Breeding dispersal and parental care in blue tits (*Cyanistes caeruleus*)

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Declaration

I declare that this thesis is my own work, except where acknowledged, and has not been submitted elsewhere in the same form for the fulfilment of a higher level degree.

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1.0 General abstract

Behaviour varies between individuals and is often thought to be adaptive. Behaviours are predicted to vary according to the circumstances of the individual, to decrease their risk of mortality or that of their offspring, or to reduce the costs associated with certain behaviours, such as territory establishment, foraging or nestling provisioning. Two of the most important behaviours determining reproductive success, and thus having potential to be adaptive, are breeding dispersal and parental care. Individual birds should be under selection pressure to minimise the costs related to these behaviours, and likely to do so in response to aspects of habitat quality, individual quality, and their own prior experience. This study examined the relative importance of these factors upon breeding dispersal and parental care in blue tits (*Cyanistes caeruleus*), additionally using repeatability analysis as a novel means to indirectly assess the influence of both individual quality and habitat.

Specifically, this study explored the influence of habitat quality and individual-specific experience upon nest-site occupancy, breeding dispersal and reproductive success. It also estimated repeatability of the breeding parameters and examined the reproductive outcome of dispersal. Mixed models suggested that nestbox occupancy increased with population density but not habitat quality, and that the probability of dispersing varied by sex, with females more likely to disperse than males, and both more likely to disperse after breeding in noisier territories. Dispersal distance was not influenced by individual or habitat quality and did not influence reproductive success. Repeatability analyses suggested that habitat quality significantly influenced reproductive success. Furthermore, clutch size was strongly repeatable for females, but not males, whereas fledging success was repeatable between individual males but not females. If individual quality is consistent through their lifetime then these results suggest that female quality is important early in the breeding attempt, but that male quality exerts a stronger influence upon final fledging success.

Both males and females increased their provisioning rate to larger broods, however, the other variables influencing each sex differed. Male provisioning rates decreased as both they, and their partner, aged, but increased when a mate was retained between breeding attempts. Females increased their provisioning rate in response to their partner's effort and provisioned at a higher rate after retaining their nest-site. However, retaining mate or nest-site did not result in higher reproductive success for either sex. The repeatability analysis suggested that females responded to the requirements of their brood, and the effort of their partner, whereas male care was less flexible. Additionally, total and male provisioning rates were repeatable for each nestbox, suggesting an influence of habitat quality. Overall, different behaviours and decisions were found to be varyingly influenced by individual, and habitat, quality and the repeatability analyses aided in assessing the relative contribution of each of these.

1. General Introduction

Individual birds exhibit differences in their behaviour when compared to members of their own species, and sex (Bell *et al*., 2009; Zhao *et al*., 2016). These differences are believed to be influenced by a range of innate and learnt processes and attributes, such as individual fitness and experience (Grieco, 2002; Herborn *et al*., 2014; Froy *et al*., 2015). Furthermore, individuals are believed to use their behaviour to adaptively increase their reproductive success, fitness and survival (Beheler *et al*., 2003; Johnstone *et al*., 2014; Bebbington and Hatchwell, 2016). Two types of behaviour which are believed to have a significant influence on reproductive success are nest-site selection, which influences dispersal (Greenwood and Harvey, 1982; Sergio and Newton, 2003; Serrano-Davies *et al*., 2017) and parental care, where individuals actively contribute to raising their offspring (Trivers, 1972; Clutton-Brock, 1991; Bebbington and Hatchwell, 2016). It is increasingly becoming acknowledged that these behaviours, while strongly influenced by aspects of the physical and social environments, are also influenced by individual-specific attributes, such as personality, prior experience, and familiarity with a nest-site or partner (Llambias *et al.*, 2008; Garcia-Navas and Sanz, 2011). However, the relative importance of these influences upon different types of behaviour, and the variation of these influences upon different individuals, are poorly understood (Garcia-Navas and Sanz, 2011).

1.1 Nest-site selection

It is widely accepted that many bird species actively select their breeding territories and nest-sites (Sergio and Newton, 2003; Meszaros *et al*., 2006; Amininasab *et al*., 2016). An explicit test of this assumption found active site-selection in blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) but not in pied flycatchers (*Ficedula hypoleuca*; Goodenough *et al*., 2009). Nest-site selection is an important behavioural process and has a strong influence upon the costs of reproduction, as nest-sites determine access to food sources and nest building materials (Hinsley *et al*., 2008; Amininasab *et al*., 2016; Mainwaring *et al*., 2017), the risk of predation (Chalfoun and Martin, 2010; Serrano-Davies *et al*., 2017) and provide essential micronutrients/calcium (Wilkin *et al*., 2009b; Sanz *et al*., 2010). Thus site-selection has implications for the reproductive success, fitness, and survival of both parents and offspring (Beheler *et al*., 2003; Mitrus *et al*., 2007; Amininasab *et al*., 2016; Zhao *et al*., 2016), which ultimately will determine future population dynamics and persistence. Furthermore, in individuals of short-lived species, such as many small passerines, habitat selection behaviours can strongly determine lifetime reproductive success (Safran, 2006). Many studies have investigated the factors influencing nest-site selection in both wild and captive birds, with a multitude of factors being found to interact at a range of spatial and temporal scales. However, these factors can be broken down into two main categories, those which are based upon physical aspects of the environment, known as abiotic factors, and those which are social or biotic, (Sergio and Newton, 2003; Safran, 2006; Aminినasab *et al*., 2016).

1.1.1 Physical environmental factors influencing nest-site selection

The most frequently studied influence upon nest-site selection is that of variation in the physical environment, with wild birds using both proximate and ultimate cues to identify suitable areas for breeding. These cues relate to various aspects of habitat quality, such as food abundance or the presence of necessary, or desirable, territory characteristics. The relative importance of these cues is known to differ at multiple spatial scales, from the landscape scale to the microhabitat (Doligez *et al*., 2003; Maicas *et al*., 2012).

At the landscape scale mobile species, such as migratory birds, are able to explore a wide-range of discrete habitat patches, gathering information on the relative quality of these for breeding (Janiszewski *et al*., 2013). At this scale it is likely that individuals searching for suitable nest-sites will use relatively simplistic cues to assess the quality of a habitat, as they are unlikely to spend long in each location, and therefore will be unable, or unwilling, to dedicate the time and energy required to achieve a detailed assessment of habitat quality. Thus, at the landscape scale, selection of nest-sites is believed to be primarily dependent upon the identification of suitable habitat patches which can be easily recognised, or upon the spatial distribution of multiple habitat types, if several different types are required simultaneously (Shave and Lindell, 2017; Wendt and Johnson, 2017). Identification of suitable breeding habitat is vital for species with specific breeding requirements, such as those which nest only in specific conditions or structures (Maziarz and Broughton, 2015). For example, sand martins (*Riparia riparia*) require suitable sandy banks for their burrows (Wernham *et al*., 2002) and there are many cavity-nesting species which require trees of a sufficient size and age (Berkunsky and Reboreda, 2009; Lambrechts *et al*., 2010). However, increasing anthropogenic disturbance of environments has altered the availability of many types of nest-sites required by specialists, and thus the availability of these is likely to be of increasing importance in determining the occupation of breeding sites, and subsequent spatial distribution of many species of wild birds (Shave and Lindell, 2017).

At the territory scale the abiotic factors influencing nest-site selection relate instead to the relative habitat quality of different areas within the same habitat patch. When selecting a breeding habitat the most important aspect of habitat quality is likely to be a suitable and reliable food source (Meszaros *et al.*, 2006). Individuals are believed to be able to make judgments about the food availability in an area based upon proximate cues, such as the composition and density of the vegetation (Sanz *et al*., 2010; Broughton *et al*., 2012; Serrano-Davies *et al*., 2017). For example, insectivorous species are more likely to settle in areas with a greater proportion of mature deciduous trees surrounding the nest, as these typically support a large invertebrate population (Southwood *et al.*, 2004; Amininasab *et al*., 2017). Areas with a greater food abundance are preferred as they reduce time spent foraging and maximise provisioning rates at the nest, increasing both parent and nestling quality (Wilkin *et al*., 2009a; Amininasab *et al*., 2016). However, the vegetation of a territory is also likely to be important in terms of predator avoidance, with studies reporting that some species preferentially nest in areas which are more densely forested, or which have a greater number of predator refuges (Amininasab *et al*., 2017). The position of the potential territory within the habitat patch is also likely to be an important factor considered by individuals prospecting for nest-sites (Maicas *et al.*, 2012; Maicas *et al*., 2014). Peripheral habitats are often found to be of a lower quality than interior ones, due to edge effects, resulting in lower reproductive success in these areas (Wilkin *et al*., 2009a). However, this influence can be reduced behaviourally, if breeding individuals are able to establish larger territories in the peripheral areas, as suggested by Krebs (1970) and Wilkin *et al*. (2006). The influence of sources of disturbance, such as anthropogenic noise or other human activities, are also known to reduce habitat quality, and thus may also be used by birds when determining which territories to select (Nyirenda *et al*., 2015). For example, Scobie *et al*. (2014) found that burrowing owls (*Athene cunicularia*) avoid areas subjected to greater road traffic noise, resulting in reduced population densities in these areas. Reijnen *et al*. (1997) report similar results found for many other species. Thus, if less-disturbed territories are available within a habitat patch it is likely that prospecting individuals will settle in these areas.

The smallest spatial scale upon which nest-site selection processes are believed to act is that of the microhabitat, which relates to the area immediately surrounding the nest-site, and the characteristics of the nest-site itself (Goodenough *et al.*, 2008; Wendt and Johnson, 2017). Predator avoidance behaviours are also likely to be acting at this scale if there is a risk of the nest being predated (Maziarz *et al*., 2016). Consequently, many open-nesting species have been found to be more likely to select areas where they can conceal their nests, such as dense undergrowth or areas with taller grasses (Latif *et al*., 2012; Fogarty *et al*., 2017; Swaisgood *et al*., 2018). Additionally, many studies have focussed upon the characteristics of the nest-site itself and how these attributes may contribute to nest-site selection on the finest spatial scale. Many variables have been found to be important here, for example, the height, and orientation, of nestbox and cavity entrance holes from the ground (Lambrechts *et al*., 2010). Entrance holes higher from the ground have been found to be preferred by great tits as they reduce the likelihood of predation (Goodenough *et al*., 2008; Goodenough *et al*., 2009; Serrano-Davies *et al*., 2017). Furthermore, nestboxes, or cavities, which are orientated toward the dominant position of the sun, the south in the northern hemisphere, are also found to be preferentially occupied, as solar radiation warms the nest, reducing the time that must be spent incubating (Lambrechts *et al.*, 2010). In contrast to this, cavities with entrance holes orientated toward the prevailing wind direction are likely to be colder, and thus require a greater energetic contribution from parents, reducing reproductive success (Goodenough *et al*., 2008). The age and previous occupation history of cavities are also likely to be of importance, as they may result in the nest-site being structurally unsound, or the nest containing a higher parasite abundance, which could lead to mortality, or reduced fitness, of some, or all, of the nestlings (Loye and Carroll, 1998; Lambrechts *et al.*, 2010; Ekner-Grzyb *et al.*, 2014).

1.1.2 Social and biotic factors influencing nest-site selection

There are also a wide range of social and biotic factors which influence nest-site selection from the landscape to the microhabitat scale. These processes may alter how habitat quality is realised, and thus the desirability of a habitat, or directly, by being used to assess habitat quality. The realised quality of a habitat is the actual quality of the habitat for individuals, after temporally variable factors have been accounted for, such as the presence of predators, which greatly lowers habitat quality. Many species are less likely to occupy a territory if there is a high risk of predation, as there is a direct risk of mortality for breeding adults and their offspring (Sergio and Newton, 2003; Mitrus *et al*., 2007). The realised habitat quality is also strongly influenced by the population density of conspecific, and heterospecific, competitors, with increased competition at high population densities reducing the resources available to all individuals occupying that habitat, and thus its quality (Arriero *et al*., 2006; Santema and Kempanaers, 2018). It has been suggested that wild birds are able to recognise that the realised quality of a habitat patch has been reduced due to high population densities or competition with higher quality conspecifics, and that these individuals will then select the next highest quality habitat patch in the area (Forsman *et al*., 2008; Szymkowiak *et al*., 2016). Furthermore, individual-level variation will occur in nest-site selection where the quality of an individual alters their ability to access resources, or breeding sites, in the presence of competition (Maicas *et al*., 2014). Individual quality may also influence nest-site selection, with females paired to low-dominance males nesting near the edge of their territory, facilitating extra-pair copulation (Mennill *et al*., 2004).

Alternatively, some species have been found to prefer areas with high densities of conspecifics, as they use this as an indicator of suitable, or high-quality, breeding habitat (Jaakkonen *et al*., 2013). This behaviour has been described in collared flycatchers (*Ficedula albicollis*; Jaakkonen *et al*., 2013), which have also been found to use moderate densities of their heterospecific competitors, tit species, in the same way (Seppanen and Forsman, 2007). This behaviour demonstrates a simplistic form of social learning, whereby individuals use the presence, or behaviour, of conspecifics and ecologically similar species to make assumptions about environmental conditions, thus informing nest-site selection decisions. As described above, this can be valuable for migratory species, which can infer habitat quality from the presence, and population density, of resident tit species (Seppanen and Forsman, 2007; Forsman *et al*., 2008). Furthermore, species can also use information about the reproductive success of other individuals to select suitable breeding habitats, with Doligez *et al*. (1999; 2002) showing that collared flycatchers select habitat patches which had a high reproductive success in the previous year, and avoid breeding in those where fledgling numbers are lower or nestlings of a lower quality. The influence of social information on nest-site selection has been studied most-frequently in migratory species and it provides an efficient method by which they can rapidly assess habitat quality, information which may otherwise be costly to acquire, in terms of both time and energy (Jaakkonen *et al*., 2013; Aplin, 2016). It is unclear to what level social information is used in non-migratory species but it is likely to be one method by which first year birds, with no breeding experience of their own, learn how to select nest-sites in subsequent years.

In contrast to social information, individuals may use personal information, that which they have gathered themselves through trial and error, to inform on selection of future nest-sites (Danchin *et al*., 2004). Many studies have examined the influence of prior experience upon nest-site fidelity in a wide range of species, and have found that individuals which are successful in one year are likely to occupy the same nest-site or, if they change nest-site, will occupy one with similar habitat characteristics (Harvey *et al*., 1979; Herlugson, 1981; Dubois and Cezilly, 2002; Marzluff *et al*., 2016). Additionally, Marzluff (1988) showed that pinyon jays (*Gymnorhinus cyanocephalus*) change the location of their nest following nest failure, doing this in response to the cause of the failure. For example, individuals which had their nests predated responded by nesting in more concealed areas, whereas those which failed due to cold weather subsequently nested in exposed areas, to benefit from solar radiation (Marzluff, 1988). However, personal information also has a social aspect, with Firth and Sheldon (2016) finding that great tits which overwintered in the same flocks were more likely to occupy bordering territories during the breeding season. Finally, individual differences in nest-site selection between birds are also believed to be driven by their personality, which is defined as being comprised of the consistent decisions, or behaviour, of individuals, which differs between individuals, but is consistent across time and space (Charmantier *et al*., 2016; Schuster *et al*., 2017). For example, in a study of the chestnut thrush (*Turdus rubrocanus*), Zhao *et al*. (2016) found that individuals exhibiting bolder personalities were significantly more likely to nest in areas with few conspecifics and that they explored these areas more rapidly. Thus, bolder individuals will experience reduced competition but may also be more vulnerable to predation, demonstrating how personality can influence reproductive success (Zhao *et al*., 2016).

1.1.3 Dispersal

Individuals which survive to breed, or which make multiple breeding attempts, must use the processes determining nest-site selection to decide whether to change location between their natal site and first breeding attempt, or between successive breeding attempts (Greenwood and Harvey, 1982; Beheler *et al*., 2003). These movements are known as natal and breeding dispersal respectively (Harvey *et al.*, 1979; Greenwood and Harvey, 1982). Understanding the factors influencing dispersal decisions is important as they determine the spatial distribution of individuals, which has a strong influence upon individual reproductive success. However, as outlined above, there are a wide range of biotic and abiotic factors likely to be influencing dispersal behaviour, as well as the confounding effects of individual quality, personality, and prior experience (Greenwood and Harvey, 1982; Clarke *et al*., 1997; Valcu and Kempenaers, 2008). Natal dispersers can only use information from observations of others, the environment, or information about the condition of their natal site (Marzluff, 1988; Doligez *et al*., 2003). However, birds making decisions concerning breeding dispersal will have their decision complicated further by an improved knowledge of multiple breeding sites and how these relate more closely to their individual fitness and personality (Dubois and Cezilly, 2002; Garcia-Navas and Sanz, 2011; Marzluff *et al*., 2016). Many of these factors have conflicting influences upon the decision to disperse, or the distance to disperse, and thus it is necessary to identify those of greatest importance, and their relative importance.

1.2 Parental care

Another important behaviour which varies between individuals and has a significant influence on reproductive success is parental care, which can be defined as any actions taken by an individual that increase the quality, and thus subsequent survival, of its offspring (Trivers, 1972; Clutton-Brock, 1991). Many different types of parental care have been studied in wild animals, ranging from species which lay eggs but provide no further care beyond this initial provision of nutrients, to species where one, or both, parents care for the young for an extended period (Wesolowski, 2004; Johnstone, 2011). The latter is known as biparental care, and has been observed in over 90% of extant bird species (Kendeigh, 1952; Clutton-Brock, 1991). Biparental care systems are believed to be favoured in birds as they increase the care provided to the brood, increasing the probability of a larger number of higher quality offspring being produced (Low *et al*., 2012). This is in turn advantageous for the parents as it ensures that they can pass their genes on to subsequent generations (Clutton-Brock, 1991). However, the level of care invested by an individual is widely found to vary based on habitat and social bird-specific factors, as well as conflict between individuals, and this variation has implications for the reproductive success of individuals.

1.2.1 Habitat quality and parental care

The physical environment and habitat quality have a strong influence upon parental care, primarily through their impact on the presence and abundance of necessary resources, but also upon the energetic and temporal costs of accessing these. One example of this is that the presence of suitable nesting material is vital for parents to be able to construct an appropriate structure to shelter, conceal, and insulate their young (Mainwaring *et al*., 2017). Similarly, the spatial distribution and abundance of suitable food items determines the rate at which food can be provisioned at the nest, strongly influencing the number and quality of offspring produced from each breeding attempt (Tremblay *et al*., 2005; Wilkin *et al*., 2009a). Other factors found to influence habitat quality, and thus parental care, for breeding birds include predation, competition, and disturbance, and these have all been described above, highlighting the importance of parents selecting a suitable nest-site for breeding (Nakagawa *et al*., 2007; Amininasab *et al*., 2017). Additionally, temporal variation in habitat quality, or realised habitat quality, may result in temporal variation in the level of investment of parental care of individuals occupying the same habitat.

1.2.2 Conflict over parental care

Variation in the level of parental care provided by individuals may also vary due to conflict inherent in biparental care systems, which impacts upon the fitness of breeding individuals, and their future survival. For example, there is conflict between both parents and offspring, as the nestlings benefit from receiving increased care, and also between the parents, as each benefits when the other invests a greater amount to the care of the brood (Johnstone and Hinde, 2006; Harrison *et al*., 2009; Bebbington and Hatchwell, 2016). It has been widely observed that breeding individuals will modify the level of parental care they provide on short time scales such as, when the needs of their offspring increase. For example, as a result of reduced temperatures in the nest, thus requiring incubation, or because of an increased brood size, meaning that more food is required at the nest (Low *et al*., 2012; Mainwaring *et al*., 2017).

Conflict between parents is believed to result in parental care behaviour being negotiated in real-time, with individuals using direct or indirect cues to monitor the level of care provided by their partner (Bebbington and Hatchwell, 2016). For example, individuals may provision the nest at a lower rate, or stop provisioning behaviour entirely, when their partner is providing low levels of care (Johnstone, 2011; Bebbington and Hatchwell, 2016). However, negotiation over care is unlikely to result in a complete withdrawal of care from the brood, as this would be disadvantageous to both parents, and it is more likely that individuals reduce their own effort slightly in response to that of their partner (Johnstone and Hinde, 2006; Cleasby *et al*., 2013). In contrast to this, individuals breeding with high quality mates, those who provide higher levels of care, would be expected to increase their own provisioning rate, maximising reproductive success. Thus, the quality of the breeding partner is likely to be an important factor influencing levels of parental care, and this will vary between years if birds change mate.

Divorce, or re-mating is also likely to be an adaptive response by which individuals can increase their reproductive success, by selecting individuals which are likely to provide higher levels of care to their offspring. For example, female blue tits increased their reproductive success following divorce, and were found to do this adaptively, when a new, higher quality mate became available (Garcia-Navas and Sanz, 2011). This also demonstrates how individual variation in parental care behaviour can contribute to the study of dispersal, as in birds it is typically females who drive mate-selection, whereas males establish territories. Thus, a female which changes mate is also likely to be one which disperses (Greenwood, 1980).

1.2.3 Individual-specific variation in parental care

The influences determining the level of parental care exhibited by an individual are also likely to vary temporally between breeding attempts, based on factors which inherently vary over time, such as individual age, or experience (Arthur *et al*., 2015). As individuals age they gain more experience from prior breeding attempts, both from personal experience and from observing others, thus the parental care that an individual provides may change to reflect different care strategies (Marzluff, 1988). For example, more experienced birds may preferentially provide larger food items, or those of a higher nutritional quality at the nest (Marzluff, 1988; Hatchwell *et al*., 1999). In short-lived birds it is likely that the benefit of prior experience, or social learning, will only be noticeable in the first few years of life, however, in longer-lived species, such as the blue-footed booby (*Sula nebouxii*) it could be much more important (Torres *et al*., 2011). Conversely, an individual's quality may reduce over time, due to senescence, and this would be expected to result in a simultaneous reduction in that individual's investment in parental care (Torres *et al*., 2011).

1.3 Assessing the consistency of behaviour – Repeatability (*R*)

In behavioural ecology there is currently a growing interest in consistent individual differences in behaviour (Bell *et al*., 2009). Previous studies suggest that despite the biotic and abiotic factors influencing these processes, many behaviours show consistent individual differences (Nakagawa *et al*., 2007). To assess this, multiple statistical methods have been developed, all centering on the estimation of repeatability (Lessells and Boag, 1987; Nakagawa and Schielzeth, 2010; Dingemanse and Dochtermann, 2013). Repeatability estimates the proportion of the total variation in the data which can be explained by differences among groups, such as different individuals or locations (Lessells and Boag, 1987; Nakagawa and Schielzeth, 2010). This means that behaviours which show high repeatability are those for which individuals show relatively low levels of variance in their behaviour but there is a high level of variance between individuals. Gray *et al*. (2005) is a good example of this, and found that the peak body mass of manx shearwater (*Puffinus puffinus*) nestlings raised by the same breeding pair were highly repeatable between years. This means that the nestlings raised by each breeding pair were a similar peak mass between years, and that nestlings raised by other breeding pairs were consistently different masses (Gray *et al*., 2005).

Repeatability estimation can be applied to the study of behaviour in the same way, as long as there is a measurable response, and repeat measurements of the grouping factor (Bell *et al*., 2009; Nakagawa and Schielzeth, 2010). Studies have shown that many behaviours exhibit some degree of repeatability, with those which are less repeatable tending to be those which are most strongly influenced by the environment, and the most repeatable being those influenced by individual phenotype, or genotype (Bell *et al*., 2009). However, repeatability has so far been applied to a relatively small group of bird species, and with most work concentrated on individual repeatability of provisioning rate (Schwagmeyer and Mock, 2003; Nakagawa *et al*., 2007). Repeatability could be a powerful tool to assess the relative influence of environmental, or individual-specific factors upon behaviour, by using both individuals and fixed points in space as grouping factors. However, this method has to date been employed in very few studies but has the potential to address some of the main questions which remain about individual variation in behaviour (Goodburn, 1991; Przybylo *et al*., 2001).

1.4 The blue tit

The blue tit is a small, insectivorous, woodland passerine, with adults weighing on average 11g (Svensson and Nilsson, 1995). Blue tits are secondary-cavity nesters which readily occupy nestboxes (Serrano-Davies *et al*., 2017), starting to form breeding territories around these in late winter and early spring, and breeding from April to early July. Blue tits are a socially monogamous species, although Kempenaers (1994) reported polygyny in 20% of males and 35% of females. Blue tits exhibit biparental care, with both parents provisioning the young in the nest (Merila and Wiggins, 1997), and in the United Kingdom breeding pairs are single brooded. Between breeding attempts individual birds often return to, or near, the territories they themselves occupied in the previous year (Garcia-Navas and Sanz, 2011). These attributes make blue tits an ideal study species to examine the influences upon nest-site selection, dispersal, and parental care, as nests can be located and the reproductive success of each monitored with relative ease.

1.4.1 Habitat quality for blue tits

The factors which constitute important aspects of habitat quality invariably differ between species, and the variables identified for study by researchers may not always reflect those of importance to the birds themselves (Krebs, 1971). However, blue tit habitat preferences have been widely studied, and thus a large body of research exists to identify those variables which are most likely to determine habitat quality (Sanz *et al*., 2010; Maicas *et al*., 2012). The most important variable determining breeding habitat quality in blue tits is believed to be food abundance (Svensson and Nilsson, 1995; Harrison *et al*., 2010). The preferred food source of blue tits provisioning a nest is phytophagous invertebrates, such as caterpillars (Perrins, 1991), the abundance of which is determined by the trees surrounding each nest-site (Przybylo *et al*., 2001; Arriero *et al*., 2006; Amininasab *et al*., 2016). For example, oak trees (*Quercus robur*) support the greatest density and biomass of invertebrates, making them the most important aspect of habitat quality for blue tits, but other deciduous trees such as beech (*Fagus sylvatica*) and hazel (*Corylus avellana*) are also known to be important (Southwood, 1961). Alternatively, evergreen trees support a low abundance of invertebrates, and as such may have a negative effect upon site selection by blue tits (Kelly and Southwood, 1999; Southwood *et al*., 2004). Studies have demonstrated the importance of the arboreal vegetation upon habitat quality for breeding blue tits by showing that reproductive success is highest when nesting in areas with a greater number of oaks, or other deciduous trees, as the energetic costs of foraging are reduced in these areas, resulting in higher fitness and survival of parents and offspring (Arriero *et al*., 2006; Wilkin *et al*., 2009a; Amininasab *et al*., 2017).

However, the realised habitat quality for blue tits is likely to be influenced by abiotic and biotic factors, as described above (Sergio and Newton, 2003; Santema and Kempanaers, 2018). One example of this is that population density, and thus competition, will reduce habitat quality for blue tits (Harvey *et al*., 1979; Serrano-Davies *et al*., 2017). Thus it is important to consider the influence of population density in studies of habitat quality concerning blue tits (Valcu and Kempenaers, 2008; Garcia-Navas and Sanz, 2011). Additionally, anthropogenic sources of disturbance, such as road traffic noise, may reduce the expected quality of specific habitats for blue tits, as found for many species (Meillere *et al*., 2015; Halfwerk *et al*., 2016). This reduction in habitat quality can have a significant enough effect to result in reduced nest-site selection, and avoidance of noisier habitats, as found for great tits (Halfwerk *et al*., 2016). Preliminary work on the influence of road traffic noise upon stress levels in blue tit nestlings suggests no effect of road traffic noise upon blue tits (Wolfenden, 2017). However, the study of road traffic noise is a relatively recent development in the literature and is not yet fully understood, and as such the influence of anthropogenic noise levels upon wild birds should be considered.

1.5 Aims and thesis outline

The broad aim of this thesis is to assess the relative importance of habitat quality, individual quality, and the prior experience of individuals, upon breeding dispersal and parental care behaviour in blue tits. Additionally, to estimate the consistency of both the breeding parameters and provisioning rates for individual males, females and nest-sites.

Chapter two uses the results of a vegetation survey, sound survey, and nine years of nestbox monitoring data collected at Lancaster University, to assess the relative influence of habitat quality, individual quality, and prior experience upon nest-site selection and breeding dispersal in blue tits. The influence of breeding dispersal as an adaptive means to increase reproductive success is also tested. Finally, repeatability estimates are used to examine the factors influencing reproductive success, and to examine the consistency of these for individual birds and nest-sites.

Chapter three makes use of three years of data on the parental care behaviour of blue tits at Lancaster University, specifically looking at the influence of habitat quality and individual-specific variables upon provisioning rates at the nest. The repeatability of male and female provisioning rates is also assessed, as well as the total provisioning rate at each nest, to examine the factors influencing consistency of parental care behaviour between individuals and nest-sites.1.6 General method

1.6.1 Study site

Fieldwork for this project was carried out in several discrete patches of woodland around the edges of Lancaster University's Bailrigg campus (Figure 1.1). This was the site of an ongoing nestbox study of a wild blue tit population (Mainwaring *et al.*, 2010), which provided an extensive amount of past data, and the necessary infrastructure, equipment and facilities to collect the data needed to address the aims of this project.

1.6.1.1 Woodland

The woodland patches which contained the nestboxes used by this study comprised an area of 15.3ha and varied in both size and shape, although most were linear and of approximately equal width (Figure 1.1). Consequently, the size of each habitat patch was deemed unlikely to influence the results of this study and not considered as a variable. The arboreal vegetation differed between areas, with the number, relative abundance, maturity, and density of trees varying across the site. The majority of woodland within the study site was classed as mixed deciduous woodland, with dominant species including oak and beech. However, there were coniferous trees present in low numbers across the site, particularly surrounding boxes 88-92, which were located in a conifer plantation.

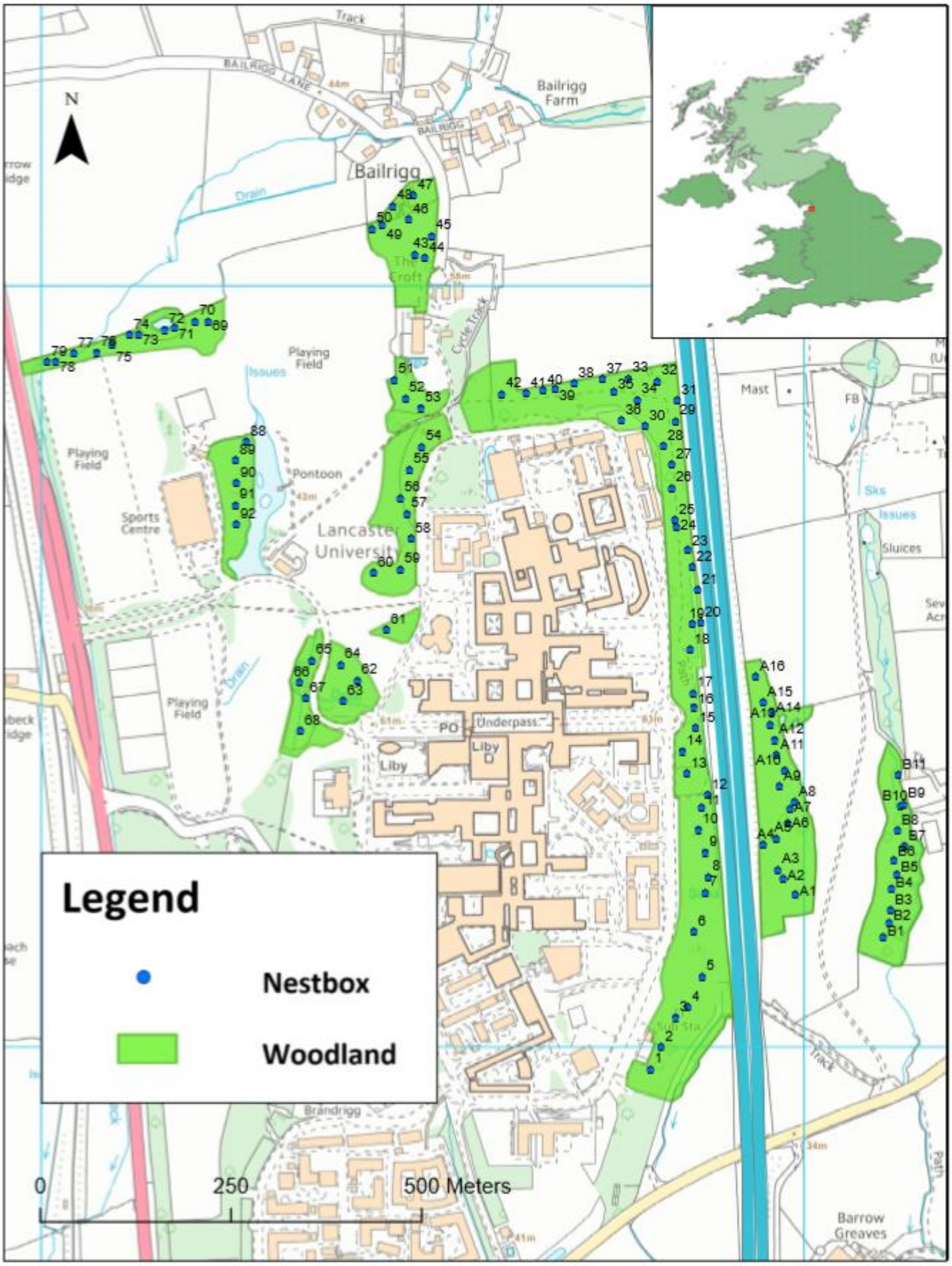

Figure 1.1: The study site at Lancaster University, United Kingdom, showing the shape and relative position of the study woodlands and the position of nestboxes within these.

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Anthropogenic food sources were available near nestboxes 43-50 but no evidence of artificial food was observed across the rest of the site and the influence on the results of this study is likely to be minimal. The landscape surrounding the study site contained multiple unmonitored woodlands, many of which were suitable habitats for blue tits. However, these areas had few mature trees, and did not contain nestboxes, and thus had limited nest sites available for blue tits to utilise during the breeding season. Consequently, it was not thought that the presence of unmonitored woodland patches near the study site would have a strong effect on the findings of this study.

1.6.1.2 Nestboxes

The study site has had 111 nestboxes maintained in their current density and configuration since late 2009 (Figure 1.1), and these were monitored for this project. The nestboxes were placed in a linear fashion parallel to the orientation of the woodland and each was, on average, 24m from its nearest neighbour. Study nestboxes were constructed from wooden planks, with an entrance hole with a diameter of 25mm, which excluded all but the study species. Additionally, the nestboxes were covered in a wire mesh with a metal plate around the entrance hole, which has proven effective in preventing nest predation by great spotted woodpeckers (*Dendrocopos major*). A more detailed description of the box dimensions, placement, and materials can be found in Mainwaring and Hartley (2008; 2016a).

1.6.2 Study species

The blue tit population studied at Lancaster University varies in size between years but uptake of the nestboxes typically ranges between 50-80% and is relatively consistent across the site. The study population is metal ringed in the nest, or when first caught, and breeding adults have been additionally marked with a unique combination of three colour rings, allowing individuals to be identified without recapture. Blue tits start to form breeding territories in late winter and early spring, then breed from April to early July. Breeding individuals frequently return to, or near, their previous breeding territories, however, high mortality between years means that many individuals are not re-sighted following fledging. Blue tits have a low life expectancy, 1.5 years for juveniles and 3 years for adults (Robinson, 2018). However, it is also possible that individuals have undergone either natal, or breeding, dispersal, leaving the study site to breed in nearby habitat patches.

1.6.3 Routine data collection

To address the aims of this study data were collected between 2010-2018 by researchers at Lancaster University. These data comprised nestbox monitoring data from the ongoing blue tit study and data from an arboreal survey of the area surrounding each nestbox.

1.6.3.1 Nestbox monitoring and breeding data

Nestboxes were monitored throughout the breeding season, with fieldwork involving regular checks of all nestboxes from the 1st of April 2018 to record the onset, and development, of nest-building, as well as identification of the adults breeding in each location (Mainwaring *et al*., 2010; Mainwaring and Hartley, 2016a; 2016b). Once nests were complete, and the nest cup had been lined, nests were checked every 1-2 days to establish the date on which the first egg was laid. Blue tits typically lay one egg a day (Cramp and Perrins, 1993), thus regular checks also allow back-calculation of first egg dates, if this was not directly observed. Nests were checked daily from day six after the first egg was laid, to establish the start date of incubation and the final clutch size.

As with Mainwaring and Hartley (2016b) nests were not checked during incubation, until a few days before the predicted hatch date, typically day 13 after the start of incubation in blue tits (Cramp and Perrins, 1993) in order to avoid disturbance at the nest during this period. Nests were checked daily from day 11 or 12 after the start of incubation, to establish when hatching began for each nest. Following hatching, nestlings were ringed from 6-14 days old, then weighed at day 14 to assess their pre-fledging body mass and condition (Wilkin *et al*., 2009a). Finally, nests were checked after all young were expected to have fledged, approximately day 21 after hatching, to establish fledging success.

The breeding parameters were recorded as counts of the number of eggs laid, young which hatched, and the number of these which fledged. Fledging success was also recorded as a binary variable for use as an additional variable in exploratory analyses. The existing data did not provide information on the nesting pair at each nest, particularly those which failed early on, and as such all relevant nesting attempts were included in analyses in Chapters 2 and 3, unless stated otherwise. Nest failures were incorporated in analyses of clutch size if they failed after laying had started but only included in analyses of hatching success if they failed after incubation had begun. Records with a value of zero for hatching success were then discounted from analyses of fledging success.

1.6.3.2 Vegetation survey

To assess the influence of habitat quality upon the behaviour and reproductive success of blue tits, the vegetation within a 50m radius of each nestbox was surveyed in 2009 and the trees encountered within each survey area were classified into three groups: deciduous, coniferous, or oak. The distance was measured between the relevant nestbox and the closest member of each category. The count of each class of tree, as well as the shortest distance from the nestbox to each, were used to represent the abundance of the food source, nutrients, and shelter that each may represent to blue tits, as well as the ease with which it could be accessed (Wilkin *et al*., 2009a). Table 1.1 shows a summary of this data.

The survey radius of 50m around each box was believed to be sufficient to encompass the entirety of a blue tit breeding territory and foraging range. Other papers within the literature most commonly used a radius of 25-50m for this type of study, as this encompasses the maximum area within which blue tits provisioning a nest will typically forage (Arriero *et al*., 2006; Amininasab *et al*., 2016). However, Tremblay *et al*. (2005) found individuals foraging up to 500m from the nest in extreme circumstances. Thus, the distance of 50m from the nest was chosen to fit ecological factors, be comparable with the existing literature, and be feasible within the time available.

Finally, the same vegetation data were used for comparison with breeding data from all years, 2010-2018. There was some evidence of trees being removed in several areas around the study site, however, the vegetation survey was not repeated as removed trees were spatially dispersed and only removed in small numbers. Furthermore, tests of the difference between multiple vegetation surveys carried out approximately ten years apart, by Amininasab *et al*. (2016), found very little difference in results. Furthermore, in managed landscapes, such as the study site, trees are typically removed only in small numbers. Additionally, the literature suggests that felling of a small number of trees does not appreciably alter habitat quality. Amininasab *et al*. (2017) examined the influence of moderate felling of trees on the reproductive output of blue tits and found no significant response, which was attributed to the territories still providing a sufficient food source, or suitable refuges from predators.

Table 1.1: Summary of the vegetation characteristics in the survey area surrounding each nestbox. Oak or evergreen trees were not found within 50m of many nestboxes, in these cases the distances reported below are an average of those nestboxes where the relevant trees were present, these values are marked with an asterisk (‘*’).

		Mean	**Max**	**Min**	**Standard deviation**
Number within 50m radius	Deciduous	152.2	371	9	68.4
	Evergreen	6.9	81	0	16.0
	Oak	11.1	51	0	13.8
Distance to the nearest tree (up to 50m)	Deciduous	1.3	24	0	3.2
	Evergreen	21.2*	>50	0	14.7*
	Oak	13.2*	>50	0	12.9*

1.6.3.3 Estimating repeatability

Repeatability can be estimated for any grouping factor for which the members of that grouping variable have two or more measurements. Therefore, the data were sorted to select all individual blue tits or nestboxes for which the response variable had a sufficient sample size. A mixed modelling approach was used to estimate repeatability (R) of the breeding parameters and provisioning rates, following Nakagawa and Schielzeth (2010). Repeatability estimates were calculated using the *rptR* package (Nakagawa and Schielzeth, 2010; Stoffel *et al*., 2017). This technique produces more accurate values for repeatability than other methods, such as the ANOVA- or correlation-based methods as it calculates the 'adjusted repeatability' (Cleasby *et al*., 2013; Schuster *et al*., 2017). Adjusted repeatability estimates adjust the value in response to the influence of the significant confounding effects, identified from the mixed models of the response, and accommodate Poisson distributed count data (Nakagawa and Schielzeth. 2010; Adams *et al*., 2015). Nestbox and bird identity were both included as random effects and used as grouping factors in *rptR*, to examine the repeatability of each response by both individual and territory. All repeatability estimates were calculated separately for males and females, as it is commonly found that the repeatability of behavioural traits differs between sexes (Cleasby *et al*., 2013; Schuster *et al*., 2017).

95% confidence intervals (CIs) and standard error (SE) were calculated around the repeatability point estimates using parametric bootstrapping based on 1000 runs, and p values calculated using likelihood ratio tests, both functions incorporated in the *rptR* package (Stoffel *et al*., 2017).

2. Controls and influences upon breeding dispersal in blue tits (*Cyanistes caeruleus)*

2.0 Abstract

Wild birds actively select their breeding sites, and those breeding over multiple years have the option to retain their nest site or undergo breeding dispersal. This decision is predicted to be influenced by habitat quality of the current nest-site, and individuals should be more likely to disperse when breeding in low-quality sites. Furthermore, aspects of individual quality and prior experience could alter a birds' likelihood of dispersing. This study investigates the relative importance of habitat quality, individual quality, and prior experience upon nest-site selection and dispersal in blue tits (*Cyanistes caeruleus*) using data collected over nine years, from 2010 to 2018. GIS systems were used to calculate dispersal distances and population densities for each nesting attempt. Repeatability was estimated for each of the breeding parameters, to assess both the influence of habitat quality and individual-specific factors for both individual birds and nestboxes.

Blue tits were found to occupy nestboxes based upon the realised habitat quality, as determined by population density, with the higher quality habitats being the only ones occupied at low population densities, but that lower quality habitats were increasingly likely to be occupied as population density increased. Secondly, males and females were more likely to disperse from noisier sites, based upon the level of road traffic noise, but not any other habitat variables, a result which may be unique in the literature. Dispersal distance was not influenced by the recorded variables, or reproductive success the previous year, and dispersing individuals did not experience any measurable changes in reproductive success following dispersal. However, the repeatability analyses indicated that habitat quality had a significant influence upon reproductive success at all stages, from clutch size to fledging success. Female quality leads to consistent clutch sizes but fledging success was more repeatable by males, suggesting that male quality has a stronger influence on final fledging success. These repeatability results are novel and have implications for future studies of dispersal, suggesting that females may benefit more from selecting a higher quality partner and territory, whereas males would benefit more from selecting higher quality territories. This study highlights the need for further investigation into the relative importance of the factors determining dispersal and suggests that the influence of habitat quality may be more complex than previously thought.

2.1 Introduction

Individuals which breed in multiple years must decide whether or not they will return to their previous breeding site or disperse and select another (Beheler *et al*., 2003; Llambias *et al*., 2008). This movement is known as breeding dispersal and has been suggested as an adaptive method by which individual birds are able to decrease the costs of reproduction and increase their reproductive success (Beheler *et al.*, 2003; Doligez *et al*., 2003; Chalfoun and Martin, 2010). For example, dispersing individuals may preferentially disperse from low-quality territories (Krebs, 1971; Valcu and Kempenaers, 2008; Cline *et al*., 2013), be searching for higher quality mates (Garcia-Navas and Sanz, 2011; Marzluff *et al*., 2016) or be responding to their own reproductive success (Marzluff *et al*., 2016). However, the relative importance of these factors differs between species and it is uncertain to what extent dispersal influences the outcome of subsequent breeding attempts (Valcu and Kempanaers, 2008; Garcia-Navas and Sanz, 2011; Marzluff *et al*., 2016).

The most common way to study the influences upon the decision to disperse or not, and how far to go, is to examine the relative costs and benefits of dispersal. Many papers have examined this by considering the habitat quality of breeding territories (Cunningham *et al*., 2016; Harts *et al.*, 2016). Wild birds have been found to use habitat quality to select their nest-sites (Chapter 1), showing that, in most cases, they are capable of recognising areas which constitute high quality breeding habitat, and this has been found to increase their reproductive success (Cline *et al*., 2013). In the context of dispersal, low-quality habitats are believed to provide few benefits, and may increase costs, such as time and energy required for foraging while provisioning nestlings. As such, individuals are expected to preferentially disperse away from these habitats, and instead occupy higher quality territories that become available near them. For example, Krebs (1971) studied this in the great tit (*Parus major*) and found that younger, less experienced birds bred on the edges of a block of woodland, but such individuals dispersed to interior territories as these became available, resulting in increased reproductive success. Marzluff *et al*. (2016), in a study of six species of songbirds, found strong support for preferential dispersal from low quality territories, and showed that individuals breeding in these typically dispersed further than individuals in areas with high habitat quality. However, there are several problems with studying solely habitat quality as a driver of dispersal, the simplest of which is that it relies upon a knowledge of all the habitat variables most likely to be determining habitat quality, information which is not always available, and can take a long time to collect.

Additionally, the realised quality of a habitat is frequently different from that which is implied by the physical attributes, such as the vegetation (Johnson, 2007). For example, biotic factors such as competition and predation reduce the resources available to each breeding pair and can increase mortality of both parents and offspring (Arriero *et al*., 2006; Forsman *et al*., 2008; Santema and Kempenaers, 2018). Thus, in territories exposed to high levels of competition, or within which a predator is present, the costs and benefits of breeding will differ from those implied by the habitat itself, and dispersal may occur in response to this (Greenwood *et al*., 1979; Chalfoun and Martin 2010). For example, in a study of the blue-footed booby (*Sula nebouxii*), Kim *et al*. (2007) found that individuals dispersed further following high breeding densities, rather than responding to aspects of habitat quality. Similarly, birds breeding under greater risk of predation, and particularly those which fail due to predation, are much more likely to disperse before breeding again (Porneluzi, 2003). Additionally, when under increased risk of predation, individuals alter the types of habitat attributes they select for, becoming more likely to disperse to territories with vegetation characteristics which aid predator avoidance, such as well-developed shrub layers and more densely packed trees (Garcia-Navas and Sanz, 2011).

Similarly to the effects of habitat quality outlined above, breeding dispersal has been suggested as a means to gain access to a higher quality mate (Llambias *et al*, 2008). However, this has been reported as being sex-specific, with females utilising this to decide whether to disperse or not, but males far less likely to do so (Greenwood *et al.*, 1979; Clarke *et al*., 1997; Garcia-Navas and Sanz, 2011). The literature suggests that there is a sex-bias in dispersal with females both more likely to disperse as well as dispersing further than males (Greenwood and Harvey, 1982; Clarke *et al.*, 1997). The same theory can explain both this bias toward female dispersal and the higher likelihood of females dispersing in response to the quality of their breeding partner, with the relative costs and benefits of dispersal determining this. Males choosing the territory location but females the nest-site within that. Dispersal has relatively few associated costs for females, as they are able to mate with any available males, and thus can select for a higher quality mate or territory (Greenwood and Harvey, 1982). However, males which choose to disperse must locate a suitable nest-site, establish a territory, and attract a mate, all before they can reproduce, thus they benefit more from retaining their breeding territory between years (Greenwood, 1980). This results in males being much less likely to disperse based upon the quality of their partner, and they are only likely to do so in response to significant disruptive events, such as predation, or if a suitable higher quality territory becomes available nearby (Garcia-Navas and Sanz, 2011). In this last case, the ability of males to disperse to a higher quality territory will be constrained by the heterogeneity of the habitat, and the spatial scale this co-varies with. If males are only dispersing short distances, but all nearby sites are similar, then this will act to encourage site-fidelity and re-use, as well as simultaneously discouraging dispersal (Switzer, 1993).

In addition to their own quality, and that of their partner, it is also believed that wild birds use information specific to themselves and their past experiences when deciding whether to disperse (Switzer, 1993; Bowers *et al*, 2014). For example, the literature suggests that the reproductive success of an individual can have a strong influence on their perception of habitat quality (Bollinger and Gavin, 1989; Haas, 1998; Llambias *et al*., 2008). A meta-analysis by Dubois and Cezilly (2002), and study of six songbird species by Marzluff *et al*. (2016), found that reproductive success can have a strong influence upon dispersal, with both males and females of a wide range of species being more likely to disperse following a breeding attempt with low reproductive success. This suggests again that the realised habitat quality will differ from that suggested by the physical environment, and thus that the previous breeding history of an individual may be of greater importance than other biotic and abiotic factors when making the decision to disperse.

However, the relative influences of the different factors determining dispersal, such as habitat quality, individual quality, and pre-dispersal reproductive success, have been found to vary between species (Dubois and Cezilly, 2002), and at times within studies of the same species. For example, Valcu and Kempanaers (2008) found that the blue tit does not undergo breeding dispersal in response to either habitat quality, or pre-dispersal reproductive success. In contrast, Garcia-Navas and Sanz (2011) found that female blue tits do use their past reproductive success to decide when to disperse, with females more likely to change nest-site following a year where either a low proportion of their brood hatched, or they had low fledging success. Additionally, Garcia-Navas and Sanz (2011) also found evidence for habitat quality influencing dispersal, with dispersing females settling in patches with a greater density of trees, thus suggesting a selection of sites with higher food availability. These conflicting results suggest that there is a need for further study of the factors influencing the decisions governing dispersal, and that this should be examined carefully to look at the reasons why the literature may report conflicting results.

Furthermore, if breeding dispersal is truly an adaptive response to improve reproductive success, as suggested in the literature (Marzluff, 1988; Beheler *et al.*, 2003), then dispersing individuals would be expected to increase their reproductive success following dispersal. This has been shown to occur in many species but is not always the case, with studies reporting that some species have no change in reproductive success following dispersal (Garcia-Navas and Sanz, 2011; Marzluff *et al*., 2016). These two results are likely to differ between species, or sexes, where reproductive success is determined by the habitat quality, or aspects of individual quality respectively (Valcu and Kempenaers, 2008). If habitat quality is of greater importance in determining reproductive success then dispersing to a higher quality territory will increase this. However, if the quality of individuals is the most important factor influencing the breeding parameters, then dispersal may have little to no impact upon these, other than as a mechanism by which predation risk, or other stressors, can be reduced.

It is also important to consider that breeding dispersal is not always a free choice, with certain variables likely to influence whether an individual changes nest-site. For example, breeding dispersal requires a suitable nest-site to exist near the former breeding site, and this to be close enough for the individual to be aware of both its location and of its occupation status. Broughton *et al*. (2010) examined the influence of this in marsh tits (*Poecile palustris*) and found that 80-90% of dispersal events occurred following the disappearance of a neighbour, making a presumably higher-quality breeding habitat available. However, this factor is likely to be of reduced importance in relatively homogeneous stands of vegetation or those with an abundance of suitable nest-sites.

To ensure that a potential disperser has contemporary information on the occupation status of alternate nest-sites they must be within an easily dispersible distance of the former nest-site, enabling regular visits at minimal cost. As mentioned previously, many non-migratory woodland species typically disperse short distances, so when considering the influence of alternative nest-sites on dispersal, the straight-line distance to each of these is likely to be less important than the structural or functional connectivity of the landscape. Habitat connectivity refers to the ease of which individuals can move through the landscape and an area with high connectivity would greatly increase the chance of suitable alternate nest-sites being identified. In contrast, in spatially discontinuous, or fragmented, habitat it is likely that the availability of alternate nest-sites will have a lower influence on breeding dispersal (Hinsley *et al*., 2008; Broughton *et al*., 2010).

The relationship between an individual and its former partner is also likely to influence the probability of breeding dispersal, namely whether divorce or mortality have occurred (Beheler *et al*., 2003; Kim *et al*., 2007). Mortality of a mate frequently leads to dispersal in the remaining partner (Broughton *et al.*, 2010), either because they cannot hold the territory or must disperse to find a mate. Divorce is more complex and usually involves the female moving to a nearby territory, most likely to take advantage of a higher quality mate or territory (Garcia-Navas and Sanz, 2011). However, divorce may not be a choice, instead occurring as a result of the female being displaced by a more dominant individual, although there is little published on this topic (Valcu and Kempanaers, 2008; Garcia-Navas and Sanz, 2011). The effects of breeding dispersal and divorce are often the same, with one generally resulting in the other (Harvey *et al*., 1979). Previous studies have examined both as different causes for a change in nest-site or partner and not explicitly as different types of event (Valcu and Kempanaers, 2008; Garcia-Navas and Sanz, 2011). The focus being on whether the change is a result of one, or more, individuals seeking either a higher-quality territory or partner.

This similarity between the effect of each causal factor may result in some bias in the identification of the variables determining breeding dispersal and requires further study.

To establish the relative influence of habitat, and individual, quality upon reproductive success a relatively small number of studies have estimated the repeatability of breeding parameters for both individual birds, and for fixed nest-sites. Theoretically, if any attribute of reproductive success is strongly repeatable for individual birds then they are unlikely to significantly influence it by dispersing. For example, Goodburn (1991) found clutch size of individual female magpies (*Pica pica*) to be strongly repeatable, but only weakly so for territories, demonstrating that females would be unlikely to disperse to increase their clutch size, but that they may do so if habitat quality influences their hatching, or fledging success. In this case, dispersal is more likely to be driven by mate-selection or be a means whereby an individual can reduce the costs of reproduction. For example, by dispersing to a territory where the risk of mortality is lower, or food is more abundant and accessible (Latif *et al*., 2012). Alternatively, high repeatability of reproductive success for each breeding territory would suggest that individual birds have much to gain from dispersing to higher quality habitats, and that occupying these will subsequently increase their reproductive success. Thus, repeatability is a powerful tool which can further assist with establishing the relative contribution of habitat quality and individual-specific attributes to breeding dispersal.

2.1.1 Aims

1. To identify the variables influencing breeding dispersal in blue tits, as well as looking at how these differ between individuals of different sexes
2. To examine the outcome of breeding dispersal, specifically in terms of reproductive success
3. To use repeatability analysis to assess the relative importance of habitat quality and individual-specific factors influencing the probability of blue tits undergoing breeding dispersal

2.2 Methods

For information on the study site, species, and collection of general data collection please refer to Chapter 1, as they have been described in the general methods section.

2.2.1 Identification of dispersal events

To study the factors influencing dispersal, the data from the 2010 to 2018 breeding seasons were used to identify all individuals breeding in at least two consecutive years. Each record of an individual breeding within the study site in two consecutive years provides a single dispersal event, as with Valcu and Kempenaers (2008) and Garcia-Navas and Sanz (2011). Birds found to be breeding more than once, but not in consecutive years, were not included in this study, as it was unclear what they had been doing in the time they were not recorded, and as such many of the variables necessary for this study could not be established.

The sex and age of those individuals selected were recorded, along with the relevant breeding parameters, and binary variables of whether the event displayed site fidelity or dispersal and whether or not breeding was successful. Information on the age of each individual was obtained from the ringing data, and recorded as that during the first known breeding attempt. Ages in this dataset were established whenever an individual was caught, and based on plumage characteristics, with this being able to categorise each bird as either a nestling, first year, or adult. The age of an individual has been found to be an important factor influencing the decisions behind dispersal and habitat selection (Kim *et al*., 2007; Wilkin *et al*., 2009a). As a result of this, the potentially confounding effect of age was controlled for by retaining only birds of one age group, those individuals found to be breeding in their first year. This group had the largest sample size (Table 2.1), maximising the reliability of results from the statistical analyses. Additionally, this ensured that all breeding attempts of the study individuals were known, reducing the likelihood of confounding effects, such as individuals having different levels of breeding experience.

Table 2.1: All birds found to be breeding in two consecutive years, thus those for which breeding dispersal could be studied, categorised by their age prior to dispersal.

Age (in years)	Count
1	172
2	8
3	10
4	4
5	1
Age unknown	47

2.2.2 Spatial variables

ArcGIS version 10.6 (ESRI, 2018) was used to plot the nestboxes on a basemap of OS (Ordnance Survey) data (Figure 2.1). The study woodlands were mapped onto this basemap and digitised, to calculate the area of each, with this being summed to give the total area of woodland containing nestboxes. The dispersal distances and population density were also calculated through use of tools in ArcToolbox.

2.2.2.1 Dispersal distances

In order to assess the extent of dispersal events it was necessary to determine the distance between subsequent breeding sites. This was calculated as a straight-line distance in metres, as with Harvey *et al*. (1979) and Garcia-Navas and Sanz (2011). The 'Generate Near Table' function was used to find the distance between all nestboxes within the study site. Individuals which did not change nestbox, thus exhibiting site fidelity, were recorded as dispersing zero metres. Finally, a binary variable was created to facilitate future analyses, this recorded whether individuals changed nestbox.

A further variable is commonly used in the literature; whether an individual has changed territory (Garcia-Navas and Sanz, 2011), however, this relies upon either extensive fieldwork to establish the exact boundaries between territories, or upon researchers deciding what constitutes a change of territory. In this latter case, a value of 50m has frequently been used for blue tits, as with Garcia-Navas and Sanz (2011). Due to uncertainties over the accuracy of this method it was not used here.

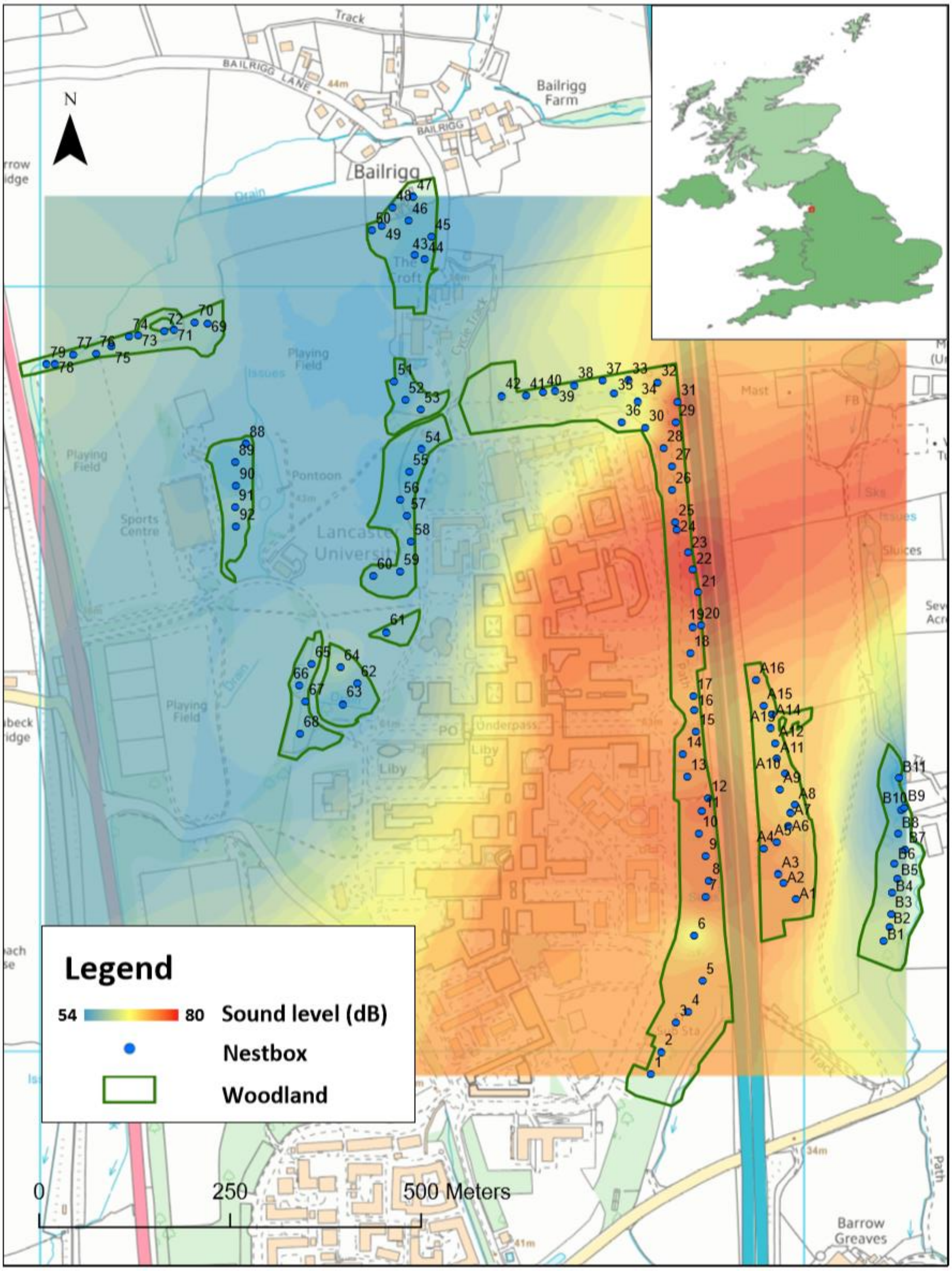

Figure 2.1: The study site at Lancaster University, United Kingdom, showing the study woodlands and the position of nestboxes within these. The road traffic noise, in decibels (dB), is shown using a colour scale with 1dB increments.

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2.2.2.2 Population density

Population density is an important variable known to influence both dispersal to, and from, habitats in bird species (Greenwood *et al*., 1979; Kim *et al*., 2007). To examine the influence of this, population density was calculated for each nestbox in each breeding season, between 2010 and 2018. This was achieved by mapping the location of each nestbox and recording the number of boxes occupied by blue tits within a 100m radius of that nestbox. The trees within the study site were generally of insufficient age to provide natural nest holes, thus using the number of occupied nestboxes should be equivalent to the number of blue tit pairs occupying an area. The distance of 100m was used as blue tit pairs are believed to typically forage within 50m of the nest during the breeding season (Tremblay *et al*., 2005), thus 100m represented the breeding pairs with which the birds occupying any one nestbox would be likely to regularly interact.

This study did not record population density as the number of breeding pairs per hectare, as is common in the literature, for example, Wesolowski (2006) and Lambrechts *et al*. (2010). However, for ease of comparison with other studies, population densities of 5 and 10 in this study convert to approximately 1.7 and 3.3 pairs per hectare, respectively.

2.2.3 Data from previous years

To examine the physical habitat variables influencing nestbox occupation, dispersal, and the breeding parameters, existing data were used from the study at Lancaster University, as well as data collected during the 2018 breeding season (Chapter 1). These data provided information on the occupancy of each of the 111 nestboxes from 2010 to 2018, recorded as a binary response variable, as well as the identity of the occupiers, if known, and it was these data which were used to identify all suitable breeding attempts for the dispersal analyses. The breeding parameters associated with each nesting attempt were also provided from this dataset and recorded as counts for each occupied nest, as well as the timing of the nesting attempt. The relevant temporal variables used in this study were the year, and the timing within the season, recorded as the first egg date, a count of how many days from the first of April, in each year, that the first egg was laid in each nest.

Existing data from a survey of the arboreal vegetation surrounding each nest were also used, these data enabled examination of the influence of the physical habitat upon nestbox occupation and dispersal, and were recorded as count data. Road noise data, were also available from a previous survey, where sound level in decibels had been recorded at all occupied nestboxes. Spatial interpolation methods were used to calculate sound levels at the nestboxes where measurements had not taken place. This was carried out in ArcMap using the ‘Inverse Distance Weighting (IDW)’ tool in the ‘Spatial Analyst’ toolset, which uses point data to produce a raster layer (Figure 2.1). The change in each measure of habitat quality was then calculated from these variables, subtracting the value of the first nesting attempt from that of the second. The same approach was then used for the other habitat variables and fledging success.

2.2.3.1 Road traffic noise

The main source of road traffic noise on the campus was the M6 motorway, which bisects the eastern side of the site (Figure 2.1). Other sources of sound disturbance included the A6, a main road to the west of the study site, and the smaller roads and paths around the campus. However, the motorway was the only sustained anthropogenic sound source within the study site, with other sources being irregular and intermittent.

Sound measurements were taken over a ten-minute period at each occupied nestbox using a Casella 346 sound level meter, with the average amplitude at each site being the value recorded. For a more detailed description of this sampling method see Wolfenden (2017). However, there were gaps in these data, and consequently, to provide a sound level in decibels for each nestbox, the data were inputted to ArcGIS. The 'Data Management' toolset was then used to generate a raster layer, which enabled prediction of sound levels at all points across the site, smoothing the data in the dataset.

2.2.4 Statistical methods

The R statistical package (R Core Team, 2017) was used for all statistical analyses and the relationships between the variables were explored following Zuur *et al*. (2010), to avoid any common statistical problems. All means are reported plus or minus one standard error.

Generalised linear models (GLMs), generalised linear mixed-effects models (GLMMs), and hurdle models were all used in the analyses for this project. GLMs were used when data were non-Gaussian but did not require random effects to be used to account for non-independence in the data. In cases where the data exhibited non-independence, GLMMs were used (Bolker *et al*., 2009; Harrison *et al*., 2018). Finally, hurdle models were employed when non-Gaussian data were determined to be zero-inflated (Yang *et al*., 2017).

Pairwise scatterplots and Pearson's correlation coefficients were used to assess collinearity between explanatory variables. Variance Inflation Factors (VIFs) were also used. These tests were carries out using the *aed* package code from Zuur *et al*. (2009) and collinearity was deemed to be present when correlations were greater than 0.4, or VIFs exceeded 3 (Zuur *et al*., 2010). When collinearity was identified one of the collinear variables was dropped from the analyses following a decision based on both ecological theory and preliminary analyses. Once the explanatory variables to include had been established, all of these were standardised and centred, to improve ease of interpretability of the model results (Schielzeth, 2010; Harrison *et al*., 2018). All possible two-way interactions between these explanatory variables were then included in each model, and sequentially dropped until only single variables, and significant interactions remained.

Model construction was then carried out by using the dredge function in the *MuMIn* package (Barton, 2018), with all possible combinations of the variables being ranked by Akaike's Information Criterion with correction for small sample sizes (AICc). The models present within the top 2 AICc values (delta AICc <2) were averaged (Galipaud *et al*., 2014; Harrison *et al*., 2018) and validated, by checking for overdispersion, and by plotting the residuals against the fitted values, the residuals against each covariate, and producing QQ-plots of the residuals (Zuur *et al*., 2009). Each averaged model was used to produce predictive plots of the variables identified as being important, and if there were a significant amount of overlapping points, these were offset from each other using the 'jitter' function in R to improve clarity.

2.2.4.1 Model of nestbox occupation

Nestbox occupancy was recorded as a binary response variable and, as such, to investigate the influence of the habitat variables upon nestbox occupancy, a GLMM with a binomial error distribution was used (Bolker *et al*., 2009). Nestbox identity was included as a random effect, controlling for autocorrelation from repeat measurements per nestbox. The habitat variables included were: the number of deciduous and evergreen trees present within a 50m radius of each nestbox, the presence or absence of an oak tree, the road traffic noise, and the population density. Year was also included, to examine stochastic effects. Any interactions which could be ecologically justified, or which were suggested by the preliminary analyses, were included in the model. Oak presence, as a binary response, was included instead of the number of oak trees, as the two variables were found to be highly collinear, and the literature suggests that oak trees are of great enough importance that their presence or absence can determine habitat quality (Chapter 1). The same model was later run with the number of oak trees included, to confirm the result found here, and this too found a negative relationship with nestbox occupancy.

2.2.4.2 Models of the breeding parameters

The data from all years, 2010 to 2018, for all occupied boxes, were used to examine the influence of the habitat variables upon the breeding parameters; clutch size, hatching success, and fledging success. These were determined to be Poisson distributed count data, and as such were also modelled using GLMMs (Harrison *et al*., 2018). The random effect, and explanatory habitat variables included, were the same as those for the model of nestbox occupation described above. However, the timing of breeding was included as an additional explanatory variable, in the form of the first egg date. The results from the three different models were very similar, showing the same key variables, thus only the model for fledging success is reported here.

2.2.4.2.1 Repeatability of the breeding parameters

The models generated above for the breeding parameters, were used to estimate the repeatability of each using the *rptR* package of Nakagawa and Schielzeth (2010) and Stoffel *et al*. (2017). These analyses followed Nakagawa and Schielzeth (2010), the full method of which is outlined in Chapter 1. The variables identified as significantly influencing the breeding parameters were included in the repeatability analyses to account for their confounding influence. To examine the influence of bird-specific and environmental influences upon repeatability, both nestbox and individual bird identity were used as grouping factors. However, to calculate the repeatability of the breeding parameters for individual birds a different dataset was used, which consisted of all individuals known to be breeding in the last three years. This was necessary because the individual bird identities were not known in the dataset for all years. This led to a discrepancy in the number of repeats of each, with an average of four repeats per nestbox and only two per individual. The estimates of repeatability are shown with the standard error, 95% confidence intervals around the estimate, and the *p* value, all of which were obtained from the *rptR* package.

2.2.4.3 Models of dispersal

Models were produced to examine the influence of environmental conditions, or reproductive success, of the first breeding attempt upon the decision to change box, and how far to disperse. Dispersal distance was measured as a straight-line distance, in metres, and was found to be zero-inflated, hence the *glmmADMB* package (Fournier *et al*., 2012) was used to fit hurdle models of the dispersal distance for both sexes together, to look for sex interactions. Hurdle models fit two GLMMs to the data to account for zero-inflation, one part with all zero values, and the other the zero-truncated values (Yang *et al*., 2017). The first of these models was a binary response, whether individuals changed nestbox between breeding seasons, or not, and modelled with a binomial error distribution and the logit link function, accounting for zero inflation in the data. The second model consisted of the values of the response greater than zero and used a truncated negative binomial error distribution, with the log link function (Fournier *et al*., 2012). The explanatory variables used in the models of dispersal were the same as those for the model of nestbox occupation, except for the additional inclusion of the sex and fledging success of the individual in the first year. The results of these models suggested that there was no interaction of sex with any of the other explanatory variables, therefore this model was not replicated for each sex.

2.2.4.4 The influence of dispersal on fledging success

To examine the influence of dispersal on fledging success, a GLM was produced with the change in fledging success between the first and second breeding attempts as the response. The explanatory variables were the change in each of the habitat variables, used in the previous models, as well as the year and fledging success of the first breeding attempt. However, to facilitate analyses, the change in the number of oaks was used in this model. This model was produced for both males and females, to look at the influence of sex, and again with whether the breeding individual had dispersed as a binary variable, or the dispersal distance, in metres, as additional explanatory variables. However, the outputs of the models which used the binary dispersal variable, and the distance, were found to be very similar, and as such only one is reported here.

2.3. Results

2.3.1 Nestbox occupation

The sample size for this analysis consisted of 111 nestboxes, with 106 of these having nine repeats and the remainder having seven. The number of nestboxes occupied by blue tits had a mean of 73.89 ± 3.12 occupied nests in each year, with this ranging from 57 to 84 between 2010 and 2018. The variables found to influence nestbox occupation were population density, oak presence, and the interaction of these two variables (Table 2.2). Nestboxes are more likely to be occupied as population density increases (Figure 2.2), and less likely to be occupied in the presence of oak trees (Table 2.2). The negative relationship between oak presence and nestbox occupation is contrary to expectations but can be explained by the interaction with population density (Figure 2.3). There was also a positive relationship between the number of oak trees and the population density (Figure 2.4).

2.3.2 Breeding parameters

Clutch size, hatching success and fledging success were found to have means of 9.37 ± 0.08, 8.30 ± 0.10, and 5.52 ± 0.15 respectively. Additionally, clutch size (n = 633) was found to be strongly significantly correlated with hatching success (rho = 0.717, df = 583, p <0.001), but only moderately so with fledging success (rho = 0.41, df = 580, p <0.001). Models of each of the breeding parameters were produced using the data from all occupied boxes from the breeding seasons since 2010. These models showed that the variables significantly influencing the breeding parameters were first egg date (Figure 2.5), the number of deciduous trees within 50m of the nest (Figure 2.6), and year (Figure 2.7). Contrary to expectations, none of the habitat variables were found to significantly influence the breeding parameters. The variables showed the same relationship with each of the breeding parameters and explained approximately 30% of the variability in the data (Table 2.3). Due to the similarities between the models, only the model for fledging success is shown here.

2.3.3 Repeatability of breeding parameters

The repeatability estimates for the breeding parameters were all moderately, to strongly, repeatable by nestbox, with fledging success being the most highly repeatable (Table 2.4). Additionally, clutch size was strongly repeatable for females, hatching success less so, and fledging success not significantly repeatable (Table 2.4). In contrast, neither clutch size or hatching success were significantly repeatable for individual males but fledging success was moderately significantly repeatable (Table 2.4).

Table 2.2: The model selection table for the global model of an averaged generalised linear mixed effects model examining the factors influencing nestbox occupation (n = 111):

> glmer(nestbox occupied (Y/N) ~ number deciduous trees + number evergreen trees + oak presence * population density (100m) + sound level (dB) + year, family = binomial)

#	Intercept	Oak Presence	Population density	Number deciduous	Number evergreen	Sound	Year	Oak presence: Population density	df	logLik	AICc	delta	weight	R2m	R2c
84	1.90	+	1.57			-0.21		+	6	-566.90	1145.9	0.00	0.14	0.19	0.32
92	1.90	+	1.67		0.16	-0.17		+	7	-565.98	1146.1	0.19	0.13	0.19	0.32
88	2.02	+	1.66	-0.16		-0.17		+	7	-565.98	1146.1	0.19	0.13	0.19	0.32
72	2.03	+	1.62	-0.20				+	6	-567.03	1146.2	0.27	0.12	0.19	0.32
76	1.90	+	1.63		0.20			+	6	-567.08	1146.2	0.35	0.12	0.19	0.32
80	1.98	+	1.68	-0.14	0.14			+	7	-566.43	1147.0	1.09	0.08	0.19	0.31
96	1.98	+	1.71	-0.11	0.11	-0.15		+	8	-565.59	1147.3	1.44	0.07	0.19	0.32
68	1.86	+	1.47					+	5	-568.68	1147.4	1.53	0.07	0.19	0.32

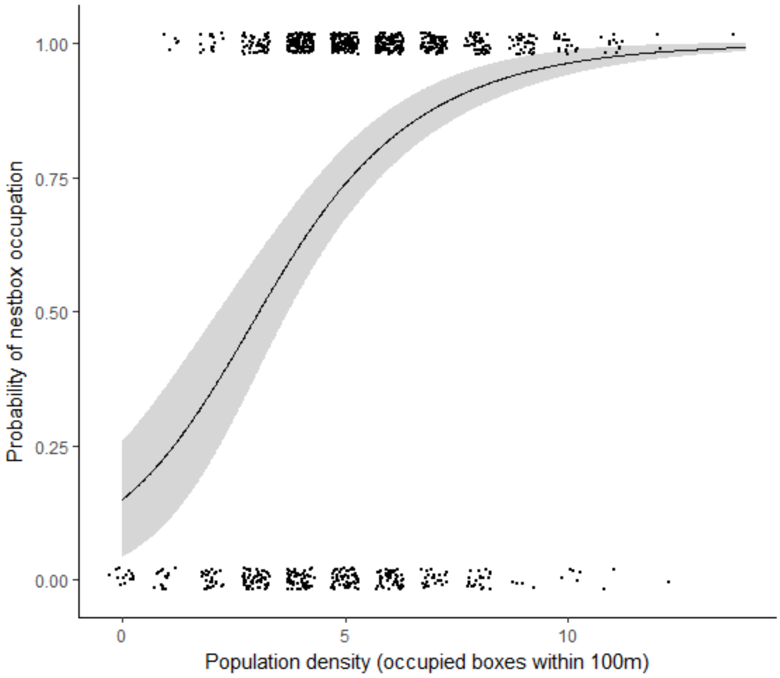

Figure 2.2: The probability of a nestbox being occupied plotted against the number of breeding pairs of blue tits within 100m, predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 111).

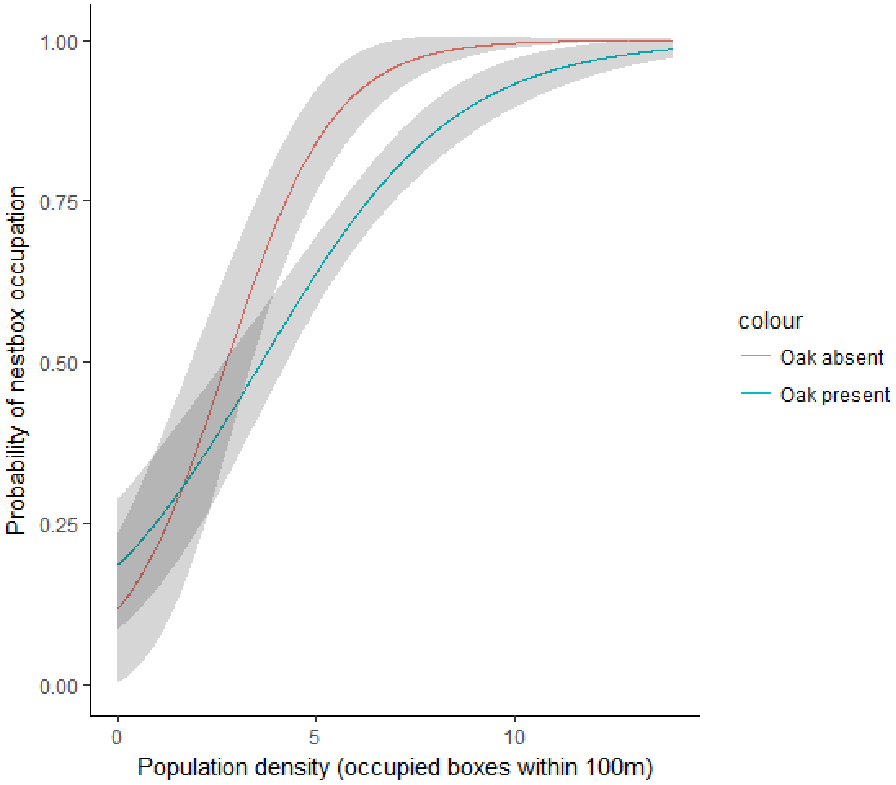

Figure 2.3: The probability of a nestbox being occupied plotted against the interaction of the number of breeding pairs of blue tits within 100m and the presence, or absence, of oak trees, predicted from the average model reported above (n = 111). The grey represents the 95% confidence intervals.

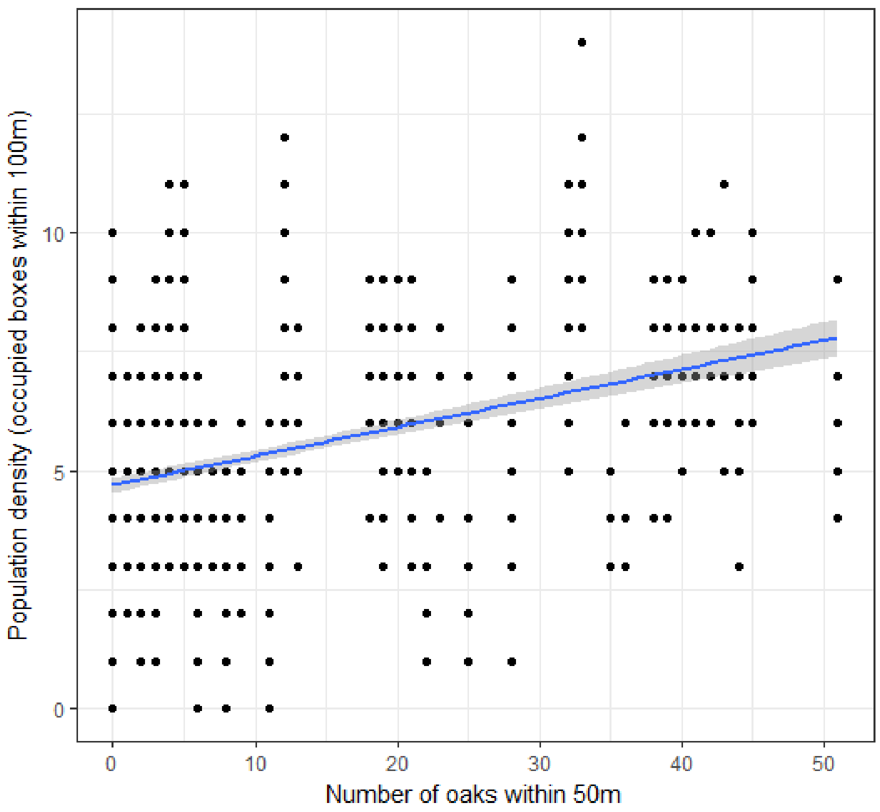

Figure 2.4: The relationship between population density (the number of blue tit pairs breeding 100m of each nestbox) and the number of oak trees within 50m (n = 111). The blue line is a trendline generated from the original data, and the shaded section shows the 95% confidence intervals.

Table 2.3: The model selection table for the global model of an averaged generalised linear mixed effects model examining the factors influencing fledging success (n = 581):

glmer (fledging success ~ number deciduous trees + first egg date + number evergreen trees + number oak trees + sound + year, family = poisson)

#	**Intercept**	**Population density**	**First egg date**	**Number deciduous**	**Number evergreen**	**Number Oak**	**Sound**	**Year**	**df**	**logLik**	**AICc**	**delta**	**weight**	**R2m**	**R2c**
88	2.11	-0.04	-0.23	0.05		0.06		+	14	-1598.02	3224.8	0.00	0.18	0.25	0.28
87	2.11		-0.24	0.05		0.04		+	13	-1599.36	3225.4	0.58	0.13	0.24	0.28
119	2.11		-0.24	0.06		0.05	-0.03	+	14	-1598.76	3226.3	1.48	0.09	0.24	0.28
120	2.11	-0.03	-0.23	0.06		0.06	-0.02	+	15	-1597.74	3226.3	1.54	0.08	0.25	0.28
71	2.12		-0.24	0.06				+	12	-1601.02	3226.6	1.81	0.07	0.24	0.28

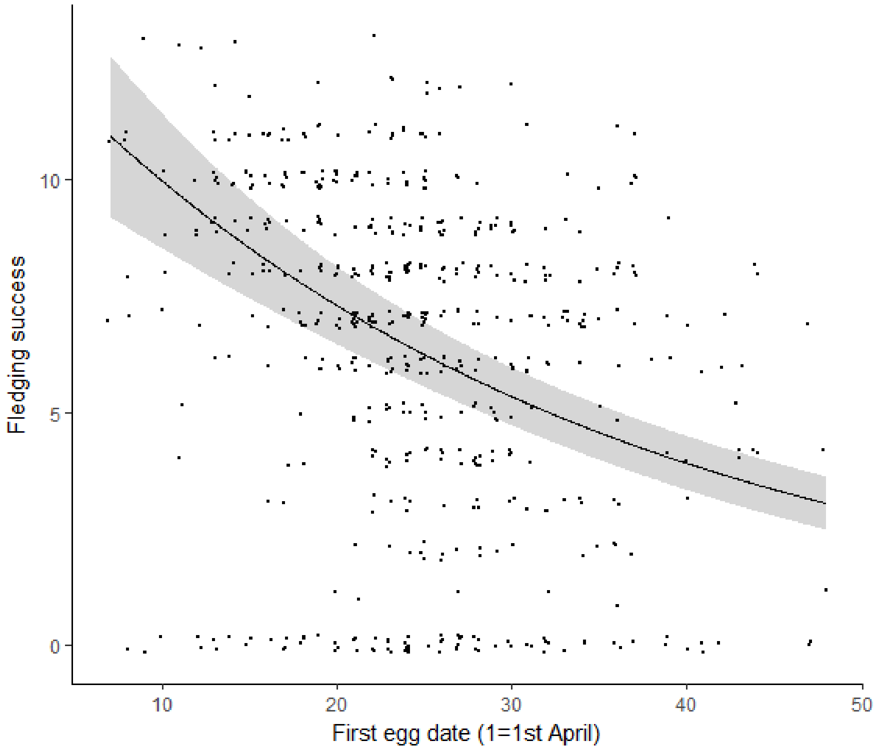

Figure 2.5: The relationship between fledging success and the date the first egg was laid in each nest, predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 581).

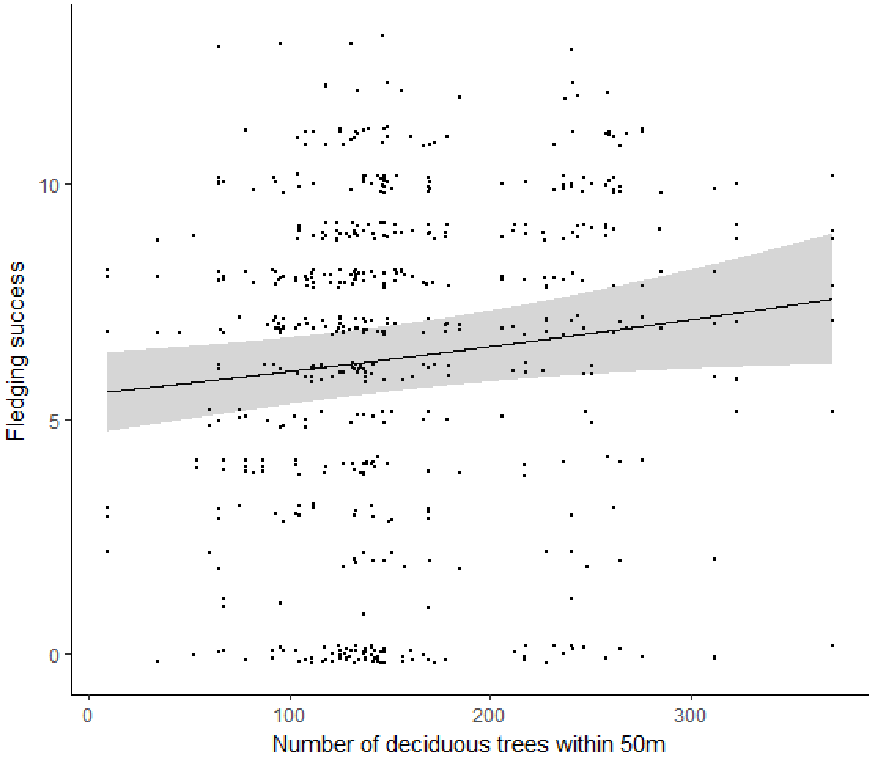

Figure 2.6: The relationship between fledging success and the number of deciduous trees within 50m, predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 581).

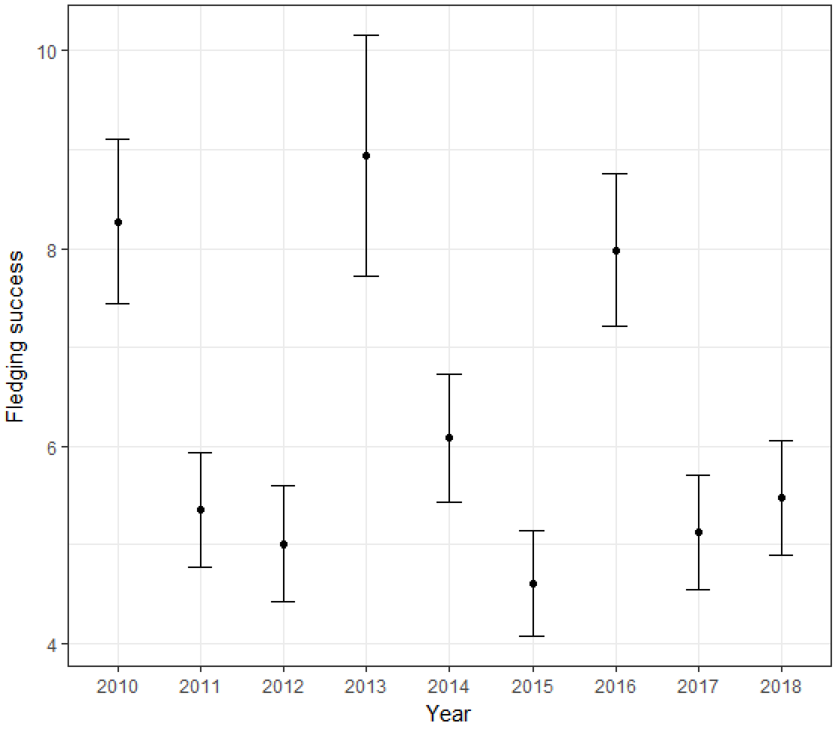

Figure 2.7: The relationship between fledging success and year, predicted from the average model reported above. The points represent the predicted values and the bars the 95% confidence intervals (n = 581).

Table 2.4: Repeatability of each breeding parameter for individual birds, separated by sex, and for nestboxes, produced using the *rptR* package. Repeatability, standard error, and 95% confidence intervals, all provided by use of *rptR*.

	Repeatability (SE)	**CI**	***p***	**n**
Clutch size by box	0.322 (0.064)	0.211, 0.467	<0.001	81
Female clutch size	0.622 (0.068)	0.495, 0.760	<0.001	89
Male clutch size	0.000 (0.079)	0.000, 0.263	0.500	81
Hatching success by box	0.301 (0.061)	0.207, 0.438	<0.001	80
Female hatching success	0.244 (0.098)	0.084, 0.485	0.018	89
Male hatching success	0.142 (0.102)	0.000, 0.387	0.139	81
Fledging success by box	0.469 (0.057)	0.353, 0.583	<0.001	80
Female fledging success	0.140 (0.101)	0.000, 0.388	0.118	89
Male fledging success	0.277 (0.106)	0.091, 0.506	<0.001	81

2.3.4. Breeding dispersal

There were 89 records of female dispersal or site fidelity, and 81 for males. Females were found to be more likely to change breeding site between seasons than males, with 78.65% of females changing nestbox, as opposed to 58.02% of males (chi-squared = 7.47, df=1, p <0.01). However, while there was a difference in the mean dispersal distance of males and females (54.64 ± 6.77m and 79.63m ± 9.30m respectively), the difference was not found to be significant (t = 1.64, df = 112.22, p = 0.10). Dispersal occurred in 63% of males whose partners disappeared, and in 78% of females in the same situation.

The first part of the hurdle model examining dispersal distance as a result of the conditions at the first breeding attempt; which treated all records as either records of dispersal or non-dispersal, found a statistically significant effect of sex and of sound (Table 2.5; Figures 2.8 and 2.9, n = 170). None of the explanatory variables were found to be significant in the zero-truncated dispersal distance part of the model, so it is not shown here. Contrary to expectations, neither the population density, nor the tree variables, of a breeding attempt were found to significantly influence dispersal.

Only the fledging success of an individual's first breeding attempt was found to be significant in determining the change in fledging success in the subsequent breeding season, this result being found for both males and females (Tables 2.6 and 2.7; Figures 2.10 and 2.11, n = 81 for males and 89 for females). Contrary to expectations, there was no influence of the change in any of the habitat variables on the change in either male or female fledging success (Tables 2.6 and 2.7). Finally, the model which looked at the change in fledging success in relation to the distance dispersed, and the changes in each of the habitat variables did not find any of the explanatory variables to be important for either males or females (n = 81 and 89 respectively), so is not shown here.

Table 2.5: The model selection table for the global model of an averaged generalised linear mixed effects model examining the factors influencing whether birds change nestbox or not (n = 170). The first part of the hurdle model:

> glmeradmb(changed nestbox Yes/No ~ number of deciduous trees + number of evergreen trees + number of oak trees + population density + fledging success at the first breeding attempt + year, family = binomial)

#	Intercept	Sex	Fledging success	Number deciduous	Number evergreen	Number Oak	Population Density	Sound	Year	df	logLik	AICc	delta	weight
66	1.41	+						0.50		4	-97.26	202.8	0.00	0.13
82	1.40	+				-0.27		0.63		5	-96.42	203.2	0.46	0.10
74	1.43	+			0.11			0.53		5	-97.05	204.5	1.71	0.05
70	1.41	+		-0.12				0.54		5	-97.06	204.5	1.73	0.05
68	1.41	+	-0.10					0.51		5	-97.11	204.6	1.84	0.05

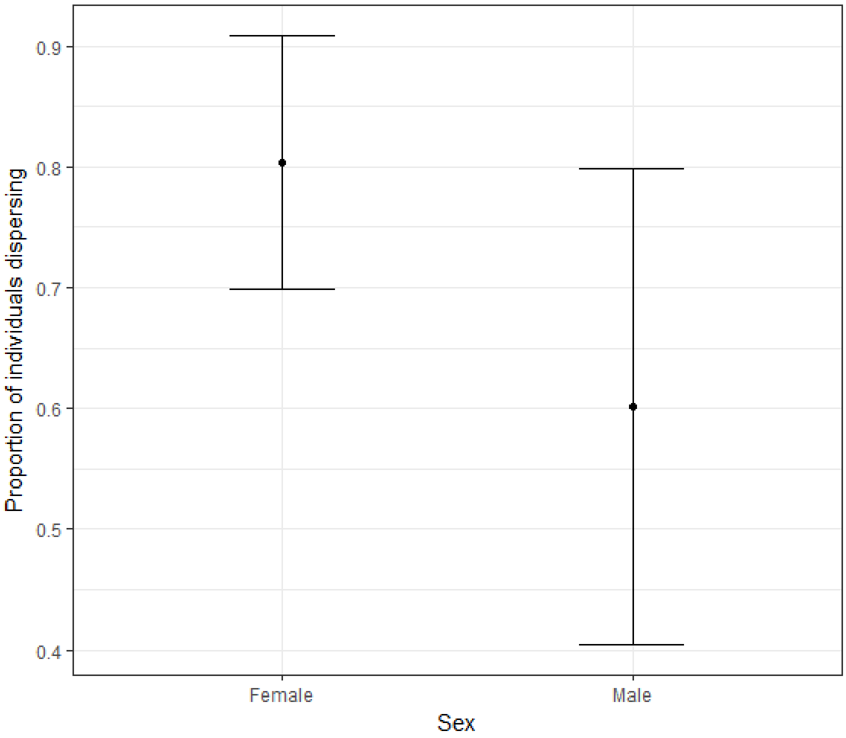

Figure 2.8: The probability of an individual dispersing following a breeding attempt and sex. The points represent the predicted values and the bars the 95% confidence intervals (n = 89 females and 81 males).

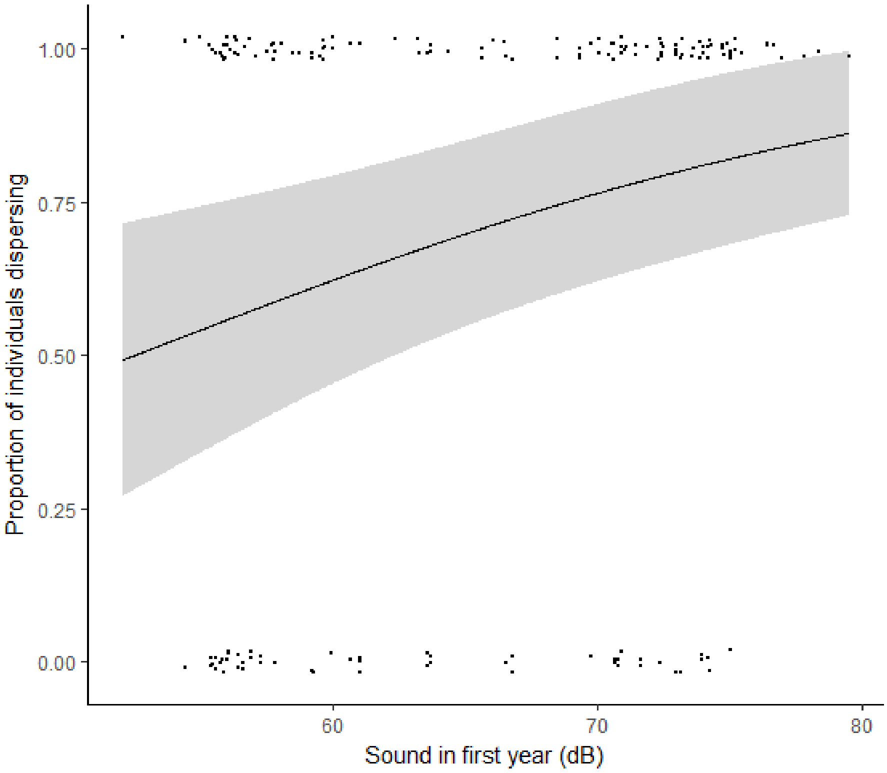

Figure 2.9: The probability of an individual dispersing following a breeding attempt, plotted against the road traffic noise experienced during that breeding attempt, in decibels. The points represent the original data and the grey the 95% confidence intervals (n = 170).

Table 2.6: The model selection table for the global model of an averaged generalised linear model examining the factors influencing the change in fledging success between first and second breeding attempts, for males (n = 81):

> glm(change in male fledging success ~ change in number of deciduous trees + change in number of evergreen trees + change in number of oak trees + change in population density + fledging success at the first breeding attempt + year of the first breeding attempt, family = binomial)

#	Intercept	Change in population density	Year	Fledging success	Change in number deciduous	Change in number evergreen	Change in number oak	Change in sound	R^2	df	logLik	AICc	delta	weight
21	-0.15			-2.56		-0.59			0.39	4	-213.70	435.9	0.00	0.09
5	-0.15			-2.56					0.37	3	-214.97	436.2	0.33	0.07
7	-0.17		+	-2.32					0.48	10	-206.78	436.7	0.75	0.06
53	-0.15			-2.72		-0.57	0.47		0.40	5	-212.94	436.7	0.75	0.06
37	-0.15			-2.72			0.50		0.38	4	-214.16	436.8	0.92	0.05
39	-0.05		+	-2.51			0.53		0.50	11	-205.72	437.2	1.30	0.05
29	-0.15			-2.57	0.31	-0.61			0.39	5	-213.33	437.4	1.53	0.04

Table 2.7: The model selection table for the global model of an averaged generalised linear model examining the factors influencing the change in fledging success between first and second breeding attempts, for females (n = 89):

> glm(change in female fledging success ~ change in number of deciduous trees + change in number of evergreen trees + change in number of oak trees + change in population density + fledging success at the first breeding attempt + year of the first breeding attempt, family = binomial)

#	**Intercept**	**Change in population density**	**Year**	**Fledging success**	**Change in number deciduous**	**Change in number evergreen**	**Change in number oak**	**Change in sound**	**R^2**	**df**	**logLik**	**AICc**	**delta**	**weight**
5	-0.01			-2.53					0.37	3	-232.40	471.1	0.00	0.10
37	-0.01			-2.60			0.49		0.38	4	-231.42	471.3	0.22	0.09
6	-0.90	+		-2.48					0.38	4	-231.54	471.6	0.46	0.08
38	-0.94	+		-2.54			0.52		0.39	5	-230.43	471.6	0.49	0.08
13	-0.01			-2.52	0.32				0.37	4	-231.99	472.5	1.37	0.05
14	-0.87	+		-2.47	0.30				0.39	5	-231.16	473.0	1.96	0.04

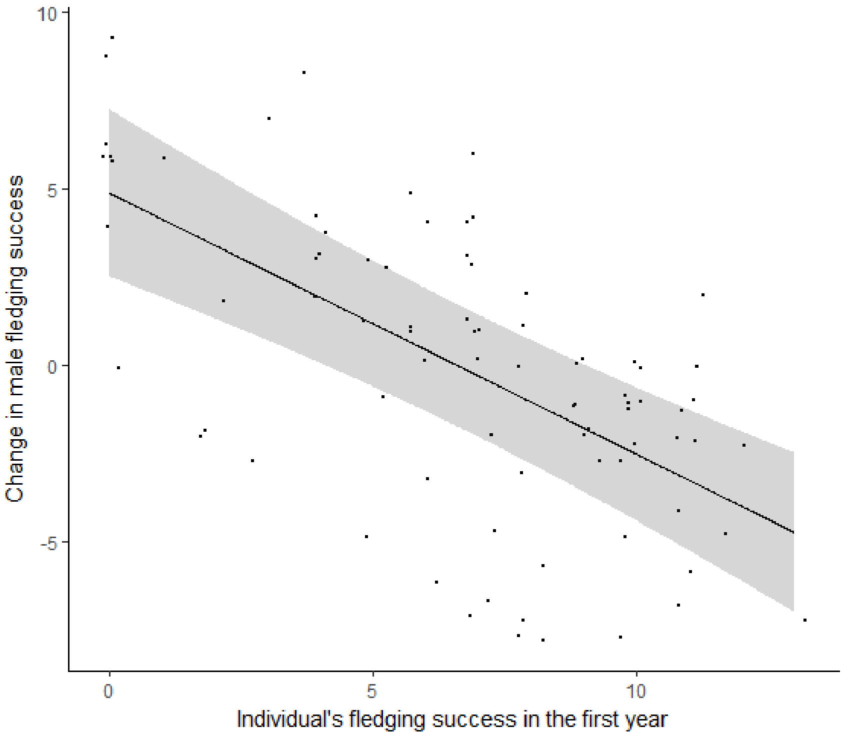

Figure 2.10: The relationship between the change in male fledging success between successive breeding attempts and the fledging success in the first year. The points represent the original data and the grey the 95% confidence intervals (n = 81).

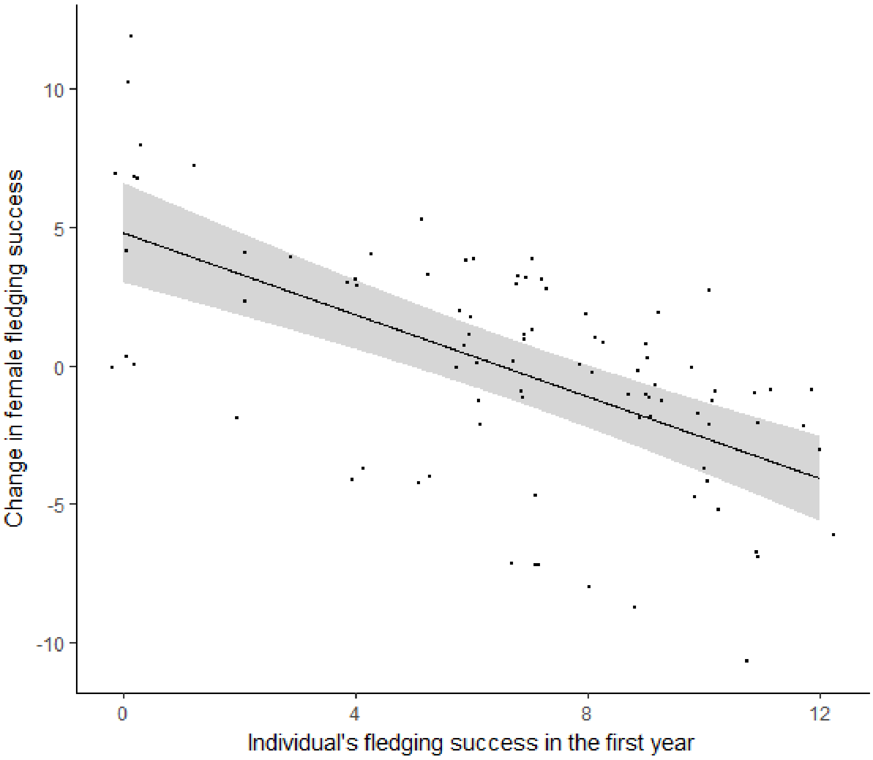

Figure 2.11: The relationship between the change in female fledging success between successive breeding attempts and the fledging success in the first year. The points represent the original data and the grey the 95% confidence intervals (n = 89).

2.4 Discussion

The results of this study indicated that there is little variation in the number of nestboxes occupied by blue tits at Lancaster University between years, but that the probability of a nestbox being occupied varied based on several variables (Table 2.2). These were population density (Figure2.2) and its interaction with habitat quality, specifically, the presence or absence of oak trees in the territory (Figure 2.3). When the influence of the physical environment upon the breeding parameters was examined, it was found that the same variables were significantly influencing each of these. These were: the timing of the brood within the breeding season (Figure 2.5), the number of deciduous trees within 50m (Figure 2.6), and the year (Figure 2.7). Furthermore, estimates of the repeatability of the breeding parameters varied between males and females, with the sexes being more repeatable at different stages of the breeding attempt (Table 2.4). Additionally, each of the breeding parameters was moderately to strongly repeatable by nestbox (Table 2.4). When the factors influencing breeding dispersal were examined, it was found that only sex and road traffic noise made an individual more likely to disperse, with females more likely to disperse than males, and individuals breeding in a noisier box also more likely to disperse (Figures 2.8 and 2.9). However, none of the habitat, or bird-specific, variables influenced the distance an individual dispersed. Finally, there was no significant difference between the habitat variables following dispersal for either males or females (Tables 2.6 and 2.7), and dispersing did not have a significant influence upon fledging success (Figures 2.10 and 2.11).

2.4.1 Nestbox occupation

Nestboxes were more likely to be occupied when the population density was higher (Figure 2.2), suggesting that blue tits preferentially choose to nest where there are high population densities. This could be a result of blue tits using a high density of conspecifics as an indication of high-quality habitat, as with pied flycatchers (Samplonius *et al*., 2017), or for the benefits from increased predator detection, and the dilution effect reducing the risk of predation (Dehn, 1990; Latif *et al*., 2012). Alternatively, it is also likely that those areas with the highest population densities were also those with the highest habitat quality, as found for blue tits by Sanz *et al*. (2010). The results of this study also suggested that the blue tits at Lancaster bred at a higher density where there were a greater number of oak trees (Figure 2.4), supporting this conclusion.

The finding that the probability of a nestbox being occupied increases with population density differs from that of Serrano-Davies *et al*. (2017) who found that blue tits breeding in a pine plantation preferentially occupied nests further away from conspecifics. This contrasting result is likely to be due to the influence of habitat quality and the spatial variation in food abundance, as blue tits breeding in evergreen woodland are known to compensate for reduced abundance of invertebrates by increasing their territory size (Tremblay *et al*., 2005). However, in mixed woodland, as at Lancaster, there is a much higher food abundance, and nestboxes are spaced approximately 25m apart, thus ensuring sufficient food availability in each territory to prevent a negative response to high population densities. However, food abundance was not measured as part of this study, so inferences based upon this are uncertain and should be addressed in future research.

Contrary to expectations, it was found that nestboxes without oak trees present within 50m were more likely to be occupied than those with oak trees present at all but the lowest and highest population densities (Figure 2.3). The literature suggests that oak trees represent the preferred habitat of blue tits, and thus should be those occupied first (Amininasab *et al*., 2016). This result is most likely to reflect birds being forced into lower quality territories as population densities increased (Sergio and Newton, 2003). However, this result may also reflect high competition for those territories with oak trees present, resulting in blue tit pairs being less able to occupy these territories, despite them being the preferred habitat (Switzer, 2002; Sergio and Newton, 2003). Additionally, it is plausible that those nestboxes near clusters of oak trees can use them for foraging regardless, reducing the benefit of nesting close to the oak trees, where interlopers will increase the time and energy required for territory defence. Figure 2.3 supports this view, showing that territories with oaks present were likely to be preferentially occupied when there was no competition, approximately zero to one breeding pair per hectare, but that at higher population densities territories without oaks were preferred.

The lack of a significant effect of the number of evergreen trees on nestbox occupation (Table 2.2) is likely to have been a result of there being few territories at Lancaster which had many evergreens, and thus there would have been no strong influence of evergreens on food abundance. Road traffic noise was also not found to influence the likelihood of a nestbox being occupied, which is as expected, as blue tits are widespread in anthropogenic environments (Pollock *et al*., 2017), suggesting that they do not regard road traffic noise as a source of significant disturbance. For example, Halfwerk *et al*. (2016), found that great tits avoid nesting in sites with greater road traffic noise, but that blue tits had no such response.

2.4.2 Breeding parameters

The negative relationship found between each breeding parameter and the first egg date (Figure 2.5), as well as the positive relationship between the number of deciduous trees within 50m of each nestbox (Figure 2.6), both suggest that habitat quality, and parental quality influenced the breeding parameters. The negative relationship between first egg date and each breeding parameter reflects the often-reported result that clutch sizes are higher for the first nests, as these tend to be those laid in both the highest quality habitats, and by the highest quality parents (Both and Visser, 2005; Tremblay *et al*., 2005). The decrease in fledging success as first egg date increases, is likely to be a result of a seasonal decline in food availability, demonstrating the importance of occupying high-quality territories.

The increase in fledging success with the number of deciduous trees (Figure 2.6) also shows the effect of food abundance. Deciduous trees support a substantial food source for foraging tits (Kelly and Southwood, 1999), thus territories with a greater number of deciduous trees will have a greater abundance of food items available, resulting in reduced foraging costs for the parents and consequently increasing the rate at which the nest can be provisioned (Stauss *et al*., 2005). However, it is surprising that oak trees were not of a greater importance, as they support a larger biomass of invertebrates than other deciduous trees (Kelly and Southwood, 1999). This could be a result of increased competition when foraging near oaks, as outlined above, or could suggest that there is sufficient food available in the study site, masking the predicted influence of oaks. Another important determinant of habitat quality is population density, which was not found to influence the breeding parameters in this study, as also found in blue tits by Arriero *et al*. (2006). The lack of a population density effect further suggests that there was not significant competition for food sources in the study site, most likely due to an abundance of food sources. However, the high disparity between clutch size and fledging success suggests that something is reducing reproductive success in these stages, perhaps as a result of increased competition for a key resource. For example, both food and micronutrients would be more difficult to access at the high breeding densities found in this study.

The variation in breeding parameters with year is due to the influence of stochastic effects, which influence both nest success, or failure, and the ability of the parents to provision the young. For example, through temporal fluctuations in local predator populations, or as a result of extreme weather events (Mainwaring and Hartley, 2016b; Brodin *et al*., 2017), which increase the energy requirements of the parents and offspring in unfavourable years, as well as influencing food availability.

2.4.2.1 Repeatability estimates of the breeding parameters

The repeatability estimates show that clutch size was very highly consistent for individual females and moderately so for nestboxes (Table 2.4). These results suggest that the primary control upon clutch size was female quality, determined by both the genotype and phenotype, which has been previously suggested by many papers, including van Noordwijk *et al*. (1987), Slagsvold and Lifjeld

(1990), Svensson (1997). A study on the repeatability of breeding parameters in magpies also found similar results (Goodburn, 1991). However, habitat quality was also important, though having a lesser influence on the repeatability of clutch size. For example, both the availability of food and natural sources of calcium, are likely to have influenced the clutch sizes recorded. Calcium is an essential micronutrient influencing the number of eggs a female can lay (Wilkin *et al*., 2009b), and is believed to be relatively constant in the environment, as it is based on soil types (Gosler and Wilkin, 2017). Thus, calcium availability could explain repeatability of clutch size by nestbox. Alternatively, it is possible that there was an interaction between habitat quality and individual quality, with each nestbox being selected by females of a similar competitive ability, explaining the moderate repeatability of clutch size found for nestboxes.

A similar result was found for the repeatability estimates of hatching success, with nestboxes exhibiting a similar level of repeatability as they did for clutch size but the estimate for female repeatability had decreased (Table 2.4). The lower repeatability of female hatching success is likely to reflect a decreasing influence of female quality as the season progresses, and after the initial input of clutch size. The observed repeatability may in fact be a result of clutch size and hatching success being highly significantly correlated, rather than females displaying repeatable hatching success. However, the nestbox and habitat quality were still significantly moderately repeatable, suggesting an influence of habitat on repeatability of hatching success. This was most likely to have been a result of the abundance of natural food sources in the environment, and the influence of this upon parental care. For example, when food is abundant females will be able to contribute more of their time to incubation, rather than foraging, which should reduce the chance of a clutch failing, and increase the number of eggs which hatch. Food abundance may also influence the quality of eggs laid, by determining egg size and nutritional content, influencing hatching success (Hargitai *et al*., 2005). Furthermore, studies have suggested that the relative food abundance of each territory is consistent across years (Amininasab *et al*., 2016; Amininasab *et al*., 2017), supporting the view that this aspect of habitat quality would result in repeatable hatching success by nestbox.

Contrasting with the results for clutch size and hatching success, fledging success was found to be strongly significantly repeatable for nestboxes, and moderately significantly repeatable for individual males, but not for females (Table 2.4). The increase in repeatability estimate of the nestbox suggests that habitat quality has a greater influence on fledging success, which is most likely to be due to the consistency of food in the environment and its influence upon provisioning rates, and thus the number of nestlings which fledge. The literature suggests that male parental care varies little between years (Nakagawa *et al*., 2007; Bell *et al*., 2009; Bebbington and Hatchwell, 2016), thus the influence of both food availability and male quality upon provisioning rate should explain the moderately repeatable result for male fledging success. Namely, the consistent provisioning rate of an individual male is likely to have a repeatable influence upon the number of their offspring which fledge, possibly by influencing the minimum, or maximum, number of nestlings that a male is able to provide care for. Contrastingly, females are believed to vary their investment in parental care based upon the demands of their offspring (Nakagawa *et al*., 2007; Cleasby *et al*., 2013), and if they do so, stochastic effects between years such as extreme weather events, which influence hatching and fledging success, will cause females to vary their level of parental care accordingly, with fledging success becoming not repeatable between years as a result.

These results contrast with those found previously for a population of blue tits by Przybylo *et al*. (2001), who found no repeatability of the breeding parameters for females, although they did find that the timing of breeding, and the condition of nestlings were consistent for territories and for males. The difference between the results of these studies could be due to the study woodlands used, with those of Przybylo *et al*. (2001) varying greatly in quality on small spatial scales, which was suggested as leading individual females to match their clutch size to the territory quality, rather than their own. However, the different statistical methods are more likely to have an influence on the results, with Przybylo *et al*. (2001) using the analysis of variance (ANOVA) method of calculating repeatability, which is commonly cited as being less accurate and less able to account for confounding effects, than the mixed modelling approach used here (Nakagawa and Schielzeth, 2010; Dingemanse and Dochtermann, 2013). Additionally, the sample sizes of Przybylo *et al*. (2001) were lower than those of this study, and are mentioned in their paper as a potential issue.

2.4.3 Dispersal

2.4.3.1 The influence of the first breeding attempt

There was little evidence that blue tits disperse away from specific conditions in this study, with only the sex of the individual (Figure 2.8), and the level of road traffic noise (Figure 2.9) found to be significantly influencing the probability of dispersal. Furthermore, none of the variables were found to significantly influence the distance that males or females dispersed, suggesting that for blue tits the more important decision is whether or not to leave a breeding site. These two decisions reflect a differing set of processes and are often confounded in the literature, although they can suggest different results, as encountered here (Mabry *et al*., 2013).

The finding that females are more likely to undergo breeding dispersal than males (Figure 2.8) is well-documented in the literature (Harvey *et al*., 1979; Greenwood and Harvey, 1982; Garcia-Navas and Sanz, 2011). Clarke *et al*. (1997) suggest that this sex-bias is likely to arise from the differential costs and benefits of dispersal. For example, males must establish a territory, defend it, and attract a female, all of which represent significant temporal and energetic costs, leading to males being more likely to maintain their current territory rather than dispersing (Garcia-Navas and Sanz, 2011). In contrast, there are far fewer costs suffered by dispersing females, as they can choose to pair with any available male and do not need to establish territories of their own (Valcu and Kempenaers, 2008). Therefore, females are likely to disperse more often, seeking access to a higher quality male, or territory, both of which increase their reproductive success (Garcia-Navas and Sanz, 2011). Similarly, females were found to be more likely to disperse following the disappearance, and presumed death of a mate. This likely reflects the role of the male in establishing the territory and may indicate that the higher probability of dispersal for females is, at least partially, in response to male mortality.

Both male and female blue tits were found to be more likely to disperse after breeding in an area exposed to greater road traffic noise (Figure 2.9). This is most likely to be a result of increasing sound levels lowering habitat quality, as suggested by Schroeder *et al*. (2012). A reduction in habitat quality could result from increased sound levels in several ways, for example, through masking of vocal communications between individuals, consequently increasing the time and energy required for territory establishment and defence (Warren *et al*., 2006; Meillere *et al*., 2015). High noise levels may also be sufficient to mask nestling begging calls, leading to parents provisioning their offspring at a sub-optimal rate (Halfwerk *et al*., 2011). However, it has also been suggested that wild birds breeding in noisier territories spend more time on anti-predator behaviour, suggesting an increased perception of predation risk (Schroeder *et al*., 2012; Meillere *et al*., 2015). As well as explaining why birds may preferentially disperse from these territories, this also has implications for reproductive success, as it reduces time spent foraging, lowering provisioning rates at the nest, and the fitness of both the parents and offspring (Schroeder *et al*., 2012).

Contrary to expectations, neither the vegetation variables, population density or fledging success were found to significantly influence the decision to disperse, or the distance between nest-sites (Table 2.5). The literature had suggested that individuals would be more likely to disperse if they had occupied a low-quality habitat, or if they had experienced low reproductive success (Bollinger and Gavin, 1989; Haas, 1998; Kim *et al*., 2007). However, a study on divorce also found no influence of reproductive success, or territory characteristics, of the former breeding attempt to influence dispersal in blue tits (Valcu and Kempanaers, 2008). This result is supported further by a study by Wesolowski (2006), of marsh tits, which suggested that there is no significant selection pressure upon birds reusing nest-sites between breeding attempts when there are other suitable ones nearby. Thus, the lack of the expected result may be due to the high availability of nest-sites in the study site, which likely exceeds that which would be expected in natural environments. The high availability of nestboxes may also have influenced the incidence of dispersal, allowing males to change nestbox while remaining within the same territory. Thus the measure of dispersal used in this study may have been biased and this could be assessed in future work.

The study site may have influenced the results in other ways as well, for instance, the majority of the woodland within the study site was mixed deciduous, thus it is possible that there was little influence of habitat in the results because territory quality did not vary considerably between areas. Additionally, the study site used in this project was not very large and there were nearby woodlands not monitored for blue tits. Hence, it is possible that this study not finding any significant influences upon dispersal distances was a result of long-range dispersers being lost from the study site. However, blue tits do not typically disperse long distances, so this is unlikely to have influenced the results significantly (Santema and Kempenaers, 2018).

2.4.3.2 The reproductive outcome of dispersal

This study found no influence of either the decision to disperse, or the distance dispersed, upon the change in fledging success between years (Tables 2.6 and 2.7). This suggests that blue tits do not gain a reproductive benefit from dispersing, regardless of whether they are moving to an area they may have experience of, such as an adjacent territory, or whether they are dispersing to a completely different habitat patch. This result is unexpected, as the literature suggests that dispersal is an adaptive process by which an individual can increase their reproductive success (Beheler *et al.*, 2003; Garcia-Navas and Sanz, 2011). Competition may be influencing the territories an individual is able to occupy (Figure 2.2), leading to individuals of a similar quality, and thus competitive ability, only being able to occupy similar quality territories when breeding, removing any influence of dispersal. The repeatability results above also suggest that fledging success is likely to be relatively repeatably by territory, therefore if an individual can only occupy territories of similar quality this may result in their reproductive success not changing (Table 2.4). Thus, it is possible that any benefit of changing nestbox will instead be noticed in the clutch size. Studies which have shown a significant change in reproductive success following dispersal have attributed this result to the quality of the breeding partner, with dispersing females in particular finding a new mate of a higher quality (Valcu and Kempanaers, 2008; Garcia-Navas and Sanz, 2011). In contrast, males can only select higher quality territories, and thus may have no consistent improvement in reproductive success (Garcia-Navas and Sanz, 2011).

The fledging success of the bird in the first year was found to be significantly correlated to the changes in fledging success for both males and females (Figures 2.10 and 2.11), which could be showing that those birds with a higher fledging success are less likely to have their fledging success alter following dispersal. This implies that higher quality individuals, those with the higher fledging success, are likely to be more repeatable, whereas lower quality individuals, which would be those whose nesting attempts failed or had low fledging success, typically improve their fledging success in subsequent years. This could be showing that there is an aspect of both individual quality upon reproductive success, and also of stochastic effects, such as extreme weather events (Mainwaring and Hartley. 2016b). However, it could also be that the significant response is merely reflecting the method used to calculate the change in fledging success, which made use of the fledging success of the first breeding attempt. If this is the case, then it is unlikely that fledging success was actually influencing the change in fledging success, and this result should be discarded.

The change in fledging success was also not found to be significantly related to the change in any of the physical habitat variables (Tables 2.6 and 2.7), further suggesting that either blue tits are not occupying improved territories following dispersal, or that this does not influence their reproductive success. This could be a result of the territories differing little, or the quality of the individual being of greater importance. It is also possible that blue tits are unable to compare the relative quality of habitats, and as such do not show a significant influence of any of the habitat variables (Bateson and Healy, 2005), although the results outlined above for nestbox occupation suggest this is not the case.

2.4.4 Conclusion and suggestions for further study

In conclusion, this study has found evidence that blue tits do make the decision to disperse in response to habitat quality, with dispersal more likely following breeding in territories subject to greater levels of road noise. This demonstrates a novel example of how increasing anthropogenic noise-levels are altering the behaviour, and spatial distribution, of populations of wild birds. However, none of the variables measured were found to influence how far blue tits dispersed, and there was no apparent reproductive benefit of dispersing. This suggests that blue tits were either unable to compare the relative quality of territories between years, or were unable to access higher quality habitats within the short distances they typically disperse. Additionally, novel evidence was found that the breeding parameters were repeatable, with female quality the most important determinant of clutch size and male quality a more important factor for fledging success. Furthermore, the breeding parameters were also found to be repeatable for nestboxes, suggesting that habitat influenced reproductive success in predictable ways, with this most likely to be resource availability.

Future projects should incorporate measures of the quality of individual birds and of breeding partners, into future research on dispersal and repeatability. This could both confirm the findings of this project and potentially identify further interesting influences upon dispersal. Furthermore, monitoring of the woodlands surrounding the study site, to examine the reproductive success of long-distance dispersers, would increase confidence in the method used here. If long-distance dispersers are not found to exhibit significantly different behaviour, or reproductive success, from those birds which remain in the study site, then it would support the results of this study, which differ from those in the literature. Finally, experimentally manipulating population density, and then reassessing the factors influencing nest-site selection, repeatability of the breeding parameters, and dispersal, could also lead to some interesting results.

3. Parental care, and its repeatability, in blue tits (*Cyanistes caeruleus)*

3.0 Abstract

Parental care is an important behaviour determining reproductive success in wild birds. Many aspects of individual and habitat quality influence parental care by altering the costs and benefits of this behaviour. However, individuals breeding in multiple years have been found to exhibit repeatable levels of parental care, with the level of repeatability varying by sex. This suggests that the costs and benefits of parental care vary between the sexes but that individual quality, personality, and experience, are likely to have a significant influence. This study examined the influence of these controls upon parental care, and its repeatability, in blue tits (*Cyanistes caeruleus*) at Lancaster University, over three years, from 2016 to 2018, along with the results of a vegetation survey of the area around each nestbox. Repeatability was estimated for the provisioning rate of breeding males, females, and for each nestbox, to assess the relative influence of habitat quality and individual-specific factors.

The results showed that the variables influencing male and female provisioning rates differed, in both their effects and in which variables were important. For example, the sexes provisioned at a similar rate at large brood sizes but females provisioned at a lower rate as brood size decreased. The other variables significantly influencing the provisioning rate of each sex were age and partner age for males, with both negatively related to provisioning rates, and the partner's investment in care for females, females increasing their investment as their partner did so. Additionally, males provisioned at a higher rate when with the same partner as the previous year, but females provisioned at a higher rate when breeding in the same nestbox, showing a significant, but sex-biased, influence of previous experience. However, reproductive success was not increased by whether an individual retained a breeding mate, or site, between years. Provisioning rates were highly repeatable for individual males, moderately so for females, and, after removing variation based upon individual identity, both male and total provisioning rate per nest were repeatable for nestboxes. These results suggest that females may be more closely matching their provisioning rate to the requirements of the brood and the effort of their partner, as predicted by the negotiation model, whereas males provision more akin to the sealed-bid model of parental care. This study has provided compelling evidence for the influences of habitat, and individual, quality and prior experience upon parental care and shown that this varies by sex. This has implications for both parental care and breeding dispersal and should be examined further in future research.

3.1 Introduction

Parental care is one of the most frequently studied behaviours in wild birds and can be defined as any actions taken by an individual that increases the quality, and survival, of its offspring at the expensive of its own future fitness (Trivers, 1972; Clutton-Brock, 1991; McNamara *et al*., 2003). Many variables have been cited as influencing parental care, with the most important believed to be related to aspects of individual, and habitat, quality (Naef-Daenzer and Keller, 1999; Chapter 1). Despite the many differing factors which influence parental care, the provisioning rates of individuals, a common measure of parental care, has been found to be moderately, to highly, repeatable for individuals breeding in multiple years (Nakagawa *et al*., 2007; Bell *et al.,* 2009; Cleasby *et al*., 2013). Additionally, these studies have typically found that males are more repeatable than females, as reported in several species, for example, the long-tailed tit (*Aegithalos caudatus*; MacColl and Hatchwell, 2003), house sparrow (*Passer domesticus*; Nakagawa *et al.*, 2007), and stitchbird (*Notiomystis cincta*; Low *et al*., 2012).

Repeatability for both male and female provisioning rates is commonly explained by the idea that individuals are provisioning the nest based upon game theory models, and that these models have a logical outcome on repeatability (Bebbington and Hatchwell, 2016). The first of these is the sealed-bid model (Houston and Davies, 1985), which states that provisioning rates only vary over evolutionary timescales, with each individual provisioning at a rate predetermined by its quality, as influenced by its genotype (Nakagwa *et al*., 2007). This model predicts that individual provisioning rates should be consistent between years and thus repeatable. However, more recent theoretical studies believe that the sealed-bid model is flawed, as it is much more likely that individuals adaptively alter their provisioning rate based upon the conditions of the current breeding attempt (Johnstone *et al*., 2014; Bebbington and Hatchwell, 2016). The negotiation model predicts that individuals instead negotiate with their partner over the level of parental care each provides (McNamara *et al*., 2003), with the negotiation varying based on the factors influencing provisioning rate (Nakagawa *et al*., 2007). The relative costs and benefits of these variables will vary between years, thus affecting the negotiation of care, resulting in inconsistent individual provisioning rates between breeding attempts (Bebbington and Hatchwell, 2016). Therefore, the negotiation model predicts that provisioning rates will not be repeatable between years.

The literature suggests that these models can explain the sex difference in repeatability of provisioning rates, where females negotiate care with both their offspring and partner, whereas male provisioning follows the sealed-bid model (Nakagawa *et al*., 2007; Cleasby *et al*., 2013). The difference in provisioning care behaviours is believed to be a result of females using provisioning rate as a measure of quality to select mates (Zhao *et al*., 2016), which has then led to this trait being repeatable between years (Bell *et al*., 2009; Schuett *et al*., 2010; Schuster *et al*., 2017). Additionally, the lower repeatability of parental care in females could be a result of females responding more closely to the needs of their brood between years, which is determined by them being more certain that the offspring are their own, and having few opportunities to have their offspring raised by other breeding pairs, thus their entire reproductive success for a year is dependent on them fledging some of their brood (Thorogood *et al*., 2011). These influences differ for the male, who can both attempt to father additional offspring through extra-pair copulations, but due to the biological processes behind reproduction, they cannot be certain of how many offspring they have (Chaine *et al*., 2015).

However, due to the aforementioned weaknesses of the sealed-bid model (McNamara *et al*., 2003), it is more likely that both parents should behave on a negotiation continuum; from complete compensation, no response, to complete matching of any changes in the provisioning rate of the partner (Hinde and Kilner, 2007; Johnstone *et al*., 2014). Hence, it becomes necessary to understand the variables influencing the negotiation process, through their influence upon the relative costs and benefits of the breeding attempt, and consequently the repeatability of parental care.

The variables most likely to be contributing to the benefits of parental care are the easiest to define, with the primary influence being the number of offspring likely to be fledged. If an individual is likely to raise more offspring from a given breeding attempt it follows that their provisioning rate should increase as well, to ensure as many young fledge as possible, maximising their reproductive success (Low *et al.*, 2012). Furthermore, individuals may adapt their provisioning rate to increase their chance of re-mating with the same partner in subsequent years. This could be a method used to retain a high-quality partner, the benefit of which could differ between sexes. For example, females may benefit from increased quality of their partner if he contributes more to parental care than other males, or if he is able to defend a larger territory, increasing access to food sources, and reducing foraging costs. Males, on the other hand, would likely benefit from higher quality females laying a larger clutch size, or better-quality eggs, both of which are likely to increase reproductive success (Slagsvold and Lifjeld, 1990; Goodburn, 1991; Nakagawa *et al*., 2007).

The costs of parental care are most likely to depend upon habitat quality, which for tits is primarily dependent upon the availability of food in the environment, with both the abundance and spatial distribution having important implications for foraging behaviour (Wilkin *et al*., 2009; Harrison *et al*., 2010; Sanz *et al*., 2010). For example, a high-quality habitat is likely to be one with many oak trees (*Quercus robur*), or other deciduous trees, but few evergreens (Perrins, 1991; Amininasab *et al*., 2016). Oaks, and other deciduous trees, support the greatest diversity and abundance of phytophagous invertebrates, the preferred food items of foraging tits (Southwood *et al*., 2004), reducing the time and effort required to find suitable food items for nestlings and leading to higher quality of both parents and offspring (Wilkin *et al*., 2009a). For example, Wilkin *et al*. (2009a) showed that a greater number of oak trees closer to the nest increased reproductive success in great tits.

Furthermore, the costs and benefits of parental care behaviour will vary based on the experience, and quality, of an individual and their partner (Froy *et al*., 2015). For example, as birds age, they will likely make small alterations to their provisioning behaviour (Grieco, 2002), potentially developing a preference for food items of a specific type, or size (Herborn *et al*., 2014). This will influence the impact of the habitat upon them and their provisioning behaviour, as is likely to differ between individuals. Similarly, older birds will have had a greater number of opportunities to observe the behaviour of others, potentially acquiring behavioural adaptations through social, or self, learning (Aplin *et al*., 2013; Aplin, 2016). Finally, birds breeding more than once will have had the opportunity to have retained both their breeding partner and habitat.

Whether an individual has retained or changed either their nest site or breeding partner is likely to influence their provisioning behaviour, through the effect of familiarity and learning. Studies of wild birds have found that they are able to remember information over the course of several months, to at least a year (Mettke-Hofmann and Gwinner, 2003). More specifically, evidence has been found that tit species are able to retain information for, at least, several months, for example, great tits (*Parus major*) recall the position of marsh tit (*Poecile palustris*) food caches and use these during the winter, when food availability is scarce (Urhan *et al.*, 2017). A similar effect is likely to happen when a bird reuses its former breeding habitat and it may benefit from increased local knowledge as to the location of food sources and predator refuges, resulting in more efficient provisioning at the nest. Similarly, re-mating with the same individual is also likely to lead to both more efficient, and higher, provisioning rates, as sexual conflict theory suggests that each parent will be less likely to withhold care, instead trusting its partner to provide a similar level of care as the previous year. Additionally, individuals may become more efficient at working together, either by relying upon their partner to engage in anti-predator behaviour or increasing their level of alternation of provisioning visits.

The processes outlined above demonstrate the main influences on the costs and benefits of parental care behaviour, and thus are the variables likely to be influencing repeatability. However, the relative importance of these variables could differ throughout the life history of an individual bird. Thus, it is necessary to investigate the influence of these factors, to better understand the processes influencing parental care behaviour in birds, and how they vary, or remain constant, temporally.

As discussed previously, the physical habitat is likely to exert a strong influence on the parental care behaviour of individuals, particularly provisioning rates. However, few studies have explicitly examined the influence of the physical habitat upon repeatability, with a paper by Niemela and Dingemanse (2017) even suggesting that this an obstacle likely to interfere with studies of the repeatability of behaviour within individuals. However, papers by Goodburn (1991) and Przybylo *et al*. (2001) have examined the influence of habitat on the repeatability of breeding parameters, such as clutch size and nestling quality. These papers found that the clutch size and timing of breeding were moderately repeatable for nest-sites regardless of the individuals occupying them, confirming that habitat can have a repeatable influence upon aspects of breeding (Goodburn, 1991; Przybylo *et al*., 2001). This suggests that birds breeding in predictable habitats may also be responding repeatably to habitat quality, with implications for the future study of habitat, behaviour and reproductive success. The nestboxes at Lancaster are spatially fixed, and the habitat around them relatively constant, thus they provide an ideal opportunity to further assess the influence of habitat quality upon repeatability.

3.1.1 Aims

1. To assess the factors influencing provisioning rates in blue tits, as well as looking at how these differ between individuals of different sexes
2. To estimate the repeatability of provisioning rate of individual blue tits breeding in multiple years
3. To estimate the repeatability of provisioning rate of blue tits by nestbox, rather than individual birds using them.

3.2 Methods

For information on the study site, species, and general data collection please refer to Chapter 1, where they have been described in the general methodology.

3.2.1 Quantifying parental care

To examine the repeatability of parental care between years, the provisioning rate for each parent was used. This is a widely used, standard measure of parental effort during the nestling stage (Thorogood *et al*., 2011; Bebbington and Hatchwell, 2016). To record provisioning rate a single adult was caught at each nest several days prior to video recording, and then sexed based on the presence of a brood patch (female) or cloacal protuberance (male) (Svensson, 2006). The individual was then marked on the tail with a spot of white correcting fluid, enabling straightforward differentiation of adults when reviewing video recordings. Provisioning behaviour was then recorded using video cameras for an hour at each occupied nestbox, between days nine and eleven after the oldest young had hatched, similar to the method used by Mainwaring and Hartley (2016a). Existing data were used from nest videos collected during 2016 and 2017, with the nests occupied during the 2018 breeding season surveyed as part of this project.

3.2.1.1 Recording videos of parental provisioning behaviour

Video recordings of parental provisioning rates at the nestbox were taken from directly opposite the entrance hole, with camcorders placed on tripods at a distance of 5-10m, dependent upon the density of the surrounding vegetation. Camcorders were placed as far from the nest as possible, within the range specified, to reduce the impact of disturbance. This distance is similar to that used by Martin *et al*. (2000), 5m, but less than that of Low *et al*. (2012), 10-20m. A distance of 5-10m is believed to have been sufficient, as the blue tits were not observed to be alarm calling once the fieldworker had left the territory and were frequently observed provisioning the nest within a few minutes after video recording had begun.

Video recording occurred only in good weather; no persistent rainfall or high winds, both of which may influence the provisioning rate by making it more difficult for adult blue tits to find their food. Provisioning behaviour was recorded for one hour at each nest, standardising any disturbance, from setting up the field equipment, across nests and providing observation of the provisioning rate per hour. A study of an ecologically similar species, the great tit, by Pagani-Núñez and Senar (2013), tested, and confirmed, the validity of using an hour as the observation length when studying nestling-provisioning rates.

Parental provisioning rates were consistently recorded between 07:00-12:30, within the range 9-11 days after the first chick in the nest had hatched. This controlled for the confounding influence of nestling age between nests and was also the peak time for provisioning during both the day and the nestling stage.

3.2.1.2 Provisioning rates

In total, parental provisioning rates were recorded at 64 nests during the 2018 field season, and the recordings were watched by a small group of researchers. To quantify provisioning rate at the nest, it is necessary to record each time an adult provides the young with food. When watching the videos, each nest visit was recorded as a feed, unless the adult was seen exiting the nest box with the same food item. Thorogood *et al*. (2011) tested, and confirmed, the assumption that each nest visit can be assumed to be a provisioning trip in the hihi (*Notiomystis cincta*), supporting the method used here.

At the time of video observation, the researchers remained blind to the sex of individual birds, recording them as marked and unmarked, to prevent bias in the dataset. Identities were then converted to sexes after the data had been compiled. Provisioning rate per hour was then recorded for each parent, at each nest, as the count of visits made by that parent during the hour-long observation period.

3.2.1.3 Determining which nests to include in the analysis

Upon watching the video recordings of provisioning behaviour, it became apparent that two of the nests had failed prior to having provisioning rate recorded, with no visits made by the parents. These videos were removed from the dataset and not included in the analyses. Additionally, several of the videos from all years 2016-2018, had all, or most, visits by only one parent, in this case, as with Burrows (2018), nests with greater than 90% of visits made by a single parent were removed from analyses (n=18, 9.7%). These videos were not included in analyses as it is uncertain to what extent a single parent is able to account for no, or minimal, investment from its partner (Harrison *et al*., 2009; Bebbington and Hatchwell, 2016; Santema and Kempenaers, 2018), and thus these nests would provide an inaccurate measure of provisioning repeatability between years.

3.2.2 Data from previous years

The influence of remaining with the same partner, or in the same nestbox, was examined using the existing ringing data. These data also provided the information on the age of each breeding individual, and the brood size when provisioning rate was monitored. These explanatory variables were compared to both the provisioning rates and the breeding parameters: clutch size, hatching success and fledging success. Age was recorded as years since hatching, brood size as a count, and both changing partner and/or nestbox were binary variables. A detailed description of the routine ringing data collection is included in Chapter 1. The tree data were also obtained from the same sources, and include counts of the number of deciduous, evergreen and oak trees within 50m of each nest, as well as the shortest distance to each of these. For the methods covering collection of these data, see Chapter 1.

3.2.3 Statistical analyses

All statistical analyses were carried out using the R statistical package (R Core Team, 2017) and preliminary analyses were carried out following Zuur *et al*. (2010). All means are reported plus or minus one standard error.

A mixed modelling approach was used to investigate the influence of bird and territory variables upon blue tit provisioning rates and breeding parameters. This approach uses random effects to account for non-independence in the dataset (Bolker *et al*., 2009; Harrison *et al*., 2018), which was present due to repeated measurements at nestboxes, and of individuals, between years. Consequently, all models were produced with both nestbox number and blue tit identity as random effects.

Collinearity between explanatory variables was assessed using pairwise scatterplots, Pearson's correlation coefficients and Variance Inflation Factors (VIFs), using the *aed* package code from Zuur *et al*. (2009). Collinearity was deemed to be present if the correlation between explanatory variables was greater than 0.4 or if VIFs were greater than three (Zuur *et al*., 2010) and collinear variables were dropped from the model based on ecological theory and preliminary analyses.

Once collinear terms had been dropped, prior to model construction, all continuous explanatory variables were standardised and centred, a process which can improve model performance and interpretation (Schielzeth, 2010; Harrison *et al*., 2018). All possible two-way interactions backed by ecological theory were included in each model and the least important dropped sequentially, until only significant interaction terms were included.

Model construction was then carried out by subjecting the response, and all explanatory variables, including those interactions which had theoretical support, to the *dredge* function in the 'MuMIn' package (Barton, 2018). All possible models were then ranked by the Akaike's Information Criterion with correction for small sample size (AICc) and if there was more than one model within the top two AICc values (delta AICc <2) then model averaging was carried out (Galipaud *et al*., 2014; Harrison *et al*., 2018). Models were checked for overdispersion and validated by plotting the residuals versus the fitted values, the residuals against each covariate, and by generating QQ-plots of the distribution of the residuals (Zuur *et al*., 2009). Predictive plots were produced of the significant variables included in each averaged model and these are shown in the results.

3.2.3.1 Models of provisioning rate

For the models of provisioning rate, the response variables were a count of the provisioning visits made by the male, the female, and the total of these during the hourly observation period. Total provisioning rate at each nest was determined to be normally distributed, and consequently was modelled using a linear mixed-effects model (LMM), however, both male and female provisioning rates were Poisson distributed, and thus modelled as generalised linear mixed-effects models (GLMMs) (Bolker *et al*., 2009). The hourly provisioning rate of each sex was modelled separately, to investigate the relative importance of different variables between males and females, and to facilitate later repeatability analyses. Additionally, the hourly provisioning rate of males and females were investigated simultaneously, to look for any important sex-interactions.

There were a considerable number of explanatory habitat variables available, thus to avoid overparameterising the model, these were reduced to only the most meaningful for each of the vegetation groups: deciduous, evergreen and oak. For all models the explanatory habitat variables used included the continuous variables of the number of deciduous trees and evergreen trees within 50m and whether an oak tree was present within the same distance, with the latter being a binary variable. The number of oak trees was initially considered in the analyses but was found to be highly collinear with oak tree presence, which preliminary analyses, and previous studies, found to be a better indicator of territory quality, thus oak presence was retained, and the number of oaks discarded. Data on the distance to each of the three classes of tree were also available but were found to be highly correlated with the number of each. The distance to each vegetation class was deemed to be less ecologically meaningful than the number, or presence, of each within 50m of the nest, and so the distance variables were removed from the models.

All models also used the age of each breeding individual, and the age and provisioning rate of its partner. Ages were also initially included as categorical variables, either first year or older, but these were found to be uninformative, so were dropped from the final models, retaining only the age in years. Additional explanatory variables included whether the breeding individual had changed breeding partner, or changed nestbox, from the previous year. These two variables were found to be collinear, however, the theory suggests they will show different effects between the sexes, and consequently all models were produced twice, once for each of these variables. Year was included as a factor variable but was found to not be related to provisioning rate, and thus was dropped from the models. Finally, brood size, the number of chicks present when provisioning rate was recorded, was included in all models of provisioning rate.

3.2.3.2 Models of the breeding parameters

GLMMs were used to assess the influence of habitat on clutch size, hatching success and fledging success. These were carried out in the same way as for the models of provisioning rate, using the same variables. However, the timing of breeding attempts is known to have a strong influence on the breeding parameters, and this was examined by including the first egg date as an additional explanatory variable in these models.

3.2.3.3 Estimation of repeatability of provisioning rate

Repeatability was estimated as described in Chapter 1, following the method of Nakagawa and Schielzeth (2010) and using the *rptR* package (Nakagawa and Schielzeth, 2010; Stoffel *et al.*, 2017). The mixed-effects models described above were used to calculate the repeatability of each relevant response and the variables identified as influencing provisioning rate included to account for confounding effects. The influence of individual bird variables and environmental variation were examined by estimating repeatability for both individual birds and nestboxes at each stage. Repeatability estimates are reported along with the standard error, 95% confidence intervals around the estimate, and the *p* value. There were three years for which provisioning rates had been recorded, and thus a maximum of three measurements of each individual nestbox and bird. However, the majority of birds with repeat measurements, thus enabling calculation of repeatability, were only recorded twice, potentially leading to wider confidence intervals than if a greater number of measurements were available (Schuster *et al.*, 2017).

3.2.3.4 Displaying the results

The models which contained the change of partner, or nestbox variables, were frequently found to be either very similar, or only one of each variable was important in each. In these cases either one model is presented, and it is stated that the other was very similar, or the model containing the important variable is reported and it is stated that the other is discarded. There was a similar result with the breeding parameters, and as such only one model is shown, that of fledging success.

Finally, it was found that repeatability estimates (*R*) differed little between the models which contained the nestbox and partner variables, typically by less than 0.01. Consequently, the repeatability estimates shown are for the models reported above, rather than duplicating the results.

3.3 Results

3.3.1 Provisioning rate

The total hourly provisioning rate of each breeding pair had a mean of 43.74 ± 1.24 nest visits per hour, with this ranging from 3-68 visits per bird. Provisioning rates were significantly correlated between individuals within breeding pairs (rho = 0.34, n = 167, $p<0.001$), with the male and female hourly provisioning rate being statistically significantly different (paired samples t-test: t = 4.45, n = 167, p = <0.001). This significant difference shows that males provision the nest at a greater rate than females (means of 23.85 ± 0.77 and 19.89 ± 0.79 respectively).

For all models of provisioning rate the most important explanatory variable was the brood size when parental provisioning was recorded (Tables 3.1 to 3.4; Figures 3.1; 3.5; 3.9), with an increase in brood size leading to an increase in total provisioning. The model averaging suggested that, for the total provisioning rate at a nest, the only other significant explanatory variables were whether the pair had changed box or partner, with changing either resulting in a similarly lower provisioning rate (Figure 3.2). However, when the data were examined for sex interactions it was found that there was an additional significant influence of sex (Table 3.2, Figure 3.3), as previously suggested by the means and t-test shown above. Examining the data for sex interactions also identified a significant interaction between sex and brood size (Figure 3.4). This interaction shows that both male and female provisioning rate increased with brood size but that female provisioning rate does so at a greater extent than males, with females provisioning at a higher rate than males for the largest broods.

The models of provisioning rate for either sex show that the variables influencing male provisioning rate are brood size, age, partner age, and whether the male has changed partner, or not, (Table 3.3; Figures 3.5 to 3.8 respectively). Whether the male had changed nestbox was not included in any of the best-fitting models. However, female provisioning rate was significantly influenced by brood size, the provisioning rate of the male, and whether they were using the same nestbox (Table 3.4; Figures 3.9 to 3.11 respectively). Changing, or keeping, a partner was not significant, although it was present in the best-fitting models. Age was also examined after excluding the outliers older than five years, with no difference in the variables identified as influencing provisioning rate.

The habitat variables were not found to be significant in any of the models of provisioning rate, although all, or some, of them were present in the best-fitting models (Tables 1 to 4). The presence of oak trees was most frequently included in the best-fitting models but was insignificant.

Table 3.1: The model selection table for the global model of an averaged linear mixed effects model examining the factors influencing total provisioning rate at a nest (n = 167):

> lmer(total provisioning rate ~ brood size + changed nestbox + female age + male age + number deciduous trees + number evergreen trees + oak presence)

#	Intercept	Female age	Brood size	Changed box	Number deciduous	Number evergreen	Oak presence	Male age	df	logLik	AICc	delta	weight	R2m	R2c
136	48.47	-2.09	13.04	+					8	-377.49	787.3	0.00	0.08	0.36	0.65
135	48.44		13.06	+					7	-379.87	787.4	0.03	0.08	0.35	0.66
152	48.33	-2.14	12.97	+		1.75			9	-375.50	788.5	1.15	0.05	0.38	0.66
151	48.31		13.00	+		1.65			8	-377.95	788.7	1.32	0.04	0.36	0.66
7	48.04		9.05	+					6	-383.70	789.0	1.68	0.03	0.31	0.64
199	48.35		13.01	+				-0.90	8	-378.46	789.3	1.93	0.03	0.35	0.65

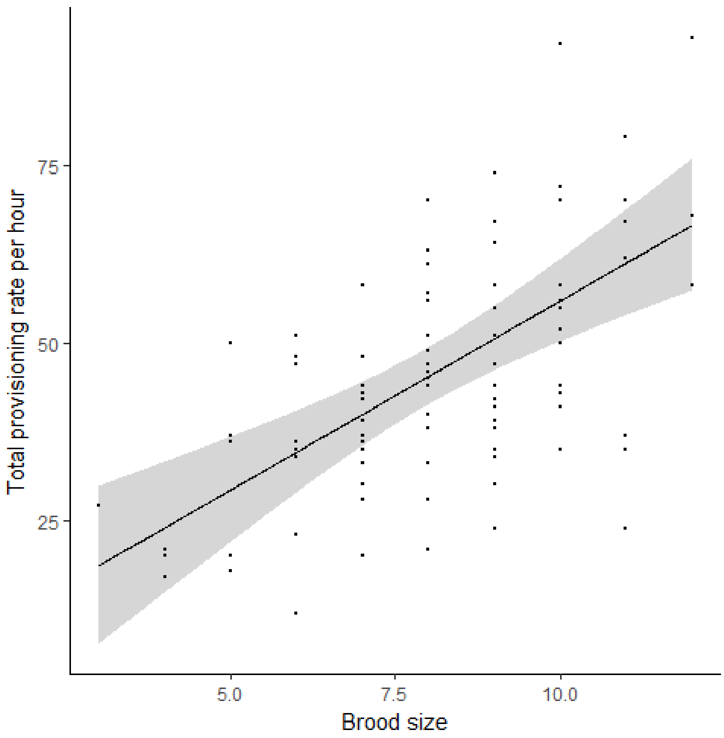

Figure 3.1: The relationship between total provisioning rate, per hour, at a nest and brood size, predicted from the average model reported above. The points represent the original data and the grey shows 95% confidence intervals (n = 167).

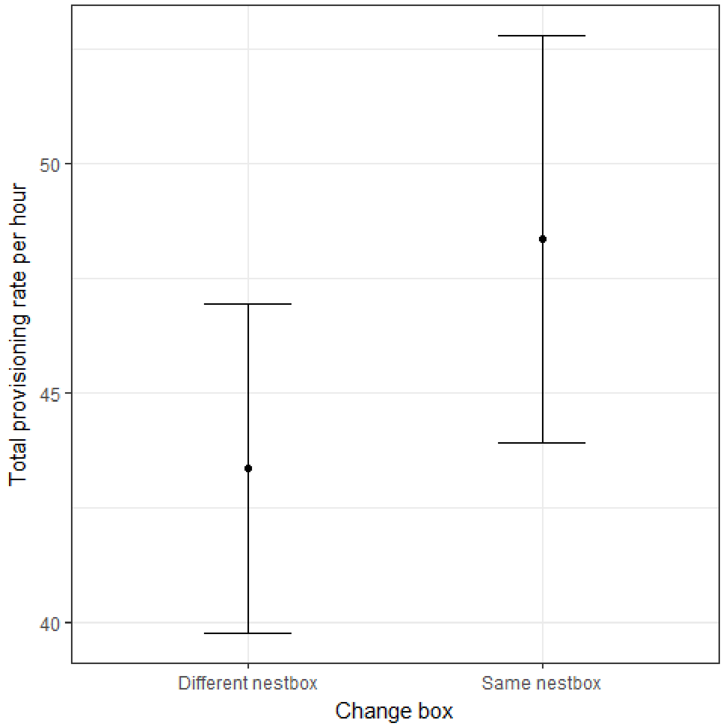

Figure 3.2: The relationship between total provisioning rate, per hour, at a nest and whether each individual had retained their breeding nestbox from the previous year. Predicted from the average model reported above. The points represent the predicted values and the bars represent the 95% confidence intervals (n = 167).

Table 3.2: The model selection table for the global model of an averaged generalised linear mixed effects model examining the factors influencing provisioning rate for both males and females, specifically checking for sex interactions (The table is split to fit onto the page, n = 167):

glmer(provisioning rate~ parent age + brood size * sex + changed nestbox + number evergreen trees + number deciduous trees + oak presence + partner provisioning rate + partner age, family= Poisson)

#	Intercept	Parent age	Brood size	Changed box	Number deciduous	Number evergreen	Oak presence	Partner age	Partner provisioning rate	Sex	Brood size:sex	df
839	3.04		0.32	+				-0.05		+	+	8
855	3.04		0.32	+		0.04		-0.05		+	+	9
775	3.05		0.31	+						+	+	7
871	3.07		0.31	+			+	-0.05		+	+	9

#	logLik	AICc	delta	weight	R2m	R2c
839	-713.46	1443.7	0.00	0.11	0.34	0.63
855	-712.73	1444.6	0.94	0.07	0.35	0.63
775	-715.27	1445.1	1.44	0.05	0.33	0.64
871	-713.36	1445.7	1.99	0.04	0.35	0.63

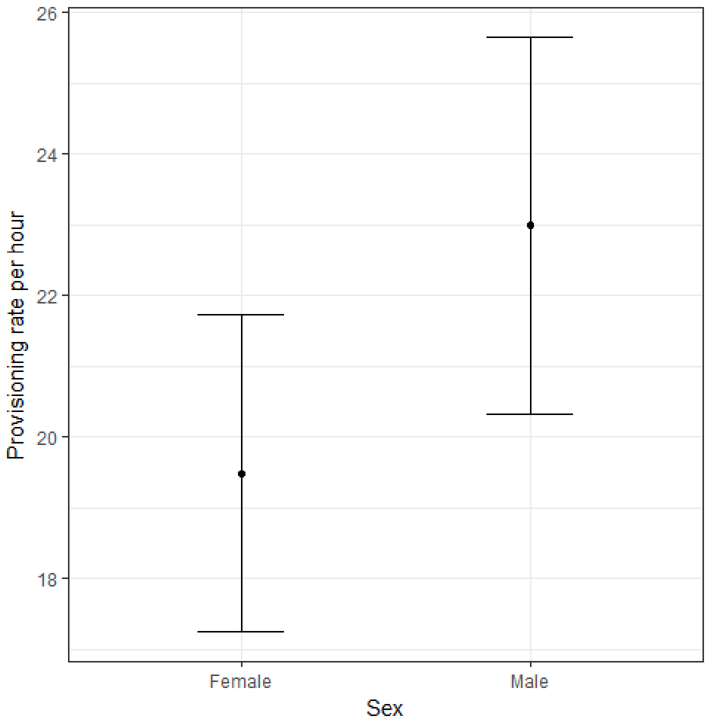

Figure 3.3: The relationship between blue tit provisioning rate, per hour, and parent sex. Predicted from the average model reported above. The dots represent the predicted values and the bars the 95% confidence intervals.

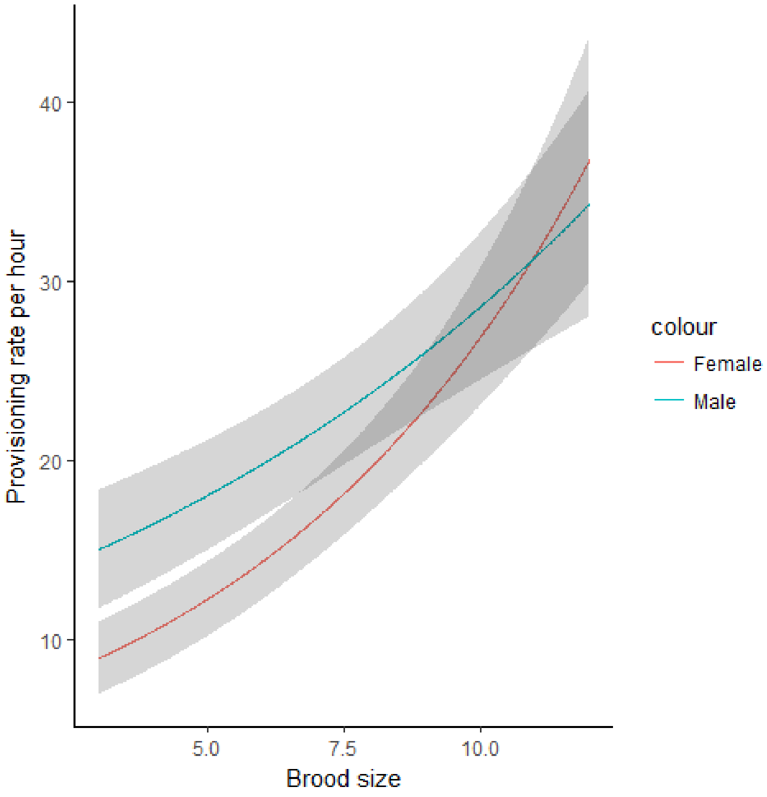

Figure 3.4: The relationship between blue tit provisioning rate, per hour, and the interaction between brood size and sex, predicted from the average model above. The lines represent males (blue) and females (red) and the grey shows the 95% confidence intervals.

Table 3.3: The model selection table for the global model of an averaged generalised linear mixed effects model examining the factors influencing male provisioning rate (n = 167):

> glmer(male provisioning rate ~ male age + brood size + changed partner + number deciduous trees + number evergreen trees + oak presence + female age + partner provisioning rate, family= Poisson)

#	**Intercept**	**Male age**	**Brood size**	**Changed partner**	**Number deciduous**	**Number evergreen**	**Oak presence**	**Female age**	**Female provisioning rate**	**df**	**logLik**	**AICc**	**delta**	**weight**	**R2m**	**R2c**
104	3.48	-0.10	0.16	+			+	-0.11		8	-339.50	696.6	0.00	0.14	0.28	0.77
72	3.31	-0.08	0.16	+				-0.11		7	-341.39	698.0	1.40	0.07	0.27	0.78
120	3.45	-0.09	0.16	+		0.05	+	-0.10		9	-339.07	698.2	1.57	0.06	0.31	0.78
232	3.48	-0.09	0.15	+			+	-0.10	0.03	9	-339.12	698.3	1.66	0.06	0.29	0.77
88	3.30	-0.08	0.16	+		0.07		-0.10		8	-340.45	698.5	1.89	0.05	0.30	0.78

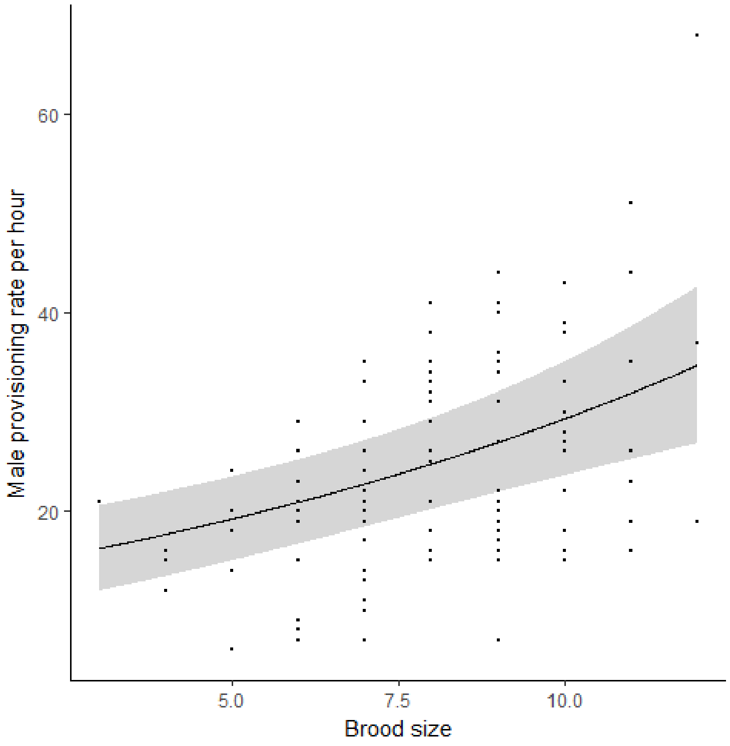

Figure 3.5: The relationship between male provisioning rate, per hour, and brood size predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 167).

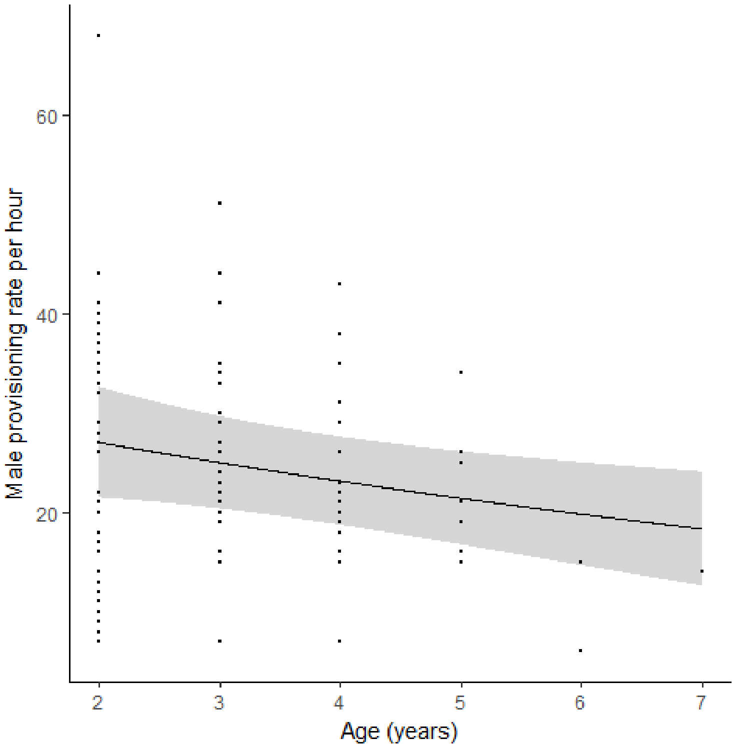

Figure 3.6: The relationship between male provisioning rate, per hour, and male age (in years) predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 167).

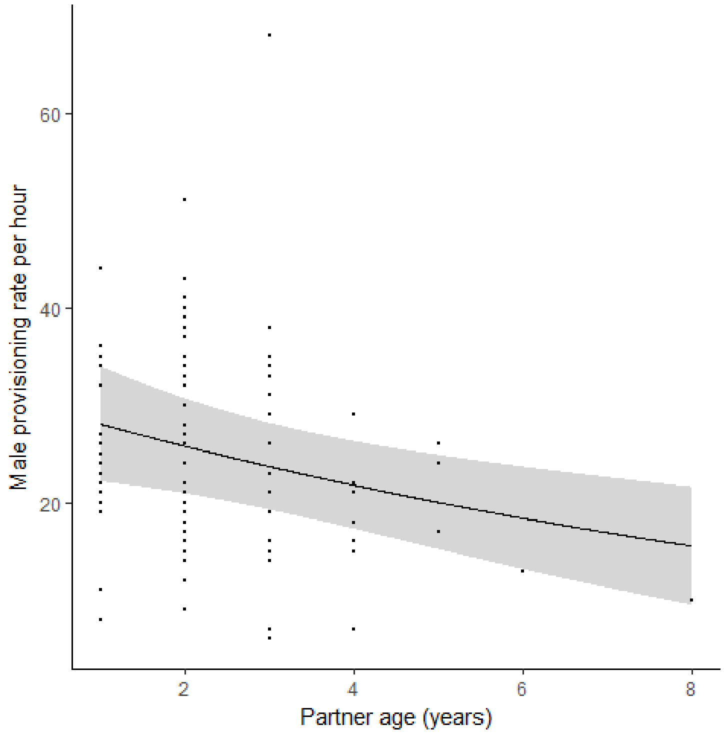

Figure 3.7: The relationship between male provisioning rate, per hour, and the age (in years) of the breeding partner predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 167).

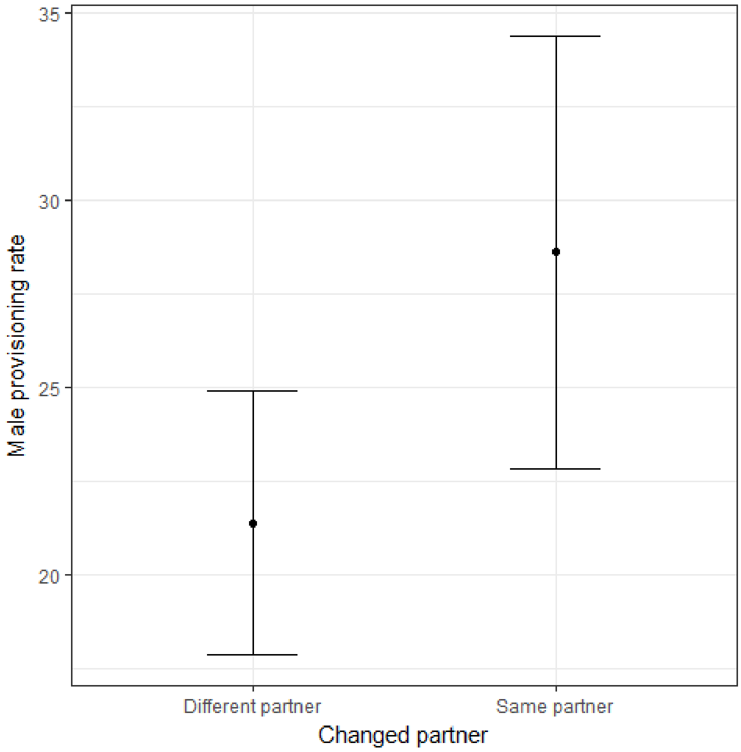

Figure 3.8: The relationship between male provisioning rate, per hour, and whether or not that male had paired with the same partner as the previous year, predicted from the average model reported above. The points represent the predicted data and the bars the 95% confidence intervals (n = 167).

Table 3.4: The model selection table for the global model of an averaged generalised linear mixed effects model examining the factors influencing female provisioning rate (n = 167):

glmer(female provisioning rate ~ female age + male age + brood size + number deciduous trees + number evergreen trees + changed nestbox + male provisioning rate + oak presence, family= Poisson)

#	**Intercept**	**Female Age**	**Brood Size**	**Changed box**	**Number deciduous**	**Number evergreen**	**Oak presence**	**Male age**	**Male provisioning rate**	**df**	**logLik**	**AICc**	**delta**	**weight**	**R2m**	**R2c**
135	3.10		0.30	+					0.09	6	-364.93	742.7	0.00	0.15	0.38	0.53
199	3.11		0.31	+				-0.04	0.08	7	-364.51	744.2	1.48	0.07	0.39	0.54
167	3.03		0.30	+			+		0.09	7	-364.60	744.4	1.65	0.07	0.38	0.54

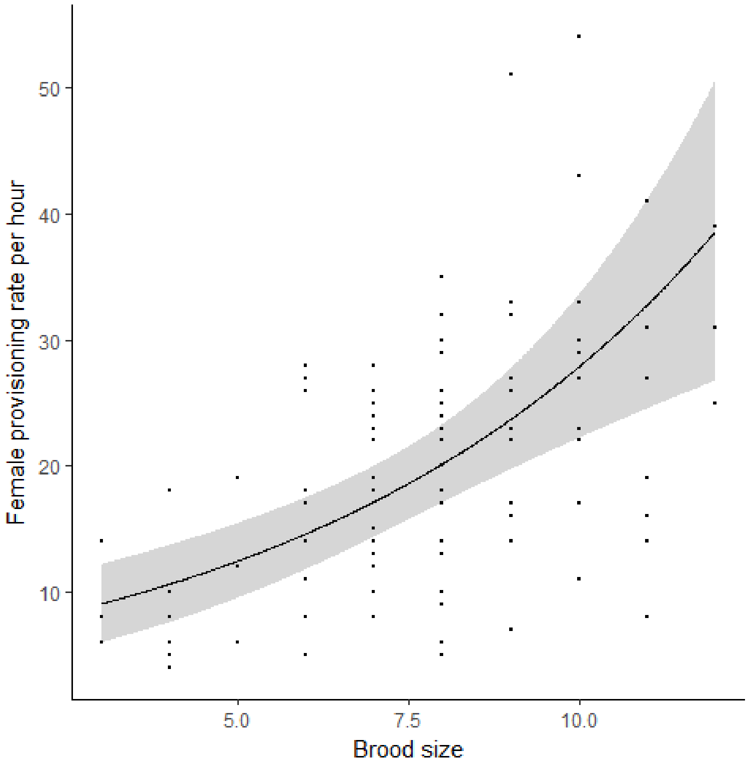

Figure 3.9: The relationship between female provisioning rate, per hour, and brood size predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 167).

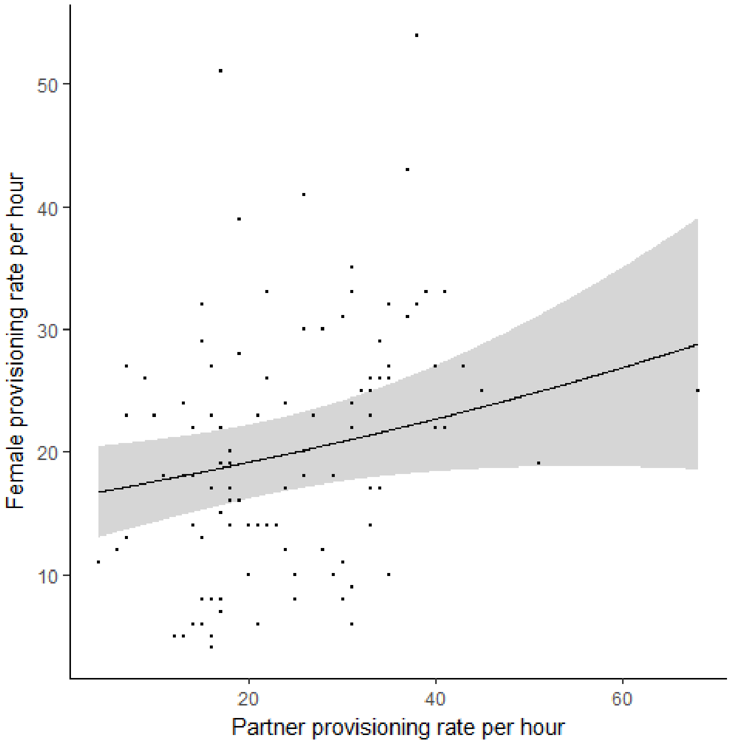

Figure 3.10: The relationship between female provisioning rate, per hour, and the provisioning rate of their partner, predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 167).

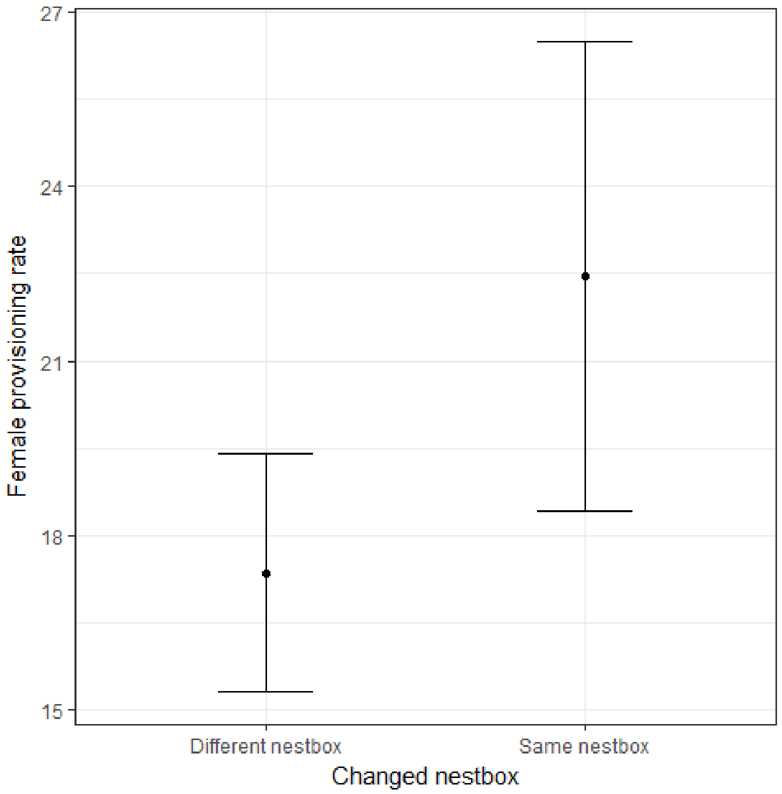

Figure 3.11: The relationship between female provisioning rate, per hour, and whether that female was using the same nestbox as the previous year, predicted from the average model reported above. The points represent the predicted values and the bars the 95% confidence intervals (n = 167).

3.3.2 Repeatability estimates of provisioning rate

The repeatability estimates suggest that provisioning rate was highly repeatable for individual males, and less so, but still significantly, repeatable for individual females (Table 3.5). Additionally, the provisioning rates attributable to the territories, rather than to individual birds, showed that male provisioning rates were moderately repeatable but that female provisioning rates were not (Table 3.5). Finally, the total provisioning rate at each box, regardless of whether it had the same male or female present, was found to be moderately repeatable (Table 3.5). Figure 3.12 shows that male provisioning rate varied less than for females, for most of the different age groups

.

Table 3.5: The repeatability of male and female provisioning rates calculated for the same individual recorded in multiple years, and of different individuals breeding in the same nestbox. Also, the repeatability of the total provisioning rate calculated by nestbox. Repeatability, standard error, and 95% confidence intervals, all provided by use of *rptR*.

	Repeatability (SE)	**CI**	***p***	**n**
Male provisioning rate by individual	0.592 (0.147)	0.075, 0.689	0.001	36
Male provisioning rate by box	0.243 (0.146)	0.000, 0.503	0.026	59
Female provisioning rate by individual	0.346 (0.186)	0.000, 0.636	0.025	36
Female provisioning rate by box	0.000 (0.076)	0.000, 0.250	1.000	59
Total provisioning rate by box	0.304 (0.131)	0.014, 0.556	0.024	59

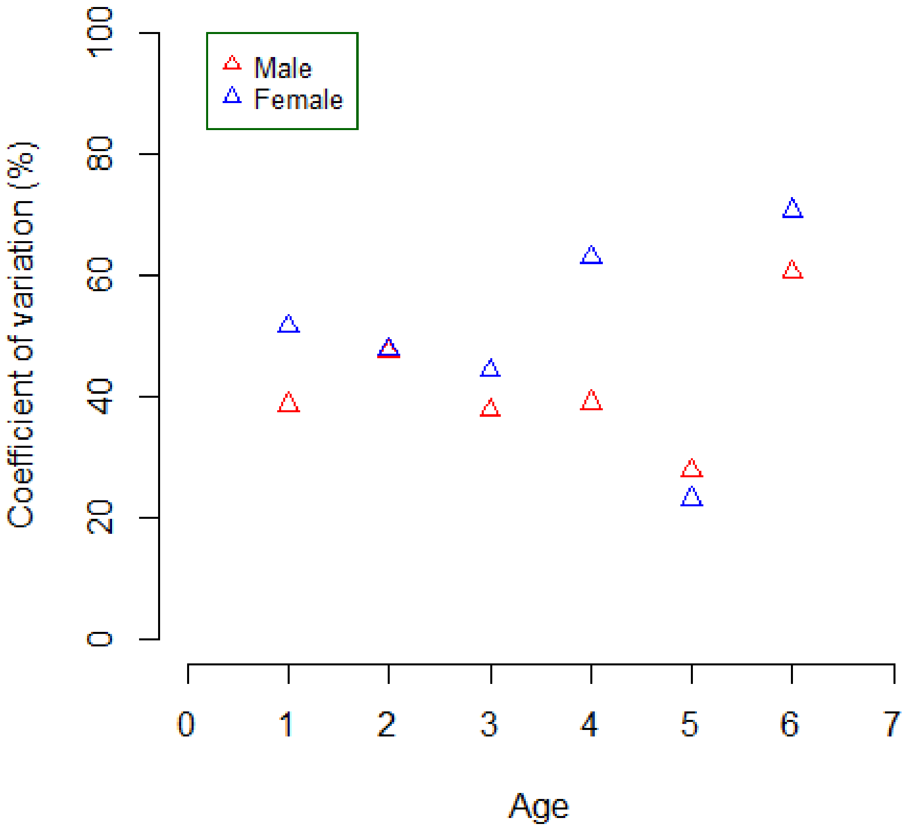

Figure 3.12: The coefficient of variation calculated for hourly provisioning rates of male and female blue tits of different ages (in years). There was insufficient sample size to calculate the coefficient of variation for birds aged 7 or 8 for either sex.

3.3.3 Breeding parameters

Preliminary analyses found that neither breeding with the same partner or nestbox had a significant effect upon the breeding parameters, they were not included in any of the best-fitting models. Furthermore, the variables influencing clutch size, hatching success, and fledging success were the same throughout all models. Consequently, only one model is displayed here, that of fledging success, and this does not contain either the influence of changing nestbox, or partner, as explanatory variables (Table 3.6). The variables found to be significantly influencing the breeding parameters were the day the first egg was laid in each nest, and the year of the breeding attempt (Figures 3.13 and 3.14). Neither the ages of the male or female, nor the habitat variables, were significant explanatory variables for any of the breeding parameters (Table 3.6).

Table 3.6: The model selection table for the global model of an averaged generalised linear mixed effects model examining the factors influencing fledging success (n = 176):

> glmer(fledging success ~ first egg date + female age + number evergreen trees + number deciduous trees + oak presence + male age + year, family = Poisson)

#	**Intercept**	**Female age**	**First egg date**	**Number deciduous**	**Number evergreen**	**Oak presence**	**Male age**	**Year**	**df**	**logLik**	**AICc**	**delta**	**weight**	**R2m**	**R2c**
75	2.15		-0.23		-0.05			+	7	-798.29	1610.9	0.00	0.12	0.30	0.42
67	2.15		-0.23					+	6	-799.44	1611.1	0.22	0.11	0.29	0.42
71	2.15		-0.23	0.04				+	7	-798.70	1611.7	0.82	0.08	0.30	0.42
107	2.15		-0.23		-0.05		0.02	+	8	-797.96	1612.4	1.43	0.06	0.30	0.43
79	2.15		-0.23	0.02	-0.04			+	8	-798.07	1612.6	1.65	0.05	0.30	0.42
99	2.15		-0.23				0.02	+	7	-799.13	1612.6	1.68	0.05	0.29	0.42
76	2.15	0.01	-0.23		-0.05			+	8	-798.14	1612.7	1.79	0.05	0.30	0.43
91	2.17		-0.23		-0.05	+		+	8	-798.18	1612.8	1.88	0.05	0.30	0.42

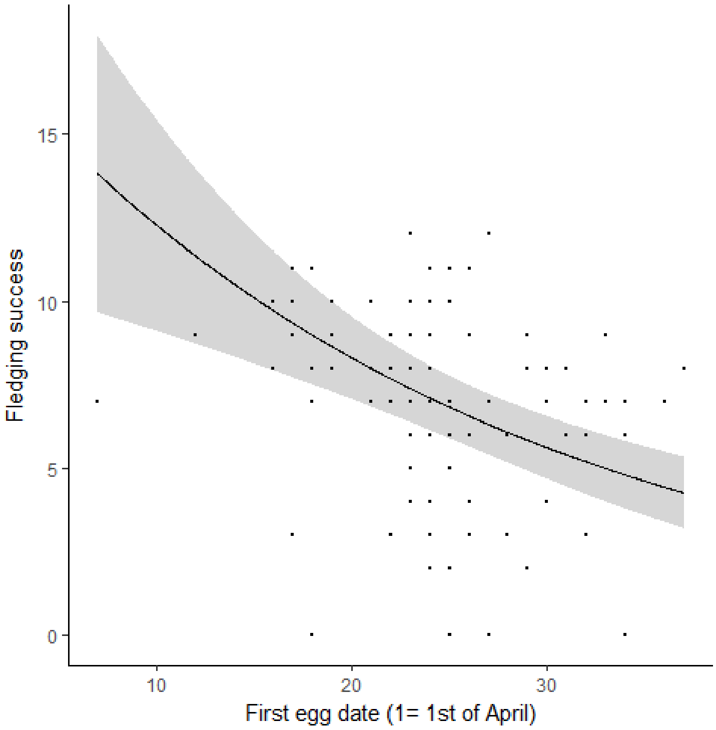

Figure 3.13: The relationship between fledging success and the date the first egg was laid in each nest, predicted from the average model reported above. The points represent the original data and the grey the 95% confidence intervals (n = 176).

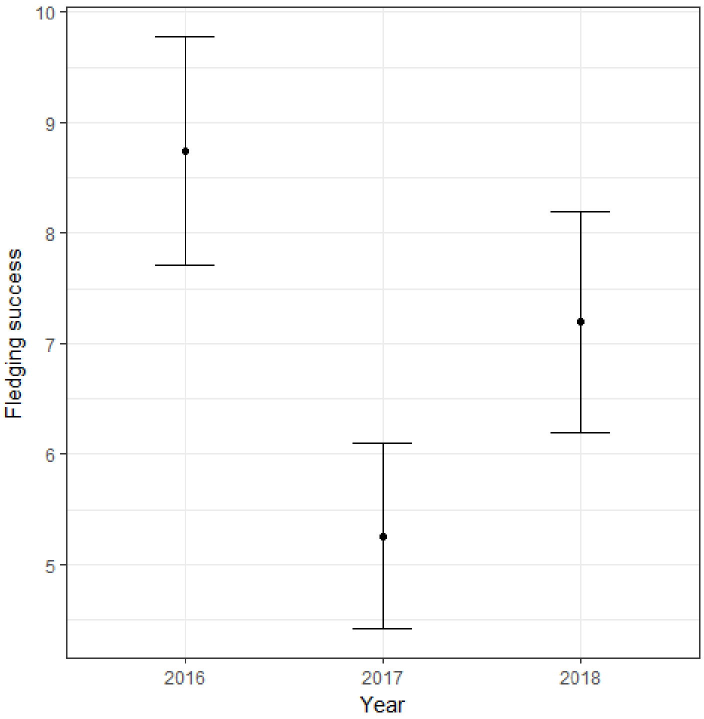

Figure 3.14: The relationship between blue tit fledging success and year, predicted from the average model reported above. The dots represent the predicted values and the bars the 95% confidence intervals (n = 176).

3.4 Discussion

The results of this study indicated that blue tit provisioning rates vary substantially and that the variation is explained by several variables (Table 3.1). Key factors driving provisioning rate include brood size (Figure 3.1) and factors specific to the breeding individual or their partner, including whether the breeding individuals had changed partner, or nest site, undergoing divorce or breeding dispersal respectively (Figures 3.2; 3.8; 3.11). Sex differences were also found in provisioning rates, with different variables significantly determining male and female provisioning rates (Tables 3.2 and 3.3). Male provisioning rate was negatively related to both age and partner age (Figures 3.6 and 3.7), but increased after retaining a partner between years (Figure 3.8). Female provisioning rate was positively related to the provisioning rate of their partner (Figure 3.10) and was higher after retaining a breeding site (Figure 3.11). Furthermore, estimation of the repeatability of provisioning rates showed these to be moderately to highly consistent for males and females breeding in multiple years. However, the analysis of repeatability of provisioning rates attributable to the territories, rather than to individual birds, showed that male but not female provisioning rates were repeatable within territories, even when the individual breeders changed (Table 3.5). Variation in breeding parameters was primarily influenced by the timing of the breeding attempt (Table 3.6; Figure 3.13) but not by the variables relating to individual age or experience of either parent (Table 3.6). The habitat variables were not found to significantly influence the provisioning rates or breeding parameters directly (Tables 3.1 to 3.4).

3.4.1 Factors influencing provisioning rate

3.4.1.1 Brood size

Brood size was found to be positively correlated with provisioning rate in blue tits in all models (Tables 3.1 to 3.4; Figures 3.1, 3.5, 3.9). The positive correlation between brood size and provisioning rate is consistent with the literature, and has been found in many species. For example, the long-tailed tit (Adams *et al*., 2015), house sparrow (Schwagmeyer and Mock, 2003; Cleasby *et al*., 2013) and house wren (*Troglodytes aedon*) (Bowers *et al*., 2014). The increase in provisioning rate, with an increased number of nestlings, is most likely to be a response to breeding individuals matching their provisioning rate to reflect the needs of their offspring; one of the primary controls on provisioning rate (Freeman-Gallant and Rothstein, 1999; Schwagmeyer and Mock, 2003; Adams *et al*., 2015). The literature supports this view, with Low *et al*. (2012) stating that many species of songbirds alter their provisioning rate to meet the needs of their brood. Additionally, studies have used experimental approaches, with supplementary feeding, to show that individuals only increase their provisioning rate with the increase in brood size when sufficient food sources are available (Low *et al*., 2012). This suggests that in the years for which provisioning data were available, food availability was not a significantly limiting factor for breeding blue tits at the Lancaster University study site.

3.4.1.1.1 Sex interactions and brood size

Parental provisioning rates were found to differ significantly between males and females, with males provisioning at a higher rate (Figure 3.3). There is no consensus in the literature concerning the relative contribution of the different sexes to total provisioning at the nest, and many studies find that there is no sex difference in provisioning rate, for example, in great tits or long-tailed tits (Wilkin *et al*., 2009a; Adams *et al*., 2015). However, there was also a significant interaction between brood size and sex (Figure 3.4), which shows that females generally provision nestlings at a lower rate than males but that, as brood size increases, females compensate for this, then provisioning at a similar rate as males at the highest brood sizes (Figure 3.4). This is an interesting result, which suggests that females match their level of parental care more closely to the requirements of their offspring than does their partner. The opposite result was reported previously by Cleasby *et al*. (2013), who found that male and female house sparrows provision at a similar rate, other than at high brood sizes, where the provisioning rates of the two sexes diverge, with females increasing their provisioning rate to a greater extent than males.

It is probable that the pattern found for female provisioning rate varying so much by brood size is due to females matching their provisioning behaviour more closely to the changing requirements of the brood. The literature supports this view, as females are often found to match their investment in parental care more closely to the needs of their offspring, whereas male provisioning rate is relatively inflexible (Nakagawa *et al*., 2007; Low *et al*., 2012). It is likely that this pattern is, at least in part, a result of females having invested more resources, and care, into each brood than males. Females are solely responsible for egg formation and laying, and thus, they are likely to invest a greater amount of care into provisioning behaviour than males will, as the success of the current brood has a greater influence on their lifetime reproductive success. Additionally, females alone brood the young in the nest but at larger brood sizes less time needs to be spent brooding, which may explain some, or all, of the increase in female provisioning rate with brood size. Contrastingly, males benefit more from holding back care and pursuing extra-pair mating, or increasing their fitness, and likelihood of surviving to breed again, increasing their reproductive success in future years (Thorogood *et al*., 2011; Low *et al*., 2012; Heist and Ritchison, 2016). As well as extra-pair copulations leading to males investing in multiple broods, they can also not be certain whether all young in each brood are theirs, whereas females know they do not have eggs amongst other broods. Thus, it is likely that females will provide as much care as possible to their brood but males distribute their care between broods, resulting in each receiving reduced care.

3.4.1.2 Influence of changing partner or breeding site

Provisioning rate was also found to be significantly influenced by whether breeding individuals had changed breeding partner, or nestbox, from the previous year (Tables 3.1 to 3.4). These two variables can be interpreted as representing divorce, and the influence of site fidelity. Both variables showed a similar pattern, with those individuals which had changed nestbox, or breeding partner, from the previous year provisioning at a lower rate (Figures 3.2, 3.8 and 3.11). Theoretically retaining a nest site should lead to increased parental care, through increased local knowledge on the spatial distribution of food items, predator refuges, and other aspects of habitat quality (Arthur *et al*., 2015), all of which results in less time needing to be dedicated to searching for food and avoiding predators. There is likely to be a similar influence of retaining breeding partner, with the theory suggesting that sexual conflict will be reduced when breeding with the same individual as in a previous breeding attempt, as each parent is less likely to withhold care if they have already bred together. Additionally, increased familiarity with a mate may lead to more efficient provisioning at the nest, either through reduced time spent watching out for predators, in the knowledge that the partner will be fulfilling that role. Greater efficiency of provisioning could also arise from increased familiarity with a partner resulting in greater alternation of nest visits, whereby parents take it in turns to provision the nest, rather than waiting for their partner to take their turn (Bebbington and Hatchwell, 2016).

However, the quality of both the breeding territory and partner may be influencing the conclusion reached above. For example, individuals which retain their nestbox may be re-occupying what they already know to be a high-quality habitat, and thus the higher provisioning rate could be a result of greater food abundance in the territory, rather than increased familiarity with the area. It is not believed that this was the case, as breeding individuals which occupied low-quality territories, or bred with low-quality partners, would be expected to increase their provisioning rate after changing box, which was not found to be the case.

Contrasting the results found in this study, Nakagawa *et al*. (2007) suggested that individuals may maintain the same level of parental care when breeding with the same partner. This could be expected to occur as a result of sexual conflict being resolved in accordance with the negotiation model of parental care (Harrison *et al*., 2009), which suggests that parental quality is important in determining the relative contribution of each member of a breeding pair (Bebbington and Hatchwell, 2016). However, this result would only be found if parental quality were consistent between both parents in consecutive years, and if there was no change in the influence of habitat quality, or other factors influencing provisioning rate.

3.4.1.2.1 Sex differences between changing partner, or breeding site

The relative importance of changing partner and nestbox varied between males and females, with changing partner having a greater influence on male provisioning rate than changing nestbox, and the opposite found for females (Figures 3.8 and 3.11). This suggests that male provisioning rate may be influenced more by the quality of their breeding partner than by that of their habitat, whereas females respond more to a change in the ecological environment. Low *et al*. (2012) also reached this conclusion, suggesting that it is a result of the relative benefit of provisioning varying between the sexes. Namely, that females provision their offspring at as high a rate as the habitat quality will allow, linked to food abundance, whereas males, who may be uncertain as to the paternity of the nestlings, will instead invest their resources into extra-pair mating or withhold care, to improve their future fitness (Potti *et al*., 1999).

3.4.1.3 Parental age

The negative relationship between male age and male provisioning rate (Figure 3.6) is unexpected, with the literature suggesting that age is likely to be reflecting the quality of the individual, as birds which survive to a greater age could be expected to be of higher quality. There was also a negative relationship between the female age and male provisioning rate (Figure 3.7). These results are contrary to expectations and there is little in the literature to explain them, although Cleasby *et al.* (2013) do state that parent, and partner age, did not influence the provisioning rate exhibited by either male or female house sparrows. The observed reduction in provisioning rate in males may be caused by them altering the type, and size, of food item they are provisioning to the nest. For example, older males may develop improved foraging skills, provisioning the nest more efficiently by preferentially providing larger food items, or multiple food items in each trip (Marzluff, 1988; Hatchwell *et al*., 1999). This mechanism would account for reduced provisioning rates at the nest (Bowers *et al*., 2014), however, Khwaja *et al*. (2017) found the size of food items delivered to the nest to be less important than the total provisioning rate. If this is the case, then a reduction in male provisioning rate may instead be a result of preferential selection of higher quality food items, such as those with a higher nutritional value (van Oers *et al*., 2015).

However, it is possible that male blue tits perceive a reduction in the quality of both themselves and that of their partner as they age, and they modify the types of food items they select to compensate. This view is tentatively supported by previous work by Nour *et al*. (1998) and Tremblay *et al*. (2005), who found that tits are capable of modifying their selection of food items to account for differing influence of habitat when provisioning nestlings. The blue tits in these studies were doing so in response to decreased habitat quality, rather than the quality of the individual, however, it is possible that the effect is the same.

Alternatively, older males may reduce their contribution to the care of the current brood to pursue extra-pair copulation. This would be an efficient method for older males to maximise their lifetime reproductive success, while not having to care for all of the offspring produced. This tactic would be especially likely to be employed by older males if they are uncertain as to their ability to reproduce successfully in subsequent years, and thus they will try to father as many offspring in each year as possible, even though this may have a detrimental effect on both their own brood and future survival. The literature suggests that males may limit their provisioning rate by investing resources in extra-pair breeding, which would support this opinion (Low *et al*., 2012). Additionally, older males are generally more dominant, thus would be expected to have more opportunities for both extra-pair copulation and polygyny. This theory is also capable of explaining the lack of an age effect for female blue tits (Table 3.4), as female reproductive success is limited by the survival of the each of their broods, thus they will invest fully in the current brood, rather than seeking additional mating opportunities.

3.4.1.4 Contribution of the partner to parental care

The contribution of each parent varies significantly, and as mentioned in the method, there are approximately 10% of nests overall where greater than 80% of provisioning visits are carried out by one parent when provisioning rate is recorded. 84% of these involve the female provisioning at the higher rate, and as such it is probable that in these cases polygyny is reducing the contribution of the male to nest provisioning. Polygyny has been observed at several of these nests during 2018 but not recorded in previous years, and in such cases the provisioning rates may be a useful way to record this behaviour.

Provisioning rates of female blue tits were found to vary based upon that of their partner, their provisioning rate increasing with that of their partner (Figure 3.10). This result can be explained by the negotiation game theory model of parental care, wherein each partner is believed to alter their investment in parental care in real-time, based upon the contribution of their partner (Johnstone and Hinde, 2006; Harrison *et al.*, 2009; Johnstone, 2011). Negotiation over parental care relies upon breeding individuals being able to access information on the level of care provided by their partner. This result suggests that female blue tits actively make use of observation of the male provisioning rate to adjust their own level of parental care, ensuring the stability of the biparental care system (Harrison *et al.,* 2009; Bebbington and Hatchwell, 2016). In a study on house sparrows, Cleasby *et al*. (2013) found that the provisioning rate of the partner was only marginally insignificant, although they had expected it to be of greater importance.

However, the negotiation model also predicts that there is negotiation between parents and offspring over the level of care provided, namely, that the parents will use begging calls, or condition of nestlings, to influence the level of care they provide (Harrison *et al*., 2009). Thus, it is possible that the result found here is, at least partially, an effect of brood size. However, this is deemed unlikely in this case, as the variables were not found to be highly collinear prior to model selection and averaging.

The lack of a significant effect between male provisioning rate and the provisioning rate of their partner provides further evidence that the male contribution to parental care is less varied (Figure 3.12). This result has been found previously, with several papers suggesting that male parental effort is closer to that which would be expected from the sealed-bid model of parental care (Nakagawa *et al.*, 2007; Bowers *et al*., 2014; Bebbington and Hatchwell, 2016).

3.4.1.5 Habitat

Contrary to expectations, neither blue tit provisioning rate, nor the breeding parameters, were found to be directly significantly influenced by the habitat variables (Tables 3.1 to 3.4). The literature suggests that habitat quality should have had a significant influence upon provisioning rate, and reproductive success, through its influence upon food abundance (Southwood, 1961; Kelly and Southwood, 1999; Sisask *et al*., 2010). Theoretically, individuals breeding in territories where food is scarce, will have to spend more time foraging, and travel further to find food items, consequently having a lower provisioning rate than individuals breeding in higher quality habitat (Stauss *et al*., 2005; Tremblay *et al*., 2005;

Wilkin *et al*., 2009a). However, some studies of the influence of habitat upon blue tits have found results which conflict with this expected finding. Consequently, the expected influence of habitat on provisioning rate may in fact be masked by individuals which have been found to do the opposite of that expected above. For example, in low-quality habitats individuals may provision nests at a higher rate, compensating for a shortage of high-quality food items by providing a greater number of smaller food items. Whereas, in high-quality habitats, parents may provision fewer, high-quality, food items to increase their future reproductive success (Nour *et al*., 1998; Tremblay *et al*., 2005). The conflicting provisioning strategies outlined above may both be utilised by individuals within the same population, and it is likely that the choice between them will vary by parental sex, quality, and experience. For example, higher quality individuals may choose to increase provisioning rate in response to lower food abundance, or may reduce provisioning rates as they age, for example as found for males in the current population.

However, the nature, and composition, of the woodland present within the study site may also have contributed to the lack of a significant response of habitat upon provisioning rate and the breeding parameters. Past studies investigating the influence of habitat quality for tits, and other small woodland passerines typically look for differences between deciduous and coniferous habitats (Tremblay *et al.*, 2005; Wilkin *et al*., 2009a). Whereas, the majority of the study woodlands used for this project consist of mixed deciduous woodland, with few coniferous trees. Therefore, there may be insufficient variation in the habitat for its influence to be expressed in provisioning rates.

The method used in this study may also have prevented the finding of a significant relationship between the habitat variables and provisioning rate, if the vegetation data used in this project were not representative of the food resource available to blue tits. This could arise in two possible ways, firstly, if the 50m radius used for the vegetation data was either too low, or too high. However, as discussed in Chapter 1, the distance used here should represent the distance within which blue tits provisioning a nest will spend most of their time (Arriero *et al*., 2006; Garcia-Navas and Sanz, 2011; Amininasab *et al*., 2016). Blue tits have been found to travel much further from the nest, but this is considered unlikely to represent a food source which would be used on a regular basis (Tremblay *et al*., 2005). Secondly, the understory was not considered, but could represent an important refuge from predators (Sanz *et al*., 2010; Amininasab *et al*., 2017), which may influence the provisioning rate as a perception of higher predation risk can lead to reduced foraging rates. Predation of breeding adults, by sparrowhawks (*Accipiter nisus*) is likely to be seasonally, and annually, important in the study site at Lancaster University (Ian Hartley, pers. comm.) and as such, may have influenced the results of this study.

It is also possible that habitat quality influences provisioning rate indirectly, by determining clutch size, hatching success, and thus brood size. For example, habitat quality is frequently reported to influence the timing of breeding attempts, with earlier laid clutches being larger, and thus producing larger broods (Table 3.6; Figure 3.13; Svensson and Nilsson, 1995; Sanz *et al*., 2010; Maicas *et al*., 2014). However, the physical environment could also be determining brood size, and thus provisioning rate, through variables not assessed in this study, such as the spatial distribution of calcium. Calcium is an important micronutrient known to be a limiting factor on the clutch size, and hatching success, of tit species (Wilkin *et al*., 2009b; Eeva *et al*., 2009; Gosler and Wilkin, 2017).

3.4.2 Repeatability of parental care

3.4.2.1 Repeatability of provisioning rate by individual

The repeatability estimates for provisioning rate show that male provisioning rate is highly consistent for the same male in different years and moderately so for individual females (Table 3.5). These repeatability values show that breeding blue tits are exhibiting consistent individual differences in provisioning rate between years. However, the value for females can only be taken as marginal proof of repeatability, as the *p* value indicates statistical significance but the confidence intervals contradict this, by overlapping with zero (Table 3.5). This contrast results from the different methods used to generate these values in the *rptR* package, and may be caused by a combination of low numbers of repeats per individual and low repeatability (Wolak *et al*., 2012; Schuster *et al*., 2017). Consequently, this result will be tentatively accepted as evidence for repeatability, as with Schuster *et al*. (2017).

These results show that parental care in blue tits is consistent between individuals breeding in multiple years, and that individuals are significantly different from each other. This suggests that individual quality, and personality, influence provisioning rates (Low *et al*., 2012). This has implications for reproductive success, suggesting that good parents are likely to remain good parents, and bad parents will remain bad ones (Bebbington and Hatchwell, 2016). However, somewhat counterintuitively, previous studies on tits have not found that variation in provisioning rate is significantly linked to the number, or quality, of fledglings (Wilkin *et al*., 2009a; Mainwaring and Hartley 2016). Mainwaring and Hartley (2016) suggest that this could be because nestlings provided with a greater food supply transfer the additionally energy, and nutrients, into aspects of quality which were not measured but increase survival in the post-fledging stage, when mortality of juvenile blue tits is high (Cramp and Perrins, 1993; MacColl and Hatchwell, 2003). Thus, higher provisioning rates, while not increasing the number of fledglings, may increase the chance of fledglings being recruited to the breeding population in subsequent years.

Additionally, the results again show that there is a sex difference in blue tit parental care behaviour, with males being much more highly repeatable than females (Table 3.5). Sex differences in estimates of the repeatability of provisioning rate have been reported previously, with males generally being found to be more highly repeatable (Schwagmeyer and Mock, 2003; Nakagawa *et al*., 2007; Schuster *et al*., 2017). Reported estimates of repeatability of provisioning rates in the literature are similar to those reported here, with estimates for males varying between 0.4 and 0.7, and 0.2 and 0.35 for females (Freeman-Gallant and Rothstein, 1999; MacColl and Hatchwell, 2003; Nakagawa *et al*., 2007). The literature suggests that this is due to males following the sealed-bid model of parental care, whereby each male provisions at a set amount, determined primarily by their quality (Houston and Davies, 1985; Nakagawa *et al*., 2007; Bebbington and Hatchwell, 2016). Male repeatability may have arisen from females using consistency of parental care as a mechanism by which to select a mate, with females benefitting from selecting higher quality males (Nakagawa *et al*., 2007; Bell *et al*., 2009; Schuett *et al*., 2010). In contrast, female provisioning behaviour is believed to be much more in line with the negotiation model, with provisioning rates altered in response to the needs of the brood, the availability of food in the habitat, and the contribution of their partner (Harrison *et al*., 2009; Low *et al*., 2012; Bebbington and Hatchwell, 2016). These conclusions are supported by the above results, which identified the key factors influencing provisioning rate in males and females.

3.4.2.2 Repeatability of provisioning rate by nestbox, independent of individual identity

The total provisioning rate at each nestbox was found to be significantly moderately repeatable, however, male provisioning rate was only marginally repeatable at each nestbox, and female provisioning rate was not at all repeatable (Table 3.5). These results were found regardless of whether the same individual, or pair, were occupying each nestbox, and suggest that both total provisioning rate, and to a lesser extent, male provisioning rate, are influenced by some aspect of the physical environment specific to each nestbox, or its surrounding territory, which is consistent between years. The literature suggests that this was most likely to be food abundance, specifically, the number of caterpillars available to the parents (Banbura *et al*., 1994; Svensson and Nilsson, 1995; Arriero *et al*., 2006). However, food abundance, determined from the vegetation data, was not determined to influence provisioning rate in this study, and consequently is unlikely to be directly causing the repeatability of provisioning rate encountered here.

Additionally, it is possible that the repeatability of total, and male, provisioning rate at each nestbox is a response of similar quality individuals occupying each nestbox between years. This might be expected, as measurements of habitat quality and food abundance have been found to be consistent between years in woodland habitats (Przybylo *et al*., 2001; Amininasab *et al*., 2016; Amininasab *et al*., 2017) and these variables should result in nestboxes being of similar attractiveness to blue tits between years, with competition then ensuring that birds of similar quality occupied each box. Males of similar quality would be expected to make similar ‘sealed-bids’, or contributions to parental care, and females of similar quality should lay similar clutch sizes (Goodburn, 1991), thus determining brood size.

Brood sizes may also be repeatable by territory due to similar levels of food available during the nestling stage, influencing nestling mortality, or the spatial distribution of micronutrients, such as calcium, in the surrounding area, which would be expected to remain constant between years (Wilkin *et al*., 2009b). However, the lack of a significant estimate of repeatability for females occupying each nestbox suggests that clutch size, and subsequently brood size, may not be influencing the repeatability of provisioning rate at each box, as females would also be expected to show a response if brood sizes were consistent (Goodburn, 1991; Freeman-Gallant and Rothstein, 1999).

3.4.3 Conclusion and suggestions for further study

In conclusion, the results of this study show that blue tit provisioning rates vary by sex, and that the variables significantly influencing this parental care behaviour also differ between the sexes. The dominant variable being the requirements of the brood and both sexes were found to alter their provisioning rates in response to this, although males varied their provisioning rates less than females. The other influence upon male and female provisioning rates differed by sex, with males responding more to the quality of their partner, and females varying their contribution to care based upon that of their partner and whether they had altered their breeding site. Additionally, male provisioning rates were found to be more strongly repeatable than those of females, and when combined with the results outlined above, this strongly suggests that male blue tits and female blue tits follow the sealed-bid model and negotiation model respectively (Houston and Davies, 1985; Harrison *et al*., 2009;

Bebbington and Hatchwell, 2016). Furthermore, novel evidence was found for total, and male, provisioning rates to be repeatable by habitat after controlling for the effect of individual identity. This suggests an interaction between habitat and parent quality, or it may be in response to provisioning rates of all males varying less than those of females.

Surprisingly, none of the habitat variables were found to influence provisioning rates directly, potentially due to parents adaptively altering their provisioning behaviour, and preferred food items in response to their habitat (Tremblay *et al*., 2005). However, the repeatability of total, and male, provisioning rate for each territory, suggests that the physical environment may be influencing provisioning rate indirectly, such as through calcium abundance (Gosler and Wilkin, 2017). Overall, this study has provided new evidence of the factors influencing parental care in blue tits, and how these vary by sex. Furthermore, the repeatability estimates are, to the best of my knowledge, the first reported for provisioning rates of blue tits and provide compelling evidence for the influence of both individual, and habitat quality on parental care.

Further research could develop this project by experimentally examining the influence of both habitat and individual quality upon parental care behaviour and repeatability, for both individuals, and nest sites. The influence of habitat quality could be assessed in one of two ways, firstly, by comparing provisioning rates, and the repeatability of these, between habitats of greatly differing quality, such as deciduous and coniferous woodland (Wilkin *et al*., 2009a; Amininasab *et al*., 2016). Secondly, by incorporating supplementary feeding, thus allowing habitat quality to be altered to the desired level, and also allowing breeding individuals, or territories, of a specific quality to be targeted. Additionally, a detailed study of the proportion of different food items being supplied at each nest, and the repeatability of this by both provisioning parent and nestbox, would also assist in clarifying the results of this study, as well as examining another mechanism by which parental personality can influence parental care, and thus offspring survival (Nour *et al*., 1998; Sisask *et al*., 2010). Furthermore, the quantity, and proportion of different prey species, available will vary based upon stochastic effects, such as cold weather, or heavy rain, during the early breeding season. Thus, examining the influence of such effects upon food availability both within, and between, years could yield some interesting results.

4. General discussion

The behaviour of wild birds varies between individuals and is often cited as a mechanism by which individuals adaptively increase their reproductive success, fitness and survival (Beheler *et al.*, 2003; Garcia-Navas and Sanz, 2011; Johnstone *et al.*, 2014). There are several ways in which this could be achieved but they all relate to the relative costs and benefits of breeding in a particular site, or with a specific partner, thus showing the importance of nest-site selection, breeding dispersal and mate selection (Greenwood and Harvey, 1982; Wilkin *et al.*, 2009a). It is becoming increasingly accepted that these costs and benefits are determined by habitat quality, individual quality, and personal experience, with an individual's prior experiences and learning, potentially altering the influence of each of these factors. However, the relative importance of these influences is poorly understood, and the literature is not always in agreement within each species (Valcu and Kempanaers, 2008; Garcia-Navas and Sanz, 2011).

Chapter two examined the habitat quality and individual-specific factors influencing breeding dispersal, as well as the reproductive outcome of dispersing. Additionally, the repeatability of the breeding parameters was estimated for both males and females, and for each nestbox, allowing further examination of the influence of habitat quality and individual-specific variables independently of those variables which had been measured. Chapter three looked at habitat and individual-specific factors influencing parental care, specifically provisioning rates, as well as the proportion of the repeatability of provisioning rate which could be attributed to either habitat, or individual variables.

4.1 Main research findings

4.1.1 Breeding dispersal and repeatability of reproductive success

The decision to undergo breeding dispersal was found to be significantly influenced by the sex of an individual and the level of road traffic noise experienced during breeding. Sex is well-known to influence post-breeding dispersal, with females more likely to disperse than males, as found here (Harvey *et al.*, 1979; Garcia-Navas and Sanz, 2011) and this is thought to be due to sex differences in the costs and benefits of dispersal (Clarke *et al.*, 1997; Valcu and Kempanaers, 2008). However, the positive relationship between road traffic noise and the probability of an individual dispersing, as the only other significant driver of dispersal, is novel and has not been reported previously. The preferential dispersal from noisier sites was most likely to be in response to masking of vocal communications (Warren *et al.*, 2006;

Halfwerk *et al*., 2011; Meillere *et al*., 2015) or an increase in the perceived predation risk (Schroeder *et al*., 2012; Meillere *et al*., 2015), both of which increase energy requirements and are likely to reduce parental and nestling quality (Schroeder *et al*., 2012). An unmeasured variable, such as increased air pollution from vehicles could also be driving this response (Sanderfoot and Holloway, 2017). Unexpectedly, no other aspects of habitat quality were found to influence the decision to disperse, and no variables influenced the distance dispersed. These results were in accordance with a previous study of blue tits (*Cyanistes caeruleus*) by Valcu and Kempanaers (2008), but differed from the majority of the literature, which strongly suggested that aspects of the vegetation surrounding each nest (Przybylo *et al*., 2001; Arriero *et al*., 2006), and previous reproductive success (Bollinger and Gavin, 1989; Haas, 1998), should have influenced dispersal. Not finding a significant influence of the vegetation characteristics, could have been a result of the vegetation being of similar quality within the typically short dispersal distances of blue tits, thus breeding individuals were unable to make decisions about the relative value of different breeding sites and did not use this information when making decisions concerning dispersal. Furthermore, there was no effect of the decision to disperse, or dispersal distance, upon the change in fledging success between years, suggesting that blue tits did not gain a measurable reproductive benefit from dispersal. This result differs from that reported in the literature, with dispersers usually found to increase some aspect of reproductive success (Beheler *et al*., 2003). it is also possible that the expected benefit of dispersing was realised in other ways, such as increased nestling quality, rather than quantity, or in higher parental survival.

The repeatability analyses indicated that female quality was the primary control upon clutch size, as clutch sizes were strongly consistent for individual females breeding in multiple years. This has been suggested previously (van Noordwijk *et al*., 1987; Slagsvold and Lifjeld, 1990; Svensson, 1997), but very rarely assessed using repeatability analysis (Goodburn, 1991). Fledging success was found to be repeatable for males, but female quality did not have a consistent, or strong, influence upon this, most likely as a result of highly repeatable male provisioning rates between years, as reported elsewhere in this thesis (Chapter 3). These results agree with those found for magpies (Goodburn, 1991) but differ from the only other study to look at repeatability of breeding parameters in blue tits, which found no repeatability of these for either parent (Przybylo *et al*., 2001). However, the lack of a response in that study could have been due to a small sample size (Przybylo *et al*., 2001) and the method used to estimate repeatability, which was less accurate than that used here (Nakagawa and Schielzeth, 2010; Dingemanse and Dochtermann, 2013). Lastly, the breeding parameters were found to be moderately to strongly repeatable by nestbox, independent of individual identity. This suggests that habitat quality did have an influence on reproductive success and that this was sufficient to exceed the influence of parental quality for hatching success and fledging success. This effect may be down to food abundance or the influence of habitat quality upon the timing of the brood, as these factors were found to influence reproductive success (Chapter 2), or the influence of an unmeasured variable, such as the availability of sources of calcium in the landscape (Wilkin *et al*., 2009b; Gosler and Wilkin, 2017). The moderately repeatable estimate of fledging success for male parents suggests that males would not significantly alter their fledging success by dispersing, whereas fledging success for female parents was not repeatable, suggesting that dispersing to access a higher quality mate or territory should increase their reproductive success. The results of these repeatability analyses are novel and highlight a method which has real potential to determine the relative contributions of habitat quality and individual-specific factors upon aspects of behaviour and reproductive success.

4.1.2 Provisioning rates and their repeatability

Provisioning rates are typically measured and used to assess the contribution of parents to parental care (Thorogood *et al*., 2011; Low *et al*., 2012). This study assessed the variables influencing male and female provisioning rates and found that these differ between the sexes. The only variable found to influence both male and female provisioning rates was brood size. Both sexes were found to provision at a higher rate when feeding a larger brood, likely due to the increased benefit of fledging a greater number of young on the lifetime success of each parent, and also in response to increased total food demand by the brood (Low *et al*., 2012; Adams *et al*., 2015). However, at lower brood sizes there was a difference in male and female provisioning rates, most likely due to females matching their provisioning rate to the requirements of the brood, whereas male provisioning rates are relatively inflexible (Nakagawa *et al*., 2007; Low *et al*., 2012). This result differs from those reported in the literature for similar species, with studies of great tits (*Parus major*) (Wilkin *et al*., 2009a) and long-tailed tits (Adams *et al*., 2015) showing no sex difference in provisioning rate, whereas house sparrows showed the opposite effect (Cleasby *et al*., 2013). These differing results are likely to reflect variation between species in behaviour, dependent upon the breeding strategy of each species (Cleasby *et al*., 2013). Male provisioning rate was also found to be negatively correlated to both the age of the male, and that of his partner. This suggests that males based their level of investment in parental care upon their own quality, and that of their partner (Cleasby *et al*., 2013). However, it is likely that older males will have developed, or learnt, more efficient foraging techniques, thus they may provision the nest at a lower rate due to increased time spent searching for larger, or higher quality, prey items (Marzluff, 1988; Hatchwell *et al*., 1999; van Oers *et al*., 2015). Males were also found to provision at a higher rate when breeding with the same partner as the previous year, suggesting that there may be a benefit to retaining a mate, perhaps from reduced sexual conflict (Parker *et al*., 2002) or more efficient provisioning at the nest (Bebbington and Hatchwell, 2016). These results suggest that male provisioning rates were determined largely by the size of their brood, their own quality, and that of their partner. Contrastingly, female provisioning rates were influenced by brood size, as discussed above, positively related to the provisioning rate of their partner, and were higher when they were breeding in the same nestbox as the previous year, but not with the same partner. These variables suggest that females adjust their level of care based upon that of their partner, a result which has been reported previously (Harrison *et al.,* 2009; Bebbington and Hatchwell, 2016). The increase in female provisioning rate when re-using a nestbox between years suggests an effect of familiarity with the territory, which may occur from local knowledge of the spatial distribution of food sources and predator refuges (Low *et al*., 2012). Surprisingly, there was no direct influence of habitat quality upon the parental provisioning rates, which would have been expected from the influence of habitat quality upon food abundance (Kelly and Southwood, 1999; Stauss *et al*., 2005; Sisask *et al*., 2010). The literature provides evidence that tits may be able to alter their provisioning behaviour in response to food availability and the demand of their offspring, and this may have masked the predicted result (Nour *et al*., 1998).

The estimates of repeatability show that parental care behaviour is significantly repeatable for individuals breeding in multiple years, with males more highly repeatable than females, as found previously in savannah sparrows (*Passerculus sandwichensis*; Freeman-Gallant and Rothstein, 1999), house sparrows (*Passer domesticus*; Schwagmeyer and Mock, 2003; Nakagawa *et al*., 2007) and stitchbirds (*Notiomystis cincta*; Low *et al*., 2012). The estimated values of repeatability are also consistent with those reported previously (Freeman-Gallant and Rothstein, 1999; Nakagawa *et al*., 2007). These results suggest that individual quality, or personality, have a strong influence upon an individual's ability to provide parental care, and that this is moderately to strongly consistent across the lifetime of an individual. Higher male repeatability is likely to have arisen from females using their partner's investment in parental care as a mechanism by which to select a mate, thus encouraging the evolution of consistency in this behaviour (Bell *et al*., 2009; Schuett *et al*., 2010). Male blue tits courtship feed their potential partner (Royama, 1966; Krebs, 1970), and it is this behaviour which could be used to select males which will provision the nest at a higher rate. In contrast, the lower repeatability of females reflects their attentiveness to the needs of the brood, females typically being found to adjust their parental care effort to the demand of their offspring (Schwagmeyer and Mock, 2003; Nakagawa *et al*., 2007). Combined with the variables found to influence provisioning rate in either sex, these results provide strong and compelling evidence that males provision as predicted by the sealed-bid model of parental care, whereas females follow the negotiation model (Houston and Davies, 1985; Nakagawa *et al*., 2007; Bebbington and Hatchwell, 2016). This suggests that males provision based upon their own quality, whereas females will respond to the quality of the male, and that of their breeding habitat. These results thus support those shown by the repeatability of breeding parameters (Chapter 2), whereby females stand to benefit by dispersing to higher quality territories, or mates, but males only benefit from finding higher quality territories. However, the repeatability of provisioning rate was also estimated for each nestbox, independent of bird identity, to examine the influence of habitat quality upon parental care behaviour, rather than just that influence arising from the measured variables. This found that male, and total, provisioning rates were moderately repeatable by nestbox but that female rates were not. This suggests that habitat quality influenced provisioning rates of males, and the total provisioning rate at a nest, either through repeatable food abundance in each breeding territory (Przybylo *et al*., 2001; Arriero *et al*., 2006; Amininasab *et al*., 2016), or as a result of other aspects of habitat quality, such as calcium availability (Wilkin *et al*., 2009b) or as a consistent association between bird quality and territory quality, with competition limiting birds of a similar quality to similar quality habitats. This repeatability of provisioning rates by nestbox and by sex suggest that individual quality is more important than habitat quality, but that it does still have an influence upon repeatability of parental care.

4.2 Suggestions for further research

The findings above contrast with the general literature concerning dispersal on two main topics and both of these would benefit from further research. Firstly, none of the measured vegetation variables were found to be influencing the decision to disperse, as found in Garcia-Navas and Sanz (2011), as previously suggested, this may have been a result of the scale of habitat heterogeneity at the Lancaster study site varying from the distances blue tits typically disperse (Santema and Kempenaers, 2018). However, it would be interesting to test this assumption, and the alternative, that blue tits were not adaptively selecting nest-sites based on their quality as determined by the results of the vegetation survey. This could be examined either by using the same methods used here as a basis for ranking those nest-sites within a suitable distance of a dispersing individual's most recent breeding attempt, and then assessing whether this ranking relates to the endpoint of dispersal. Alternatively, the number of times a nest-site has been occupied has been shown to be an accurate measure of its quality (Sergio and Newton, 2003; Janiszewski *et al*., 2013), and this could be used to quantify relative quality of all nestboxes. Ideally, an experimental approach should be used, possibly using supplementary feeding to examine whether food abundance, and thus indirectly vegetation characteristics, influence nest-site occupation.

Secondly, the interaction of breeding dispersal and reproductive success, was not found here, despite the repeatability analyses suggesting that reproductive success was repeatable for each nestbox/territory. Therefore, it is probable that some other aspect of individual, or nestling, quality was either influencing dispersal, or occurring as a result of it (Garcia-Navas and Sanz, 2011). Theoretically individuals will disperse to territories where risk of mortality, or the effort required to breed, are lower, responses which could be caused by the spatial distribution and abundance of predators and food sources (Tremblay *et al*., 2005; Chalfoun and Martin, 2010). Studying the influence of predation would be difficult but examining nests which failed suddenly at the nestling stage could be used to assess this indirectly, as complete failure at this stage is nearly always due to predation of a parent (Santema and Kempanaers, 2018). Assessing the interaction of parent, and nestling, quality upon dispersal would be much easier, and could be done using measurements of body mass, and wing and tarsus length which are routinely collected at Lancaster (Mark Mainwaring and Ian Hartley, pers. comm.) but were outside the scope of this project.

Finally, my results have shown that repeatability is an effective and efficient means by which the relative importance of variables influencing behaviour, or other measurable outcomes, can be assessed. Furthermore, it can be used to identify influences acting upon the data which were not necessarily explainable based upon the measured variables, such as suggesting an influence of calcium availability upon the repeatability of clutch size (Gosler and Wilkin, 2017). I would encourage future studies to strongly consider the use of repeatability and believe it could greatly benefit the study of ecology, being a useful measure by which to assess habitat quality, not just the repeatability of behaviour.

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