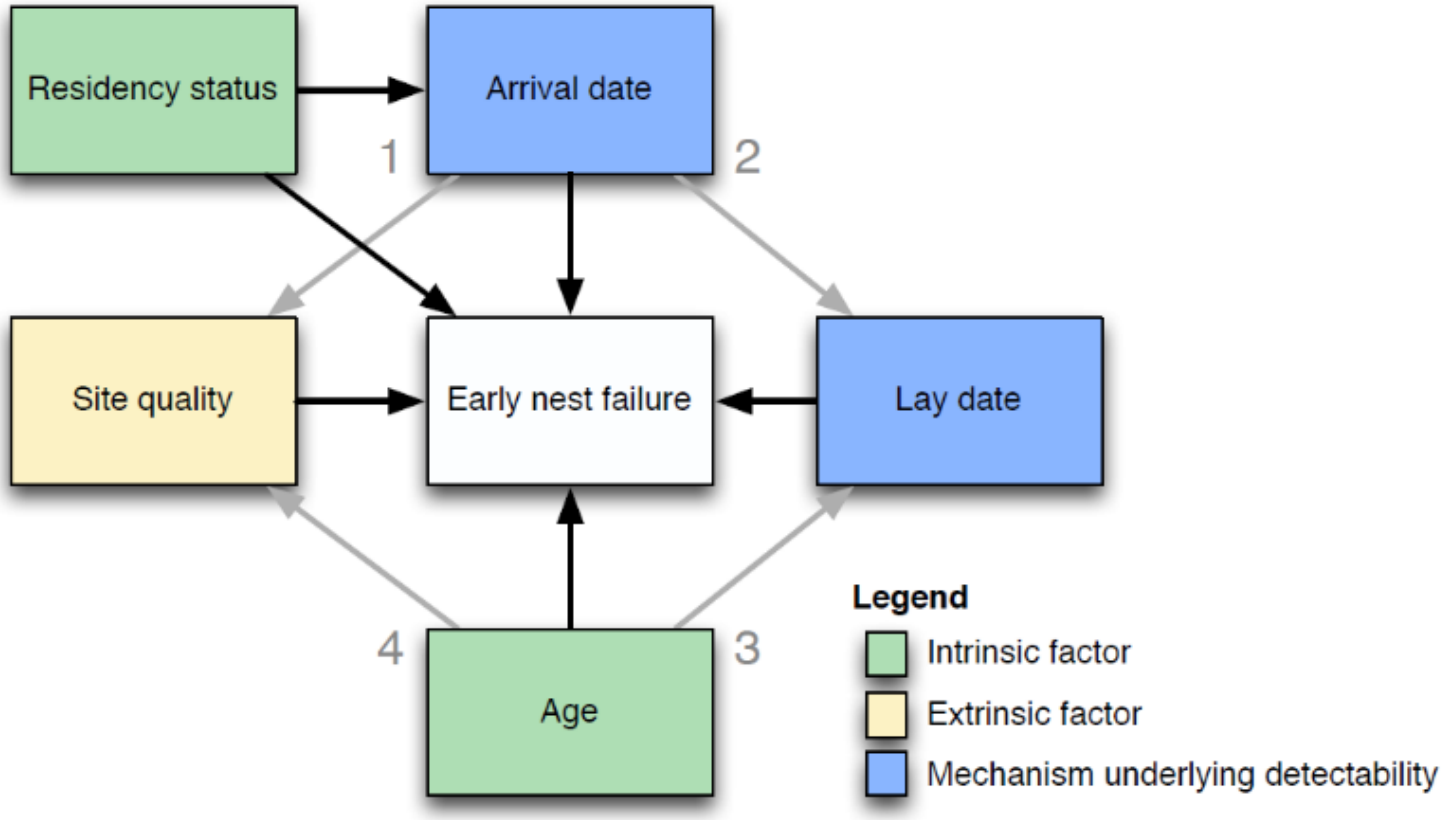


Figure 4.1: A flow diagram showing the complex interactions between factors of ecological origin examined in this thesis in relation to detectability during breeding surveys in a wild bird population. The direction of the arrows shows the direction of the relationship found within Chapter 2 of this thesis. Grey arrows indicate links that have been shown in previous studies but were not directly investigated in this thesis: (1) Lozano & Lemon (1999), Sergio, Blas & Hiraldo (2009), (2) Smith & Moore (2005), Bensch & Hasselquist (1992); (3) Newton 1988, (4) Oring et al. (1991).

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