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Title	The evolutionary ecology of personality and life history variation in an anthropogenic heterogeneous landscape
Authors	O'Shea, William
Publication date	2017
Original Citation	O'Shea, W. 2017. The evolutionary ecology of personality and life history variation in an anthropogenic heterogeneous landscape. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
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Download date	2026-11-06 13:09:32
Item downloaded from	https://hdl.handle.net/10468/5588



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The Evolutionary Ecology of Personality and Life History Variation in an Anthropogenic Heterogeneous Landscape

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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July 2017

Table of Contents

Declaration……2

Abstract……3

Acknowledgements……5

Chapter 1……6

General Introduction

Chapter 2……58

Phenology, provisioning, and life history variation in a generalist passerine across an anthropogenic heterogeneous landscape. *In revision: Oecologia*

Chapter 3……90

Do personality and innovativeness influence competitive ability? An experimental test in the great tit. *Published in Behavioral Ecology*

Chapter 4……127

Risk aversion predicts nest desertion in the great tit (Parus major)

Chapter 5……151

Proactive females have lower reproductive success in a highly fragmented landscape

Chapter 6……174

General Discussion

Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.

William O'Shea

Abstract

Across taxa, animals exhibit repeatable individual differences in behaviour. These differences, termed personality, may be heritable, linked to fitness, and thus subject to natural selection. As with many non-behavioural traits, the fitness consequences of personality may vary according to environmental conditions, but the ecological mechanisms underlying such variation are often unclear. This thesis addresses this issue, exploring the functional significance and fitness consequences of exploration behaviour, a personality trait measured in captivity, amongst great tit (*Parus major*) populations inhabiting two distinct habitat types, coniferous and deciduous woodland fragments.

Little is known of how habitat influences life history variation amongst resident populations in afforested woodland fragments, even though modern biodiversity strategies have mandated greater planting of deciduous species. Therefore, to make realistic hypotheses regarding the ecological consequences of personality variation, it was necessary to establish how the two habitats influenced life history parameters. Great tits experienced higher reproductive success in coniferous than in deciduous fragments. These differences were likely influenced by local breeding densities and thus competition, as deciduous fragments attracted higher densities of breeding pairs. Populations breeding in the two habitat types also experienced distinct seasonal changes in reproductive success. In deciduous sites, fledgling production was relatively stable while in coniferous sites it strongly declined with lay date. This thesis demonstrates that in some cases, planting regimes designed to increase biodiversity in afforested fragments may have negative consequences for resident populations.

During the winter, great tits forage in flocks on clumped resources where competitiveness may be critical for survival. Individual variation in competitiveness may reflect permanent alternative strategies arising because of correlations between behavioural traits. Competitiveness has been linked to exploration behaviour and innovativeness in the great tit, the latter of which is a behavioural trait that may have an underlying cognitive and personality component. Although indirect evidence implies that the two traits correlate with alternative foraging strategies in a social context, this has never been shown directly. Using an experimental approach, I show that innovative problem solving and personality did not correlate with competitive ability. In a separate trial, competitive exclusion led to alternative novel foraging strategies emerging amongst less competitive individuals, the first time such a pathway between the two behaviours has been demonstrated. This thesis provides valuable evidence that innovativeness may be a key trait allowing poor competitors to circumvent direct competition and access alternative resources.

One prominent theory suggests that personality is a component of life history variation, and that individual behavioural variation correlates with differential investment in reproduction and self-maintenance. These differences may be more pronounced in challenging

environments, for example when food availability is relatively low. Parental care behaviours may be a key functional mechanism linking personality with life history and fitness in different environments; however this has rarely been investigated. During incubation, female responses to predation risk were significantly repeatable within and between seasons; however there was no link between female exploration behaviour and risk aversion. More risk averse females were subsequently more likely to desert their nests before incubation, suggesting that risk aversion and desertion may be intrinsically linked. Later in the season, a comparison of females breeding in coniferous and deciduous fragments found that faster exploring females provisioned their offspring at lower rates and experienced lower reproductive success. This is contrary to what has been shown elsewhere, where exploration behaviour generally correlates positively with provisioning rates, especially in challenging conditions. Amongst males, faster explorers raised better quality offspring than slow explorers in coniferous sites, but the trend was reversed in deciduous sites which may reflect trade-offs that occur between paternal care and territoriality especially in high density areas. These results suggest that exploration behaviour may predict some aspects of parental care in the wild; however it is difficult to generalise across behavioural and environmental contexts. Despite the fitness differences observed, it is unlikely that selection will lead to changes in the genetic distribution of personality traits within populations in this landscape, because high levels of gene flow and low recruitment will maintain variation.

This thesis demonstrates the ecological relevance of personality and innovativeness, elucidating a behavioural mechanism, offspring provisioning, through which personality is linked to fitness. More generally this thesis highlights the difficulties associated with generalising the effects of personality traits across studies, and demonstrates the multitude of ways in which individual behavioural variation may influence life history in the wild.

Acknowledgements

First and foremost, I would like to thank my supervisors. Thanks to John Quinn for his support and guidance throughout my PhD, without which I would not be at this point. I'm also grateful to John O'Halloran for his encouragement and advice along the way.

Many other people have supported this project over the last few years. Huge thanks to Barry O'Mahony, my ringing trainer for all of his help and advice in various aspects of the project. Thanks also to the technicians in the Cooperage, especially Allen and Luke for help constructing the aviary when it became apparent my own carpentry skills were not up to the task, and Stuart for the GIS help. The Great Tit group were a great help during my PhD, especially Jodie Crane for her help trapping birds and Gabrielle Davidson for reading chapter drafts. I'm grateful to all my friends and colleagues in the Cooperage for their company throughout my time in BEES, especially the BEES footy crew for the Tuesday night games that have kept me sane over the past year.

Thanks to Coillte and the Castle Bernard Estate for allowing me to establish the study populations on their land. This project was supported by a Thomas Crawford Hayes Scholarship.

Finally, I would like to thank my family for their belief and constant encouragement throughout my studies.

Chapter 1

General Introduction



Introduction

Environmental heterogeneity and local adaptation

Understanding the processes that explain the origin and maintenance of biological diversity is a fundamental aim of evolutionary ecology (Roff, 1993; Futyama, 2003). Phenotypic variation arises due to plasticity and evolutionary divergence, the latter of which can be caused by to genetic drift, mutation, gene flow or natural selection (Roff et al, 1997). Although evolutionary divergence has been acknowledged as an important driver of differentiation amongst higher level taxa since the time of Darwin (Darwin, 1859), over the past century accumulating evidence has shown selection acting over increasingly smaller scales, leading to adaptive variation between populations and maintaining variation amongst individuals (e.g. Reznick et al, 1990; Wilson, 1998).

Environmental heterogeneity is ubiquitous in nature (Kotliar and Wiens, 1990) and thus populations of the same species often inhabit environments that differ in a variety of biotic and abiotic factors. (Kotliar and Wiens, 1990; Kawecki and Ebert, 2004). Within populations, genotype × environment interactions accumulate for Darwinian fitness, and over time natural selection can cause changes in the distribution of traits (Epling and Dobzhansky, 1941; Boag and Grant, 1981; Kawecki and Ebert, 2004). This may lead to the emergence of adaptive phenotypic differences between isolated populations through natural selection, sometimes over relatively small spatial scales (Kawecki and Ebert, 2004). Local adaptation is said to have occurred if resident genotypes have on average higher relative fitness than immigrant genotypes (Kawecki and Ebert, 2004). If gene flow is present, then phenotypic variation may still emerge through plastic responses to local cues; however differences between populations may not necessarily be adaptive (Sultan and Spencer, 2002; Ghalambor et al, 2007). For instance, freshwater snails (*Physella virgate*) that are raised with predatory or non-predatory sunfish species are smaller, produce thicker shells and have lower fecundity than those in the raised in the absence of predators. These traits are adaptive in the presence of predatory sunfish; however offer no advantages, and are costly in the presence of non-predatory sunfish (Langerhans and DeWitt, 2002). Thus, the adaptive nature of phenotypic plasticity relies on correct phenotype environment matching (DeWitt et al, 1998). If mismatches emerge due to inaccurate sampling of environmental information or genetic constraints, reduced fitness will result (Ghalambor et al, 2007). Identifying genes, or the corresponding phenotypic traits that confer fitness benefits in different environments is

therefore a critical step towards understanding the adaptive significance of phenotypic variation in the wild (Roff, 1997; Kawecki and Ebert, 2004).

Life history theory states that a combination of intrinsic and extrinsic constraints limit investment in growth and reproduction (Stearns, 1976), and that adaptive life history strategies (i.e. trade-offs between reproduction and self-maintenance) optimise fitness for a given environment (Stearns, 1992). Environmental heterogeneity modifies extrinsic constraints and may lead to alternative strategies emerging amongst isolated populations if traits are heritable and sufficient genetic variation exists (Stearns, 1992). For example, predation pressure influences the average age of sexual maturity and fecundity amongst populations of Trinidadian guppies (*Poecilia reticulata*) (Reznick et al, 1990; Reznick et al, 2001). Populations experiencing high predation pressure experience directional selection for earlier sexual development and more frequent broods than populations in low predation environments, as late maturing individuals are more likely to suffer mortality before breeding (e.g. Dowdall et al, 2012; Reznick et al, 2001). These populations also display consistently different adaptive foraging strategies, necessary for sustaining appropriate levels of development (Zandonà et al, 2011). Thus, environmental heterogeneity may result in natural selection acting on suites of correlated morphological, physiological and behavioural traits leading to adaptive life history divergence between populations (Stearns, 1992; Réale et al, 2010; Atwell et al, 2014).

Spatial variation in resource availability may also lead to adaptive life history divergence. Energy is critical for all aspects of life history; however under restricted resource regimes trade-offs emerge, as investment in one trait limits energy availability for others (Fig. 1.1; Zera and Harshman, 2001). Typically, populations display reduced fecundity in food restricted environments as brood size does not necessarily positively correlate with recruitment because of high offspring mortality (Stearns, 1992; Chippindale et al, 1993). Instead, populations may evolve increased reproductive lifespans (e.g. Chippindale et al, 1993) and/or increased investment in parental care, producing lower numbers of high quality offspring (e.g. Badyaev and Ghalambor, 2001). In food rich environments, energy intake is mainly limited by foraging inefficiencies and therefore life history trade-offs may not be apparent. In fact in some cases positive phenotypic correlations between traits may be observed (Fig. 1.1; van Noordwijk and de Jong, 1986). In the shorter term, phenotypic

plasticity can allow individuals to adjust reproductive investment to suit local environmental conditions (Ghalambor et al, 2007). For example, one commonly observed phenomenon is negative density dependent fecundity (e.g. Creighton, 2005). Phenotypic plasticity may be a crucial buffer following the invasion of novel habitats (Yeh et al, 2004), allowing populations to survive before the genetic assimilation of advantageous phenotypic traits also known as the "genes follow" hypothesis (Ghalambor et al, 2007); however if gene flow is constant, then adaptive phenotypic differences may not become fixed (Kawecki and Ebert, 2004).

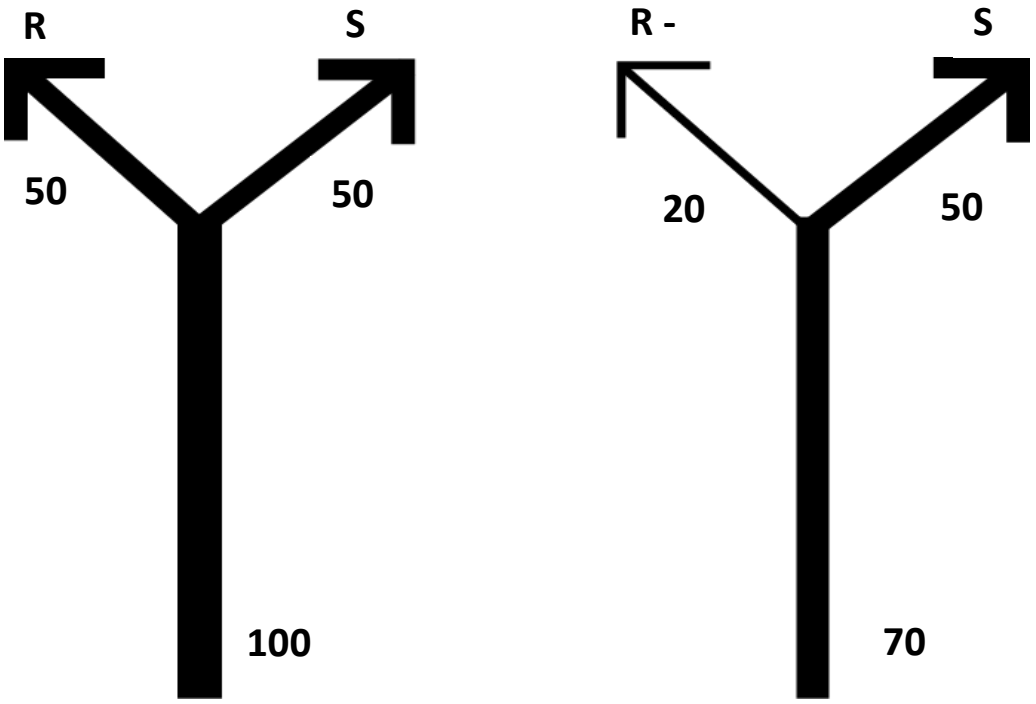


Figure 1.1. A schematic outlining energetic allocation and a physiological trade-off between reproduction (R) and self-maintenance (S) in two environments (adapted from Zera and Harshman 2001). The numbers at the bottom of the figure represent energy intake, where the environment on the right has lower resource availability (70) than the environment on the left (100). Energy allocation to respective traits is depicted by numbers near the top of the "Y". By limiting resources, trade-offs emerge between growth and reproduction (right). In the energy limited environment, reduced fecundity is observed (R-). These drawings could also represent individuals that differ in terms of their ability to acquire resources.

Similarly, temporal environmental heterogeneity can strongly influence selection on phenotypic variation. In seasonal environments, fluctuations in temperature correlate with resource availability for consumers (van Schaik et al, 1993), caused by changes in vegetation biomass (Rathcke and Lacey, 1985). Many higher trophic level consumers have evolved breeding cycles that maximise synchrony with the emergence of prey communities (Visser and Both, 2005; Nakazawa and Doi, 2011), as mismatches between food availability and reproductive requirements will result in lower fitness for individuals that display incorrect phenotypes (Singer and Parmesan, 2010). These links may span multiple trophic levels (e.g. Both et al, 2008), and have become important systems for studying the evolutionary consequences of global climate change (Parmesan, 2006). At an individual level, breeders can display considerable plasticity, matching breeding activity with annual fluctuations in temperature which influence food availability (Nussey et al, 2005; Charmantier et al, 2008), but may also respond to vegetative cues that predict local food abundance over relatively small spatial scales (Hinks et al, 2015). Between populations, differences in climate (e.g. Moore et al, 2005) or local vegetation (e.g. Charmantier et al, 2016) may lead to differences in the emergence of prey communities amongst areas that are in close proximity. If sufficient isolation exists, residents may evolve adaptive breeding cycles that coincide with peaks in local food availability. For instance, populations of *Operophtera brumata*, a polyphagous geometrid moth, display adaptive differences in egg hatch times that match bud burst of the host tree species. For moths, synchrony is essential as larvae that hatch before leaves emerge will starve; however more mature leaves have secondary metabolites that cause larval mortality so selection favours hatching times that coincide with bud burst (Singer and Parmesan, 2010). Thus, spatiotemporal environmental heterogeneity can have significant consequences for the emergence and maintenance of phenotypic variation in the wild.

Behavioural variation and animal personality

Historically, behavioural traits received less attention than morphological and physiological traits in the field of evolutionary ecology (Sih et al, 2004b; Siepielski et al, 2009). The study of behavioural variation within populations was limited to discrete traits, such as alternative foraging strategies, which are maintained by frequency-dependent selection (Barnard and Sibly, 1981). Continuous behavioural traits and individual behavioural variation within populations were generally neglected (*but see* – Huntingford, 1976). This reluctance to take an individual-based approach to the study of behaviour in the wild may have arisen because of statistical and methodological issues associated with repeated standardised measures of

behaviour or perhaps because of the difficulties associated with marking and recapturing individuals over long time periods (Réale et al, 2007). In any case, behaviour was largely treated as an optimality problem, assuming that individuals were plastic in their responses to stimuli (*reviewed in* - Clark and Ehlinger, 1987; *but see* - Krebs et al, 1978). Individual variation was considered to be noise around an adaptive population mean (Wilson, 1998).

Over the past few decades, however, accumulating empirical evidence has shown that animals exhibit limited plasticity in their behaviour (Sih et al, 2004a). Furthermore, within populations, individuals may consistently differ in their responses to identical stimuli and these differences may be repeatable, persisting over long time periods and across ontogeny in some cases (Sih et al, 2004a; Réale et al, 2007; Fucikova et al, 2009; Stanley et al, 2017). These consistent differences, termed personality, encompass a variety of behavioural traits (e.g. aggressiveness, sociality, activity, boldness) and may be conserved across situations (Sih et al, 2004a). For instance, some individuals are consistently bolder than others when foraging under different levels of predation risk (e.g. Sih et al, 2003). Inter-individual differences may also be conserved across contexts, for example individuals that are more risk prone may also be more aggressive towards conspecifics (e.g. Huntinford, 1976). These correlations between personality traits, known as behavioural syndromes, have important implications for behavioural ecology because their existence suggests that selection may not necessarily act on single behaviours in isolation (Sih et al, 2004b). Instead as with correlated morphological or physiological traits, selection depends on the fitness consequences of both traits in combination (Lande and Arnold, 1983).

Much of the work thus far on animal personalities has focused on describing the structure of behavioural syndromes and understanding the proximate causes underlying individual variation (Wolf and Weissing, 2010). Typically, personality traits are identified by repeatedly measuring behaviour under controlled captive conditions (*but see* – Duckworth et al, 2006 for an example of personality traits measured in the wild). Using a mixed model approach, it is then possible to determine the proportion of phenotypic variation explained by inter-individual variation, also known as repeatability (Falconer and Mackay, 1996). The repeatability of personality traits varies quite widely, even within species, and is viewed as the upper limit of heritability (Bell et al, 2009); however identifying individual repeatable differences in behaviour does not necessarily mean that the trait is heritable. Using a top

down approach, personality traits are then ecologically validated by correlating personality with variation in ecologically relevant traits (Réale et al, 2007).

The existence of personality traits is surprising as one would assume that complete behavioural plasticity should be favoured (Sih et al, 2004b). In reality, complete behavioural plasticity is rare because of time-lags between environmental fluctuations and subsequent behavioural responses that are caused by non-instantaneous sampling (DeWitt et al, 1998). Furthermore, environmental sampling itself is rarely optimal, and in many cases individuals have incomplete information about their environment on which to base their responses (DeWitt et al, 1998). In these cases, fixed behavioural responses may be more profitable than limited behavioural plasticity, because it allows individuals exhibiting correct phenotype-environment matches to avoid costly mistakes (Sih et al, 2003; Sih et al, 2004b; Wolf et al, 2008b; McNamara et al, 2009).

Along with the costs associated with plasticity, individual state-based differences may also promote animal personalities (Wolf and Weissing, 2010; Sih et al, 2015). State here refers to intrinsic and extrinsic factors that may influence an individual's optimal behaviour. Importantly, as state differences may arise due to genetic polymorphism or phenotypic plasticity, so too may corresponding personality phenotypes (Wolf and Weissing, 2010). Age, sex and morphological variation are just a few examples of stable state differences that may lead to the emergence of behavioural variation within populations (Wolf and Weissing, 2010). Other examples include physiological states related to life history strategies including growth rates or corresponding metabolic rates (Stamps, 2007). Faster developing individuals must consume greater amounts of resources than slower developers in order to sustain high growth rates, which can be costly to change (Mangel and Munch, 2005). The costs and benefits of behavioural traits such as aggression and risk responsiveness are likely to vary amongst individuals of different growth rates. High levels of aggression may be costly energetically, but can benefit resource acquisition necessary to sustain high growth rates. For slower developers with lower energy needs, investment in aggression has higher relative costs and is therefore not optimal. Indeed, several studies have found evidence of adaptive personality traits that correlate with different life history strategies (e.g. growth rate, fecundity and survival) within populations, known as pace of life syndromes (*reviewed in* - Biro and Stamps, 2008; Réale et al, 2010), and these positive correlations between

physiology and behaviour may be crucial for the maintenance of personality variation in the wild (Wolf and McNamara, 2012). As an individual's state may influence several behaviours at once, state-based differences also provide a powerful framework for explaining the existence of behavioural syndromes within populations (Wolf and Weissing, 2010).

Individual differences in labile states can also lead to the emergence of behavioural syndromes if behaviour reinforces state differences between individuals (Wolf and Weissing, 2010; Sih et al, 2015). For instance body condition, a proxy for energy reserves, positively correlates with predator evasion in some species (e.g. Stankowich, 2009). When foraging, individuals with greater energy reserves can afford to be more risk prone, further enhancing differences in condition between individuals (Luttbeg and Sih, 2010). Thus, state-dependent behaviour may lead to positive feedback loops emerging even if initial differences in state are relatively small (Luttbeg and Sih, 2010). Furthermore, experience performing a behaviour benefits future performance, increasing efficiency through learning (e.g. Kleim et al, 1998). Individuals may be less likely to perform alternative behavioural patterns if the costs (i.e. lower efficiency) outweigh the benefits of sticking to established, practiced patterns. This may further reinforce individual differences, promoting consistency (Wolf et al, 2008a). A recent study by Bierbach et al (2017), found that clonal fish (*Poecilia formosa*) exhibit consistent individual behavioural variation later in life even when reared under experimentally identical conditions. The authors suggest that miniscule differences in environmental cues, temperature or prey distributions led to the emergence of individual differences in behaviour. Thus, animal personality is likely to be ubiquitous in nature as even stochastic microvariation in the local environment may have significant consequences for behavioural variation through cascading positive feedback loops (Sih et al, 2015).

Natural selection and animal personality

Understanding how local environmental factors shape the phenotypic distribution of personality traits within populations is another important aspect of personality research. Personality can influence fitness (Smith and Blumstein, 2008) whereby poor phenotype-environment matches lead to reduced fitness (DeWitt et al, 1998); however if individual variation arises purely because of environmental effects (i.e. phenotypic plasticity) and the environmental variation that leads to individual variation emerging is present, then

phenotypes do not need to experience equal fitness in order to coexist within populations (Wolf and Weissing, 2010). Quantitative genetic analysis indicates that in some cases, personality traits may have a significant heritable component (*reviewed in* – Dochterman et al, 2015). If the fitness consequences of heritable traits vary according to local environmental conditions then personality may experience heterogeneous selection in different environments (Dingemanse and Réale, 2005). For example, two personality traits that are typically positively correlated are aggression towards conspecifics and risk aversion (e.g. Huntingford et al, 1976). In an environment with high levels of predation and low levels of competition, aggressive, risk prone individuals will display maladaptive behaviour resulting in lower fitness. In this scenario, selection will favour more risk averse, docile individuals leading to negative directional selection over time (Fig. 1.2a). Conversely, in an environment with low levels of predation and high levels of competition, selection should favour aggressive, risk prone individuals as these traits may positively correlate with resource acquisition and thus fitness (Fig. 1.2b). Although this is quite a simplistic example, it clearly indicates how the distribution of personality traits within populations can be shaped by local environmental conditions through fitness trade-offs (Luttbeg and Sih, 2010; Wolf and Weissing, 2010).

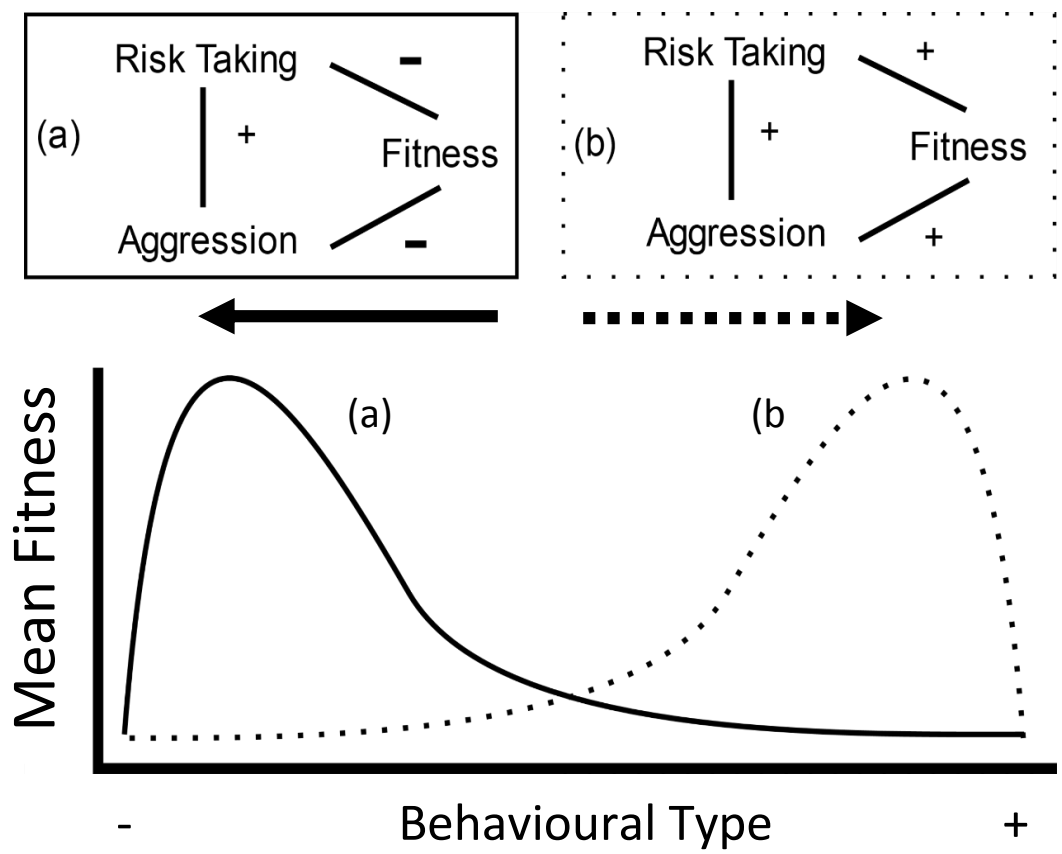


Figure 1.2. This schematic outlines the fitness consequences of a behavioural syndrome involving a positive correlation between aggressiveness and risk-taking behaviour, in two environments. (a) the solid line represents an environment with high levels of predation and low levels of competition where personality is under negative directional selection. (b) the dotted line represents an environment with low predation levels and high levels of competition where the personality traits are under positive directional selection. "+" on the x-axis indicates individuals that are more aggressive and risk prone, while "–" indicates individuals that are less risk prone and aggressive.

Identifying the fitness consequences of individual behavioural variation along environmental gradients is therefore a critical step towards understanding the adaptive significance of personality traits (Réale et al, 2007). A comprehensive literature review reveals that 28 studies have investigated the adaptive significance of a personality trait in different environmental contexts (Appendix 1.1). The majority of these studies involve one of four

traits measured under controlled captive conditions: activity in the presence of a novel object or a predator, exploration of a novel environment, or aggressiveness, which are usually viewed as proxies for behavioural syndromes (Carter et al, 2013; Appendix 1.1). A comparison of results indicates considerable between study variation regarding the fitness effects of personality traits along similar environmental gradients, which confirms that these relationships are highly species specific and difficult to generalise (Dall and Griffith, 2014; Appendix 1.1). Even within populations, a single personality trait may have variable fitness consequences among individuals of different age and sex classes which could lead to sexually or ontogenetic antagonistic selection maintaining variation in the wild. For instance Patrick and Weimerskirch (2014), investigated the fitness consequences of neophobia amongst black-browed albatross (*Thalassarche melanophrys*). In years associated with high food availability there was positive selection for boldness amongst females through reproductive success, whereas in poorer years there was negative selection acting on boldness in females. In contrast, bold males always had higher reproductive success than shy males, regardless of food availability. Boldness was linked to reproductive success via divergent foraging strategies providing a crucial link between a personality trait and a functionally significant behaviour.

Although heterogeneous selection on personality traits in different environments has been detected several times (Appendix 1.1), the underlying behavioural and ecological mechanisms that lead to these fitness differences emerging are often unclear. Thus, the aims of these types of studies should be two-fold. Firstly, to identify functional behavioural correlates of the personality traits that are likely to influence fitness. Secondly, to use these links to build ecologically relevant hypotheses that are grounded in knowledge of species-specific and in some cases population-specific behavioural and life history variation.

<u>The functional significance of personality: a case study in the great tit</u>

Research on the functional significance of personality traits in the great tit (*Parus major*) probably represents the most comprehensive work done on animal personality to date. Much of this has focused on the reactive-proactive behavioural axis which describes individual variation along a continuum (*reviewed in* - Koolhaas et al, 1999; Groothuis and Carere, 2005). At one extreme, proactive individuals are quick to explore novel

environments, aggressive, risk prone, routine forming and display a strong negative stress response to social defeat, while reactive individuals behave conversely (Groothuis and Carere, 2005). Individual variation is usually measured using a modified version of the classic "open field test", developed by Verbeek et al (1994) which involves exposing individuals to a novel environment and recording their subsequent behaviour. "Exploratory behaviour" during this assay is a repeatable and heritable trait (Dingemanse et al, 2002; Quinn et al. 2009; Nicolaus et al. 2012; Korsten et al. 2013) which has been linked with a range of ecologically significant behaviours including dispersal (Dingemanse et al, 2003; Quinn et al, 2011; Korsten et al, 2013), parental care (Hollander et al, 2008), space use (van Overveld and Matthysen, 2010; van Overveld et al, 2011; Aplin et al, 2014; Johnson et al, 2017), and social behaviours like territory defence (Amy et al, 2010; Naguib et al, 2016), dominance (Dingemanse and de Goede, 2004; Cole and Quinn, 2011), promiscuity (van Oers et al, 2008; Patrick and Browning, 2011) and social network position (Aplin et al, 2013; Snijders et al, 2014).

Exploration behaviour has been linked to survival and reproductive success in the great tit, and may be subject to heterogeneous selection along environmental gradients; however the fitness effects (i.e. viability, reproductive success) and direction of selection varies between populations (Dingemanse et al, 2004; Quinn et al, 2009; Nicolaus et al, 2016). For instance, Dingemanse et al (2004) report fluctuating patterns of viability selection on male and female great tits in the Netherlands which may have been related to fluctuations in environmental food availability and thus competition. In two food poor years where competition was higher, faster exploring females and slow exploring males were more likely to survive, with the opposite pattern observed in one food rich year. Quinn et al (2009) found evidence of heterogeneous fecundity selection acting on male great tits across two gradients: habitat quality, and population densities. In densely populated areas, faster exploring males produced less offspring than slow explorers, while in low density areas there was no evidence of directional selection acting on exploration behaviour. In higher quality habitat, faster exploring males produced less offspring than slow explorers, however in lower quality habitats, there was no detectable selection acting on exploration behaviour. Across the four years of the study, there was no evidence of heterogeneous viability selection, and female exploration behaviour was not subject to directional selection. Finally, Nicolaus et al (2016) reported evidence of heterogeneous viability selection acting on male and female exploration behaviour between years of high and low population densities. In high density

years, faster exploring individuals are less likely to survive than slow explorers, while in low density years, slow explorers were more likely to survive. There was no evidence of selection acting on personality traits via reproductive success. Thus, the effects of personality on fitness are highly context dependent in this species. Furthermore, the functional mechanisms underlying these relationships remain unclear, as there is a dearth of research investigating the relationships between personality and functional behaviours along environmental gradients in the great tit and other species.

Foraging and personality

Foraging is one candidate behaviour, as it has significant consequences for survival and reproductive success (Fritz and Morse, 1985; Lemon, 1993), and several studies have found evidence of links with exploration behaviour in great tits. One prominent argument states that differences in foraging behaviour observed between personality types are adaptive and arise because of pace of life variation, whereby proactive individuals prioritise productivity over self-maintenance (Réale et al, 2010). For instance exploration behaviour is linked to competitive ability in some contexts. Faster explorers tend to be more aggressive towards competitors (Verbeek et al, 1996) which facilitates greater access to clumped resources under scramble competition (Cole and Quinn, 2011), and may be key for overwinter survival (Gosler, 1993; Dingemanse and de Goede, 2004). However in unfamiliar or novel environments, faster explorers may have lower dominance ranks than slow explorers (Dingemanse and de Goede, 2004), because of a negative physiological stress response to social defeat which causes reduced locomotor activity (Carere et al, 2001; Carere et al, 2003). In confined or novel environments, faster explorers are unable to flee from stressful situations to recover and may suffer cascading effects of multiple defeats leading to low dominance ranks (Dingemanse and de Goede, 2004).

Furthermore as an altricial species, adult foraging behaviour during the breeding season is critical for reproductive success in the great tit (Naef-Daenzer and Keller, 1999). Faster exploring males settle in better quality territories (Both et al, 2005) but also provision their offspring at lower rates than reactive males (Barnett et al, 2012; Mutzel et al, 2013), which may be due to trade-offs between provisioning and frequent aggressive encounters with territorial intruders, as proactive males are more territorial (Amy et al, 2010). Amongst

females, proactive individuals increase provisioning rates to cope with unfavourable conditions, for instance when breeding with aggressive males or when brood demands are artificially increased (Mutzel et al, 2013; Nicolaus et al, 2015; *but see* - Patrick and Browning, 2011), as predicted by the pace of life hypothesis. This increase is not as pronounced in reactive females (Mutzel et al, 2013).

Proactive and reactive individuals may also differ in terms of space use which can influence foraging ability. Proactive individuals travel farther from unproductive patches to find food than reactive individuals (van Overveld and Matthysen, 2010; van Overveld et al, 2011). Furthermore, personality variation may be linked with patch discovery during the winter (Herborn et al, 2010), as proactive individuals that tend to forage on the periphery of flocks are more likely to move between patches (Aplin et al, 2013; Aplin et al, 2014). These differences in sociality may be due to personality specific reliance on social information (Marchetti and Drent, 2000). There is some evidence that proactive individuals rely on social information to make foraging decisions (Marchetti and Drent, 2000), whereas reactive individuals sample their local environments thoroughly (Marchetti and Drent, 2000; van Overveld and Matthysen, 2013), and therefore are more perceptive to environmental variation, facilitating optimal decisions which may be crucial during reproduction (Nicolaus et al, 2015). On the other hand, proactive individuals are more routine forming in their behaviours (Marchetti and Drent, 2000), and are willing to take risk when foraging, both in terms of space use (Quinn et al, 2011) and diet choice, with studies indicating that faster explorers are more likely to incorporate novel food items into their diet than slow explorers (Exernová et al, 2010). Studying the foraging behaviours of individuals in multiple environments could clarify these relationships, especially across environments that differ in terms of food availability and distribution. However to date no study has yet examined the links between provisioning behaviours and exploration behaviour in multiple environments, and whether this relationship influences reproductive success.

Risk aversion and personality

How individuals respond to risk is thought to be another key factor linking the reactive-proactive axis to fitness. Personality-specific differences in risk aversion may arise because of how individuals manage the trade-off between productivity and predation risk (Stamps,

2007; Biro and Stamps, 2008; Réale et al, 2010). For instance empirical evidence suggests that when starvation risk is at its highest, proactive individuals are more willing to forage in exposed areas than reactive individuals (Quinn et al, 2011). As a consequence, individuals that display traits indicative of proactivity (i.e. boldness, aggressiveness) have higher reproductive success but lower survival than reactive individuals (Smith and Blumstein, 2008).

Offspring defence represents a direct trade-off between current productivity (offspring survival) and future survival, offering an opportunity to test if indeed the reactive-proactive axis is linked to alternative life history strategies (Montgomerie and Weatherhead, 1988; Réale et al, 2010). Several studies have found evidence of individual differences in risk responsiveness during the breeding season (e.g. Kontiainen et al, 2009; Fresneau et al, 2010), which may be related to the reactive-proactive axis (Hollander et al, 2008; Cole and Quinn, 2014). For instance, proactive females are faster to return to their nests following disturbance and exposure to a novel object near the nest cavity (Cole and Quinn, 2014). However the only study to date that examined if exploration behaviour correlates with defensive behaviours in the great tit reported mixed findings (Hollander, 2008). Proactive individuals were more likely to alarm call, but were less mobile in the presence of predators against expectations. Neither of these studies investigated if parental responses were related to fitness outcomes. Therefore, identifying links between offspring defence, exploration behaviour and reproductive success, represents an opportunity to determine if life history trade-offs play a role in maintaining individual personality variation in the wild.

Individual cognitive variation

Cognition refers to the perception, processing and use of environmental information (Shettleworth, 2010). Cognitive traits such as memory, learning and innovation play a significant role in many fundamental ecological processes, influencing how individuals acquire resources (e.g. Pravosudov and Clayton 2002), avoid predation (e.g. Swift and Marzluff, 2015), invade new habitats (e.g. Sol et al, 2005), and manage social relationships (e.g. Keagy et al, 2009). Intraspecific variation in cognitive ability occurs naturally in the wild. This variation may be adaptive, arising because of phenotypic plasticity, or because of additive genetic effects (*reviewed in* - Thornton et al, 2012). Much of the early work on the

evolutionary ecology of cognition focused on intra-population comparisons which suggest that when the benefits of maintaining energetically expensive neural structures associated with greater cognitive capacity are high, natural selection may promote higher cognitive capabilities. For instance, research on black-capped chickadees (*Poecile atricapillus*) has shown that individuals from populations at higher latitudes have more hippocampal neurons and perform better in spatial memory tasks than those from lower latitudes. At lower latitudes, food is more abundant during the winter and the fitness consequences of food caching, a behaviour that relies heavily on spatial memory, are not as significant (Pravosudov and Clayton 2002). Experiments have shown that increased cognitive capacity may be associated with physiological trade-offs. For example in *Drosophila*, experimental lines selected for increased learning abilities in adulthood exhibit decreased competitive ability as larvae, compared with controls (Mery and Kawecki, 2003). This suggests that the development and maintenance of cognitive abilities are expensive and that selection may be constrained by genetic correlations with other traits. More recently, as awareness of the adaptive significance of within population cognitive variation has grown (Wilson, 1998), focus has shifted towards understanding why individual cognitive variation exists, and how it is maintained in the wild (Thornton et al, 2012; Morand-Ferron et al, 2016).

Studying the evolutionary ecology of traits, be it morphological, physiological or cognitive, requires large sample sizes. As traditional cognitive assays require substantial subject training, much of the early work on the evolution of cognition has focused on simple assays such as goal oriented problem-solving tasks, which require the performance of a novel behaviour to access a reward (*reviewed in* - Morand-Ferron et al, 2016). These trials generally require little training, allowing large numbers of individuals to be assayed repeatedly (e.g. Cole et al, 2011). The use of these tasks as a measure of cognitive ability remains controversial (Rowe and Healy, 2014; Griffin and Guez, 2014); however it is thought that innovation does have an underlying cognitive component as previous studies have shown that individual variation in innovativeness correlates with performance in operant conditioning tests (Morand-Ferron et al, 2015) and neural structures associated with higher cognitive functioning (Roth and Pravosudov, 2009; Roth et al, 2010), although they all may be simultaneously correlated with a non-cognitive trait. Despite these correlations with heritable traits (Roth et al, 2010), the only study that has attempted to estimate the heritability of innovative problem solving found that variation arose primarily due to early life environmental effects (Quinn et al, 2016). Cohorts that were exposed to harsh

environmental conditions soon after fledging were more likely to solve novel problem-solving tasks consistently throughout their lives. Innovators in the same population were also less competitive in a social context (Cole and Quinn, 2011) suggesting that innovation may enable alternative foraging strategies for less competitive individuals, allowing them to circumvent direct competition and access alternative resources through novel foraging methods thereby achieving equal fitness (Cole and Quinn, 2012).

Environmental resource availability is therefore thought to be a key factor influencing the performance of innovative behaviours in the wild. This is known as the "necessity drives innovation hypothesis" which states that in general when an individual's natural repertoire of behaviours fails to grant access to resource, innovations should be more common (Reader and Laland, 2003). Resource availability may be restricted by environmental gradients like climate or habitat, but social factors like competition may also play a role. Empirical evidence for the necessity drives phenomenon innovation is mixed (*reviewed in* – Griffin and Guez, 2014), for instance in great tits and blue tits, individuals that are less socially dominant are more likely to solve novel goal-oriented problems (Cole and Quinn, 2011; Aplin et al, 2013), and in the closely related mountain chickadee (*Poecile gambeli*), individuals from higher elevations are faster to solve novel problems than those from lower elevations (Kozlovsky et al, 2015); however amongst starlings, there is no relationship between competitiveness and problem solving (Boogert et al, 2008). In many cases, tests of the necessity hypothesis are indirect, linking innovativeness with known correlates of competitiveness. To date, no study has investigated whether competitive exclusion may directly lead to innovative behaviours occurring amongst poor competitors, as predicted by the necessity drives innovation hypothesis. Thus, one of the aims of this thesis is to examine the direct links between innovation and competition as predicted by the necessity drives innovation hypothesis.

Evolutionary ecology of anthropogenic landscapes

Modern land use has significantly degraded natural habitats worldwide (Vitousek et al, 1997; Foley et al, 2007). Much of this change has occurred due to human industries supporting a growing global population. In the past 300 years it is estimated that agriculture and timber harvesting alone have caused a net loss of approximately 10 million km^2 of natural forest habitat, while industries like fisheries, and mining operations as well as increased

urbanisation have all contributed to declines in ecosystem functioning (Foley et al, 2007). This has had catastrophic consequences for biodiversity worldwide (Pimm et al, 1995). Many extant species must adapt to survive in altered environments (Bell and Collins, 2008), and understanding how populations cope with anthropogenic change is a major aim of ecologists and conservationists alike.

Habitat loss and fragmentation are two of the most pervasive effects associated with modern land use. Habitat loss reduces the amount of habitat available within a species range, restricting access to critical resources like prey (Mortelliti and Boitani, 2007), mates (Banks et al, 2007), or breeding territories (Huhta et al, 1998). At the patch level, fragmentation amplifies negative edge effects further reducing habitat quality. Predation and parasitism rates can be higher near patch edges, as predator species from the surrounding habitat matrix are more likely to interact with residents situated closer to the edge (Murcia, 1995). As edge effects may persist for several hundred metres, they are ubiquitous in smaller fragments (Wilkin et al, 2007). Reproductive success and survival may therefore be lower amongst resident populations in smaller fragments than larger fragments, although this depends on species involved (Lampila et al, 2005). For instance Burke and Nol (2000), found that ground and shrub nesting birds had greater reproductive success in larger fragments than smaller fragments. Predation was a major cause of nest failure, and was more prevalent in smaller fragments (*see also* - Herkert et al, 2003). Conversely, studies of cavity nesting bird species breeding in woodland fragments in Belgium found no difference in reproductive success between resident populations in fragments of different size (Matthysen and Adriaensen, 1998; Nour et al, 1998). Cavity nests provide greater protection from nest predation than other types of nest, therefore the effects of fragmentation on the reproductive success of resident populations may be context specific (Lampila et al, 2005).

In modern landscapes, natural habitat is commonly replaced by economically valuable, non-native vegetation of low structural and community complexity. The benefits of intensive agriculture and forestry for local biodiversity remains controversial (Benton et al, 2003; Tscharntke et al, 2005; Brockerhoff et al, 2008; Bremer and Farley, 2010). These areas undergo regular cycles of harvesting and replanting leading to highly dynamic landscapes where natural succession is curtailed (DeFries et al, 2004). Animal communities in heavily modified areas tend to be composed of generalist species that can cope with environmental

instability (Julliard et al. 2006; Devictor et al, 2008), although factors such as the stage of the crop cycle (Sweeney et al, 2010), preceding land use (Graham et al, 2015) and patch size (Díaz et al, 1998) can all influence community structure.

Intensive management techniques designed to improve crop yields can inadvertently cause declines in environmental resource availability, contributing to an overall loss of biodiversity in modern landscapes (Benton et al, 2003). For instance, the use of pesticides on agricultural crops and the subsequent reduction in invertebrate prevalence has been linked to population crashes of farmland birds across Europe (Geiger et al, 2010). Likewise, the short rotation cycles of forestry plantations prevent natural cavities from forming, thereby reducing habitat suitability for obligate cavity nesting species (Newton 1994; Taki et al, 2011).

The structure of crops may also influence resource availability for residents. Homogeneous planting regimes maximise space use; however these areas tend to support less diverse animal communities than more heterogeneous patches (Benton et al, 2003; Pedley et al, 2011). Many non-native crop species, display significantly different life history strategies to native vegetation, including different phenologies (Dougherty et al 1994; Kuster et al, 2014). This can have cascading effects in multitrophic systems leading to mismatches between the emergence of invertebrates on non-native vegetation and the breeding cycles of higher level trophic consumers which are adapted to coincide with the emergence of critical prey in natural habitats. For instance in the Mediterranean, caterpillars, which are a key food resource for breeding blue tits (*Parus caruleus*), emerge several weeks later in evergreen than deciduous habitat. As deciduous woodland is the predominant habitat in the area, the breeding cycle of residents is adapted to the phenology of deciduous trees. Pairs breeding in evergreen habitat, many of which are immigrants, lay before the peak of food availability leading to low reproductive success (Blondel et al, 1993). In this way, homogeneous planting strategies could conceivably create ecological traps if cues that determine settlement patterns are present and attract individuals to the area (Schlaepfer et al, 2000), but if mismatches emerge between local resource availability and the breeding cycles of populations that are adapted to the phenology of the predominant native habitat.

Recent environmental directives have placed greater emphasis on conserving biodiversity in modern landscapes (Young et al, 2005; Zanchi et al, 2007). One common method employed is to plant mixed polycultures that include native vegetation. This technique increases patch productivity (Cardinale et al, 2007; Zhang et al, 2012), and supports a greater diversity and abundance of animal species (Benton et al, 2003; Felton et al, 2010; Sweeney et al, 2011) than monospecific areas. Polycultures can benefit residents over monocultures in several distinct ways. Firstly, polycultures increase within site environmental heterogeneity (e.g. wind exposure, shade, temperature), creating niche space for a more diverse ecological community than monospecific areas (Felton et al, 2010; Stein et al, 2014). For higher trophic level consumers, especially generalist species, this corresponds with increased food availability which can support higher population densities (Felton et al, 2010). Secondly polycultures exhibit greater variation in local phenology, as different plant species respond to different environmental cues, or combinations of cues (Lechowicz, 1984; Cole and Sheldon, 2017). This promotes temporal stability of food availability within heterogeneous patches for resident consumers (Stamps and Linit, 1998). Finally, many species exhibit a distinct preference for specific vegetation taxa. For instance, the great tit (*Parus major*) preferentially settles in deciduous rather than coniferous woodland (Peck, 1989; Mänd et al, 2005). Planting a variety of species of different taxa diversifies cues that determine settlement patterns of dispersing individuals, thereby increasing local abundances and species richness (Felton et al, 2010). To date, few studies have examined how different planting and management regimes influence the reproductive success of resident populations by influencing important behaviours such as foraging and reproductive investment (*but see* – Rosenfield et al, 2000; Schekkerman and Beintema; 2007).

At the landscape level, anthropogenic changes can create a heterogeneous mosaic of habitat patches, sometimes over relatively small spatial scales (Benton et al, 2003). Metapopulations may therefore be exposed to a variety of environmental selection pressures because discrete habitat patches will support different prey communities, population densities and predators depending on features like patch structure and local vegetation. In the absence of gene flow, beneficial traits may become fixed within sub-populations due to local adaptation through natural selection (Singer and Thomas, 1996; Kawecki and Ebert, 2004; Leimu and Fischer, 2008). This may lead to the emergence of spatially structured life history variation amongst isolated populations where genetic variation is large enough to prevent inbreeding depression (Kawecki and Ebert, 2004; Charmantier et al, 2016). One classic example of local

adaptation involves an island population of blue tits in the Mediterranean. Subpopulations inhabiting two distinct habitat types, evergreen oak and deciduous oak, display locally adapted life history strategies, with breeding cycles differing by almost a month between habitat types due to differences in local phenology (Charmantier et al, 2016). This phenotypic variation occurs over a smaller distance than this species is capable of dispersing, because of low levels of gene flow between populations.

In many cases, gene flow between habitat fragments is non-zero either because of high dispersal distances, or low patch isolation, or a combination of the two. Here, a constant influx of genes may prevent local adaptation from fixing beneficial traits within populations, unless behavioural mechanisms like natal habitat preference induction leads to correct phenotype environment matching amongst dispersing individuals (Davies and Stamps, 2004). If not, and gene flow is random, then evolutionary models suggest that plasticity may be favoured over specialist phenotypes in heterogeneous landscapes, because the plastic type will on average have higher fitness than non-plastic immigrants with mismatched phenotypes (Sultan and Spencer, 2002). Thus, anthropogenic change can have significant consequences for habitat quality and the ability of resident populations to adapt to anthropogenic change in heterogeneous landscapes.

The great tit study system

For this thesis I used the great tit as a study organism. The great tit is a small cavity nesting passerine found throughout much of the Western Palearctic. Its widespread distribution and preferential use of nest-boxes for breeding has made it a common study species for evolutionary ecologists because measurements of reproductive success are readily accessible (Gosler, 1993). Additionally, great tits are robust to trapping and transport, and perform well in captivity making them an ideal candidate species for behavioural studies both in captivity and in the wild.

Although great tits are adapted to mature deciduous woodland which was once common across much of Europe, they will readily settle and breed in most habitats where nest cavities are available (Gosler, 1993). Resident populations in different habitats may display considerable life history variation, including differences in fecundity (e.g. Mägi and Mänd, 2004; Riddington and Gosler, 1995), phenology (e.g. van Balen, 1973; Dhondt et al, 1984),

and survival (e.g. van Balen, 1973; Horak and Lebreton, 1998). Some of this variation is adaptive (*but see* – Dhondt et al, 1990; Postma and van Noordwijk, 2005), driven by local resource availability which can vary widely between habitat types depending on the predominant vegetation community (e.g. van Balen, 1973; Tremblay et al, 2003). Much of the comparative work carried out in great tits has focused on populations inhabiting areas dominated by coniferous tree species or deciduous tree species (e.g. van Balen, 1973; Orell and Ojanen, 1983; Massa et al, 2004; Mägi et al, 2009). Generally, deciduous woodland is viewed as optimal habitat for great tits (Gosler et al, 1993), and studies indicate that higher reproductive success in deciduous woodland may be driven by more abundant resources during the breeding season (van Balen, 1973; Sanz, 1998), but this may vary between study populations (Mägi et al, 2009). In contrast, coniferous habitat may display significantly different phenological cycles to deciduous habitat (van Balen, 1973), which can lead to low levels of environmental food availability during critical periods of the breeding season, or mismatches between resident breeding cycles and food availability thus negatively impacting reproductive success (Riddington and Gosler, 1995).

Great tits are regularly recorded breeding in fragmented landscapes (Nour et al, 1998) regardless of fragment configuration or patch isolation (Enoksson et al, 1995), due to their relatively high dispersal distances and generalist ecology (Gosler, 1993). Studies indicate that breeding densities are generally higher in natural woodland fragments than in afforested areas (Sweeney et al, 2010), possibly because of lower densities of natural cavities in managed areas (Newton, 1994) or more abundant food resources in natural habitat (Pedley et al, 2014), but perhaps also because of an innate preference for mature deciduous areas (Mänd et al, 2005). Studies have also recorded higher densities of great tits in plantations supplemented with deciduous tree species rather than pure coniferous areas during the breeding season (Sweeney et al, 2010). Whether management strategies (i.e. vegetation structure) influence the life history strategies of great tits breeding in afforested woodland fragments is unknown.

In December 2012 I established 8 nest-box (Schwegler Woodcrete Nest-box, 32mm opening) study populations in woodland fragments in the Bandon valley, Western Co. Cork, Ireland. All sites were > 2km apart. Within sites, nest-boxes were placed on trees 50 metres apart. Sites were chosen based on local vegetation characteristics and proximity to University

College Cork for safe transportation of individuals to and from the aviary. Five mixed deciduous fragments and three second rotation coniferous fragments were chosen. The predominant tree species in conifer sites were Sitka Spruce (*Picea sitchensis*) and Scots Pine (*Pinus sylvestris*), although Lodgepole Pine (*Pinus contorta*), Norway Spruce (*Picea abies*), and Douglas Fir (*Pseudotsuga menziesii*) were present in small numbers. In the mixed deciduous sites, European Beech (*Fagus sylvaticai*) and Sessile Oak (*Quercus petraea*) were the most common species, but Ash (*Frazinus excelsior*), Alder (*Alnus glutinosa*), Birch (*Betula spp.*), Sycamore (*Acer pseudoplatanus*), Spanish Chestnut (*Castanea sativa*) and some conifer species were all present in deciduous sites to some degree.

Table 1. Locations and characteristics of study populations. Sites were characterised by the taxa of the predominant tree species present. Numbers in the first column correspond with numbered sites in Fig. 1.

	Site Name	**Habitat Type**	**Site Location**
1	Ballincourneenig	Coniferous	51.837879, -8.672072
2	Ballinphellic	Coniferous	51.840546, -8.630297
3	Shippool	Mixed deciduous	51.737780, -8.630792
4	Dunderrow	Mixed deciduous	51.719555, -8.600512
5	Castle Bernard	Mixed deciduous	51.741568, -8.767775
6	Dukes Wood	Mixed deciduous	51.785965, -8.751366
7	Kilbrittain	Mixed deciduous	51.671290, -8.682011
8	Garrettstown	Coniferous	51.655159, -8.616456

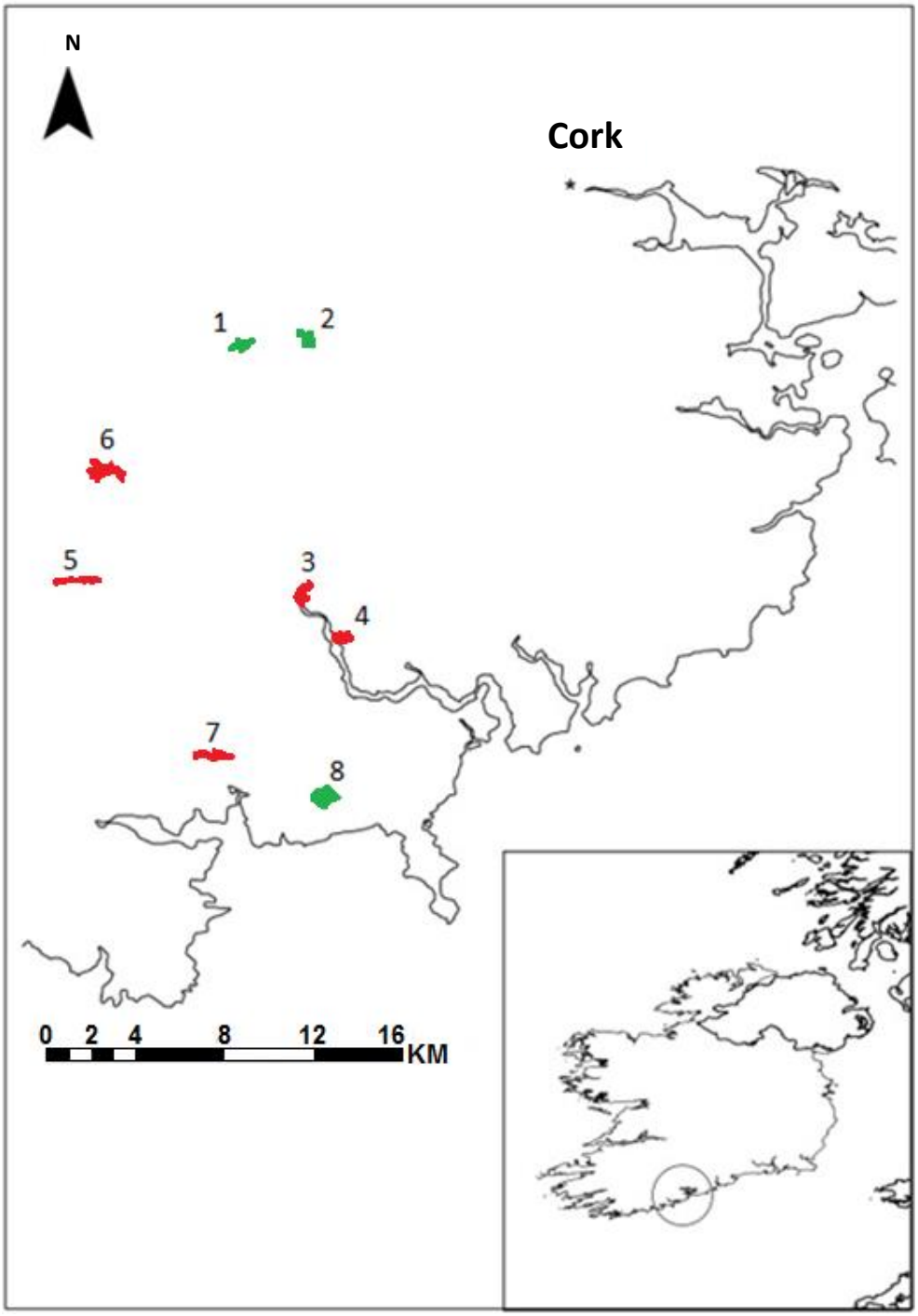


Figure 3. Map of study sites established in December 2012 in the Bandon Valley, Western County Cork. Green indicates coniferous sites, red indicates deciduous sites. Numbers next to sites correspond with numbers in table 1.





Figure 4. Pictures of the two habitat types. Above, mixed deciduous woodland. Below, coniferous habitat

Aims

In this thesis, I explore the functional significance of a personality trait, exploration of a novel environment, and examine whether personality variation is related to fitness outcomes amongst wild populations of great tits breeding in two distinct habitat types. Firstly, I establish whether important life history traits vary amongst populations of wild great tits inhabiting conifer and deciduous woodland fragments in a highly modified modern landscape. Building on previous research on personality traits in the great tit, I then explore how personality and innovative problem solving are simultaneously related to foraging behaviours in captivity. Finally, I investigate the links between personality, risk responsiveness and provisioning behaviours in great tits breeding in conifer and deciduous woodland fragments, and whether any differences that may emerge are related to individual reproductive success.

This thesis consists of four data chapters:

Chapter 2 explores how local habitat variation influences the settlement patterns, provisioning behaviour and fitness of great tits breeding in conifer and deciduous woodland fragments. Modern land management techniques have increased environmental heterogeneity, sometimes over relatively small areas. Very few studies have investigated whether this anthropogenic environmental heterogeneity leads to spatially structured life history variation emerging amongst populations in different habitat types, and the potential mechanisms underlying such differences. To do so, I established eight study populations in coniferous and deciduous woodland fragments and recorded the breeding parameters of great tits over three consecutive years. I also recorded provisioning behaviours of breeding adults during a key period of nestling growth to determine if differences in the foraging behaviours of adults were responsible for any habitat specific patterns in reproductive success that might emerge.

In **Chapter 3** I examine the links between exploration behaviour, innovative problem-solving performance and competitiveness in wild-caught captive great tits. Both traits have been simultaneously linked to competitive ability. Faster explorers are more competitive in a social context than slower explorers, while non-innovators are more competitive than innovators. The necessity drives innovation hypothesis predicts that less competitive individuals are

more likely to perform innovative behaviours in order to access alternative resources and circumvent direct scramble competition. This has yet to be shown however. I allowed dyads of great tits of known exploration behaviour and problem-solving ability to compete at a feeder designed to promote competitive interactions. I subsequently exposed dyads to the same feeder as well as a highly preferred food resource which was accessible only by the performance of a novel behaviour to test if indeed less competitive individuals were more likely to perform innovative behaviours.

In **Chapter 4** I examine how exploration behaviour correlates with predation risk responsiveness in the wild, a key mechanism thought to link the reactive-proactive personality axis to fitness. I also explore whether female responses to risk are consistent within and between breeding seasons, whether they vary throughout the season or across habitat types, and whether risk responsiveness is related to reproductive outcomes.

Finally, in **Chapter 5 I** investigate if exploration behaviour is related to reproductive investment and whether this relationship varies between conifer and deciduous habitat. I then examine if exploration behaviour covaries with adult foraging behaviours during a critical period of nestling growth in conifer and deciduous habitat. I then go on to investigate how exploration behaviour influences reproductive success, and whether habitat-specific differences in fitness emerge amongst individuals of different personality types.

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Appendix 1.1. Summary of 28 studies that have investigated the fitness consequences of personality in multiple environments. N/A indicates studies where the behavioural mechanisms underlying fitness differences amongst individuals of different personalality is unclear.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Bighorn sheep (*Ovis canadensis*)	A + J / F	Boldness	Survival	Predation pressure	Bold individuals more likely to survive high predation pressure. No effect of boldness on fitness during low predation pressure.	N/A	Réale and Festa-Bianchet, 2003
Bighorn sheep (*Ovis canadensis*)	A / F	Aggressiveness	Survival	Predation pressure	Aggressive individuals more likely to survive during high predation pressure. No effects during low predation pressure	N/A	Réale and Festa-Bianchet, 2003
Bighorn sheep (*Ovis canadensis*)	J / F	Aggressiveness	Survival	Predation pressure	No effects of aggressiveness on viability during low and high predation pressure amongst young females	N/A	Réale and Festa-Bianchet, 2003
Black turban sea snails (*Chlorostoma funebralis*)	A / M + F	Risk aversion in the presence of a predator	Survival	Predator Personality traits	In the presence of active predators, risk averse individuals more likely to survive than risk prone individuals. In the presence of inactive predators, risk prone individuals are more likely to survive.	N/A	Pruitt et al, 2012

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Black-browed albatross (*Thalassarche melanophrys*)	A / F	Boldness in the presence of a novel object	Reproductive Success	Food availability	In poor years shy females have higher reproductive success while in good years bold females have higher reproductive success.	Females that forage closer to the shore are outcompeted by males in poor years.	Patrick and Weimerskirch, 2014
Black-browed albatross (*Thalassarche melanophrys*)	A / M	Boldness in the presence of a novel object	Reproductive Success	Food availability	Bolder males have higher reproductive success than shy males across all years	Males are more competitive and thus benefit from foraging close to the shore in all years	Patrick and Weimerskirch, 2014
Common lizard (*Lacerta vivipara*)	J / M + F	Sociability	Survival	Population densities	At low densities, social individuals are less likely to survive than less social individuals. At high densities, less social individuals are more likely to survive than more social individuals	N/A	Cote et al, 2008
Common lizard (*Zootoca vivipara*)	J / M + F	Exploration of a novel environment	Survival	Population densities	Faster explorating individuals had lower survival than slow explorers at low densities. At high densities, there was no selection on exploration behaviour.	N/A	Le Galliard et al, 2015

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Coral grouper (*Plectropomus leopardus*)	A / M + F	Boldness in the presence of a predator	Survival	Temperature	At high temperatures risk prone individuals more likely to survive. No personality-specific effects of temperature on survival at low temperatures	Risk averse individuals take longer to return to resting metabolic rate. At high temperatures, this process is compromised.	Clark et al, 2017
Eastern Chipmunk (*Tamias striatus*)	J/ M + F	Exploration of a novel environment	Survival	Food availability	No effect of exploration behaviour on survival	N/A	Bergeron et al, 2013
Eastern Chipmunk (*Tamias striatus*)	A / M + F	Exploration of a novel environment	Survival	Food availability	Extreme personality values have highest survival in all environments (Disruptive selection)	N/A	Bergeron et al, 2013
Eastern Chipmunk (Tamias striatus)	A + J / F	Exploration of a novel environment	Reproductive Success	Food availability which influences age at first reproduction	Breeding at 7 months, faster exploring females had higher reproductive success. Later breeding, slower explorers had higher reproductive success than fast explorers	N / A	Montiglio et al, 2014

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Eastern Chipmunk (Tamias striatus)	A + J/ M	Exploration of a novel environment	Reproductive Success	Food availability which influences age at first reproduction	No effect of male exploration behaviour on reproductive success early in life. Later in life, slow explorers have higher reproductive success.	N / A	Montiglio et al, 2014
European Red Squirrel (*Tamiasciurus hudsonicus*)	A / F	Aggressiveness	Reproductive Success	Food availability	Low food availability, aggressive females have higher reproductive success. High food availability, docile females have higher reproductive success	N/A	Taylor et al, 2014
Great tit (*Parus major*)	A + J / F	Exploration of a novel environment	Survival	Food availability	Poor years, fast exploring females more likely to survive. Good years, slow exploring females more likely to survive	N/A	Dingemanse et al, 2004
Great tit (*Parus major*)	A + J / F	Exploration of a novel environment	Reproductive Success	Food availability	Intermediate exploration scores have higher recruitment in poor years (Balancing selection). Extreme exploration scores have higher recruitment in rich years (Disruptive selection)	N/A	Dingemanse et al, 2004
Great tit (*Parus major*)	A + J / M	Exploration of a novel environment	Survival	Food availability	Fast exploring males more likely to survive in food rich years. Slow exploring males survive in food poor years.	N/A	Dingemanse et al, 2004

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Great tit (*Parus major*)	A + J / M	Exploration of a novel environment	Reproductive Success	Food availability	No personality specific effects of male exploration scores on recruitment in food poor or food rich years	N/A	Dingemanse et al, 2004
Great tit (Parus major)	A + J / F	Exploration of a novel environment	Reproductive Success	Brood size manipulations	Faster exploring females recruited more offspring from enlarged broods than slow explorers. No effect of personality on fitness in control and reduced broods	N/A	Nicolaus et al, 2015
Great tit (Parus major)	A + J / M + F	Exploration of a novel environment	Survival	Population densities	Faster explorers have higher mortality in high population density regimes. Slow explorers have higher mortality under low population density regimes.	N/A	Nicolaus et al, 2016
Great tit (Parus major)	A + J / M + F	Exploration of a novel environment	Reproductive Success	Population densities	No effect of exploration behaviour on reproductive success under different density regimes	N/A	Nicolaus et al, 2016
Great tit (Parus major)	A + J / M	Exploration of a novel environment	Reproductive Success	Population densities	Faster exploring males produced less offspring than slow explorers under high densities. Under low densities there was no effect of exploration behaviour on reproductive success amongst males	N/A	Quinn et al, 2009

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Great tit (Parus major)	A + J / M	Exploration of a novel environment	Reproductive Success	Habitat quality	Faster exploring males produced less offspring than slow explorers in high quality territories. In low quality territories there was no effect of exploration behaviour on reproductive success amongst males	N/A	Quinn et al, 2009
Great tit (Parus major)	A + J / F	Exploration of a novel environment	Reproductive Success	Population densities	No effect of personality specific effects of local population densities on female reproductive success	N/A	Quinn et al, 2009
Great tit (Parus major)	A + J / F	Exploration of a novel environment	Reproductive Success	Habitat quality	No effect of personality specific effects of habitat quality on female reproductive success	N/A	Quinn et al, 2009
Largespring Mosquitofish (*Gambusia geiseri*)	A / F	Boldness in the presence of a predator and in isolation	Survival	Predator activity levels	No effect of boldness on survival	N/A	Blake and Gabor, 2014

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Mud Crab (*Panopeus herbstii*)	Adult / M + F	Boldness in the presence of a predator	Survival	Predator activity levels	Shy individuals had higher survival in the presence of active predators. Bold individuals had higher survival in the presence of site and wait predators	Bold individuals use refuges less than shy individuals. Refuges are also used by sit and wait predators	Belgrad and Griffen, 2016
North American Red Squirrel (*Tamiasciurus hudsonicus*)	A + J / F	Composite measure of activity, exploration and aggression	Reproductive Success	Food availability	Aggressive females recruited more offspring regardless of environmental food availability	N/A	Boon et al, 2007
Roe deer (*Capreolus capreolus*)	A + J / F	Aggression towards a predator	Reproductive Success	Open and closed habitat	Aggressive females more likely to wean offspring in open meadows than closed woodland. More docile females more likely to wean offspring in closed forests than open meadows	N/A	Monestier et al, 2015

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Siberean Chipmunk (*Tamias sibiricus*)	A + J / F + M	Boldness	Reproductive Success	Food availability	Bolder individuals produce more offspring in food poor years than shy individuals. In food rich years bolder individuals produce less offspring than shy individuals	N/A	Le Coeur et al, 2015
Socially polymorphic spider (*Anelosimus studiosus*)	A / F	Aggressiveness	Survival	Temperature	At low temperatures, aggressive individuals survive. At high temperatures docile individuals survive.	Most likely mediated by differences in metabolic rate.	Goulet et al, 2016
Socially polymorphic spider (*Anelosimus studiosus*)	A / F	Aggressiveness	Reproductive Success	Temperature	At low temperatures aggressive individuals have higher reproductive success than docile individuals. At high temperatures docile individuals have higher reproductive success than aggressive individuals	Most likely mediated by differences in metabolic rate.	Goulet et al, 2016
Stream water strider (*Aquarius remigis*)	A / M	Mating activity	Reproductive Success	Presence or absence of hyper-aggressive individuals	More active males had higher reproductive success than less active males regardless of the social setting	N/A	Sih et al, 2014

Appendix 1.1 ctd.

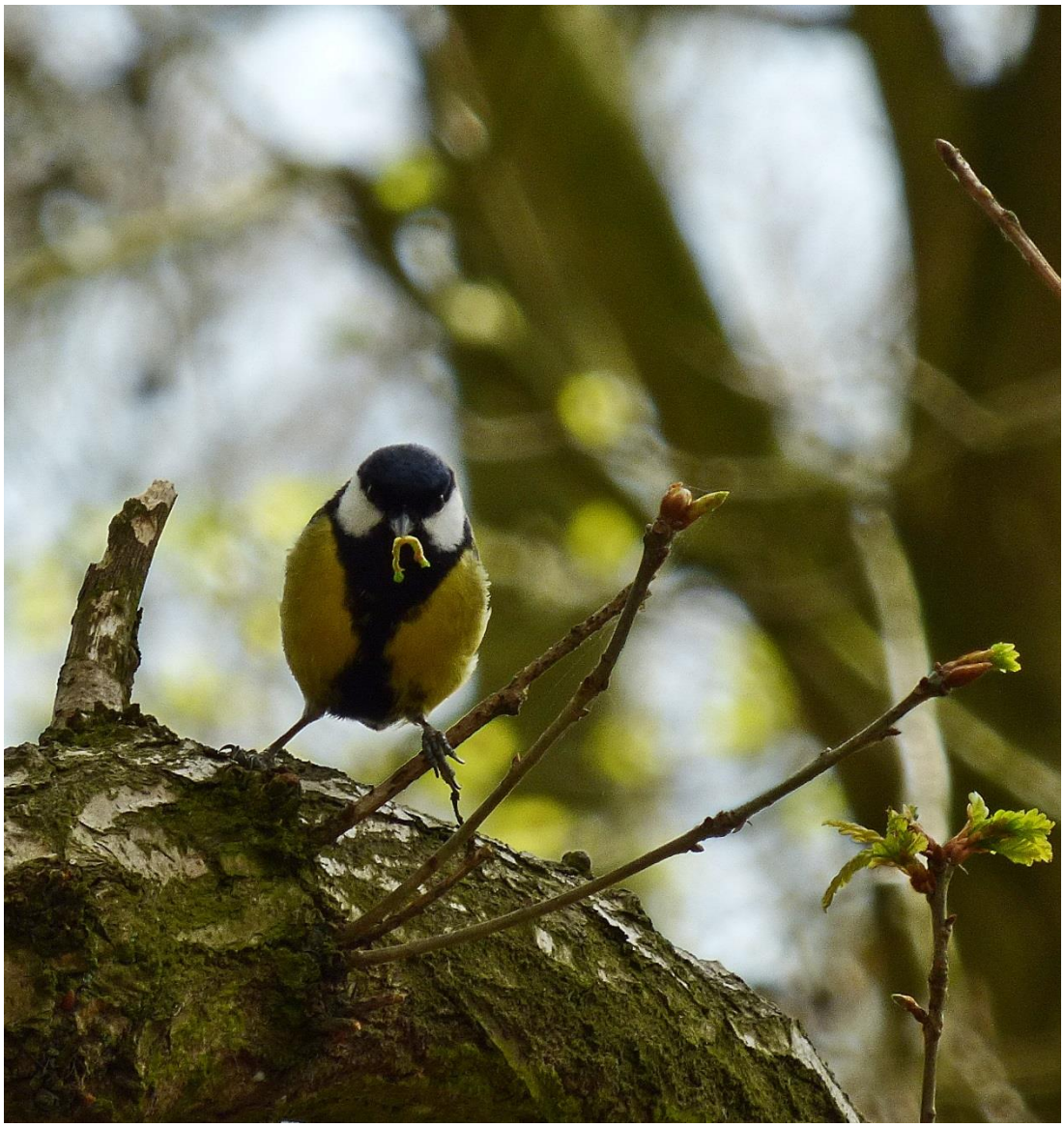
Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Three-spined stickleback (*Gasterosteus aculeatus*)	A / F	Sociability	Reproductive Success	Temperature	No evidence of temperature specific effects of personality trait on fitness	N/A	Kim and Velando, 2016
Ural Owl (*Strix uralensis*)	A + J / F	Aggressiveness	Survival	Food availability	No evidence of personality specific effects of food availability on survival	N/A	Kontiainen et al, 2009
Ural Owl (*Strix uralensis*)	A + J / F	Aggressiveness	Reproductive Success	Food availability	Agressive individuals recruit more offspring across all years.	N/A	Kontiainen et al, 2009
Water striders (*Gerris gracilicornis*)	A / F	Aggressiveness	Reproductive Success	Predator presence or absence	Regardless of predation threat, more active males had higher reproductive success than docile males	N/A	Han et al, 2016
Water striders (Gerris gracilicornis)	A / F	Activity	Reproductive Success	Male sex ratios	Regardless of sex ratio, less active females had higher reproductive success than more active females	N/A	Wey et al, 2015
Zebra Finch (*Taenioygia guttata*)	A / M + F	Boldness in the presence of a novel object	Reproductive success	Environmental sex ratios	No effects of boldness on reproductive success	N/A	Schielzeth et al, 2010

Appendix 1.1 ctd.

Species	Age/Sex	Behavioural Trait	Fitness Measure	Environmental Gradient	Description of fitness effects	Behavioural Mechanism	Source
Western Bluebird (*Sialia mexicana*)	A + J / M + F	Aggressiveness	Reproductive Success	Population densities	More aggressive individuals have lower LRS under high population densities. Aggressive individuals have higher LRS under low population densities	Aggressive individuals have less helpers, which in competitive higher density environments is essential for reproductive success. Not necessary in low density regimes	Duckworth 2008
Wild Boar (*Sus scrofa*)	A / F	Composite measure of boldness and aggressiveness	Reproductive Success	Food Availability	High food availability, aggressive females had lower reproductive success. No effect of personality on fitness in areas of lower food availability	N/A	Vetter et al, 2016
Wood frog (*Rana sylvatica*)	J / M + F	Boldness in the presence of a predator	Survival	Predator activity levels	No effect of boldness on survival	N/A	Carlson and Langkilde, 2014

Chapter 2

Phenology, provisioning, and life history variation in a generalist passerine across an anthropogenic heterogeneous landscape.



In Revision in *Oecologia* as: Phenology, provisioning behaviour, and unusual patterns of life history variation across an anthropogenic heterogeneous landscape.

Abstract

Anthropogenic factors have led to a significant degradation of natural habitats worldwide. Understanding how endemic populations survive and reproduce in modified landscapes is a major challenge for ecologists. We investigated the settlement patterns, phenology and life history of a generalist passerine bird - the great tit - in a highly-fragmented landscape, where the availability of artificial nesting-cavities was similar among deciduous and coniferous woodland fragments. We also examined the diet of nestlings and provisioning behaviours of adults during a critical period of nestling growth to determine whether habitat-specific differences in reproductive success were due to differences in nestling diet. Great tits preferentially settled in deciduous fragments, but reproductive investment and subsequent success were lower in deciduous than in coniferous habitat suggesting that birds did not follow an ideal free distribution. Clutch size tended to decline with lay date, but this depended on year and habitat type. A decline in clutch size with lay date was observed in coniferous woodland, but in deciduous woodland, clutch size was relatively stable across the season. This appeared to be adaptive in deciduous habitat where the proportion of young fledged and fledgling condition was stable throughout the season. Even though on average nests in conifer fragments were more productive, they displayed pronounced seasonal declines in the proportion of fledglings produced per egg, suggesting that breeders are not able to match reproductive investment with environmental cues linked to the phenology of food. There was no clear link between nestling diet and reproductive success. Local recruitment was negligible, suggesting that plasticity rather than divergent selection amongst populations in different habitats played a key role in driving the patterns observed. The unusual patterns we report are likely explained by the fragmented nature of the landscape, and unreliable phenological cues in a mixed-species deciduous tree community coupled with low food availability. They contrast with those reported from other populations situated in continuous woodland, demonstrating that caution is needed when generalising ecological effects across different contexts and ecosystems.

Introduction

Understanding how phenotypic variation relates to environmental heterogeneity is a fundamental aim of ecology (Schluter, 2001; Kawecki and Ebert, 2004). Populations are exposed to a variety of ecological conditions across a species' distribution (MacArthur, 1972), leading to spatially structured patterns of life history variation caused by a range of phenomena, the most significant of which is arguably local adaptation (Stearns, 1976; Kawecki and Ebert, 2004). In modern landscapes, human mediated changes are a major cause of disruption to natural environments (Saunders et al, 1991; Walther et al, 2002). These changes can significantly influence life history variation amongst populations over relatively small areas, for example by altering the environment and distorting natural cues to which populations respond (Walther et al, 2002; Kight and Swaddle, 2011). While many studies have identified correlations between phenotypic and environmental variation, the underlying behavioural and ecological mechanisms that promote such differences often remain unexplored.

Food availability is a major driver of local adaptation and the evolution of life history strategies (Stearns, 1976; Martin, 1987). Typically, resource acquisition correlates positively with reproductive investment, including fecundity (Stearns, 1976; van Noordwijk and de Jong, 1986). In temperate regions where plant phenology correlates with food availability, reproductive success in many taxa is often linked to the timing of breeding (Rutberg, 1987; Verhulst and Tinbergen, 1991). Synchrony between maximum food availability and peak energy demands of offspring maximises fitness (van Noordwijk, et al, 1995), which typically leads to seasonal declines in fecundity due to the difficulty of provisioning large broods later in the season when food is scarce (Klomp, 1970; Thomas et al, 2001; *but see* - Verhulst and Nilsson, 2008). The extent to which these relationships vary with respect to human land-use management practices, however, remains poorly understood (Brockerhoff et al, 2008).

Modern land use has significantly reduced and replaced natural woodland cover, creating isolated fragments of low structural and community complexity (Mason, 2007; Zanchi et al, 2007). Negative effects of forestry management practices are at least two-fold. Firstly, deforestation leads to fragmentation, amplifying negative edge-effects that reduce the productivity of resident communities (Saunders et al, 1991; Wilkin et al, 2007; Bueno-Enciso et al, 2016). Secondly, habitat in fragments is often degraded, or replaced by non-native species of low ecological value (Benítez-Malvido and Martínez-Ramos, 2003; Brockerhoff et

al, 2008). These factors can generate ecological traps, particularly if cues that determine settlement patterns of local species are present and similar to those of natural habitats (Schlaepfer et al, 2002). Disruptions to local phenology and the subsequent lack of food during critical periods of growth or reproduction will negatively influence the reproductive success of resident consumer populations (Hollander et al, 2013), while low levels of recruitment within fragments may prevent local adaptation arising through natural selection (Matthysen et al, 2001).

Ecological directives have led to increased emphasis on biodiversity in commercial forestry operations. While most plantations consist of fast growing monoculture patches of non-native conifer species, polycultures that include mixed deciduous tree species have become more common (Zanchi et al, 2007). Empirical studies indicate that fragments supplemented with deciduous species may support higher levels of biodiversity than conifer monocultures (Felton et al, 2010; Sweeney et al, 2011), largely because of greater understory development and more diverse invertebrate communities (Donald et al, 1998; O'Halloran et al, 2011). Deciduous habitat supports more diverse bird communities than conifer habitat, with higher densities of species that nest in cavities (Donald et al, 1998; Felton et al, 2010; Sweeney et al, 2011), which are particularly scarce in managed coniferous woodland (van Balen et al, 1982). Comparative analyses of generalist bird species, primarily using artificial nest boxes, indicate that conifer plantations tend to be suboptimal breeding habitat. Populations in conifer woodland tend to have lower fecundity and have lower reproductive success than those breeding in predominantly deciduous habitat (van Balen, 1973; Lundberg et al, 1981), though this varies according to study location and climate. The reasons for these patterns are poorly understood (Sanz, 1997; Sisask et al, 2010).

Some of the most comprehensive work studying local adaption in wild animal populations to date has come from long term study populations of blue tits (Parus Caeruleus) based in the Mediterranean. The local landscape is characterised by a heterogeneous mosaic of habitats, dominated either by deciduous oaks (Quercus pubescens) or evergreen oaks (Quercus ilex) (Charmantier et al, 2016). Due to local phenology, these habitats provide very different breeding environments for resident blue tit populations and exist in relatively close proximity (Charmantier et al, 2016). In the evergreen forests, the peak in caterpillar emergence, a critical food item for provisioning adults, is approximately one month later than in the deciduous habitat. Furthermore, the abundance and availability of caterpillars is lower in

coniferous than deciduous (Charmantier et al, 2016). Populations in both habitats display striking phenotypic differences in life history strategies. In the evergreen populations, clutch sizes are smaller, and lay dates are later, traits which have evolved in response to habitat specific food availability (Charmantier et al, 2016).

Here we examine the spatial structure of life history variation amongst resident populations in discrete woodland patches of two distinct habitat types. Although comparative studies have discovered life history variation among resident populations in fragments of different size (Nour et al, 1998; Burke and Nol, 2000; Zanette, 2000), or between continuous habitat and fragmented habitat (Nour et al, 1998; Hinam and St. Clair, 2008; Mägi et al, 2009), few have examined how the predominant vegetation community of smaller fragments influences reproductive investment, parental care and reproductive success of resident populations in combination. This approach is becoming increasingly important as natural habitat continues to be replaced by fragmented areas of commercially valuable species (Mason, 2007).

The great tit (*Parus major*) is a small cavity nesting passerine that breeds throughout much of the Western Palearctic, and uses artificial nest-boxes when provided (Gosler, 1993). Its breeding cycle is adapted to the seasonal emergence of moth larvae (Gosler, 1993), making it an important model species for the study of ecology and phenology (Charmantier et al, 2008; Hinks et al, 2015). Comparisons of life history traits recorded across the great tit distribution indicates widespread variation with regards to the timing of breeding and fecundity, influenced by an interaction of climate and habitat that together determines local resource availability (Sanz, 1998). Females tend to initiate laying activity earlier in warmer springs (Perrins and McCleery, 1989). In areas of limited resources, females tend to lay smaller clutches of heavier eggs, traits that maximise fledgling quality (Smith et al, 1989; Both, 1998; Christians, 2002). Post-hatching provisioning effort (Mägi et al, 2009; Wilkin et al, 2009) and diet breadth (van Balen, 1973; Massa et al, 2004) also varies with habitat, and strongly influences reproductive success and adult survival (Thomas et al, 2001; Wilkin et al, 2009).

We investigated how the reproductive success and offspring quality of populations in coniferous and deciduous woodland fragments were associated with reproductive investment, phenology and population densities, and whether habitat specific patterns emerged. We also explored whether the patterns observed could be explained by the

provisioning behaviours of adults and the diet of nestlings. Based on the results of previous research carried out in areas of continuous coniferous and deciduous woodland, we expected that pairs breeding in deciduous fragments would lay larger clutches than those in conifer fragments (van Balen, 1973; Riddington and Gosler, 1995; Mägi and Mänd, 2004; Blondel et al, 2006). As studies indicate that invertebrate prey communities in the two habitat types differ phenologically and quantitatively, with caterpillars more abundant in deciduous habitat (van Balen, 1973; Blondel et al, 2006), we predicted that pairs breeding in deciduous fragments would have greater reproductive success initially, but this would decline throughout the season (Naef-Daenzer and Keller, 1999). In contrast, we expected nests in conifer sites to have lower reproductive success than deciduous sites on average but with less of a decline with lay date (Mägi et al, 2009), as studies indicate that the peak emergence of caterpillars in deciduous habitat tends to be narrower than in coniferous habitat (Burger et al, 2012). We expected that adults in coniferous fragments would provision their offspring a more diverse diet (van Balen, 1973) with higher provisioning rates than pairs breeding in deciduous woodland.

Methodology

Study Site Establishment and Habitat Analysis

Nest-box study populations were established in December 2012 in eight woodland patches located in the Bandon Valley, County Cork, Ireland (n = 3 second rotation conifer, n = 5 deciduous, separated by > 2km from one another. Sites were categorized by the taxonomy of the predominant tree species present. Nest-boxes (n = 315) were placed on trees approximately 1.5 metres above the ground, approximately 50m apart (mean distance ± SD: 56.0 ± 17.5), with the locations recorded to sub-metre accuracy using a GPS (Ashtech Mobile Mapper 10).

To determine if the designation of habitat (conifer or deciduous) at the site level, was an accurate representation of habitat at the territory level, 80 previously occupied nest-boxes were randomly selected for microhabitat surveys in 2015 (28 coniferous, 52 deciduous). The canopy (including trees ≥ 6 metres) within 50 metres of the nest-box was mapped onto 10-metre grid squares. Each square was classified as one of three categories; deciduous, conifer and open, depending on the taxonomy of the predominant tree species in that area of canopy (Fig. 2.1). Open squares were areas where canopy was predominantly absent (Fig.

2.1). The data were transferred to a Geographic Information System (GIS) (ESRI 2011; ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) where we calculated the area within 50m of the nest-box that was comprised of each of the three categories.

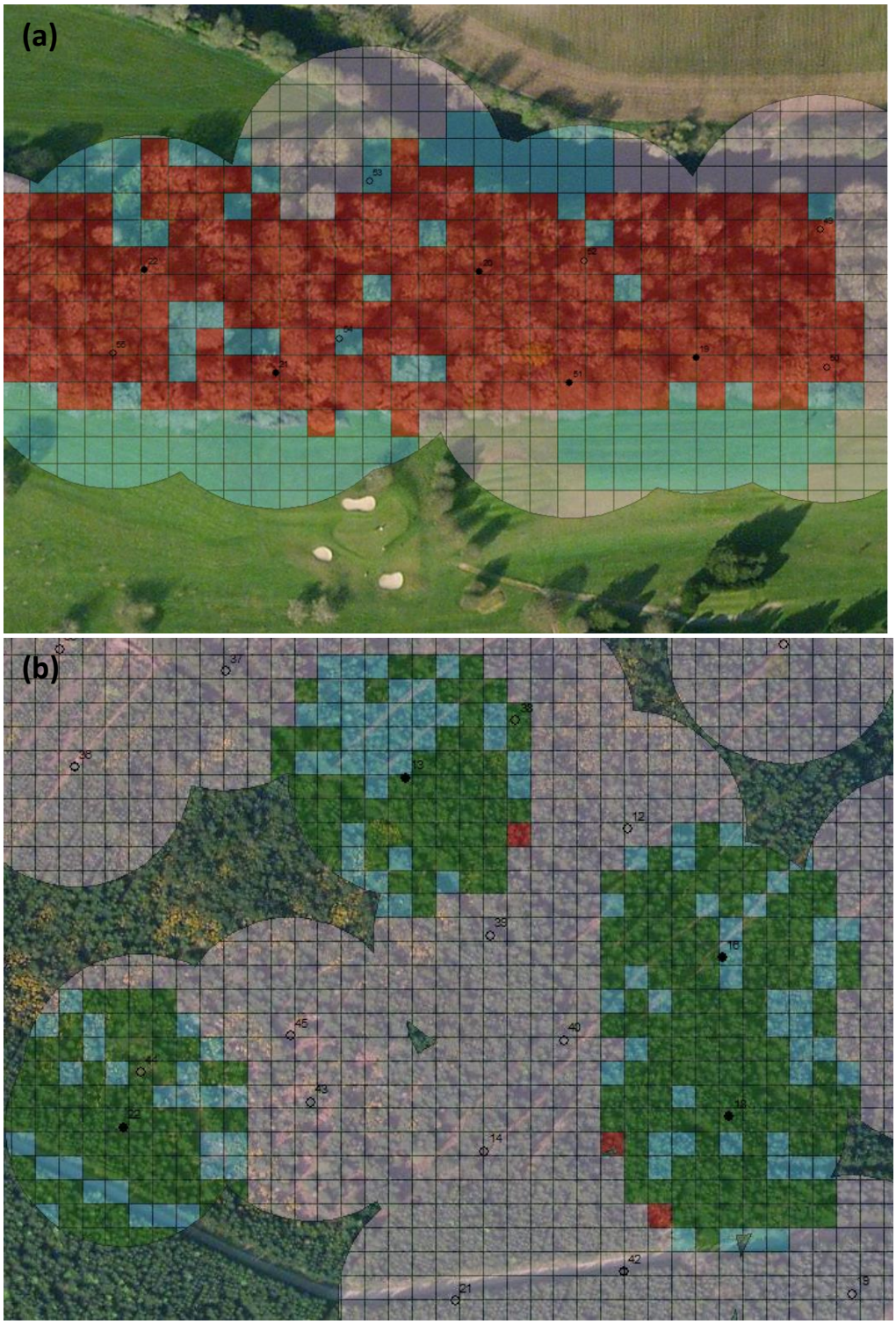


Figure 2.1. Canopy composition within 50m of occupied nest-boxes in (a) Castle Bernard, a deciduous site, (b) Garrettstown, a coniferous site. Filled dots represent occupied nest-boxes. Open dots are unoccupied nest-boxes. Numbers correspond with nest-box ID. Green squares represent predominantly conifer canopy cover within 10 x 10 metres. Red squares represent deciduous canopy. Blue squares represent open areas in the canopy. Unfilled squares were not surveyed because boxes within the area were not occupied by great tits.

Nest Recording

Nest-boxes were checked weekly from mid-April. Once pairs began to lay, nest-boxes were checked every four days to record first-egg lay-date (recorded as days since March 1). Nests were checked twelve days after the final egg was laid (based on an incubation period of thirteen days; Gosler, 1993) and every two days thereafter to record hatch date accurately. Breeding adults were trapped at least ten days after the first egg hatched. All unringed adults were fitted with a unique British Trust for Ornithology (BTO) metal band on one leg, and a passive integrated transponder (PIT) tag on the other leg. Birds were aged (older or younger than one year) and sexed based on plumage characteristics (Svensson, 1992). Wing length (mm) and body mass (g) were recorded for all adults. 15 days after the first egg hatched, all surviving nestlings were fitted with BTO rings and body mass (g) was recorded. As nestling mass at this stage of growth is asymptotic (Wilkin et al, 2009), we calculated average fledgling mass (condition) for each brood using day 15 measurements. All nest-boxes were checked post-fledgling to record unhatched eggs or ringed chicks that did not fledge. These nestlings were excluded from calculations of average fledgling mass.

Local breeding density

Tessellated polygons are geometric shapes that encompass all areas in space that are closer to the generating point than any other point (Aurenhammer, 1991). These polygons are used as models of space partitioning in wild animal populations and are used to infer likely territory sizes and local population density at the individual nest level, as densities and territory sizes are inversely related (Wilkin et al, 2006; Wilkin et al, 2007; Schlicht et al, 2014). Using a Dirichlet tessellation technique, we formed Theissen polygons around nest-boxes that were occupied by great tits during each breeding season. Low breeding densities led to excessively large polygons being generated in some cases, so we placed an upper limit of 1.76ha on all polygons. This is the maximum territory size that has been reported in the literature for great tits, and assumes that pairs predominantly use space within a 75m radius of the nest-box (Wilkin et al, 2007). 1.76ha exceeded in size 57% of territories generated for nests recorded in this study.

Nest Camera Analysis

During the 2014 and 2015 breeding seasons we used infrared nest cameras (Handykam, UK) to monitor the provisioning behaviours of breeding adults in our study sites (n = 20 conifer nests; n = 53 deciduous nests). Filming occurred between days 8 and 10 post-hatching when nestlings reach their maximum growth rate, corresponding with peak energy demands (van Noordwijk et al, 1995). To minimize disturbance, we installed dummy cameras two days prior to filming. On the morning of filming, the dummy cameras were replaced with nest cameras facing the entrance hole, to observe adults as they approached the nest-box and identify prey items (Fig. 2.2a). Filming occurred between 06:00hrs and 09:30hrs, which coincides with the peak of provisioning rates for great tit adults (Pagani-Núñez and Senar, 2013).

Due to differences in latency to resume normal foraging behaviours, the first provisioning event after 06:30hrs was used as a start point, and analysis continued until the recording ended, or until 09:30hrs. The average recording time was 2.67hrs (± SE: ± 0.36). We calculated provisioning rates as the number of times an adult entered the nest-box with a prey item divided by the total duration of the film. Prey items were classified as Lepidopteran larvae (Fig. 2.2a), adult Lepidoptera, flying insects (Adult Diptera, and Hymenoptera) or Araneae (Fig. 2.2b). Occasionally, adults would provision Coleoptera, pupae or plant matter which we grouped in one category called “other”. For 2% of visits (86 out of 4180) we were unable to identify the prey item (“unknown”). For each category, we calculated the proportion of the diet comprised of that particular prey item by dividing the number of that particular prey item by the total number of prey items provisioned. We further classified caterpillars according to their size, relative to the adults’ bill length using three categories. Large caterpillars were those of size greater than two bill lengths (Fig. 2.2b). Medium caterpillars were those of size between one and two bill lengths. Small caterpillars were those of size equal to or less than one adult bill length. Because studies have shown that caterpillar size may indicate diet quality (Naef-Daenzer and Keller, 1999), we calculated the proportion of the diet that consisted of larger caterpillars. We used the Shannon-Wiener diversity index to calculate a measure of prey diversity for each nest (Przybylo, 1995).

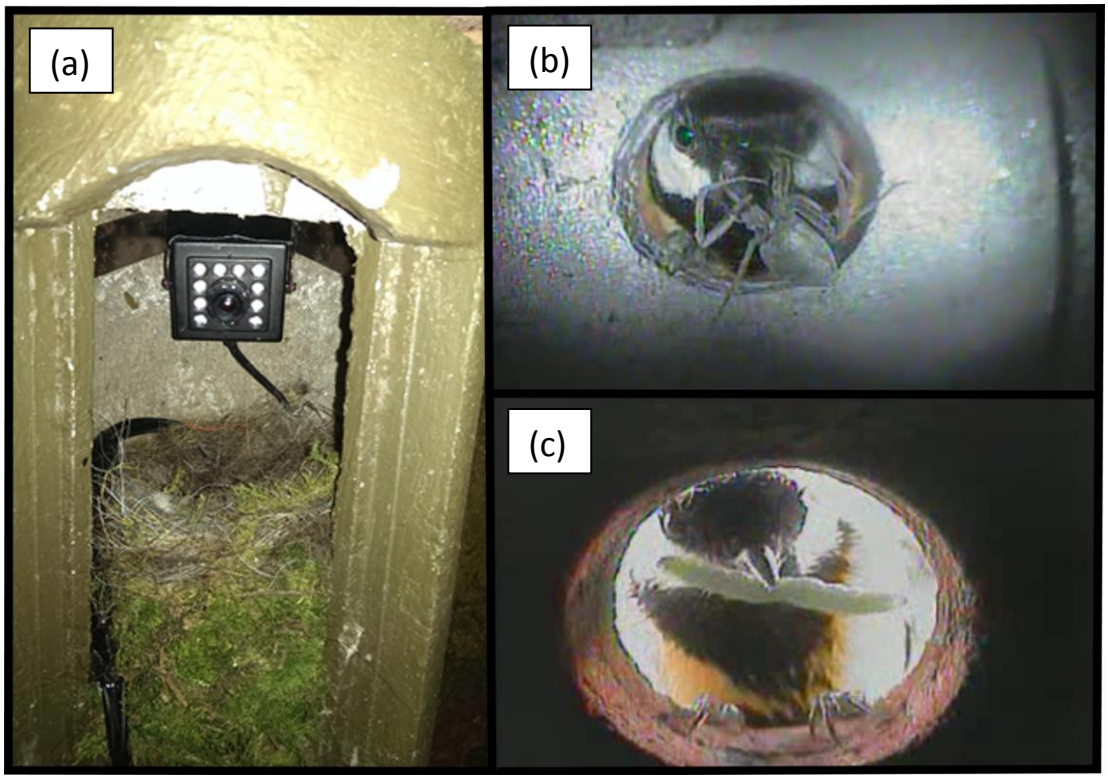


Figure 2.2. (a) Nest-box camera installed at the back of a nest-box with the face plate removed. Cameras were adjusted to focus on the entrance hole of the nest-box to observe adults as they entered. (b) An adult provisions a spider. (c) an adult provisions a large caterpillar.

Statistical Analysis

We recorded 241 breeding attempts over 3 years (n = 187 deciduous nests; n = 54 conifer nests). We disregarded any nests in which clutches were initiated 20 days after the yearly mean-centred lay date as in our experience these were likely to be replacement clutches for failed, or deserted nests early in the season (W. O'Shea, pers obs), leaving a sample of 221 breeding attempts where a clutch was laid.

All analyses were carried out using R (v.3.22, R Core Team 2015). Residual distributions were visually assessed to establish if they met the assumption of normality and suitably transformed where necessary. Likelihood ratio tests (LRT) were used to determine the significance of fixed effects in Linear Mixed Effects Models. The results reported are from global models; however applying a backwards stepwise elimination procedure for model selection, using an information-theoretic approach to model selection (Burnham & Anderson, 2002), based on comparisons of Akaike Information Criterion (AIC) values produced qualitatively similar results.

To determine if habitat type at the site level was an accurate representation of habitat at territories within sites, we entered canopy data (area comprised of conifer, deciduous and open) separately into a principle components analysis. The first component explained 67% of the total variation in the data. Deciduous canopy area and coniferous area canopy loaded heavily on PC1, with more positive values indicating predominantly deciduous territories (Spearman's Rank correlation between PC1 and deciduous area: $r_s = 0.999$, $p < 0.001$), while more negative values represented predominantly coniferous territories (Spearman's Rank correlation between PC1 and coniferous area: $r_s = -0.862$; $p < 0.001$). We then fitted a linear mixed effects model (LMM; "lme4" package; Bates et al, 2015), with PC1 as the dependent variable, habitat type (coniferous or deciduous) was included as a fixed effect, while site identity was included as a random effect (n = 80). The two variables were significantly correlated (LMM: t = 16.60; $p < 0.001$), therefore we elected to use habitat type at the site level for all further analyses.

Lay date (days since March 1; n = 217) and clutch size (n = 217) were analysed with LMM's. Habitat type (conifer or deciduous), year (2013, 2014, 2015), and capped tessellated territory size were fixed factors, and site and nest box ID were random effects. Analyses of clutch size included lay date as a fixed factor, and a lay date × habitat interaction to test for habitat specific effects of season. Plots of the data indicated that in 2014 one nest with a large clutch late in the season in a conifer site had a large influence on analyses, particularly when identifying habitat specific seasonal differences in clutch size; therefore we report analyses including and excluding this point. Initially we considered whether female age influenced laying date and clutch size as these are factors that can influence reproductive investment in other populations. We found no effect of age in either case (results reported below), and elected to reanalyse these traits without female age, including nests where we were unable to identify the female. This increased our sample size by approximately 30%, reducing our chances of committing a Type 1 error. Effects of the other terms retained in both sets of models were qualitatively similar.

The number of fledglings produced per nest was analysed using a zero-inflated negative binomial GLMM (n = 204; "glmmADMB" package; Fournier et al, 2012). 11 failed nests were disregarded from the initial sample because of desertion as a result of our activities. Mean fledgling mass (g) was rank-transformed to meet normality assumptions and analysed using a LMM (GenABEL package; Aulchenko et al, 2007; n = 121). Nest productivity is defined as

the number of fledglings (numerator) produced per egg (clutch size, denominator) and was analysed with a binomial GLMM (n = 206; “lme4” package). All models were fitted with habitat type, tessellated territory size, yearly mean-centred lay date, year, an interaction term of lay date × habitat type, and site and nest box ID as random effects. Additionally, brood size was fitted as a fixed factor in models of average fledgling mass within a brood.

Diet diversity (square-transformed) and provisioning rate were analysed using LMM’s. Age of the nestlings (8, 9 or 10) had no significant effect on provisioning rate (LM: $t = -0.353$; $p = 0.725$) and was excluded from further analyses. The proportion of the diet comprising of caterpillars and large caterpillars was analysed using binomial GLMM’s. All provisioning and diet models included habitat type, yearly mean-centred lay date, brood size on the day of filming, year, an interaction between lay date × habitat type, and nest box identity and site as random effects (n = 73). We examined determinants of provisioning rate by fitting an LMM of number of visits per hour as the dependent variable, against brood size on the day of filming, diet diversity, proportion of caterpillars, and proportion of large caterpillars as dependent variables and site and nest box identity as random factors (n = 73).

We analysed the effects of diet on fledgling mass by fitting a LMM with the average mass of fledglings as the dependent variable, brood size, diet diversity, and proportion of large caterpillars as fixed effects and site and nest box identity as random effects (n = 56). We also included a two way interaction of provisioning rate × proportion of caterpillars provisioned to test if this positively influenced fledgling mass.

We compared the average tessellated territory size in conifer and deciduous sites using a LMM. Territory size was included as the dependent variable. Habitat type was included as a fixed effect while site and nest-box identity were included as a random effect to control for repeated measures of nest-boxes. For each nest-box, we also compared the average distance to the nearest nest-box between conifer and deciduous sites using a LMM with distance to the nearest nest-box as the dependent variable, habitat type as a fixed factor, and site as a random effect. Then we fitted another LMM with distance to the nearest neighbour for each breeding attempt as the dependent variable, habitat type, and distance to the nearest nest-box as fixed effects and site as a random effect.

Results

Clutch size and lay date

Females laid earlier in conifer (mean ± se: 59.49 ± 1.06) than in deciduous woodland (mean ± se: 63.89 ± 0.56; LMM: t = 2.033; p = 0.034; Appendix 2.1; Fig. 2.3). Lay date significantly varied between years (Appendix 2.1; Fig. 2.3). Tukey post-hoc tests indicated that the differences were only statistically significant between 2013-2014 (z = -3.4733; p = 0.002) and 2013-2015 (z = -4.563; p < 0.001), but not 2014-2015 (z = -1.250; p = 0.421). Lay date was similar in juvenile and adult females (LMM: t = -1.721; p = 0.101; n = 152).

Against expectations clutches were larger in conifer woodland (mean ± se: 5.9 ± 0.17; n = 49; Table 2.1a) than in deciduous woodland (mean ± se: 4.93 ± 0.09; n = 168; Table 2.1a). Clutch size decreased with lay date (Table 2.1a) but the relationship varied between habitat types (Lay Date × Habitat Type: Table 2.1a; Fig. 2.4a). Clutch size remained relatively stable with respect to lay date in deciduous woodland but declined strongly with lay date in coniferous (Fig. 2.4a). Juvenile and adult females laid similar sized clutches (LMM: t = 1.547; p = 0.116; n = 152). Analysis of clutch size including the outlier point produced qualitatively similar results with both a negative correlation with lay date (LMM: t = -1.871; p = 0.059), and the two-way interaction between habitat type × lay date (LMM: t = 1.739; p = 0.079) close to statistical significance at the p = 0.05 level.

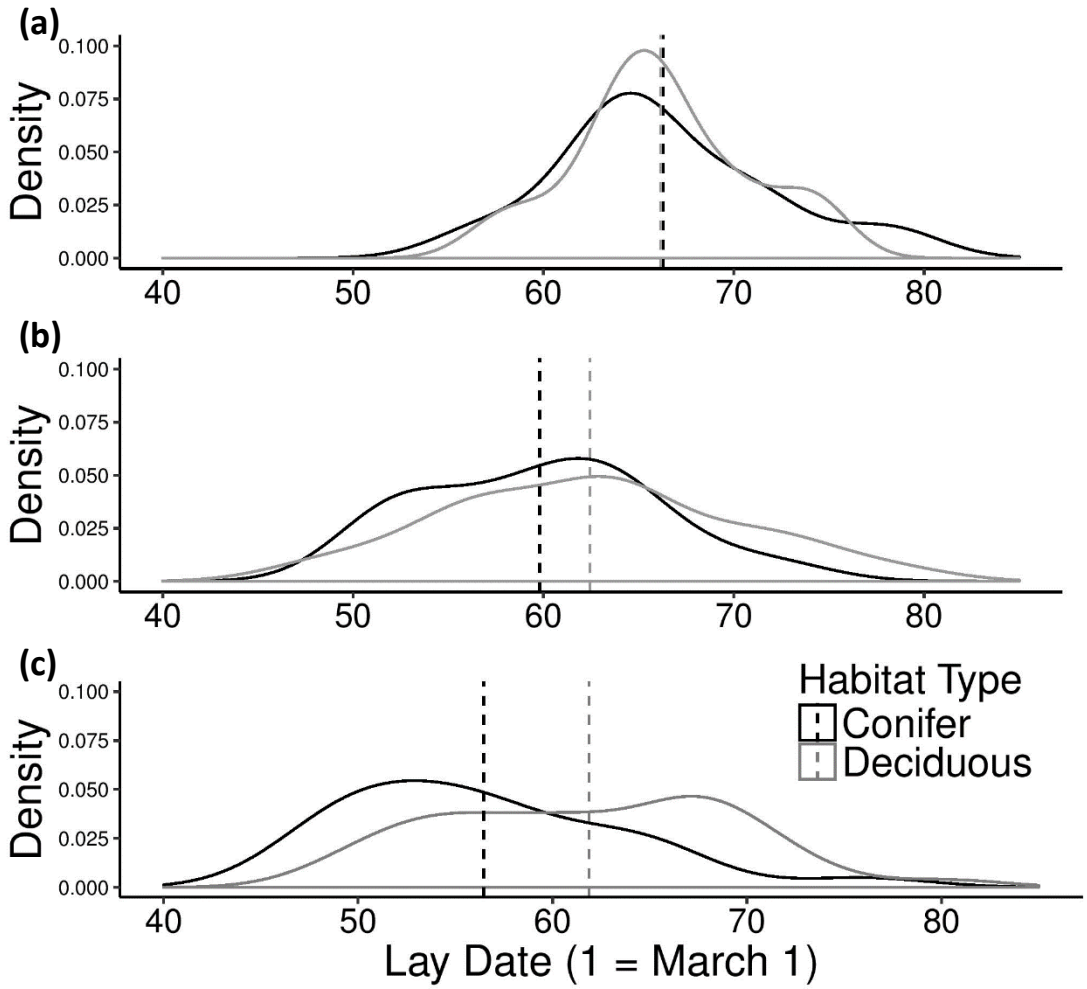


Figure 2.3. Kernel density plot of the yearly distributions of laying activity in conifer and deciduous sites (a = 2013; n = 43, b = 2014; n = 77, c = 2015; n = 102). The dashed lines represent the average lay date for the respective habitat type in a specific year. Grey is deciduous habitat, black is coniferous.

Breeding outcomes

42% of nests failed before producing fledglings. Complete nest failures were more frequent in deciduous (47% of nests failed) than in coniferous fragments (26% of nests failed; GLMM: $z = -2.315$; $p = 0.021$; $n = 217$). Nests in conifer woodland produced more fledglings (mean ± se = 4.05 ± 0.36; n = 43 coniferous nests) than those in deciduous woodland (mean ± se = 1.89 ± 0.16; n = 161 deciduous nests; zero inflated GLMM, Table 2.1b). Fledgling number declined with lay date, and there was a tendency for this decline to be more pronounced in conifer habitat (Lay Date × Habitat Type; Table 2.1b; Fig 2.4b).

The proportion of eggs that fledged was higher in conifer (0.68; n = 43), than in deciduous woodlands (0.39; n = 161; Table 2.1c). The proportion of the clutch fledged also declined with lay date (Table 2.1c). The proportion fledged declined with lay date in conifer woodlands but remained relatively constant in deciduous woodlands (habitat type × lay date interaction; Table 1c; Fig. 2.4c).

Fledglings from conifer nests were heavier (mean ± se = 17.48 ± 0.3 (g); n = 35) than those from deciduous sites (mean ± se = 16.91 ± 0.16 (g); n = 86; Table 2.1d). Fledgling mass declined with lay date in conifer woodland but not in deciduous woodland (Habitat type × lay date interaction: Table 2.1d; Fig. 2.4d). Just seven fledglings were recaptured as breeding adults in subsequent years (2.3% of fledglings recruited), a sample too small to do any further meaningful analysis.

Table 2.1. Results from linear models explaining variation in a) clutch size, b) the number of fledglings, c) the proportion of the clutch fledged, d) average fledgling mass (rank-transformed) in conifer and deciduous fragments. Models a) and d) are LMM's. Model b) is a zero-inflated negative binomial GLMM. Model c) is a binomial GLMM. Site and nest-box identity were included as a random term in all modes. P-values of LMMs assessed using LRT's. Parameter estimates and p-values of single factors reported from models excluding the interaction term.

Dependent/Independent Parameters	**Estimate ± SE**	**test statistic**	**p-value**
a) Clutch Size (n = 216) *			
Lay Date [x]	-0.024 ± 0.011	-2.152	0.030
Habitat Type [y]	-0.944 ± 0.214	-4.416	<0.001
Year(2014) [z]	-0.216 ± 0.210	-1.027	0.579
Year(2015) [z]	-0.131 ± 0.205	-0.640	n/a
Territory Size	-0.360 ± 0.220	-1.638	0.105
Lay Date [x] × Habitat Type	0.067 ± 0.028	2.402	0.015
b) Number of Fledglings (n = 204)			
Lay Date [x]	-0.018 ± 0.288	-2.190	0.029
Habitat Type [y]	-0.356 ± 0.008	-3.160	0.002
Year(2014) [z]	-0.537 ± 0.113	-3.840	<0.001
Year(2015) [z]	-0.245 ± 0.140	-2.090	0.037
Territory Size	-0.075 ± 0.145	-0.520	0.604
Lay Date [x] × Habitat Type	0.028 ± 0.017	1.690	0.092
c) Prop. Clutch Fledged (n = 204)			
Lay Date [x]	-0.076 ± 0.019	-3.881	<0.001
Habitat Type [y]	-2.182 ± 0.606	-3.584	<0.001
Year(2014) [z]	-3.058 ± 0.383	-7.977	<0.001
Year(2015) [z]	-2.037 ± 0.361	-5.648	<0.001
Territory Size	-0.738 ± 0.459	-1.608	0.108
Lay Date [x] × Habitat Type	0.148 ± 0.055	2.705	0.006
d) Average Fledgling Mass (n = 121)			
Lay Date [x]	-0.038 ± 0.605	-3.034	0.003
Brood Size	-0.119 ± 0.013	-1.892	0.058
Habitat Type [y]	-0.313 ± 0.063	-1.374	0.144
Year(2014) [z]	-0.831 ± 0.228	-4.098	<0.001
Year(2015) [z]	-0.506 ± 0.203	-2.763	n/a
Territory Size	0.342± 0.183	1.539	0.114
Lay Date [x] × Habitat Type	0.097 ± 0.027	3.639	<0.001

[x] Yearly mean-centred; [y] Conifer set to 0; [z] 2013 set to 0. [*] Results reported from analysis without outlier.

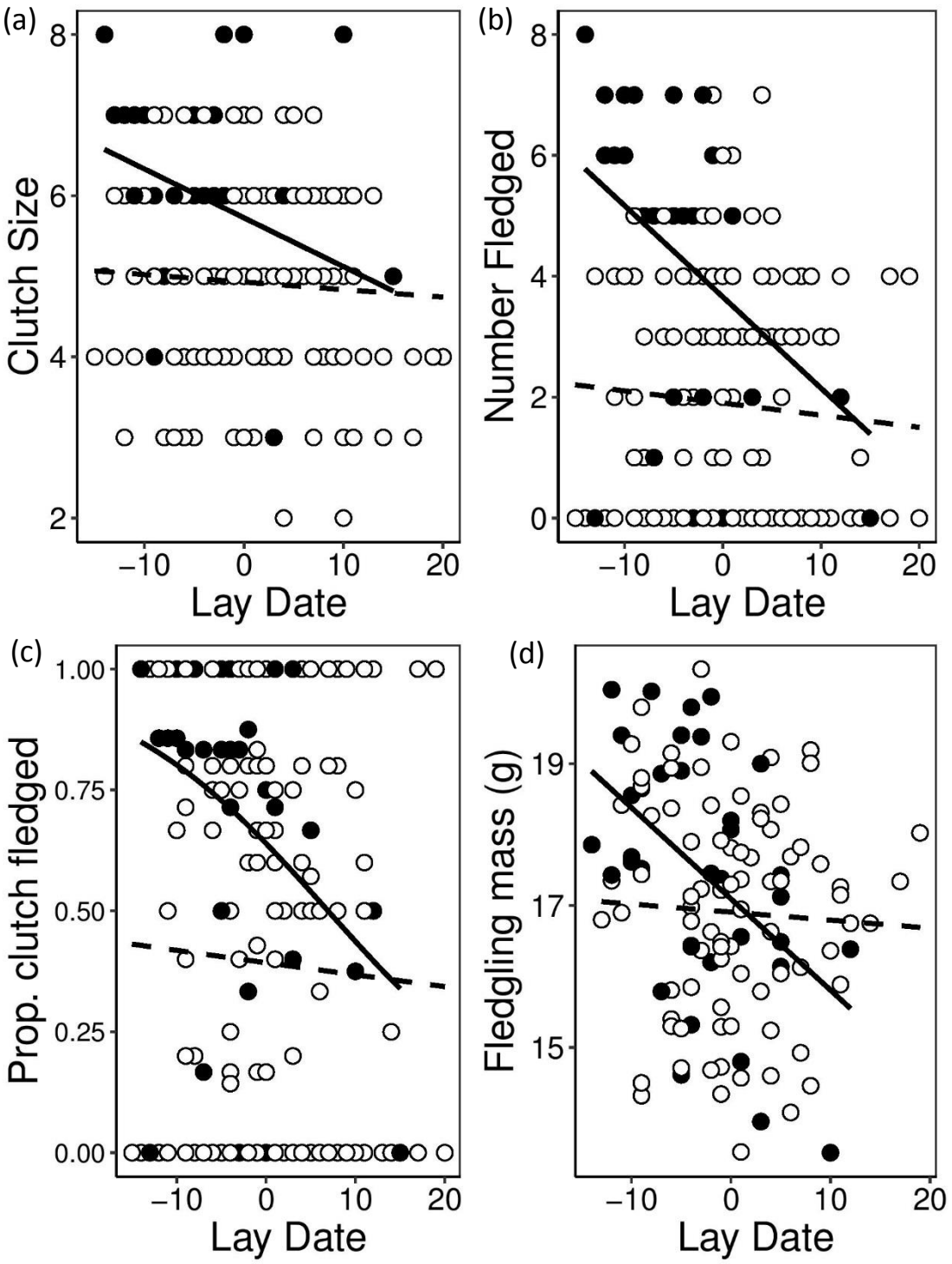


Figure 2.4. Plot of yearly mean-centred lay date and a) clutch size (n = 216), b) number of chicks fledged (n = 204), c) proportion of clutch fledged (n = 204), d) fledgling mass (n = 121) in conifer and deciduous fragments. Solid dots and lines represent nests in conifer fragments. Open dots and dashed lines represent nests in deciduous woodland fragments; solid dots and lines represent nests in conifer woodland fragments.

Provisioning rate, diet and fledgling mass

There was no significant difference in provisioning rates between birds breeding in conifer (mean ± se = 23.36 ± 1.68 visits per hour; n = 20) and deciduous woodland (mean ± se = 17.99 ± 1.01 visits per hour; n = 53; LMM: t = -1.106; p = 0.254; Appendix 2.2), controlling for brood size (LMM: t = 2.031; p = 0.038; n = 73; Appendix 2.2). Without controlling for brood size, nests in coniferous fragments were provisioned more often than those in deciduous fragments (LMM: t = -2.185; p = 0.027; n = 73). The proportion of large caterpillars in the diet correlated negatively with provisioning rate (LMM: t = -2.636; p = 0.009; n = 73), suggesting that parents needed to provision more often when food quality is lower. None of the other dependent variables related to prey proportions significantly correlated with provisioning rate (diet diversity, proportion of caterpillars; minimum *p*-value = 0.366). Diet diversity (LMM: t = 1.582; p = 0.104; n = 73), and the proportion of caterpillars in the diet of nestlings (Conifer = 55%; Deciduous = 54%; GLMM; z = -0.963; p = 0.336; n = 73), did not differ between conifer and deciduous habitat. The proportion of large caterpillars in the diet of nestlings increased with lay date in deciduous woodland, but decreased with lay date in coniferous patches (Lay date × habitat interaction; GLMM; z = 2.605; p = 0.009; n = 73; Table 2.2; Fig. 2.5).

Controlling for brood size and a habitat type × lay date two-way interaction, provisioning rate (LMM: t = -1.174; p = 0.224; n = 51) and the proportion of large caterpillars in the nestling diet (LMM: t = -1.280; p = 0.176; n = 51) did not significantly correlate with average fledgling mass (Appendix 2.3).

Table 2.2. Results of binomial GLMM with the proportion of nestling diet comprising of large caterpillars as the dependent variable (random effects = Site, nest-box; n = 73). Parameter estimates and p-values of single factors reported from models excluding the interaction term.

Parameters	**Estimate ± SE**	**t-value**	**p-value**
Lay Date [a]	0.040 ± 0.025	1.602	0.109
Habitat Type[b]	0.283 ± 0.447	0.634	0.526
Year (2015) [c]	-0.631 ± 0.250	-2.528	0.012
Lay Date × Habitat Type	0.166 ± 0.064	2.605	0.009

[a] Yearly mean-centred; [b] Conifer set to 0; [c] 2014 set to 0.

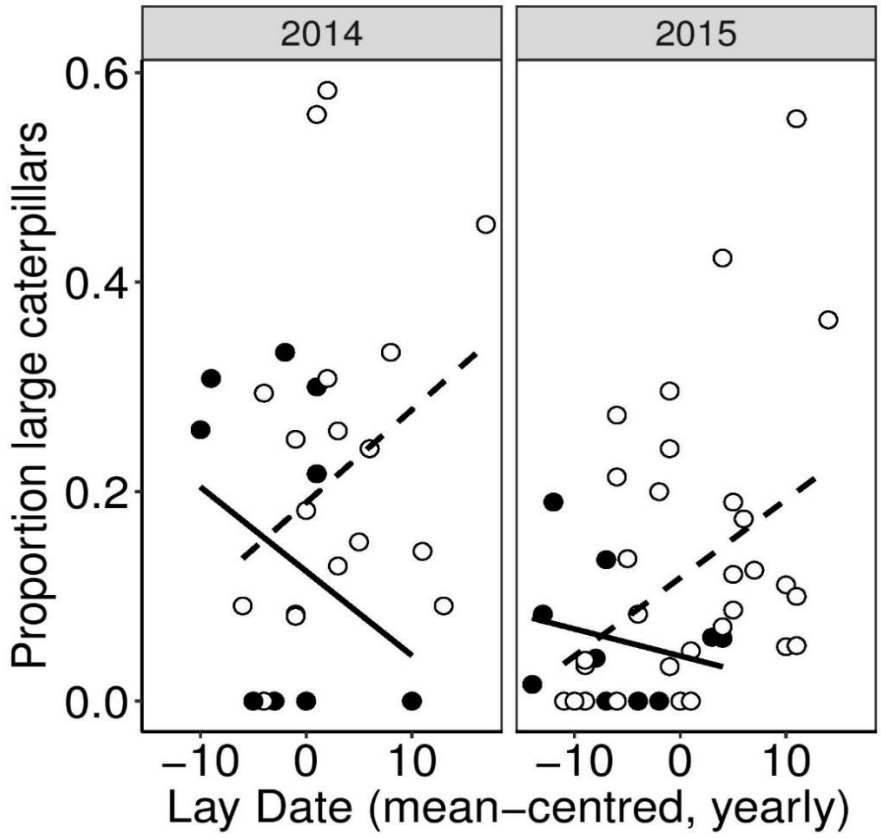


Figure 2.5. Proportion of the nestling diet consisting of large caterpillars versus lay date in 2014 (n = 10 coniferous nests; n = 20 deciduous nests) and 2015 (n = 10 coniferous nests; n = 33 deciduous nests). Solid dots and lines represent nests in conifer fragments. Open dots and dashed lines represent nests in deciduous woodland fragments; solid dots and lines represent nests in conifer woodland fragments.

Tessellated territory size and nearest neighbour distance

Tessellated territories in conifer sites were significantly larger (mean ± se = 1.74 ± 0.01; n = 54) than those in deciduous sites (mean ± se = 1.41 ± 0.03; n = 187; LMM: t = -2.498; p = 0.018). The average distance to the nearest nest-box was not significantly different between all nest-boxes in conifer (58.22 ± 2.46 (m)) and deciduous sites (56.93 ± 1.71 (m); LMM: t = -0.124; p = 0.881); however the average nearest neighbour distance was smaller in occupied deciduous (97.85 ± 4.15 (m)), than coniferous fragments (161.73 ± 17.48 (m); LMM: t = -2.262; p = 0.025). Thus, breeding densities were higher in deciduous fragments.

Discussion

Great tits nested in lower densities in conifer habitat, laid earlier in the season, produced larger clutches and had higher reproductive success than those in deciduous woodland. Clutch size declined with lay date, only in conifer woodland, but birds in conifer habitat still experienced seasonal declines in the proportion of the clutch fledged, a trend that was not as apparent in deciduous woodland fragments. Provisioning behaviours, and diet diversity were broadly similar across habitat types and were not related to reproductive outcomes.

Reproductive success and habitat quality

Great tits in coniferous woodland produced larger clutches and more fledglings than those in deciduous woodland. Provisioning rates were similar across habitat types, controlling for brood size, and there was no evidence of a difference in gross diet structure. The proportion of caterpillars provisioned across both habitat types was approximately 55%. This is low compared with other populations around Europe, where caterpillars comprise 80-90% of nestling diet (van Balen, 1973; Naef-Daenzer et al, 2000; Wilkin et al, 2009, *but see* – Mägi et al, 2009), suggesting that overall this fragmented environment represents poor quality breeding habitat for great tits. Our results are also at odds with other studies that have found significant differences in diet structure between deciduous and marginal, or coniferous habitats (van Balen, 1973; Riddington and Gosler, 1995, Charmantier et al, 2016). To support larger broods, pairs in coniferous woodland simply provisioned more of the same broad types of food as those in deciduous woodland. When necessary, provisioning adults can expand their search radius without compromising prey delivery rates (Tremblay et al, 2005), and in conifer habitat, adults may preferentially forage on discrete patches of deciduous trees along forest edges or outside of fragments, as has been suggested may be the case by Gibb and Betts (1963). Because breeding densities and therefore competition were lower in conifer habitats, this may have allowed easier access to preferential foraging habitat around fragment margins, potentially also explaining why diet structure was not significantly different between conifer and deciduous habitat, despite the different tree communities at the territory level. In deciduous woodland, females laid smaller clutches, but still fledged a lower proportion of their clutch on average than in coniferous sites. The proportion of nests that failed was also significantly higher in deciduous than coniferous woodland. Various authors have reported links between density and aspects of reproductive success (Sillett et al, 2004; Wilkin et al, 2009) and we suggest the lower success in deciduous sites may also have occurred because densities were higher than in conifer sites, though we cannot

discount the possibility that food availability was simply higher in the latter, or that differences in the energetic value of prey items may have played a role here.

The higher pair densities and lower reproductive success in deciduous fragments suggests that great tits did not follow an ideal free distribution (Pulliam and Danielson, 1991). Great tit immigration and territory settlement happens predominantly during autumn-winter (Gosler, 1993), and the cues used by immigrants may vary, including local population densities (Danchin et al, 2004), habitat (Clark and Schutler, 1999) and food availability (Brown and Brown, 1996). Preference for deciduous fragments could arise if they provide superior habitat during the winter, for instance due to beech mast availability, which strongly influences individual over-winter survival (Perdeck et al, 2000). Furthermore, conifer woodlands naturally have a lower availability of nesting holes (van Balen et al, 1982), and studies indicate that when nest-box availability is increased by the same factor in coniferous and deciduous sites, breeders still prefer to settle in deciduous areas, suggesting that there may be a natural avoidance of coniferous woodland (Mänd et al, 2005). Thus, we suggest that factors such as winter food availability, and an association between conifers and poor nest-cavity availability, led to their avoidance even though coniferous woodland provided better breeding habitat, somewhat like a perceptual trap (Patten and Kelly, 2010).

Phenology, habitat type and reproductive success

The invertebrate communities of conifer and deciduous woodland to differ qualitatively and phenologically (van Balen, 1973; Blondel et al, 2006; O'Halloran et al, 2011), and most studies report the emergence of moth larvae later in coniferous than deciduous habitat (van Balen, 1973; Blondel et al, 2006). Despite this, we found that pairs breeding in coniferous habitat laid earlier than those in deciduous habitat (Fig. 2.3), suggesting that the cues used by breeders to begin laying differ between habitat types. Alternatively, lower densities of competitors in coniferous habitat could allow females to reach their threshold laying-condition earlier than those in deciduous fragments, which can also influence laying date (Verhulst and Nilsson, 2008).

Seasonal declines in fecundity in response to environmental food availability are typical of species breeding in temperate environments (Klomp, 1970). Here, we report that clutch size declined with lay date, especially in coniferous habitat (Fig 2.4a); however in conifer sites, later nests also produced a low proportion of fledglings per egg (Fig. 2.4b). The proportion

of nestling diet comprised of large caterpillars, a nutritionally important food item (Naef-Daenzer and Keller, 1999), also decreased with lay date amongst conifer nests (Fig. 2.5). We found no link between any aspect of diet and fledgling quality possibly because our once off measure did not capture the key period food became limiting.

Female great tits can adjust their reproductive strategies according to fine scale local environmental variation (Charmantier et al, 2008; Hinks et al, 2015); nevertheless, even though clutch size declined with lay date in conifer fragments, this was still insufficient to maintain fledgling number per egg laid (Fig. 2.4c). One possibility is that the cues females responded to in conifer woodland were obscured, or not available, leading to mismatched clutch sizes (DeWitt et al, 1998). Other explanations for the decline could include seasonal changes in disease or parasite load (Merino and Potti, 1995; Merino et al, 2000), or differences in early life diet (Naef-Daenzer and Keller, 1999). Generally, studies indicate that conifer woodland is a lower quality but more stable breeding habitat for great tits when compared to deciduous woodland (van Balen, 1973; Mägi et al, 2009). In this system, it appears that the opposite is true, with higher initial reproductive success but a greater seasonal decline in coniferous fragments than deciduous fragments.

Nests in deciduous fragments fledged less chicks than those in coniferous fragments, especially early in the season, and showed only a modest decline in fledgling success with lay date. Furthermore, fledgling mass was relatively stable throughout the season in deciduous fragments. These results contrast with what has previously been reported for great tit life history traits in deciduous woodland, where typically the number of fledglings and fledgling mass decline with seasonal progression (Perrins and McCleery, 1989; Wilkin et al, 2006), a process that is primarily linked to declining food availability (van Balen, 1973). In our deciduous sites, diet diversity and provisioning rate did not change temporally, and against expectations, the proportion of large caterpillars in the diet of nestlings increased with lay date. The tree communities of deciduous fragments are relatively diverse in our study areas, due to local forestry management practices (Chapter 1). This may have led to substantial within-site phenological variation (Lechowicz, 1983) and less temporal variability in prey availability (Stamps and Linit, 1998), allowing birds to maintain relatively consistent reproductive success in terms of nestling quality and quantity throughout the season. Furthermore, territoriality decreases with seasonal progression (van Balen, 1972) which can alleviate negative density dependent effects on fecundity as has been shown previously (van

Balen, 1973). This may have also contributed to the temporal stability in reproductive success we observed in deciduous fragments here.

Conclusions

Given that recruitment rates of locally born birds are so low in these fragments, habitat-specific reproductive variation probably arises primarily through plastic responses to local cues (e.g. population densities or food availability). Plasticity facilitates reproductive success in populations that have been established in new or novel areas (Yeh and Price, 2004; *reviewed in* - Ghalambor et al, 2007) and in heterogeneous landscapes plasticity may be favoured over localised specialist strategies (Sultan and Spencer, 2002); however, it appears to have its limitations in this system, particularly in conifer fragments. The number of fledglings per egg declined with lay date for conifer nests (Fig. 2.4c), even though clutch size also declined with lay date (Fig. 2.4a). Despite this, unless dispersing juveniles match their natal woodland type to the one in which they settle through natal habitat preference induction (Davis and Stamps, 2001), local adaptation is unlikely to arise within these fragments. Our results show that patterns of life history variation can vary in surprising and complex ways across an anthropogenic landscape. They also emphasise how land management practices can have significant consequences for resident populations, leading to spatial variation in life history traits over relatively small areas.

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Chapter 2: Appendices

Appendix 2.1. Results of LMM with first egg lay date as the dependent variable (random effects = Site, Nest-box ID; n = 217). P-values assessed using LRT. Parameter estimates and p-values of single factors reported from models excluding the interaction term.

Parameters	Estimate ± SE	t-value	p-value
Habitat Type [a]	3.121 ± 1.535	2.033	0.034
Year(2014) [b]	-4.666 ± 1.344	-3.473	<0.001
Year(2015) [b]	-5.978 ± 1.310	-4.563	n/a
Territory Size	-1.306 ± 1.353	-0.965	0.286

[a] Conifer set to 0; [b] 2013 set to 0.

Appendix 2.2. Results of a LMM with the number of provisioning visits by adults per hour (rank transformed) as the dependent variable (random effects = site, nest-box; n = 73). P-values assessed using LRT. Parameter estimates and p-values of single factors reported from models excluding the interaction term.

Parameters	**Estimate ± SE**	**t-value**	**p-value**
Lay Date [a]	-0.018 ± 0.017	-1.037	0.284
Brood Size	0.196 ± 0.096	2.031	0.038
Habitat Type [b]	-0.327 ± 0.296	-1.106	0.254
Year (2015) [c]	0.200 ± 0.226	0.883	0.369
Lay Date × Habitat Type	-0.043 ± 0.042	-1.048	0.281

[a] Yearly mean-centred [b] Conifer set to 0; [c] 2014 set to 0.

Appendix 2.3. Relationship between diet composition and provisioning rate on average fledgling mass (LMM; Random Effects = Site, Nest-Box; n = 51). P-values assessed with LRT.

Parameters	**Estimate ± SE**	**t-value**	**p-value**
Brood Size	-0.232 ± 0.095	-2.451	0.014
Prop. Large Caterpillars	-1.221 ± 0.954	-1.280	0.176
Provisioning Rate	-0.021 ± 0.018	-1.174	0.224
Habitat Type	-0.405 ± 0.349	-1.159	n/a
Lay Date	-0.107 ± 0.039	-2.736	n/a
Habitat Type × Lay Date	0.125 ± 0.048	2.629	0.006

[a] Yearly mean-centred; [b] Conifer set to 0

Chapter 3

Do personality and innovativeness influence competitive ability? An experimental test in the great tit.



Published in *Behavioral Ecology as*: Do personality and innovativeness influence competitive ability? An experimental test in the great tit.

Abstract

Competitive ability is a major determinant of fitness, yet why individuals vary in their ability to compete for resources is often unclear. Rather than simply reflecting inherent differences in the ability of individuals to reach an assumed optimum behaviour quality, empirical evidence suggests that competitive ability may also reflect alternative strategies that arise because of correlations with other behaviours, such as innovativeness and personality. We examined experimentally how two behavioural traits - exploration of a novel environment (an index of the reactive-proactive personality axis) and performance in a novel lever pulling task (a measure of innovativeness) - were related to the outcomes of dyadic contests involving wild-caught great tits. Dyads were then allowed to compete freely at a feeder before being exposed to a novel string-pulling task. Although we found no significant relationship between exploration behaviour or innovativeness in isolation and competitiveness, individuals that were less competitive were more likely to spontaneously perform the string-pulling behaviour during the dyadic trials, the first direct experimental demonstration of competitive exclusion leading to innovation. Our results support the hypothesis that innovations provide a means for less competitive individuals to access resources in line with the "necessity drives innovation hypothesis", and we discuss the functional significance of innovative behaviours in wild populations.

Introduction

Competitiveness is the ability of an organism to gain access to resources in the presence of others and is a fundamental aspect of ecology (Begon et al, 2006). Individual variation in the ability to compete can lead to unequal resource acquisition during scramble competition (Kruijt and Hogan, 1967; Lekve et al, 2002). Competition can occur directly or indirectly, with the outcomes of direct competitive interactions typically determined by an asymmetry of intrinsic characteristics between competitors, including physical, cognitive and behavioural traits (Taylor and Elwood, 2003; Arnott and Elwood, 2009). Age, sex and associated morphological traits (e.g. body size, weight, and colour) can be key indicators of an individual's ability to compete and play a crucial role in reducing antagonistic interactions between unfamiliar competitors, and determining individual ranking within social hierarchies (Huntingford and Turner, 1987; Møller, 1987; Piper and Wiley, 1989; Hardy and Briffa, 2013). Despite the clear advantages to being a better competitor, the associated physiological costs, including increased energy expenditure (Praw and Grant, 1999), higher exposure to oxidative stress and stress hormones (Creel, 2001; Beailieu et al, 2014), and decreased long term survival (Johnson et al, 2013) may limit individual competitiveness. Constraints caused by links to other behavioural traits also raises the possibility that competitive ability reflects alternative life history strategies amongst individuals, covarying with behavioural syndromes (Wolf et al, 2007). Behavioural syndromes are suites of correlated behavioural or "personality" traits that display consistent variation amongst individuals (Sih et al, 2004). They include correlations of a single behaviour within a behavioural context, or across different contexts, or correlations among different behaviours (Sih and Bell, 2008).

As with other correlated traits in evolutionary ecology, behavioural syndromes can ultimately lead to fitness trade-offs by constraining behavioural plasticity in variable conditions and across contexts (Sih et al, 2012). One of the most commonly studied syndromes, the reactive-proactive axis, involves the relationship between boldness, aggression, activity, and a whole range of other behavioural traits (Koolhaas et al, 1999). Typically, boldness in novel situations positively correlates with aggressiveness and activity levels (Veerbeek, 1996), and while bolder, more risk prone, proactive individuals prioritise immediate resource gain over long term survival, the converse is true for shy individuals, who are more responsive to environmental stimuli (*reviewed in* - Réale et al, 2010).

Limited behavioural plasticity plays an important role in regulating social interactions between individuals (*reviewed in* - Briffa et al, 2015). Aggressiveness, one aspect of the reactive-proactive axis, positively correlates with social dominance in both captive and wild great tits (*Parus major*), determining resource acquisition in group foraging situations (Blanchard et al, 1988; Verbeek et al, 1996; Cole and Quinn, 2011). Proactive individuals are also more routine forming and less likely to change their behaviour in response to environmental stimuli than reactive individuals (Verbeek et al, 1994; Kurvers et al, 2010; Nichlaus et al, 2014). Evidence from wild populations supports the idea that certain personality types may be adaptive in different environments such as along ambient temperature gradients, or under different predation pressure regimes (Réale and Festa-Bianchet, 2003; Goulet et al, 2016). Density dependent selection on personality traits has been observed in several populations which may be mediated by the outcomes of competitive interactions (Dingemanse et al, 2004; Quinn et al, 2009; Nichlaus et al, 2016).

Social dominance and competitive ability have also been linked to cognition (Reader and Laland, 2003). Cognition describes how individuals perceive and process environmental stimuli and use the information to modify their behaviours (Shettleworth, 2010). Traditionally, behavioural ecologists have focused on the ecological relevance of cognitive traits across populations (Thornton and Lukas, 2012). More recently focus has shifted towards cognitive and life history variation within populations (*reviewed in* – Dukas, 2004; Thornton and Lukas, 2012; Morand-Ferron et al, 2015). Across taxa, studies have revealed genetic and phenotypic correlations between cognitive abilities and several key determinants of life history, including competitiveness (Mery and Kawecki, 2003; Cole and Quinn, 2011; Hollis and Kawecki, 2014), longevity (Burger et al, 2008) and fecundity (Cauchard et al, 2013; Cole and Quinn, 2012). Innovation – that is, the invention of a novel behaviour, or the performance of an existing behavioural process in a novel context – is one such trait, likely a composite of cognitive and personality components (Griffin and Guez, 2014a; Sol, 2015; Morand Ferron et al, 2015; Quinn et al, 2016). Individual variation in innovation is likely to be caused in part by physiological mechanisms such as stress response, which can influence motivation, metabolic rate and how individuals respond to environmental stimuli (*reviewed in* – Cockrem, 2007; Carere et al, 2010; Morand-Ferron et al, 2015). In general, the "necessity drives innovation" hypothesis argues that in circumstances where an individual's repertoire of behaviours fails to grant access to resources, innovations should be more common (Reader and Laland, 2003). Resource

exclusion can be caused by environmental gradients, for example climate or habitat, but the social environment may also contribute, by limiting access to resources for less competitive individuals. The importance of competition as an agent that promotes alternative behavioural strategies in the wild has been noted in the field of evolutionary ecology for a number of years (West-Eberhard, 1983; Gross, 1996). Innovators may circumvent direct competition with more dominant conspecifics through novel foraging strategies, allowing them to access alternative resources (Reader and Laland, 2003; Griffin and Guez, 2014a). Several studies have identified negative correlations between competitive ability and innovative propensity (Cole and Quinn, 2011; Thornton and Samson, 2012; Aplin et al, 2013); however no study has yet identified the functional mechanisms underlying this relationship.

In this study we explored the hypothesis that individual competitive ability was simultaneously linked to a component of the reactive-proactive personality axis - exploratory behaviour in a novel environment - and innovativeness in wild great tits temporarily brought into captivity. We first assayed exploration behaviour and innovativeness of captive birds in isolation. Our aim was to examine how these traits predicted aggressiveness, dominance and realized resource holding potential between great tit dyads competing at an artificial feeder under two experimental treatments. The first trial allowed the birds to access the feeder without restriction, whereas in the second trial, we restricted feeder access to a single delivery point to promote competitive interactions between the pairs. While controlling for age and sex effects that can influence dominance hierarchies amongst great tit flocks, we predicted that exploration scores would positively correlate with competitive ability and aggressiveness, and that innovators would be less competitive at the feeder, in line with previous observational studies (Cole and Quinn, 2011). In a third trial, the dyads were simultaneously exposed to an easily extracted, but less preferred food item from a feeder with a single delivery point (promoting competitive interactions) and a device containing a highly preferred valuable food resource, that required innovative problem-solving to access. We predicted that individuals that had been less competitive at the feeder during trial two would be more likely to perform this innovation than their more competitive counterparts, and that birds that had been innovative during assays in isolation would also be more likely to innovate during the experiment.

Methodology

Capture and housing

Great tits (*Parus major*) were trapped at 8 woodland sites in the Bandon Valley, Co. Cork, Ireland. Trapping occurred at supplemental feeding sites using mist nets, from January to March 2015 (n = 132) and January to March 2016 (n = 64). Birds were trapped in 2016 in order to recapture individuals and calculate between season repeatabilities. All unringed individuals were fitted with a unique British Trust for Ornithology (BTO) metal leg band on one leg, and a passive integrated transponder (PIT) tag attached to a moulded plastic ring on the other leg. Birds were aged (less than one year, or older than one year) and sexed based on plumage characteristics (Svensson, 1992). Biometrics were recorded for each individual (wing length (mm), tarsus length (mm), body mass (g)). Birds were transported to an aviary located in University College Cork within two hours of trapping. All birds arrived in the aviary before 15:30 allowing individuals time to habituate to captivity and feed before dark. A maximum of 14 great tits were trapped per catching session. All ringing activity was carried out under license from the BTO and National Parks and Wildlife Service (NPWS) Ireland, and procedures sanctioned by UCC's ethics committee and the Health Products Regulatory Authority (HPRA) of Ireland. All birds were subsequently released at the site of capture within 6 days, after further cognitive and behavioural assays.

In the aviary, subjects were housed in individual wire mesh cages (45 x 50 x 60cm) containing two wooden perches, two food bowls and a water bowl. An unset problem solving device and a dummy camera were attached to the inside of the cage to limit neophobic responses to the device when testing began. Birds were visually isolated from one another and kept under a 10h daytime/14h night-time light regime. Up to 14 birds could be housed at one time, with numbers ranging from 3 to 14 throughout the season. Subjects were fed a mixture of black sunflower seeds (15g), peanuts (15g) and mealworms (*Tenebrio molitor;* 20g), which were available in the home cage, excluding periods of enforced food deprivation prior to certain behavioural assays.

We monitored the food intake of a subsample of individual great tits in captivity during winter 2015 (n = 76). Twice per day (1030 and 1600) we removed and replaced food bowls and base trays from the cages, retrieving any food items that were dropped uneaten on the floor of the cage. The uneaten food was weighed and subtracted from the initial amount provided to estimate of food intake in the intervening period. Using caloric values

established in Gibb (1957), we calculated the caloric intake of each individual on the first day in captivity from the time of entry to captivity until 1030 the subsequent morning.

Problem Solving Assay

One hour before dark on the day of capture, we primed the problem solving devices (based on Cole et al, 2011; Fig. 3.1a). Mean time between arrival in captivity and commencement of the problem solving task was 3.19 hours (se = 0.131; range = 1-6 hrs). The task consisted of a clear Perspex cylinder attached vertically to the inside of the cage next to the front most perch. A metal platform was supported horizontally 10cm from the top of the cylinder, by a wooden lever set perpendicular to the perch (Appendix 3.1). The device was baited with 3 waxworms (*Achroia grisella),* a preferred food item for great tits (W. O'Shea, *pers obs*). In order to solve the task, individuals had to fully remove the wooden lever causing the platform and rewards to fall into a tray under the device (Fig. 3.1a). Individuals were not food deprived for this experiment; instead we placed one free waxworm underneath the device in order to attract individuals to the task. 96% of individuals ate the free waxworm provided. Two hours after light the following morning, the experiment was terminated and solving success for each individual was recorded. Birds were classified as problem solvers (S) in isolation if they successfully removed the lever from the device and accessed the rewards or as non-problem solvers (NS) if they did not fully remove the lever from the device. These trials were not filmed; however previous studies have found that solvers and non-solvers contact the devices a similar amount during trials (Cole et al, 2012; W. O'Shea, *pers obs*). Problem solving performance (PSP) was assessed in 2015 and 2016 (total sample size = 196 observations of 167 individuals; 29 repeat measures). Previous research has shown that performance in this assay is linked to individual life history variation including fecundity, reproductive success, foraging behaviour, and competitive ability in the wild (Cole and Quinn, 2011; Cole et al, 2012).

Exploration Behaviour

In the great tit, exploration of a novel environment is an assay of the reactive-proactive axis. We used an open field test method adapted from Verbeek et al, (1994) to test individual exploratory tendencies (Fig. 3.1b) in 2015 and 2016. Birds were allowed to feed for three hours following first light, after which assays were carried out sequentially on all individuals. Prior to an assay, the subjects' cage was darkened using a cover and an exit at the back of the cage was opened. The cover was kept in place until the individual flew through the

opening into the observation room, which generally occurred within seconds of opening. The observation room measured 3.5 x 3 x 2.5m and contained 5 artificial wooden trees. Trials were carried out for 2 minutes after the individual entered the observation room. Aside from the five artificial trees, subjects could land on window ledges, support beams, door frames and the entrances to the cages. During the assay, all movements were noted and classified into two categories by a hidden observer. Movements within a tree or perch were classified as hops, while movements between trees or other perches within the room were classified as flights. After the two minute period had elapsed, the observation room was darkened and the bird was returned to its original cage. All trials were scored by the same observer (WOS). The results of 8 tests were omitted (n = 6 in 2015; n = 2 in 2016) due to audible disturbances that significantly altered the behaviour of the subjects during exploration behaviour trials. The number of flights and the number of hops were entered into a Principal Component Analysis. The first component (PC1) explained 78% of the observed variance. Thus, PC1 was used as our estimate of exploration behaviour (EB) for each individual, with higher scores indicating more proactive, exploratory individuals (total sample size = 188 observations of 161 individuals; 27 repeat measures).

Competition Experiment

The experiment was carried out on birds captured in 2015. The experimental design consisted of three trials. In the first, pairs of great tits were allowed to feed at an unrestricted feeder containing peanuts which is a less preferred food type than live invertebrates for great tits (Serrano-Davies et al, *unpublished*; Fig. 3.1c). In the second, access to the peanut feeder was restricted to a single point with the aim of increasing competition between birds (Fig. 3.1d). In the third trial, in addition to the restricted access feeder with peanuts, we placed in the room highly preferred food items (mealworms and waxworms) that could only be accessed if birds performed a novel string-pulling behaviour spontaneously (Fig. 3.1e).

27 dyads were formed based on matching age and sex profiles (adult female = 5 dyads; juvenile female = 6 dyads; adult male = 8 dyads; juvenile male = 8 dyads; n = 54 individuals). Only birds captured at the same site were paired to prevent unfamiliarity potentially confounding competitive dynamics (Ydenberg et al. 1988, Lemel and Wallin 1993). Individual problem solving performance, recorded on day one in the lever pulling task was then used to pair individuals (solvers with non-solvers; n = 15 dyads). When there were insufficient numbers of solvers to create dyads, individuals were paired based on exploration score (n =

12 dyads). A range of exploration scores was calculated for all individuals tested in that week, and individuals with scores differing by more than two quartiles were paired together. One individual from each dyad was randomly selected and marked with colored tape on its PIT tag for identification purposes during the experiment. Every individual was paired only once.

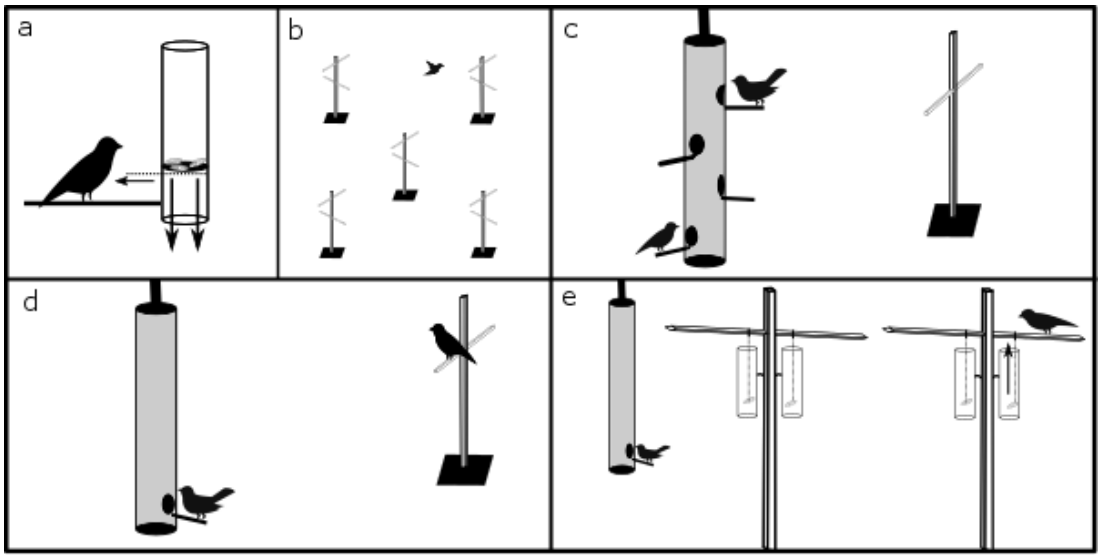


Figure 3.1. (a) Pre-trial problem solving assay based on Cole et al, (2011). Device was presented in isolation in the subjects' cage on the first day in captivity. Lever represented by dotted line, where removal resulted in access to the rewards. (b) Pre-trial exploration behaviour assay adapted from Verbeek, *et. al.,* (1994). (c) Trial 1: two subjects in the observation room with unrestricted access to feeder (n = 27 dayds). (d) Trial 2: two subjects in the observation room with restricted access to feeder (n = 27 dyads). (e) Trial 3: four string-pulling devices were added to the observation room containing a restricted access feeder. Dotted line represents string with rewards attached. Birds accessed the rewards by pulling the string upwards and grasping with their feet (n = 27 dayds).

Individuals were food deprived for one hour immediately prior to trials one and two in order to ensure all individuals were equally motivated to compete for food, after which the dyad were moved from their respective home cages to the observation room. The observation room contained three artificial trees and a wire mesh peanut feeder suspended approximately two metres above the ground from a supporting beam, with access on four sides. The feeder design ensured that individuals had to remain on the feeder to successfully feed, as the mesh aperture was smaller than the average peanut diameter. The feeder design

used in the experiment was also used at each trapping location to ensure familiarity with the feeder. Each dyad was observed for 20 minutes by a hidden observer. Total time spent on the feeder was recorded for each individual, which we used as an indicator of individual resource holding potential in the presence of a competitor (Begon et al, 2006; Lemel and Wallin, 1993). We also recorded any interactions that occurred between individuals during the experiment. These were categorized as one of the following two behaviours. Attempted challenges (aggressive behaviours) were defined as one bird landing within 15cm of the other member of the dyad, either on the feeder or at other points around the room. During the experiments, birds did not land close to one another unless attempting a displacement. The number of times a bird was displaced by its opponent (losses) was also counted. Losses were recorded when an individual left its perch after its opponent landed within 15cm (Hinde, 1952; Cole and Quinn, 2011). After the trial, the observation room was darkened and individuals were transferred to their respective cages and fed.

Following three hours of *ad libitum* feeding, the dyad was again food deprived for one hour before being reintroduced to the observation for trial two. Here, access to the peanut feeder was restricted with a cover, allowing only one individual at a time to access the feeder. The hidden observer noted individual feeding behaviours and any aggressive behaviours or displacements that occurred for 20 minutes. A locomotor activity score was recorded for a subsample of birds (n = 40) during trial 2. At a randomly selected point, the number movements (as defined during the exploration behaviour assay) performed over a two minute period were counted.

After 20 minutes elapsed, the experimental room was darkened and the observer placed four novel problem solving devices in the room, three metres from the feeder for trial three. Multiple devices of the same design were used to prevent dominant individuals from excluding subordinate competitors from both the peanut feeder and the string-pulling devices. These devices were attached to two artificial trees (two devices on each tree), and consisted of two live waxworms (*Achroia grisella*) and three mealworms (*Tenebrio molitor*) which were preferable to the peanuts available in the feeder (W. O'Shea, *pers obs*) and suspended 10cm below the perch by a string, secured with plastic cable ties. We found that the waxworms were relatively cryptic due to their colouration and immobility when suspended from the string. Because of this, we included mealworms to increase the visibility of rewards in the string-pulling devices. In order to solve this task, individuals had to pull the

string upwards until the rewards exited the tube (Fig. 3.1c). The rewards were placed within a 20cm Perspex tube, preventing access by means other than pulling the string (Appendix 3.2). A free reward of one waxworm was placed on top of a string-pulling device in order to attract individuals. After the room was illuminated, the trial began when both birds returned to their normal behaviour (performing at least one flight) and lasted 30 minutes. Time spent on the string-pulling "trees", number of interactions with the string-pulling devices (persistence) and the identity of the first individual to take the free reward from the string-pulling device were all recorded. An interaction with the device was recorded when a bird contacted the Perspex tube or the string with its feet or bill. We also measured latency to solve the string-pulling device which was defined as the amount of time between an individual first landing on the string-pulling device and a solving event. Time spent on the feeder, the number of challenges and the number of losses were recorded. All experiments were recorded by the same, single observer (WOS). After the third trial, the dyads were transferred back to their respective cages and fed *ad libitum*. A maximum of three dyads were tested per day and all trials concluded before 1700, allowing at least two hours of feeding before darkness.

Statistical Analysis

All analyses were conducted in R (v.3.22, R Core Team 2015). We examined the relationship between exploration behaviour and problem solving performance in the lever pulling task using generalized linear mixed effects model (GLMM) fitting problem solving performance (a binary variable) as the dependent variable and exploration behaviour, day of the year (Jan 1 = 1) and year as explanatory variables, individual identity and site were included as random factors to control for repeat measures of individuals (n = 188 observations of 161 individuals assayed for both exploration behaviour and problem solving performance). We also fitted an exploration behaviour × year two-way interaction to test if the relationship between exploration behaviour and problem solving performance varied between years, as evidence suggests that individual variation of performance in this style of task may be caused in part by environmental effects that can vary across years (Quinn et al, 2016). We tested if any fixed factors influenced individual exploration behaviour by fitting a linear mixed effects model (LMM) with exploration behaviour as the dependent variable and day of the year (Jan. 1 = 1), year (2015 or 2016) and sequence (order of testing 1-14) and time of day, as fixed effects and individual identity as a random effect (n = 27 individuals, 54 observations). None of our predictors significantly correlated with exploration behaviour (LRT: all fixed factors: $p > 0.05$).

We therefore calculated the unadjusted repeatability of individual exploration behaviour scores between seasons (using the rptR package which accommodates both Gaussian and non-Gaussian data (Nakagawa and Schielzeth, 2011). Repeatability of problem solving performance between seasons was also calculated using the rptR package. We assessed whether any fixed factors influenced individual solving success using a GLMM with problem solving performance as the binary dependent variable, day of the year (Jan. 1 = 1), year (2015 or 2016) and sequence as explanatory factors, and individual ID as a random effect (n = 29 individuals; 58 observations). Year was a significant predictor of solving success in our model (Percentage of first time solvers 2015: 25%, Percentage of first time solvers 2016: 14%; Z = -1.959, p = 0.037) so we calculated adjusted repeatabilities of problem solving performance controlling for year as a fixed effect (Nakagawa and Schielzeth, 2011). 95% confidence intervals were constructed via parametric bootstrapping with 1000 simulations. We retained information on individuals with only one measure of exploration behaviour and problem solving performance in our repeatability calculations (Nakagawa and Schleizth, 2010).

To determine if performance in the lever-pulling task was due to differences in motivation caused by individual stress responses to the captive environment, we examined if time in captivity, body condition on arrival or food intake prior to and during the lever pulling assay were related to solving status. We fitted a binomial GLMM with problem solving performance in the lever pulling task as the dependent variable. Time in captivity (calculated as the number of hours between arrival in captivity and the end of the problem solving assay), total caloric intake during that time period, body condition upon arrival (methods in Peig and Green, 2009), age and sex were fitted as fixed factors. We were unable to control access to food for individuals before they arrived in captivity therefore we included body condition to control for individual motivation to feed. Site was fitted as a random effect. This analysis includes only birds with food intake monitored in 2015 as we were interested in determining if variation in food seeking behaviours could have contributed to lever-pulling performance. As each individual in this sample was monitored once we did not include individual identity as a random effect (n = 76 individuals).

For the analysis of whether problem solvers or non-solvers were more competitive during trials 1 and 2 (number of aggressive challenges, number of defeats, time spent on the feeder), we restricted our analysis to individuals in the 15 dyads with different problem solving performance phenotypes. For analyses of the relationship between exploration

behaviour and the behavioural measures recorded during trials 1 and two, we included all 27 dyads, as our pairing procedure meant that no dyads consisted of two individuals of identical exploration scores.

GLMMs were initially used to test whether problem solving performance and exploration behaviour were related to the number of attempted displacements by the focal individual, and the number of times the focal bird was displaced by its opponent. Due to evidence of overdispersion (Bolker et al, 2009), a negative binomial error distribution was assumed for modelling both variables (glmmADMB package; Fournier et al, 2012). Fixed factors included in all models were treatment (unrestricted access to the feeder – trial 1, or restricted access to the feeder – trial 2), individual tarsus length as an indicator of body size, exploration behaviour, sex and age. When analysing the restricted data set containing only dyads consisting of one solver and one non-solver, we included problem solving performance in the lever pulling task as a fixed effect. Dyad identity, site code and individual identity were included as random factors in both models. A Spearman rank correlation test was used to determine if aggressiveness was consistent between trial 1 and trial 2.

The time that the focal bird spent on the feeder during each trial, was summed across individual feeder visits to calculate the time spent on the feeder, resource holding potential for trial one and trial two. Focal bird time on feeder (sec) was analysed as a proportion of total trial time (1200 seconds) initially using a GLMM assuming a binomial error distribution with a logit link function. Due to evidence of overdispersion (Bolker et al, 2009), time on feeder was modelled using a Penalised quasi-likelihood binomial GLMM (MASS package; Venables and Ripley, 2002). Fixed factors included were trial number (1 - unrestricted access or 2 - restricted access), tarsus length, exploration behaviour, sex, age, number of aggressive challenges attempted and number of times the subject was displaced (defeats) during the trials. Additionally, when analysing the restricted data set we included problem solving performance in the lever-pulling task as a fixed effect. Pair identity, site code and individual identity were included as random factors in the models. We analysed the differences in the rate of feeder visits between the first (unrestricted access) and second (restricted access) trial using a Wilcoxon Rank Sum test.

Individual string-pulling success was analysed using a GLMM assuming a binomial error distribution with a logit link function (lme4 package; Venables and Ripley, 2002). Because

solving rates in this task were low in the restricted data set (string-pulling occurred in 5 of 15 dyads), we elected to use the larger data set (n = 27 dyads) for this analysis to maximise the number of solving events, but thus excluded lever-pulling performance in isolation as a fixed factor. String-pulling success (access reward/not access the reward) was the dependent variable, while number of interactions with the string-pulling device (persistence), time spent on feeder in trial two, number of attempted challenges, number of defeats and exploration behaviour were the fixed factors. We found that the introduction of the string-pulling device led to less competition at the feeder during trial three and therefore time spent on the feeder during this trial was not representative of an individual's competitive ability. Thus, we included the measure from the trial immediately preceding (trial two) in the model. When analysing the restricted data set containing only solver and non-solver dyads we included problem solving performance in the lever pulling task as a fixed factor. Dyad identity and site were included as random factors in the model.

As hunger and in turn motivation to compete may be influenced by stress levels (Lemel and Wallin, 1993; Landys et al, 2006), we examined if more competitive individuals and less competitive individuals exhibited different activity levels during the trials, as this trait has been found to vary with circulating stress hormones (Belthoff and Dufty, 1998; Breuner et al, 1998). We fitted the number of movements recorded during a two minute period in trial two as the response variable of a Poisson GLMM. Problem solving performance, exploration behaviour and time spent on the feeder during that trial were fitted as fixed effects. To account for pair specific effects, we fitted dyad ID and site code as a random effect (n = 40 observations). Due to evidence of overdispersion (Bolker et al, 2009), we analysed the data using a negative binomial mixed effects model with the same structure as outlined above.

We used Fishers Exact test to analyse if order of arrival at the string-pulling device predicted string-pulling success, as well as to test age and sex effects on string-pulling success (n = 54). Fishers Exact tests were used to test if solving success in isolation was related to order of arrival at the string-pulling success (n = 54). A Wilcoxon Rank Sum test was used to test if mean string-pulling latency was significantly different between problem solvers in isolation and non-solvers in isolation (n = 7). We tested if opponent aggressiveness (the number of attempted displacements by opponent) was related to the amount of time spent on the string-pulling device with a Spearmans' Rank Correlation test (n = 54).

Results

Repeatability

Individual exploration behaviour did not significantly correlate with initial problem solving performance (GLMM: Z = -1.337; p = 0.181) and the relationship between exploration behaviour and problem solving performance did not vary across years (Year × exploration behaviour interaction; GLMM: Z = -1.518; p = 0.129). 23% of individuals solved the novel lever pulling task in isolation when tested for the first time (38 solvers from 167 individuals). Individual exploration behaviour for birds tested for the first time ranged between 0 and 73 movements over the two minute test period (mean ± se = 28.53 ± 1.60 movements; n = 160). Exploration behaviour was significantly repeatable between seasons in our populations (r ± se = 0.387 ± 0.155; *p* = 0.04; n = 27 between season measures). Unadjusted repeatability of lever pulling success was not significantly repeatable between seasons (r ± se = 0.111 ± 0.151; *p* = 0.060; n = 29 between season measures). Controlling for year in the analysis, adjusted repeatability of lever pulling success was significant between seasons (r ± se = 0.615 ± 0.089; *p* = 0.022; n = 29 between season measures). Problem solving performance did not significantly correlate with body condition (GLMM; z = 1.304; *p* = 0.192), time in captivity (GLMM: z = 1.736; *p* = 0.083) or caloric intake prior to and during the assay (z = 0.617; *p* = 0.516; Appendix 3.3).

Aggressive Interactions and time on feeder

At least one bird from each dyad initiated a challenge in 98% of trials during trials one and two (mean ± SD = 4.16 ± 0.64; range 0 - 48 challenges). Only 21% of challenges (112 out of 534) occurred on the feeder. Birds were more aggressive towards their opponents in trial 1 than trial 2 (GLMM: z = -3.50; *p* < 0.001; n = 15 dyads; Appendix 3.4), but none of the other fixed effects were statistically significantly related to the number of aggressive challenges at the p < 0.05 level (Minimum p-value = 0.087; Appendix 3.4). Analysis of the larger data set which also contained dyads with similar PSP scores (n = 27 dyads) produced similar results (Trial number; Negative Binomial GLMM: z = -3.07; *p* = 0.002; minimum p-value for other fixed effects = 0.237). Individual aggressiveness was highly consistent between trial 1 and 2 (r_s = 0.800, *p* < 0.001; n = 54 individuals, 27 dyads).

Individuals were displaced more by their opponents in trial 1 than trial 2 (Negative Binomial GLMM: z = -3.13; *p* = 0.002; n = 15 dyads; Appendix 3.5). Males were more likely to be displaced by their opponents than females (Negative Binomial GLMM: z = 2.10; *p* = 0.036; n

= 15 dyads; Appendix 3.5). None of the other fixed effects were statistically significantly related to the number of times the focal bird was displaced by its opponent at the p = 0.05 level (minimum p-value = 0.129; Appendix 3.5). Analysis of the larger data set which also contained dyads with similar PSP scores (n = 27 dyads) produced similar results (Trial number; Negative Binomial GLMM: z = -2.93; *p* = 0.003; minimum p-value for all other fixed effects = 0.168).

Individuals spent on average (± se) 111.26 seconds (± 9.52) on the feeder during trials one and two (range: 0 – 606s). Birds spent significantly more time on the feeder in trial 2 (restricted access) than in trial 1 (unrestricted access; GLMM : t = 2.105; *p* = 0.045; Table 3.1; n = 15 dyads). This difference was not due to an increase in the rate of feeder visits (Wilcoxon Rank Sum; W = 570.5, *p* = 0.398; n = 54), indicating the individuals were spending longer on the feeder with every visit. Lever pulling success on day 1 in isolation was not significantly related to time on the feeder subsequently during trials one and two (Table 3.1). Individual exploration behaviour did not significantly correlate with time spent on the feeder during our trials (Table 3.1). Analysis of the larger data set also containing dyads with similar problem solving performance produced similar results (Appendix 3.6); however here, birds that were more aggressive towards their opponents throughout the observation room spent significantly longer on the feeder than those individuals that were less aggressive (GLMM: t = 2.40; *p* = 0.021; n = 27 dyads; Appendix 3.6). Visualisation of the data suggested that non-solvers may be spending more time on the feeder than solvers, especially during trial 2 and that perhaps the results of this analysis were related to the relatively small sample sizes involved (Appendix 3.7). Therefore, we additionally tested if lever pulling performance was related to time on the feeder amongst dyads. The result was not significant at the p < 0.05 level (GLMM: t = -185; *p* = 0.077) More competitive individuals did not have significantly higher locomotor activity levels than less competitive individuals (GLMM: z = -0.910; p = 0.360; n = 40; Appendix 3.7).

Table 3.1. Results of a penalised quasi-likelihood GLMM analysing the relationship between behavioural traits of the focal bird and time spent on the feeder during trial 1 (unrestricted access) and trial 2 (restricted access). Random effects included in the model were site, individual identity and dyad identity (n = 15 solver/non-solver dyads, 30 individuals).

Parameters	**Estimate ± SE**	**t value**	**p-value**
Trial Number [a]	0.380 ± 0.174	2.105	0.045
Sex [b]	-0.742 ± 0.491	-10.93	0.285
Age [c]	0.016 ± -0.470	0.001	0.993
PSP [d]	-0.500 ± 0.215	-0.877	0.389
EB [e]	0.039 ± 0.091	0.512	0.613
Body Size [f]	0.156 ± 0.130	0.160	0.874
No. Challenges	0.196 ± 0.148	0.794	0.434
No. Defeats	-0.237 ± 0.187	-1.023	0.315

[a] Trial 1 set to 0; [b] Female set to 0; [c] Adult set to 0; [d] Problem solving performance in isolation, non-solvers set to 0; [e] Exploration Behaviour; [f] Tarsus Length.

String-pulling in Trial 3

7 of the 54 individuals tested spontaneously solved the string-pulling task presented during trial 3. At least one dyad member interacted with the device in 23 of 27 trials, but there were no recorded cases of two birds from the same dyad solving the string-pulling task within a trial. Individuals that solved the string-pulling task in trial 3 had spent significantly less time on the feeder in trial 2 than non-string pullers (GLMM: z = -2.187, p = 0.029; Table 3.2; Fig. 3.2; n = 27 dyads). In trial 3 the number of times an individual interacted with the string-pulling device (persistence) also positively and significantly correlated with string-pulling success (GLMM: z = 2.192, p = 0.024; Table 3.2; n = 27 dyads). Analysis of the restricted data set produced similar results (n = 15 dyads), though the negative correlation between time spent on the feeder and string-pulling success was not statistically significant at the $p < 0.05$ level (GLMM: z = -1.648; p = 0.099; n = 15 dyads). Problem solving performance in the initial lever-pulling task did not significantly correlate with string-pulling success in trial 3 (GLMM: z = 0.008; p = 0.423; n = 15 dyads).

Table 3.2. Results of a binomial GLMM analysing the relationship between competitive ability in trial 2 and string-pulling performance in trial 3, controlling for EB. Random effects included in the model were site, individual identity and dyad identity (n = 27 dyads, 54 indiv-iduals).

Parameters	**Estimate ± SE**	**z value**	**p-value**
Time on Feeder [a]	-2.644 ± 1.209	-2.187	0.029
EB [b]	-0.283 ± 0.541	-0.522	0.602
Persistence [c]	1.481 ± 0.676	2.192	0.024
No. Challenges	0.196 ± 0.559	0.351	0.726
No. Defeats	-1.925 ± 1.191	-0.777	0.437

[a] Time spent on the feeder during trial 2; [b] Exploration behaviour; [c] Number of interactions with the string-pulling device.

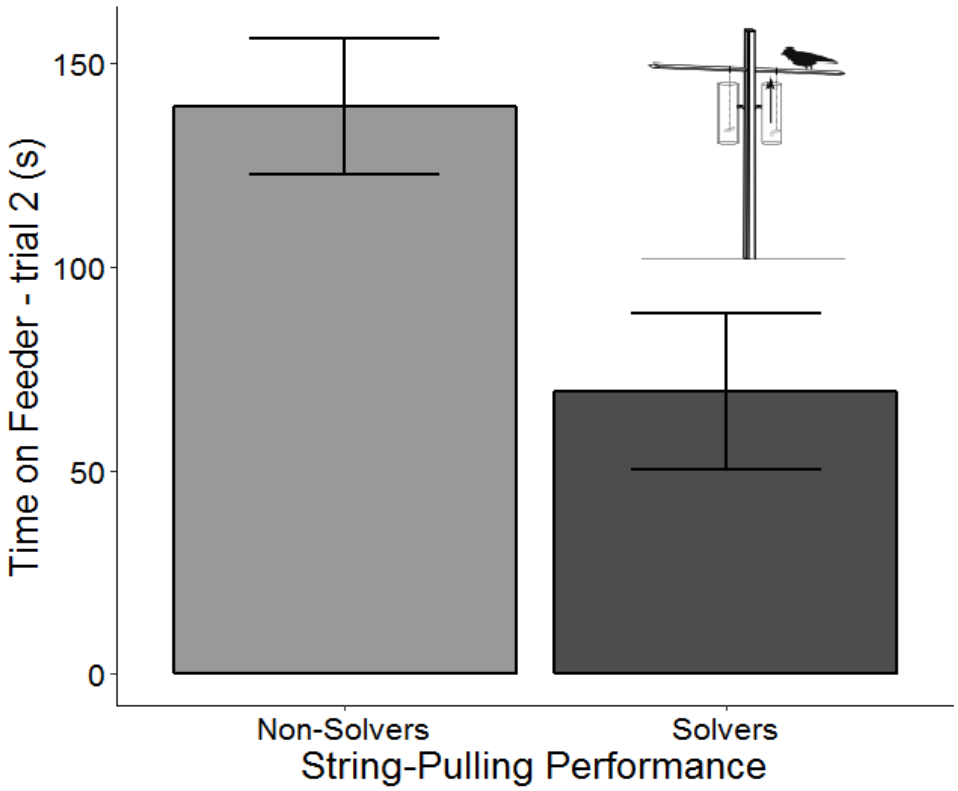


Figure 3.2. Mean time spent on the feeder during trial 2 by birds that spontaneously solved and did not solve the string-pulling problem presented in the subsequent trial 3 (n = 27 dayds). Error bars represent standard error.

Order of arrival at the device, an indicator of within dyad variation of a neophobic response to the string-pulling device, was not statistically significantly related to string-pulling success (Fishers Exact test: $p = 0.10$; n = 54). The number of times a bird was displaced in trial 3 was significantly negatively correlated with time spent on the string-pulling device in trial 3 ($r_s = -0.295$, $p = 0.030$; n = 54). We found no evidence of a significant difference between ages (Fishers Exact test: $p = 0.423$; n = 54), or sexes (Fishers Exact test: $p = 0.687$; n = 54) in the proportion of individuals that solved or did not solve the string-pulling task. Latency to solve the string-pulling task for non-lever pullers (mean (s) ± se = 1098.33 ± 344.523; n = 3) was more than twice that of lever pulling individuals (mean (s) ± se = 438.5 ± 180.88; n = 4); however the difference was non-significant at the $p < 0.05$ level (Wilcoxon Rank Sum; W = 10; $p = 0.229$; n = 7).

Discussion

We investigated the relationship between two repeatable, behavioural traits and individual competitive ability among dyads of wild caught captive great tits. The number of aggressions performed by the focal bird positively correlated with time spent feeding, indicating that within pairs, the more aggressive bird had higher resource holding potential in the presence of a competitor. We found that innovativeness, as measured by performance in a novel problem solving task in isolation, was not related to competitive ability; while less competitive individuals in a social context were more likely to perform innovative behaviours than less competitive individuals. The performance of innovative behaviours in isolation did not predict innovativeness in a social context, and exploration behaviour predicted neither aggressiveness nor resource holding potential at the feeder.

<u>Innovativeness and resource holding potential</u>

Lever pulling in isolation was not significantly related to time spent on the feeder, although this may have been caused by the relatively small sample sizes involved, limiting our ability to detect this effect. In trial 3, when presented with an alternative, preferable food reward accessible by the performance of a novel string-pulling behaviour, 13% of individuals solved the task. String-pulling success was negatively related to competitive ability in trial two, with string pullers monopolizing the feeder for less time than non-string pullers in trial two, as predicted by the necessity drives innovation hypothesis (Reader and Laland, 2003). Direct evidence for this phenomenon is scarce (Laland and Reader, 1999b; Cole and Quinn, 2011) with many studies linking innovativeness and common correlates of competitive ability in

social contexts such as age, size and dominance status (Reader and Laland, 2001; Thornton and Samson, 2012; Duffield et al, 2015). Previous studies have shown individuals experiencing stress or hunger following competitive interactions may be more likely to perform beneficial innovative behaviours (Laland and Reader, 1999a; Laland and Reader, 1999b; Duffield et al, 2015); however to our knowledge this is the first experimental evidence that shows innovative behaviours can directly benefit individuals with lower resource holding potential in a social context, by allowing access to alternative resources through novel foraging strategies. Other hypotheses, such as the "best of a bad job" hypothesis also suggest that alternative behavioural tactics can arise through social competition (Oliveira et al, 2008). We believe that our data best fits the necessity hypothesis because the string-pulling behaviour that emerges during trial 3 is wholly novel.

Our experimental design allowed us to test how innovation and competitive ability are related within age and sex classes. In contrast to other studies (Laland and Reader, 1999a; Reader and Laland, 2001; Thornton and Samson, 2012), we found no evidence that problem solving performance in either task was related to age or sex, suggesting that innovativeness may be an individual specific effect. Recent evidence shows that rather than genetic factors driving individual variation in problem solving performance (Quinn et al, 2016), environmental factors are more important in the great tit system (albeit in a different population), especially social conditions (Morand-Ferron and Quinn, 2011; Zandberg et al, 2017). In the great tit, nestlings exposed to harsh conditions where competition levels are higher, for example high local population density and poor habitat quality, are more likely to be innovators in adult life (Quinn et al, 2016). This effect does not occur in all years, but once established leads to repeatable differences in innovativeness over long periods of an individual's life (Quinn et al, 2016).

Although these studies suggest that innovativeness may arise as the result of a highly competitive environment during adult or natal life, the functional implications of innovativeness for adult life are unclear. One of the few studies to have linked problem solving performance to natural behavioural patterns found a positive correlation between innovativeness and foraging efficiency in great tits during key periods of nestling development (Cole et al, 2012; but see also Cauchard et al, 2013). Solvers may have employed alternative search patterns or handling skills, allowing them to forage over smaller areas and for shorter durations without compromising diet quality (Cole et al, 2012). Future

studies should aim to build on these results, as such links are critical for understanding the extent to which variation in innovativeness reflects alternative behavioural strategies within populations.

Cross contextual consistency in innovativeness

It has been suggested that individual differences in associative learning mediated by a perceptual motor feedback loop is a likely cognitive mechanism underlying innovative string-pulling and lever pulling behaviour (Taylor et al, 2010; Cole et al, 2011). Contact with a functional part of the device causes the reward item to move and repeating these behaviours increases the likelihood of an individual accessing the rewards. Individual variation in solving performance is thought to be driven by solvers being better at learning the association between their behavioural patterns and the reward movement caused by their behaviour (Cole et al, 2012). Given that other studies have shown that innovative problem solvers in captivity were also faster learners during an entirely different colour association task in the wild (Morand-Ferron et al, 2014), it seems that differences in cognitive ability is a likely factor underlying innovativeness (Reader et al, 2016). However evidence also suggests that individual innovativeness is highly plastic (Overington et al, 2009; Morand-Ferron et al, 2011). In this experiment, we found no evidence of a relationship between lever pulling success in isolation and string-pulling success in dyads during trial three of the experiment, when a much smaller proportion of individuals problem solved. Non-solvers in isolation took twice as long to solve the string-pulling task as solvers. These results mirror those of another great tit study population, where solvers in captivity solved similar but non-identical devices twice as fast when in the wild (Morand-Ferron et al, 2011). The lack of solving consistency across tasks in the current study did not seem to be due to variation in a neophobic response to the novel device (Griffin and Guez, 2014a), because the order of arrival at the string-pulling device was not significantly related to solving success in isolation. Persistence, measured as the number of times an individual interacted with the string-pulling device in trial 3, did correlate positively and significantly with string-pulling success in the same trials, agreeing with other studies that have found increased problem solving success with higher levels of engagement with a task (Morand-Ferron et al, 2011; Thornton and Samson, 2012; Cauchard et al, 2013; reviewed in Griffin and Guez, 2014a).

The captive environment may also unduly influence the outcomes of behavioural studies (Calisi and Bently, 2009), as individual specific stress responses can alter how subjects

respond to stimuli, including locomotor activity levels (Belthoff and Dufty, 1998; Breuner et al, 1998) and food seeking behaviours (Landys et al, 2006). Monitoring food intake prior to and during the initial problem solving trials in isolation, we found that individuals that completed the lever pulling task successfully had similar foraging patterns to those that did not succeed. Likewise, birds that had longer to habituate to the captive environment were not statistically significantly more likely to complete the task. We would argue that this indicates that outcomes of the lever pulling trial were not driven primarily by individual stress response to the captive environment. Similarly, in trial two, locomotor activity in the observation room was unrelated to feeding behaviour (time spent on the feeder) and problem solving performance. Behaviours that can be associated with stress response (increased or reduced movement), did not vary with food seeking. Although the stress involved with capture, handling and transport undoubtedly influences behaviour in captivity, the captive environment also allows experimental control of a number of critical environmental stressors associated with trials in the wild. This includes predation risk, interference through social competition and energy demands associated with variable climatic conditions (reviewed in Morand-Ferron et al, 2015). By monitoring behaviours indicative of stress, we argue that our experimental outcomes were not driven by individual stress response to the captive environment.

Innovation in a group can lead to a higher risk of aggression from kleptoparasitic members (Morand-Ferron et al, 2006) and evidence suggests that the presence of potential aggressors can reduce the probability of an individual innovating (Fragaszy and Visalberghi, 1990; Overington et al, 2009, Cronin et al, 2014), which may have explained the lack of a correlation between isolation and social contexts. The size of the observation room constrained our ability to minimise interference; a larger experimental chamber with multiple devices at various distances from the peanut feeder may have allowed us to determine if aggression avoidance played a role. In the wild, a lack of physical boundaries could allow innovators to process and consume alternative food items away from more dominant conspecifics, thereby reducing the risk of aggression. Our results indicate the complexities involved in determining the causes and consequences of innovation in a social context. Further experiments are needed to fully understand how individual state and environmental conditions influence the relationship between problem solving performance in isolation and in a social context.

Personality and resource holding potential

Individuals that performed more aggressive behaviours towards their opponents spent longer cumulatively on the feeder. This link between aggression and an individual's ability to access resources in the presence of competitors is typical of species that compete for limited resources (Begon et al, 2006), including the great tit (Gosler et al, 1996; Cole and Quinn, 2011), a species in which competitiveness is also thought to be an important correlate of winter survival when foraging on naturally clumped resources such as beech mast (Gosler, 1993; Gosler, 1996; Nichlaus et al, 2016). Aggressiveness was also consistent between trials; however we did not find the predicted positive correlation between exploration behaviour and aggressiveness towards the opponent or resource holding potential, traits that are generally thought to form part of a behavioural syndrome in great tits (Verbeek et al, 1994; Carere et al, 2005).

Several factors may explain our results. Firstly, in contrast with other similar studies on great tits, our experiment was carried out in captivity rather than in the wild (Dingemanse and de Goede, 2004; Cole and Quinn, 2011), allowing us to control the age and sex of competitors, key determinants of social dominance in this species. Failure to adequately control for these factors experimentally could exaggerate the link between exploration behaviour and competitive ability under natural conditions. Secondly, studies indicate that the relationship between exploration behaviour and aggressiveness may be context dependent (Dingemanse and de Goede, 2004). Faster exploring great tits have higher dominance ranks, but in unfamiliar environments this relationship is less pronounced or absent (Dingemanse and de Goede, 2004). Thus, one possible explanation is that in a captive environment, the relationship between exploration behaviour and competitive ability at the feeder is absent due to unfamiliar surroundings. This may explain why we found no statistically significant correlation here. Thirdly, behavioural syndromes can vary between populations depending on the environmental conditions or past evolutionary processes (Dingemanse et al, 2007). Exploration behaviour and aggression may not form a behavioural syndrome in our population where selection pressures are likely quite different. Compared to the UK and mainland Europe, for example, Ireland has relatively low populations of both the great tit and of its main predator, the sparrowhawk (Balmer et al, 2013; W. O'Shea – *unpublished data*), which may lead to lower levels of competition and predation respectively, both of which are likely important determinants of selection on behavioural syndromes (Dingemanse and Wolf, 2010).

To conclude, we present evidence that innovativeness and competitive ability are inversely related in our populations, in accordance with the necessity drives innovation hypothesis. Our experiment demonstrates that innovative behaviours can benefit less successful contest competitors, by allowing them to circumvent competition and acquire alternative resources. This suggests that innovativeness may facilitate alternative behaviours that have the potential to influence survival or other life history traits linked to fitness. To date few studies have examined the ecological significance of these behavioural correlations in the wild. We suggest future work should focus on identifying the functional behaviours that may be affected by this relationship across multiple stages of an individual's life history.

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Chapter 3: Appendices

Appendix 3.1. Lever-pulling task adapted from Cole et al, 2011.



Appendix 3.2. String pulling assay used in trial 3.



Appendix 3.3. The effects of habituation, body condition and food intake on problem solving performance in a lever pulling task in isolation (Binomial GLMM; random term = site; n = 76).

Parameters	**Estimate ± SE**	**z-value**	**p-value**
Time in captivity (hrs)	0.536 ± 0.309	1.736	0.083
Caloric Intake	0.188 ± 0.290	0.647	0.516
Sex [a]	-0.833 ± 0.063	-1.321	0.187
Age [b]	0.228 ± 0.587	0.389	0.697
Body Condition	0.434 ± 0.330	1.304	0.192

[a] Female set to 0; [b] Juvenile set to 0.

Appendix 3.4. Results of a Negative Binomial GLMM investigating the relationship between behavioural traits of the focal bird and the number of aggressive challenges attempted duri -ng trial 1 and trial 2. Random effects included in the models were site, individual identity a -nd pair identity (n = 15 dyads, 30 individuals).

Parameters	**Estimate ± SE**	**z-value**	**p-value**
Trial Number [a]	-0.670 ± 0.191	-3.50	<0.001
Sex [b]	0.532 ± 1.059	0.49	0.621
Age [c]	-1.018 ± 0.868	-1.17	0.241
PSP [d]	1.493 ± 0.873	1.71	0.087
EB [e]	0.186 ± 0.448	0.41	0.678
Body Size [f]	0.481 ± 0.545	0.88	0.377

[a] Trial 1 set to 0; [b] Female set to 0; [c] Adult set to 0; [d] Problem-solving performance in isolation, non-solvers set to 0; [e] Exploration Behaviour; [f] Tarsus length.

Appendix 3.5. Results of a Negative Binomial GLMM investigating the relationship betwee n behavioural traits of the focal bird and the number of defeats during trial 1 and trial 2. Random effects included in the models were site, individual identity and pair identity (n = 15 dyads, 30 individuals).

Parameters	**Estimate ± SE**	**z-value**	**p-value**
Trial Number [a]	-0.662 ± 0.211	-3.13	0.002
Sex [b]	2.650 ± 1.264	2.10	0.036
Age [c]	-0.859 ± 1.017	-0.84	0.399
PSP [d]	-1.496 ± 0.985	-1.52	0.129
EB [e]	-0.366 ± 0.480	-0.76	0.445
Body Size [f]	-0.831 ± 0.637	-1.30	0.192

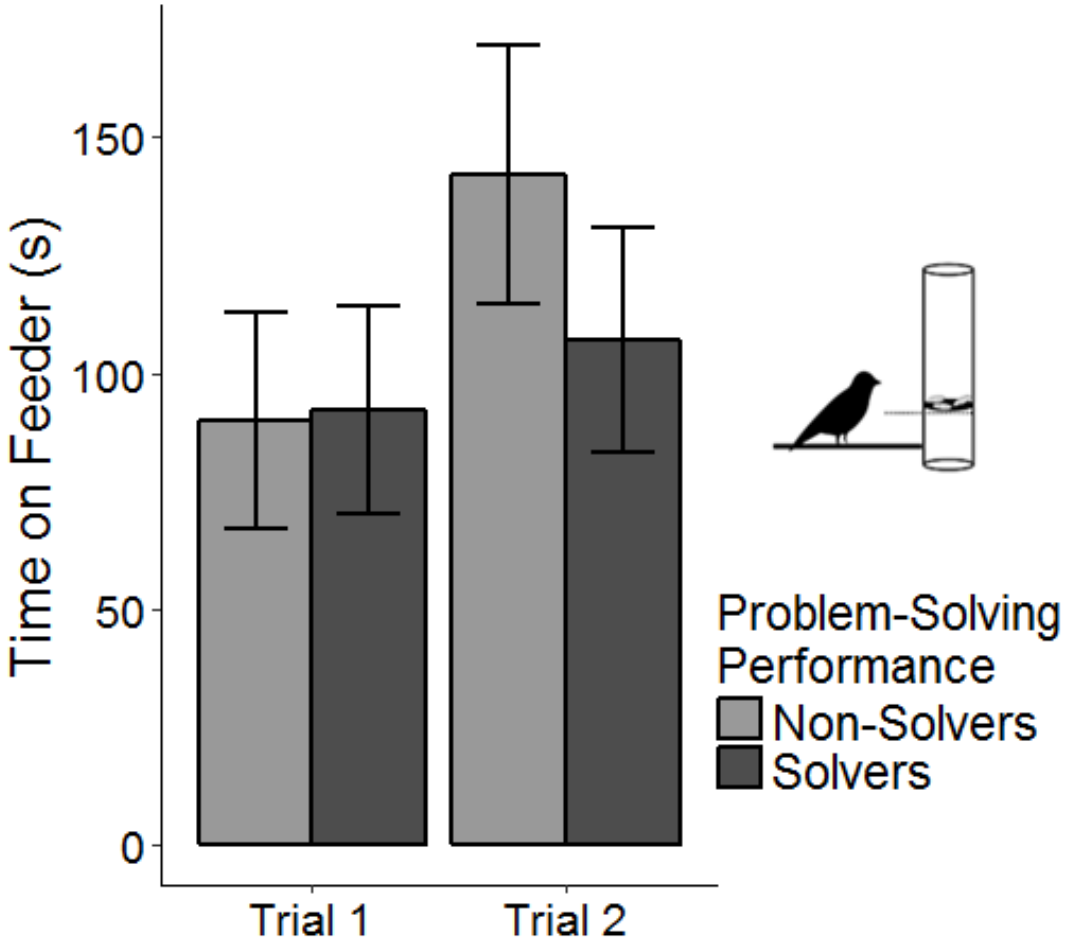
[a] Trial 1 set to 0; [b] Female set to 0; [c] Adult set to 0; [d] Problem-solving performance in isolation, non-solvers set to 0; [e] Exploration Behaviour; [f] Tarsus length.

Appendix 3.6. Results of a penalised quasi-likelihood GLMM analysing the relationship between exploration behaviour in the lever pulling task in isolation and time spent on the feeder during trial 1 (unrestricted access) and trial 2 (restricted access). This analysis is based on the larger data set which contained dyads comprised of individuals with similar problem solving performance in the lever pulling task. Random effects included in the model were site, individual identity and dyad identity (n = 27 dyads, 54 individuals).

Parameters	**Estimate ± SE**	**t-value**	**p-value**
Trial Number [a]	0.443 ± 0.124	3.548	<0.001
Sex [b]	-0.414 ± 0.322	-1.285	0.211
Age [c]	0.405 ± 0.286	1.414	0.170
EB [d]	-0.125 ± 0.110	-1.141	0.269
Body Size [e]	-0.061 ± 0.127	-0.479	0.636
No. Challenges	0.236 ± 0.098	2.401	0.020
No. Defeats	-0.107 ± 0.128	-0.838	0.406

[a] Trial 1 set to 0; [b] Female set to 0; [c] Adult set to 0; [d] Exploration Behaviour; [e] Tarsus Length

Appendix 3.7. Mean time spent on the feeder during trial 1 (unrestricted access) and trial 2 (restricted access) by problem solvers and non-solvers in the lever pulling task in isolation (n = 15 dyads). Error bars represent standard error.



Appendix 3.8. The effects of Problem solving performance, exploration behaviour and competitive ability on activity levels during trial 2 (Negative binomial GLMM; random term = dyad ID nested in site code; n = 40).

Parameters	**Estimate ± SE**	**z-value**	**p-value**
PSP [a]	-0.182 ± 0.182	-0.920	0.360
EB	0.045 ± 0.045	0.630	0.530
Time on Feeder [b]	-0.095 ± 0.095	-0.910	0.360

[a] Non-Solver in the lever pulling task set to 0; [b] Time spent on the feeder during trial 2.

Chapter 4

Predation risk aversion predicts nest desertion in the great tit (*Parus major*).



Abstract

Life history theory predicts that as environmental conditions change during reproduction, individuals should respond to the risk of predation in a way that optimizes fitness. In reality responses are constrained, due to consistent individual differences in risk responsiveness. According to the pace of life syndrome theory (POLS) these differences may be adaptive and reflect contrasting life history strategies, where more risk prone individuals generally prioritise current reproductive success and risk averse individuals prioritise their own survival. This variation has been linked to the reactive-proactive personality axis but evidence for this relationship is mixed. Here we recorded the responses of female great tits (*Parus major*) during incubation to a simulated predator disturbance and analysed the relationship between female responses and an indicator of the reactive-proactive axis - exploration of a novel environment. In line with POLS we predicted that faster exploring females would be more likely to "tight-sit", remaining on the nest, while slower exploring females would flee. 75% of females remained tight-sitting on the nest following the disturbance, while 25% fled, and female responses were significantly repeatable within and between seasons. Tight-sitting was unrelated to exploration behaviour. Tight-sitting behaviour correlated with both clutch size and reproductive success, as tight-sitting females incubated larger clutches that were less likely to fail during incubation. Furthermore, the proportion of nests that failed amongst tight-sitters was stable throughout the season; however amongst females that fled, nest failures increased with lay date. Our results suggest that exploration behaviour is not linked to POLS during this stage of the breeding season in females. Instead, a more immediate measure of risk-taking behaviour, tight-sitting, predicted female reproductive investment and subsequent success in line with the POLS theory. These results suggest that simple measures of personality do not necessarily predict important functional behavioural variation directly linked to life history variation.

Introduction

Parental care is a crucial but costly aspect of reproduction for many species (Royle et al, 2012; Santos and Nakagawa, 2012). Life history trade-offs associated with parental care vary with environmental conditions (e.g. Badyaev and Ghalambor, 2001). Therefore, breeders may display behavioural plasticity in order to optimise fitness outcomes (Westneat et al, 2011; Ghalambor et al, 2013). For instance offspring defence, one aspect of parental care, tends to increase with cumulative parental investment relative to residual reproductive value (Montgomerie and Weatherhead, 1988), and offspring viability (Greig-Smith, 1980; Brunton, 1990; Magnhagen and Vestergaard, 1993; Halupka, 1999; Albrecht and Klvaňa, 2004). However if potential costs (e.g. injury or mortality) are greater than the fitness benefits associated with offspring survival, then defensive intensity tends to be lower (Montgomerie and Weatherhead, 1988). For example if the risk of extra-pair paternity is high, males may reduce investment in offspring defence (Lubjuhn et al, 1993).

The benefits of defensive behaviours may also be influenced by reproductive timing (Curio et al, 1984). In seasonal environments, the likelihood of successfully replacing predated offspring decreases as environmental food availability declines (Verhulst and Tinbergen, 1991). Therefore, early breeders tend to defend their offspring less than late breeders (Curio et al, 1984; Hollander et al, 2008; *but see* – Weatherhead, 1989). More recently, studies have begun to focus on between individual differences in behaviour, and evidence now shows that individual responses to predation risk are not completely plastic (van Oers et al, 2003; Quinn and Cresswell, 2005; Quinn et al, 2011b). Instead, behaviours like offspring defence may vary consistently amongst individuals (Hollander et al, 2008; Kontiainen et al, 2009). These individual differences, known as personality, may be conserved across behavioural contexts leading to suites of correlated behavioural traits known as behavioural syndromes (Sih et al, 2004a; Sih et al, 2004b).

One of the best studied behavioural syndromes is the reactive-proactive axis. This describes individual personalities along a continuum (Koolhaas et al, 1999), contrasting proactive or bold individuals who tend to be more aggressive and exploratory, with reactive or shyer individuals who behave conversely (Koolhaas et al, 1999). One adaptive explanation states that these behavioural differences may be linked to individual life history variation, also known as pace of life syndromes (POLS; Réale et al, 2010). Bolder individuals prioritise current reproductive success over longer-term survival, while shyer individuals prioritise self-

maintenance, (Réale et al, 2010). Studies indicate that in some cases natural selection can act on personality traits through links with fitness (Chapter 1) and identifying the behavioural mechanisms that contribute to fitness differences amongst individuals of different personality types is critical for understanding the adaptive nature of behavioural syndromes (Sih et al, 2004a).

One such mechanism is how individuals respond to predation risk, a key selection pressure that can influence phenotypic variation in the wild (Eggers et al, 2006; Eklöv and Svanbäck, 2006; Zanette et al, 2011). Bolder, proactive individuals are less averse to risk than reactive individuals when foraging (van Oers et al, 2003; Quinn et al, 2011b; Dammhahn and Almeling, 2012), and when responding to perceived threats to their offspring (Garamszegi et al, 2008; Hollander et al, 2008; Cole and Quinn, 2014; Krams et al, 2014b; Vrublevska et al, 2015). The latter suggests that proactive individuals indeed prioritise offspring survival, and behave in a manner that increases their risk of predation as predicted by POLS (Réale et al, 2010). Due to the close links between offspring defence and fitness, heterogeneous predation pressure is likely to be an important factor maintaining personality variation in the wild (Réale and Festa-Bianchet, 2003; Dingemanse et al, 2007). However, few studies have found links between the reactive-proactive axis and behavioural indicators of parental investment that have direct fitness benefits as predicted by POLS (Mutzel et al, 2013; David et al, 2015).

In this study, we examined the responses of female great tits to a simulated predator disturbance during incubation by a human observer. Great tits and closely related cavity nesting species display similar responses to human and natural predators during the breeding season. For instance Hinde (1952), found that great tits responded to a human observer approaching the nest-box with similar vocalisations to those performed in response to the presence of a sparrowhawk near the nest-box (*Accipiter nisus*). Therefore, we assumed that our trials indicated individual responsiveness to predation risk. In response to a risk at the nest during incubation, females either flee or remain on the nest "tight-sitting" (Fresneau et al, 2014). Some also perform a deimatic hissing display (Hinde, 1952; Krams, 2014a; Umbers et al, 2017; Zub et al, 2017). Evidence from other populations suggests that the latter is an anti-predation display, which may influence predator behaviour (Krams et al, 2014a; Zub et al, 2017) and adult survival during the breeding season (Krams et al, 2014a). Tight-sitting has been described in several species as a defensive behaviour (Langham and Hulsman, 1986; Burkjedal, 1989; Fresneau et al, 2014) which can be repeatable within

seasons (Fresneau et al, 2014), and may prevent brood parasitism (Rands, 2012). To date however, the implications of tight-sitting behaviour for fitness have not yet been tested in the wild.

Our aims were firstly to establish if individual responses to predation risk, that is tight-sitting and hissing, were temporally consistent and related to one another. Secondly, we examined if exploration behaviour, a component of the reactive proactive axis in great tits that has been linked to numerous functional behaviours (Hollander et al, 2008; Quinn et al, 2011a; Quinn et al, 2011b; Cole and Quinn, 2011; Stuber et al, 2013), and is a repeatable trait in these populations (Chapter 3), correlated with tight-sitting and hissing which could indicate that the traits form part of a behavioural syndrome. Thirdly, as predicted by POLS we examined if tight-sitting positively correlated with other indicators of parental investment such as clutch size and nest age, or environmental factors that can significantly influence the value of a reproductive attempt like lay date and habitat type (Chapter 2). Finally, we examined if tight-sitting behaviour influenced reproductive success at two critical stages of the reproductive cycle, hatching and fledging.

Methodology

Nest recording

Great tit study populations were established in 5 deciduous and 3 coniferous woodland fragments located in the Bandon Valley, Western County Cork, Ireland. Nest-boxes (Schwegler Woodcrete; dimensions: 260H x 170W x 180D mm; entrance radius 32mm) were attached to trees approximately 1.5m above the ground allowing us access to the nest at eye-level without removing the nest-box from the tree. Nest-boxes were checked weekly from mid-April by two observers. Clutch initiation date (lay date, March 1st = 1), clutch size, and hatch date were recorded for each nest (see next section for details about nests visits during incubation). At least 10 days after hatching, adults were trapped at the nest-box. All unringed adults were fitted with a unique British Trust for Ornithology (BTO) metal leg band on one leg and a passive integrated transponder (PIT) tag attached to a moulded plastic ring on the other leg. Birds were aged (less than one year or older than one year) and sexed based on plumage characteristics (Svensson, 1992). 15 days after hatching, all surviving nestlings were fitted with BTO metal rings. All nest-boxes were checked at the end of the season to record any unhatched eggs or ringed chicks that did not fledge.

Simulated predation event

In 2014 and 2015 we assessed female behavioural responses to disturbance on the nest during incubation, a period that lasts for approximately 13 days in great tits (Gosler, 1993). The same protocol was used for each nest check until hatching was observed (n = 286 observations of 156 nests). The observer approached the nest-box, stood at arm's length and removed the face-plate. If there was no bird present inside the box, the observer recorded the individual as not present (NP). If a female was present, the observer remained stationary in front of the open nest-box for 20 seconds. If the bird flew at any point, the observer recorded the latency to flee (0 – 20 seconds). Birds that did not flee during the trial were given a maximum latency of 20s. Any hissing vocalisations performed during the trial were recorded and intensity was calculated as the total number of "hisses" performed by an individual during a trial. Due to the nature of the nest recording methodology, in some cases trials were carried out before clutch completion or after eggs had hatched. These results were disregarded from further analyses. A subsample of nests (n = 110) were retested before hatching to assess within-season repeatability of the behaviour (mean number of days between trials ± SD = 4.84 ± 2.45).

Exploration Behaviour

During the winter of 2014 and 2015 (Jan-March) we assessed individual exploration of a novel environment, a repeatable behavioural trait within our populations (Chapter 3). Birds were captured in study sites and transported to an aviary in University College Cork, Ireland, where they were housed individually in cages for up to one week. On the morning of the second day in captivity, individuals were allowed to feed for three hours after first light before being moved, sequentially, to an observation room containing five artificial trees. Individuals were observed for two minutes during which time all movements were counted and classified into two categories by hidden observers. Hops were movements within a tree or perch, while flights were movements between perches and trees (adapted from Verbeek, et al., 1994). After two minutes, the bird was returned to its original cage. The number of flights and hops was entered into a Principal Component Analysis, the first component of which explained 78% of the variance and had a positive loading for both behavioural measures. We therefore used PC1 as an estimate of exploratory behaviour (EB) for each individual. Higher scores indicate more exploratory individuals.

Statistical Analysis

Within- and between-season repeatability of female latency to flee (s) was estimated using Spearman's rank correlation test. For between-season repeatabilities we used the first measure taken from each season to avoid within-season habituation to the observer. Repeatabilities calculated using a generalized linear mixed effects model approach were qualitatively similar (Nakagawa and Schielzeth, 2011). Because we found the behaviour to be significantly repeatable within seasons (see results below), all further analyses include only the first measure taken for each nest. Variation within vocalisation data was low (Fig 1b), so we elected to analyse the behaviour as a binary trait (1 = performed at least one hiss vocalisation / 0 = did not vocalise) and tested within- and between-season repeatability using a binomial generalized linear mixed effects model approach (Nakagawa and Schielzeth, 2011). To test if the vocalisation and fleeing latencies were independent of each other we fitted a binomial GLMM with hissing as a binary dependent variable, and fleeing latency as an independent variable. Individual identity was fitted as a random effect. To test if female behaviours were confounded by observer identity, we fitted a censored Cox's proportion hazards model with latency to flee as a function of observer identity (Crawley, 2007), and a generalised linear model (GLM) with number of hiss vocalisations as the dependent variable and observer identity as a fixed factor. There was no significant relationship in either case (flee latency: $z = 0.174$; $p = 0.862$; vocalisations: $t = 1.539$; $p = 0.125$), therefore we do not include observer identity as a variable in further analyses.

We examined the links between the breeding environment, reproductive investment and female tight-sitting response using censored Cox's Proportional Hazards model. Female response (flee latency (s)) was fitted as the dependent variable, while yearly mean-centred lay date, clutch size, nest age (date of the test minus lay date), year and habitat type were fitted as independent variables. In approximately 30% of cases, female identity was unknown due to nest failure before trapping. As our results indicated a certain proportion of failures may have been linked to female fleeing responses (see results below), excluding nests with unknown females may disproportionately affect females with shorter fleeing latencies. We therefore analysed the complete data set, including nests with unknown females. Site and year were fitted as random effects. Additionally, to test for habitat specific effects of season on female responses, we fitted the same model with a lay date × habitat type interaction term. The analyses were repeated on a restricted data set including only females of known identity.

To test if female responses were related to exploration behaviour, we fitted a censored mixed effects Cox's Proportional hazards model with latency to flee as the dependent variable, and EB, clutch size, nest age (lay date minus the date of the test), habitat type and female age as fixed effects. Female identity, year and site were included as random effects. We also fitted an age × EB interaction term to determine if there was an age specific effect of EB on female fleeing latency.

We tested if tight-sitting behaviour was a significant predictor of nest desertion during incubation by fitting a binomial GLMM with nest failure as the dependent variable (1 = eggs did not hatch, 0 = eggs hatched), latency to flee, clutch size, yearly mean-centred lay date and the number of trials carried out per nest to control for differences in the amount of disturbance per nest. Year and site were fitted as random effects. As we were unable to identify females at nests that failed before hatching, we did not fit female identity as a random effect in this model. As studies indicate that personality types may differ in their stress responses to recurrent stimuli (Carere et al, 2001), we tested if the number of trials influenced the probability of desertion differently amongst birds of different flee latencies by fitting the same model outlined above including an interaction term of latency to flee × number of trials. We also fitted interaction terms of flee latency × lay date, and flee latency × habitat type, to test if environmental factors influenced desertion differently amongst tight-sitters and non-tight-sitters. Because of the risk of pseudoreplication causing a type 1 error (i.e. the same females deserting multiple times), we reanalysed a restricted dataset containing only breeding attempts in 2014 that began prior to the first desertion that occurred in each site. Our results were similar (see results below), in that tight-sitting behaviour was a significant predictor of desertion during incubation in the restricted dataset also (GLMM: $z = -1.987$; $p = 0.047$), suggesting that our results were not due to a type 1 error. We used a Fisher's exact test to test if the proportion of nests deserted before hatching differed between years when the predation risk trials were not carried out (2013) and years where females were subjected to systematic predation risk trials (2014 and 2015). To test if tight-sitting was related to overall nest success we fitted a poisson GLMM with number of chicks fledged as the dependent variable, flee latency, habitat type, yearly mean-centred lay date, and clutch size as dependent variables, and year and site as random effects. We then repeated this analysis without nests that failed before hatching.

All analyses were conducted in R (v.3.22, R Core Team 2015). Cox proportional hazards models were fitted using the "survival" package and the "coxme" package when specifying random terms (Therneau, 2015). Generalized linear mixed effects models (GLMM) and linear mixed effects models (LMM) were fitted using the "lme4" package (Venables and Ripley 2002). P-values of LMMs were assessed using Likelihood-Ratio tests. We applied a backwards stepwise elimination procedure for model selection, removing non-significant terms from models with a significance level of $\alpha \geq 0.10$, unless they were included as part of a significant interaction term. An information- theoretic approach to model selection (Burnham & Anderson, 2002), based on comparisons of Akaike Information Criterion (AIC) values produced qualitatively similar results. Results of non-significant terms are reported from the minimum model in which they were included.

Results

Determinants of offspring defence

75% of incubating females tested for the first time in a season remained tight-sitting on the nest for the entire 20 second trial (Mean fleeing latency ± SD: 15.54 ± 7.91 (s); n = 149; Fig. 4.1a). Female latency to flee was significantly repeatable within seasons ($r_s = 0.516$; $p = 0.001$; n = 110), and between seasons ($r_s = 0.581$; $p = 0.002$; n = 27). 16% of females tested for the first time in a season performed at least one hiss vocalisation during the trials (mean number of hiss vocalisations ± SD: 0.60 ± 1.92; n = 149; Fig. 4.1b). The likelihood of an individual hissing when disturbed was not significantly repeatable within seasons (r = 0.115; se = 0.032; $p = 0.100$; n = 110), or between seasons (r = 0.085; se = 0.067; $p = 0.392$; n = 27). The likelihood of an individual performing at least one hiss vocalisation and its fleeing latency were not significantly correlated (GLMM: z = -0.134; $p = 0.893$; n = 105).

Females incubating larger clutches took significantly longer to flee following the predation risk trial (Table 4.1). Visualisation of the data revealed that this effect was primarily driven by low numbers of tight-sitters incubating clutches of 3 eggs; 42% of females tight-sat on clutches of 3, compared to an average 76% of females tight-sitting on clutches of size greater than 3 (Figure 4.2). Neither lay date (yearly mean-centred), nor the habitat type × lay date interaction were significantly related to flee latency (Table 4.1). None of the other fixed effects significantly correlated with flee latency (Table 4.1). Restricting analyses to only known females, we found that clutch size and fleeing latencies were not significantly related (z: -0.35; $p = 0.730$; n = 105).

Exploration behaviour was not related to tight-sitting (Cox Proportional Hazards Model: z = -0.08; p = 0.93; n = 44; Appendix 4.1), and we found no evidence that the relationship between EB and tight-sitting varied across ages (EB × age interaction: z = -0.59; p = 0.55; n = 44; Appendix 4.1).

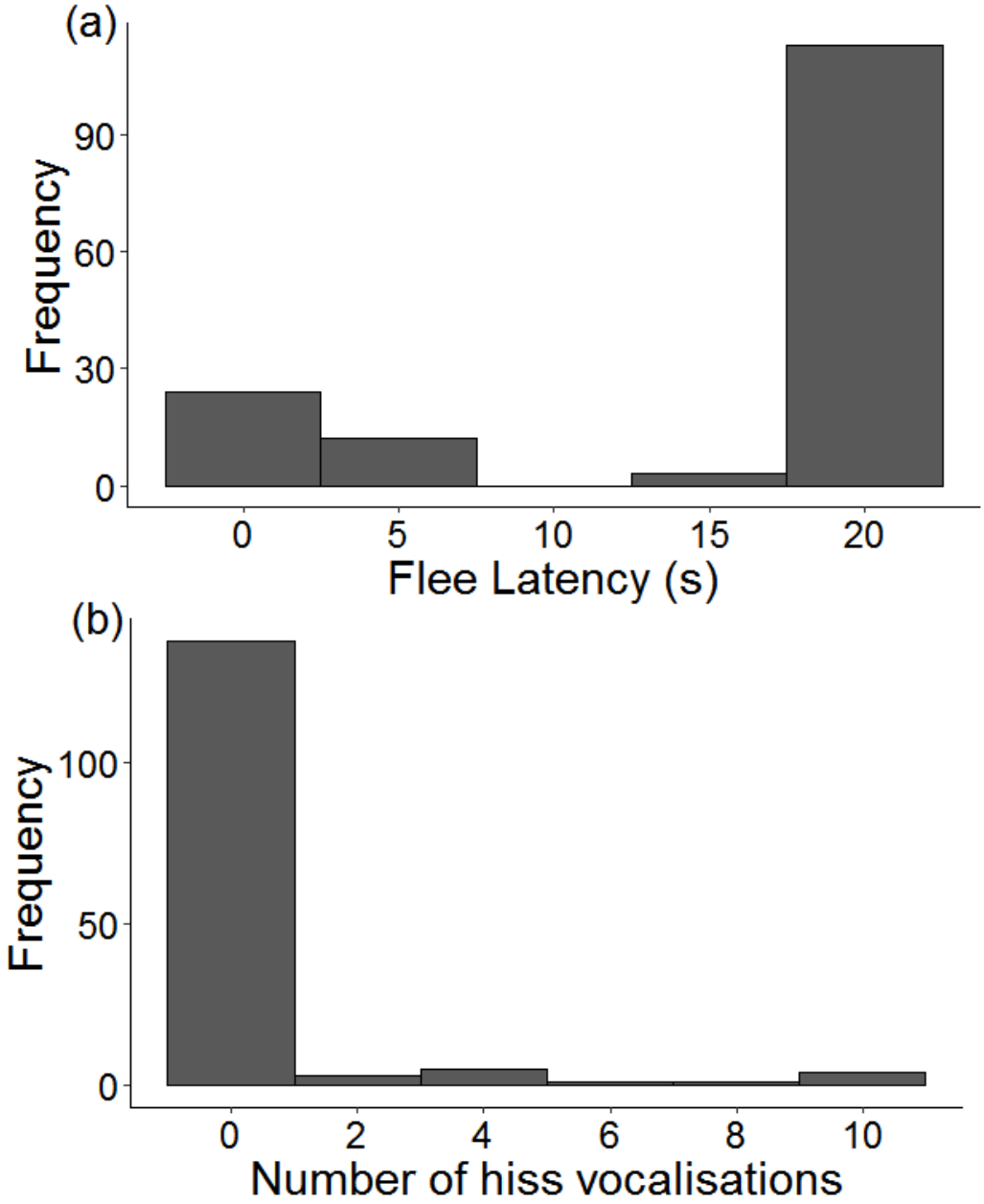


Figure 4.1. Distribution of female responses to disturbance on the nest during incubation (n = 149). (a) Counts of individuals that fled or remained on the nest. Value on the x-axis indicates latency to flee (s). Trial concluded after 20 seconds and individuals that remained on the nest at this point were designated a latency of 20 seconds. 0 indicates individuals fled immediately. (b) Counts of individuals according to the number of hiss vocalisations performed during trials.

Table 4.1. Cox proportional hazards model of female latency to flee following disturbance during incubation, as a function of reproductive investment and environmental effects (n = 149). Site and year were fitted as random effects. × denotes an interaction term. Coefficients, standard error (SE), z-values and p-values for non-interaction terms are reported from models without interaction term fitted.

Parameters	**Coefficient ± SE**	**z-value**	**p-value**
Clutch Size	0.823 ± 0.148	-2.40	0.29
Nest Age[a]	1.023 ± 0.417	0.46	0.580
Lay Date[b]	0.977 ± 0.023	-1.00	0.320
Habitat Type[c]	1.063 ± 0.482	0.13	0.900
Habitat Type × Lay Date	0.914 ± 0.063	-1.43	0.150

[a] Days since first egg laid; [b] Yearly mean-centred; [c] Conifer set to 0.

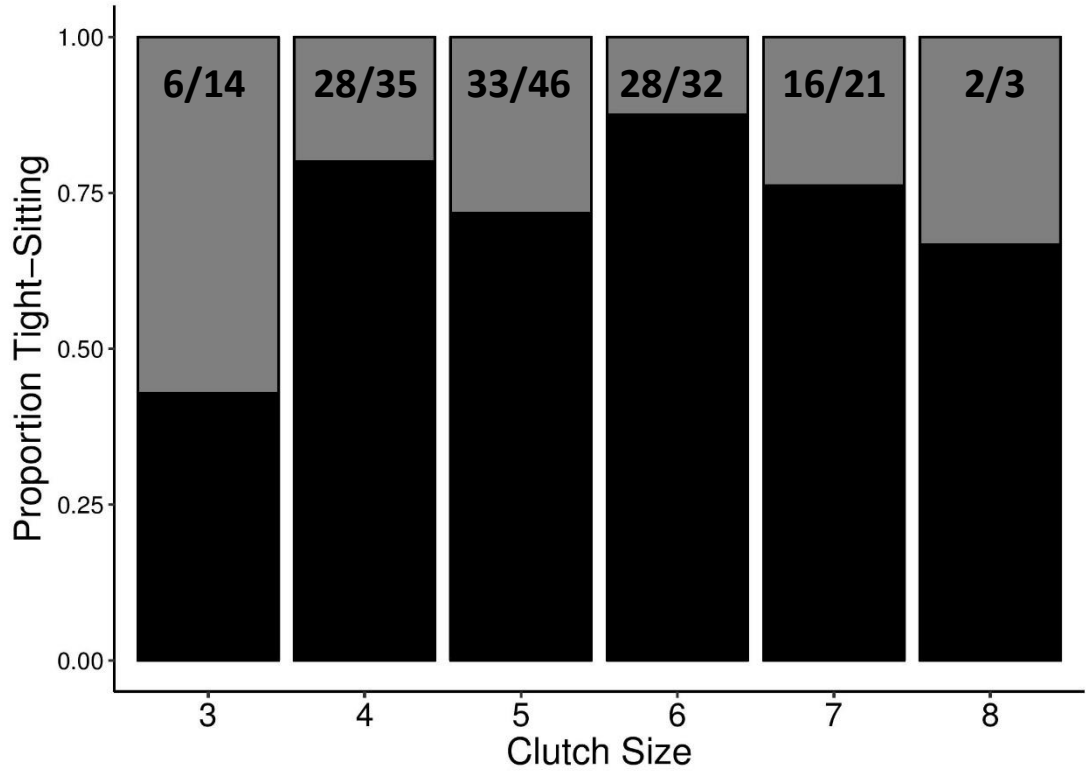


Figure 4.2. Stacked bar chart representing the proportion of females that fled the nest and tight-sat when disturbed during incubation. Tight sitters represent females remaining after 20 seconds elapsed (Black). Females that fled prior to 20s represented by grey. X-axis indicates clutch size. Numbers within bars indicate the number of tight-sitting females over the total sample size (Cox proportional hazard model: z = -2.00; *p* = 0.046; n = 149).

Tight-sitting and Fitness

Females that deserted their nests during incubation had shorter fleeing latencies (mean ± SD: 8.54 ± 2.65; n = 13) than those at nests that did not desert before hatching (mean ± se: 16.42 ± 0.62; n = 136; Fig. 4.3; Table 4.2). None of the other single-term fixed effects correlated with desertion including clutch size and lay date (Table 4.2). The two-way interaction term of number of trials × flee latency was not significantly related to desertion during incubation (Table 4.2). The two-way interaction between lay date × fleeing latency was significantly related to desertion (Table 4.2); desertion rates were constant across the season in tight-sitting females, but increased with lay date in females that fled the nest (Table 4.2; Fig 4.4). Desertion rates did not significantly differ between 2013 (4/45 nests deserted before hatching), and 2014/2015 (13/149 nests deserted; Fisher's exact test: p = 0.7674). The number of fledglings was not related to fleeing latencies (GLMM: z = -0.416; p = 0.678 Appendix 4.2). Restricting analyses to only nests where eggs successfully hatched, tight-sitting was not significantly related to the number of nestlings fledged (GLMM: z = -0.833; p = 0.405; n = 136).

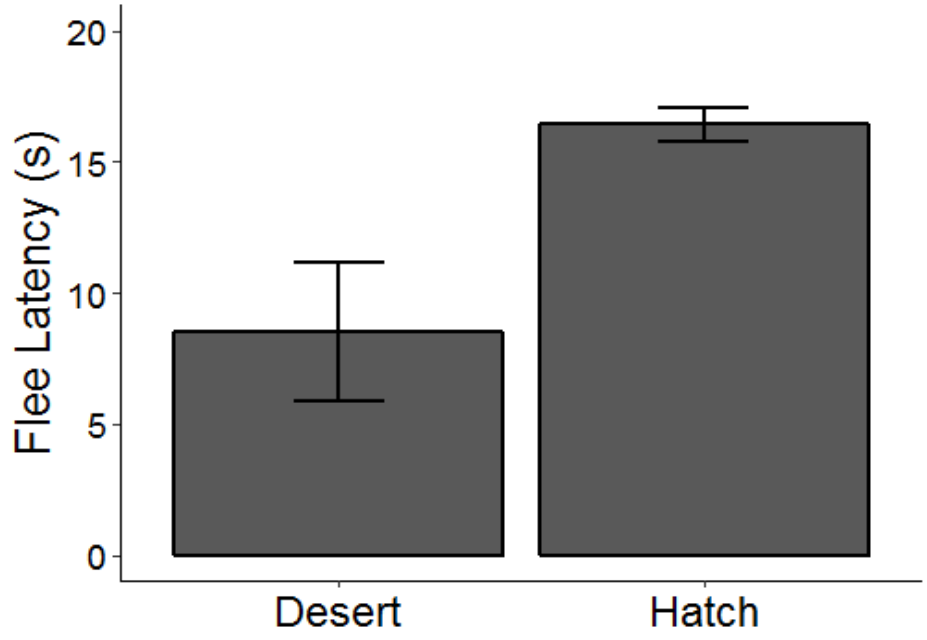


Figure 4.3. Average fleeing latencies amongst females that deserted their clutches during incubation (mean ± SD: 8.54 ± 2.65; n = 13), and those that successfully hatched nestlings (mean ± se: 16.42 ± 0.62; n = 136).

Table 4.2. Binomial GLMM with desertion during incubation (1 = desert; 0 = did not desert) as the dependent variable (n = 149). Year and site were fitted as random effects. × denotes interaction term. Estimates, standard error (SE), z-values and p-values of non-interaction terms reported from models without the interaction terms fitted.

Parameters	**Coefficient ± SE**	**z-value**	**p-value**
Flee Latency	-0.114 ± 0.033	-3.447	0.001
Clutch Size	-0.256 ± 0.283	-0.904	0.366
Number of Trials	-0.641 ± 0.501	-1.280	0.201
Habitat Type[a]	-0.259 ± 0.935	-0.276	0.782
Lay Date[b]	0.067 ± 0.039	1.692	0.091
Flee Latency × Number of Trials	-0.054 ± 0.061	-0.883	0.377
Flee Latency × Lay Date	-0.016 ± 0.006	-2.708	0.007
Flee Latency × Habitat Type	-0.019 ± 0.109	-0.172	0.864

[a] Conifer set to 0; [b] Yearly mean-centred.

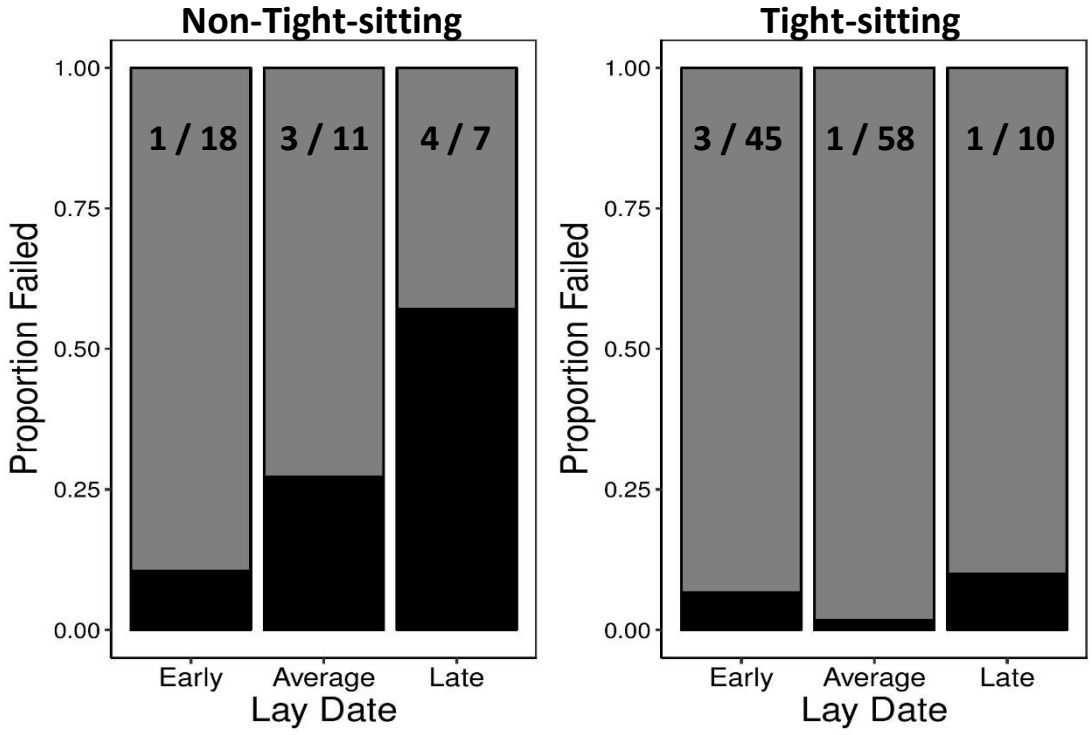


Figure 4.4. Stacked bar chart indicating the proportion of nests that failed prior to hatching versus categorised yearly mean-centred lay date for tight-sitting females and those that fled. Lay date split equally into 3 categories: Early = -15 to -4, Average = -3 to 7, Late = 8 to 19. Numbers within bars equal the number of nests failed (black) and the total number of nests in that category.

Discussion

Female tight-sitting behaviour was repeatable but did not correlate with a known proxy for the reactive-proactive axis, exploration behaviour, suggesting that the two behaviours do not form a behavioural syndrome. Tight-sitting behaviour correlated with clutch size, an indicator of female investment in the reproductive attempt. Individual tight-sitting behaviour correlated with a measure of fitness from the early stages of breeding, as the nests of tight-sitting females were less likely to fail during incubation than nests of females that fled. A more representative measure of fitness, the number of fledglings, was not significantly related to tight-sitting behaviour.

Determinants of offspring defence

Tight-sitting behaviour was significantly repeatable both within and between seasons. Hissing was not repeatable within or between seasons, and was not related to tight-sitting. The proportion of individuals that hissed in response to predation risk (16%) was much less that has been reported in other studies where it is a repeatable behavioural trait (70-80% of incubating females hiss; Krams, 2014a). This suggests that the prevalence, repeatability and thus adaptive significance of this trait is population specific, although we cannot rule out that females hiss less in response to humans rather than natural nest predators which have been used as a stimulus in other studies. For instance, Krams and colleagues (2014a), reported much higher occurrences of hissing vocalisations; however in that study, incubating females experienced a woodpecker head entering the nest-hole which may be a more realistic representation of a predation event. Comparative studies with identical methodology across the great tit range recording the prevalence of hissing behaviour could elucidate the environmental selection pressures that promote this form of deimatism within populations. Females incubating larger clutches were less likely to flee in response to disturbance, an effect driven primarily by females incubating clutches of just three eggs (Fig. 4.2). Positive correlations between nest defence and clutch size are well established in the literature (Montgomerie and Weatherhead, 1988), and may arise because of the associated higher reproductive value and greater energetic investment associated with larger clutches (Pettifor et al, 2001; Visser and Lessells, 1991).

Tight-sitting was not significantly related to exploration behaviour which suggests that against expectations, the trait is not linked to the reactive-proactive axis in this population. Evidence is mixed as to whether the reactive-proactive axis is linked with behaviours

indicative of parental investment as predicted by pace of life syndrome theory. For instance, links between exploration behaviour and provisioning rates have been recorded in the closely related blue tit (Mutzel et al, 2013), but not in great tits (Patrick and Browning, 2011).

Likewise, risk taking at the nest has been linked with exploration behaviour in several other populations (Hollander et al, 2008; Cole and Quinn, 2014), but here we found no evidence of a relationship. There are several potential explanations for our results. Firstly, behavioural syndromes are a property of populations rather than species (Bell et al, 2005; Dingemanse et al, 2007) and may emerge in environments where ecological pressures favour specific correlations between behavioural traits (Wilson, 1998; Bell, 2005; Dingemanse et al, 2007). Indeed, predation pressure appears to be a key environmental variable that leads to the emergence of aggression-boldness syndromes (Bell, 2005; Dingemanse et al, 2007; Evans et al, 2010). Thus, the lack of a relationship here between exploration behaviour and tight-sitting may be adaptive, arising because of homogenous environmental factors across populations, such as lower densities and diversities of natural nest predators (McDonald, 2002; Balmer et al, 2013). This may also explain why hissing responses were rare here compared to populations in mainland Europe (Krams et al, 2014a). Alternatively, our measure of exploration behaviour may not be an accurate proxy for the reactive-proactive axis, perhaps due to methodological issues with our exploration assays, although this seems unlikely as they were based on methods used widely in the literature (Verbeek et al, 1994; Dingemanse et al, 2002; Hollander et al, 2008; Carter et al, 2013). Finally, individual state-based differences are thought to underlie personality and behavioural syndromes (Wolf and Weissing, 2010). The two behaviours observed here may not be linked to the same underlying state. Therefore, although consistent individual behavioural variation exists, differences are not correlated across behavioural contexts. For instance, studies have found links between exploration behaviour and metabolic rate or stress responsiveness (*reviewed in* – Koolhaas et al, 1999; Groothuis and Carere, 2005; Careau et al, 2008; Baugh et al, 2013); however links between individual differences in exploration behaviour and physiological reproductive investment (i.e. clutch size) in the great tit are often not present (Dingemanse et al, 2004; Both et al, 2005; Mutzel et al, 2013; Nicolaus et al, 2015), even though the latter clearly influences risk aversion during this period of the breeding season (Montgomerie and Weatherhead, 1988).

Tight-sitting and fitness

Nests incubated by females that fled in response to predation risk - a trait that was repeatable across years - were more likely to fail before hatching, resulting in potentially reduced fitness for these risk averse females. As nests failed due to incomplete incubation, it appears that females that flee their nests were more likely to abandon the reproductive attempt, particularly later in the season when reproductive outcomes were less likely to be successful (Chapter 2). Desertion ends investment in the current reproductive effort and conserves residual reproductive value (Székley et al, 1996). Studies indicate that females may be more likely to desert their clutches during incubation if the expected fitness benefits of raising current offspring are low due to poor environmental conditions (Ackerman and Eadie, 2003; Ouyang et al, 2012). A major prediction of the pace of life theory is that life history trade-offs maintain variation in strategies within populations (Réale et al, 2010). Identifying females earlier in the season is essential to test this hypothesis and determine if the relationship between tight-sitting and desertion is adaptive, which may be the case if both strategies result in similar subsequent lifetime reproductive success.

Nest failure was independent of the number of trials carried out, suggesting that nest predation trials did not trigger abandonment directly and that desertion and tight-sitting may be intrinsically linked. We also found no difference between the proportion of nests abandoned before hatching in 2013 when tight-sitting behaviour was not assessed, and the proportion of nests abandoned in 2014/2015 when trials were carried out. Although this does not prove that abandonment was unrelated to disturbance, as nests in 2013 were systematically checked to record reproductive parameters, it suggests that the addition of further disturbances caused by repeated predation-risk trials did not lead to increased rates of abandonment amongst incubating females.

Tight-sitting was related to reproductive outcomes during the incubation stage but not at the fledgling stage. Analyses including and excluding nests that failed during incubation indicate that there was no significant difference between tight sitters and non-tight sitters in terms of the number of nestlings fledged. This suggests that despite desertions and the smaller clutches laid by females that fled, tight sitters did not have higher reproductive success. The reasons for this are unclear. Perhaps tight-sitting may correlate with another aspect of parental care later in the season, which has negative consequences for reproductive success, thus constraining reproductive outcomes.

To conclude, we have identified a repeatable behavioural trait, tight-sitting, that is significantly related to female reproductive investment and reproductive outcomes. Exploration behaviour, a component of the reactive-proactive axis does not predict tight-sitting behaviour; however risk averse females are more likely to desert their nests, particularly during periods of the season associated with reduced reproductive outcomes. Identifying females during incubation could elucidate if risk averse females have higher survival rates than risk prone tight-sitters indicating that the correlation between the two traits is adaptive, as predicted by POLS.

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Chapter 4: Appendices

Appendix 4.1. Cox proportional hazards model of female latency to flee as a function of exploration behaviour, controlling for reproductive investment (n = 42). Female identity, site and year were fitted as random effects. × denotes an interaction term. Coefficients, standard error (SE), z-values and p-values for non-interaction terms are reported from models without interaction term fitted.

Parameters	**Coefficient ± SE**	**z-value**	**p-value**
EB	0.951 ± 0.595	-0.08	0.93
Clutch Size	-2.584 ± 0.859	-0.30	0.76
Nest Age[a]	0.239 ± 1.270	0.45	0.65
Female Age[b]	2.322 ± 1.187	0.68	0.50
Habitat Type[c]	-0.320 ± 1.183	-0.96	0.34
EB × Female Age	-0.786 ± 1.330	-0.59	0.55

[a] Days since first egg laid; [b] Juvenile set to 0; [c] Conifer set to0.

Appendix 4.2 Poisson GLMM with the number of chicks fledged as the dependent variable (n = 149). Year and site were fitted as random effects.

Parameters	**Coefficient ± SE**	**z-value**	**p-value**
Lay Date[a]	-0.014 ± 0.010	-1.454	0.146
Clutch Size	-0.143 ± 0.054	-2.659	0.008
Habitat Type[b]	-0.602 ± 0.274	-2.195	0.028
Flee Latency	-0.003 ± 0.008	-0.416	0.678

[a] Yearly mean-centred; [b] Conifer set to 0.

Chapter 5

Proactive females have lower reproductive success in a highly fragmented landscape.



Abstract

The adaptive significance of personality variation remains unclear. Although the role of habitat heterogeneity in maintaining personality variation is thought to be key, few studies have examined the fitness consequences of personality in different environments. We studied how individual exploration of a novel environment, a commonly assayed component of the reactive-proactive axis, and a repeatable trait in these populations, was related to provisioning behaviour and fitness outcomes in wild great tits across coniferous and deciduous woodland fragments. The reactive proactive axis has been positively linked to competitive ability and the pace of life syndrome, and negatively to responsiveness to environmental conditions, suggesting links with life history variation arise in a variety of ways. We found no relationship between male or female exploration behaviour and clutch size as a measure of reproductive investment. Female exploration behaviour was negatively correlated with fledgling number when controlling for clutch size, a relationship that was observed across both habitat types. Female provisioning appears to be a key factor underlying this relationship as faster exploring females provisioned at a slower rate than slow explorers controlling for brood size. This result is contrary to what has been reported elsewhere, where higher provisioning rates facilitate greater reproductive success for faster exploring females. Male exploration behaviour was negatively related to fledgling condition in deciduous fragments, a relationship that was reversed in coniferous fragments. Our results suggest that although the effects observed are context and sex specific, individuals at the slow end of this personality axis are likely to be favoured across our study system.

Introduction

Identifying the fitness consequences of traits along environmental gradients is a critical step towards understanding the adaptive significance of phenotypic variation and how traits evolve in the wild (Futuyama, 2005). Traditionally, studies have focused on morphological or physiological traits that can be measured with minimal error, while the study of behavioural phenotypes in an evolutionary ecological framework has been neglected due to difficulties involved with obtaining standardized individual measurements (Sih et al, 2004b; Réale et al, 2007; Siepielski et al, 2009). Increasingly, standardised protocols for measuring and analysing individual behavioural variation are being used to further our understanding of why consistent individual behavioural variation, or personality, arises (Sih et al, 2004b; Dingemanse and Wolf, 2010; Sih et al, 2015).

The term personality refers to consistent among individual differences in behavioural patterns (Sih et al, 2004a). These individual differences may also be conserved across behavioural contexts (e.g. aggressiveness towards competitors and boldness when foraging), forming suites of correlated personality traits known as behavioural syndromes (Sih et al, 2004a). Much of the early research on personality focused on describing behavioural syndromes and understanding the proximate causes underlying individual variation. Empirical evidence suggests that personality emerges because of underlying individual differences in state that constrain behaviour (Dingemanse and Wolf 2010; Wolf and Weissing, 2010; Sih et al, 2015). States may include fixed traits like sex or morphology, but labile traits may also lead to individual personality emerging if initial state differences are reinforced by behaviour, creating positive feedback loops (Wolf and Weissing, 2010; Sih et al, 2015). Individual growth rate, a trait that is often tightly linked to variation in life history strategies, is an example of a state that generally has a strong influence on behaviour (Stamps, 2007; Biro and Stamps, 2008). Faster growing individuals tend to be more risk prone and aggressive when foraging, whereas slower growing individuals invest less in costly behaviours like aggression, prioritising self-maintenance (Stamps, 2007; Biro and Stamps; 2008; Réale et al, 2010). As individual differences in state may arise due to phenotypic plasticity or genetic polymorphism, so too may the corresponding personality traits (Wolf and Weissing, 2010).

More recent work has focused on the ultimate causes of personality and how individual variation is maintained in the wild (Dingemanse and Wolf, 2010). If variation arises purely

due to phenotypic plasticity, then environmental heterogeneity will cause differences in the distribution of personality traits between populations in various environments, regardless of fitness differences amongst phenotypes (Wolf and Weissing, 2010). However several studies have found evidence of an additive genetic component to personality (e.g. Dingemanse et al, 2002; Quinn et al, 2009), and since personality can influence fitness (Smith and Blumstein, 2008), this implies that personality traits may evolve in the wild through natural selection (Dingemanse and Réale, 2013).

As with morphological or physiological phenotypes that display limited plasticity, incorrect personality-environment matching will decrease the fitness of mismatched individuals (DeWitt et al, 1998). Mismatches may arise due to social factors such as the distribution of behavioural types within a population, leading to frequency dependent selection (Wolf and McNamara, 2012). Environmental heterogeneity can also cause phenotype-environment mismatches, leading to personality-specific fitness differences among individuals along environmental gradients (Wolf and Weissing, 2010). Several studies have found evidence of contrasting patterns of natural selection acting on personality traits along environmental gradients related to temperature (e.g. Goulet et al, 2016; Clark et al, 2017), food availability (e.g. Dingemanse et al, 2004; Patrick and Weimerskirch, 2014), population densities (e.g. Quinn et al, 2009; Nicolaus et al, 2016), and predation pressure (e.g. Réale and Festa-Bianchet, 2003; Pruitt et al, 2012), as well as differences in the phenotypic distribution of personality traits among populations in different environments (e.g. Biro and Post 2008; Dubuc-Messier et al, 2017). In many cases however, the behavioural mechanisms that lead to these differences emerging are unclear.

Foraging is one of the most fundamental behaviours in the natural world, and can have significant fitness consequences (Ritchie, 1990; Lemon, 1993). Foraging efficiency may be influenced by a variety of local factors including resource distribution (e.g. Tremblay et al, 2004), competition (e.g. Svanbäck and Bolnick, 2007) and predator densities (Milinski and Heller, 1978), which may vary widely between habitats. As personality may limit certain aspects of individual foraging ability, for instance because of aversion to risky situations (Quinn et al, 2012), or because of differences in information use (van Overveld and Matthysen, 2013; Kurvers et al, 2010), or space use (van Overveld and Matthysen 2009), this may lead to maladaptive behaviours emerging in some contexts with negative consequences for fitness. Personality-specific foraging tactics are therefore seen as a key factor driving

fitness differences among behavioural types in different environments; however, few studies have examined how personality influences foraging behaviours in the wild along environmental gradients (*but see* – Patrick and Weimerskirch, 2014).

The reactive-proactive continuum is a widely studied axis of personality. At one extreme, proactive individuals are exploratory, aggressive and routine forming in their behaviour, while at the other, reactive individuals are less bold, less aggressive and more sensitive to environmental variation (*reviewed in* - Koolhaas et al, 1999). The reactive-proactive axis has been linked to fitness via reproductive success (e.g. Mutzel et al, 2013), but the direction and strength of these relationships may be context dependent (Dingemanse et al, 2004; Quinn et al, 2009; Nicolaus et al, 2016). There is some evidence that proactive individuals may invest more in reproduction, reproducing earlier and producing larger broods than reactive individuals due to correlations between life history strategies and personality, also known as pace of life syndromes (POLS; Réale et al, 2010; Montiglio et al, 2014; Dubuc-Messier et al, 2017). The success of these strategies may be highly dependent on environmental resource availability (Boon et al, 2007), and differences may only emerge when resource availability does not limit reproductive investment (Nicolaus et al, 2016). Furthermore, proactive and reactive individuals may also display different foraging tactics (van Overveld and Matthysen, 2009), including differences in activity (Mutzel et al, 2013; but see – Patrick and Browning, 2011), and prey choices (Exernová et al, 2007; Serrano-Davies et al, submitted). For altricial species, parental foraging behaviours have significant consequences for reproductive success (Mutzel et al, 2013); however there is a dearth of information regarding the links between personality, foraging and fitness across environments with different resource distribution and availability (*but see* - Patrick and Weimerskirch, 2014).

In this chapter, we examined the links between a repeatable component of the reactive-proactive axis, exploration behaviour (EB) and reproductive success in wild great tit (*Parus major*) populations established in two habitat types, deciduous and coniferous fragments. Chapter 2 showed that breeding densities are higher in deciduous fragments than coniferous fragments, which may influence competition and thus reproductive success (Wilkin et al, 2006). Prey diversity was similar between habitat types, although adults provision at lower rates in deciduous fragments suggesting that competition or local food availibility limits foraging ability (Chapter 2). Although it appears that individuals settle preferentially in deciduous habitat (Chapter 2), populations breeding in coniferous fragments laid larger

clutches and had greater reproductive success than those in deciduous fragments (Chapter 2). Previous studies have shown that EB may influence the acquisition of high quality territories in great tits, with faster exploring males acquiring and defending territories which had hosted more successful reproductive attempts in previous years (Both et al, 2005). Therefore, we predicted that male EB would negatively correlate with lay date and positively correlate with clutch size in both habitat types, as mates of faster exploring males would have greater access to the resources necessary for reaching threshold breeding condition. In line with the POLS hypothesis, we predicted that faster exploring females would lay earlier and lay larger clutches than slower exploring females, but that the relationship would be more pronounced in coniferous sites where local breeding densities and thus competition is lower. Previous studies have shown that male provisioning and subsequent reproductive success correlates negatively with EB, as more aggressive males may compromise parental investment due to overinvestment in territorial behaviours (Duckworth, 2008; Mutzel, 2013). Therefore, we predicted a negative correlation between male EB and provisioning rates and fledgling mass in both habitat types. We expected the relationship to be stronger in deciduous fragments where higher breeding densities could lead to more frequent territorial intrusions. Amongst females, we predicted that faster exploring females would provision at higher rates, and would produce more fledglings than slow females in line with POLS, especially in coniferous fragments where local competition for resources is lower. Caterpillars are an important food item for breeding great tits, and nestlings provisioned caterpillar rich diets attain higher quality at fledging (Wilkin et al, 2009), which predicts recruitment (Monrós et al, 2002). Assuming that male EB predicted territory quality, we also expected that faster exploring males would provision more caterpillars than slow exploring males, and that to compensate for low levels of preferable prey slow exploring males would provision their offspring a more diverse diet.

Methodology

Nest recording

Nest-box study populations were established in three coniferous, and five deciduous woodland patches in the Bandon Valley, Western Co. Cork, Ireland in December 2012. From April 2013 and every year thereafter, nest-boxes were checked weekly to ascertain nest building progress and to record first egg lay date. Nests were rechecked regularly once laying activity was discovered to accurately record clutch size and hatching date. Breeding adults were trapped at least ten days after the first egg hatched. All unringed individuals were fitted

with a British Trust for Ornithology (BTO) metal ring on one leg and a passive integrated transponder (PIT) tag on the other leg. Individual sex and age (greater than one year or less than one year), were assessed based on plumage characteristics (Svensson, 1992). Fifteen days post hatching, all surviving nestlings were fitted with BTO rings and nestling mass was recorded. All nest-boxes were checked at the end of the season to record the identity of any ringed nestlings that did not survive to fledgling and unhatched eggs. We calculated average fledgling mass per nest based on measurements taken on day fifteen, as changes in nestling mass between day 15 and fledging are negligible (Wilkin et al, 2009).

Parental provisioning and nestling diet

Parental provisioning behaviours at the nest were recorded between days eight and ten post-hatching, during the 2014 and 2015 breeding seasons. Dummy cameras were installed two days prior to filming to minimise disturbance. On the morning of filming, the dummy cameras were removed and replaced with nest cameras facing the entrance hole, positioned to record adults as they approached the nest-box. Filming occurred between 0600h and 0930h, coinciding with the daily peak of provisioning rates for adults.

When analysing the recordings, the first provisioning event after 0630hrs was used as a start point and analysis continued until the recording ended, or until 0930hrs. The sex of adults was determined by sex-specific behavioural and plumage characteristics. From each video we recorded individual provisioning rates, calculated as the number of times an individual entered the nest-box with a prey item divided by the recording duration. We also recorded the prey items provisioned, specifically the proportion of prey items provisioned that consisted of caterpillars. Diet diversity was also estimated using the Shannon-Weiner index, with prey items classified as Lepidopteran larvae, adult Lepidoptera, flying insects (Adult Diptera, and Hymenoptera) or Araneae. Occasionally, adults would provision Coleoptera, pupae or plant matter which we grouped in one category called “other”.

Exploration behaviour

During the winter (Jan-March) of 2014 and 2015, we assessed individual exploration of a novel environment, a repeatable personality trait in our populations. Birds were trapped at artificial feeding stations in the woodland fragments and transported to an aviary in University College Cork where they were housed individually in cages for up to one week. During the captivity period, birds were fed *ad libitum* sunflower seeds, peanuts and

mealworms, except for periods of food deprivation before certain behavioural assays. Birds had access to water at all times. On the morning of the second day in captivity, individuals were allowed to feed for three hours after first light, before being moved sequentially to an observation room containing five artificial trees. The majority of movements by birds were within and amongst trees; however, other perches were available within the room for birds to land on. Movements were classified as either flights or hops (Verbeek et al, 1994), with hops assessed as movements within a tree or perch, and flights as movements between perches and trees. After two minutes, the birds were returned to their home cages. All individuals were released at their site of capture. The number of flights and hops was entered into a Principal Component Analysis, the first component of which explained 78% of the variance and had a positive loading for both behavioural measures. We therefore used PC1 as an estimate of exploratory behaviour (EB) for each individual. Higher scores indicate more exploratory individuals. After a maximum of 5 days in captivity, individuals were returned to their site of capture. As great tits are relatively sedentary, we expected to observe a proportion of the individuals assayed during the winter, breeding in the nest-boxes provided the following spring.

Statistical Analysis

All analyses were conducted in R (v3.22, R Core Team 2015). The residual distributions were assessed visually and Shapiro-Wilk tests were used to determine if the data was normally distributed. When necessary, the data were appropriately transformed. All continuous fixed factors were mean-centred and rescaled by dividing by 1 standard deviation (Schielzeth, 2010). Linear Mixed Effects Models (LMM) and Generalised Linear Mixed Effects Models (GLMM) were fitted using the "lme4" package (Bates et al, 2015). Likelihood-Ratio tests (LRT) were used to assess the significance of fixed effects of LMMs. As data included relatively few breeding attempts where the behavioural phenotypes of both adults were known (n = 11 nests in conifer fragments, n = 17 nests in deciduous fragments), we examined the relationship between exploration behaviour and the reproductive success of males (n = 55 breeding attempts by 42 males) and females (n = 55 breeding attempts by 38 females) separately. Analyses were conducted on reproductive data collected from 2013 to 2015, and as previous studies have found that exploration behaviour is stable over the time periods involved here (Dingemanse et al, 2002), we used the first measure of exploration behaviour recorded for each individual. We applied a backwards stepwise elimination procedure for model selection, removing non-significant terms from models with a significance level of $\alpha \geq$

0.10, unless they were included as part of a significant interaction term. An information-theoretic approach to model selection (Burnham & Anderson, 2002), based on comparisons of Akaike Information Criterion (AIC) values produced qualitatively similar results. Results of non-significant terms are reported from the minimum model in which they were included.

LMM's were fitted to analyse the relationship between EB and lay date and average fledgling mass. GLMM's with a poisson error structure were fitted to analyse clutch size and the number of fledglings produced. Fixed factors included in each model were individual EB, habitat type (conifer/deciduous), individual age (juvenile/adult), and year (2013/2014/2015). Models also controlled for the preceding breeding parameters. In the analysis of clutch size, yearly mean-centred lay date was also included as a fixed factor. In the analyses of the number of fledglings, yearly mean-centred lay date and clutch size were also fitted as fixed factors. In the analyses of average fledgling mass, brood size and yearly mean-centred lay date were also included as fixed factors. Interaction terms of EB × habitat type were also fitted to explore habitat specific effects of EB on reproductive traits. Site and individual identity were fitted as random effects in all models to control for repeated measures and site-specific effects. Sample sizes differed between analyses of fledgling mass and other dependent variables due to nest failures where fledgling mass was unavailable.

Individual provisioning rates (Square root transformed for females) and diet diversity (square transformed) were analysed using LMM's, while the proportion of caterpillars provisioned was analysed using a GLMM with a binomial error structure. Fixed factors included in all models were habitat type, year and EB. An interaction terms of EB × habitat type was also fitted. Brood size was included as a fixed factor in analyses of provisioning rate. Yearly mean-centred lay date was included as a fixed factor in analyses of diet diversity and proportion of caterpillars provisioned. Site and individual identity were fitted as random effects in all models. Finally, we examined if female provisioning rates were related to the number of chicks fledged from a nest by fitting a GLMM with a Poisson error structure. The number of chicks fledged was the dependent variable. Female provisioning rate, lay date, habitat type, year and brood size on the day of filming were dependent variables. Female ID, and site were fitted as random effects.

Results

EB was not significantly related to lay date or clutch size in males or females (Table 5.1). Controlling for clutch size, EB was negatively correlated to the number of fledglings but only in females (Table 5.2; Fig. 5.1a). Fledgling condition was not significantly related to EB in females (Table 5.2). In males, we found a significant interaction between EB × habitat type (Table 5.2). In conifer fragments fledgling mass increased with male EB but in deciduous fragments, fledgling mass declined with male EB (Fig 5.1b).

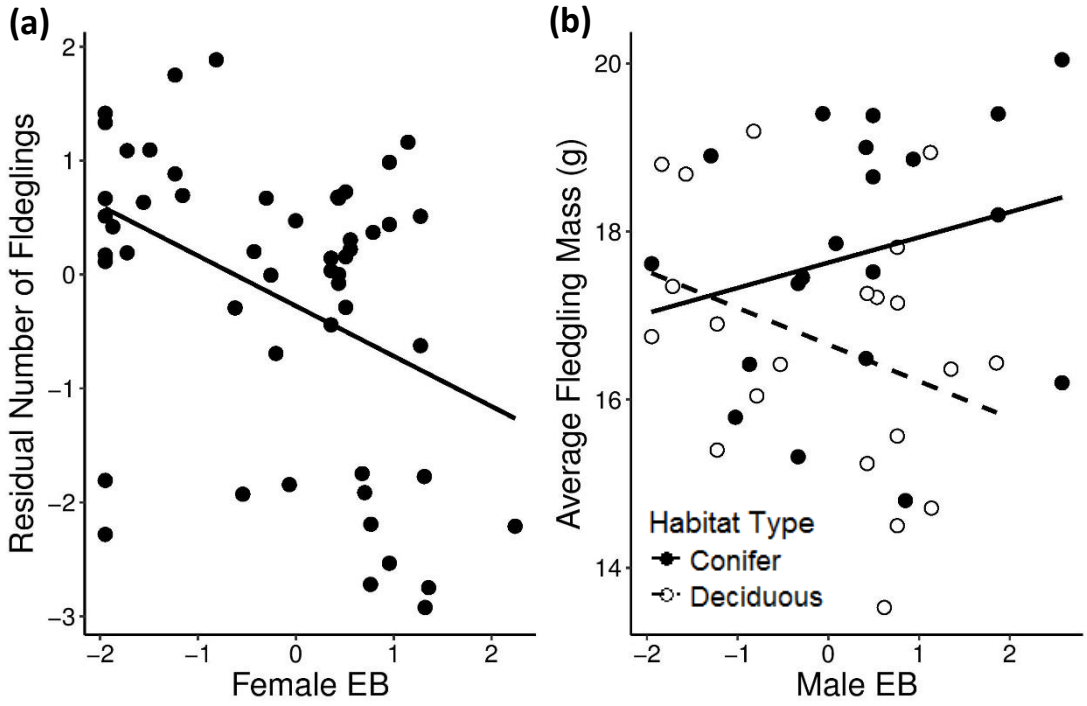


Figure 5.1. (a) Plot of female exploration behaviour and the number of fledglings produced across deciduous and woodland plots (n = 55). (b) Plot of male EB and average fledgling mass (n = 41). Filled dots and solid lines indicate nests in conifer sites, open dots and dashed lines indicate deciduous nests.

Table 5.1. Analyses of the relationship between exploration behaviour and pre-natal traits in male (n = 55) and female (n = 55) great tits. Lay date analysed using LMM, clutch size analysed using poisson GLMM (random effects: individual ID, site). P values assessed for LMM's using Likelihood Ratio Test. × denotes an interaction term. Regression coefficients and p-values of individual fixed effects shown from models fitted without interaction terms. N/A indicates fixed effects not included in models.

	Lay Date				**Clutch Size**			
	Males		**Females**		**Males**		**Females**	
Fixed effects	**β ± SE**	**p-value**	**β ± SE**	**p-value**	**β ± SE**	**p-value**	**β ± SE**	**p-value**
EB	-0.34 ± 0.87	0.724	-0.03 ± 0.77	0.932	0.04 ± 0.05	0.03	0.03 ± 0.05	0.491
Habitat [a]	5.16 ± 2.35	0.071	6.95 ± 2.88	0.017	-0.14 ± 0.12	0.231	-0.20 ± 0.12	0.09
Age [b]	-2.76 ± 1.36	0.048	-0.67 ± 1.80	0.694	-0.05± 0.13	0.725	0.07 ± 0.12	0.569
Year (2014) [c]	-6.62 ± 1.44	<0.001	-3.61 ± 2.87	0.013	-0.07± 0.19	0.726	-0.04 ± 0.19	0.835
Year (2015) [c]	-11.17 ± 1.32	-	-6.72 ± 2.70	-	-0.02 ± 0.17	0.906	-0.10 ± 0.16	0.526
Lay Date[d]	N/A	N/A	N/A	N/A	-0.04 ± 0.06	0.505	-0.02 ± 0.07	0.769
EB × Habitat	-0.38 ± 1.83	0.81	0.641	0.508	0.03 ± 0.10	0.75	-0.06 ± 0.12	0.596

[a] Conifer set to 0; [b] Juvenile set to 0; [c] 2013 set to 0; [d] Yearly mean-centred.

Table 5.2. Analyses of the relationship between exploration behaviour and reproductive success in male and female great tits. Number of fledglings was analysed using Poisson GLMM (n = 55 male observations, n = 55 female observations), average fledgling mass (n = 41 male observations, n = 40 female observations) was analysed using LMM (random effects: individual ID, site). P values assessed for LMM's using Likelihood Ratio Test. × denotes an interaction term. Regression coefficients and p-values of individual fixed effects shown from models fitted without interaction terms. N/A indicates fixed effects not included in models.

	Number of Fledglings				**Average Fledgling Mass**			
	Males		**Females**		**Males**		**Females**	
Fixed effects	**β ± SE**	**p-value**	**β ± SE**	**p-value**	**β ± SE**	**p-value**	**β ± SE**	**p-value**
EB	-0.03 ± 0.07	0.694	-0.24 ± 0.07	0.001	-0.13 ± 0.21	0.547	-0.25 ± 0.20	0.18
Habitat [a]	-0.51 ± 0.16	0.002	-0.54 ± 0.19	0.003	-1.01 ± 0.58	0.063	-0.75 ± 0.44	0.075
Age [b]	0.09 ± 0.18	0.606	0.56 ± 0.18	0.003	-0.19 ± 0.54	0.691	0.17 ± 0.49	0.698
Year (2014)[c]	-0.47 ± 0.25	0.056	-0.56 ± 0.18	0.002	-1.37 ± 0.75	0.168	-1.45 ± 0.65	0.068
Year (2015)[c]	-0.19 ± 0.19	0.324	-0.49 ± 0.21	0.146	-0.84 ± 0.64	N/A	-0.67 ± 0.57	N/A
Lay Date [d]	-0.01 ± 0.10	0.910	-0.19 ± 0.10	0.066	-0.22 ± 0.29	0.386	0.004 ± 0.26	0.986
Fecundity [e]	0.192 ± 0.082	0.020	0.56 ± 0.08	0.496	-0.11 ± 0.27	0.701	-0.01 ± 0.29	0.969
EB × Habitat	-0.15 ± 0.13	0.267	-0.09 ± 0.16	0.591	-0.89 ± 0.40	0.017	0.15 ± 0.51	0.74

[a] Conifer set to 0; [b] Juvenile set to 0; [c] 2013 set to 0; [d] Yearly mean-centred; [e] Clutch Size for Number of Fledglings, Brood Size for Fledgling condition.

There was a significant negative relationship between exploration behaviour and provisioning rate in females (Table 5.3; Fig 5.2). Male provisioning rate and EB were not significantly related (Table 5.3). The proportion of caterpillars provisioned and diet diversity were not significantly related to EB in males or females (Appendix 5.1).

Table 5.3. Relationship between male (n = 29) and female (n = 32) exploration behaviour and provisioning rates (LMM: random effects: Individual Identity, site and year). For analyses of females, provisioning rate was square-root transformed to achieve normality. P-values assessed for LMM's using Likelihood Ration Tests. × denotes an interaction term. Test statistics and p-values of individual fixed effects shown from models without interactions fitted.

	Males		**Females**	
Fixed effects	**β ± SE**	**p-value**	**β ± SE**	**p-value**
EB	-0.72 ± 1.12	0.504	-0.39 ± 0.13	0.001
Habitat [a]	-7.73 ± 2.43	0.019	0.28 ± 0.37	0.409
Year [b]	4.56 ± 2.85	1.000	0.55 ± 0.29	0.062
Brood Size	2.59 ± 1.26	1.000	0.55 ± 0.15	0.004
EB × Habitat	-0.29 ± 1.85	0.860	0.14 ± 0.31	0.628

[a] Conifer set to 0; [b] 2014 set to 0.

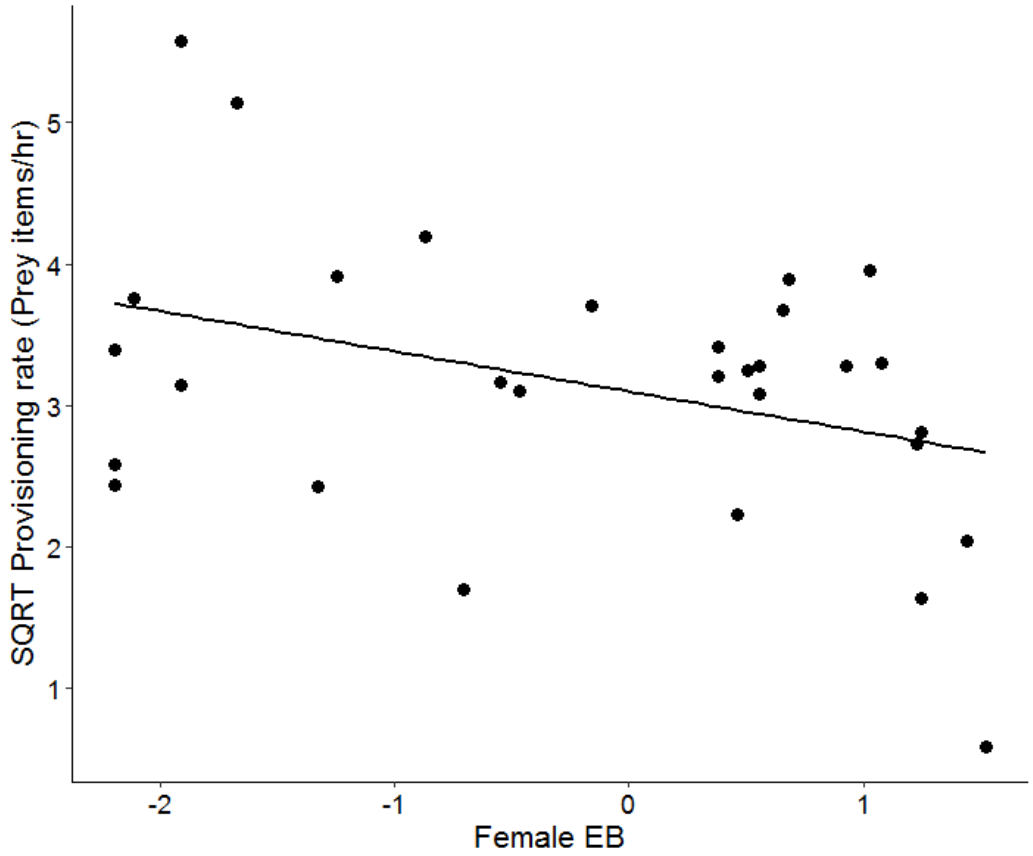


Figure 5.2. Plot of female provisioning rate (number of prey items per hour) and female exploration behaviour across deciduous and woodland plots (n = 32).

Discussion

We found no evidence that male EB was related to lay date or clutch size. Faster exploring females laid the same sized clutches as slow explorers. However they fledged fewer chicks. These differences may be linked to the lower provisioning rates observed amongst faster exploring females. Male EB was negatively related to offspring quality in deciduous sites as we had predicted; however, we did not find a link between male EB and provisioning behaviours.

Reproductive timing and clutch size

Average laying date did not differ between faster and slower exploring individuals across both conifer and deciduous fragments. Under controlled captive conditions, fast exploring female great tits tend to lay earlier than slow exploring females (Groothuis, et al, 2008; *but see* - Visser et al, 2011), but evidence from wild populations is mixed (Both et al, 2005; Mutzel et al, 2013). In our study area, average lay date differed significantly between habitat types but female EB had no influence on lay date in either. This suggests that females of different personality types respond to cues that promote laying activity in a similar manner. Likewise, we found no links between male EB and lay date in either habitat type. Hypothesised paths between male EB and lay date are primarily based on the ability of faster exploring males to secure better territories (Both et al, 2005; Nager et al, 2007). The lack of a relationship with lay date could indicate that EB does not significantly influence the ability of males to secure a high-quality territory in these populations as has been shown elsewhere (Mutzel et al, 2013). However we cannot rule out the possibility that the poor breeding habitat provided by these fragments in general (Chapter 2) prevents females reaching breeding condition early, thus negating any potential differences that may arise due to EB across habitat types.

Exploration behaviour did not significantly correlate with clutch size in males or females. For birds breeding in seasonal environments, clutch size is directly linked to fitness (Pettifor et al, 2001), and is influenced by local environmental factors such as breeding densities and habitat quality (Chapter 2; van Balen, 1973; Both et al, 2000; Wilkin et al, 2009). Studies have shown that given the opportunity, proactive females will invest more in the current reproductive attempt than reactive individuals, in line with POLS theory (Réale et al, 2010; Mutzel et al, 2013; Nicolaus et al, 2015). Therefore, we predicted that faster exploring females would lay larger clutches than reactive females, particularly in less densely populated conifer fragments where resources may not be as limited by local competition,

which was not the case. Previously we found that in these populations, EB does not correlate with another aspect of parental care, offspring defence, as would be predicted by POLS (Chapter 4). It may be that in these populations EB is not related to pace of life, or perhaps the relationship between EB and clutch size is mediated by underlying environmental factors which we are unable to account for here. For instance, low environmental resource availability can limit female investment in fecundity by constraining egg production (Nager et al, 1997) leading to smaller broods than parents are capable of raising successfully (Nicolaus et al, 2015).

Provisioning and Reproductive Success

Faster exploring females produced fewer fledglings of the same quality than slower exploring females, an effect present across both habitat types. As recruitment rates are extremely low in these fragments (Chapter 2), we are unable to confirm if fledgling production corresponds with offspring survival which is a more direct measure of fitness. However the number of fledglings produced is a strong predictor of fitness in the great tit generally (McCleery et al, 2004). As our analyses of fledgling success controlled for original clutch size, which did not correlate with EB, our results suggest that slower exploring females lay clutches that are closer to an optimal size given environmental conditions, than faster exploring females (Pettifor et al, 2001; Nicolaus et al, 2015).

Information use is an important component of the reactive-proactive axis. Reactive individuals are sometimes reported to sample environmental information more thoroughly than proactive individuals (Mathot et al, 2012; Overveld & Matthysen 2013), and are therefore better able to match key reproductive traits with environmental conditions (Nicolaus et al, 2015). Proactive individuals display physiological and behavioural adaptations that may mitigate these differences (Groothuis, et al, 2008; Mutzel et al, 2013), and increased investment in brood provisioning may be an important mechanism that allows proactive individuals to compensate in unfavourable breeding conditions (Mutzel et al, 2013; *but see* – Patrick and Browning, 2011). Interestingly we did not find this here. Faster exploring females provisioned their offspring at lower rates than slow exploring females during a critical period of nestling growth. This difference was not due to better diet quality which can lead to lower provisioning rates (Chapter 2; Wilkin et al, 2009), as in fact nestling diet structure did not vary between female personality types. Instead, it appears that faster exploring females are less efficient foragers across these fragments. Previous studies have

shown that provisioning rates are a key trait linking proactivity with reproductive success (Mutzel, *et al,* 2013), which we confirm here. However the relationship we report between reproductive success and EB is negative whereas previous links were positive.

Amongst males, exploration behaviour did not correlate with the number of fledglings produced, provisioning rates or diet structure, though we did find a habitat specific effect of EB on nestling condition. Faster exploring males produced heavier fledglings in low-density conifer fragments than slower exploring males, but the opposite was true in high-density deciduous fragments (Fig. 5.1a). Studies indicate that proactive males that are more territorial than reactive males (Amy et al, 2010), may suffer reduced reproductive success in high density areas because frequent aggressive interactions with territorial intruders may lead to decreased paternal investment in the breeding attempt (Duckworth, 2008; Barnett et al, 2012; Mutzel et al, 2013). Furthermore, proactive individuals take longer to recover following social defeat (Carere et al, 2001), which may enhance the negative consequences of repeated aggressive encounters for paternal care. Although we found evidence of the ultimate predicted effect, the predicted proximate cause - male provisioning rates - did not vary with EB. Further work is needed to establish the underlying relationship here. One potential explanation is that differences in provisioning rates between personality types arise earlier in the nesting season when offspring are younger. Studies have shown that circulating hormones levels which strongly influence territoriality (Levin and Wingfield, 1992), decrease towards the end of the breeding season (Beletsky et al, 1990). Thus, male EB and correlations with territoriality may have had a stronger influence on early nestling provisioning which would not have been detected by our filming protocols.

Conclusion

Our results provide evidence linking a personality trait with reproductive success. We have also confirmed that provisioning is a key functional behaviour linking EB and fitness, as has been shown elsewhere (Barnett et al, 2012; Mutzel et al, 2013). While previous studies have found a positive relationship between EB and reproductive success (Mutzel et al, 2013), here we report the opposite amongst females. It appears that habitat may influence the fitness of personality types differently; however this relationship is sex specific. The majority of breeding females involved in this study are immigrants and are unlikely to be adapted to local conditions (Chapter 2). If information use, or environmental responsiveness plays a role in shaping reproductive decisions (Nicolaus et al, 2015), reactivity may be favoured amongst

immigrants to these fragments; however as recruitment is low and immigration rates are high (Chapter 2), the likelihood of local adaptation arising through natural selection is low unless natal habitat preference induction occurs in this population.

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Chapter 5: Appendices

Appendix 5.1. Analyses of the relationship between exploration behaviour and provisioning behaviours in male (n = 29) and female (n = 31) great tits. Proportion of the diet comprising of caterpillars was analysed using binomial GLMM, diet diversity calculated using the Shannon-Weiner Index was analysed with LMM (random effects: individual ID, site). Male diet diversity was X^2 transformed. P values assessed for LMM's using Likelihood Ratio Test. × denotes an interaction term. Regression coefficients and p-values of individual fixed effects shown from models fitted without interaction terms. Bold indicates significant effects related to EB.

	Proportion of Caterpillars Provisioned				**Diet Diversity**			
	Males		**Females**		**Males**		**Females**	
Fixed effects	**β ± SE**	**p-value**	**β ± SE**	**p-value**	**β ± SE**	**p-value**	**β ± SE**	**p-value**
EB	-0.12 ± 0.21	0.559	-0.10 ± 0.16	0.535	-0.07 ± 0.11	0.502	-0.004 ± 0.08	0.967
Habitat [a]	-0.98 ± 0.55	0.076	-0.20 ± 0.16	0.721	0.002 ± 0.31	0.994	0.13 ± 0.171	0.450
Year [b]	0.04 ± 0.60	0.954	-0.35 ± 0.24	0.142	0.10 ± 0.33	0.750	0.37 ± 0.18	0.036
Lay Date [c]	0.46 ± 0.27	0.084	-0.18 ± 0.14	0.184	0.07 ± 0.13	0.560	0.25 ± 0.09	0.004
EB × Habitat	0.18 ± 0.38	0.641	0.06 ± 0.35	0.862	-0.09 ± 0.25	0.691	0.07 ± 0.18	0.694

[a] Conifer set to 0; [b] 2014 set to 0; [c] Yearly mean-centre

Chapter 6

General Discussion



The overarching aim of this thesis was to explore the functional significance of animal personality (**Chapter 3, 4, 5**) and the fitness consequences of personality variation in an anthropogenic landscape (**Chapter 4 and 5**), where environmental heterogeneity occurs over relatively small spatial scales (**Chapter 2**). Personality can influence fitness (Smith and Blumstein, 2008) and may be subject to natural selection (Dingemanse et al, 2005); however studies examining the fitness consequences of individual behavioural variation in multiple environments are lacking, even though these studies are essential for understanding the adaptive significance of animal personality in the wild (Réale et al, 2007; **Chapter 1**).

Studying the evolutionary ecology of any trait requires large sample sizes (Kingsolver et al, 2000), and there is often a trade-off between the number of data points, and the ease at which a trait can be measured. Therefore, rapid standardized behavioural assays in captivity are often favoured over natural behavioural observations resulting in situations where personality variation is linked to fitness, but the functional mechanisms underlying the links are unclear (Appendix 1.1: **Chapter 1**). I addressed this issue in this thesis by investigating the links between exploration behaviour measured in captivity and functional behaviours that can significantly influence fitness, namely foraging ability under contest competition and two aspects of parental care, offspring defence and adult provisioning behaviours.

<u>Environmental variation and reproductive success in coniferous and deciduous fragments</u>

The fitness consequences of personality traits vary within a species, and even within populations (e.g. Dingemanse et al, 2004; Quinn et al, 2009; **Chapter 1**). Thus, in order to build ecologically relevant hypotheses, one must have a foundational knowledge of the study system in question (Dall and Griffith, 2014). Before I established these great tit study populations in 2012, little was known of the breeding biology of Paridae in Ireland (*but see* – Perry, 2003), or within fragmented forestry plantations in general, even though this habitat is common across Western landscapes (Watts, 2006). I addressed these issues in **Chapter 2** by examining life history traits, foraging behaviours and reproductive success of breeding great tits in coniferous and deciduous woodland fragments

In modern landscapes, human mediated change can create significant environmental variation over relatively small spatial scales, altering the availability of critical resources within discrete habitat patches (Andrén, 1994). For mobile generalist species capable of surviving in multiple environments like the great tit, habitat selection most likely depends on

local cues, including factors such as population densities or food availability (e.g. Orians and Wittenberger 1991; Doligez et al, 2004). One major issue with anthropogenic change is that it can disrupt natural cue-habitat quality correlations, resulting in settlement patterns that do not follow an ideal free distribution (Pulliam and Danielson, 1991; Schlaepfer et al, 2002). In this system for example, great tits preferentially settled in deciduous fragments, but also experienced low reproductive success in these fragments, rather like an ecological trap. Why great tits prefer deciduous woodland remains unclear. It may be an innate behaviour (Mänd et al, 2005) that evolved in response to the high densities of natural cavities that exists in mature deciduous woodland relative to other habitat types (van Balen, 1982). Another possibility is that deciduous woodland provides better overwinter habitat than coniferous sites due to beech mast availability, which may be critical for survival (Perdeck et al, 2000). Generally, even during the winter when supplementary food was continuously available in both habitat types, densities of great tits at feeders was much lower in coniferous than deciduous fragments which suggests that coniferous habitat is indeed avoided in this system, though it may simply be that feeders were just easier to find in deciduous woodlands.

Life history trade-offs may emerge in environments where energy intake is limited by extrinsic constraints such as local competition or food availability (Stearns, 1989). These trade-offs are governed by priority rules which determine resource allocation, but typically, lower fecundity is observed in energy restricted environments as there is a minimum energy threshold necessary for self-maintenance, while individuals may forgo breeding under extreme circumstances (Zera and Harshman, 2001). Clutch size was consistently lower in deciduous than in coniferous woodland fragments, contrary to *a priori* expectations based on previous comparative studies (Sanz, 1998). Furthermore, subsequent reproductive success was also lower in deciduous sites. It is unclear whether the patterns observed arose because of environmental food limitations, or because of high local breeding densities and thus competition in deciduous sites. Elucidating this remains an important goal for future work, because if indeed food availability is lower in deciduous than coniferous sites, this suggests that management strategies designed to improve biodiversity (Zanchi et al, 2007) may in some cases have negative consequences for resident communities of higher order consumers. Similarly, the fact that nestling diet structure did not vary between habitats was surprising given that vegetation communities were considerably different at the territory level. It may be that because of the highly managed nature of the landscape, only generalist invertebrate communities are capable of colonising both habitat types (Oxbrough et al,

2012). Another possibility is that in coniferous sites, adults travel further and forage on discrete patches of deciduous trees, on or near patch edges predating similar invertebrate communities as has been shown in other populations (e.g. Gibb and Betts, 1963; Tremblay et al, 2004; Strauss et al, 2005). If so, this may provide a physiological cost to raising larger broods in coniferous sites (Tinbergen and Verhulst, 2000), which could result in higher mortality, or reduced future reproductive success through carry-over effects (Tinbergen and Verhulst, 2000; Thomas et al, 2001). Because great tit breeders are relatively sedentary, estimating survival based on year to year breeding records is reasonably accurate (e.g. Quinn et al, 2009); however in this system, high levels of nest failures before adult trapping means that this measure is unreliable, particularly in deciduous sites. Therefore, identifying adults early in the season will be crucial for discovering if fecundity-mortality trade-offs exist in coniferous sites. Of course, if food availability is simply higher in coniferous sites, it may be that trade-offs are not present because energy intake is not extrinsically limited (van Noordwijk and de Jong, 1986).

As well as influencing spatial variation of reproductive success in this landscape, it appears that habitat differences also cause temporal divergence in breeding strategies. Great tits are capable of considerable phenological plasticity, matching breeding cycles to microenvironmental cues (Hinks et al, 2015) or annual fluctuations in temperature (Nussey et al, 2005) which may be key for population persistence. In this system, great tits breeding in coniferous sites exhibited earlier laying, and a decline in clutch size with lay date; however in deciduous sites clutch size was temporally stable. Whether this variation was an adaptive response to local conditions, or caused by seasonal changes in food availability which hampered egg formation amongst later breeding females in coniferous sites is unclear. Asynchronous hatching caused by early onset incubation is typical of mismatched breeding cycles in great tits and may also lead to increased brood mortality (Barrientos et al, 2017). By investigating incubation regimes of females in coniferous sites it may be possible to determine if later breeders begin incubation before clutch completion, which would provide circumstantial evidence that temporal changes in life history are a response to environmental conditions rather than limited energy availability. Alternatively, as no link between changes in nestling diet and reproductive success was present, it may be that the observed decline in reproductive success with lay date in coniferous sites is due to other factors such as disease. For instance, conifer plantations in Ireland support high populations of biting midges (*Ceratopogonidae*) compared to other habitat types (Pedley et al, 2014).

These invertebrate populations can peak in May and June, coinciding with the great tit nesting period in Ireland (Sanders et al, 2012). Biting midges are known carriers of malarial parasites of the genus *Haemoproteus* that may negatively influence nestling condition and fledging rate (Krams, et. al., 2013).

It is unlikely that this system is representative of a metapopulation in the strictest sense (Hanski, 1991), as great tits are capable of breeding in connecting marginal habitats like ditches and hedgerows where cavities are available (Gosler, 1993; Riddington and Gosler, 1995). In fact in this landscape, marginal habitat such as hedgerows is the predominant habitat type, with woodland representing only 10% of land cover in Ireland (Forest Service, 2013). Furthermore, as the majority of this woodland is comprised of coniferous monocultures, its suitability for breeding great tits is low (van Balen, 1982), and point counts indicate that without nest-box provisioning, great tit breeding densities in afforested plantations occur at less than 0.5 birds per hectare (Sweeney et al, 2010a; Sweeney 2010b). Therefore, by supplying artificial nesting cavities, the suitability of afforested fragments for breeding increases dramatically. However as the breeding cycle of great tits in natural cavities in Ireland is unknown, it is unclear whether nest-box provisioning increased populations to supra-optimal levels thus decreasing reproductive success particularly in deciduous sites (Mänd et al, 2005). It may be possible to determine if higher population densities are the cause of low reproductive success in deciduous sites by carrying out density reduction experiment using a paired plot design (Fig. 6.1).

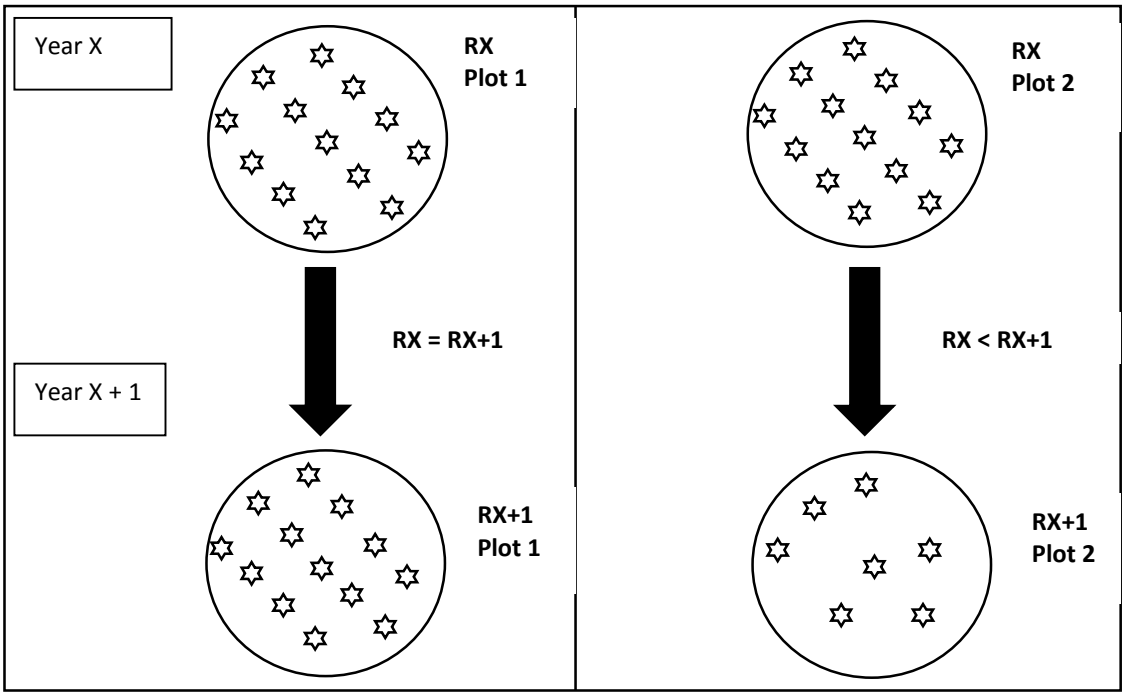


Figure. 6.1. Outline of a nest-box removal experiments in a paired plot design. Nest-boxes denoted by stars. R's symbolise reproductive success in year x and year x+1 respectively. If reproductive success is strongly influenced by local breeding densities, removal of nest-boxes from the plot should increase reproductive success compared to control plots

The high levels of immigration, and low levels of recruitment observed are typical of fragmented populations of mobile species, and may promote plasticity over genetic adaptation (Lambrechts et al, 1999; Matthysen et al, 2001; Sultan and Spencer, 2002) as random geneflow will prevent local adaptation from occurring unless selection is particularly strong (Kawecki and Ebert, 2004) or behavioural mechanisms such as assortative breeding are a barrier post settlement (Postma and van Noordwijk, 2005). Another possibility is that gene flow is non-random because dispersing offspring select breeding habitat based on natal habitat preference induction. Although evidence for this phenomenon is mixed (Davies and Stamps, 2004), experimental studies on hand raised coal tits (*Parus ater*) show that while juveniles raised under controlled conditions without habitat cues exhibit a strong innate preference for coniferous habitat, groups raised in a specific habitat show a preference for the habitat type in which they are raised late in life (Gruenberger and Leisler, 1990). Currently, investigating this phenomenon in the system would be difficult as study populations are further than 2km apart which is the average great tit dispersal distance (Verhulst et al, 1997); however adding nest-boxes along hedgerows between woodland fragments of similar and contrasting vegetation structure could be a really interesting design

to determine if breeding habitat is influenced by natal habitat (Figure 6.2). Furthermore this design could provide valuable information about the dispersal distances of great tits in general; for example do juveniles that were raised in challenging natal habitat disperse further, or does some form of natal habitat preference induction exist? Experimental manipulations of natal conditions by increasing or decreasing densities could elucidate mechanisms. Very little is known of juvenile great tit post-fledgling movements and as movement between patches is generally restricted to hedgerows (*but see* – van Overveld et al, 2011), establishing nest-boxes in this habitat could be very enlightening, regarding the spatial ecology of great tits in modern landscapes.



Figure 6.2 Typical landscape in Ireland consisting of irregularly shaped woodland patches separated by agricultural fields, bounded by hedgerows.

Chapter 2 provides valuable information about this study system. Against expectations, diet structure was largely similar across both habitat types, suggesting that the availability of critical resources like caterpillars are similar in both coniferous and deciduous fragments. Instead, differences in life history between habitats are probably influenced strongly by local competition. More generally, these results show that management strategies like planting regimes can cause spatiotemporal environmental variation for resident populations in afforested areas, and that caution is needed when generalising environmental effects across different ecosystems.

Competitive ability and individual behavioural variation

Chapter 3 explores the functional significance of individual behavioural variation for foraging strategies in a social setting. Exploration behaviour (EB), and problem-solving performance are independent repeatable traits in this system and have been simultaneously linked to foraging ability in a social context (Cole and Quinn, 2012). Faster explorers may be more competitive due to higher levels of aggression (Verbeek et al, 1994), while problem-solvers are less competitive which may reflect adaptive phenotypes, indicative of alternative foraging strategies (Cole and Quinn, 2012). Evidence of the latter is mainly indirect however (**Chapter 1**), and thus I addressed this using dyadic contests in captivity.

Exploration behaviour did not correlate with aggressiveness or competitive ability during the captive trails. Relationships between exploration behaviour and dominance are context specific, and may be strongly influenced by environmental conditions and the social setting (Verbeek et al, 1999; Dingemanse and de Goede, 2004). Proactivity has been linked to stress responses, whereby faster explorers display reduced activity following a social defeat (Carere et al, 2003). Faster explorers have an active coping style and may flee from stressors, but in unfamiliar environments like the aviary where these trials took place, escape is not possible. Thus in this situation, the captive environment may have unduly influenced competitive dynamics within dyads. Another possibility is that in these populations, aggressiveness and exploration behaviour do not form part of the same behavioural syndrome due to population specific selection pressures, for example predation pressure (e.g. Dingemanse et al, 2007). Further tests under more realistic conditions in the wild could elucidate this (e.g. Cole et al, 2012).

Innovation as measured in the lever pulling task in isolation tended to correlate with competitive ability at the feeder across age and sex categories as predicted; however the relationship was not statistically significant. This trend warrants further study as it suggests that our analysis may have been limited by the small sample sizes involved in this study. Furthermore in a separate trial, individuals that were less competitive were more likely to innovate in order to access alternative resources. This provides valuable evidence for the necessity drives innovation hypothesis (Reader and Laland, 2003). Much of the previous evidence has been indirect, linking innovativeness with common correlates of competitive ability such as body size (Duffield et al, 2015), and age (Reader and Laland, 2001). **Chapter 3** shows that innovation can directly benefit individuals that are excluded from a common resource by facilitating access to alternative resources.

Why some individuals are more likely to innovate than others remains unclear. The mechanisms underlying individual variation in goal oriented problem-solving are probably related to several different traits. Firstly, there may be a cognitive component to performance, related to perception and operant conditioning (Taylor et al, 2012). Several studies have found that individual variation correlates with associative learning abilities, which strengthens this argument (e.g. Griffin et al, 2013; Morand-Ferron et al, 2015), although it may be that the two traits correlate with an underlying non-cognitive component. Motor diversity may also play an important role in problem-solving (Guez and Griffin, 2016). Comparative studies have shown that species with larger motor repertoires are consistently more likely to problem-solve (Griffin and Guez, 2014). Similarly, interindividual variation in motor diversity has been shown to correlate with problem-solving performance (Benson-Amram and Holekamp, 2012; Griffin et al, 2014). The fact that greater motor diversity affords a better chance of performing the "correct behavioural pattern" is easy to comprehend, but what is less clear is how individual variation in behavioural repertoire arises. Experience probably plays a major role here (Griffin et al, 2014). For example, as an individual gains more experience handling specific food items, motor diversity may actually decrease as using neglected behavioural patterns may decrease foraging efficiency. In this manner, less competitive individuals that are forced to forage and process a wider variety of food items may be more likely to innovative simply because they practice and regularly use a greater diversity of behavioural patterns. This may also explain why food deprivation does not generally lead to increased solving performance (Cole et al, 2012; Griffin and Guez, 2014; *but see* – van Horik and Madden, 2016), as increases in physiological motivation (i.e. hunger)

should not impact behavioural repertoire breadth, although as far as I can tell this is yet to be tested explicitly. Finally, persistence may also increase solving performance as time spent interacting with a task increases the likelihood of solving (Guez and Griffin, 2016). Results from **Chapter 3** seem to support this pathway, as individuals that made contact with the string-pulling device more often, were more likely to access the rewards.

One puzzling aspect of **Chapter 3** was that problem-solving performance in isolation did not predict performance in a social context. This lack of cross-contextual consistency in innovativeness has been observed previously in great tits and other species (Overington et al. 2009; Morand-Ferron et al, 2011). As visual access to the task appears to be a key factor influencing problem-solving (Taylor et al, 2012), vigilance towards competitors or predators may compromise performance. Indeed, studies indicate that the presence of potential kleptoparasitic conspecifics may decrease individual innovative propensities in the wild (Overington et al, 2009). One natural follow up would be to investigate this relationship further. For example, if the devices are shielded from view but still in a social context, are innovations more likely to be performed by subordinate individuals? Furthermore, innovators spent less time on the string-pulling device when their opponent was hyper-aggressive, presumably to avoid antagonistic interactions with aggressive individuals. It would be interesting to understand how this behaviour manifests in more complex social settings. For example are innovators simply less likely to innovate in the presence of any competitor, or can they discriminate between individuals, and thus still perform innovations in the presence of less aggressive competitors. One key aspect of social interactions is that competitors can assess opponents and must decide the correct behaviour given the circumstances (Arnott and Elwood, 2009). Understanding how problem-solving behaviour is related to an individuals' perception of its opponent could be an interesting avenue of research for future work.

The findings in **Chapter 3** suggest that problem-solving in captivity may reflect alternative foraging strategies rather than simply poor competitiveness in a social context. Empirical evidence from the wild strengthens this claim, with two studies showing that problem-solving ability positively correlates with foraging efficiency during the breeding season and fledging success (Cole et al, 2012; Wetzel, 2017). Whether performance in food based tasks correlates with other functional behaviours in the wild that might be related to fitness is unknown; however if indeed there is a cognitive component to problem-solving, then the

behaviour may correlate with any number of functional traits that are related to perception or learning. For instance, nest building may have significant fitness consequences through its effects on incubation behaviours (Hilton et al, 2004; de Heij et al, 2006), and has previously been linked to problem-solving ability (Keagy et al, 2009). Determining the best materials to use in the wild relies on past experience, learning and perception of the structural properties of available materials (Bailey et al, 2014). Thus, nest building could be another potential functional mechanism relating problem-solving to fitness in the wild.

Despite the costs associated with lower competitive ability in a social setting, the only study to date that investigated the relationship between problem-solving and survival found no such links, suggesting that alternative strategies may lead to equal realised competitive ability (Cole et al, 2012). Instead, problem solvers in the population were more likely to desert their nests following a perceived predation attempt, suggesting that female solvers experienced greater negative stress responses to disturbance (Cole et al, 2012). Whether trade-offs linked to problem-solving maintain individual variation remains unclear, as quantitative genetic analysis of problem-solving in great tits found that this trait arose almost wholly through permanent early life environmental effects (Quinn et al, 2016). This suggests that regardless of the fitness consequences of problem-solving, individual variation will persist, making the best of a bad job. Whether non-heritability is the case across populations remains unclear, as the contribution of additive genetic effects to a trait may vary within a species (e.g. Dingemanse et al, 2004; Quinn et al, 2009).

Comparative studies across environments could be useful for identifying the generality of trade-offs. For instance, are the differences in foraging efficiencies observed in high quality oak woodland, carried over, or amplified into poorer quality habitat where food availability may not be as high? Evidence suggests that environmental parameters can have a strong selective influence on cognitive traits that may be linked to problem solving. For instance chickadees from urban environments and high latitudes are better at spatial memory tasks and problem-solving than those from rural populations and low latitudes respectively (Pravosudov and Clayton, 2002; Kozlovsky et al, 2017); however currently, evidence of the functional mechanisms underlying population divergence is severely lacking. Initially, a second major aim of this thesis was to explore the functional significance of innovative problem-solving performance across the two habitat types. Due to the relatively low proportion of individuals that solved the task, coupled with low breeding densities in this

system, I was unable to attain sufficient sample sizes to test hypotheses statistically. For instance from coniferous habitat, only 5 of the 41 individuals that were tested in captivity and subsequently bred in coniferous fragments, were problem solvers. In comparison in deciduous sites 74 individuals that were assayed subsequently bred, with 19 of these being problem solvers. Adapting the methodology used to record performance from a binary measure to a continuous measure, could alleviate some of these issues. For instance a latency to solve, or trials to criterion approach could allow for greater flexibility in analyses of individual performance (Morand-Ferron et al, 2015). This comparative work could provide valuable evidence regarding the functional significance of problem-solving in the wild, of which there is a dearth of research at the moment.

Personality, parental care and fitness

According to the pace of life theory, personality reflects a behavioural component of alternative life history strategies, and that individual variation is adaptive, reflecting optimal behaviour for a given strategy (Réale et al, 2010). As proactives prioritise productivity over self-maintenance, this should be reflected in differential investment in parental care (Roulin et al, 2010), although these differences may only emerge in certain environments (Nicolaus et al, 2015). In **Chapter 4** I examined the links between proactivity and offspring defence, which reflects a direct trade-off between parental survival and productivity, while in **Chapter 5** I took a comparative approach examining the links between exploration behaviour and provisioning behaviours amongst breeders in coniferous and deciduous sites.

In **Chapter 4**, there was no evidence of a link between exploration behaviour and female response to predation risk during incubation. Despite this, female responses were repeatable both within and between years, suggesting that the two traits represent distinct personality traits in this system and are not part of the same syndrome. Although studies have shown that faster exploring females are more risk prone at the nest during incubation (e.g. Cole and Quinn, 2014), to date only one study has found links between exploration behaviour and offspring defence in great tits, and evidence in this study was mixed (Hollander, 2008). Phenotypic correlations may not necessarily be conserved within a species (**Chapter 3**) and may be highly context specific (Garamszegi et al, 2012). This cross-contextual inconsistency may arise for several reasons. Firstly methodological differences between studies including differences in captive conditions, techniques and observers likely influence the recorded behaviour, leading to some between-study variation in traits under consideration (Carter et al, 2013). I would argue that this is unlikely to be the case here as exploration behaviour was

measured under standardised conditions, and infrastructural factors should influence all individuals to the same extent and the assay should still capture individual variation within populations. Another possibility is that local environmental selection pressures have selected against a correlation between exploration behaviour and risk taking. For instance, both modelling and empirical studies suggest that predation pressure may be a key factor leading to the emergence of aggression-boldness syndromes (Bell, 2005; Dingemanse et al, 2007; Luttbeg and Sih, 2010). Thus, the results from **Chapter 4** may arise because of lower densities of predators in this system. Indeed the fact that the prevalence of deimatic hissing, which is a functional defensive behaviour (Krams et al, 2017; Zub et al, 2017), was very low compared to other populations suggests that predation pressure may not exert a strong selective influence on these populations. Alternatively, differences in the methodology used to assay female risk aversion between this and other studies may have lead to the differences in female responses observed. Finally, perhaps tight-sitting represents a different response to predation risk than offspring defence. For instance in the two previous studies that have investigated exploration behaviour and offspring defence (Hollander et al, 2008; Cole and Quinn, 2014), female risk aversion was measured outside of the nest-box, where females had time to assess the threat before reacting. Here, I measure an instantaneous response to a predation threat in isolation. This measure may be more akin to a startle response and thus represent a different but equally valid response to predation (Quinn and Cresswell, 2005). To support this, studies on blue tits have found that female responses in predation risk trials similar to the one described in **Chapter 4** do not correlate with responses when threats are observed from outside the nest-box (Fresneau et al, 2014). Another possibility is that the measure of tight-sitting here was not sufficient to measure individual variation. Tonic immobility may last for tens of minutes (Quinn and Cresswell, 2005; Cockrem, 2007), thus a 20 seconds assay may not necessarily capture individual variation and that individual behaviour in a longer assay would be related to EB. Further experimental work is needed to elucidate this. By comparing female responses across different scenarios it may be possible to determine if risk responsiveness correlates across behavioural contexts. For example, we might expect that tight-sitting (Fig. 6.1a) would be strongly correlated with female responses when presented with a threat immediately upon leaving the nest-box (Fig. 6.3c), but perhaps less so with discovering a threat upon returning to the nest-box (Fig. 6.3b). If all three behaviours correlate and are not related to EB, then this would suggest that risk aversion and exploration behaviour do not form a behavioural syndrome in this population.

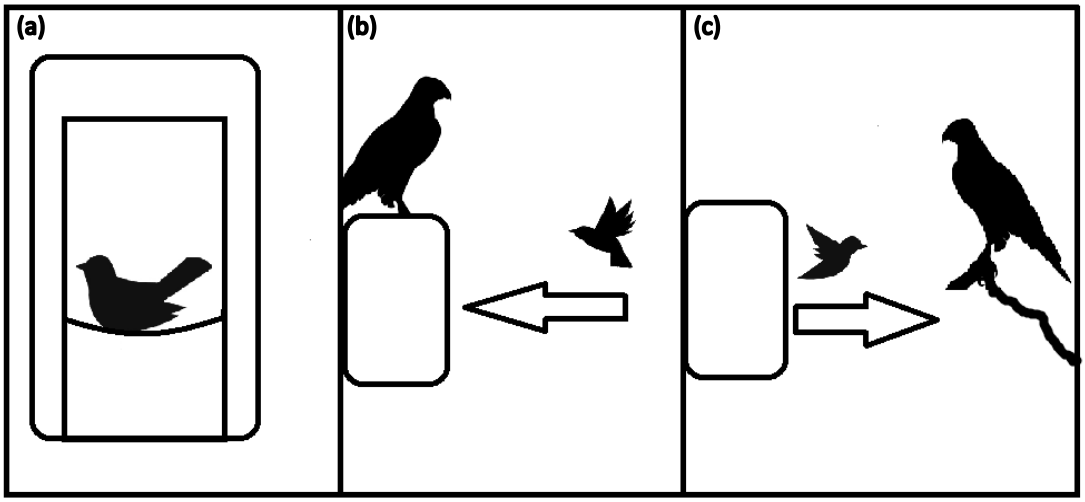


Figure 6.3 (a) Female tight-sitting response during disturbance. (b) Female response to predation threat at the nest-box. (c) Female response to predation threat immediately upon leaving the nest.

Female responses were significantly related to reproductive investment, as females incubating smaller clutches were less likely to "tight-sit" on the nest and fled in response to risk. Furthermore, nests incubated by non tight-sitting females were more likely to fail during incubation due to desertion, a trend that increased with lay date. Desertion may be an adaptive behaviour which conserves residual reproductive behaviour during periods of poor environmental conditions (Székely et al, 1996; Ouyang et al, 2012). The results from **Chapter 4** suggest that tight-sitting behaviour may be indicative of female investment in the reproductive attempt; however what is unclear is whether the two traits are intrinsically linked, or whether they represent differences in environmental responsiveness. For example fleeing may represent low reproductive investment similar to what is predicted by the pace of life syndromes hypothesis (Réale et al, 2010) and thus desertion is an adaptive behaviour for a slower pace of life. In contrast, these behaviours may also represent differences in individual responsiveness where individuals that flee are more responsive to environmental variation, and thus desert their nests particularly later in the season in response to changing environmental conditions. From **Chapter 4** it seems more likely that the latter is the case, because clutch size was not a significant predictor of desertion. Differentiation between two hypotheses could be accomplished by reducing residual reproductive value (RRV) amongst individuals of the same age. RRV is thought to be the key state variable underlying different pace of life syndromes (Réale et al, 2010). If the two traits, tight-sitting and desertion, are intrinsically linked to life history, one would expect to find lower desertion and higher levels

of tight-sitting amongst non-tight-sitting individuals that were manipulated. In contrast, tight-sitters should not change their behaviour. If tight-sitting reflects differences in responsiveness, then manipulating residual reproductive value should not lead to behavioural changes amongst tight sitters and non-tight sitters alike.

Whether the correlations between the traits are adaptive depends on whether females that desert their offspring have lower mortality and thus equal lifetime reproductive success. Life history trade-offs may be a key process maintaining personality variation in the wild (Wolf et al, 2007; Biro and Stamps, 2008). In order to determine if that is the case here, it will be necessary to identify females before they desert their nests. This could be accomplished using non-invasive PIT tag technology to determine if all behavioural types have equal lifetime reproductive success.

When the opportunity arises, proactive individuals may invest more in reproduction than reactive individuals (e.g. Nicolaus et al, 2015), thus when measuring the fitness consequences of personality traits in a single environment may not be possible to determine if relationships between personality and fitness are absent because there is no link, or because environmental factors are constraining or promoting reproductive investment amongst a specific personality type. Therefore, comparative studies between populations in different environments, or experimental manipulations may permit a better understanding of links between personality traits and fitness. In **Chapter 2** I established that population densities were higher in deciduous than in coniferous sites, and that because diet structure was the same, differences in clutch size and reproductive success between the two habitat types were probably driven by high local competition in deciduous sites.

Exploration behaviour was not related to clutch size. The reasons for this remain unclear, but it may be that the environment limits reproductive investment amongst all females equally. Faster exploring females had lower reproductive success, fledging fewer chicks than slower explorers, regardless of habitat type. This suggests that proactive females lay larger clutches than they are capable of raising given environmental conditions, perhaps because of differences in environmental information use (e.g. Nicolaus et al, 2015). These differences in reproductive success may be in part driven by lower provisioning rates amongst proactive females in both conifer and deciduous sites. As diet structure did not vary with EB, it could suggest that proactive females are simply less efficient foragers than reactive females. This

is the opposite to what has been shown previously, whereby proactive individuals are capable of increasing provisioning rates to cope with unfavourable conditions, and display higher reproductive success (e.g. Mutzel et al, 2013; *but see* – Patrick et al, 2011). Higher provisioning rates amongst proactive females may arise because these individuals are less risk prone (Quinn et al, 2012). Furthermore, proactive individuals are more routine forming when foraging (Marchetti and Drent, 2000) which may be beneficial in environments where critical resources are abundant and foraging requires little searching. In this system, adults provision a wide variety of prey items switching rapidly between provisioning events (**Chapter 2**). Perhaps this style of provisioning is more suited to reactive individuals that are less routine forming in their foraging behaviours (Verbeek et al, 1994). One way of investigating provisioning differences would be to monitor space use by radio tracking females of different personality types. For instance, reactive individuals are more perceptive to environmental change as they spend more time sampling environmental information (van Overveld and Matthysen, 2013). This could permit more informed foraging decisions about when to switch between patches, rather than making costly trips to prey depleted areas (Marchetti and Drent, 2000). If indeed this was the case, one might expect to find that proactive individuals are more likely to return to the same areas in consecutive foraging trips, whereas reactive individuals would move to new areas more often.

Amongst males, exploration behaviour negatively correlated with average fledgling mass in deciduous habitat, while in coniferous habitat, there was a positive correlation. Exploratory males are more territorial, approaching speakers more closely than reactive individuals during playback experiments (Amy et al, 2010), and may neglect provisioning due to frequent aggressive encounters with territorial intruders (Duckworth, 2006). In more densely populated areas, aggressive males may therefore suffer reduced reproductive success, similar to the patterns we observed here, although we did not find a link between male exploration behaviour and provisioning behaviours. Perhaps these differences are cumulative, and our relatively brief recording window was not sufficient to detect provisioning differences between individuals. Using less disruptive PIT tag technology to record provisioning rates over longer periods could elucidate this.

Another factor not explored in **Chapter 5** is that reproductive success is a composite trait in great tits, and may be dependent on both male and female behaviour (Both et al, 2005; Mutzel et al, 2013). Although ideally, I would have examined how parental personality traits

in combination influenced reproductive success in both habitats, the relatively low number of nests where this data was available, especially in coniferous sites, made this impossible. Studies indicate that assortative mating amongst personality types in great tits results in higher reproductive success. Although the exact mechanisms underlying this relationship are unclear, it may be that faster explorers are better at obtaining and defending high quality territories, while slow explorers have higher quality offspring (Both et al, 2005). Alternatively, faster exploring females may be better able to cope with paternal neglect caused by higher territoriality amongst faster exploring males (Mutzel et al, 2013). Finally, for offspring, it may be easier to adjust begging behaviour to parents of the same personality type rather than dissimilar pairs, assuming that personality influences parental response to offspring begging (Roulin et al, 2010). The weakness of studies involving assortative mating in great tits is that they were carried out in single environments, therefore the generality of the findings are unclear. For example if paternal neglect is a major cost to disassortative pairs, in this system disassortative mating may not be as costly in coniferous sites due to the lower population densities, whereas the costs may be higher in deciduous sites. This could be a really interesting avenue of investigation for future research and a natural follow on from the body of work in this thesis.

The likelihood of personality evolving in response to local conditions through natural selection in these fragments is low, as recruitment rates are negligible and gene flow is high. One unanswered question is how personality variation is maintained at the landscape level. If the patterns observed in these sites are replicated across the metapopulation as a whole, then exploration behaviour may be experiencing negative directional selection. One potential explanation is that variation is maintained by non-equilibrium dynamics (Wolf and Weissing, 2010). In many species, exploration behaviour correlates with dispersal (Cote et al, 2010). More exploratory, aggressive individuals may disperse further and settle in newly established habitat (Dingemanse et al, 2003; Duckworth and Badyaev, 2007). As sites become established, slower explorers begin to immigrate and thus population densities rise. Habitat suitability decreases for exploratory individuals and the personality undergoes negative directional selection (Duckworth and Badyaev, 2007), similar to the patterns observed here. Modern anthropogenic landscapes are extremely dynamic and constantly undergoing changes (**Chapter 1**), therefore non-equilibrium dynamics may play a role in maintaining personality variation. As I did not begin assaying exploration behaviour until the winter of 2014/2015 when populations were well established, it wasn't possible to test if the

phenotypic distribution of personality shifted over time, as would be expected if faster explorers were more likely to settle in newly established populations. Thus, future studies could examine these trends in newly established sites.

Conclusions

The fact that exploration behaviour has been linked with such a wide range of functional behaviours in the great tit (**Chapter 1**) is remarkable given its nature (i.e. movements in a novel environment over a 2 minute period) and the ease with which it can be measured. Using simple standardized assays to quantify individual behavioural variation can facilitate the collection of large amounts of data, and provides a useful approach for studying the evolutionary ecology of individual behavioural variation. However this thesis, alongside the body of work carried out on personality variation in the great tit, highlights the fact that generalising the effects of exploration behaviour within the species can be challenging.

In anthropogenic landscapes which are now widespread, environmental heterogeneity exposes metapopulations to widely different selection pressures over relatively small spatial scales. Studying the evolutionary ecology of personality within fragments is important as it provides a better understanding of how evolutionary processes can be shaped by human impacts. A major aim of this thesis was to address a knowledge gap, involving the functional significance of exploration behaviour in multiple environments. Although clearly, ecological conditions differ between the two habitat types, generally, reactivity was favoured across habitat types. This is surprising given that previous studies have shown that environmental heterogeneity, including differences in resource availability and population densities can have differential fitness effects on exploration behaviour in the great tit (Quinn et al, 2009; Nicolaus et al, 2016). Importantly, I identified a key proximate mechanism, provisioning behaviour, that links exploration behaviour to fitness; however further work is warranted to better understand how personality evolves in this landscape. Natural selection is unlikely to act on a single trait in isolation, due to correlations that exist between traits (Roff, 1997). In this thesis, I show that three unrelated, repeatable traits, problem-solving, risk aversion and exploration behaviour are related to functional behaviours that could simultaneously influence individual life history variation in the wild, illustrating the complexities involved with understanding how natural selection acts on individual behavioural variation.

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