Personality and cognitive variation in a wild population of the great tit (*Parus major*)

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ABSTRACT

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The evolutionary processes that shape individual variation in continuous behavioural traits remain poorly understood. While the emerging discipline of animal personality is providing increasing evidence that consistent individual differences in behaviour have significant fitness consequences, cognitive traits are yet to be explored in the same manner. My general objective in this thesis was twofold. First, I aimed to examine the ecological significance and fitness consequences of the cognitive trait innovative problem solving-performance, using a population of great tits (*Parus major*). Second, I aimed to explore the mechanisms underlying the functional significance of 'exploration behaviour' a captive measure of the reactive-proactive personality axis, focusing specifically on foraging and risk-taking behaviour. This two-trait approach was expected to shed light on whether personality and cognition simultaneously influence fundamental behaviours.

By carrying out behavioural assays on birds temporarily held in captivity, I showed that success at solving a food-motivated problem was repeatable within individuals, consistent between two different tasks and independent of exploration behaviour. Problem-solving performance was positively related to clutch size and fledgling number, established when birds were released back into the wild. Furthermore, when rearing offspring, solvers had shorter working day lengths than non-solvers and foraged over smaller ranges without compromising either provisioning quantity or quality. However, solver females were also more likely to desert their broods than non-solvers and consequently there was little evidence to suggest that directional selection acted on problem-solving performance. In comparison to non-solvers, solver males were also found to be poorer at competing for limited food resources during the winter. Together these findings suggest that costs and benefits are associated with problem-solving performance, which together may act to maintain variation in this trait.

My thesis also provides some of the first evidence that exploration behaviour is related to both foraging and risk-taking behaviour in the wild. In comparison to relatively slow explorers, fast exploring males were better competitors at feeders during the winter. Relatively fast and slow explorers also differed in a number of foraging behaviours during offspring provisioning, although not always in the direction predicted from captive work on other populations. Finally, while exploration behaviour was positively correlated with risk-taking behaviour amongst breeding females during incubation, it did not predict nest desertion in response to the risk associated with being trapped by field workers. Collectively these findings suggest that personality measured in captivity has specific but not general power to predict behaviour in the wild.

An important facet of evolution is that natural selection is rarely likely to act on a single trait in isolation owing to correlations between traits. This thesis demonstrates how important behaviours in the wild can be simultaneously linked to multiple sources of consistent behavioural variation. It also represents the first large-scale investigation of how variation in a cognitive trait relates to natural behaviour, reproductive life-history variation and fitness in wild animals. Using this individual-based approach in a natural setting may prove to be a useful tool for understanding how selection acts on cognitive traits.

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Author Contributions

Main Contributors

Ella F. Cole had independent intellectual input into all aspects of the thesis, collected three years of behavioural assay data and three years of field data. Also analysed data, wrote drafts and incorporated co-authors comments to produced final versions of all chapters.

John L. Quinn (supervisor and co-author of all chapters) secured funding and conceived the initial project proposal. Also provided intellectual input, guidance on experimental design, research techniques and analytical methods throughout, and gave detailed comments on all chapter drafts.

Julie Morand-Ferron (co-author of Chapters 4 and 5) had intellectual input, assisted in the collection of behavioural assay data (winter 2009-10), and commented on Chapters 3, 4 and 5.

Additional Contributors

Dominic L. Cram (co-author of Chapter 2) assisted in the design of the primary problem-solving task and collection of problem-solving data (January – March 2007).

Amy E. Hinks (co-author of Chapter 4) collected and analysed the radio-tracking data used in Chapter 4, and commented on a draft of this chapter.

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CHAPTER 1

General introduction



No one supposes that all individuals of the same species are cast in the very same mould

- *Darwin*

General Introduction

Individual variation: the study of fine-scale evolutionary processes

Heritable individual differences can be viewed as the raw material on which selection acts within populations (Darwin, 1859). Up until the mid 20th century, evolutionary biologists mainly considered natural selection as a process causing differences between higher-level taxa (Wilson 1998). However, over the last 60 years natural selection has been shown to operate over increasingly smaller scales. By the 1980s it was widely accepted that selection can maintain variation between individuals of the same species, via population specific selection regimes (e.g. Reznick & Endler 1982; Endler 1986). In recent decades, further evidence has accumulated to suggest that variable and antagonistic selective pressures may act to maintain individual differences within single populations (e.g. Price et al. 1984; Wilson 1998; Garant et al. 2007; Svensson & Sinervo 2004). Thus differences between individuals are increasingly viewed as a *product* of natural selection (Wilson 1998). Identifying and understanding the processes that lead to this genetic variation within natural populations remains a fundamental aim of evolutionary ecology (Roff, 1997).

For decades, genetic variation has been studied intensively in the wild and in captive populations, revealing a number of key mechanisms thought to maintain individual differences. One of these processes is antagonistic selection acting on genetically correlated fitness-related traits (Lande & Arnold, 1983). For example in the medium ground finch (*Geospiza fortis*), bill depth and bill width are highly

genetically correlated with one another, and are both under selection but in opposing directions (Price et al. 1984). The relative strength of selection on these traits fluctuates between years depending on food availability, and in some years this results in both traits failing to show the expected evolutionary response Price et al. 1984). Similar contrasting patterns of selection can also maintain variation in a trait when selection patterns vary between life-history stages within the same individual (Schluter & Smith 1986; Blondel et al. 2002). For example, in female song sparrows (*Melospiza melodia*), tarsus length is both negatively correlated with juvenile survival, and positively correlated with adult reproductive success (Schluter & Smith 1986). Hence, where fitness traits are intercorrelated, selection can act to constrain evolutionary change.

In addition to antagonistic selective forces acting within individuals, the direction and intensity of selection acting on traits can fluctuate over small temporal and spatial scales (Price et al. 1984; Grant & Grant 1995; Svensson & Sinervo 2004; Wilson et al. 2009; Van de Pol et al. 2010; Garant et al. 2007; Parker et al. 2011). Recent work on a population of great tits (*Parus major*) demonstrated that selection on a number of life-history traits varied depending on both local breeding density and habitat, leading to different life-history strategies being favoured in different parts of the population (Garant et al. 2007). The scale of this environmental heterogeneity was small relative to the great tit's average dispersal distance, meaning that gene flow is likely to prevent local adaptation, thus maintaining genetic variation (Dias & Blondel 1996). Heterogeneity in social environmental factors can also lead to maintenance of variation via frequency-

dependent selection, where the success of a particular phenotype is dependent on the frequency that it occurs in the population (Maynard Smith 1982; Allen & Greenwood 1988; Endler & Greenwood 1988; Svensson and Sheldon 1998; Sinervo & Calsbeek 2006). For example, in African lions (*Panthera leo*) the most productive litter size is dependent on the size of the litter of female neighbours (Packer & Pusey, 1995). From these examples it can be seen that both social and non-social environmental heterogeneity can cause the optimal phenotype for a trait to vary considerably over time and space, hence maintaining genetic variance. Knowledge of correlations between traits and the spatial and temporal scale at which selection is acting may therefore be critical to understand the microevolutionary dynamics in wild populations.

Behavioural variation and the concept of personality

In comparison to morphological and life-history traits, behaviour has received less attention in the field of evolutionary ecology. A notable exception is work on discrete behavioural differences between individuals, for example alternative mating strategies, that can be maintained by frequency-dependent selection (e.g. Sinervo & Lively 1996). Continuous behavioural traits, in contrast, have not yet been subject to the same level of detailed investigation (Mazer & Damuth, 2001). Much of this neglect is thought to stem from a reluctance to take an individual-based approach to the study of behaviour (Réale et al. 2007). In behavioural ecology, it has generally been assumed that individuals are largely plastic in their behaviour, allowing them to behave optimally in all contexts (Sih et al. 2004a).

Individual behavioural variation has therefore often been considered to reflect stochastic noise around a behavioural optimum (Wilson 1998).

However, over the last 20 years evidence has accumulated showing that animals exhibit limited plasticity in their behaviour, either across different situations (e.g. foraging behaviour under different environmental conditions) or different contexts (e.g. foraging vs. antipredator behaviour) (Wilson et al. 1994; Wilson 1998; Koolhaas et al. 1999; Gosling 2001; Sih et al. 2004a). In addition to this lack of flexibility, when subjected to identical environmental conditions, individuals of the same species will often behave differently to one another. For example they may differ in their sociality (e.g. Cote & Clobert 2007), aggressiveness (e.g. Huntingford 1976) or risk-taking behaviour (e.g Wilson et al. 1994; Van Oers et al. 2004). These consistent differences between individuals - termed personality or temperaments (Gosling, 2001) - have now been demonstrated in a broad range of species, and are widely considered to be ubiquitous in nature (Sih et al. 2004a). Early work on animal personality aimed to characterise personality dimensions and understand the proximate mechanisms causing individual differences (reviewed in Sih et al. 2004b). However, in recent years greater emphasis has been put on exploring the adaptive explanation for personality, and developing a conceptual framework in which to do so (reviewed in Smith & Blumstein 2008; Réale et al. 2007; Réale et al. 2010; Dingemanse & Wolf 2010; Wolf & Weissing 2010).

Much of current personality research centres on two main questions: what are the ultimate mechanisms causing within-individual consistency, and how are between-

individual differences in behaviour maintained in natural systems (Wolf & Weissing, 2010). Why consistent behavioural differences arise is puzzling because of the intuitive expectation that natural selection should favour complete behavioural plasticity (Sih et al. 2004b). Explanations for the existence of individual consistency include the possible benefits associated with consistency (Dall et al. 2004; McNamara et al. 2009) and the costs of being flexible, such as the behavioural errors caused by limited or noisy environmental information (Sih et al. 2004a; Mcelreath & Strimling 2006). Parallels have been drawn between personality and the fear response, where rather than responding differently to each threatening situation, animals have a state of fear that can be induced by many circumstances (see Dall et al. 2004). This cross-contextual consistency is thought to make it easier for individuals to behave appropriately and rapidly in response to a stimulus, thus avoiding costly mistakes (Rolls, 1999). In addition to these theories, many adaptive models of personality have shown how consistency can arise if behaviour is linked to consistent differences in state, such as residual reproductive value or productivity (Dall et al. 2004; Wolf et al. 2007; Dingemanse & Wolf 2010; Wolf & Weissing 2010). For example one theory proposes that a life-history strategy that prioritises growth or current productivity, will be reflected by increased foraging activity across contexts (i.e. aggressive, predation-risk prone), whereas a strategy that prioritises survival will be associated with more cautious behaviours (i.e. low aggression, risk-aversion) (Stamps 2007; Biro & Stamps 2008).

In contrast to traditional behavioural ecology theory, personality theory predicts that the limited plasticity displayed by animals will result in particular behavioural

types (e.g. aggressive individuals) behaving optimally in some contexts, but exhibiting seemingly maladaptive behaviours in others (Figure 1a, Sih et al. 2004b; Dall et al. 2004). This concept fundamentally influences the study of behavioural evolution, as it implies that we cannot understand behavioural adaptations by studying them in isolation, but instead must observe behaviour across a range of contexts. For example, to understand how selection is acting on parental care behaviour, it may also be important to consider how this trait is linked to competitive ability and aggressiveness (see Figure 1b). Viewed in this way, it can be predicted that different personality types will be suited to different situations or environmental conditions. This in turn suggests that personality variation is likely to be maintained by spatio-temporal heterogeneity in selection pressures relating to variation in factors such as predation pressures, food availability, and the social environment (Wilson et al. 1994; Wilson 1998; Sih et al. 2004a; Dall et al. 2004; Wolf et al. 2008; Réale et al. 2010).

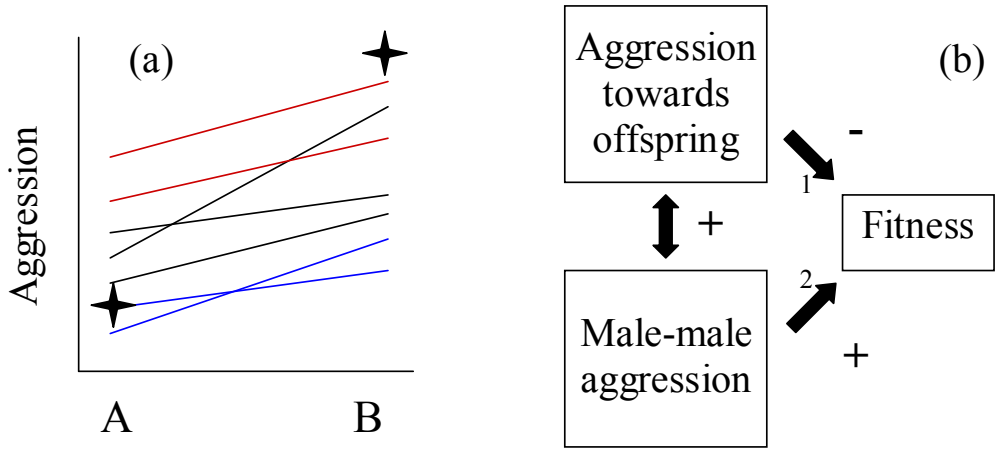


Figure 1. Limited behavioural plasticity and fitness (adapted from Sih et al. 2004b): (a) a plasticity plot showing individual variation in "aggression" across two contexts (A & B), where each line represents an individual and the stars signify the optimum level of aggression for each context, and (b) an example of a positive behavioural correlation across contexts produced by behavioural tendencies that carry over between contexts. The red individuals in figure (a) are highly aggressive and therefore may perform well in competition with other males but at a cost of high aggression towards offspring, whereas the less aggressive individuals (blue) will show the opposite pattern. Whether aggressive or passive individuals are favoured in a given situation will depend on the relative strength of selection on male-male competition and parental care behaviour (represented by arrows 1 & 2).

Empirical work exploring how selection acts on personality in natural populations has shown that patterns of selection fluctuate over time and space, and between the sexes (e.g. Réale & Festa-Bianchet 2003; Dingemanse et al. 2004; Boon et al. 2008; Quinn et al. 2009). For example, work on a Dutch great tit population demonstrated that annual adult survival related to personality, but that the direction of selection apparently alternated between years and was always opposite for males and females (Dingemanse et al. 2004). The behavioural mechanisms leading to this annual variation in selection pressures are largely unknown, but are thought to be linked to changes in winter food resources affecting competition between individuals. Fluctuating selection pressure such as those reported in this study, where different behavioural types are favoured under

different conditions, are therefore likely to maintain higher levels of within-population genetic variation than expected from mutation alone (Dingemanse et al. 2004; Burger & Gimelfarb 2002). Consequently, it appears that the same types of mechanisms that are thought to act on morphological and life-history variation may also be maintaining behavioural variation in wild populations - a concept with wide reaching ecological and evolutionary implications (Sih et al. 2004a; Nettle 2006; Réale et al. 2010).

Cognitive ability – the functional significance of individual differences

It is generally recognised that individuals differ in their ability to solve goal-orientated cognitive tasks (e.g. Vonk & Povinelli 2011; Seibt & Wickler 2006; Overington et al. 2011a; Biondi et al. 2008) and this variation can be consistent between different types of tasks (e.g. Galsworthy et al. 2002; Matzel et al. 2003; Overington et al. 2011a; Bouchard et al. 2007; Banerjee et al. 2009), and can have a significant heritable component (Tolman 1924; McGuire & Hirsch 1977; Lofdahl et al. 1992; Galsworthy et al. 2005). Individual differences in cognitive ability have generally not been considered using the same framework as personality variation (see: Penke et al. 2007; Réale et al. 2007). Instead, traditionally the study of animal cognition has largely focused on either identifying proximate causes of variation in ability, or scrutinised small numbers of captive individuals to establish the level of causal understanding animals possess about various problem-solving tasks (see Shettleworth 2010). However, in recent years the link between cognition and ecology has received growing attention (Healy & Braithwaite 2000; Reader & Laland 2003; Dukas 2004; Emery 2006; Roth et al. 2010; Lefebvre 2011).

Cognition can be defined as the mechanisms by which animals acquire, process, store, and act on information from their environment (Shettleworth, 2010). These cognitive processes are thought to fundamentally influence how animals acquire and manage resources, avoid predation, invade new habitats, and maintain social relationships (e.g. Cheney et al. 1986; Curio 1988; Pravosudov & Clayton 2002; Sol et al. 2002; Turner et al. 2006; Keagy et al. 2009), and are therefore likely to have considerable ecological importance. Indeed variation in cognitive traits is generally assumed to reflect adaptive differences, where high performance allows animals to occupy more cognitively demanding niches (Lee 1991; Stephens 1991; Reader & Laland 2003; Dukas 2004; Shettleworth 2010). Support for this hypothesis mostly comes from between-species comparisons (Dukas & Real 1991; Sherry & Healy 1998; Healy et al. 2005; Nicolakakis et al. 2003; Sol et al. 2005). For example it has been demonstrated that bird taxa with larger relative brain sizes and higher innovation rates are more successful at establishing themselves in novel environments (Sol et al. 2005), and vole species with larger home ranges have better spatial memories (Sherry & Healy 1998). Although these interpecific comparisons suggest that variation in cognitive performance is adaptive, more fine-scale comparisons are required to establish whether variation in these traits is indeed linked to fitness (Raine & Chittka 2008).

Research on the black-capped chickadee (*Poecile atricapillus*) has provided some insight into the adaptive significance of intraspecific variation in cognitive performance (Pravosudov & Clayton 2002; Roth & Pravosudov 2009; Roth et al. 2010, 2011). Using a common garden approach, it has been demonstrated that

individuals from the northern extreme of the species range, where conditions are relatively harsh, have more hippocampal neurons, better spatial memories and are better at solving novel foraging problems, than those from the southern extreme where food is more abundant (Roth et al. 2010, 2011). Although this work suggests that there may be fitness benefits associated with being a good problem solver, and that positive, directional selection for this trait might be expected under harsh environmental conditions, this hypothesis has yet to be tested directly (Boogert et al. 2011). Indeed, while cognitive traits such as learning have been shown to have fitness consequences under laboratory conditions (reviewed in Dukas 2008), very little is known about the functional significance and fitness consequences of individual differences in cognitive performance in natural populations (but see: Keagy et al. 2009). Indeed no study has attempted to measure selection on a cognitive trait under natural conditions. One reason for this is likely to be that sufficient sample sizes needed are often difficult to obtain for cognitive traits, the measurement of which commonly requires extensive subject training or repeated trials (e.g. Weir et al. 2002; Tebbich & Bshary 2004; Heinrich & Bugnyar 2005).

A recent study in barn swallows (*Hirundo rustica*) overcame this difficulty by using relative head size as a proxy for brain size (and hence cognitive capacity) (Møller, 2010). Birds with relatively large heads were found to arrive earlier from spring migration, were less likely to be recaptured (despite continuing to breed in the study colony), and also aggregated in larger colonies than smaller-headed birds. While these results suggest that there may be fitness benefits associated with traits such as navigation and learning ability, and the capacity to deal with socially

complex environments (Møller, 2010), they provide only indirect evidence for these hypotheses. Understanding how selection acts on cognitive traits therefore remains a fundamental knowledge gap in the field of animal cognition, and is one of the key aims of this thesis.

The distinction between cognitive and personality traits

In the study of human individual differences, general cognitive ability and personality are treated as distinct types of traits (Cronbach 1949; Moutafi et al. 2005; Penke et al. 2007; Winter & Barenbaum 1999). This distinction is also often adopted in the study of animal personality (see Réale et al. 2007). In human research, it has been proposed that this distinction is significant as it reflects different kinds of selection pressures acting on these traits (Penke et al., 2007). As previously discussed, personality variation is likely to be maintained by balancing selection, where both extremes of the same trait are favoured by selection to the same degree, but in different contexts or under different environmental conditions. In contrast it has been suggested that directional selection should act to winnow variation in general cognitive ability, and that any genetic variation will be the result of mutations (i.e. mutation-selection) (Penke et al., 2007). This distinction is based on the premise that cognitive abilities are directly, invariably and positively related to fitness (Réale 2007). Although this has not been tested directly in wild populations, evidence from both comparative studies and selection experiments in the lab suggest that, at least for certain cognitive traits, this is unlikely to be the case (e.g. Safi et al. 2005; Köhler & Moyà-Solà 2004; Kawecki 2010).

In addition to benefits, cognitive traits are also likely to be associated with considerable costs (Dukas, 2004). Engaging in cognitively demanding behaviours can be associated with both time and energy costs (e.g. Dukas & Visscher 1994), as well as increased predation risk (Reader & Laland 2003). In addition to the costs associated with exhibiting specific behavioural actions, cognitive traits are also likely to incur intrinsic costs, such as those caused by developmental or genetic trade-offs (Kawecki, 2010; Niven, 2005). This is because the development and maintenance of neural structures required for cognitive tasks are energetically costly (reviews in: Dukas 2004). In humans, for example, the brain only accounts for 2% of an adult's body weight, but it consumes about 20% of the resting metabolic rate (Clarke & Sokoloff 1999). Experimental work studying correlated responses to selection in *Drosophila melanogaster* has demonstrated evolutionary trade-offs between learning ability and other ecologically relevant traits such as competitive performance and senescence (reviewed in Kawecki 2010).

In addition to trade-offs caused by differential allocation of limited resources, cognitive traits and other fitness-related behaviours may be linked via pleiotropic effects, leading to behavioural trade-offs (Strobel, 2007). For example in humans, a polymorphism in the gene encoding the catecholamine-metabolising enzyme catechol-O-methyl transferase has been linked to high scores on the personality axis 'neuroticism' and to better performance in cognitive tasks involving working memory (reviewed in Strobel 2007). In non-human animals individual variation in cognitive ability has been linked to a range of other behaviours (although not yet at the genetic level) such as high stress reactivity (Pfeffer et al. 2002), willingness to

approach novel objects (Seferta et al. 2001; Bouchard et al. 2007; Overington et al. 2011a), and exploration (Overington et al. 2011a; Guillette et al. 2009; Guillette et al. 2010; Titulaer et al. 2012; Amy et al. 2012). In several taxa cognitive performance can be negatively related to dominance or competitive ability – traits which are themselves likely to be under significant selection (Laland & Reader 1999; Reader & Laland 2001; Reader & Laland 2003; Katzir 1983).

Whether a cognitive trait is favoured by selection will therefore depend on the relative costs and benefits of that trait in a given situation and environment. Consequently, like personality axes, in some contexts cognitive traits are likely to be subject to balancing selection (Strobel, 2007). Some evidence for contrasting patterns of selection acting on cognitive abilities in nature comes from comparative work in bats. It has been demonstrated that, relative to the ancestral state, brain size in bats has increased in behaviourally flexible species and those inhabiting structurally complex habitats, but has been reduced in species occupying less cognitively demanding niches (Ratcliffe et al. 2006; Safi et al. 2005). However, whether similar patterns of heterogeneous selection may act to maintain variation in cognitive traits between and within natural populations has yet to be demonstrated. Indeed very little is known about the potential fitness pay offs for animals with different cognitive abilities under natural conditions (Raine & Chittka, 2008). One of the main aims of this thesis is therefore to investigate both the functional and adaptive significance of individual variation in a simple cognitive trait.

Studying individual variation – the ecological validity of standardised assays

Researchers studying personality are ultimately interested in the consistent differences in natural behaviour in the wild. However, in comparison to morphological and life-history traits, behaviours are more difficult to measure without ambiguity in large numbers of individuals. It is perhaps partly for these reasons that individual behavioural variation has been relatively understudied by behavioural ecologists (Réale et al. 2007). To overcome these difficulties researchers generally measure easily-quantifiable behaviours under controlled conditions (but see Duckworth 2006). The tests used to assay these behaviours are often taken from classical animal behaviour research, such as the 'open field test' (Walsh & Cummins, 1976), which has been adapted for use in a wide range of study species (e.g. open field assay in great tits (Verbeek et al. 1994), barnacle geese (Kurvers et al., 2009), Trinidad killifish (Fraser et al. 2001), North American red squirrels (Boon et al. 2007), and sheep (Villalba et al. 2009)). Use of these simple assays has provided great insight into correlations between different behaviours and the underlying proximate causes of variation; however the functional significance of this variation generally remains less clear. To examine the adaptive significance of variation in these tests, researchers compare the survival and reproductive success of assayed individuals once released back into the wild (see Dingemanse et al. 2004; Boon et al. 2007, 2008; Quinn et al. 2009). Inferences about the mechanisms leading to fitness differences between behavioural types are therefore often based solely on behaviour measured during standardised assays in captivity (and often under highly artificial conditions).

However, behaviour in these assays can be context specific (e.g. Van Oers et al. 2005; Bell & Sih 2007), and where studies have compared specific behaviour across captive and wild contexts, captive assays do not always predict wild behaviour in the expected direction (e.g. Van Overveld & Matthysen 2010; Morand-Ferron et al. 2011; Dingemanse & de Goede 2004; Hollander et al. 2008). Determining the ecological validity of standardised assays therefore remains an important step in understanding how selection operates on consistent behavioural differences.

A case study: personality in the great tit

Probably the best-studied non-human personality axis is the reactive-proactive personality continuum (reviewed in Koolhaas et al. 1999; Groothuis & Carere 2005). This axis has been studied particularly extensively in rodents and great tits, where in comparison to relatively reactive individuals, more proactive individuals can be characterised by rapid exploration of a novel environment, short latencies to feed in the presence of novel objects or after being startled, high aggression, a high tendency to form routines, lack of flexibility in response to environmental stimuli and a high reactivity to social defeat (reviewed in Groothuis & Carere 2005). Work on the great tit represents the most comprehensive study of the functional significance of personality to date (see Figure 2). In this species 'exploration behaviour of a novel environment' (continuous measure from slow to fast), an assay of the reactive-proactive personality continuum, has been linked to a broad range of ecologically relevant behaviours such as dispersal (Dingemanse et al. 2003; Quinn et al. 2011), nest and territory defence (Amy et al. 2010; Hollander

et al., 2008), dominance (Dingemanse & de Goede 2004), promiscuity (Van Oers et al. 2008; Patrick et al. 2011) and space use (Van Overveld & Matthysen 2010; Van Overveld et al. 2011).

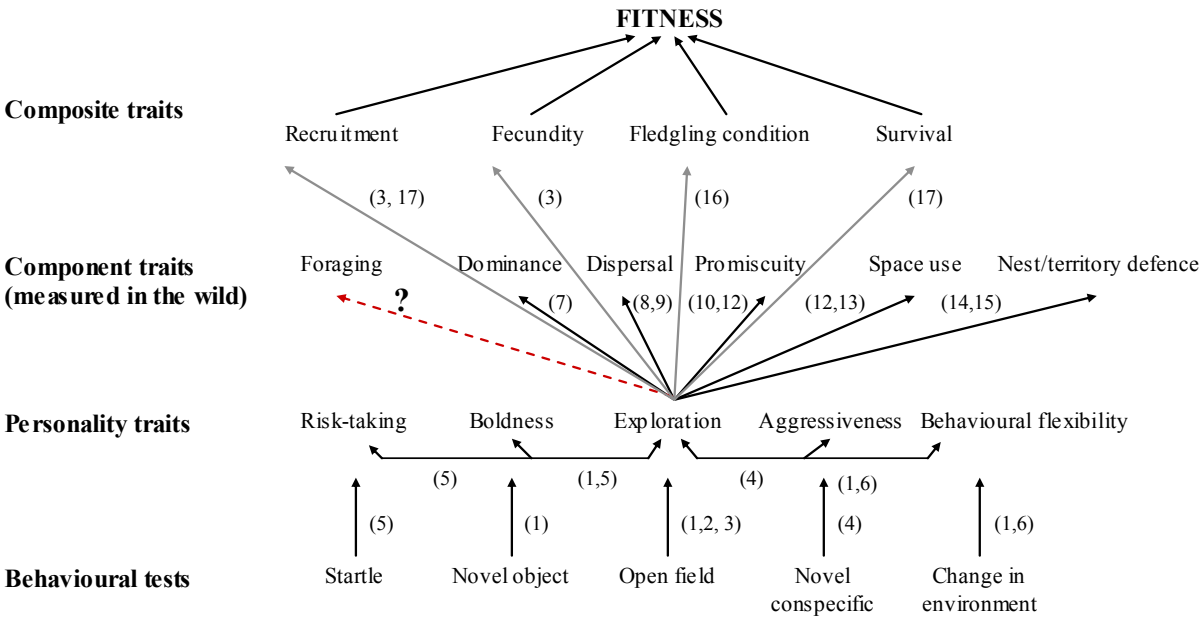


Figure 2. A flow diagram showing the framework for the study of personality in the great tit, and the links demonstrated between captive measures, behaviour in the wild and fitness (adapted from Réale et al. 2007). Black arrows indicate direct relationships between two variables, grey arrows indicate links with fitness related traits, and red dashed line represents an unexplored relationship. Number in figures: (1) Verbeek et al. (1994); (2) Dingemanse et al. (2002); (3) Quinn et al. (2009); (4) Verbeek et al. (1996); (5) Van Oers et al. (2004); (6) Marchetti & Drent (2000); (7) Dingemanse & de Goede (2004); (8) Dingemanse et al. (2003); (9) Quinn et al. (2011); (10) Van Oers et al. (2008); (11) Patrick et al. 2011; (12) Van Overveld & Matthysen (2010); (13) Van Overveld et al. (2011); (14) Hollander et al. (2008); (15) Amy et al. (2010); (16) Both et al. (2005); (17) Dingemanse et al. (2004).

However, for several key behavioural categories, the significance of the reactive-proactive axis for behaviour in the wild remains largely unknown. Obtaining food resources is a major challenge faced by animals, and foraging efficiency has been shown to have significant fitness consequences (e.g. Fritz & Morse 1985; Ritchie 1990; Lemon 1993; Lescroël et al. 2010). Several captive studies on great tits have demonstrated differences in the way relatively fast and slow birds forage (Verbeek

et al. 1994; Marchetti & Drent 2000), and therefore it has been suggested that foraging may represent an important mechanism linking personality to fitness (Both et al. 2005; Quinn et al. 2009). However, very little is known about how personality influences natural foraging behaviour in this species. A recent study that measured the response of great tits to the abrupt removal of artificial feeders in the wild, found that relatively fast explorers moved to new foraging areas whilst slower individuals remained within the vicinity of the site of the feeder (Van Overveld & Matthysen 2010). This observation directly contrasts with predictions based on captive behaviour, where fast birds continued to visit feeding sites after food is withdrawn and slow birds more readily extend their searching to new sites (Verbeek et al. 1994; Drent & Marchetti 1999; Marchetti & Drent 2000). This example demonstrates the need for work examining how the reactive-proactive axis relates to natural foraging behaviour, in order to better understand the functional significance of this trait.

Another mechanism that is thought to play a key role in linking the reactive-proactive axis to fitness is how individuals respond to risk. This is because relatively reactive and proactive individuals are predicted to differ in how they manage the inherent trade-off between productivity and avoiding the risk of predation (Van Oers et al. 2004; Sih et al. 2004a; Biro & Stamps 2008; Wolf et al. 2007). Indeed evidence from a range of species suggests that reactive individuals have higher survival but lower reproductive success than proactive individuals (reviewed in Biro & Stamps 2008; Smith & Blumstein 2008). Risk responsiveness is thought to be an important behavioural mechanism driving these effects (Wolf et

al., 2007). However work on captive great tits has shown that risk-taking behaviour can be highly context-dependent (Van Oers et al. 2005); therefore it cannot be assumed that individuals that are relatively bold in captive assays are also categorically more risk-prone in the wild. Moreover, the only study in this species to compare personality in captivity to risk-taking behaviour in the wild reports mixed findings (Hollander et al. 2008). One of the aims of this thesis is therefore to further investigate the functional significance of exploration behaviour - a key captive measure of personality - by exploring how this trait relates to in both foraging and risk-taking behaviour in the wild.

Study system and traits of interest

In this thesis I use the great tit study system to explore the functional significance of a simple cognitive trait and a personality trait. Cognitive performance is often defined as the speed or success of individuals at solving problems in functionally significant contexts such as feeding, spatial orientation, or communication (Roth & Dicke 2005). One way to quantify this is to present individuals with novel tasks requiring a solution that is not part of the animal's normal repertoire (Roth & Dicke, 2005). At the interspecific level, food-related problem solving in these types of tests has been shown to correlate with taxonomic counts of innovations in the wild (Webster & Lefebvre 2001). Innovativeness, defined as the ability to solve novel problems or find new solutions to old problems (Kummer & Goodall, 1985), has itself been linked to residual brain size, tool use, and learning ability across avian and primate taxa (see: Lefebvre 2011; Reader et al. 2011), and is increasingly viewed as an important component of animal cognition (Lefebvre et al. 2004; Roth

& Dicke 2005; Boogert et al. 2011). In this thesis I therefore use success in a novel food-related problem-solving task to quantify individual variation in cognitive performance.

Great tits are small cavity-nesting passerines with a broad geographical range, spanning Europe, large parts of Asia and northern Africa (Gosler 1993). This ability to occupy a wide variety of different habitats has been shown to be a hallmark trait of innovative species (Overington et al. 2011b). Indeed anecdotal evidence suggests that great tits are highly inquisitive in response to novelty (Gibb 1957) and are capable of considerable innovative foraging behaviour (Fisher & Hinde 1949; Hinde & Fisher 1951; Duyck & Duyck 1984; Estók et al. 2010). For example, it was recently observed in a Hungarian population of great tits that individuals systematically searched for and killed bats for food (Estók et al., 2010). A recent study compiled records of innovations (i.e. behaviours not previously observed within taxa) for 803 bird species in 76 families, and found that the great tit ranked among the top 20 species for food-related innovation propensity (Overington et al. 2009). Innovative problem solving is therefore likely to be an ecologically relevant trait in this species.

The second trait I examine in this thesis is the personality trait 'exploration behaviour of a novel environment' (hereafter exploration behaviour), which is a captive-measured behaviour often used as a proxy for the reactive-proactive personality axis. As previously discussed this behavioural axis has been extensively studied in the great tit (Groothuis & Carere 2005, see Figure 2).

Previous work on my study population has shown that exploration behaviour is influenced by both additive genetic and environmental sources of variation and also predicts dispersal behaviour, promiscuity and reproductive fitness (Quinn et al. 2009; Quinn et al. 2011; Patrick et al. 2011). Personality research has demonstrated that great tits provide an excellent study organism for examining the functional significance of behavioural variation. Not only are wild great tits easy to catch and assay in captivity, but they readily breed in nest boxes at high densities, and are tolerant of frequent human disturbance during reproduction (Cramp & Perrins 1993). This means that the reproductive behaviour of large numbers of individually tagged birds can be monitored, providing detailed measures of reproductive success and life-history variation. Tits will also readily feed from artificial feeders and are central-place foragers during the breeding season, so their foraging behaviour can be easily observed and quantified (reviewed in Perrins 1979, Gosler 1993). Indeed the behaviour, life histories and trophic interactions of the great tit have been extensively studied, and as a result this species has been used as a model system for many aspects of biology (Perrins 1991; Perrins 1979; Gibb & Betts 1963; Gosler 1993).

Fieldwork for this thesis was conducted at Wytham Woods, a mixed deciduous woodland, 385ha in size in Oxfordshire, UK (51° 46’ N, 1° 19’ W). Wytham is composed of a mixture of ancient semi-natural woodland, eighteenth, nineteenth and twentieth century plantations and secondary regenerated wood pasture (Wilkin et al. 2006). The predominant tree species are oak (*Quercus robur*), beech (*Fagus sylvatica*), sycamore (*Acer pseudoplatanus*) and ash (*Fraxinus excelsior*).

Wytham contains 1020 nest boxes (Figure 3), which are monitored as part of a long term study which began in 1947 (Gibb 1950). The quality of habitat for breeding great tits is highly heterogeneous. Pedunculate oak trees (*Quercus robur*) are an important component of great tit breeding habitat as their foliage supports large populations of winter moth larvae, the great tit's main food source during the breeding season (Summerville et al. 2003; Perrins 1979). As part of a larger project I was involved in mapping all the oak trees in Wytham with a diameter at breast height of 30cm or greater, allowing for habitat quality to be easily quantified.



Figure 3. Satellite image of Wytham Woods, black circles show the locations of great tit nest boxes (N = 1020).

Thesis aims and overview

This thesis investigates the functional significance of two behavioural traits, innovative problem-solving performance and exploration behaviour, with two broad aims. The first is to use an empirical framework borrowed from personality research to carry out the first large-scale study into the ecological significance and fitness consequences of a simple cognitive trait. The second is to simultaneously explore the functional significance of exploration behaviour, building on previous personality work in the great tit. To do this I investigate how variation in this trait relates to behaviour in wild, concentrating particularly on foraging and risk-responsiveness, traits that are proposed to represent key behavioural mechanisms driving relationships between personality and fitness. Studying both a cognitive trait and a personality trait in the same individuals will allow me to establish the extent to which these two traits simultaneously correlate with functionally significant behaviour in nature.

This thesis consists of five data chapters:

- In **Chapter 2** I build on preliminary work carried out by previous students to develop a standardised assay of spontaneous problem-solving performance that quantifies variation between individuals in my study population, and can be carried out rapidly on hundreds of wild-caught individuals. I then examine the extent to which success in this assay is repeatable over time and consistent between different problem-solving tasks, and test whether variation relates to exploration behaviour and a number of state and motivational factors.

- In **Chapter 3** I explore the possibility that problem-solving ability is negatively correlated to competitive ability, a relationship that has been demonstrated in several taxa, which may represent a behavioural trade-off and therefore a potential cost of high problem-solving performance. To do this I observe birds, previously assayed for problem solving and exploration behaviour in captivity, at feeders in the wild where competition is high. In addition I simultaneously explore the functional significance of exploration behaviour in a competitive foraging context by testing whether this trait can predict competitive ability at feeders (and hence ability to secure limited food resources).
- In **Chapter 4** I go on to examine how problem-solving performance and exploration behaviour relate to *natural* foraging behaviour, by measuring the quality and quantity of food brought back to the nest during offspring provisioning, as well as the size of birds' foraging ranges. Here I aim to test the hypothesis that innovative foraging allows individuals to better exploit their environment and forage more efficiently, as well as test several hypotheses based on captive studies linking exploration behaviour to foraging performance.

- In **Chapter 5** I examine the fitness consequences of variation in problem-solving performance by establishing how performance relates to various life-history traits and fitness components, and testing whether directional selection is occurring on this trait. I also test the hypothesis that the

benefits of innovative problem solving may be more pronounced under poor environmental condition, where food is more difficult to locate.

- Finally, in **Chapter 6** I explore how exploration behaviour covaries with risk responsiveness in the wild, a possible behavioural mechanism thought to link the reactive-proactive personality axis to fitness. To do this I establish whether exploration behaviour predicts how individuals respond to two different kinds of risk in a reproductive context: novelty at the nest and trapping by humans.

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CHAPTER 2

Individual variation in spontaneous problem-solving performance among wild great tits



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Individual variation in spontaneous problem-solving performance among wild great tits

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Behavioural traits generally and cognitive traits in particular are relatively understudied in an evolutionary ecological context. One reason for this is that such traits are often difficult to characterize among large numbers of individuals, without the influence of diverse environmental effects swamping intrinsic individual differences. We conducted standardized assays on a natural population of great tits, *Parus major*, to quantify and characterize individual variation in problem-solving performance, a simple cognitive trait often linked to innovative foraging ability. Forty-four per cent of 570 birds solved a food-motivated, lever-pulling problem and this proportion was consistent across three seasons. Individual performance was consistent within and across captivity sessions, across seasons, and between two different problem-solving tasks (lever and string pulling). Problem-solving performance was not explained by differences in latency to approach the empty task, nor latency to feed after human disturbance. Variation was unrelated to body condition, while age and natal origin explained significant but minimal amounts of variation, the importance of which varied between seasons. Problem-solving performance did not covary with exploration behaviour of a novel environment, suggesting that individual differences in problem solving represent an independent source of behavioural variation in our population. Rather than simply reflecting covariance with state or with other behavioural traits, our results suggest that variation in problem-solving performance represents inherent individual differences in the propensity to forage innovatively. We suggest that standardized problem-solving assays may prove ideal for studying the evolutionary ecology of simple cognitive traits.
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The link between cognition and ecology has received growing interest in recent years (see Healy & Braithwaite 2000; Dukas 2004; Biernaskie et al. 2009; Roth et al. 2010). Cognitive processes are likely to have considerable ecological importance because they fundamentally influence how individuals acquire and manage resources, avoid predation, invade new habitats, and maintain social relationships (Cheney et al. 1986; Curio 1988; Pravosudov & Clayton 2002; Sol et al. 2002; Turner et al. 2006; Keagy et al. 2009). Individual variation in cognitive traits is therefore likely to influence survival and reproductive success (Gailey et al. 1985; Morse & Stephens 1996; Egas & Sabelis 2001). Little is known about the underlying causes of such variation in wild populations (Roth et al. 2010). One reason for this is that behavioural traits are influenced by a great variety of environmental factors making it difficult to identify intrinsic causal factors (Merilä & Sheldon 2001). Another is that the large sample sizes needed for the study of individual variation are often difficult to obtain, especially for cognitive traits, the measurement of which commonly requires extensive subject training or repeated trials (e.g. Weir et al. 2002; Tebbich & Bshary 2004; Heinrich & Bugnyar 2005). Here we attempted to overcome these difficulties by examining a variety of sources of individual variation in a simple cognitive trait, problem-solving performance, using rapid assays among large numbers of wild-caught great tits, *Parus major*, temporarily held in captivity under standardized conditions.

In recent years a growing number of studies have quantified repeatable or consistent behavioural differences between individuals from natural populations (Bell et al. 2009). However, we know of no similar repeatability estimates for cognitive traits. Repeatability is defined as the proportion of phenotypic variation explained by differences between individuals (Lessells & Boag 1987), which can be caused by a variety of factors: genetic, developmental and environmental (Réale et al. 2007; Bell et al. 2009). Selection experiments and common garden studies have provided considerable evidence that genes play an important role in shaping cognitive abilities (McGuire & Hirsch 1977; Lofdahl et al. 1992; Galsworthy et al. 2005; Roth et al. 2010). Developmental factors also affect cognitive performance (Vince 1958, 1960; Laland & Reader 1999; Reader & Laland 2001;

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Botero et al. 2009). For example, juvenile birds direct more attention to novel problems than adults (Vince 1958, 1960; Greenberg 2003) and female guppies, *Poecilia reticulata*, are more likely to forage innovatively than males (Laland & Reader 1999). In addition, environmental conditions can also influence cognitive traits (Cooper & Zubek 1958; Seibt & Wickler 2006; Arnold et al. 2007). For example, the diet of blue tit, *Cyanistes caeruleus*, nestlings has been shown to influence their spatial-learning ability as adults (Arnold et al. 2007). Social environmental factors can also be important. High cognitive performance is often more prevalent among subordinates, which frequently lose out in competition for limited resources (Laland & Reader 1999; Reader & Laland 2000), and drops in social rank can be associated with an immediate improvement in problem-solving performance (Bunnell & Perkins 1980). Empirical data therefore suggest that consistent individual differences in cognitive traits can be caused by a wide range of factors.

Individual variation in cognitive ability may also covary with other behavioural traits. Correlated suites of behaviours, also called behavioural syndromes or personality, have been documented in a wide variety of taxa (reviewed in Gosling 2001; Sih et al. 2004; Réale et al. 2007). For example, in the great tit, in contrast to 'proactive' individuals, 'reactives' are relatively neophobic (Verbeek et al. 1994), less aggressive (Verbeek et al. 1996), explore new environments more slowly and thoroughly (Verbeek et al. 1994), are more responsive to their environment (Verbeek et al. 1994), are less likely to form routines and readily explore new feeding options (Drent & Marchetti 1999). It has been suggested that because 'reactive' individuals explore their environment more thoroughly than 'proactive' individuals, and are better able to adjust their foraging behaviour when faced with environmental change, they may perform better in some cognitive tasks (Benus et al. 1987; Verbeek et al. 1994; see Sih & Bell 2008 for discussion). In contrast, it has also been proposed that bolder, fast-exploring individuals may readily acquire information about novel situations and learn novel tasks more quickly than shyer, slow explorers (Sneddon 2003). Few studies have investigated cognitive performance in the context of personality, and those that have report conflicting results, so the generality of this relationship remains unclear (see Carere 2003; Sneddon 2003; Guillette et al. 2009). Evidence from a variety of taxa suggests that neophobic individuals are less likely to engage in novel feeding situations and consequently are unlikely to solve problems or innovate (Searle 1949; Seferta et al. 2001; Webster & Lefebvre 2001; Greenberg 2003; Bouchard et al. 2007). However, several studies also demonstrate that a significant amount of variation in learning ability remains after controlling for neophobia and exploration behaviour (Galsworthy et al. 2002; Matzel et al. 2003; Bouchard et al. 2007).

We used a wild population of great tits to quantify and characterize individual variation in spontaneous problem-solving performance. Individual variation in novel problem solving is poorly understood but may reflect general cognitive ability (Roth & Dicke 2005) and innovativeness (Laland & Reader 1999; Webster & Lefebvre 2001). The great tit is a generalist species with an extensive geographical range (Gosler 1993). Great tits frequently investigate novel objects in the wild (Gibb 1957) and anecdotal evidence suggests considerable innovative foraging behaviour; examples include the opening of milk bottle tops (Fisher & Hinde 1949; Hinde & Fisher 1951), the tapping of acorns to determine the presence of hidden larvae (Ennion 1962), the use of a pine needle to extract larvae from bark (Duyck & Duyck 1984), and predation of pipistrelle bats, *Pipistrellus pipistrellus* (Estók et al. 2009). Food-related problem solving may therefore be an ecologically relevant trait for this species.

Our aims were (1) to determine whether problem-solving performance was consistent within individuals, across short and long time periods, and between two different tasks; (2) to establish whether our assay measured goal-oriented problem-solving propensity, rather than quantifying general activity, neophobia or motivational differences; (3) to examine the relationship between a well-studied personality trait, exploration behaviour of a novel environment (henceforth, exploration behaviour), and problem-solving performance; and (4) to determine whether state variables such as sex, age and natal origin could account for observed individual differences in problem-solving performance.

METHODS

Study Site and Catching Procedure

All behavioural assays were carried out on great tits caught from a wild population in Wytham Woods (51°46′N, 1°20′W), Oxfordshire, U.K. We caught 662 individuals using mist nets at temporary feeders erected at sites throughout the wood during the winters of 2006–2007, 2007–2008 and 2008–2009, between November and March. From here onwards these three winter catching periods are referred to as seasons. Additionally, birds were caught in the final week of each season by removing them from their nestboxes after dusk. All birds were caught under ringing licences from the British Trust for Ornithology (BTO). Birds were aged (adult or juvenile if less than 1 year old) and sexed based on plumage (Svensson 1992), and biometrics (wing length, mm, and body mass, g) were taken. All unringed individuals were fitted with a unique BTO metal leg-ring. During the 2007–2008 and 2008–2009 seasons all great tits were also fitted with a unique passive integrated transponder (PIT, EM4102 tag, HID Global GmbH, Walluf, Germany) measuring 12.4 mm × 2.1 mm, which was attached to a celluloid split colour leg-ring. Up to 16 birds per catching session were transported in individual bird bags to the nearby John Krebs field station. Great tits were taken into captivity under Natural England licence.

On arrival at the field station, usually mid-afternoon, birds were housed singly in wire cages (45 × 45 cm and 68 cm high) and were visually isolated from one another. Two housing rooms were used, with a minimum of two and a maximum of eight occupied cages per room. Each cage contained three dowel perches, the unset problem-solving devices and bowls containing fresh water, husked sunflower seeds and mealworms, *Tenebrio molitor*. The birds were kept under a natural light regime using automated timers and the housing rooms were kept at ambient temperature (ranging from 3 to 16 °C) and ventilated using an air conditioning system. All birds were released within 24 h with the exception of a subsample of 80 birds during the 2007–2008 season that were kept in captivity for 4 days to carry out a battery of repeat trials and an object neophobia assay. All birds were released at the catching site.

Problem-solving Assay

All individuals (with the exception of 92 birds from the 2006–2007 season that were used in separate experiments, see below) were presented with a lever-pulling task on the afternoon they were housed ($N = 570$). The device used in this task consisted of a vertical transparent Perspex tube containing a platform, which was supported by a horizontal lever (Fig. 1a, b). The device was baited with four waxworms, *Pyralis farinalis*, placed on the platform. To solve the task, birds had to remove the lever from the device, causing the platform to drop and the waxworms to fall into a feeding dish. When the task was set, a single waxworm was placed in this dish to attract the bird to the device. This waxworm was eaten by the vast majority of birds (99% of birds, $N = 298$, ate the freely available waxworm in winter 2010). All birds were exposed to this task for approximately 3 h without being disturbed: 1 h before the aviary lights went off in

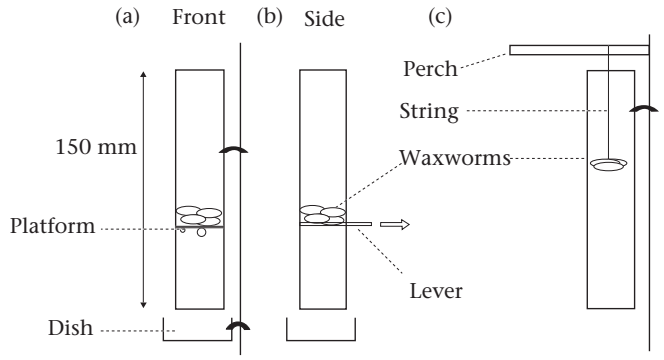


Figure 1. Problem-solving devices: (a) front view of the lever-pulling device as it appears to the bird, (b) side view and (c) string-pulling device. The lever-pulling device consisted of a transparent Perspex tube containing a platform supported by a horizontal lever. To solve the task, the bird had to remove the lever, releasing the platform and food reward. The string-pulling device consisted of a food reward suspended on the end of an 8 cm string, hung from a perch and protected by a transparent Perspex tube. To solve this task, the bird had to lift the string from above.

the evening and 2 h the morning after when the aviary lights had come on. Birds were not food deprived during this trial; however, the food reward in the device (waxworms) was highly preferable to the standard food available in the cage (E. F. Cole, personal observations).

Repeatability and Consistency

In addition to the overnight trial, subsamples of birds from the 2006–2007 and 2007–2008 seasons ($N = 51$ and 80, respectively) and all birds caught in the 2008–2009 season ($N = 218$) were also presented with the lever-pulling task again on the day after capture to test the individual repeatability of solving performance within a captivity session. Here birds were given 90 min to solve the problem, and were food deprived for 30 min preceding the trial and for the trial duration. In 2007–2008 the birds were moved to new cages just before they were presented with the daytime task for logistical reasons; similarly, they were also given access to their roosting boxes during these trials in 2006–2007 and 2007–2008, which meant they could avoid observing the problem-solving device. These factors probably contributed to the lower solving rates for this assay in these two seasons (see Results).

To assess whether performance in the lever-pulling task represented a more general propensity to problem solve, all birds assayed during the 2007–2008 and 2008–2009 seasons were also presented with a string-pulling task during the afternoon of the day after capture (Fig. 1c). Here birds obtained their food reward (three waxworms) by lifting an 8 cm string from the top of a Perspex tube. Birds were food deprived for 30 min preceding the trial and during the 60 min trial itself. During the 2007–2008 season, a subsample of birds ($N = 80$) was presented with this task a second time during the second evening in captivity to assess individual repeatability of string-pulling performance.

Over the 3-year study 67 individuals were taken into captivity twice, with a minimum of 2 weeks between captivity sessions, allowing us to estimate the repeatability of performance, both within and between the two tasks over longer time periods.

Characterizing Problem-solving Performance

Activity levels

To confirm that success in our lever-pulling task was a measure of goal-oriented problem-solving propensity rather than random activity in the cage, during the 2006–2007 season a subsample ($N = 45$) was presented with the daytime lever-pulling task (as described above) without the device being loaded with a food reward. A further subsample ($N = 47$) was presented with the normal loaded task. Both groups were experiencing the task for the first time in this trial and did not undergo any other problem-solving tests. If problem solving was motivated by food and not merely a reflection of individual activity levels, we predicted birds would primarily solve the device in the presence of food.

Neophobia

To determine whether individual variation in problem-solving performance could be explained by variation in neophobic response, we measured object neophobia among a subsample of individuals ($N = 61$) taken into captivity during the 2007–2008 season. Neophobia was assayed by comparing an individual's latency to feed with and without a novel object placed next to a food dish (modified methods from Greenberg 1984). This test was carried out on the morning before birds were released after all other assays had been completed. Normal food bowls were first removed from a bird's cage and three waxworms were placed in a dish permanently attached to the inside of the cage. The bird was then shut out of its roosting box and given 30 min to feed from the dish. Six birds did not feed during this period of habituation to the new feeding regime, and were therefore excluded from the experiment. Immediately after this initial 30 min period, the dish was refilled with three waxworms and the bird was randomly presented with either a novel object (white plastic disc, 10 cm in diameter, with six protruding, 2 cm long, coloured pipe cleaners) next to their food dish or the control treatment where only the food was added; the bird was then given 30 min to feed. Immediately after this, the final phase of the test was carried out, which involved the opposite treatment; either experimental or control. Latency to feed from the dish in the experimental and control treatments was extracted from video footage (Sony Handycam DCR-SR33E camcorder).

During the 2008–2009 season, 10 of the 16 housing cages were fitted with PIT detectors (Francis Scientific Instruments Ltd, Cambridgeshire, U.K.), positioned so that they acted as a perch in front of the lever-pulling device. All birds were fitted with PIT tags and therefore we could quantify the time it initially took individuals to approach the device when housed, a measure that we assumed reflected neophobia directed towards the device.

Exploration Behaviour

All birds underwent exploration behaviour assays on the morning after capture. Birds were released into a novel room (Verbeek et al. 1994) in which their movements were recorded for 8 min using an event recorder (Psion Workabout, with Observer mobile software, Noldus Information Technology, Wageningen, The Netherlands). Information on the number of hops, the number and duration of flights, and the areas of the room utilized were then entered into a principal components analysis, and the first component (all major loadings referred to increased activity) used in a general linear model (GLM) to produce an exploration behaviour score for each bird from the parameter estimates derived from using individual as a fixed effect, controlling for time of year (see Quinn et al. 2009 for further details).

Ethical Note

The protocols outlined were all subject to ethical review by the Department of Zoology (Oxford) ethical committee. Behaviour during captivity was closely monitored to ensure that any deterioration in health could be noticed quickly. Birds invariably began feeding shortly after they were transferred into their housing cages. One of the 662 individuals taken into captivity stopped eating but

recovered after being transferred to a heated cage and fed sugar water with a pipette. Changes in body mass between capture and release (mean ± SE = −0.73 ± 0.033 g) were well within the great tit's natural range of diurnal mass fluctuations (Macleod et al. 2005). All birds were released at the site of capture, where there was a supply of supplemented food to allow birds to feed before dusk. The PIT tags weighed approximately 0.13 g, small compared to the normal diurnal fluctuations of great tits (1.1 ± 0.02 g; Macleod et al. 2005). This added weight results in no adverse effects in terms of individual survival or body condition (Nicolaus et al. 2008).

Statistical Analysis

At the population level, solving-rate consistency between seasons was calculated using binary two-sample tests (Z statistic estimated with a normal approximation). A binary two-sample test was also used to test whether solving performance was goal oriented. Individual repeatability in solving performance between trials and consistency across tasks was calculated using GLMs, assuming a binomial error distribution, and using individual identity as the explanatory factor, adapted from Lessells & Boag's (1987) measure of repeatability. A logistic binary regression was used to determine which effects influenced solving performance. These included fixed factors age (juvenile/adult), sex, natal origin (immigrant/resident-born), cage (1–16) and room (1/2), and the continuous variables body condition and exploration behaviour. 'Days since 1 September' (September date) was also included as a continuous variable to control for a variety of possible time-of-year effects, such as hunger-related motivation and experience. Body condition was estimated for each bird by dividing the residual from a regression of body mass against the time of day birds were caught, by its wing length. Early environmental factors such as diet (Perrins 1991) and habitat types (Blondel et al. 1993) are likely to vary between years, and therefore we included interactions between age and season, and natal origin and season. Only first tests were included for birds that were taken into captivity multiple times. Main effect statistics were calculated including all main effects without interactions, dropping each one from the full model to test its significance; statistics for the interaction terms were estimated from full models containing all interactions. Nonparametric tests were used to test the relationships between neophobia measures and problem-solving performance. All analyses were conducted in either SPSS (SPSS Inc., Chicago, IL, U.S.A.) or Genstat (VSN International, Hemel Hempstead, U.K.).

RESULTS

Rate of Problem Solving

Forty-four per cent of birds solved the overnight lever-pulling task and this was remarkably consistent over the three seasons (Fig. 2). Fewer birds (26%) solved the daytime lever-pulling task but this was not consistent across seasons (Fig. 2). This inconsistency can be attributed to the lower daytime solving rates in 2006–2007 and 2007–2008, which we attribute to differences in methodology (see Methods). The string-pulling task was solved by 25% and this rate was consistent across seasons (Fig. 2). Therefore fewer than half of all birds solved our main problem-solving tasks, demonstrating individual variation in problem-solving propensity in our population.

Behavioural Repeatability and Consistency

Using scores from all individuals that were taken into captivity twice over the 3-year period, we found that both lever-pulling and string-pulling performances were repeatable within individuals over time (Table 1, Fig. 3a, b). Solving success in both tasks was also repeatable for individuals repeatedly assayed a year or more apart (Table 1). Again lever-pulling and string-pulling performances were consistent when we compared performance within a single captivity session (Table 1). Comparing performance between the two different

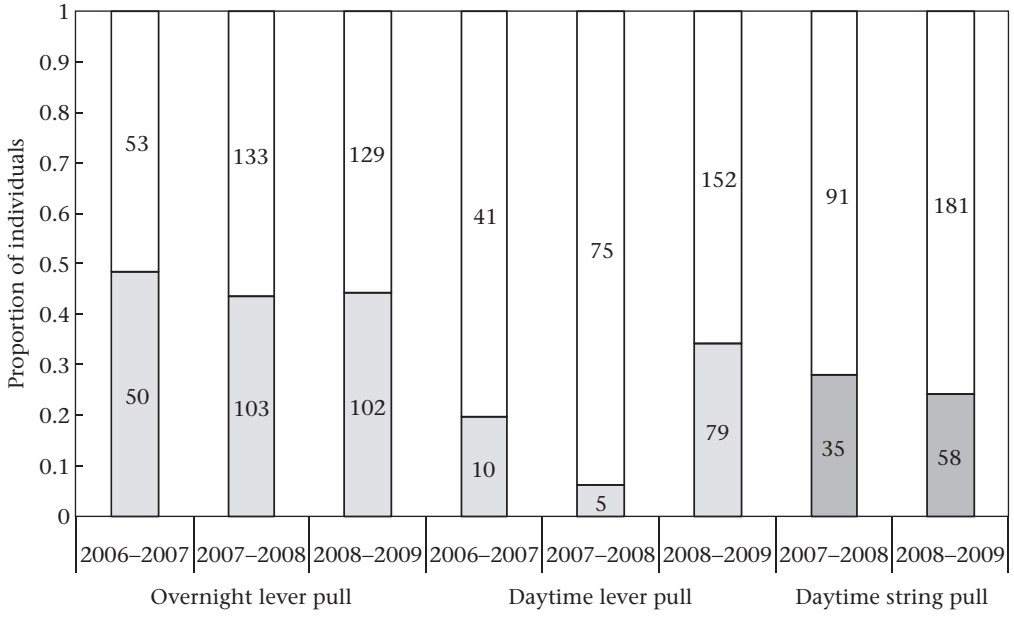


Figure 2. Proportion of individuals that solved the different tasks. Light grey represents solvers of the lever-pulling tasks, dark grey solvers of the string-pulling task and white nonsolvers. The numbers inside the bars correspond to the number of individual solvers and nonsolvers in each season. The proportion that solved the overnight task did not differ significantly between seasons: comparison of seasons 1 and 2: two-sample binomial test: $Z = 0.736$, $P = 0.462$; comparison of seasons 1 and 3: $Z = 0.744$, $P = 0.457$; comparison of seasons 2 and 3: $Z = 0.052$, $P = 0.958$. The proportion that solved the daytime lever-pulling task differed significantly between seasons: comparison of seasons 1 and 2: $Z = 2.341$, $P = 0.019$; comparison of seasons 1 and 3: $Z = -2.029$, $P = 0.042$; comparison of seasons 2 and 3: $Z = -4.623$, $P < 0.001$. The proportion that solved the string-pulling task did not differ significantly between seasons: comparison of seasons 2 and 3: $Z = 0.732$, $P = 0.464$.

Table 1
Repeatability of individual lever-pulling and string-pulling performance within and between captivity sessions

		Year	*N*	Repeatability	SE	*P*
Within captivity session	Lever-pulling performance between the overnight and daytime trials	All	347	0.34	0.05	<0.001
	String-pulling performance between the overnight and daytime trials	2007–2008	80	0.37	0.10	<0.001
Between captivity sessions	Lever-pulling performance between years	All	35	0.27	0.16	0.046
	Lever-pulling performance between captivity sessions over 3 years	All	67	0.40	0.10	<0.001
	String-pulling performance between years	All	23	0.54	0.15	<0.001
	String-pulling performance between captivity sessions over 3 years	All	47	0.37	0.13	<0.01

Performance between captivity sessions includes all repeated trials in which birds were taken into captivity twice with at least 2 weeks between sessions, whereas performance between years only includes birds taken into captivity twice with a year or more between sessions. Repeatability was estimated using methods from Lessells & Boag (1987).

tasks also showed a marked consistency in individuals' solving propensity both within and between captivity sessions (Table 2).

Characterizing Problem-solving Performance

None of the individuals presented with an empty problem-solving device solved the task, and this was significantly fewer than the number that solved the loaded task (binomial two-sample test: $Z = -3.635$, $N = 92$, $P < 0.001$).

Birds demonstrated marked consistency in the time they took to feed in the control and neophobia trials in captivity (Spearman rank correlation: $r_S = 0.360$, $N = 55$, $P = 0.007$). However, latency to feed was similar in the neophobia and control trials (Wilcoxon signed-ranks test: $T = -1.593$, $N = 55$, $P = 0.111$; neophobia: mean $\pm$ SE $= 358 \pm 63.1$ s; control: mean $\pm$ SE $= 467.2 \pm 82.2$ s). Rather than quantifying neophobia, therefore, this test provided a repeatable measure of motivation to feed after human disturbance. This measure did not significantly explain any of the observed individual variation in problem-solving performance (Mann–Whitney *U* test: $U = -0.726$, $P = 0.726$; solvers: mean $\pm$ SE $= 473 \pm 152$ s, $N = 18$; nonsolvers: mean $\pm$ SE $= 464 \pm 99$ s, $N = 37$). Furthermore body condition also did not explain variation in problem-solving performance (Table 3).

The time taken to approach the lever-pulling device when initially housed, which was measured in a subset of individuals during the 2008–2009 season, did not differ between solvers and nonsolvers (Mann–Whitney *U* test: $U = -0.624$, $P = 0.533$; solvers: mean $\pm$ SE $= 493 \pm 66$ s, $N = 69$; nonsolvers: mean $\pm$ SE $= 561 \pm 73$ s, $N = 70$). This suggests that variation in solving performance was not explained by device neophobia.

Variation in exploration behaviour was unrelated to variation in solving performance (Table 3).

State and Environmental Sources of Variation

There was no difference in solving performance between males and females (Table 3). Juveniles tended to solve the lever-pulling task more often than adults (Table 3), an effect that was present in only one of the three seasons (Table 3, Fig. 4a). Residents were also more likely to solve the task than immigrants and again this effect was present in only one of three seasons (Table 3, Fig. 4b). Birds solved the lever-pulling task more often with increasing September date (Table 3, Fig. 4c). Overall, the model explained just 10.7% of the observed variation in problem-solving success, which is small relative to the individual variation reported above.

DISCUSSION

Spontaneous problem-solving performance in our assays was goal oriented and consistent within individuals over time and between two distinct tasks. Individual variation was independent of differences in body condition, latency to approach the empty device, latency to feed after human disturbance and exploration behaviour. Males and females did not differ in their problem-solving performance and only a minimal amount of individual variation was accounted for by differences in age and natal origin. Together, these results suggest that, rather than reflecting motivational differences or covariance with other behavioural traits such as activity and exploration, the variation we characterize may largely represent inherent individual differences in the propensity or ability to solve problems related to innovative foraging.

Both lever- and string-pulling performances were relatively consistent within individuals between trials, both within captivity sessions and over long time periods, suggesting that consistent individual differences in performance exist within the population. Our levels of behavioural consistency are comparable with those of

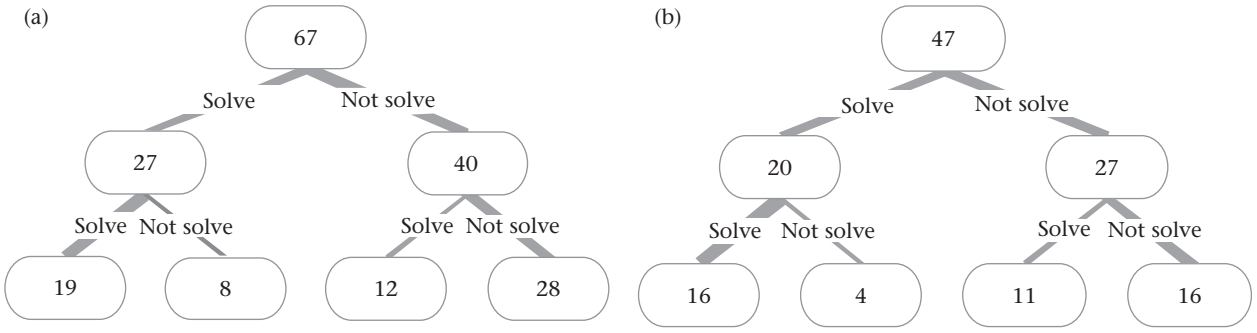


Figure 3. Decision trees showing the repeatability of problem-solving performance over time. Primary branches represent solvers and nonsolvers of the first trial and secondary branches represent solvers and nonsolvers of the same task when taken into captivity again (minimum gap between tests = 2 weeks) for (a) lever pulling and (b) string pulling. Branch width represents the proportion of individuals that solved/did not solve the task, and numbers in the boxes indicate the numbers of individuals in each category.

Table 2
Consistency of individual performance between the lever-pulling and string-pulling tasks

		Year	*N*	Repeatability	SE	*P*
Within captivity session	Daytime lever-pulling and daytime string-pulling performance	2007–2008 & 2008–2009	297	0.24	0.05	<0.001
Between captivity sessions	Overnight lever-pulling and daytime string-pulling performance, between years	All	23	0.31	0.15	0.035
	Overnight lever-pulling and daytime string-pulling performance, between captivity sessions over 3 years	All	46	0.35	0.13	0.017

Consistency was estimated using a measure of individual repeatability (adapted from Lessells & Boag 1987).

other behavioural traits (reviewed in Bell et al. 2009). Repeatability estimates for behavioural traits are generally higher when the interassay interval is short (Bell et al. 2009), but our assay was repeatable for assays conducted a year or more apart. Taken together with the fact that solving performance was not influenced by body condition, these results suggest that performance is largely independent of state factors.

By definition, goal-oriented behaviour is expected to be repeatable because successful behaviour is reinforced by a reward (Skinner 1938). However, if the individual consistency in solving performance we observed was solely the result of reinforcement we would expect consistency to reduce as the period of time elapsed between trials increased (Shettleworth 1998). We did not find support for this, as our estimates for within and between captivity sessions are comparable. In addition, we found solving performance to be relatively consistent between the two distinctly different problem-solving tasks, even when the gap between the two tasks was 2 weeks or longer. Together, these results suggest that our assay captures consistent individual variation in the ability to solve foraging-related tasks.

Birds did not solve the task in the absence of a food reward, demonstrating that solving the task was motivated by the food, rather than a result of random activity patterns. Furthermore, although our trials were preceded by human disturbance and used relatively novel devices, both of which could have influenced motivation to solve tasks, several lines of evidence suggest this is unlikely. First, we failed to detect any evidence of object neophobia using Greenberg's (1984) approach, because there was no increase in latency to feed with novel objects compared with control trials. This may be because novel objects in a novel environment can elicit a less intense response than in a familiar one (Greenberg & Mettke-Hofmann 2001). We also found no relationship between solving performance and latency to approach the problem-solving device

Table 3
Binomial logistic regression model to establish whether variation in problem-solving performance can be explained by both state and environmental factors

	Overnight lever-pulling task		
	df	*W*	*P*
Season	2	0.597	0.742
September date	1	5.265	**0.022**
Age	1	3.281	0.070
Sex	1	0.014	0.905
Natal origin	1	2.043	0.153
Exploration behaviour	1	0.341	0.559
Body condition	1	0.775	0.379
Test time	1	5.033	0.754
Room	1	0.240	0.624
Cage	15	21.020	0.136
Age*Season	2	6.124	**0.047**
Natal origin*Season	2	9.402	**0.009**

The model was run first without the interactions to give all the main-term statistics and then with the interactions. September date refers to days since 1 September; age is classed as either juvenile or adult, and natal origin classed as Wytham born or immigrant. *P* values significant at the 0.05 level are shown in bold. $N = 509$ individuals.

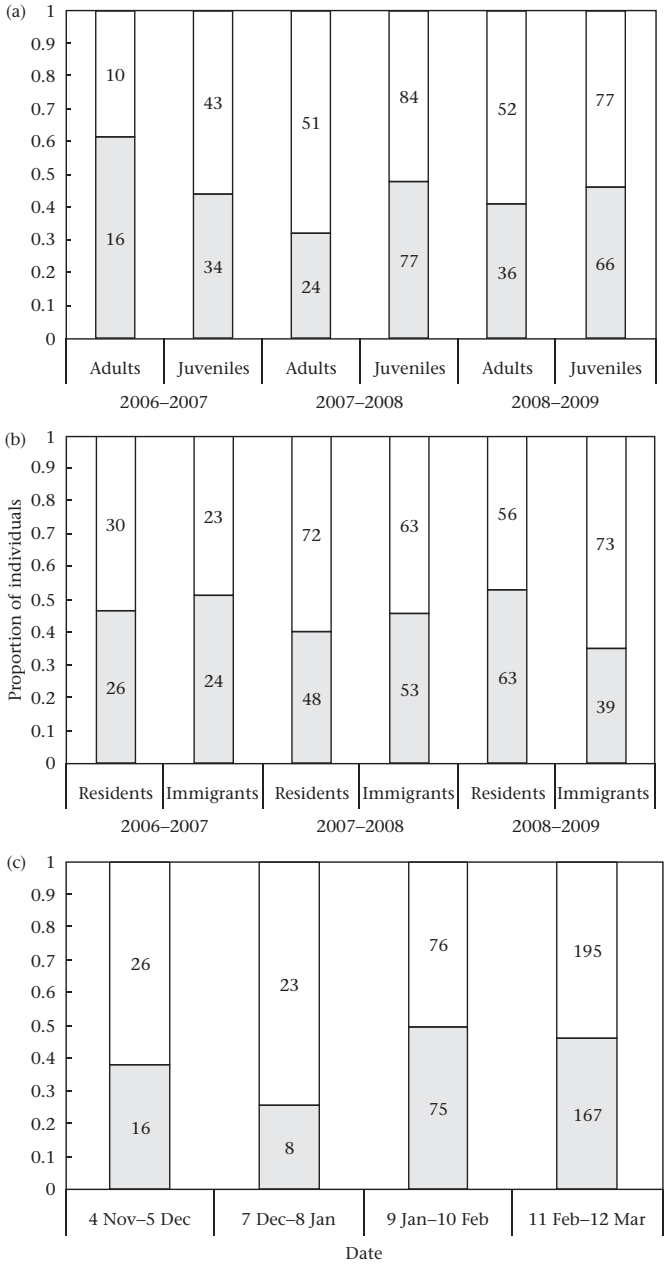


Figure 4. Factors contributing to individual variation in solving success in the overnight lever-pulling task: (a) age, (b) natal origin and (c) time of year. Light grey represents solvers of the lever-pulling tasks and white nonsolvers. See Table 3 for statistics. The numbers inside the bars correspond to the number of individual solvers and nonsolvers in each category.

when initially housed, suggesting that neophobia directed towards the task itself does not account for the variation we observed in problem solving. Neophobia, therefore, seems not to have been a factor in our system. In addition, both object neophobia (Verbeek et al. 1994) and response to stress (Carere et al. 2003; Carere & van Oers 2004) have been shown to covary with exploration behaviour in great tits but we found no link between exploration behaviour and problem-solving performance in our population. Finally, we found no relationship between solving performance and time to feed in the control trial after freely available food had been placed in the food dish. As both of these assays were preceded by human disturbance, the absence of a relationship suggests that response to disturbance did not account for the observed variation in problem solving. Even though we cannot rule out the possibility that our results might have been influenced by these possible confounding effects, our additional analyses suggest these factors are unlikely to be a major driver in problem-solving variation.

We found no support for either a positive or negative relationship between exploration behaviour and problem-solving performance. This supports previous work on the great tit that found no difference between fast and slow explorers in performance in foraging tasks requiring associative learning and spatial memory (Carere 2003). In contrast, a recent study on a related species, the black-capped chickadee, *Poecile atricapilla*, found a positive relationship between readiness to enter a novel environment and learning speed in an acoustic discrimination task (Guillette et al. 2009). It seems, therefore, that links between exploration behaviour and problem-solving performance are likely to be task and species dependent, which is unsurprising given that behavioural correlations can differ between populations of the same species (Dingemanse et al. 2007).

Great tits were more likely to solve tasks as the winter progressed. A similar time-of-year effect is observed in exploration behaviour, where individuals become 'faster' closer to the breeding season (Dingemanse et al. 2002; Quinn et al. 2009). Aviary temperature decreased with September date, but we suspect it is unlikely that the change in solving rate was a result of temperature change because, throughout the winter, there was a consistent difference in temperature between the two housing aviary rooms (approximately 4 °C), which did not account for any variation in performance. Post hoc analysis shows that the effect was observed in both adults and juveniles (binary logistic regression: age*time of year: $W_2 = 0.37$, $P = 0.847$), suggesting that cumulative experience does not explain this seasonal trend. Therefore the change in solving performance observed may reflect changes in foraging behaviour or intrinsic motivational levels. Alternatively, differential overwinter survival rates of solvers and nonsolvers could be important, or variation in their catchability, resulting in solvers being more likely to be caught later in the season when conditions are harsher.

Little variation in solving performance was accounted for by differences in age and natal origin. We found a tendency for juveniles to be more likely to solve the task than adult birds, but only in some seasons. Therefore variation cannot be explained by greater curiosity among juveniles alone, a phenomenon commonly observed in birds (Vince 1958, 1960; Greenberg 2003). We also found that immigrants were more likely to solve the task in one of the three seasons. These season effects suggest that problem-solving performance may be influenced by early environmental factors that vary between years and habitat types. Several studies have found that variation in factors, such as natal diet and foraging experience, result in individual differences in cognitive abilities later in life (e.g. Cooper & Zubek 1958; Seibt & Wickler 2006; Arnold et al. 2007). Furthermore, a recent interspecific cross-fostering experiment demonstrated that early learning has a strong and lasting effect on the foraging behaviour of wild great tits (Slagsvold & Wiebe 2007). A multitude of biotic and abiotic factors influence relative prey abundance and foraging conditions between years (Gibb 1950; Perrins 1979). In addition these factors are likely to affect different populations in different ways. For example, whereas great tits breeding in oak-rich habitats, such as Wytham, rely mainly on winter moth larvae, *Operophtera brumata*, to feed their young, birds breeding in coniferous or garden habitats are dependent on different prey species (van Balen 1973; Perrins 1979). Therefore a 'good food year' in Wytham may not be a good year for external populations, resulting in the relative behavioural phenotypes of residents and immigrants varying between years. Clearly more detailed analysis using data on natal habitat quality and fledging conditions is required to establish whether these sorts of cohort effects are occurring in our population.

The functional significance of problem-solving performance remains poorly understood. Interspecific comparative analyses have shown positive relationships between innovative foraging ability and success in both invading new habitats and dealing with seasonal environmental change (Sol et al. 2002; Lefebvre et al. 2004). At the individual level, recent work on the black-capped chickadee demonstrated that nestlings taken from a harsh environment, where food is difficult to locate, are better problem solvers than those from a favourable one (Roth et al. 2010). This suggests that the ability to problem solve may allow individuals to survive in conditions where foraging is particularly difficult. In our population, individual variation in problem solving may largely represent inherent differences in an independent behaviour trait. The relative importance of different proximate sources of variation and their functional significance remain to be determined in our population, but we suggest that the use of simple assays such as ours may provide new insight into the evolutionary ecology of cognition.

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CHAPTER 3

Personality and problem-solving performance explain competitive ability in the wild



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Personality and problem-solving performance explain competitive ability in the wild

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Competitive ability is a major determinant of fitness, but why individuals vary so much in their competitiveness remains only partially understood. One increasingly prevalent view is that realized competitive ability varies because it represents alternative strategies that arise because of the costs associated with competitiveness. Here we use a population of great tits (*Parus major*) to explore whether individual differences in competitive ability when foraging can be explained by two traits that have previously been linked to alternative behavioural strategies: the personality trait 'exploration behaviour' and a simple cognitive trait, 'innovative problem-solving performance'. We assayed these traits under standardized conditions in captivity and then measured competitive ability at feeders with restricted access in the wild. Competitive ability was repeatable within individual males across days and correlated positively with exploration behaviour, representing the first such demonstration of a link between a personality trait and both competitive ability and food intake in the wild. Competitive ability was also simultaneously negatively correlated with problem-solving performance; individuals who were poor competitors were good at problem-solving. Rather than being the result of variation in 'individual quality', our results support the hypothesis that individual variation in competitive ability can be explained by alternative behavioural strategies.

Keywords: competitive ability; innovative problem-solving; exploration behaviour; personality; *Parus major*; alternative strategies

1. INTRODUCTION

Competition for limited resources is a fundamental ecological process in most natural systems [1] and competitive ability can have major consequences for individual fitness [2–4]. Although empirical studies show that individual state is an important determinant of competitive ability—for example, sex, age or body size (reviewed by Piper [5])—much individual variation over and above these state-dependent effects has yet to be explained (e.g. [6]). Traditionally, competitive ability has been assumed to primarily reflect either 'individual quality' or random error. This contrasts with an increasingly prevalent view that variation in competitive ability is adaptive and arises because the benefits of competitiveness can be outweighed by associated costs [7–12]. Commonly, these costs might include fighting [13], higher exposure to stress hormones [14] and elevated metabolic rate leading to increased food demands [15,16]. Consequently, under some circumstances, relatively poor competitors can paradoxically outperform good competitors [17,18], suggesting that variation in competitive ability may reflect alternative behavioural strategies. The extent to which alternative strategies might explain variation in competitive ability in natural systems, however, remains largely untested.

In this paper, we test whether variation in competitive ability can be explained simultaneously by links with two sources of behavioural variation that reflect alternative behavioural strategies. The first of these is referred to as the proactive–reactive axis, and represents perhaps the best-studied personality axis in non-human animals [19]. In contrast to individuals at the 'reactive' end of the continuum, 'proactives' are bolder, more aggressive and more risk-prone (reviewed by Sih *et al.* [7]). Potential explanations for how behavioural correlations are maintained within populations are diverse (reviewed by Dingemanse & Wolf [20] and Wolf & Weissing [21]). One theory with increasing empirical evidence links variation in proactivity to life-history variation, suggesting that proactives tend to sustain high productivity but at a potential cost to survival, while reactives do the opposite [8–10]. Proactives should therefore have higher realized competitive ability in order to meet the demands of their faster pace of life [9,10]. Indeed, a positive relationship between the proactive–reactive behavioural axis and both social dominance and competitive ability has been demonstrated in rodents [22,23], fish [24,25] and birds [26–28]. However, several studies have found that proactive individuals take longer to recover from social defeat than reactive individuals, and under some conditions are poorer competitors [29,30]. The only study to date that has examined links between the reactive–proactive axis and competitive ability in the wild found contrasting correlations within the same population, suggesting that this relationship may be dependent on the physical and social environment [31].

In addition to the reactive–proactive axis, competitive ability has also been linked to another source of behavioural variation: the tendency to innovate or problem-solve

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[32–34]. The 'necessity drives innovation' hypothesis predicts that good competitors monopolize access to limiting resources, forcing poor competitors to innovate [32,34,35]. Although it is often assumed that the observed variation in innovativeness is temporary (i.e. not consistent over time) and arises through phenotypic plasticity, it may equally represent more permanent, inherent differences between individuals. Irrespective of whether these differences are temporary or permanent, innovative foraging can be viewed as an alternative foraging strategy that helps some individuals avoid costs associated with intense competition [34,36], a hypothesis that is largely supported by empirical evidence from primates, fish and birds [32–34,37,38]. Individual consistency in innovativeness has rarely been assessed, however, and the extent to which inherent, long-term individual differences in innovativeness may contribute to variation in competitive ability remains unclear.

In this paper, we explore whether individual variation in competitive ability when foraging is linked simultaneously to the reactive–proactive behavioural axis, as assayed by 'exploration behaviour in a novel environment', and innovative problem-solving performance using a wild population of great tits (*Parus major*). Exploration behaviour is heritable, and correlated with a range of ecologically significant behaviours in several different populations, including ours [39–44]. Great tits are a generalist species [45], and anecdotal evidence suggests that they frequently investigate novel objects in the wild [46] and are capable of considerable innovative foraging behaviour [47–49]. Food-related problem-solving is therefore thought to be an ecologically relevant trait for this species, which we hypothesized would influence competition between individuals. Problem-solving performance is also repeatable and independent of exploration behaviour in our population [50].

To date, most studies that have tested for links between competitive ability and other behavioural traits in the same individuals simultaneously did so under laboratory conditions (but see [31,51]). Furthermore, few studies measure competitive ability directly (i.e. through food intake), which is important because subdominant individuals could potentially compensate by increasing foraging efficiency [52]. Great tits live in flocks during the winter, and competition for clumped, but limited food resources is intense [45]. Using observations of competitive interactions and food intake in the wild, we measured both social dominance and competitive ability for birds that had undergone behavioural assays in captivity. We then tested whether competitive ability could simultaneously be predicted by proactivity and problem-solving performance.

2. METHODS

(a) *Study site, catching procedure and housing*

All behavioural assays were carried out on great tits in the context of a long-term study population at Wytham Woods, Oxfordshire, UK (51°46′ N, 1°20′ W). All birds were caught between September and March, from 2005 to 2009 (see the electronic supplementary material for details of trapping procedure). Unringed individuals were fitted with a unique BTO (British Trust for Ornithology) metal leg-ring, and were aged (adult or juvenile if less than 1 year old) and sexed based on plumage [53]. Biometrics were also taken (wing length, millimetres, and body mass, grams). Birds caught in the 2007–2008 and 2008–2009 winters, and in the 2007 and 2008 breeding seasons, were also fitted with a unique passive integrated transponder (PIT), attached to plastic leg ring, which was automatically detectable at feeders using antennae (see below). Birds were then taken into captivity (under a Natural England licence), where exploration behaviour and problem-solving performance were assayed under standardized conditions. All individuals were subsequently released back into the wild, where dominance and competitive ability were measured at eight experimental sites.

(b) *Captive behavioural assays*

(i) *Exploration behaviour*

Here, we use an assay of 'exploration behaviour in a novel environment' (hereafter exploration behaviour) as our measure of proactivity. In great tits, exploration behaviour is thought to reflect general activity levels, and has been shown to correlate with boldness, aggressiveness and risk-taking under captive conditions [26,54,55]. On the morning after capture, all birds underwent exploration behaviour assays. The assay room was based on the design used by Verbeek *et al.* [54], and consisted of a rectangular room containing five artificial trees. An event recorder was used to record the number of hops, the number and duration of flights, and the areas of the room used, for 8 min. These data were then entered into a principal component analysis, and the square-root of the first component (all major loadings referred to increased activity) used in a general linear model (GLM) to produce an exploration behaviour score for each bird from the parameter estimates derived from using individual as a fixed effect, controlling for time of year (see [41] for further details).

(ii) *Problem-solving performance*

Birds caught between November 2007 and March 2009 were presented with a problem task on the afternoon they were housed. The device used consisted of a vertical transparent Perspex tube containing a platform, which was supported by a horizontal lever. Four waxworms (*Galleria mellonella*) were placed on the platform to bait the device. To solve the task, birds had to remove the lever, causing the platform to drop and the waxworms to fall into a feeding dish (full methods in [50]). Forty-four per cent of birds solved the task. In contrast to other studies (e.g. [56]), solving performance was unrelated to exploration behaviour, neophobia towards the problem-solving device, motivation to feed from freely available food and residual body mass as a measure of body condition [50]. Solving propensity was repeatable over periods of up to a year and across different types of foraging-related tasks, suggesting our assay measures a biologically significant trait that we assume reflects a tendency to innovate, specifically to solve food-related problems [50].

(c) *Field observations: competitive ability and dominance*

Competitive ability and related traits were measured at eight feeders distributed throughout the woods during January to March 2009. On the morning of observation, the multiple-access-point peanut feeder used to attract birds to the catching site was replaced with a single-access-point feeder containing peanut granules (approx. 2 mm^3; Jacobi Jayne Ltd, Herne Bay, UK). Tits generally prefer to take food away from feeders to protective cover before handling [57].

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We assumed that by using smaller food items, we forced birds to either stay on the feeder for prolonged periods or visit more often in order to feed effectively, thus increasing the competition over access to the food. The feeder was also fitted with a PIT tag reader (Francis Scientific Instruments, Cambridge, UK) at the feeding hole, which logged the time and ID of visits by tagged birds. The tag reader has previously been demonstrated to detect the vast majority of visits by tagged individuals [58]. Birds were given 30 min to acclimatize to this change, and then their behaviour at the feeder was monitored for approximately 150 min using a Handycam DCR-SR33E camcorder (Sony Corporation, Tokyo, Japan). Monitoring was always carried out at the same time of day, beginning at approximately 9.00 h and ending by 12.00 h. The following day the procedure was repeated at the same site, allowing us to measure the repeatability of competitiveness in our sample. We note that this only allowed us to assess the repeatability of behaviour of birds that visited the feeder on both days, which we assume did not lead to bias. For an unrelated experiment, the feeder was positioned either near protective cover (a thicket or bushy area) or in the open on the first day, and in the opposite position on the second day. This was randomized across days and controlled for in all models.

The video footage and the PIT tag data were then analysed to establish the number and duration of all visits, as well as all competitive interactions (displacements and challenges) involving focal individuals (see the electronic supplementary material for details). Competitive ability was estimated as the amount of time that each individual had sole access to the food resource. To test whether this was a good predictor of the amount of food consumed, we also recorded the number of food items consumed on 100 randomly selected visits.

We used information on competitive interactions to establish whether our measure of competitive ability correlated with dominance status. Male great tits are invariably dominant over females [59], which was confirmed by our data: only 2 per cent of all displacement events involved a female displacing a male ($n = 301$), even though 42 per cent of all individuals visiting the feeders were female. We initially intended to construct sex-specific dominance hierarchies for all individuals, but only detected sufficient interactions between known birds to produce a male hierarchy for one of the eight sites (containing nine individuals, based on 41 aggressive interactions, for six of which we also collected data on visit duration). We were therefore unable to test the link between the total amount of time spent feeding and dominance for females, and consequently restricted our analyses to males (although inclusion of data, where available, for both sexes did not significantly change the results). Note also that the general lack of aggressive interactions is expected since physical fights are rare in great tits, and instead the outcome of contests is generally determined by physical assessment and posturing [45]; moreover, the dominance hierarchies of the flocks had probably already been established before we began our observations, reducing the probability of contests [45].

Dominance ranks were derived for the nine individuals for whom we had sufficient interaction data using David's scores [60,61] (see the electronic supplementary material). Scores were calculated using methodology from Gammell *et al.* [62]: the proportion of wins (P_{ij}) by individual i in his interactions with another individual j is the number of times (α_{ij}) that i defeats j divided by the total number of interactions (n_{ij}) between i and j; thus $P_{ij} = \alpha_{ij}/n_{ij}$. The proportion of losses by i in interactions with j is $P_{ji} = 1 - P_{ij}$. The David's score for each member i of a group is calculated with the formula

$$\mathrm{DS} = w + w_2 - l - l_2,$$

where $w = \sum P_{ij}$, $w_2 = \sum w$ (weighted by the appropriate P_{ij} values of those individuals with which i interacted), $l = \sum P_{ji}$ and $l_2 = \sum l$ (weighted by the appropriate P_{ji} values of those individuals with which i interacted).

(d) *Statistical analysis*

We initially tested whether the total time spent on the feeder (TTF) was an appropriate proxy for competitive ability in a feeding context by testing whether TTF predicted (i) the amount of food an individual consumed using a linear regression, and (ii) dominance measures using two-tailed Pearson's correlations and linear mixed models (LMMs). An LMM was also used to rule out the possibility that TTF merely reflected the order in which birds arrived at the feeder. TTF repeatability was estimated using Pearson's correlations. We tested whether TTF was influenced by both exploration behaviour and problem-solving performance using an LMM, with the following fixed effects: 'age' (juvenile/adult), 'natal origin' (Wytham-born/immigrant), 'treatment', 'wing length', 'exploration behaviour' and 'problem-solving performance' (solve/not solve). Effect significance was tested by dropping terms individually from the full model, and non-significant terms were removed via backwards elimination.

A previous study on great tits found that the dominance–exploration behaviour relationship was context-dependent [31]: fast-exploring territorial males had relatively high dominance ranks, but the relationship was reversed in non-territorial males. We tested this by assuming a bird was 'territorial' if it bred in Wytham, either in 2008 or 2009 (LMM, controlling for 'age' and 'treatment'). The same study also found that the distance between a territorial male's nest-box and the feeder predicted social dominance; we tested this using straight-line distance from the breeding nest-box. The random terms 'bird ID' and 'location' were included in all mixed models, and all tests were two-tailed.

3. RESULTS

(a) *Competitive ability*

TTF predicted the number of food items consumed by individuals (Linear regression: $F_{1,98} = 101.5$, $p < 0.001$; figure 1) and was significantly repeatable across days (Pearson's correlation: $r = 0.455$, $p = 0.014$, $n = 27$). Dominance score was positively correlated with both TTF (Pearson's correlation: $r = 0.892$, $p = 0.017$, $n = 6$) and the total number of times an individual displaced another male from the feeder (Pearson's correlation: $r = 0.930$, $p = 0.007$, $n = 6$). TTF was also correlated with the total number of same-sex displacements caused by males (considering all birds; LMM: $F_{1,84} = 15.35$, $p < 0.001$; figure 2). TTF was unrelated to the order in which birds first visited the feeder during trials (LMM: $F_{1,82} = 0.51$, $p = 0.476$). Together, these results suggest that the total amount of time spent at the feeder is an appropriate proxy for competitive ability.

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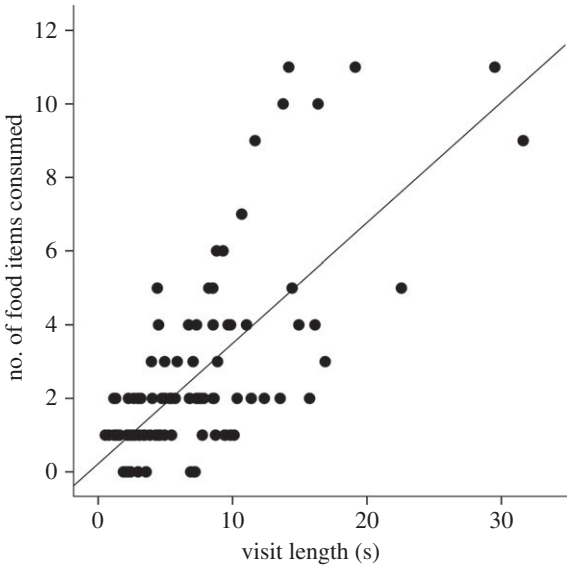


Figure 1. Relationship between the number of food items consumed by great tits and visit length ($n = 100$).

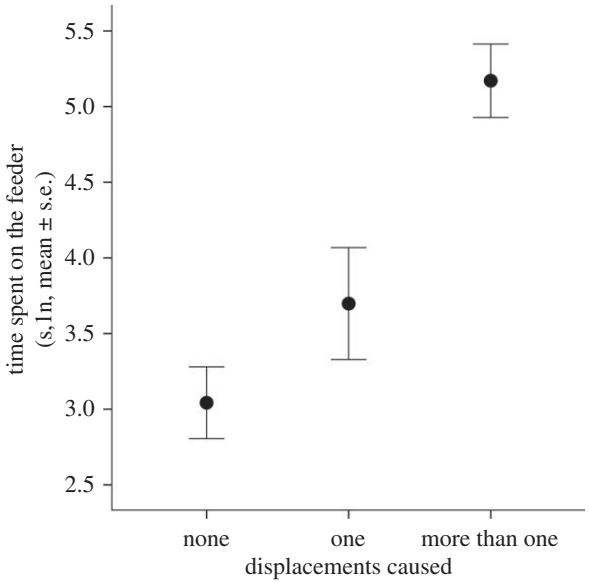


Figure 2. Relationship between the amount of time individual great tits spent feeding and the number of times they displaced another male from the feeder. Where individuals were recorded on more than 1 day, their feeding times and number of displacements were averaged across days ($n = 62$).

(b) *Competitive ability, exploration behaviour and problem-solving*

Fifty-three males of known exploration behaviour and problem-solving performance visited the feeders during our trial (exploration behaviour, mean ± s.e. = 0.829 ± 0.062; solving rate, 25 solvers and 28 non-solvers). TTF was higher in juveniles than in adults (LMM: $F_{1,41} = 7.65$, $p = 0.008$; table 1), but there was no difference between Wytham-born and immigrant birds, nor did body size (as estimated by wing length) predict TTF (table 1). TTF correlated positively with exploration behaviour (LMM: $F_{1,39} = 6.45$, $p = 0.015$; figure 3 and table 1), but correlated negatively with problem-solving performance (LMM: $F_{1,43} = 4.53$, $p = 0.039$; figure 3 and table 1); that is, fast explorers and non-solvers had significantly more access to the feeder than slow explorers and solvers. Finally, the relationship between exploration behaviour and TTF was independent of territoriality (LMM: interaction term: $F_{1,40} = 1.34$, $p = 0.254$) and distance from the breeding territory (LMM: $F_{1,38} = 0.89$, $p = 0.352$).

4. DISCUSSION

Our results suggest that individual differences in competitive ability may be explained by two sources of behavioural variation: a heritable personality trait (exploration behaviour) and a repeatable cognitive trait (innovative problem-solving). In males, competitive ability was itself repeatable and correlated positively with both dominance rank and exploration behaviour, but negatively with problem-solving performance. The repeatability of competitive ability was assessed over a short time period, and only among those individuals that visited the feeder on consecutive days. The stability of competitive ability over longer time periods and in different social or physical conditions is unknown, though we note that exploration behaviour and problem-solving performance are repeatable in our population over years [41,50], suggesting that competitive ability may also be stable over longer time periods. To our knowledge, this is the first demonstration that a repeatable measure of competitive ability correlates in a contrasting manner with multiple behavioural traits that are often believed to represent independent, alternative behavioural strategies. It is also one of only a small number of studies to examine correlations between multiple behavioural traits of any kind in the same individuals simultaneously in the wild (but see [51,63]).

During winter, great tits compete for clumped but limited food resources, and suffer significant mortality from starvation, which is especially pronounced among subordinate individuals [64]. The amount of time an individual has access to a limited food resource is therefore likely to be a good indicator of competitive ability. Indeed, we found that time spent on feeders strongly predicted the amount of food consumed by an individual. Direct antagonistic interactions were relatively uncommon at the feeders in our experiment, probably because dominance hierarchies are also partly determined by physical assessment and posturing, neither of which are easy to detect [45]. Nevertheless, based on the interactions that did occur we found that the number of times individual male great tits displaced other males was a strong predictor of total time spent on the feeder (TTF). Our feeders represented a clumped food resource, which we assumed mimicked patterns of variation in the distribution of natural winter foods, such as beech mast (seed crop from *Fagus sylvatica*). Although we cannot rule out other sources of uncontrolled variation, together the effects observed support previous findings linking dominance status to feeding success in free-living great tits [65].

Proactivity, as measured by exploration behaviour, was a predictor of competitive ability when foraging. Several studies have demonstrated a positive relationship between the proactive–reactive axis and competitive ability in captivity [22,23,25–28], but the present study is one of the first to demonstrate this effect under largely natural conditions (but see [31]), and the first to show a direct link with the ability to acquire resources in the wild at the level of the individual. Most models describing adaptive

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Table 1. Factors contributing to variation in the amount of time individuals had access to the feeder. TTF was log-transformed to achieve normality. *p*-values derived from dropping individual terms from a linear mixed model. This minimum model was derived via backward elimination, removing non-significant terms. All terms shown were also significant in the full model (with n.s. terms: immigration status, wing length and treatment). The model also included random terms location (variance ± s.e. = 0.330 ± 0.304; likelihood ratio test: $\chi^2 = 4.49$, d.f. = 1, $p = 0.026$) and bird ID (variance ± s.e. = 0.189 ± 0.368; likelihood ratio test: $\chi^2 = 0.260$, d.f. = 1, $p = 0.610$). $n = 80$ records for 53 individuals.

fixed terms	estimate ± s.e	*F*	*p*
constant	4.400 ± 0.335	n.a.	n.a.
age[a]	−0.889 ± 0.322	7.65	0.008
exploration behaviour	0.894 ± 0.352	6.45	0.015
problem-solving performance[b]	−0.685 ± 0.322	4.53	0.039

[a]Juvenile set to 0.
[b]Non-solver set to 0.

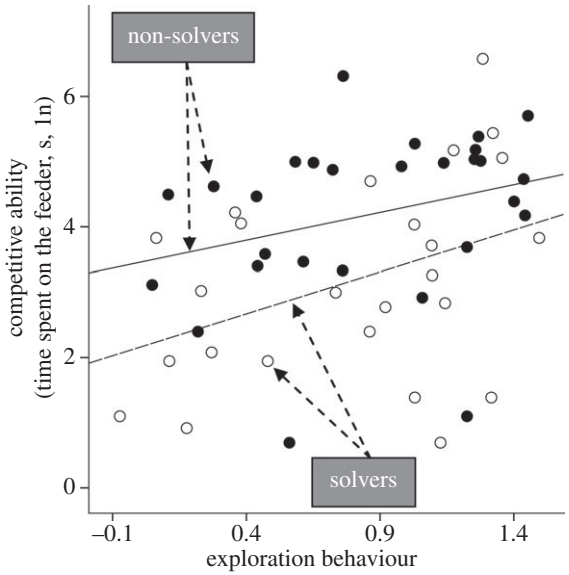


Figure 3. Relationship between competitive ability (TTF) and exploration behaviour for solvers and non-solvers. Data plotted are the feeding times for each individual (averaged across days for birds observed more than once) and the lines are fitted regression lines ($n = 53$).

personality variation explain the behavioural differences on the basis of differences in state [21]. Recent theories have viewed life-history strategy as the key state variable, suggesting that proactive individuals adopt a behavioural strategy that maximizes productivity, whereas reactives maximize survival [8–10]. Our findings are consistent with this idea, indicating that different personality types may reflect alternative life-history strategies [9,10]. Despite this link between competitive ability and proactivity, previously we reported no survival selection on exploration behaviour in our population [41], contrasting with the variable survival selection on exploration behaviour reported for another population of great tits [66]. However, the selective consequences of behavioural correlations are probably moderated by other ecological factors (e.g. the severity of weather conditions, food shortages or population density). They are also likely to be influenced by correlations with other traits that have not been measured, which themselves may be population-specific [67,68]. Understanding selection on any personality axis can therefore only be achieved by measuring partial selection gradients on all correlated, functionally significant traits simultaneously.

Individuals who performed poorly in a problem-solving task in captivity spent more time monopolizing the feeder compared with those who performed well. This agrees with the 'necessity drives innovation hypothesis', which predicts that subordinate individuals adopt alternative foraging strategies to avoid the costs associated with intense competition. Female great tits were no better at solving problems than males [50], to whom they are invariably subordinate [69], suggesting a restricted individual, rather than a general, effect of necessity on innovativeness. The 'necessity drives innovation hypothesis' implies a causal link between competitive ability and innovativeness, but nevertheless consistent individual differences in innovative foraging instead may lead to differences in realized competitive ability. Previously, we have shown that problem-solving performance is consistent over long time periods among individuals in our population [50], suggesting that the link between competitive ability and innovativeness may be the result of genetic or permanent environmental factors, rather than more transient environmental effects. Inherent individual differences in innovative problem-solving are therefore likely to contribute to variation in competitive ability, but it remains to be seen whether the phenotypic correlation observed occurs at the genetic level.

In contrast to the traditional idea that conspecifics are ecologically equivalent, many generalist species are composed of relatively specialized individuals that vary in their preference for, and productivity when using, different foraging methods [70]. In great tits, older individuals are thought to use a wider variety of food sources than younger birds [45]. Indeed, we found that first-year males spent more time on the feeder than adults, even though they are normally subordinate [71]. This supports previous work on our population showing that, even when competition at artificial feeders was relaxed, first-years used feeders more than adults [58]. Variation in competitive ability for a specific resource may therefore arise because the value of the resource differs between individuals. In this way, both adults with better knowledge of other food sources and innovative foragers that use an alternative foraging strategy will have a lower realized competitive ability as they rely more on sources of food other than the one subject to intense competition. This argument implies a causal link between problem-solving performance and competitive ability, which we are unable to establish in this study. If the phenotypic correlation proves to have a genetic basis, this would have important evolutionary implications because it would mean that individuals within the same population would be subject to different selection pressures owing to resource-specific ecological interactions [70,72].

An important facet of evolution is that natural selection is rarely likely to act on single traits in isolation owing to correlations between traits [73,74]. Few

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attempts have been made to establish the extent to which consistent variation in multiple behavioural traits measured under standardized conditions in captivity is correlated with functionally significant behaviour in nature (but see [51]), let alone examine the genetic basis [75,76] or selective consequences [12,51] of these associations. The behavioural correlations shown here suggest how individuals with different competitive abilities may be able to coexist; the evolutionary significance of these patterns now needs investigation.

The protocols outlined in this paper were all subject to ethical review by the Department of Zoology (Oxford) ethical committee.

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SUPPLEMENTARY MATERIAL

Catching procedure, housing and exploration behaviour assay

Most birds were caught using mist nets at temporary feeders erected at sites throughout the wood between September and March, from 2005 to 2009, though a few were removed from nest boxes when roosting after dusk. Birds were caught under licence from the British Trust for Ornithology (BTO). Up to 16 birds per catching session were transported in individual bird bags to the nearby John Krebs field station. Great tits were taken into captivity under a Natural England licence. PIT tags (EM4102 tag, HID Global GmbH, Walluf, Germany) measuring 12.4 mm × 2.1 mm were attached to celluloid split colour leg-rings. The event recorder used for the exploration behaviour assays was a Psion Workabout, with Observer mobile software (Noldus Information Technology, Wageningen, the Netherlands).

Competitive ability and dominance

At all but one of the sites competitive ability was assessed after birds had been released from captivity. However, at one of the eight sites, for logistical reasons competitive ability was assessed before birds were caught. Although the order of events should not influence our results, site was controlled for in all statistical models (see statistical analysis). The majority of individuals included in analyses underwent behavioural assays directly prior to the competitive ability observations (i.e. winter 2008-2009); a small number (N=14) of birds that were present during the competitive ability observations had not been taken into captivity that year, but had been assayed in previous years. As both exploration

behaviour and problem-solving performance are repeatable between years [48; 59], this had no bearing on the analyses here.

When analysing the video footage, displacements were defined as 'an individual arriving at the feeder within 50 milliseconds of the previous bird' and a challenge as 'an individual posturing or making physical contact with the focal bird but failing to displace it from the feeder'. Dominance ranks were derived for the nine individuals for whom we had sufficient interaction data using David's scores. This measure uses aggressive interactions between dyads to rank individuals, while taking into account the relative strengths of the opponents [67]. We chose to use this method, as opposed to those that involve rearranging a dominance matrix so that some numerical criterion, calculated for the whole matrix is minimised or maximised, because our matrix contained a significant proportion of unknown dyad interactions. Therefore a measure of an individual's overall success was deemed a more appropriate method.

When constructing the dominance hierarchy, only individuals that interacted with at least two other birds within the hierarchy were included (i.e. a quarter of the other individuals, N=9). All but one individual interacted with at least three of the other eight individuals that made up the hierarchy. The hierarchy was formed using information on 21 of the 36 possible dyad interactions that could have occurred between individuals. There was only one inconsistency (an instance where a bird lost to an individual below it in the hierarchy) in the hierarchy once constructed; we therefore were confident that the David's Score approach captured the dominance relationships in our dataset in a satisfactory way.

CHAPTER 4

Explaining variation in natural foraging behaviour:

the role of personality and problem-solving performance



Explaining variation in natural foraging behaviour: the role of personality and problem-solving performance

Ella F. Cole, Julie Morand-Ferron, Amy E. Hinks & John. L. Quinn

ABSTRACT

Individuals differ in how they exploit their environment when foraging and this in turn can influence productivity and fitness. Personality and cognitive traits are thought to be important drivers of foraging behaviour but evidence for this idea is lacking from studies under natural conditions. We temporarily took wild great tits (*Parus major*) into captivity and assayed the continuous personality trait 'exploration behaviour' and the binary cognitive trait 'problem-solving performance'. We then quantified the foraging behaviour of these birds once released back into the wild using a combination of nest box cameras, passive integrated transponder (PIT) tags, and radio-telemetry to examine several aspects of offspring-provisioning behaviour and ranging behaviour. Relatively fast explorers provisioned a higher proportion of good quality prey items to their young than slow explorers during the early nestling phase. During the late nestling phase slow explorers provisioned at a higher rate than fast explorers when food availability was low, indicating that relatively slow explorers may cope better in low-quality environments. Problem-solving performance but not exploration behaviour was related to ranging behaviour, with solvers foraging over much smaller ranges than non-solvers. During the early nestling phase, solvers also had shorter working day lengths, and solver males provisioned a higher proportion of good quality prey items than either females or non-solvers, while these effects were not significant in the late nestling phase. These findings provide rare field-based evidence that a simple cognitive trait may predict foraging efficiency. Taken together our results show how behaviour of fundamental ecological significance, foraging, can be simultaneously influenced by two independent sources of consistent individual variation in the wild.

INTRODUCTION

Obtaining sufficient food is a major challenge faced by animals, and therefore natural selection is likely to favour efficient foragers (Pyke 1984; Stephens & Krebs 1986). Empirical work has established that variation in foraging behaviour can be both heritable (e.g. Wallin 1988; Hedrick & Riechert 1989; Lemon 1993) and have considerable consequences for fitness (Fritz & Morse 1985; Ritchie 1990; Lemon 1991; Lescroël et al. 2010). Optimal foraging research has demonstrated that animals are able to discriminate between food patches of different profitability, and make foraging decisions that maximise their productivity (reviewed in Stephens & Krebs 1986). However, individuals within the same population also show marked differences in both foraging performance (Smith & Sweatman 1974; Clayton & Krebs 1994a & b; Chittka & Dyer 2003; Burns 2005), and preference for particular foraging sites and food types (Van Burkirk & Smith 1989; Partridge 1976). Traditionally, this individual variation in behaviour has often been viewed as stochastic noise surrounding a behavioural optimum (Wilson 1998). Only recently have researchers begun to consider that differences in foraging behaviour may be adaptive, sometimes reflecting alternative strategies (see: Bolnick et al. 2003; Burns & Dyer, 2008; Muller & Chittka, 2008). Two factors that may give rise to individual variation in foraging are differences in ability to exploit certain resources, and correlations between behaviours across different contexts (i.e. personality) (Burns 2005; Laland & Reader 1999). The aim of this chapter was to examine whether individual differences in foraging behaviour among great tits while provisioning offspring might be explained by variation in both a personality and a cognitive trait.

Personality can be defined as behavioural differences between individuals that are consistent over time and/or across contexts, as is considered to be ubiquitous in nature (Gosling 2001; Wilson 1998; Sih et al. 2004; Smith & Blumstein 2007; Réale et al. 2010). Perhaps the most extensively studied non-human personality axis is the reactive-proactive continuum in great tits (*Parus major*). Extensive captive work has demonstrated that, relative to 'proactive' birds, 'reactive' individuals are relatively neophobic, slow to explore new environments, less aggressive, and more risk-adverse (reviewed in Groothuis & Carere 2005). Due to the lack of plasticity exhibited by individuals between contexts, theory predicts that selection will favour different personality types under different environmental conditions or contexts (Sih et al. 2004; Dall et al. 2004; Réale et al. 2010), but the functional significance of personality in the wild remains poorly understood (Réale et al 2007). Recent work in the great tit has revealed that the reactive-proactive continuum is linked to a broad range of ecologically relevant behaviours such as dispersal (Dingemanse et al. 2003; Appendix A, published as Quinn et al. 2011a), nest and territory defence (Hollander et al. 2008; Amy et al. 2010), risk-taking behaviour (Appendix B, published as Quinn et al. 2011b, Chapter 6), dominance and competitive ability (Dingemanse & de Goede 2004; Chapter 3, published as Cole & Quinn 2012), promiscuity (Van Oers et al. 2008; Patrick et al. 2011) and space use (Van Overveld & Matthysen 2010, Van Overveld et al. 2011). However, very little is known about how personality influences natural foraging behaviour, despite the fact that foraging performance is well known to influence survival and reproduction, and is a likely mechanism linking personality to fitness (discussed in Both et al. 2005; Quinn et al. 2009).

Work on animals in captivity provides several lines of evidence to suggest that personality influences the way individuals collect and act on information in their environment, factors that are likely to affect foraging behaviour. First, more reactive individuals that are relatively slow to explore novel environments (hereafter 'slow explorers') are thought to be more thorough in their exploration than relatively fast explorers (hereafter 'fast explorers'). During exploration assays, slow explorers spend more time moving around small areas of space (Verbeek et al. 1994; Fox et al. 2009) or contacting novel objects (Hessing et al. 1994). Second, in artificial foraging scenarios fast explorers are quicker than slow explorers to form foraging routines, and slower to break these routines when food distribution changes (Verbeek et al. 1994; Drent & Marchetti 1999). Whether these differences observed in captivity extend to a wild context is largely unknown. One field study where food was abruptly removed from artificial feeders found that slow exploring great tits stayed close to feeders whereas fast birds moved away, contrasting with findings from captivity that fast birds are more routine-like in their behaviour (Van Overveld & Matthysen 2010). The only study to date that has examined how exploration behaviour relates to natural foraging behaviour focused on a single behavioural measure, and reported no effect of personality on the provisioning rate of adult great tits (Patrick & Browning 2011). Consequently there remains a need for research that examines how personality relates to different facets of foraging behaviour in the wild.

In addition to the reactive-proactive axis, foraging behaviour can also be linked to cognitive ability. It is generally recognised that individuals differ in their ability to

solve cognitively challenging problems (e.g. Vonk & Povinelli 2011; Seibt & Wickler 2006), and like personality traits, these differences can be consistent within the individual (Laland & Reader 1999; Banerjee et al. 2009; Cole et al. 2011). Foraging behaviour can be cognitively demanding, suggesting that differences in cognitive performance between individuals may influence foraging efficiency (see Boogert et al. 2011). Innovative foraging - where individuals feed on novel food types or adopt new foraging techniques – has been shown to correlate with a range of cognitive traits across taxa, and is considered to be an important component of animal cognition (Roth & Dicke 2005; Lefebvre 2011; Reader et al. 2011). Innovativeness is thought to allow individuals increase their food intake or enhance their feeding efficiency (Lee 1991; Reader & Laland 2003). Support for this idea comes mainly from anecdotal studies (e.g. Grant & Grant 1989) and comparative work showing that more innovative and large-brained taxa are more successful at establishing themselves in novel environments and less likely to suffer population decline (Sol et al. 2002, 2005; Shultz et al. 2005). These studies indicate that innovative foraging may help animals to survive in novel, challenging or changing environments (Sol et al. 2005; Shultz et al. 2005). However, the importance of innovative behaviours for the foraging performance and fitness of individuals remains largely unexplored. Indeed very little is known about how consistent individual differences in any cognitive trait influences foraging behaviour under natural conditions (but see Raine & Chittka 2008).

In this study we use a population of wild great tits to explore how variation in the reactive-proactive axis (as assayed by exploration behaviour), and innovative

problem-solving performance, relate to foraging behaviour when provisioning offspring in the wild. In altricial species, such as the great tit, parental foraging performance is the major determinant of reproductive success (Naef-Daenzer & Keller 1999, Haywood & Perrins 1992), but foraging is likely to be cognitively challenging (Gosler 1993). When provisioning young, great tits must locate large numbers of cryptic prey items, distributed in temporal and spatial patches across a structurally complex environment (Perrins 1979; Golser 1993). Great tits are central place foragers and therefore they can be readily monitored bringing food back to the nest (e.g. Betts 1955; Royama 1970), making them an ideal study species for this topic. Furthermore, much is known about their foraging behaviour (reviewed in Perrins 1979; Gosler 1993). Caterpillars, especially those of the winter moth (*Operophtera brumata*), are the preferred food provisioned to nestlings because they are easier to ingest and have a shorter handling time than other small invertebrates (Gosler 1993; Bańbura et al. 1999). Great tits also preferentially select large caterpillars from their environment, which is presumed to reflect an efficient foraging strategy requiring fewer foraging trips (Naef-Daenzer et al. 2000; Wilkin et al. 2009). Nestlings fed on caterpillar-rich diets have been shown to fledge in better condition, a key determinant of subsequent survival and recruitment selection (Wilkin et al. 2009).

We used a combination of nest box cameras, PIT tag technology and radio-telemetry to quantify working day lengths, provisioning rate, prey composition, and space use during foraging among individual great tits. Our primary objective was to explore how two sources of behavioural variation – problem-solving

performance and exploration behaviour – might simultaneously influence foraging during offspring provisioning, a key determinant of fitness. The two traits are apparently uncorrelated (see Chapter 2) which led to the expectation that they should influence foraging in different ways. In addition to testing the covariance between these traits and foraging, we also explore the possibility that these relationships will depend on local food availability, which may be expected for several reasons. Differences in foraging efficiency between solvers and non-solvers might only become apparent when food is particularly scarce and difficult to find (Reader & Laland 2003). Similarly, because slow explorers are more flexible in their behaviour in captivity, it has been hypothesised that these individuals should do better when conditions are more changeable or unpredictable (Marchetti & Drent 2000; Guillette et al. 2010). Conversely, routine-forming fast birds may be more productive when food is abundant because they can readily locate rich food patches, and their routine-like behaviour should allow them exploit abundant food more efficiently. To address these questions we examined foraging behaviour along both temporal and spatial gradients of food availability. First, however, we examined whether the various foraging variables we measured during offspring provisioning correlated with reproductive success in order to assess whether links between our captive measures and provisioning behaviour are likely to have any fitness consequences.

METHODS

Study population and study site

We used a nest box population of great tits at Wytham Woods (51°46'N, 1°20'W), a 385 hectare, mixed but primarily deciduous woodland in Oxfordshire, U.K. We trapped birds at artificial feeders throughout the winter between January 2007 and March 2010, and took them into captivity where their exploration behaviour and problem-solving performance were assayed. In addition to BTO metal leg-rings, all individuals were fitted with a unique PIT tag (EM4102 tag, HID Global GmbH, Walluf, Germany) measuring 12.4 mm × 2.1 mm, which was attached to a celluloid split colour leg-ring. This tag was detectable automatically by PIT detecting equipment used at the nest (see below). Once the behavioural assays were complete, all birds were released back at the site of catching.

Captive assays

Problem-solving performance: Birds were brought into captivity where they were housed singly in wire cages, arranged so that individuals were visually but not acoustically isolated from one another (see Chapter 2 for further housing information). Problem-solving performance (hereafter PSP) was assessed using a novel foraging task in their home cages. The device used consisted of a vertical transparent Perspex tube containing a platform baited with four waxworms (*Galleria mellonella*), which was supported by a horizontal lever. To solve the task birds had to remove the lever, causing the platform to drop and the waxworms to fall into a feeding dish. Birds were presented with the task in the evening and their success was recorded the following morning (giving them three hours of daylight

in which to attempt the problem). They were not food deprived during the trial, but the reward provided in the device was a highly preferred food source (E. Cole, pers. obs.). At the end of the trial, birds were classified as either solvers or non-solvers based on their success in the task (see Chapter 2 for full methodology). Previously we showed that solving performance is repeatable over time and consistent with performance in a different task (see Chapter 2), suggesting that it may reflect general food-related problem-solving ability of individuals.

Exploration behaviour: On the morning after capture, birds also underwent an exploration behaviour (hereafter EB) assay. Each housing cage was connected to the novel assay room by a sliding trapdoor, so that birds could be moved between rooms without handling. The assay room was based on the design used in Verbeek et al. (1994). The trial began when the bird entered the room and lasted for 8 minutes. Throughout the trial the number and duration of flights, the number of hops and the areas of the room the bird used were recorded, using a hand held computer (Psion Workabout with Observer software, Noldus Information Technology, Nottingham, UK). Exploration scores were then produced from these data, by first running a principal components analysis on the raw data, and then using the first component from this analysis (all major loadings referred to increased activity) to estimate individual parameters in a General Linear Model (GLM), controlling for time in the season and number of observations per bird (see Quinn et al. 2009 for further details). Previous work on our population has demonstrated that EB is repeatable and shows modest heritability (Quinn et al. 2009).

Breeding data

The breeding attempts of all great tits occupying nest boxes in Wytham are monitored as part of a long-term study (see McCleery et al. 2004). Regular visits were made to nests to determine the lay date, clutch size, hatch date and brood size of each breeding attempt. All adults were caught and identified (when nestlings were approx. 7 days old), allowing us to locate birds that had been assayed in captivity. BTO rings and PIT tags were fitted to all untagged birds and a sub sample of assayed individuals were fitted with radio-tags (see below). Nestlings were weighed to provide a measure of fledging condition when 14 days old (once they reached asymptotic body mass (Perrins 1979)). Several weeks after fledging all nests were checked to establish how many nestlings had fledged successfully.

Foraging behaviour during offspring provisioning

Home range estimates: In 2009 eleven adults that had previously been assayed in captivity were fitted with PIP3 single-celled radio-tags (Biotrack Ltd, tag dimensions: 14mm × 7mm × 4mm, antenna length: approximately 10cm in length, mass: 0.65g). Radio-tags were attached to birds using Rappole harnesses (Rappole & Tipton 1991) made from 0.5mm cotton-covered elastic, which lopped over both legs (Figure 1). These harnesses were designed to wear through and drop off after several weeks, although where possible, birds were recaptured at the nest to remove the tags once radio-tracking had finished.

Individuals were tracked for an average of 235 minutes (SD = 61.1, range = 135-335 minutes) over 3 to 6 days when nestlings were between 8 and 13 days old. Birds were located by triangulation from two locations simultaneously using handheld antennae. The two tracking positions were at a distance of 50-75m from each other, and from the nest box of interest, to ensure that the bearings within the central part of the home range were most accurate (White 1985). Bearings were taken at the two radio-tracking locations once every minute. If it was not possible to obtain a good bearing within 5 seconds, then the location fix was classed as unsuccessful (on average 51.7 fixes per hour were successful). Fix accuracy was estimated by comparing the fixes of birds when at the nest box (the timing of which was known from the data PIT detectors installed on the nest boxes) to the known location of the nest box (national grid coordinates). Using this technique, location errors were found to be normally distributed, with an average of 6.99m (SD = 2.36m), which is small relative to individual home ranges.

Radio-tracking fixes were then used to estimate home range size for each bird, which can be defined as the area most often utilised by an individual (Kenward 2001). These home range estimates were generated using harmonic mean-centred minimum convex polygons in Ranges7 v2.2 software (Anatrack Ltd, http://www.anatrack.com). Utilisation distribution plots, produced in Ranges7, were used to establish the size of minimum convex polygon that was most likely to exclude erroneous or anomalous location fixes (in terms of percentage of all fixes). These utilisation distribution plots indicated the use of 90% core sizes, thereby excluding occasional 'excursions'. Observations of these excursions have revealed

that birds occasionally travel outside their normal home range to visit rare resources, such as water for bathing (Naef-daenzer 1994).

Provisioning behaviour: During the 2009 and 2010 breeding season we monitored parental provisioning behaviour in birds that had previously been assayed in captivity. We used nest box cameras and PIT detectors to measure four components of provisioning behaviour (see below). Great tits alter their provisioning rate and prey composition throughout the provisioning period (Perrins 1979; Gosler 1993). Nestlings are unable to regulate their body temperature until they are approximately a week old (Perrins 1979) and therefore the male undertakes a larger proportion of provisioning during the early nestling phase, feeding both the young and the brooding female. The female gradually increases the amount of time she spends foraging until both sexes are provisioning at equal rates (Kluijver 1950). Between the age of 7 and 10 days old, nestlings reach their maximum growth rate and therefore require large amounts of energy (Perrins 1979; Noordwijk et al. 1995). This demand is best met by the provisioning of a large number of caterpillars, which represent preferred prey (Bañbura et al. 1999; Wilkin et al. 2009). Here, we monitored provisioning at two stages: (1) when nestlings were 6 days old (early nestling phase; in 2010) and (2) when they were 10-11 days old (late nestling phase; in 2009 and 2010). Because the early nestling phase occurs before adult birds were caught (i.e. before the locations of previously assayed birds became known), we located assayed birds by scanning nest boxes of incubating females with a handheld PIT tag reader (Francis Scientific Instruments, Cambridge).

The different provisioning variables measured were as follows:

i) Working day length: PIT tags allowed us to record when birds were present at the nest by fitting nest boxes with PIT tag detectors (Francis Scientific Instruments, Cambridge), which recorded the time and identity of any tagged individual that came within range of the detector (approx. 10cm). PIT detectors were fitted to nest boxes during the early afternoon, and were removed mid-morning the following day. Working day length was calculated by subtracting the time elapsed between when birds stopped provisioning in the evening and resumed again the following morning (i.e. overnight break) from 24 hours. The detectors used to collect these data at the two nestling phases differed in their appearance. Early in the nestling phase parents are more likely to desert their broods in response to disturbance at the nest (Kania 1989). Therefore to minimise the change in the appearance of nest boxes during the early nestling phase we used detectors that were build into nest-box face-plates (see Figure 2a). Parents are far less likely to desert in response to disturbance later in the provisioning period (Kania 1989). Because we only had a limited number of the smaller face-plate detectors, we used larger detectors placed outside the entrance of the nest boxes during the late phase (Figure 2b). Aside from this difference in appearance, the two types of detectors were identical in the way that they recorded data. Working day length data were collected for 50 individuals of known EB/PSP phenotype during the early nestling phase and for 146 individuals during the late nestling phase.

ii) Provisioning rate: Small cameras (Handykam, UK) fitted inside nest boxes were used to measure the rate at which birds delivered prey to the nest. During the late

nestling phase these were placed on the back wall of the nest box opposite the entrance, allowing a clear view of birds entering and leaving the nest. In the more sensitive early nestling phase, we minimised change in appearance of the nest box interior by placing the cameras in the roof of the nest box, looking down at the nest. From this view it was still possible to identify prey items held in the beak of provisioning parents. Dummy nest box cameras were placed in the nest boxes when the PIT detectors were installed (Figure 2c), although filming did not take place until the following morning. This allowed birds to habituate to changes to their nest box before observation. Although there was a noticeable effect on the frequency at which parents visited the nest immediately after equipment was installed, birds resumed normal behaviour within an hour (E. Cole, pers. obs.). Provisioning rate peaks between 6 and 9 am (S. Patrick thesis 2008), and therefore to maximise the amount of data we could collect, birds were filmed within this provisioning peak. During the early and late nestling phases, each nest was filmed for approximately 180 and 90 minutes respectively; the early nestling sample duration was longer because parents provision at a lower rate at this time.

Provisioning rate for each parent was measured as the number of food items successfully delivered to the nest, divided by the duration of the video (in hours). The identity of the bird entering the nest was obtained from the PIT detectors. To account for the fact that some individuals took longer to resume feeding after videoing began, each bird's latency to make their first successful visit was subtracted from the length of the video, when calculating provisioning rate. As we were only able to film each nest for a short period, we used the PIT-detector data

(which spanned a greater time period) to determine whether this short video sample was representative of overall provisioning behaviour. To do this, provisioning rate during the morning (as described above) was compared to provisioning rate during the evening (5-7pm) estimated from the PIT data, within individuals. For the measure of evening provisioning rate (PIT data only), it was not possible to differentiate between when a bird enters or exits the nest. Therefore provisioning rate was calculated as the number of minutes in an hour where the presence of the focal bird (either entering or leaving the nest) was detected at least once (or 'visit minutes', see Wilkin et al. 2009; Patrick & Browning 2011). Morning 'provisioning rate' and evening 'visit minutes' were highly correlated, suggesting our measure of provisioning rate from the video footage is representative of individual behaviour (Linear regression: $R = 0.610$, $P < 0.001$, $N = 49$; $R = 0.657$, $P < 0.001$, $N = 165$, for early and late nestling phases respectively, see Appendix 1).

Although several published studies have used 'visit minutes' as a measure of provisioning rate (e.g. Wilkin et al. 2009; Knowles et al. 2010; Patrick & Browning 2011), it is yet to be established how closely this measure matches actual visit rate. We were able to test this as, during the morning period, we have both camera and PIT-detector data. By comparing actual provisioning rate (from the cameras) and 'visit minutes' (from the PIT data) within individuals for the same time period, we demonstrated a near perfect correlation between these measures (Linear regression: $R = 0.967$, $P < 0.001$, $N = 44$, see Appendix 2).

iii) Prey type: The video footage outlined above was also used to identify each prey item in order to calculate the proportion of food items that were caterpillars.

iv) Caterpillar size: Caterpillars were classified as small, medium or large relative to the size of the bird's bill, allowing us to calculate the proportion of caterpillars that were medium-large in size. Data on both provisioning rate and quality were collected for 48 individuals of known EB/PSP phenotype during the early nestling phase and 123 during the late nestling phase (these sample sizes differ from the ones given for working day length because, due to equipment failure, we did not have both camera and PIT detector data for all nests).

Temporal and spatial food gradients

To test the hypothesis that the relationships between EB/PSP and provisioning behaviour may depend on local food abundance, we measured two proxies for food availability based on temporal and spatial gradients. The first was related to the timing of breeding in relation to the annual peak in the abundance of winter moth (*Operophtera brumata*) caterpillars, the major food source of most *Parus* species (Perrins 1965). The degree to which birds synchronise their breeding with this short peak in food abundance strongly influences the number and condition of nestlings fledged by a pair (Visser et al. 2006). A standard measure of the timing of this food peak is the date by which half of the total number of caterpillars has emerged (the 'half-fall date,' see Charmantier et al. 2008). We calculated the disparity with this peak for each nest as the number of days between the annual half-fall date and the date when nestlings were 9 days old (which corresponds to

the peak demand when nestlings require most food (Keller & Van Noordwijk 1994). This measure provides a more accurate temporal measure of food availability than timing of breeding alone.

Winter moth larvae are found at highest densities in foliage of the pedunculate oak (*Quercus robur*) (Summerville et al. 2003). Previous work has demonstrated that birds breeding in nest boxes with a greater number of oak trees within a 75m radius breed earlier, lay larger clutches and fledge young in better condition (Wilkin et al. 2007; Wilkin & Sheldon 2009). During the winter of 2011 all of the oak trees in Wytham that had a diameter at breast height of 30cm or greater were mapped (see Appendix 3). We then calculated the number of oak trees within a 75m radius of each nest box (hereafter habitat quality), which we assumed was correlated with food availability. These scores were produced using GIS software (MapInfo 10.5), by mapping the locations of all oak trees and nest boxes, and then calculating the number of oak trees within a 75 m buffer around each nest box (see Wilkin et al. 2007 for details of methodology).

Statistical analysis

First, to assess the consequences of provisioning behaviour for reproductive success, we determined whether either the number of young that fledged successfully from the nest, or the average fledging mass of a brood, was related to the four main provisioning variables. Variables were averaged across both parents to provide a single measure for a given nest (single parent nests were excluded from analyses (see below)). Home range was excluded from this analysis due to

small sample size (N = 2 nests where both parents were radio-tracked). For logistical reasons, including equipment failure, there were some nests for which only PIT detector (i.e. working day length) or camera data (provisioning rate and prey composition) was collected. Therefore, in order to utilise all the data, two separate analyses were run: one examining the relationship between reproductive success and working day length, and the other the relationship between reproductive success and provisioning rate, prey type and caterpillar size. All analyses were carried out using General Linear Models (GLMs), and in addition to the provisioning variables, included the terms: lay date, disparity, habitat quality and brood size (and year in the case of the late nestling phase analyses). Brood sizes was included in the fledging success analysis to determine whether differences in parental provisioning behaviour influenced fledging success, after accounting for variation due to the number of nestlings being provisioned. Where the same pair bred together in successive years, only the first attempt was included. All models were simplified by backwards elimination of non-significant terms.

We then tested the relationship between both EB and PSP, and the five provisioning variables, including range size. Single parents, whose partners have deserted or been predated compensate by working harder, and consequently their behaviour is unlikely to represent that expected under the normal bi-parental system (Alatalo et al. 1988). These birds were excluded from all analyses. All analyses examining the link between provisioning traits and EB and PSP were carried out using Linear Mixed Models (LMMs), or Generalised Linear Mixed

Models (GLMMs). Nest box was always included as a random factor to account for the fact that pair behaviour was unlikely to be independent of one another. Where error structure was not normally distributed, and could not be transformed (i.e. for the proportion data: prey type and caterpillar size), GLMMs were used assuming binomial error. The binomial totals for these models were the total number of identifiable items (in the case of prey type) or the total number of caterpillars (in the case of caterpillar size). All models also included the fixed effects: age (first year or older), sex, brood size, disparity and habitat quality. For the late nestling phase analysis, year (2009/2010), and lay date were also included as fixed effects. Lay date was not included in the early nestling phase analysis, as in 2010 (the year that these data were collected), birds bred very late with respect to the caterpillar peak, and therefore there was a close linear relationship between lay date and disparity, making the inclusion of both factors in any analysis inappropriate. Where provisioning data was collected for the same individuals in successive years, only the first observation was included in the analysis to prevent pseudo-replication (there was insufficient power to include individual ID as a random factor).

In addition to the main effects PSP and EB, we also tested for interactions between these traits and individual age and sex. Male and female tits differ in their foraging behaviour (Gosler 1993; Bañbura et al. 2001), and during the early nestling phase, have different care roles (discussed above). Age interactions were assessed because of the general possibility that foraging experience gained by birds may influence any inherent differences among PSP or EB phenotype (Slagsvold & Wiebe

2007; Slagsvold & Wiebe 2011; Grieco et al. 2002). To test the hypothesis that the influence of EB and PSP on provisioning behaviour might depend on local food availability, we also tested for interactions between these traits and both disparity and habitat quality. Due to the number of variables included in these analyses, final models were derived by backwards, stepwise model simplification. All analyses were carried out in GenStat v13.1.

RESULTS

Reproductive consequences of provisioning behaviour

Controlling for differences in brood size, during the early nestling phase, pairs that work longer days had a tendency to fledge more offspring ($t = 1.76$, $P = 0.096$, $N = 20$; note that the effect just fell short of significance in the full model including non-significant terms: $t = 2.02$, $P = 0.058$, $N = 20$, Table 1). Fledgling number was also positively related to working day length during the late nestling phase ($t = 1.99$, $P = 0.049$, $N = 96$, Table 1). Provisioning rate positively correlated with fledgling number in the late nestling phase ($t = 2.30$, $P = 0.024$, $N = 78$, Table 2), but this relationship was not significant in the early phase. We also found that during the early nestling phase, pairs that provision a larger proportion of caterpillars to their young fledged more offspring ($t = 2.42$, $P = 0.024$, $N = 27$; Table 2). Relative caterpillar size was unrelated to fledgling number, and none of the provisioning variables covaried with fledging mass, a measure of offspring condition (see Table 1 & 2). Therefore three of the four provisioning variables measured were related to fledgling number, an important life history trait closely associated with fitness, though not necessarily across early and late nestling stages.

EB and provisioning behaviour

Neither home range size nor working day length were related to EB (see Table 3 & 4). During the early nestling phase, slow explorers delivered prey to the nest at a higher rate than fast explorers, but only amongst adults (EB × age: $F_{1, 40} = 5.17$, $P = 0.028$, Figure 3). Again during the early nestling phase, fast males provisioned a greater proportion of caterpillars than slow males, but no such effect was observed amongst females (EB × sex: $F_{1, 38} = 7.23$, $P = 0.011$, Figure 4). In addition to prey type, EB was strongly positively correlated with the proportion of medium-large caterpillars provisioned, irrespective of sex ($F_{1, 37} = 22.12$, $P < 0.001$, Figure 5).

Provisioning rate was influenced by an interaction between EB and disparity during the late nestling phase ($F_{1, 101} = 4.21$, $P = 0.043$). Amongst poorly timed nests, slow birds provisioned at a higher rate than fast birds (Figure 6a & b). With the exception of this effect on provisioning rate, other provisioning variables were unrelated to interaction terms between EB and food availability (see Table 3 & 4). In summary, EB covaried with both provisioning rate and quality, although no effects spanned both the early and late nestling phases.

PSP and provisioning behaviour

PSP related to provisioning behaviour in three different ways. First, solvers had ranges almost one-third the size of non-solvers ($F_{1, 6} = 14.88$, $P = 0.010$, Figure 7). Second, solvers had significantly shorter working day lengths than non-solvers during the early nestling phase ($F_{1, 38} = 5.54$, $P = 0.024$, Figure 8, Table 3). Finally, solver males provisioned a greater proportion of medium-large caterpillars than

females or non-solvers during the early nestling phase (PSP × sex: $F_{1, 36} = 4.89$, P = 0.033, Figure 9). Neither of the latter two effects were present during the late nestling phase.

Neither provisioning rate nor prey type were linked to PSP, in either the early or the late nestling phases (see Tables 3 & 4). In addition, no interactions between PSP and gradients of food availability were significant (P>0.1 for all interactions), suggesting that the effects of PSP on provisioning were not dependent on food abundance.

DISCUSSION

We demonstrated a range of differences in how individuals of different personality types and cognitive abilities forage during offspring provisioning. Three of the four provisioning traits we measured related to fledgling success and were therefore likely to be of ecological relevance. Relatively fast exploring personality types in captivity provisioned young during the early nestling phase with higher quality food than slow explorers. However, amongst poorly timed nests (when food availability was assumed to be low) slow explorers were able to provision at a higher rate than fast explorers during the late nestling phase. At the same time our cognitive trait, PSP, also predicted several aspects of provisioning behaviour. Birds that solved tasks in captivity had much smaller foraging ranges than non-solvers, and during this early nestling phase, solvers also worked shorter days, while solver males provisioned more medium-large sized caterpillars.

Personality and provisioning behaviour

EB was unrelated to home range size. Although our sample size was small, these results are in agreement with the only other similar work in great tits (Van Overveld & Matthysen 2010), which also found that fast and slow individuals do not differ in the amount of space they use while foraging. The similarity in the results is notable because the studies were conducted at different times of year, when both feeding behaviour and space use are considerably different (Gosler 1993).

Captive and field studies on *Parus* species suggest that fast and slow explorers are likely to differ in their foraging behaviour. It can be predicted from work on captive great tits that slow explorers, who are more responsive to changes in their environment and more thorough in their exploration, may be better at locating good quality prey items (Verbeek et al. 1994; Drent & Marchetti 1999). However, fast exploring great tits are quicker to form foraging routines in captivity than slow explorers (Drent & Marchetti 1999), and both fast exploring great tits and blue tits (*Cyanistes caeruleus*) have been shown to possess more explorative foraging strategies than slow explorers in the wild (Herborn et al. 2010; Van Overveld & Matthysen 2010). These findings could indicate that fast explorers are more efficient foragers. Here we find that during the early nestling phase, fast males provisioned a higher proportion of their preferred food, caterpillars (Gosler 1993), than slow males, and fast explorers of both sexes provisioned a greater proportion of larger caterpillars. This suggests that the more exploratory, routine-forming nature of fast explorers may be beneficial when foraging during the breeding

season. This seems feasible because caterpillar abundance at different patches within a bird's foraging range changes over time (Naef-Daenzer et al. 2000), therefore birds should constantly explore their environment to collect information on relative prey abundance. Indeed, evidence from radio-tracking work suggests that, in addition to repeatedly returning to profitable patches, birds keep exploring other sites continuously (Naef-Daenzer & Keller 1999). Highly-exploratory individuals may therefore be able to keep better track of food locations, allowing them to collect better quality prey.

Although fast explorers may generally be more explorative than slow explorers, slow individuals are thought to be more flexible in their behaviour, suggesting that they may do better in changeable or uncertain environments (Verbeek et al. 1994; Drent & Marchetti, 1999; Marchetti & Drent 2000). We found that amongst birds that had timed their breeding poorly during the late nestling phase, slow birds provisioned at a higher rate than fast birds, suggesting that they may be more efficient forgers when resources are less predictable. However we found no evidence to support the prediction that routine-forming fast explorers are better foragers amongst well-timed nests, where food was likely to be most abundant. Furthermore we note that the influence of EB on other provisioning traits did not depend on food availability and therefore these findings provide mixed support for the responsiveness hypothesis.

Adult birds delivered a higher proportion of larger caterpillars during the early nestling phase and worked shorter days during the late nestling phase, compared

to first year breeders (see Table 3 & 4). One explanation for this is that because great tits tend to reoccupy the same or similar territories in subsequent years (Harvey et al. 1979), repeat breeders may be able to use their previous experience to forage more efficiently (Gosler 1993). Indeed, the relative timing of leaf development and presumably caterpillar emergence for individual oak trees is highly repeatable between years (A. Hinks thesis, 2011), suggesting that knowledge of a particular area may be beneficial to foraging tits. We also found that a negative relationship between EB and provisioning rate was only present amongst adults (i.e. experienced breeders). These findings indicate that different personality types may differ in the extent to which they use previous experience – a hypothesis that is worthy of further exploration.

We have assumed that links between EB and provisioning reflect intrinsic differences in foraging behaviour, but alternative factors could play a role. First, provisioning behaviour may reflect differences in parental investment between individuals, due to factors such as certainty of paternity (Winkler 1987; Burley 1988; Sheldon et al. 1997; Sheldon 2000; Sheldon 2002) which several studies have shown is linked to personality in great tits (Van Oers et al. 2008; Patrick et al. 2011). In our population fast males might be expected to invest less in their brood because they sire fewer within-pair young than shyer males (Patrick et al. 2011). In contrast we found that under some conditions fast birds in fact provision better quality food items than slow males. Second, differences in motivation are also likely to influence provisioning behaviour. Parents respond to increased begging rates by provisioning at a faster rate (Bengtsson 1983; Hinde 2005), and therefore

reducing prey quality (Wright et al. 1998). Fast-exploring nestlings have been shown to beg at a higher rate than slow nestlings (Carere et al. 2005), and as EB is heritable (Dingemanse et al. 2002; Drent et al. 2003; Quinn et al. 2009), it can be predicted that increased begging amongst fast nestlings will lead to higher provisioning rates amongst fast parents. Contrary to this expectation, we find that, under some circumstances, fast birds provision at a *lower* rate, and deliver better quality prey items than slow explorers, suggesting that differential begging is unlikely to explain our results. To summarise, the relationships we observe between provisioning behaviour and EB seem likely to reflect differences in how individuals exploit their environment. This hypothesis could be further explored in captivity by comparing the feeding efficiency of fast and slow birds when presented with a complex foraging environment.

Problem solving and provisioning behaviour

Little is known about the functional significance of variation in cognitive traits at the intraspecific level, primarily because the vast majority of empirical studies in this field have focused on studying small numbers of individuals under laboratory conditions (but see: Biro et al. 2003; Gajdon et al. 2006; Keagy et al. 2009; Appendix C, published as Morand-Ferron et al. 2011). One exception is a recent study on bumble-bees (*Bombus terrestris*), which demonstrated that colonies performing better on associated learning tasks in captivity were more productive foragers in the wild (Raine & Chittka 2008). We took a similar approach and found that problem-solvers in captivity foraged over significantly smaller areas than non-solvers. On the one hand this effect could be caused by intraspecific competition

forcing solvers to maintain small home ranges, because in our population solvers have relatively low realised competitive ability at feeders in winter (Chapter 3, published as Cole & Quinn 2012). Equally, the smaller foraging ranges of solvers agrees with the prediction that innovative problem solving allows individuals exploit their environment more effectively (Lee 1991; Reader & Laland 2003). Several lines of evidence support this as the more likely hypothesis. First, despite having smaller home ranges, there was no difference in the provisioning rate between solvers and non-solvers, suggesting that solvers were able to find the same amount of food as non-solvers, but over a much smaller area. Second, extensive ranging behaviour in breeding great tits is observed amongst individuals that cannot find food in the vicinity of their nest (A. Hinks thesis, 2011). Indeed travelling far from the nest is likely to be costly for parents, both in terms of time and energy (e.g. Thomas et al. 2001). More efficient foragers are therefore likely to have more time for non-provisioning behaviour such as brooding young nestlings, and nest and self maintenance - factors that are likely to contribute to both nestling and parental survival. Indeed in Chapter 5 we show that, amongst birds that successfully reared offspring, solver females fledged more young than non-solvers, without compromising fledgling condition, suggesting that nestlings may directly benefit from this increased efficiency.

In further support of the foraging efficiency hypothesis, solvers also worked significantly shorter days than non-solvers during the early provisioning phase. Although we found that working day length is positively correlated to fledgling number, elsewhere we show that solvers fledge more young than non-solvers (see

Chapter 5). We also found that solver males provisioned a greater proportion of larger caterpillars than the non-solvers or females during the early nestling phase. This indicates that at least under some conditions, solvers may be better at locating good quality prey items. Notably, we find no evidence to suggest that any of these provisioning differences between solvers and non-solvers were dependent on food availability.

Summary and conclusions

The majority of effects we observed between EB or PSP and provisioning behaviours were detected only during the early nestling phase. No single effect was present at both stages, suggesting that relationships between EB, and PSP, and provisioning behaviour are likely to depend on other factors that vary between these stages. We assumed an individual's behaviour was independent of its partner's, but this is unlikely to be true, particularly during the late nesting phase when males and females provision at equal rates in a coordinated manner (Gosler 1993; Royama 1970). Pair coordination may therefore mask some individual differences in provisioning behaviour. Despite the restricted nature of the EB and PSP effects, we show that the provisioning behaviours measured here are linked to fledgling success, suggesting that variation in provisioning between the different behavioural phenotypes may have significant consequences for fitness. We further explore how PSP relates to life-history variation and fitness in Chapter 5 (see also Appendix E, published as Cole et al. 2012).

To our knowledge, this represents the only study to explore the relationship between personality, cognitive performance and foraging behaviour under natural conditions. Our findings provide evidence that both personality and problem-solving performance, measured in captivity, reflect differences in the way individuals forage during offspring provisioning. Furthermore, they demonstrate how foraging, a behaviour of fundamental ecological significance, can be simultaneously influenced by two independent sources of consistent individual variation. These links highlight the need to take an integrated approach to the study of behaviour, as selection is unlikely to act on any single trait in isolation. Demonstrating how different fitness-related traits are inter-correlated with one another represents an important step towards understanding the mechanisms that maintain individual variation in behaviour within populations.

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FIGURES AND TABLES

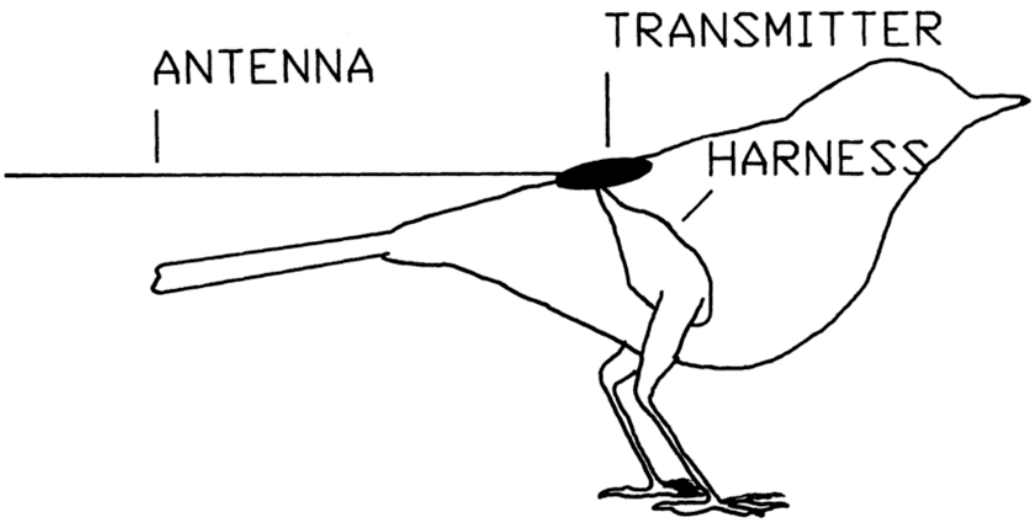


Figure 1. Diagram showing the position of the radio-tracking transmitter (reproduced from Rappole & Tipton 1991).



Figure 2. Equipment used to record provisioning behaviour: (a) face-plate PIT detector used during the early nestling phase to minimise change in appearance to the nest, (b) circular dectector used during the late nestling phase and (c) dummy nest box camera installed opposite the nest box hole, to allow birds to habituate the presence of equipment prior to data collection.

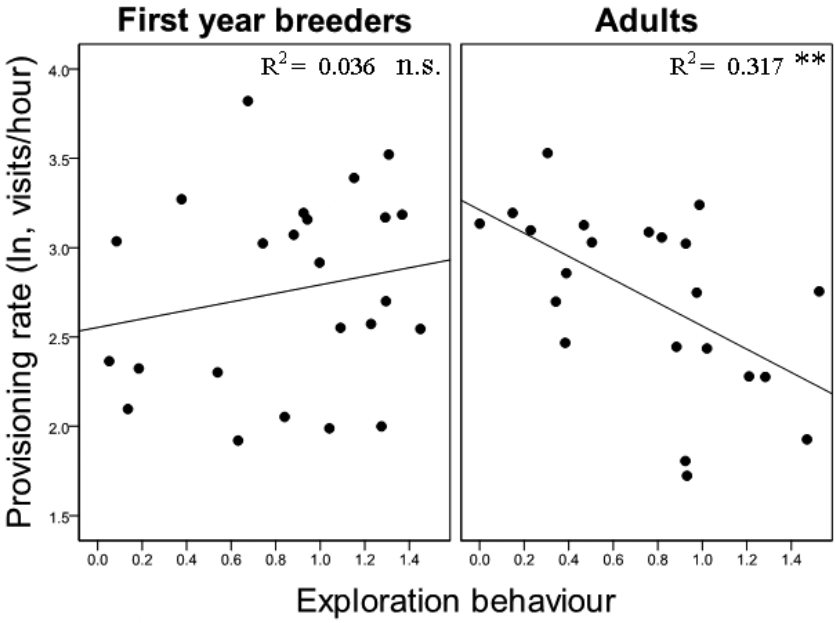


Figure 3. Relationship between provisioning rate (ln transformed) and EB during the early nestling phase (N = 46), for birds less than one year old (first year breeders) and older birds (adults). ''**'' indicates P < 0.01.

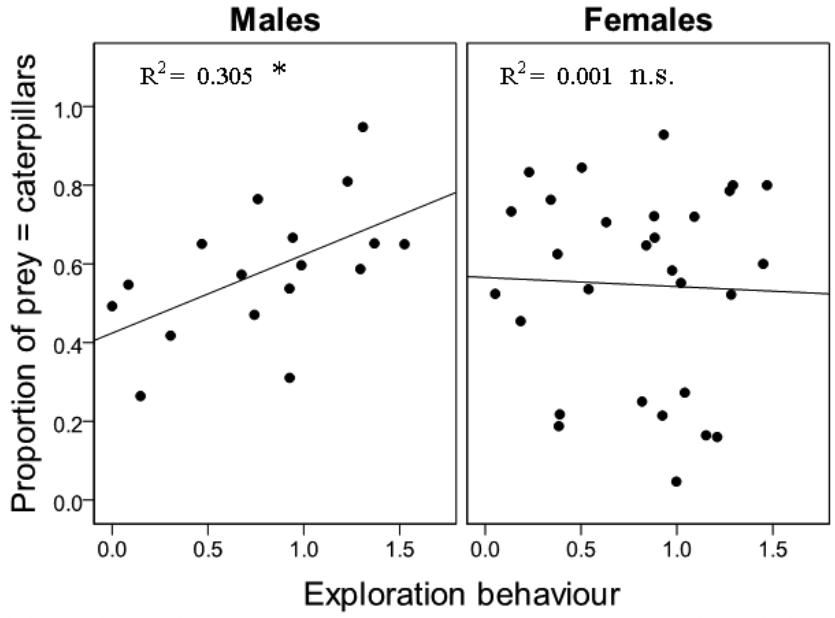


Figure 4. Relationship between prey type and EB, during the early nestling phase for males and females (N = 46). ''*'' indicates P < 0.05.

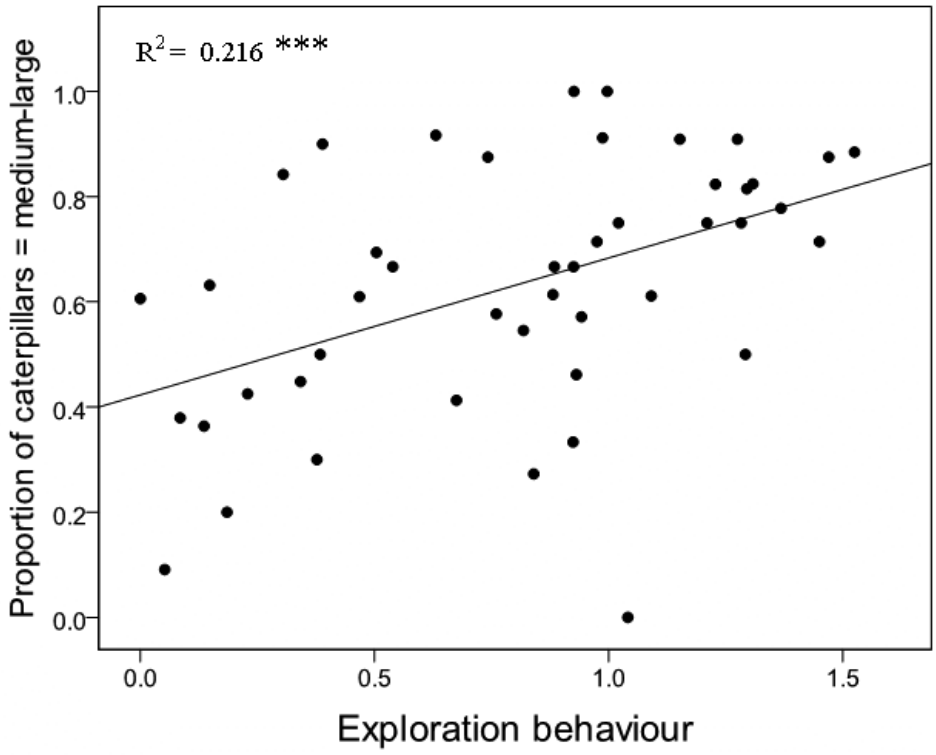


Figure 5. Relationship between the proportion of caterpillars provisioned that were medium-large in size and EB, during the early nestling phase (N = 46). ‘‘***’’ indicates P < 0.001.

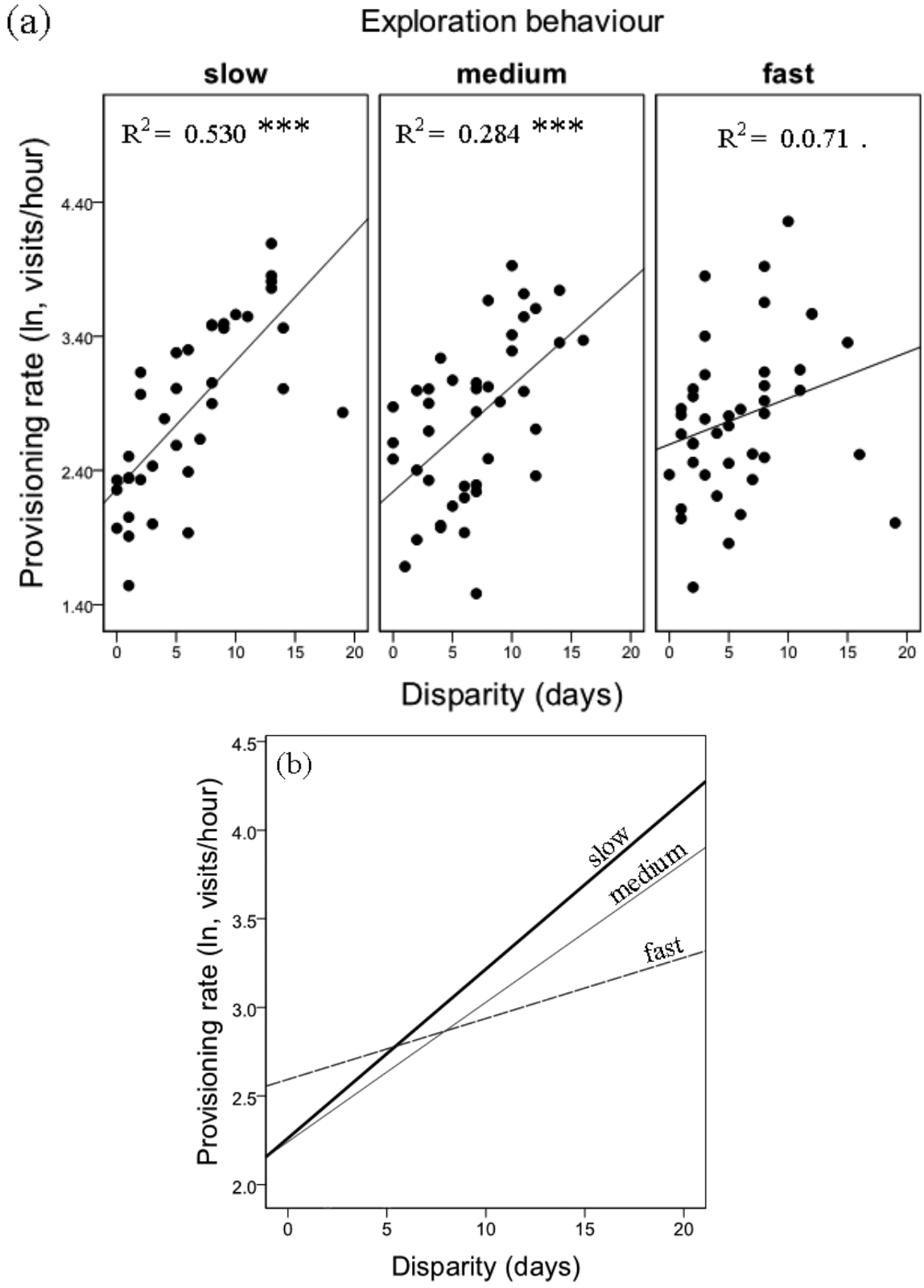


Figure 6. Relationship between provisioning rate (ln transformed) and breeding disparity for different exploration phenotypes during the late nestling phase: (a) split by panels and (b) overlay of the lines of best fit (N = 118). ‘‘***’’ indicates P < 0.001.

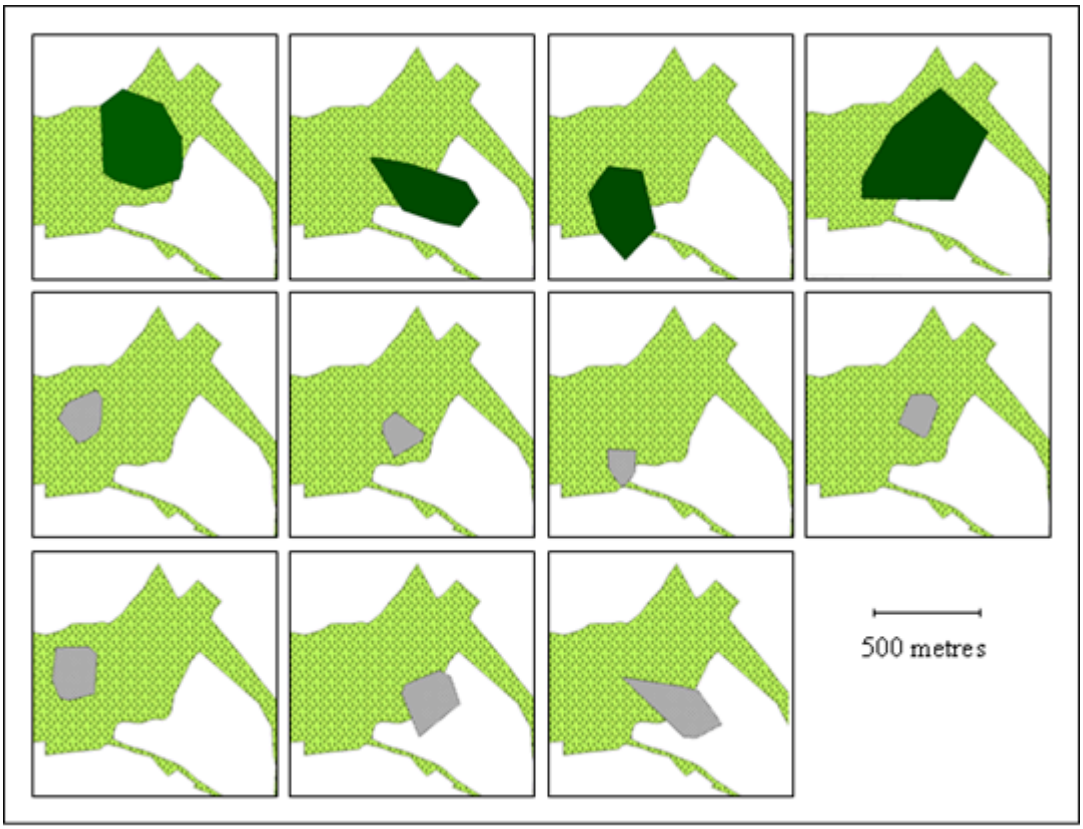


Figure 7. Graphical representations of the home range sizes of non-solvers (green) and solvers (grey), N = 11.

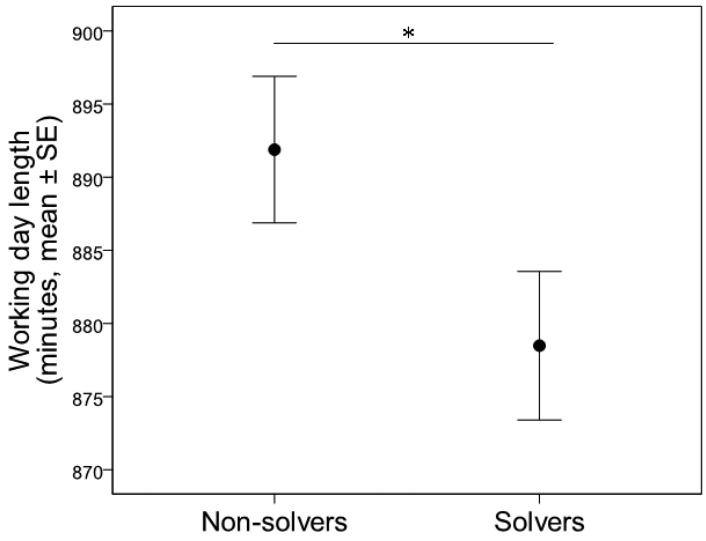


Figure 8. The average working day length of solvers and non-solvers during the early nestling phase (N = 46). ''*'' indicates P < 0.05.

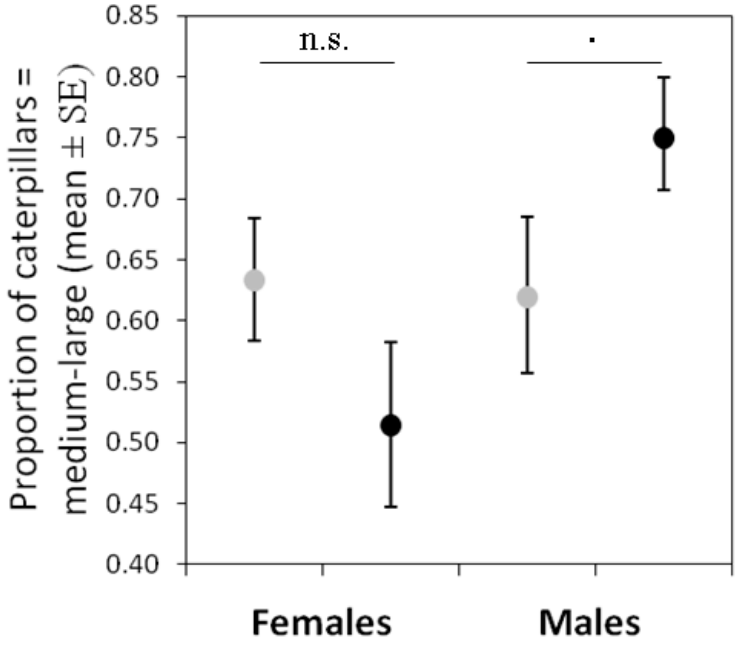


Figure 9. Proportion of caterpillars provisioned that were medium-large in size by solvers (black) and non-solver (grey) males and females, during the early nestling phase (N = 46). ''.'' indicates P < 0.06.

Table 1. Relationship between two measures of reproductive success and working day length, during early and late nestling phases.

	EARLY NESTLING PHASE						**LATE NESTLING PHASE**					
Term	Fledgling number (N=20)			Fledging mass (N=20)			Fledgling number (N=96)			Fledging mass (N=94)		
	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P
Constant	-17.27 ± 9.710			19.815 ± 0.419			-5.15 ± 3.16			19.16 ± 0.174		
Working day length (min)	**0.020 ± 0.011**	**1.76**	**0.096***				**0.007 ± 0.004**	**1.99**	**0.049**			
Brood size	0.993 ± 0.144	6.89	<.001				0.827 ± 0.054	15.39	<0.001			
Disparity				-0.141 ± 0.041	-3.52	0.002				-0.091 ± 0.024	-3.78	<0.001

Models were derived by backward elimination of non-significant terms. Full models contained effects: working day length (average of pair at a nest), disparity, lay date, brood size, habitat quality (and year in the case of the late nestling phase model). * Working day length just fell short of significance at the 0.05 level in the full model (test statistic and p value from full model: t = 2.05, P = 0.058, mean ± se = 0.024 ± 0.012). Effects of provisioning traits are shown in bold.

Table 2. Relationship between two measures of reproductive success and provisioning rate, prey type and caterpillar size, during early and late nestling phases.

	EARLY NESTLING PHASE						**LATE NESTLING PHASE**					
Term	Fledgling number (N=27)			Fledging mass (N=27)			Fledgling number (N=78)			Fledging mass (N=77)		
	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P
Constant	-0.762 ± 0.483			19.734 ± 0.349			1.519 ± 0.468			19.357 ± 0.162		
Provisioning rate							**0.023 ± 0.010**	**2.30**	**0.024**			
Proportion of caterpillars (prey type)	**0.950** ± **0.393**	**2.42**	**0.024**									
Brood size	1.016 ± 0.048	21.29	<.001				0.790 ± 0.049	16.17	<0.001			
Disparity				-0.142 ± 0.036	-3.90	<.001	-0.048 ± 0.024		0.050	-0.111 ± 0.022	-5.05	<.001

Models were derived by backward elimination of non-significant terms. Full models contained the provisioning variables: provisioning rate, prey type, and caterpillar size (all averaged within pairs), as well as lay date, disparity, brood size and habitat quality (and year in the case of the late nestling phase model). Effects of provisioning traits are shown in bold.

Table 3. Relationship between four provisioning variables and PSP and EB, during the early nestling phase, controlling for a range of fixed effects.

Term	**Working day length (min) (N=46)**			**Provisioning rate (feeds/hour) (N=46)**			**Proportion of caterpillars (N=46)**			**Caterpillar size (N=42)**		
	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P
Constant	893.2 ± 5.22			2.561 ± 0.094			0.198 ± 0.164			0.294 ± 0.203		
PSP [a]	**-15.534 ± 6.599**	**5.54**	**0.024**							**-0.404 ± 0.318**	**0.11**	**0.738**
EB				**0.080 ± 0.191**	**2.19**	**0.147**	**1.415 ± 0.526**	**0.06**	**0.810**	**1.185 ± 0.270**	**22.12**	**<0.001**
Age [b]				-0.099 ± 0.118	0.74	0.394				0.671 ± 0.225	6.12	0.018
Sex [c]				0.5625 ± 0.111	27.58	<0.001	0.049 ± 0.210	0.12	0.737	-0.010 ± 0.268	3.44	0.074
Disparity							-0.131 ± 0.033	13.71	<0.001			
EB * Age				**-0.644 ± 0.283**	**5.17**	**0.028**						
EB * Sex							**1.414 ± 0.526**	**7.23**	**0.011**			
PSP * Sex										**0.963 ± 0.435**	**4.89**	**0.033**

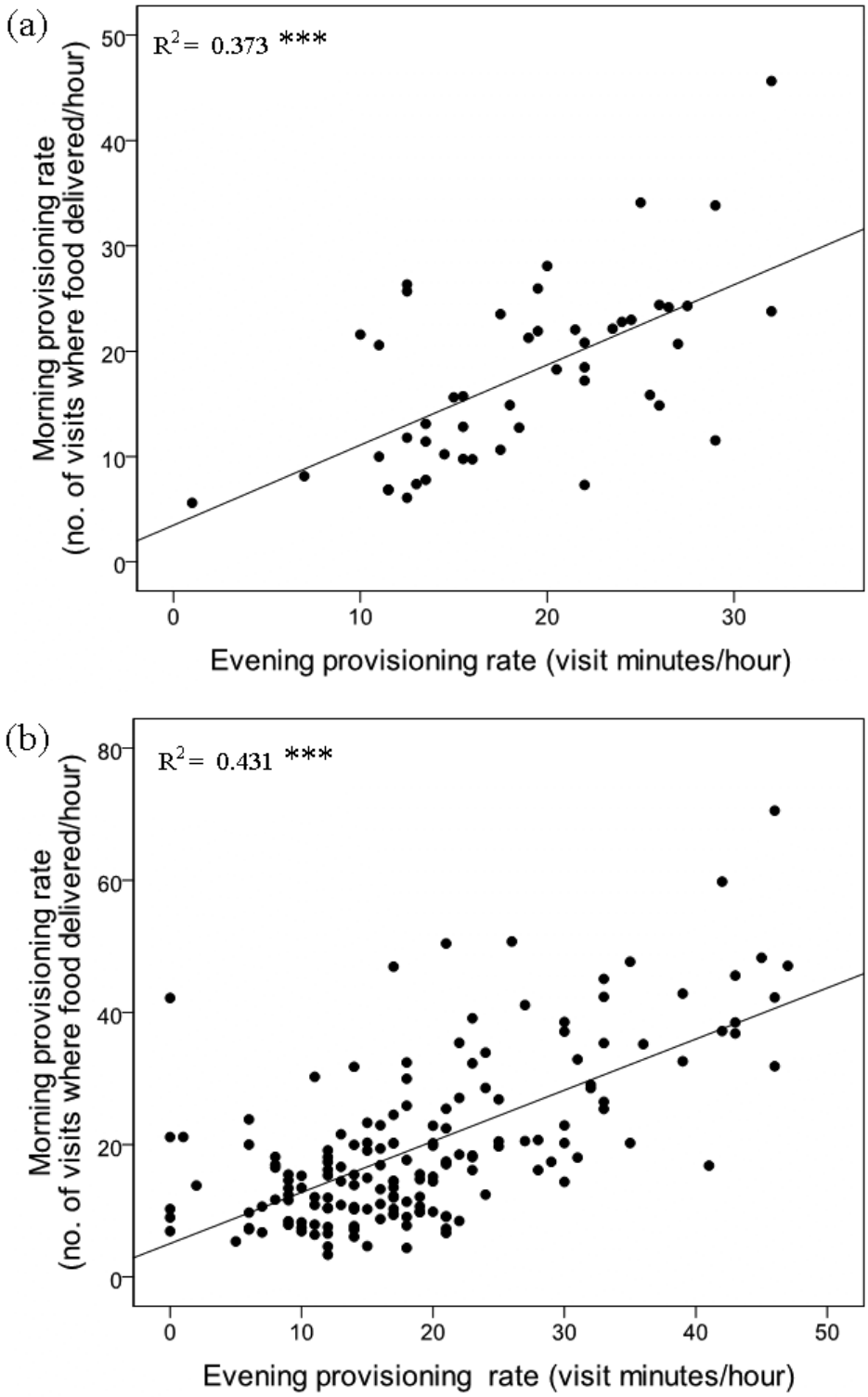
[a] Non-solver set to zero, [b] first year age class set to zero, [c] female set to zero. Models were derived by backward elimination of non-significant terms. In addition to PSP and EB, all full models contained the terms: age, sex, brood size, disparity and habitat quality, and nest box ID (random effect). For each model, two way interactions between EB/PSP and sex, age, disparity, and habitat quality were tested. Where interactions are present in the minimal model, the main effect F and P values shown are taken from the minimal model excluding interactions. Estimates and standard errors displayed are those from the full minimal model including significant interactions. EB and PSP effects are shown in bold. All significant main or interactions terms involving PSP or EB were also significant at the P = 0.05 level in full models, prior to model simplification.

Table 4. Relationship between four provisioning variables and PSP and EB, during the late nestling phase, controlling for a range of fixed effects.

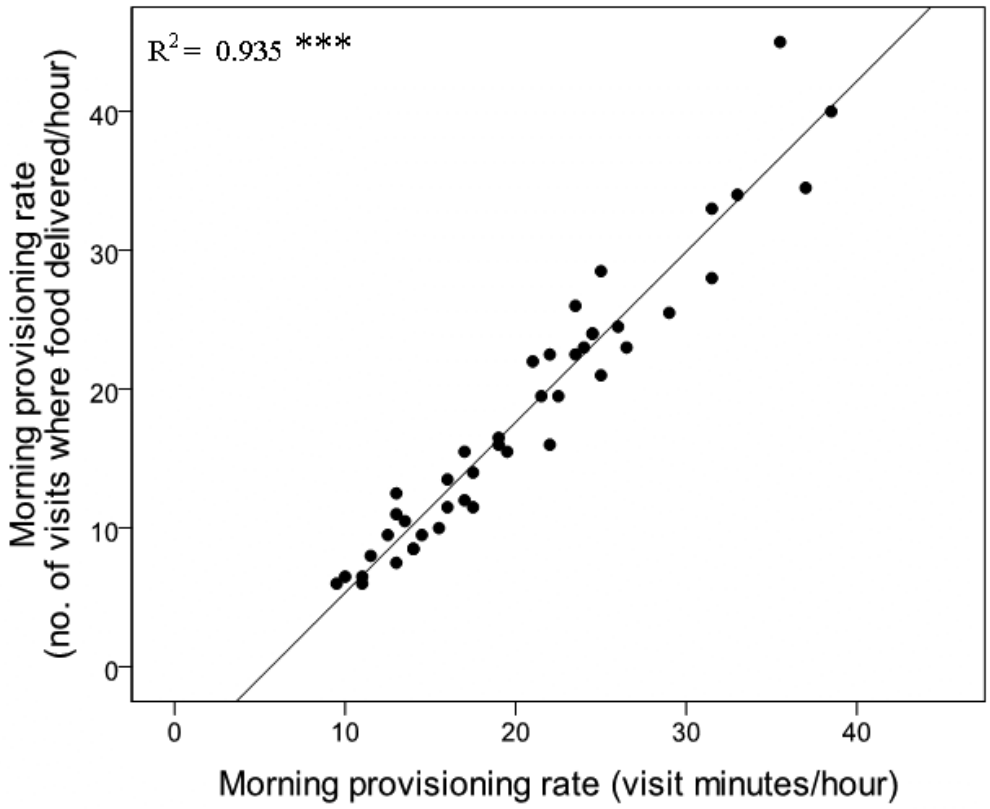
Term	**Working day length (min) (N=146)**			**Provisioning rate (feeds/hour) (N=118)**			**Proportion of caterpillars (N=123)**			**Caterpillar size (N = 123)**		
	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P
Constant	906.5 ± 4.860			2.806 ± 0.048			1.014 ± 0.127			1.252 ± 0.124		
PSP [a]												
EB				**0.066 ± 0.100**	**0.54**	**0.463**						
Age [b]	-10.261 ± 4.864	4.45	0.037									
Sex [c]	-33.340 ± 3.764	78.47	<0.001				0.536 ± 0.135	15.89	<0.001			
Disparity				0.077 ± 0.011	52.89	<0.001	-0.098 ± 0.021	20.69	<0.001	-0.071 ± 0.026	7.29	0.008
Lay date	1.478 ± 0.500	8.81	0.004	-0.032 ± 0.008	14.78	<0.001						
Brood size	4.004 ± 1.450	7.63	0.007									
Year [d]	14.821 ± 5.989	6.12	0.015									
EB * Disparity				**-0.045 ± 0.022**	**4.21**	**0.043**						

[a] Non-solver set to zero, [b] first year age class set to zero, [c] female set to zero, [d] 2009 set to zero. Models were derived by backward elimination of non-significant terms. In addition to PSP and EB, all full models also contained terms: age, sex, brood size, disparity, lay date and habitat quality, and nest box ID and year (random effect). For each model, two way interactions between EB/PSP and sex, age, disparity, and habitat quality were tested. Where interactions are present in the minimal model, the main effect F and P values shown here are taken from the minimal model excluding interactions. Estimates and standard errors displayed are those from the full minimal model including interactions. All significant main effects of PSP or EB were also significant at the P = 0.05 level in full models, prior to model simplification, with the exception of the interaction between EB and disparity, which dropped to a non-significant tendency (W_1 = 3.15, p = 0.080, e ± se = -0.043 ± 0.025).

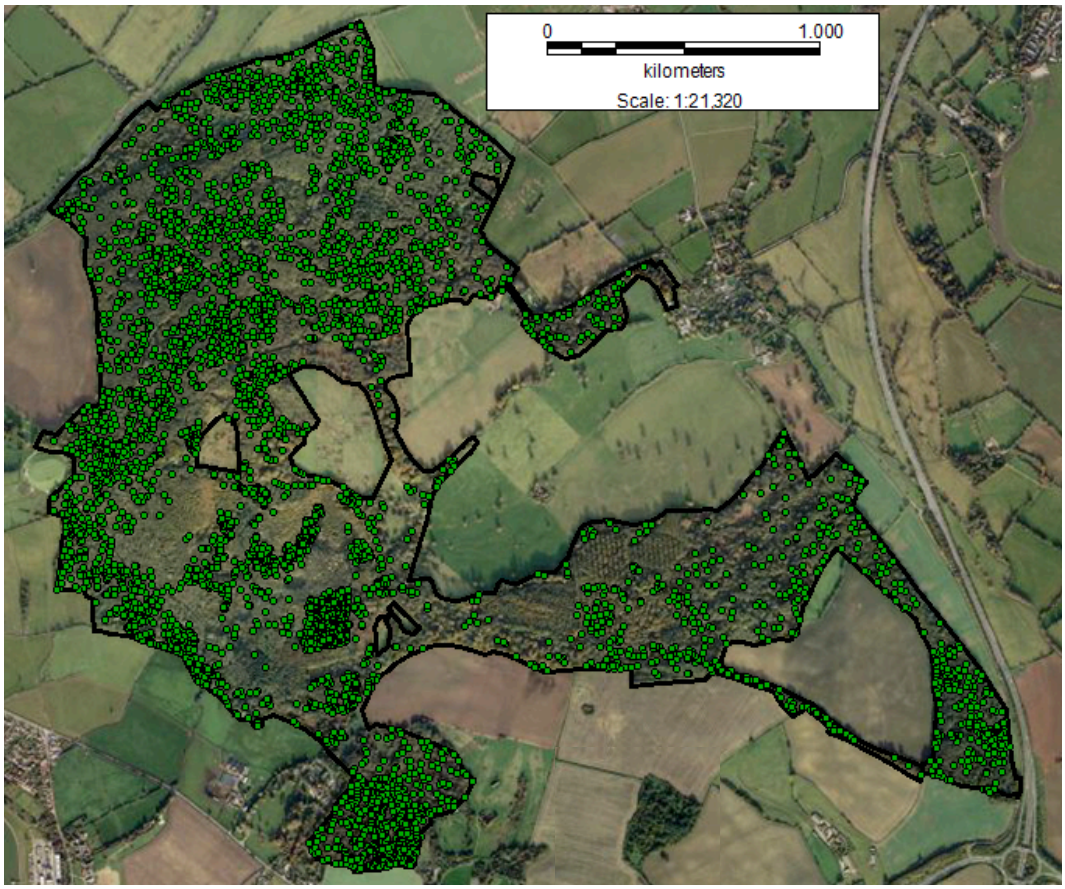
APPENDICES



Appendix 1. Relationship betweeen morning provisioning rate and evening provisioning rate for (a) the early nestling phase (N =49) and (b) the late nestling phase (N = 165). "***" indicates P < 0.001.



Appendix 2. Relationship between morning provisioning rate measured using the video footage, and the visit minute measure of provisioning rate taken from the PIT detector data for the same time period (N = 44). ‘‘***’’ indicates P < 0.001.



Appendix 3. Satellite image of Wytham Woods, showing the location of all oak trees above 30cm diameter at breast height (green circles, N = 5425).

CHAPTER 5

Innovative problem solving, life-history variation and fitness in the great tit



Innovative problem solving, life-history variation and fitness in the great tit

Ella F. Cole, Julie Morand-Ferron & John L. Quinn

ABSTRACT

Innovativeness correlates with a range of cognitive abilities, and is thought to allow animals to exploit their environment more efficiently, thereby giving them a selective advantage. Although it is widely assumed that natural selection should favour greater cognitive performance among individuals, evidence for this hypothesis is lacking from natural populations. Here we use a wild population of great tits (*Parus major*) to examine whether individual innovative problem-solving performance is related to reproductive life-history variation and fitness. Over four winters we assayed problem-solving performance among wild-caught birds temporarily taken into captivity and subsequently monitored their reproductive performance in the wild. Problem-solver females and those mated to problem-solver males produced relatively large clutches. This effect was not due to solvers beginning their breeding attempts earlier or occupying better quality habitats. Solver females were more likely to desert their brood prior to fledging, though among non-deserters, solvers fledged significantly more offspring than non-solvers. Perhaps as a result of these contrasting links with different life-history traits, we found little evidence of recruitment selection on problem-solving performance, either within or across years. This is the first large-scale study to examine the consequences of individual cognitive performance for life-history variation and fitness in a natural population. Our results suggest that although higher cognitive ability can lead to higher reproductive success, equally important negative effects counteracted these benefits, leading to no overall selection on cognitive ability. The ecological mechanisms that lead to these effects remain to be elucidated.

INTRODUCTION

Cognition can be defined as the mechanisms by which animals acquire, process, store, and act on information from their environment (Shettleworth 2010). Cognitive processes allow animals to respond to their environment and modify their behaviour, and are therefore likely to have important ecological and evolutionary implications (Dukas 2004). Innovativeness - the ability to solve novel problems or find new solutions to old problems (Kummer & Goodall 1985) - is a form of behavioural flexibility that is increasingly viewed as an important component of animal cognition (Lefebvre et al. 2004; Roth & Dicke 2005; Boogert et al. 2011). Indeed, innovativeness has been shown to correlate with residual brain size, tool use, and learning ability across avian and primate taxa (Lefebvre 2011; Reader et al. 2011). Different species vary considerably in their propensity to innovate, and evidence from comparative work suggests that this interspecific variation may reflect adaptive differences (reviewed in Lefebvre et al. 2004; Reader & Laland 2003). For example in birds, more innovative taxa survive better when introduced to new habitats (Sol et al. 2005) and British bird species with larger telencephalons, an area of the brain associated with problem solving, are less likely to suffer population decline (Shultz et al. 2005).

Differences in novel problem-solving ability also exist within species (e.g. Seibt & Wickler 2006; Biondi et al. 2008; Vonk & Povinelli 2011; Overington et al. 2011a). This variation can be relatively consistent over time and between different tasks, and can be independent of motivation suggesting that it represents inherent individual differences, caused by genetic or permanent environmental effects

(Laland & Reader 1999; Banerjee et al. 2009; Cole et al. 2011; Overington et al. 2011a). Selection for innovativeness is expected if this type of behavioural flexibility allows individuals to exploit novel or existing resources more efficiently, especially when resource supply is particularly low or variable (Grant & Grant 1989; Dukas 1998; Reader & Laland 2003). A recent study in black-capped chickadees (*Poecile atricapillus*) provided some support for this, by demonstrating that individuals from the northern extreme of the species range are better at solving novel foraging problems than those from the southern extreme, where food is more abundant (Roth et al. 2010). Although this work suggests that there may be fitness benefits associated with being a good problem solver, and that we might expect positive, directional selection for this trait under harsh environmental conditions, this hypothesis has yet to be tested directly. Indeed, very little is known about the fitness consequences of any cognitive trait under natural conditions (but see: Raine & Chittka 2008; Keagy et al. 2009).

In addition to benefits, cognitive traits may also be associated with costs. Evidence suggests that cognitively demanding behaviours can be associated with both time and energy costs (e.g. Dukas & Visscher 1994) as well as increased predation risk (Reader & Laland 2003). In addition to costs associated with exhibiting specific behavioural actions, cognitive traits are also likely to incur intrinsic costs caused by developmental or genetic trade-offs (Niven 2005). For example work on *Drosophila melanogaster* has demonstrated that preferential allocation of limited resources to the development of learning ability can result in reduced competitive ability (Mery & Kawecki 2003). This evidence suggests that, under certain

conditions, the costs of a cognitive trait such may outweigh the benefits, causing high performing individuals to be at a selective disadvantage (Kawecki 2010). Selection for innovative ability is therefore likely to depend on the relative costs and benefits of this trait in a particular environmental context. One expectation is that innovativeness may only be advantageous in particularly poor quality environments, where resources are scarce (Reader & Laland 2003).

Using a wild population of great tits (*Parus major*) we examined the fitness and life-history correlates of novel problem-solving performance, a trait that is thought to reflect innovativeness (Laland & Reader 1999; Webster & Lefebvre 2001) and general cognitive ability (Roth & Dicke 2005). Great tits provide an excellent study system to examine the fitness consequences of innovativeness; not only have their life histories and ecology been intensively studied (reviewed in Perrins 1979; Gosler 1993), but great tits are generally inquisitive in response to novelty (Gibb 1957), and occupy a wide variety of habitats (Gosler 1993) - a hallmark trait for innovative species (Overington et al. 2011b). Indeed anecdotal evidence suggests that great tits are capable of considerable innovative foraging behaviour (e.g. Fisher & Hinde 1949; Hinde & Fisher 1951; Duyck & Duyck 1984; Estók et al. 2010). Consequently, food-related problem-solving ability is likely to be an ecologically relevant trait for this species. Great tits are therefore ideal for examining how innovativeness influences reproductive success at different life-history stages, and under varying degrees of food availability.

Here we measured individual variation in innovative problem-solving performance under standardised conditions, by taking individuals into captivity for short time periods. Birds were then released back into the wild, where their subsequent breeding attempts were closely monitored, allowing us to compare various life-history traits and fitness components of birds that did and did not solve our problem-solving task. We also tested whether the local habitat quality of solvers and non-solvers were likely to differ and therefore confound any link with life-history variation. To address the hypothesis that the fitness benefits of innovativeness might depend on environmental conditions, we tested whether any of these reproductive differences between good and poor problem solvers varied along temporal and spatial gradients of food availability. Finally we tested whether directional selection is occurring on this trait in our study population using standardised selection differentials (Lande & Arnold 1983).

METHODS

Study population and study site

This work was carried out in the context of a long term study population of great tits at Wytham Woods (51°46'N, 1°20'W), Oxfordshire, U.K. Wytham woods is a mixed deciduous woodland, c. 385 hectares in size, containing 1020 nest boxes. All birds for this study were trapped in the winter (November – March) between January 2007 and March 2010. Great tits were caught using mist nets at temporary feeders erected throughout the wood. Unringed individuals were fitted with a unique BTO (British Trust for Ornithology) metal leg ring. Birds were then taken into captivity under a Natural England licence where problem-solving performance

was assayed under standardised conditions. All individuals were subsequently released back into the wild, at the site of catching.

Captive problem-solving assay

At the field station birds were housed singly in wire cages (45 × 45 × 68 cm), with opaque sides to visually isolate them from one another (see Chapter 2 for full housing information). All individuals were presented with a novel problem task on the afternoon they were housed to assess problem-solving performance (hereafter PSP). The problem device consisted of a vertical transparent Perspex tube containing a platform, which was supported by a horizontal lever. Four waxworms (*Galleria mellonella*) were placed on the platform to bait the device. To solve the task birds had to remove the lever, causing the platform to drop and the waxworms to fall into a feeding dish. Birds were classified as either solvers or non-solvers based on their success in this task (see Chapter 2 for full methodology). Previously we demonstrated that individuals in our population differ consistently in their propensity to solve this task, and that these differences are maintained over time spans of up to a year, and across different types of novel foraging problems (see Chapter 2). Performance in this task is likely to reflect an individual's ability to solve novel foraging problems, and is therefore a suitable measure of cognitive performance (Roth & Dicke 2005).

Monitoring reproductive attempts

A team of fieldworkers monitored the reproductive attempts of all birds between April and June each year, as part of the long-term study of the tit population (see

Perrins 1979; McCleery et al. 2004). Nest boxes were visited regularly to establish the lay dates (April date; April 1st = 1), clutch sizes, and hatch dates. Additional visits were made to catch and identify the parents (when nestlings were approx. 7 days old), and to ring and weigh the nestlings prior to fledging (at 14 days old). Adults were trapped using a spring-loaded trap, placed inside the nest box; any unringed birds were ringed with a unique BTO ring. Nestlings were weighed when 14 days old to provide a measure of their condition. Nestlings reach asymptotic body mass before they are two weeks old, meaning their mass at this point reflects condition at fledging (Perrins 1979). All nests were checked after fledging was complete to establish how many nestlings had done so successfully, and nests were classified as failed if no young fledged successfully. As each nestling was individually banded, we were able to establish how many young from each nest recruited to the breeding population the following year (see below).

Life-history variation

Over the four breeding seasons 247 females and 221 males of known PSP bred in Wytham (totalling 382 and 316 breeding attempts respectively). In order to examine how PSP might influence individual behaviour at different stages of reproduction, we assessed the covariance between PSP and six life-history traits (see below), controlling for preceding life-history traits where appropriate. In addition, we tested whether solvers and non-solvers differed in the quality of their breeding habitat, which is known to influence reproductive success (Wilkin et al. 2007; Wilkin & Sheldon 2009).

Life-history traits

(i) Timing of breeding (lay date) – the date that a female begins to lay her clutch is strongly linked to reproductive success, with young hatching from early nests generally being more likely to survive post fledging than those from late nests (Perrins 1965; Perrins 1970). Not only is more food available for the nestlings in early nests, but fledglings from early nests are also likely to have a competitive advantage over late nestlings (Perrins 1979). Food availability for the laying female is thought to be an important determinant of lay date in great tits (Perrins 1970; Kallander 1974).

(ii) Clutch size – the number of eggs a female lays is closely linked to the number of recruits to the breeding population she produces (Boyce & Perrins 1987). Clutch manipulation experiments strongly suggest that each female lays the number of eggs that will maximise recruitment for her brood (Pettifor et al. 1988; Pettifor et al. 2001).

(iii) Nest failure (whether or not all young died between adult trapping and fledging) - approximately 13% of nests where the young were alive at adult trapping fail before fledging (see Chapter 6). Although some nests also fail prior to adult trapping, they cannot be included in analyses as the identity of parents at these nests is unknown. The nest boxes used by our study population are virtually predator proof (McCleery et al. 1996). Nest failure can therefore either be attributed to desertion - which is normally caused by inability to feed fledglings or increased danger to offspring or adult survival (e.g. high predation risk) (Gosler 1993), or parental mortality (Perrins 1979).

(iv) For successful nests, the number of young fledged from the nest - this is a good predictor of recruitment selection to the breeding population (Pettifor et al. 1988).

(v) The average fledging mass of young (hereafter fledging mass) – this trait is also strongly correlated with recruitment (Verboven & Visser 1998), and provides a measure of average offspring condition.

(vi) Number of young that successfully recruited to the breeding population the following year.

Measures of food availability

To establish whether the reproductive consequences of PSP were dependent on foraging conditions, we used two proxies for local food availability. The first was the disparity between when parents had chicks in the nest and the annual peak in caterpillar abundance, a measure that correlates strongly with both fledgling number and condition (Visser et al. 2006). The second measure was the number of oak trees within a 75m radius of each nest box (hereafter habitat quality). Oak trees are the preferred food source of the winter moth larvae (Summerville et al. 2003), and great tits breeding in oak rich habitats have been shown to breed earlier, lay larger clutches and fledge young in better condition (Wilkin et al. 2007; Wilkin & Sheldon 2009). Full details of how disparity and habitat quality were calculated for each breeding pair are outlined in the methods section of Chapter 4.

Statistical analysis

For all analyses the effects of male and female PSP were analysed separately because PSP was known for both parents in only 28% of our sample nests. Restricting our analysis to these nests would therefore have reduced sample size considerably. Relationships between PSP and the six life-history traits were tested using Linear Mixed Models (LMMs) and Generalised Linear Mixed Models (GLMMs), containing the random factors year (2007-2010), and bird identity to account for multiple breeding attempts per individual. GLMMs were used to test the relationships between PSP and both nest failure (fail/succeed) and recruitment (assuming binomial and Poisson error structure, respectively). All other relationships were tested using LMMs. All models controlled for the fixed effects bird age, lay date, breeding disparity and habitat quality (unless one of these terms was the response variable). In addition, in the model explaining variation in nest failure, brood size was included as a fixed effect, as this has been shown to strongly influence nest failure rate (see Chapter 6). Because the disparity score for each nest was calculated using the hatch date for that breeding attempt, disparity was not included as a fixed effect in the model explaining variation in lay date (which is highly correlated to hatch date). To establish whether relationships between PSP and life-history measures were dependent on food availability, we tested the interactions between PSP and both disparity and habitat quality, for each life-history trait. All P-values were derived from dropping each term from the full model (excluding interactions), and final models were derived by backwards, stepwise model simplification..

Standardised directional selection coefficients were estimated using Generalised Linear Models (GLM) of two measures of reproductive success: fecundity, defined as the total number of young that successfully fledged from the nest (including nests where no young fledged) and recruitment, defined as the number of young successfully recruited to the breeding population the following year. Both fecundity and recruitment were standardised within year. Selection estimates and standard errors were derived from models with normal errors. The significance of these was tested with an F-statistic against a normal distribution for fecundity but with a Wald (W) statistic against a Poisson error structure for recruits (following methods from Lande & Arnold 1983).

RESULTS

Habitat quality and life-history variation

There was no difference in breeding habitat quality between solvers and non-solvers, either for females or males ($F_{1, 245} = 0.73$, $P = 0.393$; $F_{1, 218} = 0.02$, $P = 0.392$, respectively). Neither female nor male PSP covaried with lay date (see Tables 1 & 2). These relationships were therefore unlikely to confound other links between PSP and reproductive success.

Solver females laid larger clutches than non-solvers ($F_{1, 231} = 4.47$, $P = 0.039$) and there was a non-significant tendency for females paired with solver males to lay larger clutches than females paired to non-solvers ($F_{1, 185} = 3.30$, $P = 0.071$). A post-hoc analysis was conducted to establish the combined effect of male and female PSP on clutch size, considering nests where the PSP of both parents was known.

The number of solver parents was found to be a strong predictor of clutch size ($F_{2, 116} = 5.25$, P = 0.007, Figure 1).

Nest failure was related to female but not male PSP; the nests of solver females were significantly more likely to fail before fledging than non-solvers (Figure 2, $W_1 = 6.22$, P = 0.013, N = 368, see Tables 1 & 2). This was also true when restricting data to females that were known to survive beyond the breeding season ($W_1 = 4.36$, P = 0.039, N =134), suggesting that the elevated nest failure among solvers was a result of desertion rather than adult mortality. To establish whether the nests of solver females were more likely to fail because these females laid larger clutches (and therefore had larger broods) we conducted a post-hoc analysis testing the interaction between female PSP and brood size with respect to nest failure. This interaction was not significant, suggesting the effect of female PSP was independent of brood size (interaction term: $W_1 = 0.33$, P = 0.564, N = 242). While there was no difference in nest failure rate between solver and non-solver males, nest failure was influenced by an interaction between male PSP and habitat quality (PSP × habitat quality: $W_1 = 3.95$, P = 0.047, N = 308). Whereas the nests of male solvers were less likely to fail with increased habitat quality, this relationship was not present amongst non-solver males (Figure 3). This interaction effect was not present in females.

Amongst those females that did successfully rear young to fledging, solver females fledged significantly more offspring than non-solvers ($F_{1, 182} = 4.10$, P = 0.044, Figure 4). This effect did not occur in males (see Table 2). Average fledging mass

did not differ between solvers and non-solver females or males (see Tables 1 & 2). With the exception of the interaction between male PSP and habitat quality, none of the interactions between life-history traits and breeding disparity or habitat quality were significant ($P > 0.1$ for all interaction terms).

Recruitment and selection

Solvers and non-solvers did not differ in their recruitment success, either amongst females or males (see Tables 1 & 2). Indeed we found little or no evidence to suggest that either fecundity selection or recruitment selection is acting on this trait at the population level (see Table 3).

DISCUSSION

By carrying out rapid assays on hundreds of individuals under standardised conditions and then monitoring their reproductive performance, we conducted the first large-scale investigation of how variation in a cognitive trait influenced reproductive life-history variation and fitness in wild animals. Previously we demonstrated consistent and persistent individual differences in innovative problem-solving in great tits in our study population (Chapter 2). Given that some of this variation is likely to have an additive genetic basis, innovativeness is expected to be the target of natural selection. The results from this study demonstrate that variation in innovative problem-solving performance is linked to three important life-history traits: clutch size, nest failure and fledgling number. However we find little or no evidence to suggest that directional fecundity or recruitment selection is acting on this trait in our population.

Innovativeness and life-history variation

Innovativeness is thought to allow individuals to better exploit their environment and consequently forage more efficiently (Lee 1991; Reader & Laland 2003). Problem solvers were therefore expected to lay larger clutches and raise more young successfully than less innovative individuals. After controlling for other known sources of variation, we confirmed that female problem solvers produced larger clutches than non-solvers. A large body of experimental research suggests that great tit females optimise their clutch size to correspond with the number of nestlings that they (and their mate) can adequately feed and ultimately recruit to the breeding population (Perrins & Moss 1975; Pettifor et al. 1988; Pettifor et al. 2001). The findings that solver females laid larger clutches than non-solvers, and providing their nest was successful, were capable of maintaining this difference through to fledging without compromising fledgling quality suggest that solvers are better able to rear large broods. This hypothesis, is further supported by the findings reported in Chapter 4, which indicate that solvers may be more efficient foragers than non-solvers.

Although the effect of male PSP on clutch size fell short of significance, an analyses including nests where the PSP of both parents was known revealed that clutch size was largest when both parents were problem solvers. This finding provides the first tentative evidence that females mated to males of different cognitive abilities vary in a key life-history trait (Boogert et al. 2011). In many birds, including great tits, the male feeds the female during egg laying and incubation (Lack 1940). Although supplementary feeding experiments have shown that the amount of food

a female consumes is unlikely to limit the number of eggs she can produce (reviewed in Meijer & Drent 2008),,there is some evidence to suggest that males can use courtship feeding to influence how much a female investments in her clutch (Carlson 1989). A study in red-backed shrikes (*Lanius collurio*) found that providing only males with additional food significantly increased their partners' clutch size (Carlson 1989). As male courtship feeding can be a good predictor of provisioning behaviour (Niebuhr 1981; Wiggins & Morris 1986; Green & Krebs 1995), it can be hypothesised that females use courtship feeding to assess their mates' potential or intention to provision nestlings effectively, and adjust their clutch size accordingly. Indeed a study that tested experimentally whether female red crossbills (*Loxia curvirostra*) use information on male foraging ability to make reproductive decisions found that females associated preferentially with good foragers (Snowberg & Benkman 2009). Some of the clutch size variation we observed might therefore have been caused by females varying their reproductive investment based on the problem-solving performance of their partners. Alternatively, these traits may be linked via a third trait that females use as an indicator of male quality or cognitive capacity, such as song complexity (Boogert et al. 2008) or carotenoid-based plumage colouration (Mateos-Gonzalez et al. 2011).

In contrast to females, we found no link between PSP and fledgling number in males. Although we have no clear explanation for why this might be, males and females tits are known to differ in their prey choice and provisioning behaviour (Bańbura et al. 2001, Gosler 1993, Chapter 4). For example male blue tits have been found to provision a higher proportion of good quality food items than

females (Bańbura et al. 2001). These sex differences in parental care may therefore affect how the foraging ability of males and females influences nestling survival.

Work on wild bird populations suggests that traits such as innovative problem solving and tool use may be particularly beneficial in poor quality environments, where food is difficult to find (Roth et al. 2010; Tebbich et al. 2002). We find no evidence to suggest that solvers performed especially well when food availability is low. One reason for this may be that the spatial scale of variation in food availability within our study site is too small to observe an effect. Indeed previous work on our population has shown that birds failing to synchronise their breeding attempts with local food availability forage over a larger area compared to synchronised birds (Hinks thesis 2011). The ability of birds to extend their foraging range may therefore act to partially mitigate the effects of variation in food availability at a small spatial scale.

Innovativeness and nest desertion

In contrast to the positive correlations between innovative problem solving and several fitness related traits discussed above, female problem solvers were more likely to desert their nests than non-solvers. Nest desertion is commonly associated with low resource availability causing parents to be unable to provide sufficient food to raise a brood to fledging (Gosler 1993; Einloft-Achenbach & Schmidt 1984). However, it seems unlikely that the higher nest failure amongst solvers was due to parents being unable to find enough food since, amongst successful birds, solvers fledged *more* offspring than non-solvers without

compromising fledging mass. Indeed, small broods require *less* provisioning but were more likely to be deserted than large broods (irrespective of parental PSP), suggesting that food availability was not the predominant factor causing nest desertion in this study.

Rather than being a result of lack of food, offspring desertion can also represent adaptive response, which occurs when the benefits of rearing offspring no longer outweigh the costs to personal survival (and therefore future reproduction) (David & Tait 1980; Mock & Parker 1986; Pöysä et al. 1997). One factor affecting this trade-off is the probability of personal survival, which amongst breeding great tits is largely influenced by predation (Perrins 1979; McCleery & Perrins 1991). In Chapter 6 we show that some indivuduals in our population desert in response to being trapped at the nest by humans. Such trapping and handling is known to elicit a neuroendocrine stress response comparible to that produced when exposed to predators (Silverin 1998; Cockrem 2007). In a reproductive context, this neuroendocrine stress response is thought to cause individuals to redirect resources away from reproduction towards personal survival (reviewed in Wingfield & Sapolsky 2003). Moreover, individuals vary in the intensity of this stress response, with those exhibiting a larger hormonal response reducing their parental care more than those showing only a mild response (Lendvai & Chastel 2010; Miller et al. 2009). It therefore seems likely that nest desertion may represent an adaptive response amongst individuals with high stress reactivity, where personal survival is prioritised over current reproductive effort (see Chapter 6 for further discussion).

One possible explanation for our finding that solvers desert more often than non-solvers is that solvers are more responsive to the stress associated with being trapped. Indeed problem-solving performance can covary with stress responsiveness in birds (Pfeffer et al. 2002), and we have previously shown that the startle response, an anti-predation behaviour, tends to be more pronounced in solvers than in non-solvers (Appendix D, published as Dunn et al. 2011). Solvers may be generally more responsive to stress than non-solvers, and therefore more sensitive to predation risk – a possibility we feel warrants further investigation.

Desertion in great tits has been linked to female, but not male, nutritional condition, suggesting that desertion may be initiated primarily by females (Hõrak et al. 1999). If true this could explain why female PSP alone predicts nest failure. We did find that amongst solver males failure rate decreased with increased habitat quality which may indicate that the relative importance of environmental factors leading to nest desertion differ between solvers and non-solvers phenotypes.

Perspectives and conclusions

We found contrasting relationships between PSP and i) clutch size and fledgling number, and ii) nest failure, which we suggest is likely to explain why there was little evidence of directional fecundity or recruitment selection acting on these traits across the population. This suggests that contrasting links between PSP and different life-history traits may help maintain variation in PSP within our

population. Although the positive effect of PSP on clutch size and fledging number is likely caused by improved foraging efficiency and better exploitation of the available habitat, the mechanisms underpinning the relationship between female PSP and nest desertion remain elusive. Furthermore, we note that the relationships demonstrated in this study are correlative, and that further work is required to explore the mechanisms linking PSP and life history variation outlined here. This work highlights the importance of considering all stages of reproduction when examining how behavioural traits may influence fitness. Genetic correlations between behavioural traits that lead to life-history trade-offs are known to sometimes cause individuals to behave in surprising and suboptimal ways (Sih et al. 2004; Duckworth 2006). In our case we suggest that high nest failure amongst solvers could be caused by a correlation between PSP and stress reactivity. The potential importance of correlations among behavioural traits has only recently begun to be recognised in behavioural ecology (Sih et al. 2004; Réale et al. 2007).

To date most studies demonstrating the adaptive significance of cognitive traits have done so by experimentally manipulating cognitive capabilities in captivity (e.g. Dukas & Duan 2000; Dukas & Bernays 2000). Very few studies have examined the fitness consequences of natural individual variation in cognitive traits in the wild. One exception is recent work in the satin bowerbird (*Ptilonorhynchus violaceus*) demonstrating that males with better problem-solving performance received a greater number of copulations (Keagy et al. 2009). A notable drawback of this study is that the problem-solving task given to the birds related directly to maintenance of the bower, a trait that is known to greatly influence copulation rate

(Coleman et al. 2004). The link with fitness may therefore reflect selection for a secondary sexual trait rather than cognitive ability per se, though the two may be genetically correlated. In contrast, our study examines the link between reproductive behaviour and an independent measure of cognitive performance quantified outside the breeding season in a novel environment. Here we have shown that it is possible to examine the effect of a simple cognitive trait, measured under standardised conditions, on important life-history variation and fitness correlates in the wild, and hope that this work will encourage similar studies on cognitive traits.

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FIGURES AND TABLES

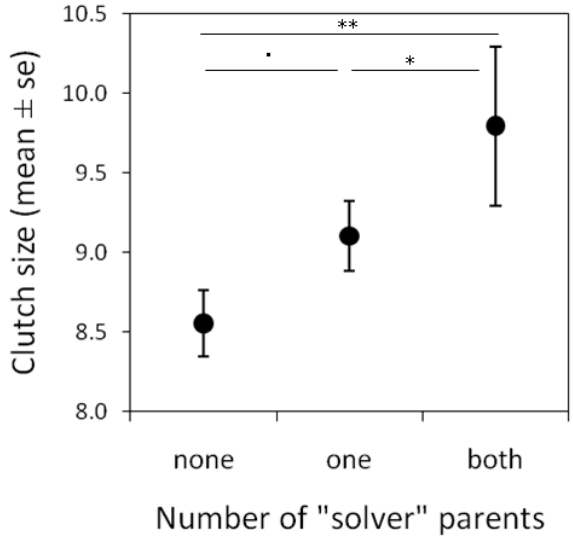


Figure 1. Clutch size and the number of "solver" parents at a nest, including nests where the problem solving-performance of both parents was known. Where a pair bred together in successive years, clutch size was averaged across breeding attempts (N = 136 pairs in which at least one parent's PSP was known; both parents non-solvers, N = 49; one solver parent, N= 65 (male only, N = 33; female only, N = 32); two solver parents, N = 22). ''**'' indicates P < 0.01, ''*'' indicates P < 0.05, and ''·'' indicates P < 0.06.

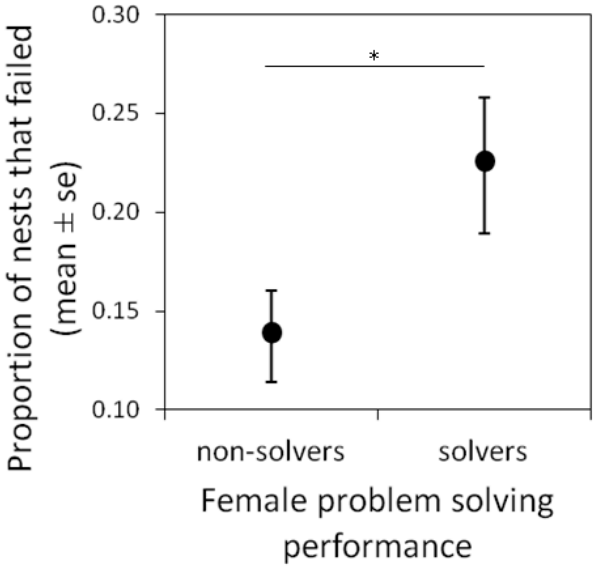


Figure 2. Nest failure between when adults were trapped and offspring fledged in relation to female problem-solving performance. Data plotted are the back transformed mean effects from a GLMM with binomial error structure (repeated observation for females breeding in successive years were accounted for using female ID as a random factor, N = 382 breeding attempts for 246 individuals; non-solvers, N = 147; solvers, N = 99). ''*'' indicates P < 0.05.

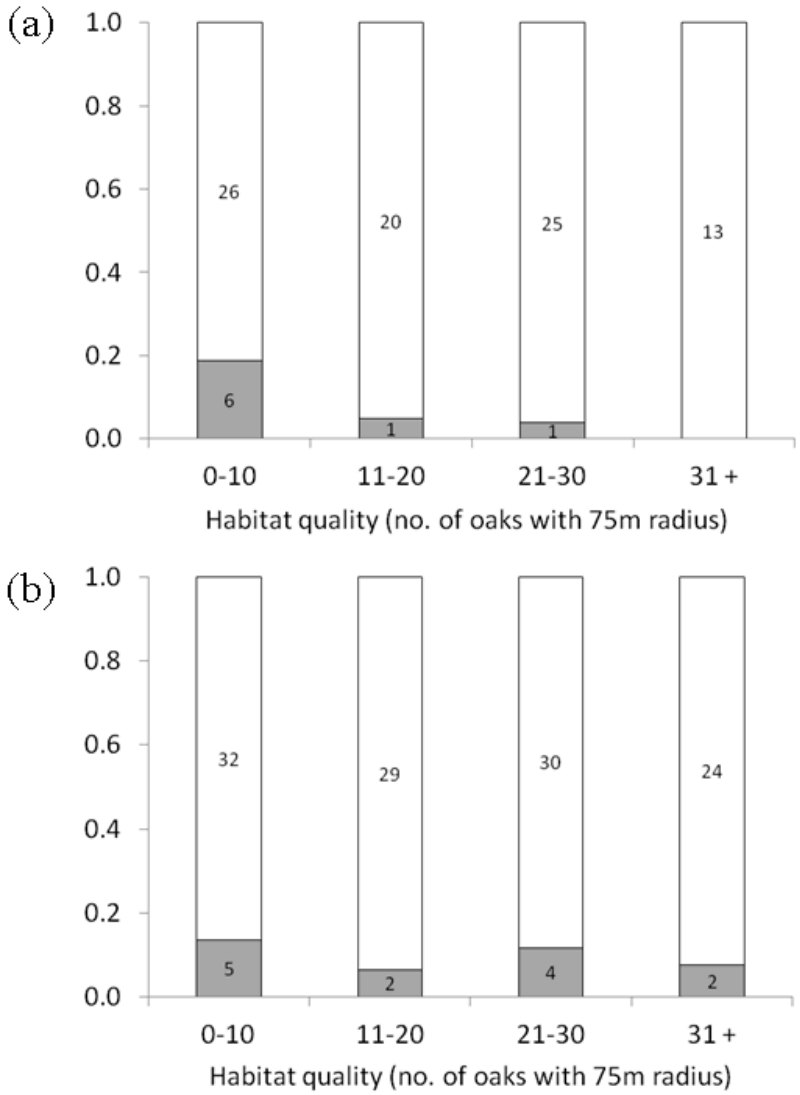


Figure 3. The relationship between the proportion of nests that failed between adult trapping and fledging, and habitat quality. Failed nests shown in grey for (a) solver males and (b) non-solver males. (N = 221). The continuous variable 'habitat quality' has been binned here into four discrete categories for illustrative purposes.

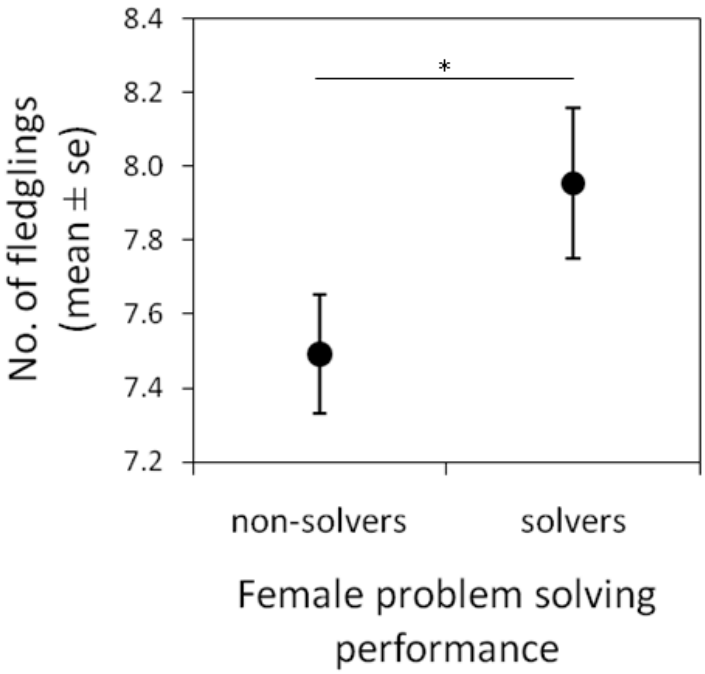


Figure 4. The number fledglings in relation to female problem-solving performance. Where a female bred in successive years, fledgling number was averaged across breeding attempts (N = 214 individuals; non-solvers, N = 132; solvers, N = 82). ‘‘*’’ indicates $P < 0.05$.

Table 1. The relationship between female problem-solving performance (PSP) and successive life-history traits through reproduction. . Separate statistical models are shown for each trait.

Term	Lay date (N = 373)			Clutch size (N = 368)			Nest failure (N = 368)			Number of fledglings (N = 307)			Average fledging mass (g) (N = 307)			Number of recruits (N = 368)		
	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	W	P	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P
Constant	18.32 ± 1.758			8.820 ± 0.266			-1.871 ± 0.295			7.465 ± 0.298			18.21 ± 0.210					
Lay date	-	-	-	-0.067 ± 0.016	17.19	<0.001				-0.114 ± 0.026	18.89	<0.001	-0.066 ± 0.0.17	14.40	<0.001			
Disparity	-	-	-	-0.053 ± 0.024	4.97	0.027				-0.151 ± 0.038	15.56	<0.001	-0.118 ± 0.025	21.52	<0.001			
Brood size	-	-	-	-	-	-	-0.326 ± 0.083	15.39	<0.001	-	-	-	-	-	-	-	-	-
Age[a]	-1.944 ± 0.475	16.75	<0.001															
PSP[b]				0.400 ±0.189	4.47	0.036	0.742 ± 0.297	6.22	0.013	0.479 ± 0.237	4.10	0.044						

[a] First-year breeder and [b] non-solver set to zero. Each column represents a separate model. Models were derived by backward elimination of non-significant terms. All full models included fixed effects: PSP, age (categorised as either first-year breeder or older), lay date (date first egg was laid), disparity (difference in days between the annual peak in caterpillar abundance and the date when nestlings were 9 days old; see supplementary methodology), habitat quality (oak density within 75m of the nest) and brood size, unless indicated by a dash in the table (see methodology for further details). In addition to fixed effects controlled for in the table, all models also contained random terms bird identity and year. Model results from GLMMs (for nest success, binary error structure; number of recruits, Poisson error structure) and LMMs. For each model the interactions between PSP and both disparity and habitat quality (number of oaks within a 75m radius of nest box) were tested. All interactions were non-significant at the P = 0.05 level (P > 0.1).

Table 2. The relationship between male problem-solving performance (PSP) and successive life-history traits through reproduction. Separate statistical models are shown for each trait.

Term	Lay date (N = 308)			Clutch size (N = 308)			Nest failure (N = 308)			Number of fledglings (N = 273)			Average fledging mass (g) (N = 273)			Number of recruits (N = 308)		
	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	W	P	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P
Constant				9.008 ± 0.268			-1.781 ± 0.283			7.887 ± 0.259			18.42 ± 0.115			-0.882 ± 0.202		
Lay date	-	-	-	-0.060 ± 0.019	10.47	0.001				-0.105 ± 0.023	20.07	<0.001	-0.033 ± 0.014	5.26	0.026	-0.053 ± 0.020	7.06	0.008
Disparity	-	-	-	-0.065 ± 0.028	5.31	0.022				-0. 114 ± 0.036	10.15	0.002	-0.073 ± 0.022	11.10	0.002			
Habitat quality							-0.061 ± 0.020	9.62	0.002									
Brood size	-	-	-	-	-	-	-0.434 ± 0.112	15.08	<0.001	-	-	-	-	-	-	-	-	-
PSP [a]						[b]	-0.017 ± 0.391	<0.001	0.965									
PSP* habitat quality							-0.091 ± 0.046	3.95	0.047									

[a] Non-solver set to zero, [b] PSP was the last term to be removed from the model: W = 3.30, P = 0.071, estimate ± SE = 0.337 ± 0.186. Models were derived by backward elimination of non-significant terms. Each column represents a separate model. All full models included fixed effects: PSP, age (categorised as either first-year breeder or older), lay date (date first egg was laid), disparity (difference in days between the annual peak in caterpillar abundance and the date when nestlings were 9 days old; see supplementary methodology), habitat quality (oak density within 75m of the nest) and brood size, unless indicated by a dash in the table (see methodology for further variable details). In addition to fixed effects controlled for in the table, all models also contained random terms bird identity and year. Model results from GLMMs (for nest success, binary error structure; number of recruits, Poisson error structure) and LMMs. For each model the interactions between PSP and both disparity and habitat quality (number of oaks within a 75m radius of nest box) were tested. Only interactions with P values < 0.1 are shown.

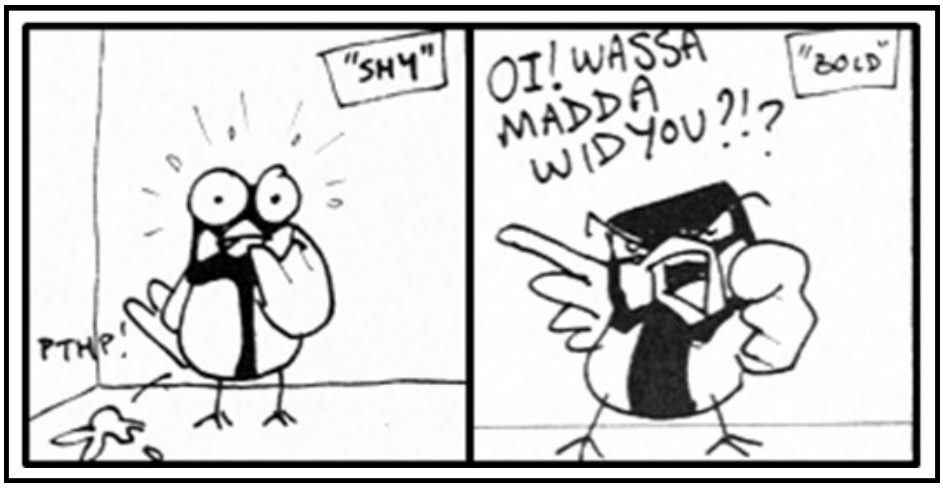
Table 3. Directional selection coefficients for problem-solving performance within years and sexes using two fitness measures, the number of offspring fledged (fecundity) and the number of offspring recruited to the breeding population (recruitment).

		Fecundity, S ± SE		Recruitment, S ± SE	
	N	Female	Male	Female	Male
2007	105	-0.17 ± 0.12	-0.10 ± 0.12	-0.06 ± 0.12	-1.44 ± 0.71*
2008	153	0.04 ± 0.11	-0.09 ± 0.12	-0.21 ± 0.41	0.03 ± 0.44
2009	146	-0.08 ± 0.13	-0.02 ± 0.11	-0.46 ± 0.31	0.02 ± 0.32
2010	142	0.07 ± 0.10	0.03 ± 0.09	0.16 ± 0.36	0.32 ± 0.31

P-values for fecundity were estimated assuming normal error, and for recruitment assuming a Poisson error. All parameters are from models assuming a normal error. * indicates $P < 0.05$.

CHAPTER 6

Examining the link between personality in captivity and risk-responsiveness in the wild



Examining the link between personality in captivity and risk responsiveness in the wild

Ella F. Cole & John L. Quinn

ABSTRACT

The behavioural mechanisms that link personality to fitness variation are poorly understood. One mechanism thought to play a key role is how individuals respond to risk. Relatively reactive and proactive individuals are expected to differ in how they manage the inherent trade-off between productivity and survival, with proactive individuals being more risk-prone and reactive individuals adopting a more cautious, risk-averse strategy. In the great tit (*Parus major*) the reactive-proactive personality axis has been well characterised in captivity and linked to fitness, but few studies have tested whether this axis relates to risk-taking behaviour in the wild. We used a population of wild great tits to test whether 'exploration behaviour', a captive assay of the reactive-proactive personality axis, can predict risk responsiveness in two unrelated contexts during reproduction. We show that female risk-taking behaviour, experimentally measured at the nest during incubation by attaching a novel object to the top of nest boxes, was repeatable over days and correlated positively with exploration behaviour. In contrast, we found little evidence that exploration behaviour predicts whether birds deserted their brood in response to the increased risk experimentally proven to be associated with being trapped and handled by humans at the nest. Our results provide evidence that exploration behaviour represents differences in risk-taking behaviour between individuals in the field, but may have limited power to predict behaviour across multiple wild contexts.

INTRODUCTION

Faced with identical environmental conditions, individuals of the same species often differ in their behaviour. Moreover, this between-individual variation can be consistent over time and across various contexts and situations (Koolhaas et al. 1999; Gosling 2001; Wilson 1998; Sih et al. 2004a). For example, whereas some individuals are aggressive towards both conspecifics and predators, others are consistently more cautious (Huntingford 1976). This behavioural phenomenon - termed personality – challenges the traditional approach taken in optimality modelling that assumes animals show infinite plasticity in their behaviour (Sih et al. 2004b). Much of the initial research on personality has focused on characterising suites of correlated behaviours in captivity, and understanding the proximate mechanisms causing these individual differences (reviewed in Sih et al. 2004b). In recent years greater emphasis has been put on describing links between personality and life history variation in the wild (reviewed in Smith & Blumstein 2008). However the underlying mechanisms that give rise to these links remain very poorly understood.

To date the mechanisms that link fitness to personality have usually been inferred from observational study under captive conditions (e.g. Réale & Festa-Bianchet 2003; Boon et al. 2007). However the validity of this approach is unclear for several reasons. First, captive environments in which individuals are observed are often highly artificial, and therefore unlikely to be representative of the general social and ecological conditions experience by individuals in the wild. Second, individuals may differ in their response to being held in a captive environment,

which could act to mask or accentuate natural variation in behaviour (Herborn et al. 2010). Third, work in captivity and in the wild has demonstrated that the correlations between behaviours can be context dependent (e.g. Dingemanse & de Goede 2004; Van Oers et al. 2005; Bell & Sih 2007; Coleman & Wilson 1998, Appendix B, published as Quinn et al. 2011). These points suggest that in order to understand how selection operates on personality, it is important to assess the ecological validity of captive assays by examining how they relate to behaviour in the wild (Réale et al. 2007).

One of the best-characterised, non-human personality axes is the reactive-proactive continuum in the great tit (reviewed in Groothuis & Carere 2005). Extensive work in captivity has shown that individuals who are relatively fast to explore novel environments (proactive individuals) are less neophobic (Verbeek et al. 1994; Drent et al. 2003; Carere et al. 2005), quicker to resume feeding after being startled (Van Oers et al. 2004a) and quicker to engage in aggressive interactions (Verbeek et al. 1996; Carere et al. 2005) than slow-exploring (reactive) individuals. This personality axis of variation has been linked to fitness in several populations, suggesting considerable functional significance (Dingemanse et al. 2004; Both et al. 2005; Quinn et al. 2009). One mechanism that is thought to play a key role in linking the reactive-proactive axis to fitness is how individuals respond to risk, for example in the context of the trade-off between foraging and predation (Van Oers et al. 2004a; Sih et al. 2004a; Biro & Stamps 2008; Appendix B, published as Quinn et al. 2011) or between current verses future reproductive success (Wolf et al. 2007; Réale et al. 2010). Indeed these

trade-offs are central to several theories developed to explain how personality variation arises (Stamps 2007; Biro & Stamps 2008; Wolf et al. 2007; Réale et al. 2010). These models are increasingly supported by empirical evidence showing that proactive individuals have higher reproductive success than reactive individuals, but reduced survival (reviewed in Biro & Stamps 2008; Smith & Blumstein 2008). However, despite the fact that risk responsiveness is thought to be an important behavioural mechanism driving these effects (Wolf et al. 2007), few studies have related personality in captivity to risk-taking behaviour in ecologically relevant contexts to test this assumption (but see Hollander et al. 2008; Briffa et al. 2008; Herborn et al. 2010, Appendix B, published as Quinn et al. 2011).

It has been hypothesised that hormonal stress responsiveness involving the secretion of glucocorticoids, is itself a consistent trait within individuals with fitness consequences (Cockrem & Silverin 2002; Cockrem et al. 2009; Evans et al. 2006; Bonier et al. 2009), may be a key physiological mechanism underlying personality differences (Koolhaas et al. 1999). However, captive work on a range of taxa provides conflicting evidence for this idea (reviewed in Koolhaas et al. 2010; Coppens et al. 2010). In the great tit, some studies have demonstrated that reactive individuals show a more acute stress response (Carere et al. 2003; Carere & Van Oers 2004), while others have found that more proactive individuals take longer to recover from social stress (Verbeek et al. 1999; Carere et al. 2001), and show a greater physiological and hormonal stress response to handling by humans than reactive individuals (Fucikova et al. 2009; Stöwe et al. 2010). This lack of a clear

relationship between these traits raises questions about the power of the reactive-proactive personality axis to predict how individuals cope with highly stressful situations in the wild.

In this study we use a wild population of great tits to examine whether 'exploration behaviour of a novel environment' (hereafter EB), a captive assay of the reactive-proactive axis, predicts how individuals respond to two different kinds of risk during reproduction: novelty at the nest and trapping by humans. Great tits begin breeding in their first year of life and, in the UK, usually have only one breeding attempt per year (Gosler 1993). Adult great tits are at significant risk of predation by sparrowhawks (*Accipiter nisus*) during offspring provisioning (Perrins 1979). In addition, tit nests in the UK are commonly predated by both great spotted woodpeckers (*Dendrocopos major*) and weasels (*Mustela nivalis*) (McCleery & Perrins 1991), and by a number of other avian and mammalian predators in other parts of the species' range. Weasels not only pose a threat to eggs and nestlings, but also to adults as they can kill parents that defend their nest (Dunn 1977; Perrins 1979). In high risk situations, parents of iteroparous species may reduce investment in, or even abandon their reproductive attempt, favouring personal survival over current reproductive effort (Holt 1994; David & Tait 1980; Harris 1980; Harfenist & Ydenberg 1995). How individuals respond to risk during reproduction is therefore likely to significantly impact on both survival and reproductive success.

Our aims in carrying out this study were two-fold. First, we tested whether female EB predicted risk-taking behaviour at the nest during incubation, experimentally measured by recording the latency to resume normal behaviour after being subjected to a stimulus that is assumed to be perceived as risky (see: Verbeek et al. 1994; Van Oers et al. 2004a; Arnold et al. 2007). Animals often show caution in response to novel objects or environments, which is thought to reflect avoidance of the unknown risks associated with novelty (Richard et al. 2008). Here we measure the response to a novel object associated with the nest. Second, we tested whether a bird's EB could predict how they responded to trapping and handling by humans, an event that is routine in monitored avian populations during reproduction but which is likely to represent an acute risk. Trapping and handling by humans elicits a similar physiological and behavioural stress response in birds as exposure to model predators (Müller et al. 2006; Cockrem 2002; Silverin 1998), and human disturbance is widely considered to be perceived as a risk of predation by nesting birds (Beale & Monaghan 2004; Frid & Dill 2002; Cockrem 2007). Previous work has shown that trapping can cause parents to reduce their parental care or abandon their breeding attempt (Kania 1992; Lendvai & Chastel 2010; Miller et al. 2009). First we demonstrate experimentally that the trapping procedure carried out in our study population does cause individuals to desert their breeding attempt, and then test whether parental EB predicts desertion behaviour.

METHODS

Study population

This work was conducted using a long-term study population of great tits (see Charmantier et al. 2008; McCleery et al. 2004) at Wytham Woods, Oxford, UK (51° 46′ 26.57″ N, 1° 18′ 38.71″ W). Wytham Woods contains 1020 great tit nest boxes distributed over 385 ha of mixed, largely deciduous woodland. Breeding attempts in nest boxes by all individuals are monitored annually by a team of fieldworkers, between April and June (see McCleery et al. 2004 for details). Nest boxes are visited regularly throughout the breeding season to establish the lay date, clutch size, hatch date, and brood size of each breeding attempt. In addition, the parents at each nest are caught and identified when nestlings are approximately 7 days old (see below), and any unringed individuals are fitted with a unique BTO metal leg-ring. All nests are subsequently visited when nestlings are 14 days old to ring and weigh surviving nestlings prior to fledging.

EB assays in captivity

Birds were caught over the course of six winters (between September and March, from 2005 to 2010) using mist nets at temporary feeders erected at sites throughout the wood, under licence from the British Trust for Ornithology (BTO). Any unringed individuals were fitted with a unique BTO metal leg-ring and were aged (first winter, or older) and sexed based on plumage (Svensson 1992). Great tits caught in the 2007-2010 winter, and the 2007-2010 breeding seasons were also fitted with a unique passive integrated transponder (PIT, EM4102 tag, HID Global GmbH, Walluf, Germany) measuring 12.4 mm × 2.1 mm, attached to colour

rings. Birds were then transported to the nearby John Krebs field station for behavioural assay (under a Natural England licence), where they were housed individually in indoor aviaries (see Chapter 2 for further details).

All birds underwent EB assays on the morning after capture, following identical procedure to that used by Quinn et al. (2009). Each individual housing cage was connected to the novel assay room by a sliding trapdoor. At the start of the assay birds could be moved between rooms without handling. The EB assay began when a bird entered the novel room (based on the room design used in Verbeek et al. 1994), where their movements were recorded for 8 min using an event recorder (Psion Workabout, with Observer mobile software, Noldus Information Technology, Wageningen, The Netherlands). Information on the number of hops, the number and duration of flights, and the areas of the room utilised were then entered into a principal components analysis. The square-root of the first component (all major loadings referred to increased activity) was then used to estimate individual effects in a general Linear Model (GLM), controlling for the time in the season and number of observations per bird to produce an EB score for each bird (see Quinn et al. 2009 for further details).

Risk-taking behaviour in the wild

We assayed risk-taking behaviour of females during incubation in the 2009 breeding season (April-June). Individually PIT tagged female great tits that had previously been assayed for EB in captivity were located in their nest boxes using a handheld PIT-tag reader (Francis Scientific Instruments Ltd, Cambridgeshire, UK).

Nest boxes were scanned at night as females invariably roost in their nest boxes during the laying period prior to incubation (Gosler 1993). Risk-taking behaviour was then assayed for 43 individuals, at day 9 or 10 of incubation, by video recording (using a Handycam DCR-SR33E camcorder, Sony, UK) from a distance of 10m the latency to resume incubation after a small black and white flag (148 x 105 mm) had been fixed to the roof of the nest box (Figure 1). After the flag was attached to the box, the female was gently encouraged to leave the nest, by removing the face-plate of the nest box (and if necessary lifting her gently off the nest with one finger). Trials were only run if a female was present at the nest at the start of the assay. The flag was removed after 40 minutes, regardless of whether the female had returned to the nest; birds that did not return within the 40 minutes were scored as 'non-returning' (see statistical methods).

A random subset of individuals (N = 22) was given a repeat trial the following day, to assess repeatability of risk-taking behaviour. The flag used for this repeat trial had a different pattern to the one used the previous day (either spotted or chequered, randomly assigned) to minimise any habituation to the assay. Finally, a separate random sample of females (N = 37) was assigned to a control treatment, where the same assay procedure was followed, but no flag was attached to the nest box. This was done to establish whether latency to return to the nest was related to the novel object, rather than a result of human disturbance alone. These control trials were randomised over time with respect to the experimental trials, to control for variation due to timing of breeding.

EB and response to adult trapping

We aimed to test whether parental EB predicts whether parents desert their brood in response to trapping by humans. A review on the effects of trapping birds at the nest at different reproductive stages found that trapping great tits can result in significant nest desertion (Kania 1992). However, desertion rate reduces the later in the reproductive attempt that birds are caught (Kania 1992), presumably because the value of the brood increases as nestlings get older (Gosler 1993). Here we experimentally tested the assumption that the trapping procedure, carried out in our study population as part of the standard monitoring protocol, is directly responsible for nest desertion. As part of the standard protocol, most breeding adults are caught at the nest when nestlings are 7 days old (median age = 7 days, IQR = 1, N = 3724 breeding attempts 2005-2010) using trap-doors placed inside the nest boxes that are triggered by a bird entering the nest. Birds are then transferred from the nest box into a bird bag, before being processed and then released back at their nest. The processing procedure, which takes approximately 5 minutes, involves taking biometric measurements and collecting a blood sample via brachial venepuncture from all individuals, and ringing and PIT-tagging untagged birds.

We experimentally tested the effect of our specific trapping protocol by comparing the rate of desertion caused by the normal trapping procedure to that caused by not trapping until later in the nestling period. This was done during the 2011 breeding season, by randomly assigning great tit nests to one of two treatments: normal trapping (adults trapped when nestlings were 7 days old) and late trapping

(adults trapped when nestlings were 10 days old). All broods were subsequently visited when 14 days old to determine whether the nest had failed, where failure was defined as there being no live nestlings remaining in the nest. 'Late trapping' nests were also visited when nestlings were 7 days old, so that brood survival between 7 and 14 days old could be compared between treatments (see Figure 2). Once this assumption had been tested, we examined whether an individual's EB could predict whether or not they deserted their nest in response to human trapping.

Statistical analysis

We established whether females took longer to return to the nest in the presence of the novel object than in the control treatment using a Mann-Whitney U test, and tested for habituation to the trial across days using a Wilcoxon matched-pairs test. A spearman's rank correlation was used to assess repeatability of risk-taking behaviour in the wild. We used a proportional hazards survival analysis to test whether latency to return to the nest could be predicted by EB, which accounted for the fact that some individuals did not return within the 40 minute trial (9 out of 43). Lay date and clutch size were also included in this model to control for motivational differences caused by variation in brood value (see below).

A two-sample binomial test was used to establish whether nest failure differed between the normal and the late trapping treatments (comparing the number of failed nests between day 7 and day 14 between treatments). We then used Generalised Linear Mixed Models (GLMM), with binomial errors and a logit link

function, to establish whether nest desertion after adult trapping could be predicted by the EB of either parent. Only nests that were trapped when nestlings were 7 days old or younger were included in the analysis, as it is only trapping at this stage that causes significant desertion (see results). In addition, we only included in our analysis birds that were subsequently trapped again in Wytham, either during the winter or in following breeding seasons, to exclude nests that failed due to adult mortality. We note that this restriction may have resulted in the exclusion of some deserted nests where the parents died shortly after the breeding season.

For 84% of nests in our sample the EB of only one parent was known; therefore separate analyses were run to test the effects of male and female EB. Nevertheless we also ran a model with a much-reduced dataset to test for the interaction between male and female EB. In addition to EB, all models contained the random factors year (2005-2010) and bird ID, and the fixed effects, bird age (juvenile or adult), brood size, lay date, local habitat quality (see below) and whether both members of the pair were caught. Brood size was controlled for as this relates directly to brood value (Williams 1966). Low food availability is likely to increase desertion rate, as adults breeding in these conditions may be unable to collect sufficient food to feed themselves and their young (Einloft-Achenbach & Schmidt 1984; Gosler 1993). To control for this, timing of breeding and local habitat quality were included in models, as both of these factors will influence the amount of food available for provisioning parents and therefore the risk of nestling starvation (Perrins 1979; Gosler 1993). Previous work on our population has shown that the

number of pedunculate oak trees (*Quercus robur*) within a 75m radius of the nest box can be used as a proxy for habitat quality (Wilkin et al. 2007; Wilkin & Sheldon 2009). We calculated these scores using GIS software (MapInfo 10.5), by mapping the locations of all oak trees and nest boxes, and then calculating the number of oak trees within a 75 m buffer around each nest box. Finally, at a small proportion of nests only one adult is ever caught, either because the second parent has deserted or been predated, or because they avoid the nest when trapping is taking place. The number of parents trapped at a nest was therefore controlled for in all analyses because single parents, or parents paired with highly risk averse individuals may themselves be more likely to desert the nest. For the male and female models all terms were retained in the final model. To reduce the likelihood of a Type II error due to small sample size, the model testing for an interaction between female and male EB was simplified via backwards elimination of non-significant variables.

Ethical Note

The captive protocol outlined was subject to review by the Department of Zoology (Oxford) ethical committee. After being held in captivity, all birds were released at the site of capture, where there was a supply of supplemented food to allow birds to feed before dusk. In the wild risk-taking behaviour assays, nine of the 43 females did not return to the nest within the 40 minute trial. However all 43 females resumed incubation after the trials and none of their nests failed before hatching. The ethical issues associated with our trapping procedure only became apparent to us immediately before the 2011 breeding season, and any desertions

caused by trapping in previous field seasons was unintentional. The trapping-induced desertions caused in the 'normal trapping' treatment during 2011 were deemed necessary to establish that nest failure was a direct result of human disturbance.

RESULTS

EB and risk-taking in the wild

Females took significantly longer to return to the nest during the risk treatment than the control treatment (Mann-Whitney U test: U = -1.398, N = 80, P = 0.028, experimental median = 23.77 minutes, IQR = 11.87, control median = 15.07 minutes, IQR = 17.81), confirming that birds were reacting specifically to the novel object. Response to novelty was repeatable within individuals over two days (Spearman's rank correlation: r_s = 0.442, N = 22, P = 0.039), and there was no habituation to the assay across days (Wilcoxon matched-pairs test: W = 84, N = 22, p = 0.924). Relatively fast explorers resumed incubation faster than slow explorers (Proportional hazard survival analysis: X^2 = 5.341, N = 43, P = 0.021, Figure 3). Neither lay date nor clutch size were significant predictors of response to novelty (Proportional hazard survival analysis: X^2 = 0.280, P = 0.591; X^2 = 1.941, P = 0.164, N = 43, respectively).

EB and nest desertion in response to trapping

None of the nests in the late trapping treatment failed (Figure 4) but 12.5% failed during the normal trapping treatment, a difference that was statistically significant (two sampled binomial test: Z = 2.837, p = 0.005, N = 132, Figure 4). As predicted,

this strongly suggests that the trapping procedure caused some individuals to desert their broods.

We examined the general causes of nest failure amongst birds that were known to have survived the breeding season and found that nests where the male was not caught were significantly more likely to fail than those where both parents were trapped (W_1 = 28.97, P < 0.001, N = 200). There were only two cases where the male but not the female was trapped; therefore this factor was not a significant predictor of nest failure amongst males (W_1 < 0.01, P = 0.982, N = 163). Larger broods were far less likely to fail than small broods (W_1 = 10.21, P = 0.001, N = 163; W_1 = 15.13, P < 0.001, N = 200 for the male and female sample respectively, Figure 5). Nests were also more likely to fail if they were in poor quality habitats, estimated by the number of oak trees within a 75m radius of the nest box (W_1 = 4.05, P = 0.044, N = 163; W_1 = 3.41, P = 0.065, N = 200 for the male and female sample respectively). Neither male nor female age predicted nest failure (W_1 = 0.65, P = 0.419, N = 163; W_1 = 0.68, P = 0.408, N = 200, respectively).

There was no relationship between nest failure rate and male EB (W_1 = 0.53, P = 0.468, N = 163), and a non-significant tendency for the nests of relatively fast females to be more likely to fail than those of slow females (W_1 = 2.95, P = 0.086, N = 200). Finally, there was no evidence for an interaction between male and female EB with respect to nest desertion (interaction term: W_1 = 0.10, P = 0.755, N = 63).

DISCUSSION

We examined the ecological validity of personality variation by testing whether EB, a captive assay of the reactive-proactive axis, can predict how individual great tits respond to different types of risk during reproduction. Female risk-taking behaviour in response to novelty at the nest was repeatable across days and correlated positively with EB, demonstrating that personality measures in captivity predict risk responsiveness in the wild. In contrast there was little evidence linking parental EB to desertion behaviour, suggesting the ability of personality measures in captivity to predict general effects in the wild may be limited.

Risk aversion during incubation

The idea that behaviour assayed in captivity reflects behaviour in the wild has received mixed empirical support (Briffa et al. 2008; Dingemanse & de Goede, 2004; Herborn et al., 2010; Hollander et al., 2008; Van Overveld & Matthysen, 2010; Wilson & Mclaughlin, 2007). Here we show that EB measured in captivity predicts female risk-taking behaviour during incubation (both of which are repeatable); with relatively slow explorers taking longer to resume incubation than faster explorers. This supports findings from the only other study to examine the link between personality and risk responsiveness during reproduction, which showed that EB was positively correlated to the rate of alarm calling towards a human intruder at the nest (Hollander et al. 2008). Furthermore, these findings support captive work on other populations suggesting that EB and risk-taking represent a behavioural syndrome in the great tit (Groothuis & Carere 2005)

Incubating great tits normally leave their eggs for time spans of around 10 minutes in order to feed (Gosler 1993). Evidence from several bird species has shown that more attentively incubated clutches hatch sooner, and have a higher hatching success (Perrins 1979; Gorman et al. 2005; Komdeur et al. 2002). In response to risk at the nest most females in our study remained away from the nest longer than 10 minutes, and a number of individuals did not resume incubation until after the novel object had been removed 40 minutes later. Although it is not known how long these birds would have stayed away if the threat had not been removed, great tits have been observed to abandon their breeding attempt in response to novelty at the nest for prolonged periods (E. Cole, pers. obs., A. Hinks pers. comm.). Our findings therefore suggest that when faced with risk, slower females may jeopardise their reproductive attempt, providing support for the theory that reactive individuals prioritise survival over current productivity (i.e. current reproductive effort), whereas more proactive individuals do the opposite (Stamps 2007; Biro & Stamps 2008; Wolf et al. 2007; Réale et al. 2010).

Risk aversion during provisioning

Previous work has shown that, in comparison to other hole-nesting birds, great tits are relatively sensitive to disturbance during reproduction (reviewed in Kania, 1992). Here we demonstrate that trapping adults at the nest when nestlings are one week old can cause a significant level of nest desertion in this species. Whether this represents an adaptive response remains unclear but in general stress responses among breeding animals are thought to cause a reallocation of resources from reproduction to survival (Wingfield & Sapolsky, 2003, Lendvai &

Chastel, 2010; Miller et al. 2009). Evidence that deserters may be individuals that invest more strongly in their own survival comes from work in great tits showing that females that abandon their brood after being trapped are in better nutritional condition than non deserters, independently of brood size (Hõrak et al. 1999). Alternatively, in our experiment trapping may simply have triggered an unusually extreme stress response that has negative effects on behaviour, such as impairing decision making (Lima 1998; Cockrem 2007). Nevertheless, this work provides strong evidence that risk to parents is an important determinant of parental care - a consideration that has received comparatively little attention in studies on breeding birds (see Lima 1998; Lendvai & Chastel 2010).

In contrast to the positive relationship between EB and risk-taking behaviour we observed during incubation, we found little evidence that EB is linked to nest desertion in response to being trapped at the nest. Amongst females there was a non-significant tendency for relatively fast explorers to desert at a higher rate than slower individuals. Recent work on captive bred selection lines found that fast great tits showed a stronger hormonal stress response to handling stress than slow birds (Stöwe et al. 2010). In several bird species, individuals showing high stress reactivity in response to trapping reduce their parental care more than less stress reactive individuals (Lendvai & Chastel 2010; Miller et al. 2009). It is therefore possible that differences in stress reactivity may explain the tendency we observe. However, in a different study fast great tits were demonstrated to show *lower* stress reactivity in response to social defeat than slow birds (Carere et al. 2003),

suggesting the relationship between these traits is not straight forward and could be context dependent.

Correlations between behavioural traits can often be highly dependent on the context in which they are observed (e.g. Dingemanse & de Goede 2004; Van Oers et al. 2005; Bell & Sih 2007; Coleman & Wilson 1998). For example, in captive great tits, the relationship between EB and risk-taking behaviour can be dependent on social context, despite strong phenotypic and genetic correlations between these traits within the same context (Van Oers et al. 2004a; Van Oers et al. 2004b; Van Oers et al. 2005). Although both novelty at the nest during incubation and trapping and handling during nestling rearing are likely to be perceived as increased risk by great tits, the contexts of the risks are considerably different. During nestling provisioning males visit the nest frequently, and therefore the probability of both parents being present near the nest after trapping is likely to be higher than during incubation, when the male visits less often (Perrins 1979; Gosler 1993). The presence of conspecifics can increase risk taking behaviour in slow exploring great tits of both sexes, and decreasing risk-taking behaviour in fast females (Van Oers et al. 2005). This could explain why we find little evidence for a relationship between EB and risk responsiveness during trapping, where a conspecific is more likely to be present. We note that we were unable to control for the presence of the mate, nor mate behaviour immediately after trapping, both of which are likely to influence the risk-taking behaviour of the focal individual (Van Oers et al. 2005).

In addition to sociality, other contextual differences between our two risk treatments could influence the relationship between EB and risk responsiveness. While novel objects have been shown to elicit a hormonal stress response in captive Japanese quail, (*Coturnix japonica*) (Richard et al. 2008), trapping and physically restraining wild animals is likely to trigger a much more acute response (Silverin 1998). The severity of the two stressors we used in this study are therefore likely to differ considerably. Although it has been proposed that hormonal stress reactivity represents a key proximate mechamism causing personality differences (Koolhaas et al. 1999; Carere et al. 2003), recent findings have challenged this view by showing that this relationship is not as clear as previously presumed (Martins et al. 2007; Koolhaas et al. 2010; Coppens et al. 2010; Lendvai et al. 2011). Indeed, it has been suggested that hormonal stress reactivity and the reactive-proactive behavioural axis should be viewed as two distinct axes of individual variation, both of which may influence behaviour in a given context (Koolhaas et al. 2010; Coppens et al. 2010, see Figure 6).

Despite a number of studies examining the link between the reactive-proactive axis (or boldness) and hormonal and physiological stress reactivity in the great tit, the relationship between these traits remains unclear (see: Carere et al. 2003; Carere & Van Oers 2004; Fucikova et al. 2009; Stöwe et al. 2010). If stress reactivity and the reactive-proactive axis are not closely linked, it can be predicted that in relatively high stress situations (such as being trapped and handled) behaviour will be largely dictated by an individual's stress reactivity rather than their boldness (see Figure 6). This may explain why we find only weak evidence for

a link between EB and nest desertion. As many behaviours are likely to be influenced by both boldness and stress reactivity, it may therefore be the *interaction* between these two axes that predicts a behavioural response in a given context. Evidence for this idea comes from work on the greylag goose (*Anser anser*), showing that innovative foragers can be characterised by being both bold explorers and highly reactive to environmental stressors (Pfeffer et al. 2002). Further work, comparing risk responsiveness and stress reactivity towards different stressors in the same individuals, is clearly needed to establish the relative importance of these traits for predicting how individuals respond to challenging situations.

In conclusion, the results from this study suggest that correlations between behavioural traits in captivity and the wild are likely to be largely dependent on the context in which they are measured. While our findings provide evidence that EB, measured in captivity, is related to risk-taking behaviour in the wild, they also suggest that EB has limited power to predict risk responsiveness across multiple wild contexts. We suggest that knowledge of other sources of consistent individual variation, such as stress reactivity, may be important in order to understand how individuals respond to challenging situations in nature.

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FIGURES AND TABLES



Figure 1. Photograph of a nest box during the risk-taking trial during incubation, showing the novel flag attached to the roof of the nest box.

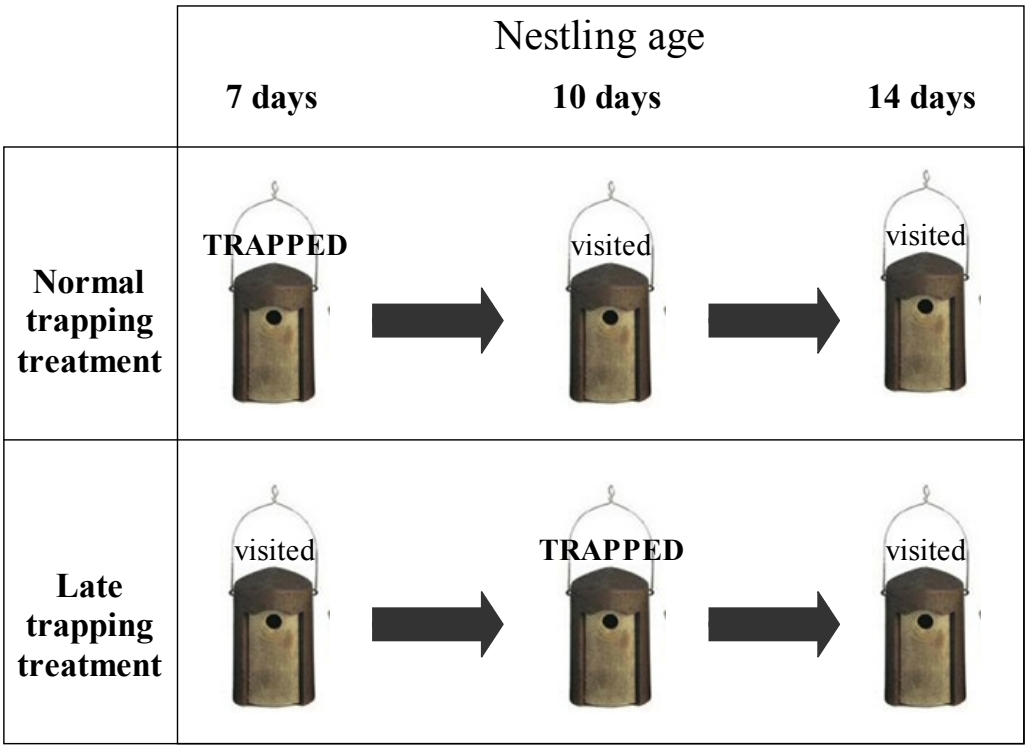


Figure 2. Experimental design for the trapping experiment. All nest boxes were visited repeatedly, first when broods were 7 days old, then subsequently at 10 and 14 days old (N = 72 and 60 nests for normal and late trapping respectively).

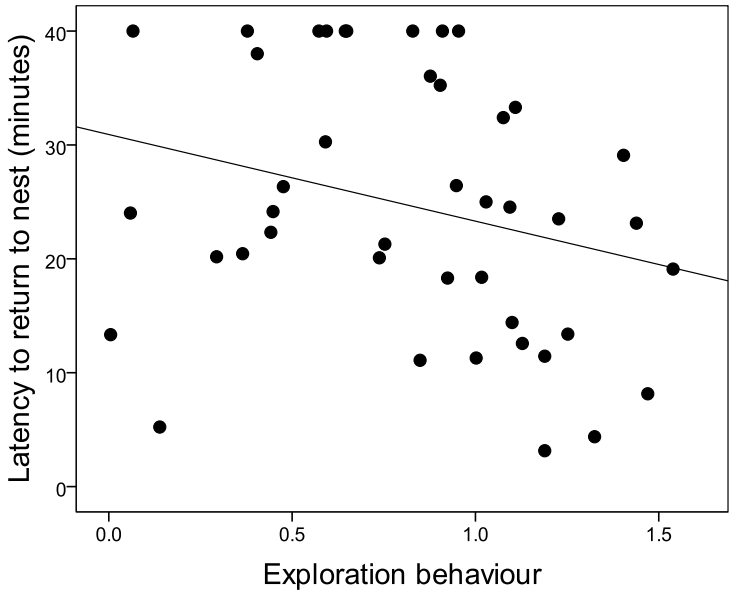


Figure 3. Relationship between response to novelty (latency to return to the nest) and exploration behaviour (N = 43).

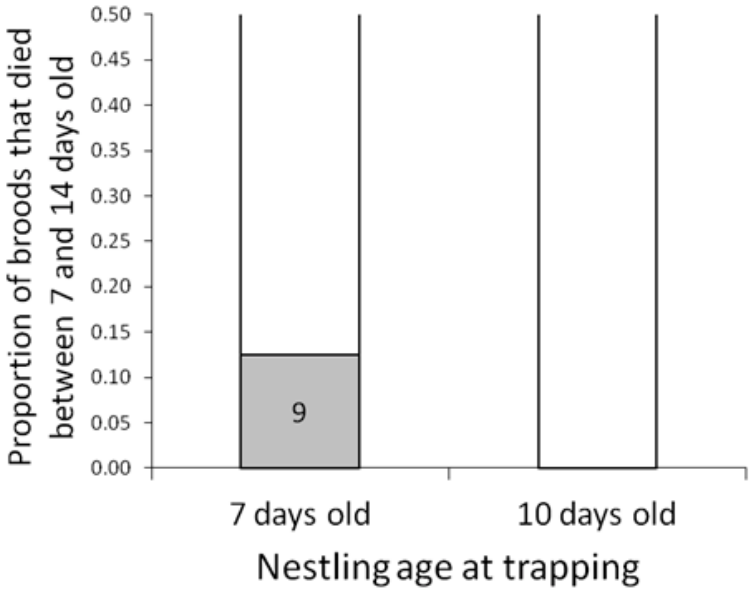


Figure 4. The difference in nest desertion rate between nests where parents were caught when broods were 7 and 10 days old respectively. The grey bars represent dead broods and white bars live broods (N = 72 and 60 nests for normal and late trapping respectively).

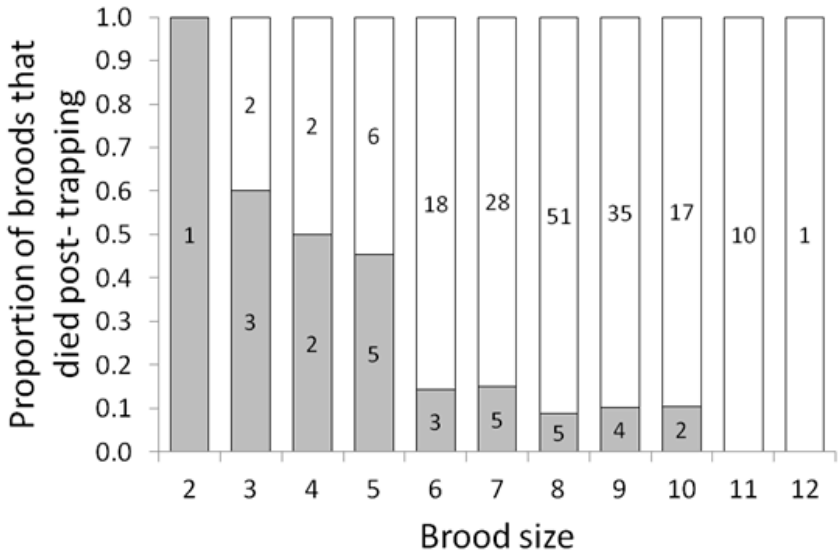


Figure 5. Relationship between nest failure rate and brood size. Where individual females bred in successive years, only their first breeding attempt was included (N = 200).

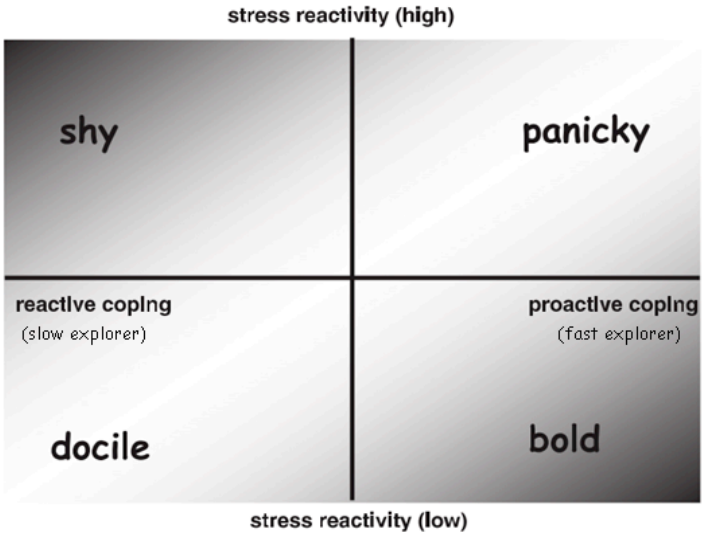


Figure 6. Diagram depicting the reactive-proactive (slow-fast) personality continuum and stress responsiveness as orthogonal axes of variation (adapted from Koolhaas et al. 2010). Under this assumption, in high stress situations both relatively fast and slow explorers that are also highly responsive to stress may act in a similar way to each another (represented in by the "shy" and "panicky" behavioural types). In contrast, in situations that are less stressful, the reactive-proactive axis (slow-fast) may be a better predictor of behavioural response than the stress reactivity axis.

Table 1. Full model results from GLMMs analysing the associations between nest failure (between adult trapping and when brood is 14 days old) and parental EB.

	Females (N = 200)			**Males (N = 163)**		
Term	Estimate ± SE	W	P	Estimate ± SE	W	P
Constant	-2.075 ± 0.358			-2.227 ± 0.578		
Lay date	0.060 ± 0.043	2.05	0.152	0.031 ± 0.046	0.46	0.499
Brood size	-0.519 ± 0.133	15.13	<0.001	-0.474 ± 0.148	10.21	0.001
Habitat quality	-0.037 ± 0.020	3.41	0.065	-0.053 ± 0.026	4.05	0.044
Partner caught [a]	-2.990 ± 0.555	28.97	<0.001	13.70 ± 593	0.00	0.982
Age [b]	-0.398 ± 0.482	0.68	0.408	0.437 ± 0.540	0.65	0.419
EB	1.050 ± 0.611	2.95	0.086	-0.392 ± 0.540	0.53	0.468

[a] Parameter for 'partner not caught' set to zero; [b] juvenile set to zero. All non-significant terms were retained. All models also contained random terms bird ID and year.

CHAPTER 7

General discussion



Early sailors knew their maps were not perfect, but imperfect maps were better than no map at all

- *Samuel Gosling & Oliver John*

General Discussion

Aims and motivation

The primary aim of this thesis was to investigate the ecological significance and fitness consequences of between-individual variation in cognitive performance. This work was motivated by a fundamental knowledge gap regarding how cognitive traits are adapted to the environment (Raine & Chittka 2008). While the proximate causes of individual variation in cognitive traits have been studied for many decades, the evolutionary and ecological processes that shape such variation within populations remain elusive. Comparative studies have provided limited, indirect evidence for the intuitive expectation that increased cognitive capabilities can increase survival (e.g. Sol et al. 2005; Sol et al. 2007). Furthermore, interspecific comparisons have suggested that costs associated with cognition also play an important role in shaping variation (e.g. Safi et al. 2005), an issue that has been largely ignored in evolutionary studies of cognition (Dukas 2004). One reason for the general lack of empirical studies on the evolutionary ecology of cognitive traits is that obtaining the large sample sizes required to study these questions effectively is a major challenge in the traditional cognition paradigm. In this thesis I therefore used an approach from the emerging field in behavioural ecology of animal personalities, and carried out rapid assays on large numbers of wild-caught individuals taken into captivity. Whereas personality studies assay temperament traits such as 'exploration behaviour' and 'startle response', I conducted simple

tests of problem-solving propensity. I then monitored the behaviour and reproductive success of these same individuals when released back into the wild.

The second key aim of this thesis was to examine the ecological validity of personality variation, an area that is often neglected in studies of personality. Researchers studying personality are faced with an inherent trade-off between how easily traits can be measured under standardised conditions, and their apparent functional significance. Exploring the adaptive significance of variation requires large sample sizes (Dingemanse & Réale 2005), which has often resulted in quick and simple assays being favoured. This approach therefore commonly leads to situations where personality variation is linked to fitness, but the behavioural mechanisms causing these patterns are unknown and must be predicted from behaviour observed during standardised assays (e.g. Réale & Festa-Bianchet 2003; Boon et al. 2007). However, behaviour in these assays can be highly situation specific (e.g. Van Oers et al. 2005), and does not always relate to behaviour in the wild in the manner expected (e.g. Dingemanse & de Goede 2004; Van Overveld & Matthysen 2010; Hollander et al. 2008). A greater knowledge of the ecological relevance of personality assays would therefore improve our ability to understand the adaptive significance of personality variation. In this thesis I explored how a captive assay of personality related to foraging and risk-taking behaviour in the wild – traits that are proposed to be key behavioural mechanisms driving relationships between personality and fitness (Stamps 2007; Wolf et al. 2007). The rationale for studying personality and cognitive traits in parallel was initially to understand if personality influenced problem-solving performance but

when this was shown not to be the case, to establish whether these traits simultaneously influence functionally significant behaviours.

Individual variation in problem-solving performance

Investigating the functional significance of consistent individual differences involves a number of key steps (see Table 1). The first is to establish methodology for reliably quantifying consistent variation between individuals. In **Chapter 2** a captive assay of problem-solving performance (PSP) was developed that captured significant variation within our population. We found that this variation was relatively consistent over time and between two different tasks, supporting work in other species that individuals differ consistently from one another in their ability to solve cognitive problems (e.g. Banerjee et al. 2009; Overington et al. 2011; Vonk & Povinelli 2011). Furthermore we demonstrated that performance was unrelated to latency to approach the empty task, latency to feed after human disturbance, and exploration behaviour, suggesting that variation in PSP represents inherent individual differences in the propensity to solve innovative-foraging problems. A further study showed that, when presented with a similar problem-solving task in the wild, individuals that were successful in captivity solved three times faster than those that were unsuccessful in captivity (Appendix C, publsihed as Morand-Ferron et al. 2011). However, success in captivity did not predict success in the wild, suggesting that solving performance is, to some degree, dependent on context.

Goals	Components	
(1) Develop experimental tests to measure trait	• Variation between individuals • Repeatability • heritability	✓ ✓
(2) Validate test	• Ecological validity • Physiological validity	✓
(3) Link trait variation to fitness	• Correlation with fitness indices • Measuring selection	✓ ✓
(4) Determine broad-scale patterns of variation	• Intraspecific population comparisons • Interspecific comparative studies	

Table 1. Four-step framework outlining how to study the evolutionary ecology of consistent behavioural variation (adapted from Réale et al. 2007). Areas of investigation covered by this thesis are indicated by a tick.

Once the methodology for capturing variation has been established, the functional significance of these individual differences can then assessed by linking the assayed trait to ecologically important traits and fitness components (see Table 1). A key prediction that I tested is that innovative problem solving allows individuals to better exploit their environment (Lee 1991; Reader & Laland 2003). In **Chapter 5** we demonstrated that birds that problem solved in captivity produced larger clutches than non-solvers. Providing their nests did not fail, female solvers also fledged more young. This represents amongst the first evidence from a natural population that individual cognitive ability is related to fitness (but see Keagy et al. 2009). While these findings could suggest that solver females are better at obtaining the resources they require to raise a large brood, they could feasibly be the result of solvers being able to produce larger clutches in ways that are not directly related to any cognitive process. One way to distinguish between these hypotheses would be to experimentally increase the clutch size of non-solvers, to establish whether they are equally capable of raising large broods as solvers. Further evidence that solvers may be more efficient foragers comes from work

presented in **Chapter 4**, where we showed that solvers work shorter days during the early nestling phase than non-solvers, and forage over much smaller ranges without compromising either the quantity or quality of provisioning. Notably however, we found little evidence that the types of prey collected differed between solvers and non-solvers. Furthermore we find no evidence to suggest that differences in foraging efficiency or reproductive success between solvers and non-solvers are more pronounced when food availability is particularly low, as might be expected if solvers were inherently better at locating food. Captive work, comparing how solvers and non-solvers differ in their efficiency in finding food in complex environments, may help to elucidate the mechanisms causing the differences we observe in the wild.

Evolutionary studies on cognition have often focused on benefits while ignoring costs (discussed in Dukas 2004). I demonstrated that PSP is associated with substantial costs related to low realised competitive ability amongst males (**Chapter 3**) and high rates of nest desertion after being trapped at the nest amongst females (**Chapter 5**). Innovative foraging can be viewed as an alternative foraging strategy that helps some individuals avoid costs associated with intense competition (Reader & Laland 2003; Bolnick et al. 2003). Solvers may therefore have lower realised competitive ability because they are able to utilise alternative food sources. Although I did not test this directly by observing behaviour away from the feeders, evidence from **Chapter 4** suggests that solvers and non-solvers differ in their foraging behaviour. To explore the idea that "good competitors" and "good problem solvers" may represent alternative foraging strategies, we plan to

replicate the methodology used in **Chapter 3** in captivity but provide alternative, less obvious food sources. Under the alternative strategy hypothesis it might be expected that solvers should more readily explore these alternative feeding options.

One potential theory to explain the negative relationships between PSP and both competitive ability and nest desertion is that PSP may be linked to stress reactivity - a relationship that has previously been demonstrated in another bird species (Pfeffer et al. 2002). Both social defeat, and trapping or handling by humans, are known to represent severe stressors to wild birds (Cockrem 2007; Koolhaas et al. 2010). In **Chapter 6** we provide some support for this, showing that a large proportion of nest failure after adult trapping in our population can be attributed to the trapping procedure. Further evidence that stress-reactivity and cognitive performance may be linked comes from work showing that the magnitude of an individual's hormonal stress response can influence their cognitive performance, with individuals experiencing an intermediary state of stress having the highest performance (reviewed in Mendl 1999). Stress reactivity could therefore represent an important proximate mechanism contributing to individual differences in cognitive performance (Pfeffer et al. 2002). One avenue for further research would be to explore the underlying hormonal and neuro-endocrine correlates of PSP (i.e. the 'physiological validity' of variation, see Table 1). Our findings indicate that further investigation of the link between problem-solving performance and stress reactivity may help shed light on the potential costs of cognitive traits.

Perhaps due to the contrasting relationships between PSP and clutch size, and PSP and nest failure, in **Chapter 5** we find that there is little or no directional fecundity or recruitment selection acting on PSP in our population. It may be the case that antagonistic patterns of selection are acting on this trait at different life-history stages (or situations), leading to variation in PSP within our population. These processes may therefore be comparable to those that maintain variation in morphological traits such as the example of tarsus length in female song sparrows discussed in **Chapter 1** (Schluter & Smith 1986). Due to the findings from **Chapter 6** regarding the detrimental effects of trapping on adult great tits, from 2012 birds in the Wytham population will not be trapped until later in the nestling period. If high nest failure amongst solvers is a result of response to trapping, we may expect positive directional selection on PSP once the trapping protocol changes. However, high stress at other life-history stages, such as competition for limited resources in the winter, may also negatively impact on the fitness of problem solvers.

A further step that can be taken to investigate the adaptive significance of behavioural variation is to examine the broad-scale patterns of these differences, through use of interpopulation and interspecific comparative studies (see Table 1). In contrast to studies on personality traits, the vast majority of evolutionary ecological studies of cognition have involved comparing traits between species or populations (reviewed in Reader & Laland 2003; Shettleworth 2010). Indeed this was the main reason for the *within* population focus in this thesis. As the first study of its kind, it remains to be seen whether patterns observed in our population will also be found elsewhere. Personality research on great tits has demonstrated that

very different patterns of selection can be observed to act on the same trait in different populations (Dingemanse et al. 2004; Quinn et al. 2009). Our work could therefore be extended, not only by replicating this study on different populations which may be subject to different selection regimes, but also by using a common garden approach to compare the PSP of great tits amongst populations that vary along an environmental gradient. For example, birds from deciduous woodlands could be compared to individuals from evergreen woodlands where PSP may be particularly beneficial due to the relatively low food availability in these habitats (Perrins 1979). One area where interspecific comparisons could prove useful is in assessing the generality of trade-offs between cognitive and other fitness-related traits. For example, a similar trade-off to the one demonstrated in **Chapter 3** between competitive ability and cognitive performance has also been found in *Drosophila melanogaster* (Mery & Kawecki 2003). Identifying common trade-offs across populations and species is likely to prove useful in understanding how selection acts on individual differences in cognitive performance.

Although we do not measure the heritable component of PSP in this thesis, this trait is relatively consistent over time and between tasks and is therefore likely to exhibit non-zero heritability (Lynch & Walsh 1998). One avenue for future research would be to explore the genetic basis of this trait by the use of evolutionary genomics. Van Oers & Mueller (2010) recently reviewed the use of genomics in the study of animal personality, and suggested that identifying links between genetic polymorphisms and behavioural traits will prove a useful tool in understanding the adaptive significance of behaviour (Van Oers & Mueller 2010).

Currently a project is underway to sequence the great tit genome, generating a dataset of approximately 9 million SNP genotypes for 10,000 different SNPs. As we collected DNA (blood) samples from the vast majority of our assayed birds, this raises the exciting possibility of being able to explore links between PSP and genes or genome regions. In addition to additive genetic effects, differences in state (e.g. Laland & Reader 1999; Appendix D, published as Dunn et al. 2011) and permanent environmental effects (e.g. Girvan & Braithwaite 1998; Arnold et al. 2007) are also likely to play a key role in shaping cognitive abilities. Large-scale analyses on the Wytham great tit population have found that natal environmental effects can have a wide-reaching influence on life-history variation (Wilkin & Sheldon 2009). We have extensive information about natal conditions for approximately half of the individuals we assayed (i.e. those born in Wytham) and therefore hope to use this dataset to explore the influence of natal environmental effects on PSP. This work would represent the first large-scale investigation of the proximate causes of variation in a cognitive trait in a wild population.

Exploring the functional significance of exploration behaviour

The great tit has now been the subject of a large body of personality research; in no other species is so much known about the proximate causes, ecological significance and fitness consequences of consistent behavioural variation (reviewed in Groothuis & Carere 2005; Dingemanse & Réale 2005, also see **Chapter 1**). Only by carrying out these extensive studies to assemble a comprehensive picture of how personality influences behaviour across multiple ecological situations can we fully understand the adaptive significance of this biological phenomenon. In this thesis I

build on existing work in the great tit by testing links between exploration behaviour (EB), a commonly used captive measure of the reactive-proactive personality axis, and foraging and risk-taking behaviour in the wild - two potential behavioural mechanisms that are likely to cause fitness differences between personality types.

In our population EB has previously been shown to be influenced by both additive genetic and environmental sources of variation (Quinn et al. 2009), and predicts dispersal, promiscuity and reproductive success (Quinn et al. 2009; Appendix A, published as Quinn et al. 2011a; Patrick et al. 2011, see Figure 1). In **Chapter 3** we showed additionally that EB is related to competitive ability for limited food resources, a trait that was itself found to be repeatable across days. Although measures of proactivity have been linked to dominance or food intake in a range of taxa under captive conditions (reviewed in Biro & Stamps 2008, also see Chapter 3), our findings represent the first demonstration of a positive relationship between a measure of the reactive-proactive axis and both competitive ability and food intake in the wild. This suggests that different personality types may vary in their ability to secure limited food resources during the winter.

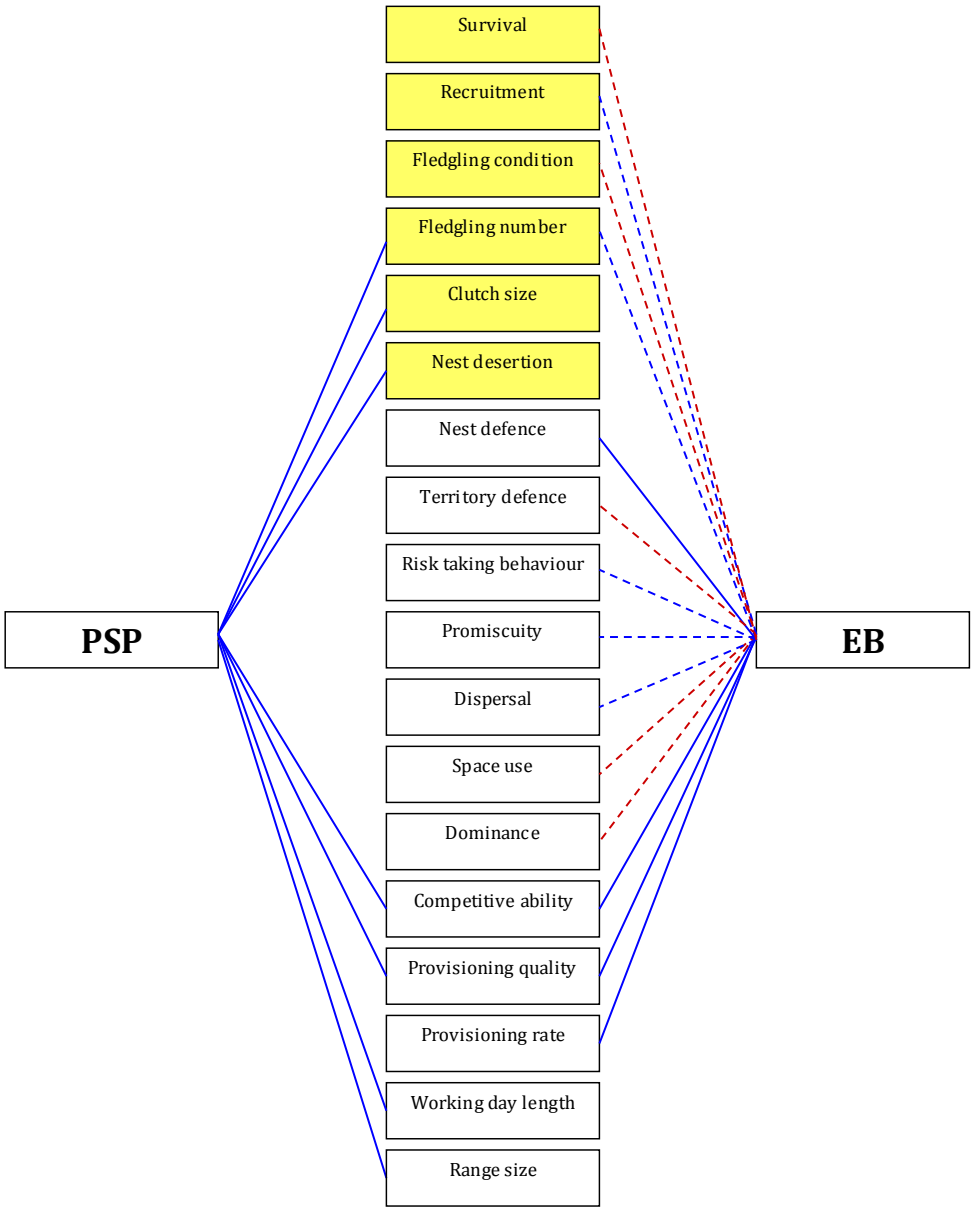


Figure 1. Demonstrated links between EB and PSP assayed in captivity, and behavioural (white) and life-history/fitness components (yellow), measured in the wild. Blue lines represent relationships shown in the Wytham great tit population (solid lines refers to those shown in this thesis), and red lines show relationships demonstrated in other populations. Studies included in the diagram (with relationships demonstrated shown in brackets): Dingemanse et al. 2004 (EB and both survival and recruitment), Both et al. 2005 (EB and fledgling condition), Quinn et al. 2009 (EB and both fledging number and recruitment), Chapter 5 (PSP and nest desertion, clutch size and fledgling number), Hollander et al. 2008 (EB and nest defence), Amy et al. 2010 (EB and territory defence), Appendix B, published as Quinn et al. 2011b (EB and risk-taking behaviour), Chapter 6 (EB and risk-taking behaviour), Van Oers et al. 2008 (EB and promiscuity), Patrick et al. 2011 (EB and promiscuity), Dingemanse et al. 2003 (EB and dispersal), Appendix A, published as Quinn et al. 2011a (EB and dispersal), Van Overveld & Matthysen 2010 (EB and space use), Van Overveld et al. 2011 (EB and space use), Dingemanse & de Goede 2004 (EB and dominance), Chapter 3, published as Cole & Quinn 2012 (PSP, EB and competitive ability), Chapter 4 (PSP, EB and range size, working day length, provisioning rate and prey quality).

Additionally, in **Chapter 4** we demonstrated that EB was related to several aspects of foraging behaviour during offspring provisioning. While personality types did not differ in the size of their foraging ranges, supporting previous work in another population (Van Overveld & Matthysen 2010), fast explorers were found to provision a higher proportion of good quality prey items to their young than slow explorers, during the early nestling phase. In addition, during the late nestling phase relatively slow explorers provisioned at a higher rate than fast explorers when food availability was particularly low. This latter finding provides tentative support for work in captivity which suggests that slow explorers may cope better in unpredictable environments (Marchetti & Drent 2000). We found no effects that spanned both the early and late nestling phase. Assuming general effects are not simply masked by confounding factors that we did not consider, this finding is puzzling because general differences in foraging performance have been proposed as an important mechanism influencing relationships between EB and fitness in great tits (see Both et al. 2005; Quinn et al. 2009). The work presented in this thesis, suggests that captive assays of EB have specific but not general power to predict foraging behaviour during offspring provisioning. To date only a small number of studies have explored the link between EB and foraging either in captivity or the wild (Verbeek et al. 1994; Drent & Marchetti 1999; Marchetti & Drent 2000; Patrick & Browning 2011). This topic would benefit from further work exploring both the nature and generality of relationships between personality and foraging, for example at other times of the year, in other populations and in other species.

Several theories proposed to explain how personality variation arises and is maintained in populations suggest that the reactive-proactive axis is inherently linked to life-history variation, with proactive individuals tending to sustain high productivity but at a potential cost to survival, while reactives do the opposite (Wolf et al. 2007; Biro & Stamps 2008; Réale et al. 2010). The work in this thesis provides support for this theory from three separate contexts: in comparison to relatively slow individuals (i) fast males had higher competitive ability, (ii) in some situations fast birds provided their offspring with better quality food and (iii) fast females were more risk-prone in response to the presence of a novel object at the nest (**Chapter 6**). These three lines of evidence all suggest that relatively fast individuals may prioritise current productivity (either in terms of food intake during the winter, or current reproductive effort during the breeding season) over self-maintenance or long term survival. Further support for this theory comes from an additional study on our population showing that EB predicts how individuals managed the key trade-off between foraging and antipredation behaviour (Appendix B, published as Quinn et al. 2011b). However, it must be noted that if EB was closely linked to this life-history trade-off between current verses future productivity, slow individuals might be expected to have higher survival, which does not appear to be the case in the Wytham study population (Quinn et al. 2009), though such effects may be masked by other ecological factors.

Despite demonstrating a positive relationship between EB and risk-taking behaviour in response to novelty, in **Chapter 6** we find little evidence that EB predicted parental nest desertion after being trapped at the nest. This is perhaps

surprising given that trapping and handling by humans is likely to be perceived as an increased risk to personal survival (Silverin 1998; Cockrem 2007). One possible explanation for these findings is that desertion behaviour is determined by stress responsiveness rather than by the reactive-proactive axis. Although stress responsiveness (as measured by the hypothalamic–pituitary–adrenal axis) has been suggested as one of the main proximate, physiological mechanism causing differences in proactivity (Koolhaas et al. 1999), more recent studies have challenged this view (reviewed in Koolhaas et al. 2010; Coppens et al. 2010). Indeed, it has been proposed that stress reactivity may represent an independent axis of consistent individual variation (Koolhaas et al. 2010). This raises the possibility that the reactive-proactive behavioural axis may have restricted utility in predicting how individuals respond to stressful situations in nature.

Perspectives on studying the adaptive significance of personality

In the great tit, EB has now been linked to a diverse range of ecologically relevant traits and fitness components (see Figure 1). It is quite remarkable that such a simple (and seemingly arbitrary) trait can predict so many different behaviours, each of which is likely to have consequences for fitness. Studying personality by assaying easily-quantifiable behaviours in captivity, such as EB, is a useful approach to take for several reasons. First, this methodology allows for easy interpopulation comparisons that can provide insight into the generality of proximate mechanisms underlying personality and the conditions under which suites of correlated behaviours arise (e.g. Dingemanse et al. 2007; Korsten et al. 2010; Dingemanse 2011). An overarching aim of personality research is to

determine under what sets of ecological conditions different personality types may be favoured. A second advantage to the captive assay approach is that these simple measures can potentially be used as proxies for wild behaviours, thus allowing researchers to use long-term datasets to map how the behavioural profile of a population changes with varying social and non-social environmental factors, without the need to measure multiple, complex behavioural traits in the wild. A key requirement of this approach is that the captive behaviour being assayed should reliably predict important fitness-related behaviours in the wild. EB is likely to influence fitness simultaneously via links with many different traits (see Figure 1). However the sheer number and complexity of these relationships, many of which are context-, state- or sex-specific, makes it challenging to predict how selection is likely to act on this trait. Consequently, it remains uncertain how feasible it will be to fully understand the adaptive significance of EB in the great tit. Perhaps it is most likely to prove useful when dramatic and discrete changes in the ecological conditions occur leading to strong potential for selection. This might include prolonged severe weather, a rapid increase in predator number or sudden change in woodland quality due to habitat management.

In contrast to quantifying personality variation under captive conditions using a top-down approach, an alternative bottom-up approach is to identify key behavioural correlations in nature, involving traits that have clear links to fitness. In the western bluebirds (*Sialia mexicana*), a species that is currently undergoing range expansion, consistency in aggressiveness across different contexts has been shown to lead to a counterintuitive negative relationship between male nest

defence and reproductive success, caused by aggressive males investing little in parental care (Duckworth 2006). However, aggression in this species is also genetically correlated to dispersal behaviour (Duckworth & Kruuk 2009), with aggressive males being better at colonising new habitats, and having higher reproductive success in these populations than less aggressive males (Duckworth 2008). Consequently, in this species there is evidence to suggest that contrasting patterns of selection are acting on the aggression-dispersal axis, which are dependent on population age (Duckworth 2008). Such clear-cut examples of behavioural trade-offs in nature may be rare and are probably difficult to find; therefore both this bottom-up approach and the captive-assay approach are likely to play an important role in revealing the adaptive significance of personality variation.

Concluding remarks

An important facet of evolution is that natural selection is rarely likely to act on a single trait in isolation owing to correlations between traits (Roff 1997; Price & Langen 1992). In this thesis I show how problem-solving performance and exploration behaviour, two independent sources of consistent behavioural variation, simultaneously affect several traits that are likely to have consequences for fitness (see Figure 1). This adds support to what is a growing realisation amongst behavioural ecologists that traits do not evolve independently, and therefore understanding how individuals behave in any given situation requires knowledge of correlated behaviours in other contexts. In this thesis I show that exploration behaviour, a captive assay of the reactive-proactive behavioural axis

relates to behaviour in several different ecologically relevant contexts, shedding light on possible mechanisms that may act to maintain variation in personality in the great tit. This work also highlights the need for caution when generalising behavioural differences observed in captivity to a wild context.

The main body of my thesis applied an empirical framework used in animal personality research to explore the functional significance of cognitive variation, a topic that is rarely studied at the scale of the individual. I demonstrate that a simple standardised test can be used to capture meaningful individual variation in cognitive performance, allowing for large numbers of individuals to be assayed. By following these individuals in the wild I show that problem-solving performance predicts a number of ecologically relevant behaviours and has significant reproductive benefits (see Figure 1). These findings largely support predictions that innovative problem solving may allow individuals to better exploit their environment. Problem-solving performance was also found to be associated with costs that may arise through correlations with other traits. That there were both benefits and costs to being a good problem solver, suggests that contrasting patterns of selection acting at different life-history stages may lead to variation in performance amongst individuals. The precise nature of the fitness costs of higher cognitive performance, and the situations or environments in which they arise is a topic that warrants further investigation. My thesis has demonstrated the feasibility of examining the ecological significance and fitness consequences of cognitive traits, and will therefore hopefully encourage similar studies. Ultimately, in order to understand the fitness consequences of individual variation in cognitive

ability in nature, the costs and benefits of higher cognitive performance must be examined across a range of environments and ecological contexts.

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Appendix A

Scale and state-dependence of the relationship between personality and dispersal in a great tit population

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Scale and state dependence of the relationship between personality and dispersal in a great tit population

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Summary

1. Dispersal is a key process in population biology and ecology. Although the general ecological conditions that lead to dispersal have been well studied, the causes of individual variation in dispersal are less well understood. A number of recent studies suggest that heritable temperament – or personality – traits are correlated with dispersal in the wild but the extent to which these 'personality-dispersal syndromes' are general, how they depend on an individual's state and on spatial scale and whether they are temporally stable, both within and across individuals, remains unclear.

2. Here, we examine the relationship between exploration behaviour – an axis of personality that appears to be important in animals generally – and a variety of dispersal processes over 6 years in a population of the great tit *Parus major*.

3. Exploration behaviour was higher in immigrant than in locally born juveniles, but the difference was much larger for individuals with a small body mass, though independent of sex, representing one of the first examples of a state-dependent effect in a personality-dispersal syndrome.

4. Despite a temporal trend in exploration behaviour at the population level, the difference between immigrants and locally born birds remained stable over time, both across and within individuals. This suggests that the personality difference between immigrants and locally born birds is established early in development, but that the process of immigration interacts with both personality and state.

5. We found that the number of immigrant parents a locally born bird had did not influence exploration behaviour, suggesting either the difference between immigrants and residents was environmental or that the effect is overridden by local environmental sources of variation.

6. In contrast to previous work, we found no evidence for links between personality and natal dispersal distance within the population, either in terms of an individual's own exploration behaviour or that of its parents.

7. Our results suggest that there are links between individual differences in personality and dispersal, but that these can be dependent on differences in state among individuals and on the scale over which dispersal is measured. Future work should aim to understand the differences between dispersal within and between populations and the ways in which personality and state interact to determine the outcome of these processes.

Key-words: behavioural syndrome, dispersal, emigration, great tit, immigration, personality, state

Introduction

Dispersal has a key influence on a wide range of processes in natural populations (Hamilton & May 1977; Comins, Hamilton & May 1980; Greenwood 1980; Greenwood & Harvey 1982; Rannala & Mountain 1997; Clobert *et al*. 2001; Sakai *et al*. 2001). Understanding the factors that influence dispersal decisions by individuals, and the spatial scale over which they occur, therefore remain important objectives in ecology and evolution. Individual variation in dispersal has been linked to a variety of factors, including natal conditions caused by parental life-history decisions (Pärt 1990; Verhulst, Perrins & Riddington 1997; van der Jeugd 2001), individual physiological profiles and body condition (reviewed in Dufty & Belthoff 2001). Morphological variation has long been

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known to influence dispersal tendency (reviewed in Ims & Hjermann 2001), sometimes leading to integrated suites of traits underlying different dispersal strategies (Zera & Denno 1997; Roff 2001). Phenotypic correlations between dispersal and other behavioural traits have also been shown to drive variation in the propensity to disperse (Cote *et al*. 2010a). In particular, correlations with temperament traits are receiving much attention because they often capture variation in many different behavioural traits simultaneously. These correlations are said to reflect 'personalities' at the individual level, behavioural syndromes at the population level (Wilson *et al*. 1994; Wilson 1998; Sih *et al*. 2004; Bell 2007; Reale *et al*. 2007) and dispersal syndromes in the specific instance of behavioural traits being correlated to dispersal. As these temperament traits are limited in plasticity, and have often been shown to be heritable, their linkage with dispersal is potentially of importance, because it suggests that dispersal involves the simultaneous flow of suites of behavioural traits and that any selection on dispersal behaviour will have multiple correlated effects.

Three main types of consistent behavioural trait are known to be involved in dispersal syndromes (Cote *et al*. 2010a): aggression, sociality and exploration behaviour, the latter term here including boldness and activity level. Several important issues are emerging in dispersal-syndrome research. The first is that while the link between dispersal and 'exploration behaviour' seems primarily positive (Myers & Krebs 1971; Wilson *et al*. 1994; Wilson 1998; Fraser *et al*. 2001; Dingemanse *et al*. 2003; Krackow 2003; Sih *et al*. 2004; Bell 2007; Reale *et al*. 2007), the direction and strength of the relationship between dispersal and both aggressiveness and sociability is highly system-dependent; as yet, too few studies exist to understand this variation. A second emerging issue concerns the scale over which these effects occur. Most studies to date are from captive or semi-captive populations and demonstrate correlations between consistent behavioural variation and dispersal over very small spatial scales. Three notable exceptions have involved a much greater range of scales. The first showed a dispersal syndrome within a single-stream population of Trinidad killifish *Rivulus hartii* (Fraser *et al*. 2001), two others in the great tit *Parus major* (Dingemanse *et al*. 2003) and the common lizard *Lacerta vivipara* (Meylan *et al*. 2009) occurred at the meta-population level, while the final example was detected along the entire range-expansion front of the western bluebird *Sialia mexicana* in the USA (Duckworth 2006a, 2008; Duckworth & Badyaev 2007; Duckworth & Kruuk 2009). Another emerging issue concerns the proximate causes of behavioural-dispersal syndromes. Although often assumed to have a genetic basis, this has rarely been tested, either indirectly or directly. Quantitative genetic analysis showed that aggressiveness and dispersal were genetically correlated in western bluebirds (Duckworth & Kruuk 2009), while natal dispersal distance in the great tit was predicted by paternal exploration behaviour alone, which may indicate genetic factors are more likely to play a role than maternal effects at the laying stage (Dingemanse *et al*. 2003). A fourth issue is whether dispersal syndromes are state-dependent. Dispersal is often strongly state-dependent in animal populations, especially in relation to sex, age, physiology and morphological traits such as body condition (Dufty & Belthoff 2001; Ims & Hjermann 2001; Clobert *et al*. 2009; Meylan *et al*. 2009). Complex correlations between state and multiple behaviours may involve a combination of genetic, environmental, G × E or developmental factors (Meylan *et al*. 2002, 2009; Meylan & Clobert 2005), but even phenotypic evidence for state-dependent personality-dispersal syndromes is scarce. A fifth emerging issue concerns the within-individual permanence of dispersal syndromes. One study has demonstrated that sociability was consistent over 3 weeks spanning the dispersal period in a semi-natural population of mosquitofish (Cote *et al*. 2010b); consistency was also reported over 1 year in a semi-captive population of common lizards (Cote & Clobert 2007), but the stability of personality differences with respect to dispersal under natural conditions remains untested. Lastly, it is largely unknown to what extent dispersal syndromes are stable with respect to population-level processes such as changes in population density, or population history. In the common lizard, sociability remained consistent from birth to 1-year post-dispersal within experimental populations, and this was independent of the original population's density (Cote & Clobert 2007). In contrast, the aggression-dispersal syndrome in western bluebirds breaks down over time within specific parts of a geographic range, dependent on year since colonisation (Duckworth & Badyaev 2007; Duckworth 2008). Although personality traits are sometimes strongly influenced by environmental factors (Carere *et al*. 2005; Groothuis & Carere 2005; Arnold *et al*. 2007; Costantini *et al*. 2008; Groothuis *et al*. 2008; Quinn *et al*. 2009), they are also heritable and may be the target of strong selection (Dingemanse *et al*. 2004a; Boon, Reale & Boutin 2008; Smith & Blumstein 2008; Quinn *et al*. 2009). Hence, we might expect to see changes in the mean characteristics of populations' dispersal syndromes over small spatial and temporal scales.

Our aim was to explore these emerging issues in the context of a natal-dispersal syndrome involving 'exploration behaviour in a novel environment' (exploration behaviour or EB) in a long-term study population of the great tit. Extensive work on dispersal has been conducted in this species, revealing sex-biased natal dispersal to be the major dispersal event shaping population genetic structure (Greenwood, Harvey & Perrins 1978; Verhulst, Perrins & Riddington 1997; Szulkin & Sheldon 2008; Szulkin *et al*. 2009). Exploration behaviour was one of the first personality traits to be linked to dispersal under natural conditions in an animal population (Fraser *et al*. 2001; Dingemanse *et al*. 2003). It is also heritable (Dingemanse *et al*. 2002; van Oers *et al*. 2004; Quinn *et al*. 2009), correlates with variation in a range of other types of behaviours – including dominance (Verbeek, Boon & Drent 1996; Verbeek *et al*. 1999; Dingemanse & de Goede 2004b), aggression (Carere *et al*. 2005) and territory defence (Amy *et al*. 2010) – and potentially represents a cause of gene flow within and between populations. Our main objectives were the following: (1) to test for an association between explora-

tion behaviour and immigration; (2) to examine whether natal dispersal distance within the study population was correlated with the exploration behaviour of the individual or of their parents; (3) to test whether any links between exploration behaviour and dispersal were state (sex, body mass and body size)-dependent or (4) likely to have a genetic basis as indicated by the effect of parental origin (immigrant vs. locally born parents) on individual exploration behaviour; and (5) to test whether any effects were stable within individuals.

Materials and methods

STUDY POPULATION AND DISPERSAL

This work was carried out as part of a long-term study on a population of great tits at Wytham Woods, Oxford, UK. The study site consists of a discrete ca. 385 ha area of mixed woodland that is effectively isolated from other woodland by surrounding agricultural and urban landscapes. Great tits are socially monogamous and in Wytham breed almost exclusively in nest boxes distributed throughout the woodland (Perrins 1970). Population density has increased markedly over the last 20 years (Garant *et al.* 2004) and was relatively high from 2004 to 2009, the period over which the data analysed here were collected. Mean nest box occupancy by great tits was 37·6% (range 28–46%; $N = 1021$ nest boxes). Reproductive success is monitored annually by a team of up to 10 fieldworkers and nest boxes checked at least weekly during spring. When nestlings are c. 7 days old, the parents are caught at the nest and are aged as adults (if more than 1 year old) or as immature (< 1 year old) and are either ringed for the first time or identified by an existing metal leg-ring. All young are ringed and weighed when 14 days old (see McCleery *et al.* 2004 for further details), allowing immigrants to be distinguished from Wytham-born birds (natal origin), establish the natal site of Wytham-born birds, and thus the natal dispersal distance for locally born recruits. All nest boxes had previously been mapped with the aid of a GPS system (Wilkin *et al.* 2006), and the natal dispersal distance from the natal site to first-breeding or settling site was determined as the straight-line distance. The dispersal distances of birds classed as immigrant are unknown. While there is evidence that a small proportion of immigrants are born to great tits breeding in marginal habitats close to the boundary of the study site (e.g. in hedgerows and gardens), 95% of immigrants are thought to originate elsewhere (Verhulst, Perrins & Riddington 1997) and can thus be classed as genuine dispersers from adjacent populations more than 1 km away from the study site.

Exploration behaviour assays

Assays were conducted over five winters, from February to March 2005 and from September to March in the subsequent four winters. Birds were usually caught with mist-nets at sunflower-seed feeders in the woods, weighed, aged and sexed based on plumage (Svensson 1984), identified and brought into captivity at Wytham field station, ca. 2 km from the centre of the wood, usually for not more than 24 h; a minority of birds were caught during nocturnal checks of nest boxes for roosting birds. Birds were individually housed, and assays were conducted the following morning between 08.00 and 13.00 h. An assay commenced 20 s after a bird was first coaxed from its cage through a trapdoor leading to an adjoining novel environment room and lasted for 8 min, after which the bird was coaxed back into its cage. The assay room design was based on (Verbeek, Drent & Wiepkema 1994). The frequency and location of all movements were recorded using a hand-held computer, generating 12 closely related behavioural measures; the first component (PC1) from a principal components analysis had a positive loading for all measures, reflecting a combined measure of activity levels and propensity to explore novel objects and areas (Quinn *et al.* 2009). PC1 was right skewed and was therefore transformed ($PC1_T$) by the equation $PC1_T = \sqrt{(PC1 + (PC1_{min} \times -1))}$ where $PC1_{min}$ was the smallest (negative) value of PC1 in the data set and was used as the basis of our measure of EB for objectives 1–3.

A total of 2258 EB assays were conducted on 1805 individuals from February 2005 to March 2010, of which 627 (34·7%) were immature (i.e. in their first winter) immigrants and 709 (39·3%) were locally born immature birds. Among birds that were first assayed as adults, 244 had been ringed as nestlings in Wytham, and 226 were immigrants from outside, of which 77·9% and 73·5%, respectively, had been recorded as breeding birds previously. The link between personality and natal dispersal distance could be studied directly for 252 locally born birds that were assayed as immature birds and recruited to the population in their first year, for an additional 34 that recruited when older and for 81 that were first assayed as adults (total $N = 367$). Of the 367 immature birds that were assayed or recruited at any stage, two or more siblings of known EB recruited from 58 nests, yielding possible within-brood comparisons from 58 nests, for which within-brood comparisons of same-sexed siblings were possible from 17 nests for males and 17 nests for females. Of the 252 locally born birds assayed in their first winter, two or more siblings of known EB recruited from 34 nests, allowing within-brood comparisons from 11 nests for males and 8 nests for females.

The indirect link between parental personality and offspring dispersal distance within populations could be estimated for 139 different fathers (recruiting 232 offspring from 168 breeding attempts) and 134 mothers (recruiting 232 offspring from 167 breeding attempts) that were subject to personality assays and also recruited offspring to the breeding population; the relationship between mid-parent EB values and offspring dispersal distance could be estimated for the 86 male–female pairings that generated dispersal distances for 132 offspring. These sample sizes are several times larger than those used in an earlier study of this question (Dingemanse *et al.* 2003).

ANALYSES

Objectives 1 and 3 were both tested in similar models, where the response variable was the $PC1_T$ values from the first assays conducted on individuals, and controlled for days since 31 August, or 'Day', because EB increases over time within seasons. Objective 1 tested whether EB differed between immigrant and resident immature birds (natal origin, two-level factor). Objective 3 tested whether any dichotomy in EB between residents and immigrants was dependent on state (sex, body mass, body size) or variation in EB among cohorts at the population level, tested by two-way interactions between natal origin and the relevant variable. Because birds were caught at different times of the day and season, both of which factors have a large influence on body mass, we used residual body mass (henceforth, body mass) when first captured as immature birds in winter based on the equation mass = 0·136*h – 0·004*day + B_i*-cohort + 1·154 (males) – 0·079 (immature birds), where B_i denotes a cohort-specific parameter (not shown), and the parameter for females was set to 0. Wald statistics for each of these variables were 271·9, 82·0, 66·3, 969·6 and 3·6, respectively; all had P values < 0·001, except for age, where $P = 0·057$. The model accounted for 38·8% of the variation, while quadratic terms for hour and time of season were not significant. Body size was estimated from the first principal

component of wing length (mm) and tarsus length (mm), with latent vectors of 0·14 and 0·99, respectively. This component, henceforth referred to as body size, accounted for 92·3% of the variation in these two linear measures but was only weakly correlated with body mass ($r = 0{\cdot}156$, $P < 0{\cdot}001$, $N = 2007$).

Objective 2 asked whether EB and natal dispersal were correlated within the study population. Here, we used a series of models to test whether 'natal dispersal distance' (√transformed to improve error normality) was predicted by the individual's own EB or that of either parent (see Dingemanse *et al*. 2003). Here, EB was an explanatory variable and corrected beforehand for several fixed effects, including date within the season and the number of times the bird had been assayed; all assays were included in a GLM of $PC1_T$, and the parameter estimate for an individual added to the constant was used as the corrected EB (full details given in Quinn *et al*. 2009).

Objective 4 asked whether the link between EB and natal origin was likely to have a genetic basis. Many immigrants are thought to originate >2 km from the boundaries of our study area (Verhulst, Perrins & Riddington 1997). Therefore, we were unable to measure the EB of birds from the external population that did not immigrate to our study population and cannot determine whether the difference between immigrants and residents reflects a fixed difference at the population level, a process of selection within the external population, or developmental changes at the individual level because of the process of immigration. However, we can make some inferences based on comparisons of the effect of parental origin on the phenotype of their offspring. Therefore, we asked to what extent having zero, one or both parents born locally had on the EB of their offspring. If the link between natal origin and EB is caused by the immigration process itself, or an environmental effect on EB in the source-immigrant population, we expected no link between parental origin and the EB of their offspring. Alternatively, a link between parental origin and offspring EB would suggest either a genetic basis to the syndrome, or that selection acted on EB in the source-immigrant population.

Finally, objective 5 tested whether EB was consistent over time within individuals. Here, we used the first $PC1_T$ values for individuals when they were assayed for the first time as immature birds and again when assayed for the first time as adults, which was available for 61 immigrants and 74 residents. All analyses were conducted using GLMs or LMMs. For the GLMs in objectives 1, 3 and 4, the analyses shown include multiple offspring from an unknown number of immigrant birds and a small number of the same nests within Wytham. We elected not to present analyses for single birds per nest for the local birds, because this could not be done for immigrants, but all analyses gave similar results whichever approach was taken. For objective 2, nesting attempt was also included as a random effect to account for multiple offspring dispersing from the same nest. We did not include either paternal or maternal identify in this analysis because (i) doing so often prevented the models from converging, presumably because most individuals had only one datum and (ii) doing so made no difference to the fixed effects when convergence did occur. The statistical significance of random effects was tested using log-likelihood ratio tests and of fixed effects using Wald statistics. All analyses were conducted in Genstat or SPSS.

Results

EB AND NATAL ORIGIN

We found a clear effect of natal origin on exploration behaviour: EB scores among immigrant first years were on average 11% higher than among locally born first years (predicted means ± SE: 1·07 ± 0·018 and 0·968 ± 0·016, respectively), controlling for significant between- and within-season effects (Table 1). The analyses in Table 1 were repeated on immature birds that subsequently bred in the population ($N = 515$), and the natal origin main effect remained unchanged ($W = 5{\cdot}923$, $P = 0{\cdot}015$; $B \pm \text{SE} = -0{\cdot}094 \pm 0{\cdot}039$ for local birds), showing that the effect detected in winter was not driven by any qualitative difference between immigrants that did and did not breed, and that the effect had a direct impact on the breeding population.

Mean EB varied at the population level from year to year (Table 1; Fig. 1), but the difference between immigrants and locally born birds was independent of this variation (cohort × natal origin, $W = 2{\cdot}28$, d.f. = 5, $P = 0{\cdot}809$; model otherwise similar to Table 1; Fig. 1), suggesting that whatever caused the annual variation in EB among cohorts had equivalent effects in immigrant and locally born birds.

EB-DISPERSAL SYNDROME WITHIN THE MAIN POPULATION

As previously shown for this population (Verhulst, Perrins & Riddington 1997), natal dispersal distance among birds born in Wytham was greater for females than for males in this sample ($W = 41{\cdot}49$, $P < 0{\cdot}001$; median and, in parentheses, IQ range for males and females were 496 m (607 m) and 737 m (885 m); full LMM is in Table 2a). There was no evidence for a relationship between an individual's EB score and natal dispersal distance (Table 2a). This was true when the analysis was repeated only on those birds that had already bred and therefore undergone post-natal dispersal before being assayed ($W = 0{\cdot}33$, $P = 0{\cdot}569$, $B \pm \text{SE} = 1{\cdot}267 \pm 2{\cdot}219$, $N = 115$); therefore, the assaying procedure itself did not explain the lack of an association between EB and natal dispersal distance. Similarly, there was no main effect of parental EB, either for each parent separately (paternal, Table 2b; maternal, Table 2) or using mid-parent values (Table 2d) on the natal dispersal distance of their offspring.

Table 1. GLM of exploration behaviour among immature great tits with respect to natal origin (resident vs. immigrant) and other fixed effects in Wytham. $N = 1278$, including multiple individuals born from the same nesting attempt; selecting only the first individual originating from each parental nest attempt had no substantial effect on the model

Fixed terms	*B*	SE	*W*	*P*
Constant	0·847	0·068	n/a	n/a
Sex[a]	0·041	0·024	2·87	0·090
Day	0·002	0·000305	41·82	< 0·001
Natal origin[b]	−0·101	0·025	17·41	< 0·001
Cohort	–	–	26·01	< 0·001
Residual body mass (g)	−0·005	0·012	0·14	0·712

[a]Females set to 0.
[b]Immigrants set to 0.

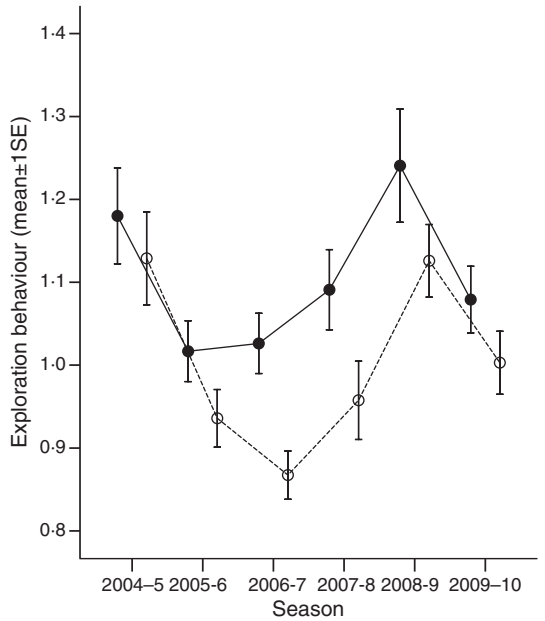


Fig. 1. Variation in exploration behaviour among immature great tits with respect to time and natal origin. (● immigrants; ○ residents). The natal origin effect on exploration behaviour was maintained over time.

We were also able to make within-family comparisons for 34 families where >1 same-sexed offspring were assayed and recruited to the breeding population at any stage of their life. The differences in EB and natal dispersal distance for sibling dyads were not correlated for males (r_s = −0·10, P = 0·701, N = 17) or for females (r_s = −0·201, P = 0·439, N = 17), agreeing with the previous analyses showing no link between within-population dispersal and EB. Similar results were obtained for the smaller sample of birds that were assayed when immature and recruited in their first summer of life. Finally, to allow direct comparison with a similar study elsewhere (Dingemanse *et al.* 2003), we also repeated all of the analyses in Table 2 using the numbers of hops and flights in the first 2 min as our measure of EB (corrected for other fixed effects as done for our main estimate of EB); all of the effects remained non-significant, and conclusions as to statistical and biological significance are unchanged (analyses not shown). Collectively, our analyses show that a dispersal-EB syndrome existed at the between-population scale but not within our main study population.

THE INFLUENCE OF STATE

There was a tendency for EB to be marginally higher among males than females (predicted means ± SE: 1·04 ± 0·017 vs. 0·995 ± 0·017), but the difference between immigrants and locally born birds was independent of sex (Natal origin × Sex, W = 0·17, P = 0·682). Immigrants tended to be lighter than locally born birds (W = 2·738, P = 0·098: mean residual mass, which corrects for sex as well as other fixed effects = −0·051 ± 0·042 SE vs 0·042 ± 0·038 SE), while the difference in EB between immigrants and residents was more pronounced for light birds (body mass × natal origin, W = 6·97, P = 0·008, B ± SE = 0·066 ± 0·0·025; Fig. 2; controlling for season, day, sex), an effect that was independent of sex (body mass × natal origin × sex, W = 0. 49, P = 0·486). The body mass × natal origin effect was driven

Table 2. The influence of (a) an individual's own exploration score, (b) paternal exploration score, (c) maternal exploration score and (d) mid-parental score (mean of paternal and maternal) on (natal dispersal distance (m))$^{1/2}$. All analyses are linear mixed models. Sample sizes were 252, 232, 232 and 132 for (a), (b), (c) and (d), respectively; d.f. = 1 for all terms, except for those in which year was involved, in which case d.f. = 4

Random terms	Log-likelihood ratio	P	Component ± SE	Fixed terms	Wald	P	B ± SE
(a)							
Nesting attempt	0·53	0·467	46·93 ± 20·11	Constant			26·02 ± 2·219
Residual			66·17 ± 19·15	Sex	26·36	< 0·001	−6·615 ± 1·288[a]
				Individual EB	1·09	0·297	1·609 ± 1·539
				Year	5·32	0·259	n/a
(b)							
Nesting attempt	0·49	0·484	26·51 ± 37·43	Constant			35·12 ± 4·457
Residual			89·58 ± 37·66	Sex	10·61	0·001	−4·658 ± 1·430[a]
				Paternal EB	1·23	0·268	1·961 ± 1·767
				Year	7·57	0·186	n/a
(c)							
Nesting attempt	0·00	1·00	1·899 ± 33·200	Constant			30·90 ± 6·11
Residual			110·9 ± 34·7	Sex	9·03	0·003	−3·308 ± 1·382[a]
				Maternal EB	0·02	0·900	0·399 ± 1·578
				Year	4·02	0·548	n/a
(d)							
Nesting attempt	2·91	0·088	76·00 ± 31·65	Constant			26·47 ± 4·728
Residual			50·59 ± 28·02	Sex	2·96	0·090	−3·174 ± 1·845[a]
				Mid-parent EB	0·16	0·692	−1·195 ± 3·010
				Year	1·32	0·857	n/a

[a]Female set to 0.

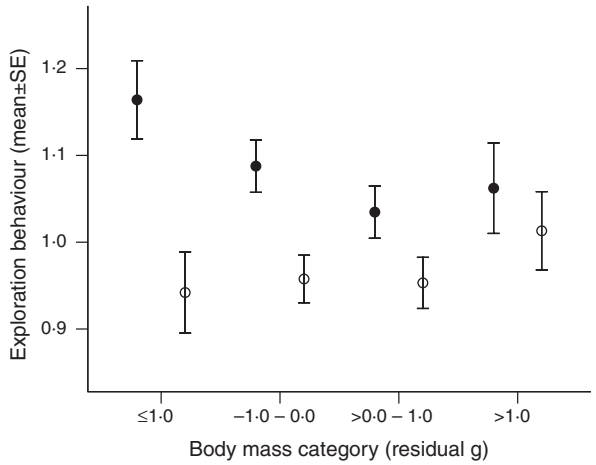


Fig. 2. State-dependent association between exploration behaviour ($PC1_T$; see text) and natal origin (● immigrants; ○ residents) in Wytham great tits (N = 1276) from 2004 to 2009. The state variable, body mass, was residualised on time of day, sex and other factors (see text) and categorised based on cuts at mean and ± 1SD points.

by a positive correlation between exploration behaviour and body mass among local-born immature birds (W = 4·47, P = 0·035, B ± SE = 0·036 ± 0·017, N = 676; controlling for day, sex, season) and no effect of exploration behaviour on body mass among immigrants (W = 2·506, P = 0·114, B ± SE = −0·029 ± 0·018, N = 602, controlling for day, sex, season).

There was no difference in body size between immigrants and local-born birds (W = 0·01, P = 0·919, N = 1268; controlling for day, season and sex), and the link between natal origin and EB was not influenced by body size (body size × natal origin, W = 0·46, P = 0·497, B ± SE = 0·008 ± 0·012; controlling for season, day, sex); this result was similar even when body mass × natal origin was also included, which itself remains significant. Therefore, body mass per se rather than body size seemed to be the source of the state-dependent effect on EB.

Within the population, there was no evidence that state-dependent effects could have masked an underlying link between natal dispersal distance and an individual's EB. This was true for body mass (EB × body mass, W = 0·16, P = 0·687) and body size (EB × body size, W = 0·46, P = 0·499). It was also true for sex (EB × sex, W = 0·33, P = 0·568) and for interactions between sex and both body mass (EB × body mass × sex, W = 0·54, P = 0·464) and body size (EB × body size × sex, W = 3·03, P = 0·083).

PARENTAL ORIGIN

Of the 645 locally born offspring, 149, 357 and 139 had zero, one and two locally born parents, respectively (including only birds where both parents were known). There was no difference in EB among offspring between these three groups (W = 3·520, d.f. = 2, P = 0·173; controlling for cohort, sex and day in a LMM with nesting attempt as a random effect; predicted means ± SE were 1·002 ± 0·037; 0·963 ± 0·026; 1·045 ± 0·040). Similarly, the effect was not parent specific because there was no difference in EB between birds born to an immigrant mother and those born to resident mothers (N = 186 and 149, respectively, W = 1·11, P = 0·292), or between birds born to an immigrant father and those born to resident fathers (N = 167 and 149, respectively, W = 0·26, P = 0·613, N = 347). All of the preceding effects were uninfluenced by time since the parents had immigrated (i.e. parental age; results not shown). We cannot discriminate between those resident offspring that emigrate and those that die; to test whether the estimates of EB with respect to parental origin might be biased because of this, we tested whether there was any difference in local recruitment to the population with respect to parental origin over the years when this study was conducted. However, we found no significant difference in recruitment rate between offspring whose parents were locally born or immigrants (both parents locally born: −0·602 ± 0·236; back-transformed predicted recruitment rate = 0·548 recruits per breeding attempt), both parents immigrants (−0·569 ± 0·238, 0·566 recruits per breeding attempt); one of each type (−0·636 ± 0·229, 0·529 recruits per breeding attempt; W = 0·50, d.f. = 2, P = 0·779, N = 1495 breeding attempts from 2004 to 2009); GLMM with Poisson error and a log-link function; mother identity, father identity and year were included as random effects; lay date, brood size and average fledgling mass were all significant fixed effects – not shown).

Recruitment data for birds assayed during the winter were available for birds born up to the 2008 breeding season (assayed in the 2008–2009 season), and of these, 235 of 506 immigrant birds (46·4%) and 286 of 577 (49·6%) locally born immature birds subsequently recruited to the Wytham breeding population. There was no difference in recruitment rate between these two groups (W = 1·464, P = 0·226, controlling for: date of assay (W = 9·146, P = 0·002); sex (W = 0·0009, P = 0·985); cohort (W = 11·853, d.f. = 4, P = 0·018). EB did not predict the likelihood of recruitment (W = 2·00, P = 0·158, B ± SE = −0·205 ± 0·145, logit scale; other effects same as previous model) and this was equally true for immigrants and residents (EB × natal origin, W = 0·387, P = 0·534). Taken together, these results and those in the preceding paragraph suggest that, at the between-population level, the dispersal-EB relationship is not influenced by differences in recruitment likelihood or by direct parental (e.g. genetic) effects.

STABILITY WITHIN INDIVIDUALS

Analysis of data from individuals assayed when both immature and adult showed that EB did not change with age and that birds consistently differed from one another over time (Age fixed effect and bird random effect in Table 3). Within-individual changes in EB were independent of natal origin (Age × Natal origin, Table 3; Fig. 3). The preceding tendency for immigrants to be smaller than local-born birds was not detected (W = 0·11, P = 0·732) among those immature birds that subsequently recruited to the population, while the

Table 3. Linear mixed model of exploration behaviour with respect to natal origin and age for 115 individuals (N = 294 assays) that were assayed when immature and again as adults

Random terms	Log-likelihood ratio	P	Component ± SE
Individual	76·63	< 0·001	0·132 ± 0·024
Residual (Bird × Age)	n/a	n/a	0·099 ± 0·011
Fixed terms	**Wald**	**P**	**B ± SE**
Constant	n/a	n/a	1·120 ± 0·129
Age	0·05	0·824	0·024 ± 0·067[a]
Natal origin	5·71	0·019	−0·154 ± 0·087[b]
Sex	1·75	0·189	0·103 ± 0·078[c]
Day	10·96	0·001	$1{\cdot}74 \times 10^{-3} \pm 5{\cdot}27 \times 10^{-4}$
Cohort (year)	9·37	0·100	[d]
Age × Natal origin	0·78	0·379	−0·041 ± 0·083[e]

n/a is not applicable.
[a]Adult parameter set to 0.
[b]Immigrant set to 0.
[c]Females set to 0.
[d]Parameters not shown.
[e]Parameter of immature residents shown.

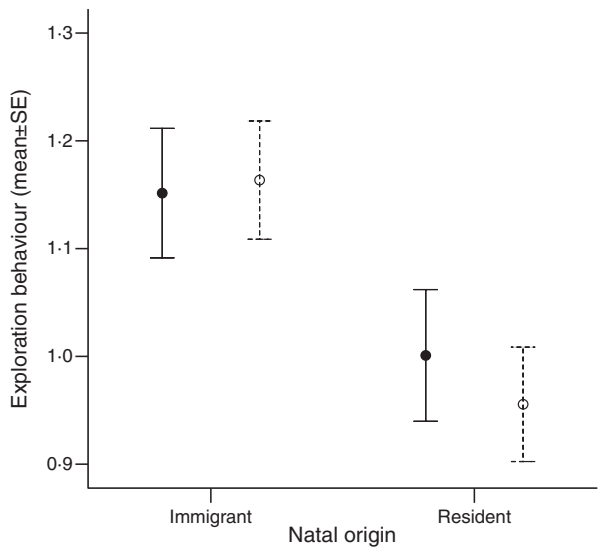


Fig. 3. Exploration behaviour and natal origin among great tits that were assayed when immature (●) and again as adults (○).

difference in EB between immigrants and locals was no longer influenced by body mass (body mass × natal origin, W = 0·038, P = 0·846, B ± SE = −0·001 ± 0·040, N = 515). This was not caused by any detectable size-dependent recruitment effect because the probability of assayed immature birds recruiting to the population was not influenced by body mass (W = 0·024, P = 0·877, B ± SE = −0·010 ± 0·064; controlling for season, sex, time of season, natal origin), by natal origin (W = 1·311, P = 0·252, B ± SE = 0·144 ± 0·126 for local birds) or the interaction between the two (W = 0·250, P = 0·617, B ± SE = −0·063 ± 0·127). Together, these analyses suggest that the difference between resident and immigrant birds is consistent over an individual's lifetime after immigration.

Discussion

Here, we provide evidence for a link between the personality trait 'exploration behaviour' and dispersal, and that the link is at least partially state- and scale-dependent. Immigrants to our study population had higher exploration scores than locally born birds; this difference was consistent across years and between the sexes, but was state-dependent because it was primarily present in light individuals. In contrast, despite large sample sizes relative to similar studies (Dingemanse *et al*. 2003), we found no evidence for any relationship between within-population dispersal distance and EB, whether assessed within individuals or within families.

THE EXPLORATION BEHAVIOUR-DISPERSAL SYNDROME

Exploration behaviour among immigrants was on average 11% or 0·23 standard deviations higher than among residents in our study population. Furthermore, the difference between residents and immigrants occurred in each cohort, despite annual variation in mean exploration behaviour between years. Annual fluctuations in environmental conditions and in selection on EB have both occurred over the course of this study (Quinn *et al*. 2009; Quinn *et al*. unpublished), either of which might drive these cohort-specific fluctuations, but the consistency of the syndrome indicates resilience to this population-scale process. The effect may also be robust across studies because the difference between immigrants and residents we detected was similar to that reported for a Dutch study population, where exploration scores were about 14% higher among immigrants (estimated from Fig. 2 in Dingemanse *et al*. 2003). In other systems, personality-dispersal syndromes have tended to be population specific. For example, correlations between a variety of (non-dispersal related) behavioural traits among three-spined sticklebacks seem to be population specific across Californian (Bell & Stamps 2004) and Welsh (Dingemanse *et al*. 2007) populations. Similarly, the aggressiveness-dispersal syndrome in the western bluebird in the USA is prominent only in populations far from those of the congeneric mountain bluebird *Sialia currocoides* with which it competes for breeding sites. However, too few replicate studies exist to generalise about the spatial or temporal robustness of dispersal syndromes involving behavioural traits at the between population level.

In contrast to both a previous study of a Dutch great tit population (Dingemanse *et al*. 2003), and also several other studies of similar exploration behaviour syndromes in other species (Cote *et al*. 2010a), we found no evidence of a link between exploration behaviour and natal dispersal distance amongst individuals born within our population. Moreover,

there was no evidence of a positive correlation between natal dispersal distance and paternal, maternal or mid-parent exploration behaviour. The sample sizes were quite large for these analyses (N = 132–252), and the standard errors for the effects were thus relatively small; analyses gave similar results when repeated on an alternative 2-min assay used in the Dutch study. Population differences in ecology and in the precise way EB influences dispersal are likely to explain different effects across studies. While the present study was carried out in a single continuous woodland in a landscape dominated by agriculture, the Dutch study site (Westerheide) is almost contiguous with the much larger Hoge Veluwe national park in central Netherlands (Dingemanse *et al*. 2003). Dispersal over Westerheide may be less constrained than in a more fragmented landscape where the strength of selection against emigration might be relatively strong, perhaps decoupling any correlation between exploration behaviour and dispersal distance within our population, which would not necessarily affect the difference in EB between immigrant and resident birds. Against this constraint hypothesis, in fact great tits in Wytham dispersed over larger distances than those in Westerheide (females, 935 vs. 643 m; males 648 vs. 498 m; from Dingemanse *et al*. 2003), possibly because Wytham is larger (385 vs. 250 ha). Similarly, females dispersed 44% further than males in Wytham but only 30% further in Westerheide. Other unknown ecological factors undoubtedly are at play, but more generally, EB is likely to influence the dispersal process within populations in different ways across populations. Natal dispersal can be viewed in three distinct phases – departure from the natal site, transience and settlement (Clobert *et al*. 2001, 2009; Cote *et al*. 2010a) – and EB has the potential to influence each of these processes through correlations with a variety of different behavioural traits, for example dominance and responsiveness, both of which are also likely to be important determinants of condition-dependent and 'informed' dispersal (see Clobert *et al*. 2009), which influence dispersal decisions at multiple stages.

STATE DEPENDENCE OF THE SYNDROME

The difference in exploration behaviour between residents and immigrants was independent of sex because both male and female immigrants had higher scores than male and female residents, respectively. However, immigrants with small body mass had higher EB scores than locally born birds with a similar body mass. Previous work on this population suggested state-dependent effects in the immigration process, with larger birds born in external, low-quality habitats being more likely to immigrate successfully into Wytham (Verhulst, Perrins & Riddington 1997). Indeed numerous studies show that dispersal is often dependent on an individual's state, for example on morphological or physiological phenotype (Clobert *et al*. 2001, 2009), but very few studies provide evidence for state-dependent links between dispersal and behavioural phenotypes (Holekamp 1986; Ims 1990; O' Riain, Jarvis & Faulkes 1996; De Fraipont *et al*. 2000; Meylan *et al*. 2002). Body size or condition play a role in most of these studies, as it does in ours, and may be generally important in behavioural syndromes.

The link between exploration behaviour and body size may shed light on the behavioural mechanisms causing the EB-dispersal syndrome in our population. These mechanisms generally remain poorly understood but are hypothesised to be driven by differences in the outcome of social interactions (Dingemanse *et al*. 2002). While fast birds tend to be relatively dominant (Verbeek, Boon & Drent 1996; Verbeek *et al*. 1999), which may facilitate the immigration process (Chitty 1967; Krebs 1978), slow birds are better able to cope with social defeat (Carere *et al*. 2001), which may facilitate remaining in high-quality natal habitats where competition is stronger, and social defeat is therefore more frequent (Dingemanse *et al*. 2003). It is plausible that the outcome of these interactions is modulated by body mass, which can be a determinant of social status (Gosler & Carruthers 1999), and we suggest that the pattern in Fig. 2 may be explained by the dominance/social defeat model outlined in Fig. 4a (see legend for description). Figure 4b shows an alternative exploration behaviour/dispersal model where fast birds are more mobile generally and are therefore likely to both emigrate and immigrate, irrespective of body size. This model could not explain the pattern in Fig. 2 because, on average, immigrants were faster than local birds. In reality, the processes involved are likely to be more complicated than indicated in Fig. 4a. For example, the influence of EB on social interactions could be density or frequency-dependent. Furthermore, in the great tit fast explorers are dominant in some circumstances but slow explorers are dominant in others (Dingemanse & de Goede 2004b) and in the common lizard, dispersers from high population densities tend to be repelled by conspecific odour (asocial), while dispersers from low-

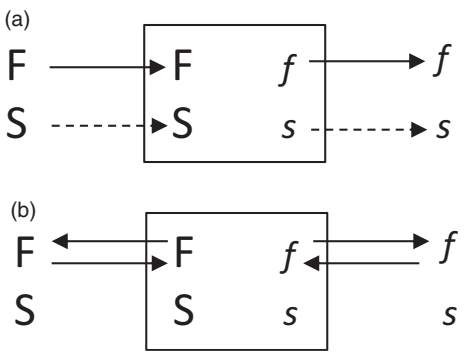


Fig. 4. Proposed models of the exploration behaviour/dispersal syndrome in our population. Both body mass (heavy = uppercase and light = lowercase) and exploration behaviour (f or F = fast and s or S = slow) are continuous phenotypes but for simplicity are shown here as discrete. (a) The dominance/social defeat model: heavy birds of all types are likely to immigrate to Wytham, but especially heavy, fast birds because they are also aggressive and more dominant; light birds are more likely to emigrate because they are less dominant, but light slow birds less so because they are better able to cope with social defeat. (b) The exploration behaviour/dispersal model: fast birds are more mobile generally and therefore likely to both emigrate and immigrate, irrespective of body mass.

density areas tend to be attracted to the odour (sociable; Cote & Clobert 2007). Although we show that the exploration behaviour-dispersal syndrome is body-mass dependent, clearly further research is needed to understand how this effect arises. Furthermore, if dominance plays a role in the body-mass dependent effect, it remains unclear why body size did not give a similar effect within the population, given that this measure can also predict dominance status (Garnett 1981). The answer is likely to be non-trivial because body mass is determined by body size, muscle condition and fat reserves (Gosler & Carruthers 1999), each of which may relate to dominance in different ways, dependent on the relative importance of the risks of foraging and predation (Gosler 1996, 2001; Gosler & Carruthers 1999; Gosler & Harper 2000).

CONSISTENCY OF THE SYNDROME

We found that the difference in exploration behaviour between immigrants and residents was maintained over the first year of life post-immigration. Elsewhere, we reported exploration behaviour was repeatable in this population (Quinn *et al*. 2009) but the analysis here further suggests that immigrants did not change their exploration behaviour once they had become established in the population over time, suggesting that the differences in exploration behaviour between immigrants and residents were permanent. One study showed that sociability was correlated with dispersal and that it was consistent within individuals before, and 10 months after, dispersal in a semi-captive population of lizards (Cote & Clobert 2007), though sociability could still have changed differentially with respect to dispersal status over time despite this consistency. In another study, a number of behavioural differences between philopatric and dispersing common lizards were found to be stable over periods of up to 10 months after the dispersal phases, even when both maternal and natal environmental conditions were manipulated (Meylan *et al*. 2009). This consistency suggests an inherent, possibly genetic, cause of these syndromes, but direct evidence for a genetic basis to dispersal syndrome linked to consistent behavioural variation is rare (Duckworth & Kruuk 2009). Exploration behaviour is heritable in our population (Quinn *et al*. 2009) but is also influenced by permanent environment effects (Quinn *et al*. 2009). The lack of an association between parental origin and the difference in exploration behaviour between immigrants and residents in the current study suggests that the syndrome may be largely environmental. We cannot distinguish between emigration and death among individuals that were born locally in our population but that did not recruit, but nevertheless, our recruitment analysis suggested the estimates of EB with respect to parental origin may not be biased because of differential emigration with respect to parental origin, though we acknowledge our approach is indirect. We did not measure EB before dispersal took place and therefore could not test directly whether the difference between immigrants and residents arose as a result of changes within individuals during the immigration process itself, whether it results from selection for a particular part of the external population, or whether the external population differs from the main study population with respect to mean EB phenotype (a difference that might have either environmental or genetic causes). Furthermore, G × E effects could equally explain the difference and we note that identifying the genetic basis of dispersal syndromes clearly remains a major challenge in the field (Duckworth 2006b).

Conclusions

Our data suggest that the exploration behaviour-dispersal syndrome in great tits from Wytham is independent of sex and large-scale population-level processes, albeit under a restricted set of environmental conditions – for example, population density has been consistently high over the course of this study (Quinn, J.L., Patrick, S., Cole, E.F., Bouwhuis, S., & Sheldon, B.C. *et al*. unpublished). They support the growing view that consistent behavioural differences over and above those associated with commonly studied condition factors may have important implications for our understanding of the causes and consequences of dispersal. Although our measure of personality is heritable in this study population, the dispersal syndrome seems to be largely state-dependent and is not influenced by parental origin. Unless this latter effect can be explained by G × E, given the effect size (0·23 SD) of the difference between immigrants and residents, together these analyses point to a limited impact of the syndrome on gene flow into the population. Our data also showed that the syndrome was dependent on spatial scale in our population because it was detected only in the context of differences between immigrants and residents, and not within-population variation in natal dispersal. Although this questions the generality of the effects found elsewhere, it also demonstrates that explaining differences in the existence of syndromes between populations is a major challenge.

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Appendix B

Personality predicts individual responsiveness to the risks of starvation and predation

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Personality predicts individual responsiveness to the risks of starvation and predation

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Theory suggests that individual personality is tightly linked to individual life histories and to environmental variation. The reactive–proactive axis, for example, is thought to reflect whether individuals prioritize productivity or survival, mutually exclusive options that can be caused by conflicts between foraging and anti-predation behaviour. Evidence for this trade-off hypothesis, however, is limited. Here, we tested experimentally whether exploration behaviour (EB), an assay of proactivity, could explain how great tits (*Parus major*) respond to changes in starvation and predation risk. Individuals were presented with two feeders, holding good or poor quality food, which interchanged between safe and dangerous positions 10 m apart, across two 24 h treatments. Starvation risk was assumed to be highest in the morning and lowest in the afternoon. The proportion of time spent feeding on good quality food (PTG) rather than poor quality food was repeatable within treatments, but individuals varied in how PTG changed with respect to predation- and starvation-risk across treatments. This individual plasticity variation in foraging behaviour was linked to EB, as predicted by the reactive–proactive axis, but only among individuals in dominant social classes. Our results support the trade-off hypothesis at the level of individuals in a wild population, and suggest that fine-scale temporal and spatial variation may play important roles in the evolution of personality.

Keywords: personality; plasticity; life-history variation; predation; starvation; trade-off

1. INTRODUCTION

The coexistence of discrete behavioural differences between individuals in populations has been relatively well studied and can often be explained by frequency-dependent selection acting on, for example, alternative mating strategies [1,2]. In contrast, understanding the adaptive significance of individual variation in continuous behavioural traits remains a major challenge. Recently, focus has centred on personality or behavioural syndromes within animal populations, that is, behavioural traits that are consistent over time, across situations or correlate with other behavioural traits [3–6]. How consistent behavioural differences arise is puzzling because of the intuitive expectation that natural selection should favour complete behavioural plasticity. Potential explanations for how behavioural consistency is maintained within populations are diverse and most are supported only by scant empirical evidence [7–10]. While costs associated with plasticity are thought to be a major proximate driver of behavioural consistency, links with individual state, life-history variation and the selective consequences of environmental heterogeneity and uncertainty are also thought to be pivotal [5–10]. Experimental evidence for any of these processes in natural populations at the level of individuals, however, remains scarce [7–10].

State dependency has long been a key concept in decision-making [11] and is central to many recent models developed to explain personality [12–15]. Some of these view variation in life-history strategy as the key state variable; for example, one model suggests that selection should favour consistent boldness and aggressiveness for individuals with low-residual reproductive value, but the opposite for those with high-residual value [14]. Another model suggests a life-history strategy that prioritizes growth or productivity, or that minimizes starvation risk, will be reflected by increased foraging activity and consistently predation-risk-prone behaviour across situations; on the other hand, a strategy that prioritizes survival leads to selection for consistently predation-risk-averse behaviour [7]. The reactive–proactive personality axis is common in many vertebrate groups and has been linked to this trade-off because, at one end of the continuum, reactive or responsive individuals tend to be slow but thorough-exploring, cautious and shy, compared with those at the other end of the continuum, where proactive routine-forming individuals tend to be fast but superficial-exploring, bold and predation-risk prone [16]. Existing evidence suggests that proactives tend to sustain high productivity but at a potential cost to survival, while reactives do the opposite (reviewed by Smith & Blumstein [17]). To meet the demands of their faster pace of life, proactives should, therefore, be relatively starvation-risk averse, but as a result may be more predation-risk prone than reactives. In other words, the constraints on behavioural plasticity caused by personality

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arise because they reflect differences in state, or in this case, consistent differences in how individuals manage the trade-off between foraging and anti-predation behaviour.

Evidence in support of the trade-off hypothesis is growing [18–20] but limited for several reasons. First, in many studies where links between personality and productivity have been inferred, the underlying mechanisms remain unclear because (i) the nature of the risks associated with the behavioural decisions is poorly characterized or unknown [21–23] and (ii) responses to experimental changes in these risks have not been examined [8]. Second, other studies have only considered how personality is linked to variation in predation risk [19,24–26]. This infers indirect links with the risk of starvation or poor self-maintenance, but the extent to which personality might simultaneously influence responses to starvation-risk variation directly is unclear. This is important because the absolute levels of starvation and predation risk may be independent. Third, some of the most influential experimental studies to date have compared differences between discrete subpopulations [18,27], which make it difficult to draw direct conclusions about individual behavioural consistency, or to control for how other factors simultaneously influence behavioural decisions. Experimental tests on how personality influences the way individuals respond to variation in predation and starvation risk are therefore needed.

Using a long-term study population of the great tit, *Parus major* (reviewed by Verhulst *et al.* [28] and McCleery *et al.* [29]), our aim was to examine whether the reactive–proactive axis predicts key foraging decisions made in the context of the trade-off between foraging and anti-predation behaviour. Studies in our population and elsewhere have shown that an assay of 'exploration behaviour in a novel environment' (EB) among wild great tits temporarily taken into captivity is a good proxy for the reactive–proactive axis. Not only is EB repeatable within individuals but it is also heritable, under selection [21,25,30–32], and correlates with a variety of different behaviours, including dispersal [33,34], promiscuity [35,36] and dominance [37,38]. Although EB has been linked to risk-taking and foraging behaviour [25,39], the significance of these effects under natural conditions has yet to be tested. Moreover, the importance of EB in the context of the trade-off between foraging and predation has not been examined.

We recorded the behaviour of free-ranging, tagged tits visiting feeders using passive integrated transponder (PIT) loggers. After assaying EB among wild birds temporarily taken into captivity, we monitored how the proportion of time birds spent feeding on a feeder with good quality food (proportion of time on good food, or PTG), rather than on a second feeder 10 m away with poor quality food, changed with respect to (i) experimentally manipulated variation in predation risk (feeders were either in a 'safe' or 'dangerous' position from predators) and (ii) natural variation in perceived starvation risk, which we assumed increased from the evening to the morning because birds are unable to feed for up to 12 h overnight [40]. First, we tested whether (i) great tits traded-off the need to feed against the risk of predation, expecting that PTG would be lower when the good quality feeder was in the dangerous position compared with when in the safe position, and that PTG would be higher in the morning when starvation risk is highest. We then used a mixed-model approach to test whether individuals (ii) differed consistently from one another with respect to PTG [3,41], and (iii) varied in their responsiveness to a change in predation or starvation risk. Finally, we tested the hypothesis that personality is linked to the trade-off by asking whether EB explains the behavioural responses observed to changes in feeder position and time of day. Our general expectation was that relatively fast-exploring birds should prioritize foraging at the expense of being predation-risk prone, but slow-exploring birds should prioritize minimizing predation risk but at the expense of being starvation-risk prone. Nevertheless, we expected this effect could be moderated by the well-known link between dominance and both EB [37] and age or sex [42]. In Wytham, competition among feeders containing poor quality food can be intense when in the safe position [38]; therefore, we expected the least-dominant individuals in the population, slow-exploring females and juveniles, could be forced to feed more in the dangerous position, when the poor quality food was in the safe position.

2. METHODS

(a) *Study population*

The field experiment was conducted in the context of a long-term study of the great tit [29] at Wytham Woods, Oxford, UK (51°46′26.57″ N, 1°18′38.71″ W) between January and March 2009. Wytham Wood is a 338 ha mixed deciduous forest 6.5 km outside Oxford, UK. From 2006 to 2008, the entire breeding population and their offspring were individually tagged with both metal and PIT tags during the breeding season. Immigrants and older birds were also caught during winter and PIT tagged, which in 2009 occurred at each of the eight trial locations in the days before or after the trials, at which time birds were also taken into captivity for behavioural assays (§2*c*). Biometric data including age and sex were recorded for all birds. Great tits are social, form loose flocks in winter and have a generalist feeding habit, foraging primarily on invertebrates, seeds and beech mast in winter. Their main predator in winter, the sparrowhawk (*Accipiter nisus*), is also the main predator of adult songbirds generally across most of Eurasia [43], and can attack prey at speeds of up to 25 m s^{-1} [44]. Typically, they rely on ambush before their prey have had time to escape [45,46].

(b) *Experimental setup*

Two-day trials were carried out at eight different sites around Wytham. Twenty-four hours before the 2-day trial, a single bird feeder was placed at an experimental site with a mix of good quality peanuts (whole-nuts) and poor quality peanuts (granules), both supplied by Jacobi Jayne Ltd, in order to attract birds to the area and to acclimatize them to the food used during subsequent trials. Note that it was expected *a priori* that the whole-nuts would be perceived as good quality (see electronic supplementary material) which was supported by the analysis reported below. On the first day of the trial itself, which followed immediately after the acclimatization period, single feeders were placed in two different 'feeder positions' at around midday: the low predation risk or 'safe' position (2–3 m near dense undergrowth), and the 'dangerous' position in the open approximately 10 m from the safe feeder, away from any protective cover. One of the feeders contained whole-nuts and the other granules.

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Both feeders were left in place for a 24 h treatment, after which the position of the feeders was switched and left for a second 24 h treatment. Conditions were best for the birds during the treatment in which the whole-nut feeder was in the safe position and the granules in the dangerous position. The order of the two treatments was randomly allocated across sites, but ensuring best and worst conditions occurred on the first day at an equal number of sites.

An antenna was placed below the single, food-access points at each feeder. Visits by birds with PIT tags on leg rings were then detected and recorded by a data logger with a resolution of one-sixteenth of a second. This potentially gave samples for the morning and the afternoon periods ('time of day' fixed effect) in both the first and second 24 h treatments, i.e. a maximum of four samples per individual. In all analyses, we used PTG as our response variable, that is, the proportion of time during any one of these sample periods that an individual spent on the good quality (whole-nut) food, using the total time on the whole-nut and granule feeders as the denominator. PTG was assumed to be a concise estimate of the behavioural decisions made when presented with feeders of different starvation and predation risk. Many birds visited only one of the two feeders during each treatment; however, our test of the trade-off hypothesis does not depend on birds making informed choices by visiting both feeders within either treatment, because we explore how EB influences changes in the decisions made across treatments, although we note that the feeders were so close to one another and visible that birds were probably aware that both feeders were present.

(c) *Exploration behaviour assays in captivity*

To assay EB, birds were taken under licence from Natural England and brought to the John Krebs Field Station, Oxford, UK and housed individually on a natural light–dark cycle in 45 × 45 × 68 cm wire cages, and given food and water ad libitum. A total of 16 cages were available for housing, eight on each side of a large observation room to which the cages were connected by a trap door. Details of the EB assay are provided elsewhere [31] and further information is provided in the electronic supplementary material. All birds were released back at the capture site within 24 h of being caught.

(d) *Data analysis and predictions*

In the focal winter, a total of 156 individually tagged great tits visited a feeder at least once during each experimental treatment at any site. Four of these were recorded at more than one site on multiple trials, giving a total of 164 individual trials. Individuals were included only if they were recorded in the morning and, or, in the afternoon, during both 24 h treatments ($n = 131$ individuals). We had five general objectives or predictions. First, we used linear-mixed models (LMMs) to estimate the individual component of variation in PTG, generating repeatability estimates by expressing the individual component of variation as a proportion of total sample variance [47]. Second, we tested whether individuals traded-off the risks of starvation and predation by asking whether PTG changed with respect to the following fixed effects in a LMM: (i) feeder position, (ii) time of day, and (iii) their interaction. Third, we tested whether there was significant variation in PTG plasticity across treatments, or more specifically whether individuals varied in the extent to which they traded-off starvation and predation when risk changed. This was carried out by testing the following so-called I × E random effects: individual × feeder position, individual × time of day or individual × feeder position × time of day as random effects in a LMM [41]; note that all E were categorical variables. Finally, we tested whether changes in PTG across the predation or starvation-risk categories were influenced by EB using fixed effect interactions (EB × time of day and EB × feeder position), or whether these effects were age- or sex-dependent (four possible three-way fixed effect interactions between EB, feeder position, age and sex). All four three-way interactions were included initially but only the final model in which all variables were significant is shown. We used LMMs with location and individual identity as random effects in all models, unless otherwise stated, with feeder position, age, sex and EB as fixed effects using GENSTAT v. 13 [48]. We followed standard protocol in REML analyses [49] where initially the random model is established using the REML deviance (or a REML-deviance-based Akaike Information Criterion (AIC) or Bayesian Information Criterion (BIC)), while including the full fixed model with all interactions. The fixed model is then simplified using F statistics with numbers, or F statistics with numbers of denominator degrees of freedom estimated using standard methods [50]. PTG was logit transformed according to the equation logit(100 × (time at whole-nut feeder)/(total time detected during treatment)), where zero values for the numerator and denominator were substituted with the smallest non-zero proportion. Errors approximated to a normal distribution. Further information is provided in the electronic supplementary material.

3. RESULTS

(a) *The starvation–predation trade-off*

PTG was lower when the whole-nut feeder was placed in the dangerous position, and in the afternoon when the risk of starvation lowest (feeder position and time of day; table 1 and figure 1). Furthermore, PTG was especially low when the whole-nut feeder was in the dangerous position in the afternoon (feeder position × time of day, figure 1). Therefore, individuals traded-off their need to forage efficiently against the need to minimize predation risk; the way this happened was dependent on the relative size of these two risk factors.

(b) *Repeatability of poor quality food*

PTG showed low–moderate repeatability across the morning and afternoon periods when the whole-nut feeder was in the safe position ($r = 0.17$; individual variance component ± s.e. = 1.234 ± 0.594, log-likelihood test = 4.89, $p < 0.027$) and moderately high repeatability across periods when in the dangerous position ($r = 0.45$; individual variance component ± s.e. = 10.66 ± 2.15, log-likelihood test = 29.78 $p < 0.001$). However, PTG was not repeatable across morning and afternoon periods over both treatments ($r = 0.05$; individual variance component ± s.e. was 0.82 ± 0.66, log-likelihood test = 1.70, $p < 0.19$). Therefore, consistent individual differences in PTG were detected within treatments but this consistency disappeared across treatments, pointing to substantial behavioural plasticity.

(c) *Individual variation in foraging plasticity*

Our analysis suggested significant individual plasticity variation in PTG across safe and dangerous positions

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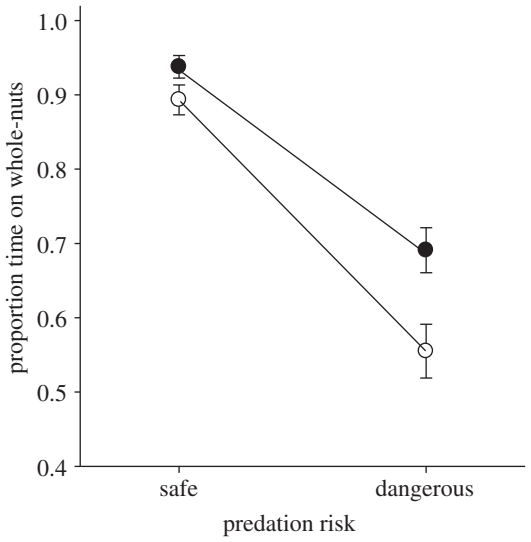


Figure 1. Change in the proportion of time spent on the good quality, whole-nut feeder (PTG) with respect to predation risk (safe and dangerous) and starvation risk (filled circles represent morning, high risk; open circles represent afternoon, low risk) treatments.

Table 1. Linear mixed model of PTG (the proportion of time individuals spent on the whole-nut rather than the granule feeder). 'EB', exploration behaviour; 'I', individual; 'feeder', feeder position; 'time', time of day. The I × time × feeder random effect just fell short of significance (log-likelihood = 2.7, $p = 0.11$). log-l, log-likelihood.

random model

effect	log-l	component ± s.e.
I	6.59**	−5.34 ± 1.32
location	24.41***	1.48 ± 0.93
I × location	4.62*	4.60 ± 1.39
I × feeder	28.49***	5.62 ± 1.49
I × time	7.07*	−1.01 ± 0.71
residual	—	9.21 ± 1.18

fixed model

effect	F (d.d.f.)	B ± s.e.
constant	—	3.24 ± 0.62
feeder	71.27 (116.0)***	2.25 ± 0.65[a]
time	4.68 (95.6)*	−1.81 ± 0.49[a]
age	1.13 (55.9)[n.s.]	−0.83 ± 0.43[a]
sex	1.18 (49)[n.s.]	−0.60 ± 0.59[a]
EB	0.6 (38.1)[n.s.]	0.61 ± 0.99
sex × feeder	0.68 (115.9)[n.s.]	0.75 ± 0.83[b]
sex × time	0.37 (97.1)[n.s.]	−0.30 ± 0.50[c]
EB × feeder	0.02 (114.5)[n.s.]	1.91 ± 1.39[a]
EB × time	8.49 (94.9)**	−3.87 ± 0.83[a]
EB × sex	0.01 (49.5)[n.s.]	−0.07 ± 1.29[a]
age × time	4.01 (94.4)*	1.04 ± 0.52[d]
feeder × time	11.57 (143.6)***	1.94 ± 0.64[e]
EB × feeder × sex	3.92 (114.0)*	−3.63 ± 1.83[f]
EB × time × sex	13.66 (98.1)***	4.04 ± 1.09[g]

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, n.s. > 0.05.
[a]Dangerous, morning, adult or female set to 0.
[b]Males in safe position; all other levels set to 0.
[c]Male in afternoon; all other levels set to 0.
[d]Juvenile in afternoon; all other levels set to 0.
[e]Afternoon in safe position; all other levels set to 0.
[f]Refers to male in cover position; all others set to 0.
[g]Males in afternoon; all other levels set to 0.

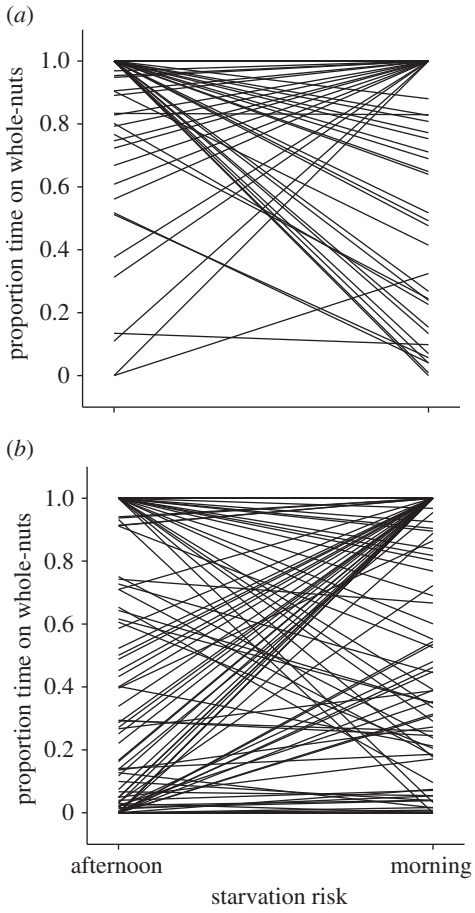


Figure 2. Reaction norm plots showing individual plasticity in the proportion of time spent on the good quality, whole-nut feeder (PTG) with respect to time of day when the whole-nut feeder was placed in the (*a*) safe ($n = 144$ birds) and (*b*) dangerous ($n = 133$ birds) positions, and the low quality granule feeder was placed in the opposing positions. Each line is drawn from raw data for separate individuals ($n = 2$ per individual); some birds that spent all time on one feeder type are obscured.

(individual × feeder position, table 1). While most individuals avoided the whole-nut feeder when this was in the dangerous position, some showed no change and others increased their use of whole-nuts (see electronic supplementary material; figure 1). There was also significant plasticity variation across morning and afternoon periods (individual × time of day, table 1), which suggested that while PTG was higher in the morning among the majority of individuals when presumably hungry, for some birds the opposite was true (figure 2). This temporal plasticity variation appeared to be most pronounced when the whole-nut feeder was in the dangerous position (figure 2*b*) and was less evident when in the safe (figure 2*a*; individual × time of day × feeder position, $p = 0.11$, log-likelihood = 2.70; model otherwise the same as in table 1). Therefore, individuals varied in the extent to which the proportion of time they spent feeding on the whole-nut feeder changed simultaneously along two different risk gradients.

(d) *State, exploration behaviour and foraging plasticity*

PTG was not directly age- or sex-dependent (main effects in table 1). Similarly, there was no overall variation between

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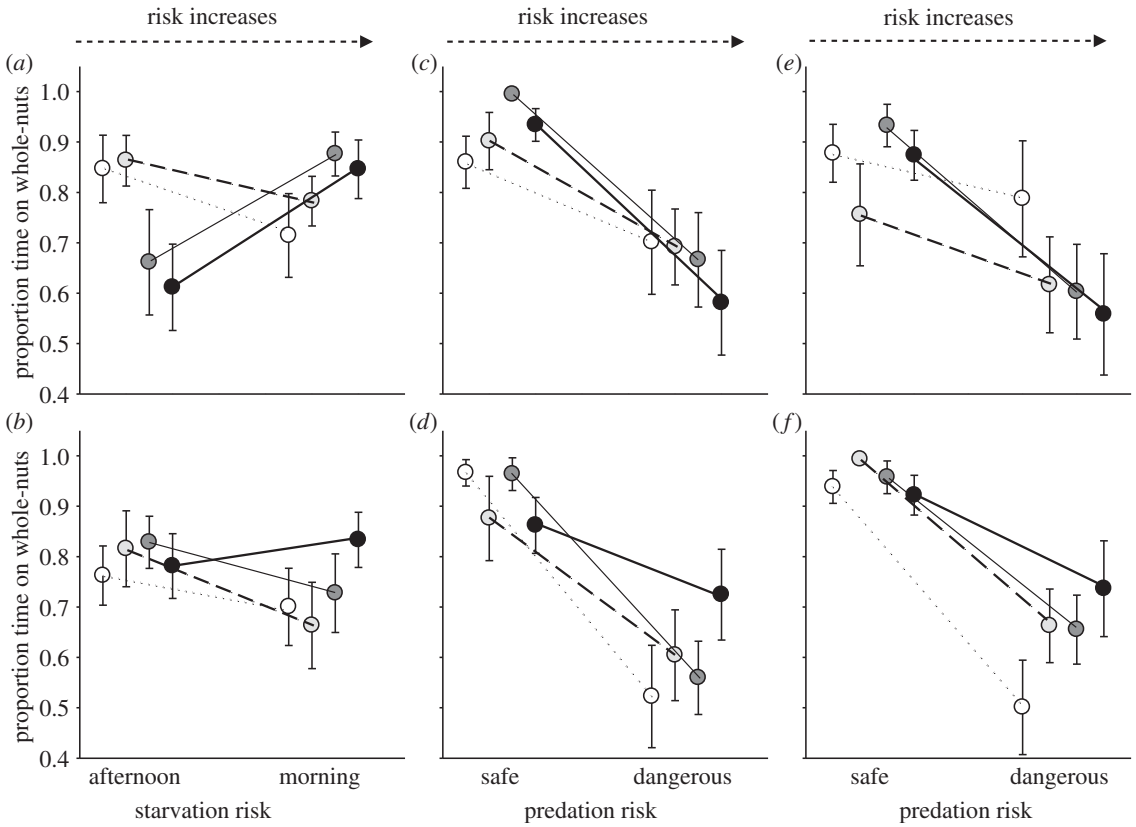


Figure 3. Exploration behaviour (EB: white circles, 0.12; light grey circles, 0.55; dark grey circles, 0.98; black circles, 1.40) and plasticity in the proportion of time spent on the good quality, whole-nut feeder (PTG) rather than on the granule feeder, with respect to a change in starvation risk for (*a*) females, (*b*) males and a change in predation risk for (*c*) females, (*d*) males, (*e*) juveniles and (*f*) adults. EB is split into four categories of equal width; values shown are the mid-range value for four equal intervals from −0.1 to 1.6. Data are raw means of individual values averaged across feeder position (*a*,*b*) or time of day (*c*–*f*) treatments. Sample sizes for individual points varied (mean ± s.d. = 16.12 ± 3.86, range 10–26 observations).

the sexes in how they responded to time of day or feeder position (two-way interactions in table 1). There was a marginally significant difference between adults and juveniles in their response over time of day (age × time of day, table 1), but the effect was negligible (back-transformed logits from morning to afternoon were, for males 0.99 and 0.96, and for first winter birds, 0.97 and 0.97). Therefore, individual variation in PTG when conditions changed could not be explained by age or sex.

PTG plasticity with respect to a change in time of day was linked to EB (time of day × EB, table 1). This suggested that while slow-exploring individuals showed little or no change, fast explorers reduced their PTG in the afternoon, an effect that appeared to be only present in females (EB × time of day × sex, $F_{1,110} = 13.7$, $p < 0.001$, figure 3*a*,*b*).

PTG plasticity with respect to feeder position was not related to EB across all individuals (feeder position × EB, table 1) but was related to EB within sexes (EB × feeder position × sex, table 1; figure 3*c*,*d*). Among females, PTG varied relatively little across feeder positions for slow-exploring individuals, while the opposite was true for fast females. Among males, the opposite pattern was observed. Finally, there was a tendency for PTG plasticity with respect to feeder position to vary with age (EB × feeder position × age, $F_{1,110} = 3.7$, $p = 0.057$ when dropped before the final model was selected). This suggested that among first winter birds, fast individuals showed greatest plasticity in PTG with respect to predation-risk variation but among adults, slow birds showed the greatest plasticity (figure 3*e*,*f*).

4. DISCUSSION

Great tits traded-off the risks of starvation and predation during this study because they prioritized feeding on good quality food—that is, they became more starvation-risk averse—when starvation risk was highest in the morning or predation risk was lowest near cover. Our analyses demonstrated significant individual plasticity variation (individual × environment or I × E effects) simultaneously across two risk gradients. Although this variation was not directly related to sex or age, it was linked to our measure of personality, EB, in a sex- or age-dependent manner.

(a) *Individual consistency and plasticity variation*

Most empirical research on phenotypic plasticity has been at the level of changes within populations over time, or differences between genotypes in different locations or subpopulations, often focusing on non-labile traits under experimental conditions [51]. Here, we show that although PTG differed consistently between individuals within treatments, individual great tits varied substantially in the extent to which they traded-off the risks of starvation and predation when two different types of risk changed. There was relatively little variation between

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individuals when the whole-nut feeder was in the safe and the granule feeder was in the dangerous position, as most individuals behaved in a starvation-risk-averse manner because there was little cost involved with doing so. Repeatability was low in this treatment because the majority of individuals behaved similarly and therefore we do not emphasize the lack of consistency across treatments. Instead the plasticity variation or I × E is notable for two reasons. First, it explained a significant amount of variation over and above the individual random effects. Detecting significant I × E is often difficult [3,52,53] even when reaction norm plots visually suggest substantial plasticity variation [54]. Second, our results suggest plasticity variation along two independent 'gradients', linked to spatial and temporal variation in the risks of predation and starvation, respectively. Plasticity variation along even a single axis emphasizes the limitations of studying variation using average effects, but this demonstration of two simultaneous forms of plasticity variation further emphasizes the limitations of looking at mean effects alone across a heterogeneous environment [5,41]. Finally, most previous attempts to quantify plasticity variation using a mixed-model approach have been on life-history and morphological traits [55,56]. A recent review identified 14 studies that examined I × E in a range of behaviours [3], half of these using a mixed-model approach and two in the context of predation risk [57]. Our current study, however, represents the first clear demonstration of significant individual variation in behavioural plasticity in the context of the trade-off between foraging and anti-predation behaviour.

(b) *Exploration behaviour and the starvation–predation trade-off*

EB is influenced by both additive genetic and environmental sources of variation in the Wytham population [31,58], where it also predicts dispersal, competitive ability, promiscuity and reproductive fitness [31,34,36,38]. Here, we show that EB also predicts how individuals managed the key trade-off between foraging and anti-predation behaviour, adding to the idea that it represents an important personality axis of variation [4]. Our results show that EB correlated positively with a tendency to prioritize feeding on high quality food when starvation risk was naturally highest in the morning (for females), and to do the same when predation risk was experimentally increased (for males and adults), supporting the hypothesis that personality reflects life-history variation [4,7,10,14,59]. In addition to being one of the few experimental tests of the hypothesis [8], this represents perhaps an advance on previous findings for several reasons. First, previous studies have suggested that personality variation probably arises because of variation in risk or other environmental factors across a relatively large spatial scale—across populations or in spatially isolated niches within populations [26,60]. In contrast, our predation-risk categories were only 10 m apart within locations, suggesting that personality variation can be linked to fine-scale environmental variation within a population. Second, although some personality traits have previously been linked to foraging behaviour [61,62], here we show that personality predicts responses to changes in the risk of starvation specifically, which was the strongest effect involving EB. Slow females showed relatively little change in PTG during the day but fast females showed highest starvation risk aversion in the morning when starvation risk is generally thought to be highest.

Against predictions of the trade-off hypothesis, however, slow females and slow juveniles were less responsive than fast females and fast juveniles, respectively, to a change in predation risk. There was a tendency for slow females and juveniles to have relatively lower access to the poor quality, granule feeder when in the low predation-risk position, or relatively higher dependency on the granule feeder when in the high predation-risk situation. This unexpected tendency to be more, not less, predation-risk prone is likely explained by differences in competitive ability at the low quality feeder when near cover. Previous research shows that competition is high at poor quality, granule feeders when near cover [38]. Given the positive correlation between dominance and EB in our population [37,38], and the tendency for females and juveniles to be subdominant in this species generally [42], slow females and juveniles were likely to be the least-dominant individuals, explaining their relatively high usage of the good quality feeder in the dangerous position but their lower usage of the poor quality feeder in the safe position. Also against predictions of the productivity hypothesis, EB did not predict how males responded to a change in starvation risk, reasons for which are not readily surmised. Therefore, we conclude that support for the trade-off hypothesis in our population is strong but nevertheless dependent on an individual's state (age and sex) and the specific risk-gradient.

(c) *General conclusions*

Two broad conclusions can be drawn from our field experiment. First, foraging behaviour in the context of the trade-off between foraging and anti-predation behaviour is influenced by multiple sources of individual variation: consistent differences within environments, plasticity variation across environments and state-dependent links with a personality axis of variation. They support the assertion that mean effects alone are unlikely to explain behavioural decisions made [7,18,19,63] and add to the growing evidence that simple personality traits predict constraints on behavioural variation generally. Nevertheless, few studies have yet to establish whether such constraints have a genetic basis in natural populations [64,65]. Second, our results support general theoretical expectations about the evolution of personality because EB was linked to important axes of life-history and environmental variation [7,8,10]. Furthermore, uncertainty is an important element of many theoretical models [7,8,10,13,15] and in our study is reflected in the mismatch between the perceived and actual risks associated with the fine-scale spatio-temporal gradients we consider. While selection estimates for personality traits and behavioural syndromes are still relatively scarce [17], elsewhere the absence of annual survival selection in EB in our population is reported [31]. This lack of survival selection could be explained by fine-scale fluctuating selection inferred by the fine scale of the risks we examine, though we note that it could also be explained by generally high levels of

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plasticity, a possibility that is supported by the strongly context-dependent link between personality and the trade-off. Finally, we note that the possibility of such an evolutionary mechanism does not preclude a role for frequency-dependent selection, because the costs and benefits for different personality types that arise owing to either (i) the risks of starvation or predation or (ii) competition are likely to be frequency-dependent.

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Appendix C

Who are the innovators? A field experiment with 2 passerine species

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Original article

Who are the innovators? A field experiment with 2 passerine species

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Ecological and evolutionary drivers of innovativeness among species are relatively well studied, but the significance of similar variation within species is much less well understood. Using automated foraging devices, we conducted the first large-scale study of novel problem-solving performance in a wild bird population to test whether variation in innovativeness can be explained by inherent individual differences and by factors related to the "necessity drives innovation" hypothesis. We detected 20145 visits by 236 great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) and found consistent individual differences in the propensity to solve and in the time spent at devices between successive solutions in the field. Although individuals that were successful in a similar version of the task in captivity solved 3 times faster in the wild than those that were unsuccessful in captivity, success in captivity did not predict success in the wild. Thus, innovative propensity varies among individuals but it is also context dependent. Juveniles were more likely to solve the problem in the wild than adults, supporting the necessity drives innovation hypothesis. We found no evidence for social learning at problem-solving devices in the wild. The consistent individual differences in novel problem-solving performance we report suggest that innovativeness may be of adaptive significance within our population. Our results also suggest that selection for innovativeness may occur primarily among juveniles. *Key words:* age differences, innovation, personality, problem solving, social learning, state. *[Behav Ecol]*

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INTRODUCTION

Innovation—solving a novel problem or finding a new solution to an old one—is a process by which individuals can broaden their behavioral repertoire (Kummer and Goodall 1985) and is therefore an important aspect of behavioral plasticity (Reader and Laland 2003). The propensity to innovate can have important ecological and evolutionary implications. For instance, innovative bird taxa are more likely to survive when introduced to novel environments (Sol et al. 2005) and show a greater number of species per taxon, suggesting a link between innovativeness and speciation rates (Nicolakakis et al. 2003).

Despite the potential importance of innovation in population responses to anthropogenic perturbations and its central role in the appearance of local traditions and culture, conceptual and empirical work on innovation is still in its infancy (Ramsey et al. 2007). One important challenge in the field is judging the novelty of the behavior against the established repertoire of an individual or a population. An extensive study by Van Schaik et al. (2006) on wild orangutans established that 3000 observation hours were required to obtain a stable inventory of the population's behavioral variants. Detailed knowledge of this kind is rarely available. An alternative approach is to examine the success and efficiency of individuals presented with a novel problem, most often in the foraging context (e.g., Fragaszy and Visalberghi 1990; Laland and Reader 1999a; but see Keagy et al. 2009). Studies using this "novel problem" approach reveal a significant amount of interspecific variation in problem-solving performance, with species that are generally more dependent on manipulative foraging and less neophobic being better at solving novel tasks (Webster and Lefebvre 2001; Day et al. 2003; Seibt and Wickler 2006).

In addition to interspecific variation, it is generally recognized that individuals differ in their propensity to innovate, but the evolutionary significance of this variation is poorly understood (Reader 2003). We suggest that this is for 3 main reasons. First, most studies have scrutinized isolated individuals in captivity (but see Biro et al. 2003; Gajdon et al. 2006; Keagy et al. 2009; Boogert et al. 2010), where conditions are unlikely to reflect realized innovation rates in natural social and environmental conditions (Morand-Ferron et al. 2004). Because the cross-contextual consistency of individual innovative tendencies has rarely been assessed (Pfeffer et al. 2002), it is generally unknown whether results from the lab can be used to draw general conclusions on individual variation in innovativeness in a natural selective environment. Second, evaluating consistency of individual differences in the propensity to innovate is essential when assessing whether the observed phenotypic variation is likely to have an additive genetic basis and therefore to be of evolutionary significance (Roff 1997; Bell et al. 2009). Whether individuals consistently differ in their propensity to innovate has never been measured explicitly under natural conditions (Bell et al. 2009). The third reason is that, over and above inherent individual differences, it remains unclear what factors (e.g., sex, age, and dominance rank) influence the propensity to innovate (Reader 2003). Not only would these factors lead to heterogeneous selection on innovativeness within the population, they could also influence how novel behaviors spread through the population via social learning (Laland 2004; Van de Waal et al. 2010).

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The "necessity drives innovation" hypothesis states that innovation occurs predominantly when established behaviors are unsuccessful. It therefore predicts a negative relationship between competitive ability and innovativeness because good competitors enjoy better access to limiting resources (Laland and Reader 1999a, 1999b; Reader and Laland 2003). Although this relationship has been demonstrated in wild primates (Reader and Laland 2001) and male guppies (Laland and Reader 1999b), other studies have found no relationship (Gajdon et al. 2006; Bouchard et al. 2007) or even a positive relationship between social dominance and innovativeness (Boogert et al. 2006). Juveniles are expected to innovate more frequently than adults because they are usually subordinate and show a greater propensity to explore new objects (Greenberg and Mettke-Hofmann 2001; Biro et al. 2003; Biondi et al. 2010). Contrary to this prediction, a review on wild primates (Reader and Laland 2001), as well as a study on captive families of callitrichid monkeys (Kendal et al. 2005), found adults to be more innovative than juveniles. Although small and food-deprived guppies could find a novel food source more quickly than larger and well-fed conspecifics (Laland and Reader 1999b), recent avian studies report no effect of body condition (Boogert et al. 2010; Overington 2010; Cole et al. 2011) or motivation (Keagy et al. 2009) on problem-solving success. Empirical tests thus provide conflicting evidence for the necessity drives innovation hypothesis.

Here, we use the novel problem approach to explore individual variation in innovative problem solving among mixed-species flocks of wild passerines and compared the consistency of individual performance in the wild and in captivity for great tits (*Parus major*). We also include data from the wild for the closely related blue tit (*Cyanistes caeruleus*). We follow captive studies using the novel problem approach and operationally define innovators as those individuals that solved the problem and noninnovators as individuals not solving the problem. Previous work on great tits from our population shows that innovative problem-solving performance in captivity differs consistently between individuals, that these differences are maintained over time spans of up to a year and across different types of novel foraging problems, and are unrelated to other personality traits, including neophobia and exploration behavior (Cole et al. 2011; Cole EF, Quinn JL unpublished data). Great tits and blue tits form the core of winter mixed-species flocks in Wytham (Hinde 1952) and are ideal models for the study of innovative problem solving for several reasons. First, they are known to spontaneously innovate at high rates in the wild (Fisher and Hinde 1949; Estók et al. 2009; Overington et al. 2009). Second, great and blue tits born or breeding in Wytham are fitted with a unique passive integrated transponder (PIT) tag, allowing the behavior of large numbers of marked individuals to be remotely monitored in the field. Finally, social dominance hierarchies have been well studied in these species, enabling a test of the necessity drives innovation hypothesis: great tits are dominant over other tit species (Hinde 1952); males are dominant over females, and within sexes adults are dominant over juveniles (Saitou 1979; Barluenga et al. 2000); larger individuals are dominant over smaller ones (Garnett 1981; Maynard-Smith and Harper 1988; Barluenga et al. 2000); and individuals closer to their breeding territory are usually dominant over those breeding further away (Brian 1949; Drent 1983; De Laet 1984). Moreover, subdominant individuals face a greater risk of starvation and are therefore known to carry a larger amount of body reserves than dominant individuals (Gosler 1996; Gosler and Carruthers 1999).

We tested the following predictions: 1) individuals differ consistently in the probability of solving a novel foraging problem in the wild; 2) individual problem-solving performance in captivity predicts performance in the wild; lack of an effect would suggest plasticity in the propensity to innovate depending on the environmental conditions. If innovation is indeed driven by necessity, we also predict: 3) subdominant individuals—blue versus great tits, females versus males, juveniles versus adults, smaller individuals, and individuals further away their breeding territory—to show increased use of problem-solving devices, be more likely to solve the problem and reach their first solution more quickly than dominant individuals; and 4) a positive relationship between body reserves and problem solving in the field. Finally, 5) we examine the possibility that the solution to this novel foraging problem was learned socially by examining whether innovations occurring later in the course of our field experiments were characterized by increased efficiency (Boogert et al. 2008), assuming that the amount of social information potentially available to naive individuals in the wild increased with the number of successful innovators and therefore with time.

MATERIALS AND METHODS

Study site and general protocol

The study took place in Wytham Woods (lat 51°46′N, long 1°20′W), Oxfordshire, UK, from 2 February to 15 March 2010. Five locations in different areas of the Woods were chosen so as to maximize the distances, and minimize the differences, between the locations (i.e., presence of an open area with dense cover nearby). A multiaccess feeder filled with black husked sunflower seeds was installed at a location 5–7 days prior to catching to increase the local density of birds. We then used mist nets to consecutively catch 2–3 batches of 5–16 great tits over 3 days; all birds were caught under ringing licenses from the British Trust for Ornithology. Birds were aged (adult or juvenile if less than 1 year old) and sexed based on plumage (Svensson 1992). We recorded wing length, mass, and fat score (Gosler 1996) for all individuals caught. Fat score is inversely related to individual quality (Gosler and Carruthers 1999) and is correlated across seasons within individuals (Gosler and Harper 2000). All unringed individuals were fitted with a unique metal leg-ring and unique PIT tag (Core RFID ltd Warrington, UK) which was attached to a celluloid split color leg-ring. Birds were transported singly in bird bags to the nearby John Krebs field station, where they were housed in individual cages, and isolated visually but not acoustically from each other. We examined individual performance on an overnight lever-pulling task and released birds at their point of capture 24–48 h later (see below for details). Two days after releasing the last batch of birds at a location, we installed 6 automated lever-pulling devices and ran field observations for 5–7 days before removing the devices and proceeding to the next location.

Captive assays

The general procedure in captivity was similar to that detailed in Cole et al. (2011). One hour before lights-off on the day of catching, each lever-pulling device was baited with 4 waxmoth larvae (*Pyralis farinalis*). These devices were made of a vertical perspex column, and a single shelf held in place by a lever, which had to be removed by the bird to gain access to the reward. Lever-pulling success (yes or no) was assessed at 08:00 h on the next day, that is, 2 h after sunrise. Around 15:00 h, individuals were released at their point of capture.

Field observations

We used 6 automated lever-pulling devices (Figure 1; see also Supplementary Material), each installed on a 1.5 m wooden

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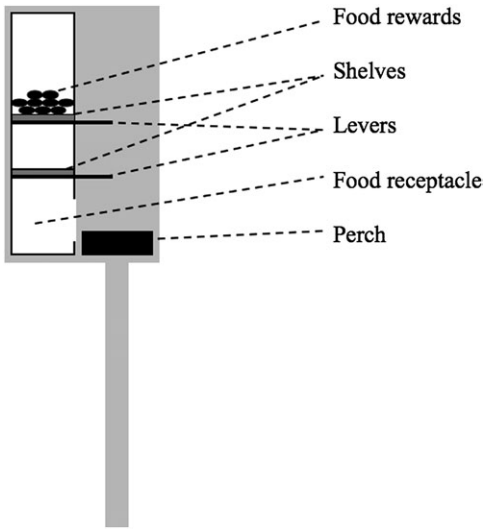


Figure 1
Schematic depiction of a lever-pulling device used in the field (not to scale). The device (left) was made up of a transparent perspex tube and 2 shelves held by metallic sticks. The perch (right) was equipped with a PIT tag reader. Both components were connected to a battery-operated logger from which the data could be exported and saved using a laptop. Each device was baited with 30 sunflower seeds sitting on the top shelf; both sticks had to be pulled in either order, to release the 30 seeds in the bottom compartment where they could be collected by birds.

pole planted in the ground, 1–4 m from tree cover. We assumed the use of many devices per location reduced the probability of monopolization by dominant individuals (Drea 2006; Boogert et al. 2008). Each device was made from a transparent perspex tube and 2 shelves held by metallic levers. These devices required the same type of solution as the task in captivity, that is, pulling a lever out, which caused the food to fall from a shelf into a receptacle where it was available for consumption. The automated devices, however, required 2 levers to be removed in either order before accessing food, compared with one lever in the captive task. The second lever allowed us to examine acquisition of double lever-pulling behavior as an additional measure of problem-solving propensity that can be used to compare the behavior of captive solvers versus nonsolvers in the wild. Once pulled out, the levers had to be replaced by the experimenter, thereby preventing individuals from pulling levers on a device depleted of its rewards. The timing of the removal of each lever was automatically recorded by a battery-operated data logger. A PIT reader located in the perch, 2 cm away from the perspex lever-pulling device, recorded the timing and duration of visits by marked individuals. The perch was small enough so that only one bird could sit on it at a time.

After installation, we baited each device with 30 sunflower seeds and left the site. Sunflower seeds were also provided in a standard multiaccess feeder installed at each location 5–7 days before capture and after each daily observation period; birds should therefore be familiar with this food type. We checked the devices every 40 min and rebaited those that had been successfully opened with 30 sunflower seeds, leaving the other devices untouched. We ran this protocol for approximately 6 h per day between 10:00 and 17:00 h, 5–7 days per location, depending on weather conditions (no observations under rain or snow). The devices were left at the site for the whole duration of the experiment in order to minimize disturbance at experimental locations and reduce neophobia responses by the birds.

We used 86 min of video footage recorded at 3 locations to check 1) the rate of error in attributing solving events to PIT-tagged versus non-PIT individuals; 2) the rate of nondetection of PIT-tagged individuals; and 3) the duration of detection gaps when a PIT-tagged bird was still present at the device but stopped being detected, for instance when a bird hopped on other parts of the device than the perch but then returned to the perch without leaving the device. The percentage of visits by PIT-tagged individuals was 70.4% ($N = 100$ of 142 visits by PIT and non-PIT birds). All 9 levers pulled out during these 86 min were properly attributed to PIT versus non-PIT individuals. The rate of nondetection was 13 of 99 visits (13.1%), but all of these except one (3 s) were for visits shorter than 2 s, suggesting that nondetection had a very low probability of leading to nonattribution of a solving event to a PIT-tagged bird. Maximal gap in detection records within a same visit by an individual was 12 s (mean ± standard deviation = 6.71 ± 2.64). We therefore defined a "visit" as a collection of detections separated by less than 12 s. We defined an "attempt" as a visit made to a baited device, which could be solved (i.e., with 1 or 2 levers to be removed before obtaining the food reward). We defined a successful "solving event" as an attempt leading to the device being opened, with 30 sunflower seeds becoming freely available to any bird for each solution.

The species, sex, age (adult or juvenile), and wing length (used here as a measure of body size; Gosler et al. 1998) of all marked individuals was recorded when they were initially ringed; sex and wing length of individuals ringed as nestlings and not caught as adults were therefore not available. Nest-box coordinates (Wilkin et al. 2006) were used to calculate a linear distance between breeding territory and the experimental location used by PIT-tagged individuals. We used Wytham coordinates for nest-boxes occupied in the 2010 breeding season, or in 2009 if the bird had not been recorded in 2010. For Wytham breeders detected at 2 ($N = 5$) or at 3 experimental locations ($N = 1$), we used the last location to calculate distance from territory.

Statistical analyses

When examining which variables predicted whether an attempt would lead to solving or not, we used a generalized linear mixed-model (GLMM with Laplace approximation, family = binomial with logit link, package "lme4") (Bolker et al. 2008). We included random factors for "location" and "individual" to control for nonindependence of data points collected at the same location and to take into account pseudoreplication caused by including several attempts per individual (Bolker et al. 2008). We also used a binomial GLMM including a random factor for location when analyzing the characteristics of birds that solved at least once in the field versus those that never solved. There was no overdispersion in the GLMMs (Crawley 2007). We used a linear mixed-model (LMM; package "nlme") including a random factor for location when examining determinants of the total number of visits to devices (log-transformed) and latency to first solution by successful individuals (log-transformed number of seconds spent at baited devices before first solution, $N = 33$). In order to examine the significance of individual differences in behavior, we compared models differing only in the presence or absence of a random intercept for individual using likelihood ratio tests (Pinheiro and Bates 2000; Bolker et al. 2008). For these tests, we provide information on the proportion of variance accounted for by individual differences in behavior (repeatability; Nakagawa and Schielzeth 2010). All analyses were conducted in R version 2.9.2 for Mac (R Development Core Team 2010).

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Table 1

Predictors of individual problem solving success (0 or 1) when visiting a baited device under natural conditions in Wytham Woods

Attempt leads to solving or not

	Estimate ± SE	*Z*	*P*
Device state	0.30 ± 0.16	1.88	0.060
Duration of visit	0.06 ± 0.01	5.15	<0.001
Time of day	−0.03 ± 0.04	−0.76	0.449
Previous attempts	0.05 ± 0.01	7.33	<0.001

Analyses are from a GLMM of 4775 attempts by 197 individual great and blue tits (family = binomial, link = logit). "Location" and "individual" were included as random effects.

Device state is 1 or 2 (reference) levers to pull for the device to be solved, Duration of visit in seconds, Time of day to the closest hours, Previous attempts are the number of visits to baited devices by this individual before the current attempt.

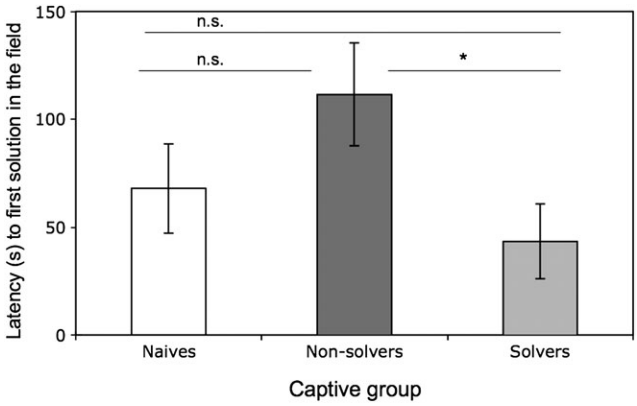


Figure 2

Latency to first solution in the field in relation to captivity group: naives ($N = 13$), captive nonsolvers ($N = 13$), and captive solvers ($N = 7$). Latency was defined as the mean ± SE number of seconds spent at baited devices before an individual's first solving event in the field. "n.s." indicates no significant difference in Tukey post hoc comparisons, whereas the "*" indicates $P < 0.05$.

RESULTS

Problem solving in the wild

We detected 20145 visits by 236 PIT-tagged birds (173 great tits and 63 blue tits) over 31 days of observation. The number of visits by individual birds to the devices ranged from 1 to 750 (median = 38, mean ± standard error [SE] = 83.5 ± 7.0). We recorded a total of 313 solving events over 4775 attempts (proportion of successful attempts = 6.6%). Forty-three individuals (18.0%) removed at least one lever, and 33 (13.8%) solved the device either by pulling the second lever or both levers within a visit. Even when restricting the dataset to the 117 birds that visited the device as frequently as the solver with the smallest number of visits (42 visits for a total duration of 99.5 s spent at devices), the proportion of successful individuals was still quite low, with only 28.2% of birds solving 1–61 times (median = 4, mean ± SE = 9.5 ± 2.4).

The probability of success increased with duration of attempt and number of previous attempts and tended to be higher when only one lever remained to be pulled out rather than 2 but was independent of time of day (Table 1). Controlling for these effects, there were significant individual differences in problem-solving success among birds that visited devices at least once while they were baited (repeatability = 0.86; Likelihood ratio test: $\chi^2 = 333.9$, degrees of freedom [df] = 1, $P < 0.001$). Successful individuals were consistent in the time they needed to reach each successive solution (repeatability = 0.34; Likelihood ratio test: $\chi^2 = 30.4$, df = 1, $P < 0.001$), and this time decreased over successive solving events (LMM: $F_{1,302} = 32.0$, $P < 0.001$).

Problem solving in captivity versus in the wild

We assayed and released a total of 177 great tits near the 5 experimental locations. Among these birds, 96 (54.2%) were subsequently detected at devices in the wild. The probability of detection of captive solvers (40/68 = 58.8%) did not differ from that of captive nonsolvers (56/109 = 51.4%) (chi-square test: $\chi^2 = 0.15$, df = 1, $P = 0.700$). Among the 36 captive solvers that made at least one attempt in the wild, 8 (22.2%) also solved in the wild versus 11 of 52 (21.1%) for nonsolvers, suggesting captive solvers were no more likely to solve than captive nonsolvers (chi-square test: $\chi^2 = 0.01$, df = 1, $P = 0.905$). Including individuals assayed in 2009 according to the same captive protocol and now exhibiting one or more problem solving attempts in the field ($N = 9$, total = 97) did not change this conclusion (chi-square test: $\chi^2 = 0.03$, df = 1, $P = 0.865$). Captive solvers and nonsolvers did not differ in total number of visits (2 groups *t*-test: $t = 0.31$, df = 94, $P = 0.761$), mean duration of attempts (2 groups *t*-test: $t = -0.94$, df = 86, $P = 0.353$), total number of levers pulled out (2 groups *t*-test: $t = -0.05$, df = 94, $P = 0.960$), or percent successful attempts in the wild (Mann–Whitney test: $U = 917$, $n = 88$, $P = 0.823$).

However, among successful individuals in the wild, captive solvers reached their first solution 3 times faster than captive nonsolvers; neither of these 2 groups differed significantly from naive birds, that is, not taken into captivity in 2010 (Figure 2; Analysis of variance: $F_{2,30} = 5.56$, $P = 0.009$; Tukey post hoc comparisons: solvers vs. nonsolvers: $P = 0.007$; solvers vs. naive: $P = 0.245$; nonsolvers vs. naive: $P = 0.142$). Among individuals that pulled out at least one lever in the wild, a similar proportion of captive solvers (6/10 = 60%) and nonsolvers (8/15 = 53.3%) were capable of pulling both levers in one attempt (chi-square test: $\chi^2 = 0.11$, df = 1, $P = 0.742$).

Individual determinants of problem solving in the wild

We found no effect of species, sex, or wing length on the total number of visits to problem-solving devices in the field; however, juveniles visited the devices more often than adult birds (Table 2). This was not due to juveniles using the devices earlier in the season, or visiting devices faster than adults at each location (date of first visit: LMM: $F_{1,170} = 1.38$, $P = 0.242$; order for first visit within a location: LMM: $F_{1,170} = 2.07$, $P = 0.152$). There was no effect of species, sex, or wing length on the probability of solving the problem at least once in the field, but there was a tendency for juveniles to be more likely to solve than adults ($P = 0.069$; Table 2; Figure 3). An additional analysis excluding other non-significant terms suggested a slightly stronger effect (Figure 3c; GLMM: Wald test: $z = 2.03$, $P = 0.042$). The higher problem-solving success of juveniles was not due to increased efficiency as the observed age-class effect disappeared when controlling for total duration of attempts (GLMM: Wald test: age class: $z = 0.62$, $P = 0.537$; attempts: $z = 4.96$, $P < 0.001$). Instead juveniles seemed more perseverant than adults because they engaged in longer unsuccessful attempts (mean ± SE = 4.12 ± 0.17 s

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Table 2

Predictors of (a) total number of visits (log-transformed) and (b) overall solving success (binary response) by individual great and blue tits under natural conditions in Wytham Woods

	(a) Total number of visits			(b) Solved at least once or not		
	Estimate ± SE	F	P	Estimate ± SE	Z	P
Species	−1.32 ± 1.24	1.14	0.287	−1.70 ± 2.06	−0.83	0.408
Sex	0.10 ± 0.37	0.08	0.782	0.39 ± 0.57	0.68	0.500
Age	1.62 ± 0.32	26.0	<0.001	1.17 ± 0.65	1.81	0.069*
Wing length	0.007 ± 0.10	0.01	<0.942	−0.02 ± 0.14	−0.17	0.867

Estimates and their standard error as well as value of the statistic and statistical significance were generated from LMM and GLMM models, respectively ($n = 176$, df = 1, 167). Each model included a random effect for "location." Species is *Cyanistes caeruleus* or *Parus major* (reference set to zero), Sex is female or male (reference set to zero), Age is juvenile or adult (reference set to zero).

*$P = 0.042$ when Age was included in a reduced model on its own.

vs. 2.73 ± 0.31 s, respectively; LMM: $F_{1,193} = 18.04$, $P < 0.001$). Individuals visiting devices located closer to their breeding territory did not use them more often (LMM: $F_{1,103} = 0.17$, $P = 0.680$) and were no more likely to solve the problem (GLMM: Wald test: $z = 1.19$, $P = 0.233$) than birds further away from their territory. Fat score at capture did not predict total number of visits to the devices (LMM: $F_{1,85} = 0.12$, $P = 0.730$) or problem-solving success in great tits (GLMM: Wald test: $z = -0.95$, $P = 0.344$).

Controlling for captivity group (Figure 2: captive solvers, captive nonsolvers, or naive birds), the latency to the first solution by great tits in the field did not depend on sex (LMM: $F_{1,20} = 0.07$, $P = 0.793$), wing length (LMM: $F_{1,20} = 0.03$, $P = 0.870$), or fat score (LMM: $F_{1,10} = 0.97$, $P = 0.349$). The numbers of blue tit solvers ($N = 5$), adult solvers ($N = 3$), and the number of solvers with known distance from their breeding territory ($N = 12$) were too low to examine the effect of these variables on latency to the first solution in the field.

Social learning in the wild?

The date of initial contact with a problem-solving device in the field did not predict latency to first solution (within locations: LMM: $F_{1,27} = 0.01$, $P = 0.919$; over all locations: linear regression: $F_{1,31} = 0.13$, $P = 0.721$), suggesting that individuals that had potentially more time to acquire social information were not more efficient innovators. Moreover, the latency to first solution did not decrease with an increasing number of first solutions being recorded at a location (in fact this latency increased: LMM: $F_{1,27} = 8.6$, $P = 0.007$), suggesting that the innovation process was not influenced by the potential accumulation of social information in the local population.

DISCUSSION

Our automated lever-pulling devices allowed us to conduct the first large-scale empirical investigation of individual differences and cross-contextual consistency in problem-solving performance in a wild bird population. Despite the very high number of attempts, only a small proportion of individuals solved the problem, suggesting it was a nontrivial task for tits. The probability that a bird solved the problem increased over successive attempts and the time spent trying to open baited

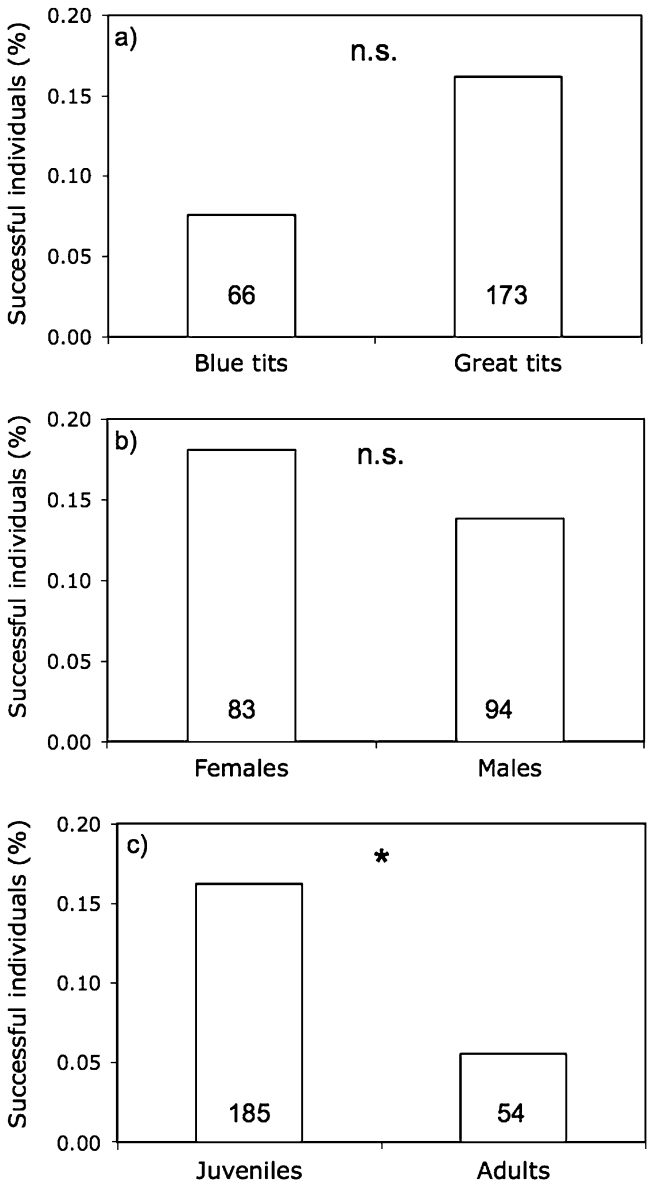


Figure 3
Percentage of individuals that solved the problem at least once in the field according to (a) species, (b) sex, and (c) age class. Numbers in bars indicate sample size for each category. "n.s." indicates no significant difference in a GLMM on problem-solving success, whereas the "*" indicates $P < 0.05$.

devices decreased between successive solutions, demonstrating increased individual performance over time: Birds were learning the solution. However, we found no evidence for social learning of the solution in the field. Individuals differed consistently in the probability of solving the task at each attempt, and in the time spent at devices between successive solving events, pointing to quantitative sources of variation in performance on this task in the wild; an additive genetic basis to at least part of this variation would suggest our measure of innovative problem solving is the target of natural selection. Recent studies on behavioral variation have emphasized the importance of measuring consistency when drawing conclusions about the evolutionary significance of behavioral variation under natural conditions (Dingemanse and Réale 2005; Oers et al. 2005; Sih and Bell 2008). Two studies have

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examined performance of marked individuals on different tasks in the field and report nonsignificant correlations in problem-solving performance (Keagy et al. 2009; Boogert et al. 2010). However, to our knowledge, our study is the first to explicitly assess cross-contextual and temporal within-task consistency in innovative problem solving under natural conditions.

The propensity to solve in captivity did not predict the propensity to do so in the wild, which contrasts with the consistency reported previously in this population for a similar task in captivity, both across sessions and years (Cole et al. 2011). Moreover, a similar proportion of captive solvers and nonsolvers was capable of pulling both levers during the same attempt in the field. This lack of cross-contextual consistency is surprising considering that both tasks required birds to pull out lever(s) to access food. Indeed, captive solvers innovated 3 times faster in the wild than captive nonsolvers, suggesting that they benefited from their recent experience with a task requiring similar motor actions and/or that they were inherently better at solving problems. The use of an innovative food-processing technique in individual Carib grackles (*Quiscalus lugubris*) also did not correlate between the isolated captive context and the natural social context (Morand-Ferron et al. 2004). Differential individual tendencies to scrounge (Beauchamp 2001; Giraldeau and Dubois 2008; Kurvers et al. 2009) and/or differential responses to predation risk (Quinn and Cresswell 2005; Rieucau et al. 2010) or to the social context (Magnhagen and Staffan 2005; Stöwe et al. 2006; Piyapong et al. 2010) in nature could result in weak cross-contextual consistency if these tendencies are uncorrelated with innovativeness in captivity. Scrounging was indeed observed in the field, as each reward consisted of 30 seeds while a bird could carry only one seed at a time. Although scrounging was not an option when none of the devices were solved or when rewards were depleted, previous visits providing scrounging opportunities might have led to exclusive investment in this alternative tactic by some individuals (Giraldeau and Caraco 2000). It is also possible that captive solvers suffered interference or invested more than captive nonsolvers in antipredatory or social vigilance while attempting to solve the problem, although we did not detect a difference in mean duration of attempts between these 2 groups.

We report significant individual differences in the probability of solving a novel problem in a wild population (reviewed in Reader 2003). These individual differences could not be explained by species, sex, body size, distance to breeding territory, or fat score. It is possible that these variables would have had an impact if socially dominant individuals could monopolize the devices (Fragaszy and Visalberghi 1990; Gajdon et al. 2004), which we tried to avoid by providing 6 devices at each location. However, we found juveniles to be more likely than adults to solve the problem at least once in the field; a similar, but weak effect, was also observed in our captive assays (Cole et al. 2011). This effect was unlikely to be due to a difference in physical strength, as juveniles in their first winter are as heavy and large as adult great tits (Gosler 1993). Because the difference in innovativeness between juveniles and adults in the field disappeared when controlling for total duration of attempts, and because juveniles used devices more frequently and engaged in longer unsuccessful attempts than adults, we conclude that juveniles are more innovative because they make greater use of alternative food sources and are more perseverant rather than because they have better technical or cognitive abilities. A similar finding was observed in captive caracaras (*Milvago chimago*) presented with a novel problem: Although juveniles opened more lids for food in total, once controlling for effort they were no more efficient than adults (Biondi et al. 2010). Few studies have examined individual differences in innovative problem solving in the wild, but those that have done so report no age effect (Keagy et al. 2009), or they report increased success in adults (Gajdon et al. 2006). Our findings, along with those from Biro et al. (2003), bring support to the necessity drives innovation hypothesis, which predicts increased innovation rates in poor competitors and therefore in juveniles compared with adults (Laland and Reader 1999a, 1999b; Reader and Laland 2003).

Socially mediated learning by captive nonsolvers in the wild could have led to reduced individual consistency across contexts; however, we found no evidence for social learning in the wild. Contrary to results obtained for starlings (*Sturnus vulgaris*; Boogert et al. 2008), individual tits contacting the task later during the course of our trials were no more efficient at solving than those that contacted the task earlier in the trial. Moreover, the latency to the first solution in the field did not decrease with an increase in the number of innovations recorded at a location and therefore with a potential increase in the number of demonstrators to learn from. Social information should have been readily available to naive observers in our system because devices were installed near and facing protective tree cover heavily used by birds. Previous research has shown that great tits can engage in observational learning in captivity (Marchetti and Drent 2000) and use local enhancement for locating patchily distributed food sources in the wild (Sasvari 1992). It is possible that tits used mainly local enhancement rather than observational learning at our devices, which might have increased their efficiency at finding the devices but not their efficiency at solving the problem. Examining novel problem-solving performance of individuals in isolation and in captive groups as well as in the wild when birds are territorial during the breeding season (Gosler 1993) should provide a better understanding of social influences on the expression of innovative propensities in this system.

In conclusion, our observations suggest substantial plasticity in innovativeness across captive and natural environments. In the wild, the probability of solving the task and the time spent at baited devices between each solving event were repeatable within individuals; these consistent individual differences suggest that innovativeness could be the target of natural selection in our population (Roff 1997; Bell et al. 2009). Juveniles were more likely to solve a novel foraging problem than adults, lending support to the necessity drives innovation hypothesis, and therefore suggesting that selection on innovativeness is likely to occur primarily among juveniles. The novel system described has provided new insight into the sources of variation underlying the propensity to innovate under natural conditions, which we hope will encourage further research on the evolutionary ecology of innovativeness.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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Appendix D

Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits

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ORIGINAL PAPER

Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits

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Abstract The evolution and ecology of consistent behavioural variation, or personality, is currently the focus of much attention in natural populations. Associations between personality traits and parasite infections are increasingly being reported, but the extent to which multiple behavioural traits might be associated with parasitism at the same time is largely unknown. Here, we use a population of great tits, *Parus major*, to examine whether infection by avian malaria (*Plasmodium* and *Leucocytozoon*) is associated with three behavioural traits assayed under standardized conditions. All of these traits are of broad ecological significance and two of them are repeatable or heritable in our population. Here, we show weak correlations between some but not all of these behavioural traits, and sex-dependent associations between all three behavioural traits and parasite infection. Infected males showed increased problem-solving performance whereas infected females showed reduced performance; furthermore, uninfected females were four times more likely to solve problems than uninfected males. Infected females were more exploratory than uninfected females, but infection had no effect on males. Finally, infected males were more risk-averse than uninfected males but females were unaffected. Our results demonstrate the potential for complex interactions between consistent personality variation and parasite infection, though we discuss the difficulty of attributing causality in these associations. Accounting for complex parasite-behaviour associations may prove essential in understanding the evolutionary ecology of behavioural variation and the dynamics of host–parasite interactions.

Keywords Risk-taking behaviour · Malaria · *Plasmodium* · *Leucocytozoon* · Problem-solving performance · Exploratory behaviour

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Introduction

Personalities or behavioural syndromes have been described across a wide range of taxa (Gosling and John 1999; Sih et al. 2004b) and can be defined as consistent behavioural differences between individuals. These differences can take the form of behavioural correlations within the same trait across the same or different contexts or correlations between different behavioural traits (Gosling and John 1999; Sih et al. 2004b; Réale et al. 2007). Personality variation is currently the focus of much research, especially in the context of a range of traits that can be easily measured under standardized conditions, for

example exploration behaviour, aggressiveness, boldness, or sociability. One reason for this focus is that these traits effectively represent personality axes of variation because they predict behaviour in a whole range of other traits, and therefore have major consequences for a variety of ecological and evolutionary processes (Sih et al. 2004a; Réale et al. 2007), including susceptibility to parasitism (Barber and Dingemanse 2010; Boyer et al. 2010).

Parasites are ubiquitous in animal populations and links between parasite infection and host behaviour can arise through a variety of mechanisms (Moore 2002; Lefèvre and Thomas 2008; Lefèvre et al. 2009). Altering host behaviour may be adaptive for trophically transmitted parasites by increasing the likelihood of transmission (Sanchez et al. 2008) but can also arise as a by-product of the diversion of host energy reserves to parasites (Edelaar et al. 2003), or as a side effect of non-target host infection (Webster 2001; Lefèvre et al. 2008). It is also well documented that the threat of parasitism can generate avoidance behaviours that would otherwise not be observed (Hart 1990). Finally, numerous studies suggest that a range of behavioural traits may make individuals more susceptible to directly, vector- and trophically transmitted parasites (Wilson et al. 1993; Moore 2002; Barber and Dingemanse 2010; Boyer et al. 2010). Several challenges face these latter studies. The first is the possibility that parasitism was the underlying cause, not consequence, of the behavioural variation. Secondly, it is rarely known whether these traits are consistent within individuals and therefore the adaptive significance of these associations remain unclear. Thirdly, studies that have examined behavioural associations with parasitism have tended to focus on one specific behavioural trait rather than on examining associations with a suite of behaviours (Valkiunas 2005; Holmstad et al. 2006). It therefore remains unclear how general the associations between parasitism and behaviour are likely to be within individuals, and predictions will differ depending on the nature of transmission of the parasite. Finally, the extent to which these associations are sex dependent are not well understood. Numerous mechanisms could lead to sex differences in the association between infection and behaviour. For example, sex differences in behavioural traits associated with latent toxoplasmosis in humans, where effects occur as a side effect of non-target host infection, are thought to be mediated by the alteration of dopamine levels (Lindová et al. 2006; Flegr et al. 2008), which counteract symptoms among infected women (Lindová et al. 2006). Testosterone suppresses the immune system (Oppliger et al. 2004), and male birds with higher plasma testosterone levels tend to have a higher intensity of avian malaria infection (Saino et al. 1995). The sexes can also differ in their behaviour, both during and outside the breeding season (Gosler 1987) which may lead to a differential likelihood of infection.

Avian malaria is an extremely widespread, vector-transmitted parasite amongst birds (Valkiunas 2005) and can have lethal and sub-lethal effects on both individuals and populations (Van Riper et al. 1986). Detrimental associations have been found between avian malaria infection and many life-history traits (e.g. Dufva 1996; Merino et al. 2000; Møller et al. 2004; Knowles et al. 2010), although the mechanisms underlying these associations are unknown. These associations may be sex specific: for example, Møller et al. (2004) found infection by malaria parasites to delay arrival date in male swallows but not females. However, little is known about the sex-specific nature of associations between avian malaria and behaviour, as many studies focus on the effects of infection on one sex (Dufva 1996; Merino et al. 2000; Knowles et al. 2010).

In this paper, we use a natural population of a generalist passerine bird, the great tit *Parus major*, to examine associations between malaria infection and three contrasting behavioural traits. Two malaria parasite families, *Plasmodium* and *Leucocytozoon*, are known to be present at high prevalence within parts of our study population (Wood et al. 2007; Cosgrove et al. 2008) and reach their highest prevalence in autumn (Cosgrove et al. 2008). A previous study experimentally demonstrated that *Plasmodium* infection has a direct and substantial effect on female reproductive fitness in blue tits, *Cyanistes caeruleus* (Knowles et al. 2010), confirming that functionally significant effects of malaria on behaviour in great tits are plausible.

The behavioural traits we focus on—exploration behaviour of a novel environment, problem-solving performance and startle latency—were chosen because they are easily measured under standardized conditions (van Oers et al. 2004; Quinn et al. 2009; Cole et al. 2011), they have broad ecological significance (Greenberg 2003; Réale et al. 2007) and because they have been associated with parasite infection in other systems (Holmstad et al. 2006; Garamzegi et al. 2007; Boyer et al. 2010). Highly exploratory individuals may be more likely to become infected (Wilson et al. 1993) because host activity level is known to increase susceptibility to parasitism generally (Boyer et al. 2010). Malaria prevalence varies spatially in our system (Wood et al. 2007), so more exploratory individuals may be more likely to come across the vectors of avian malaria and become infected. Performance in novel problem-solving tasks is thought to provide a measure of general cognitive ability (Roth and Dicke 2005) and innovativeness (Laland and Reader 1999; Webster and Lefebvre 2001). Because innovative foraging behaviour has been associated with avian malaria infection across species (Garamzegi et al. 2007), we also expected that individual variation in problem-solving performance might be linked to malaria infection. Latency of response to a startle stimulus is a measure of risk-taking or anti-predation behaviour, as not

responding to a sudden movement by fleeing increases the likelihood of falling prey to a predator. Infection by malaria parasites has been associated with an increased likelihood of freezing, as opposed to fleeing, in both chaffinches (Valkiunas 2005) and willow ptarmigan (Holmstad et al. 2006) but conversely, in a trophically transmitted acanthocephalan parasite system, it has also been shown to increase escape behaviour (Médoc et al. 2009).

Our aim was to investigate the extent to which *Plasmodium* and *Leucocytozoon* infections are associated with variation in exploration behaviour, problem-solving performance and startle response simultaneously among wild-caught birds temporarily taken into captivity. Exploration behaviour and problem-solving performance are also the subject of intense study in our population; elsewhere we demonstrate that both are repeatable and the former is heritable (Quinn et al. 2009; Cole et al. 2011). Due to the potentially diverse ways in which associations between parasitism and behaviour may arise, we did not make any a priori predictions regarding the direction of effects we expected. However, we expected differences between the sexes because of hormonally mediated variation observed in other species (Lindová et al. 2006; Flegr et al. 2008) and because the sexes intrinsically differ in their behaviour during reproduction which could lead to differences in exposure to vectors. We show sex differences in associations between malaria infection and each behavioural trait and discuss whether direction of causality can be inferred from the patterns observed.

Materials and methods

Study site and catching procedure

Great tits were captured in mist nets at feeding stations within Wytham Woods, Oxford, UK, during October 2008 and 2009. We chose this period because malaria peaks in detectability at this specific time of the year and shows low prevalence for much of the rest of the year (Cosgrove et al. 2008). Following capture, birds were aged and sexed according to plumage characteristics (Svensson 1992), weighed, and all unringed individuals were fitted with a unique BTO metal leg ring. They were then taken into captivity at Wytham Field station, approximately 2 km from the capture site. Birds were housed as per Quinn et al. (2009) for no more than 48 h and were blood-sampled by venipuncture of the brachial vein just before release.

Behavioural assays

At 17:00 h on the day of capture, a problem-solving task, consisting of a vertical transparent Perspex tube containing a platform supported by a horizontal lever, was presented to each bird. The device was baited with peanuts placed on the platform. To solve the task, birds had to remove the lever from the device, causing the platform to drop and the peanuts to fall into a feeding dish positioned below the device (Cole et al. 2011). When the task was set, a single peanut was placed in this feeding dish to attract the bird to the device. Birds were not food deprived during this trial; however, the food reward in the device was preferred to the standard food available in the cage (E. Cole, personal observation). The device was then left overnight and at 08:00 h the following morning, whether or not the bird had solved the problem (defined as removing the lever either completely, or sufficiently to release the bait) was recorded and used as the response variable. The likelihood of solving this task is unrelated to activity level per se and represents individual differences in the ability to forage innovatively (Cole et al. 2011).

The exploration behaviour (EB) of each bird was assessed between 08:00 and 12:00 during the morning following capture, using methods described more fully in Quinn et al. (2009), differing only in that the assay duration was shortened from 8 to 2 min. Previous work has shown the 2- and 8-min assays to be highly correlated (Quinn et al. 2009). An assay commenced 20 s after a bird was first coaxed from its cage through a trapdoor leading into an adjoining novel environment room and lasted for 2 min, after which the bird was coaxed back into its cage. The assay room was based on Verbeek et al. (1994). The frequency and location of all movements were recorded using a handheld event recorder (Psion Workabout, with Observer mobile software, Noldus Information Technology, Nottingham, UK), generating 12 behavioural measures (see Appendix S1 of Quinn et al. 2009); the first component (PC1) from a principal components analysis had a positive loading for all measures, reflecting a combined measure of activity levels and propensity to explore novel objects and areas. Square root transformation led to an approximately normal distribution, and this was used as the measure of exploratory behaviour. We ignored repeat assays and did not correct for within-seasonal temporal variation, as reported previously (Quinn et al. 2009), because all assays were undertaken at the same stage of the season.

Immediately following the EB assay, the response of each bird to a startle stimulus was assessed by instigating the sudden movement of a stick from the corner of the novel environment room, controlled remotely using a length of colourless line fed under the door. This was carried out between 2 and 4 min after the end of the EB assay, when the bird was on either of the two trees closest to the stimulus stick. This trait could not be assessed for a number of individuals (n=26) who did not land on either of these two trees within 4 min of the end of the EB assay.

Assays were recorded using a video camera (Handycam, DCR-SR33E, camcorder, Sony, UK) and videos analysed subsequently to determine (1) whether each bird reacted to the movement of the stick by leaving the tree and (2) the time taken to react to the movement of the stick, defined as the time taken between the start of the movement stimulus and the bird's feet leaving the tree (±0.05 s). Examination of the startle response times showed a clear bimodal distribution, with birds either reacting immediately to the movement of the stick, or reacting to the sound of the stick hitting the floor (or not reacting at all). Thus, birds were split into those that either did or did not react to the initial movement of the startle stimulus (defined as leaving the perch before the noise of the stick hitting the floor was audible), which was used as the response variable.

Parasite screening

DNA was extracted from blood samples using a standard ammonium acetate method and screened for parasites using the protocols of Waldenström et al. (2004) for detection of infection by *Plasmodium* spp., and Hellgren et al. (2004), for detection of infection by *Leucocytozoon* spp. The presence of *Plasmodium* was established using primers HaemNF and HaemNR2 nested within HaemF and HaemR2 (Waldenström et al. 2004), and *Leucocytozoon* spp. were detected using primers HaemFL and HaemR2L nested within primers HaemNFI and HaemNR3 (Hellgren et al. 2004). Reactions for detection of *Plasmodium* were carried out in a working volume of 25 μl containing 50–200 ng template DNA, 1.25 mM dNTPs, 3 mM $MgCl_2$, 0.4 μM of each primer, 1× GoTaq Flexi Buffer (Promega, Madison, WI) and 1 U GoTaq Flexi (Promega, Madison, WI); the protocol for detection of *Leucocytozoon* differed only in that the concentration of $MgCl_2$ was 1.5 mM. Multiple positive controls of DNA from birds with known infections and negative controls containing deionised water in place of DNA were included on each plate to ensure successful amplification of target DNA and lack of contamination respectively. The protocol of Waldenström et al. (2004) also detects *Haemoproteus* spp., however this parasite is known to occur at a very low prevalence of ~0.8% at our study site (Cosgrove et al. 2008) and thus we assumed that all infections detected using this protocol were *Plasmodium*.

The PCR protocol for first round reactions consisted of a denaturation step of 94°C for 3 min followed by 20 cycles of 94°C for 30 s, 50°C for 30 s and 72°C for 45 s, with a terminal extension step of 72°C for 10 min; the protocol for second round reactions contained 35 cycles but otherwise consisted of an identical thermal profile. PCR reactions were carried out on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, California).

Statistical analysis

Statistical analyses were carried out in R (R Core Development Team 2009). Associations between behavioural variables were established using a χ^2 test (for the binary variables, problem-solving performance and startle response) and two binomial generalised linear models (for associations between exploratory behaviour and each of the two binary variables).

Three generalised linear models were used to determine whether parasite infection status was associated with problem-solving performance, exploration behaviour or startle response. Capture and natal areas can also be associated with behavioural variation in our population (Quinn et al., unpublished data) and the likelihood of parasitism (Wood et al. 2007). We therefore controlled for any effects of these two factors on all three response variables and the likelihood of parasite infection separately. Where these terms were found to influence a behavioural variable they were included in further analysis (full model results are provided in Appendices 1 and 2 in the Electronic supplementary material).

All models were fitted with parasite infection status, age, sex and year as main effects. To determine whether behavioural responses to parasitism differed between years, age classes or sexes, we also fitted the appropriate two-way interactions. The startle response model also included the distance of the bird from the startle stimulus to control for any effects that proximity to the stimulus may have on the response. We also repeated these tests for effects of each parasite family separately.

Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that did not were removed in a stepwise fashion until only those terms that improved the fit of the model at α=10% remained. Following model simplification, each non-significant main effect was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons and likelihood ratio tests at α=10% to ensure lack of association with the response variable at and validate the robustness of the MAM. Although model simplification by stepwise deletion has been criticised in the literature (Whittingham et al. 2006; Mundry and Nunn 2009), a recent study validated stepwise deletion as a method of model selection and established that it performed just as well as other methods of producing predictive models (Murtaugh 2009). In addition, simplification of our models made no difference to the terms considered to significantly influence the response variables.

The interactions between infection status and sex were significant for all three behavioural traits. Post hoc analyses were subsequently conducted on each sex separately to

establish whether opposing trends were present in both sexes or whether a significant trend was present in only one sex and not in the other. The structure of models used in these analyses was identical to those used previously, but without the main effect of sex.

To determine whether any associations were also found with the number of parasite infections a bird had, the above three models were rerun, substituting the parasitized or not parasitized term with the number of parasite infections (0, 1 or 2).

Results

Infection rates and behavioural correlations

In total, 59 male and 32 female great tits were assayed during October 2008 and 2009. No sex biases were found in infection rates, with 56% of females infected with at least one parasite, compared with 61% of males; 40% of females and 41% of males were infected by *Plasmodium* spp., and 38% of females and 39% of males were infected by *Leucocytozoon* spp. Older birds were more likely to be infected (χ_1^2=6.80, p=0.009), but infection rate was not significantly influenced by natal area (GLM, F=0.86, p=0.54) or capture site (GLM, F=0.06, p=0.94) in our sample.

Problem-solving performance (PSP) was not significantly linked to EB (GLM, $t_{1,\ 88}$=1.46, p=0.14), a result that we also report elsewhere using a much larger sample size (Cole et al. 2011) and therefore these two behavioural traits are independent of one another. In contrast startle response was not independent of the other two variables because it correlated, although not significantly, with both PSP (χ^2=3.31, p=0.07) and EB (GLM, $t_{1,\ 62}$=1.80, p=0.07), with problem solvers and faster explorers both more likely, although not significantly, to show a startle response.

Problem-solving performance

The likelihood of a bird solving a problem overnight did not differ significantly between the sexes (males, 46% solved and females, 50% solved), but was predicted by an interaction between sex and whether a bird was infected (GLM, $z_{1,\ 86}$=3.56, p=0.0004). Male birds were more likely to solve if infected (GLM, $z_{1,\ 57}$=3.27, p=0.001; Fig. 1a), whereas infected females were less likely to solve (GLM, $z_{1,\ 29}$=−3.12, p=0.002; Fig. 1a). We also note that amongst uninfected birds, females were far more likely to solve problems than males (Fig. 1a). The proportions of birds solving also differed between years (GLM, $z_{1,\ 87}$=2.65, p=0.008), with 60.5% solving in 2008 compared with only 37.3% solving in 2009. Age did not significantly influence the likelihood of solving (GLM, LRT=0.07, p=0.80) and there was no evidence for the effects of infection differing between age classes (age×infection, LRT=0.01, p=0.92) or between years (year×infection, LRT=0.05, p=0.82).

Sex differences in associations were also found when the analyses were carried out for each parasite family separately (*Plasmodium* spp.: GLM, $z_{1,\ 86}$=2.21, p=0.04, Fig. 1b; *Leucocytozoon* spp.: GLM, $z_{1,\ 86}$=2.93, p=0.003, Fig. 1c; for full model details see Table 1 and Online Appendix 1 in the Electronic supplementary material). An interaction between the number of parasite infections and sex also influenced problem-solving performance (GLM, $z_{1,\ 86}$=3.24, p=0.001), with a higher percentage of solvers with an increasing number of infections in males but no linear trend in females (Fig. 2a; full model details are given in Table 2).

Exploratory behaviour

Exploration behaviour did not differ significantly between the sexes (males, 0.95±0.06 and females, 1.01±0.07), but was predicted by an interaction between sex and parasite infection status (GLM, $F_{1,\ 86}$=4.16, p=0.05). No evidence was found for a relationship between male exploration behaviour and infection status (GLM, F_1=0.14, p=0.71; Fig. 1d); however infected females were more exploratory (GLM, $F_{1,\ 29}$=6.18, p=0.02; Fig. 1d). Adults were more exploratory than juveniles (GLM, $F_{1,\ 87}$=8.89, p=0.004; juvenile, 0.86±0.04 and adult, 1.17±0.09). Exploration behaviour did not differ significantly between years (GLM, F_1=0.69, p=0.41), and there was no evidence for the effects of infection differing between years (year×parasite, F_1=0.28, p=0.60) or between age classes (age×infection, F_1=1.73, p=0.19). Sex differences in associations were also found when examining associations with *Plasmodium* spp., although this was not significant for *Leucocytozoon* spp. (*Plasmodium* spp.: GLM, $F_{1,\ 81}$=4.35, p=0.04, Fig. 1e; *Leucocytozoon* spp.: GLM, $F_{1,\ 81}$=2.97, p=0.09, Fig. 1f; for full model details see Table 1 and Online Appendix 1 in the Electronic supplementary material). Exploratory behaviour was also influenced by an interaction between sex and the number of parasite infections (GLM, $F_{1,\ 81}$=4.39, p=0.04), with exploration in females increasing with a higher number of infections (Fig. 2b; full model details are given in Table 2).

Startle response

Whether or not a bird responded to a sudden movement did not differ significantly between the sexes (males, 85% reacted and females, 79% reacted), but was predicted by an interaction between sex and infection status (GLM, $z_{1,\ 59}$=

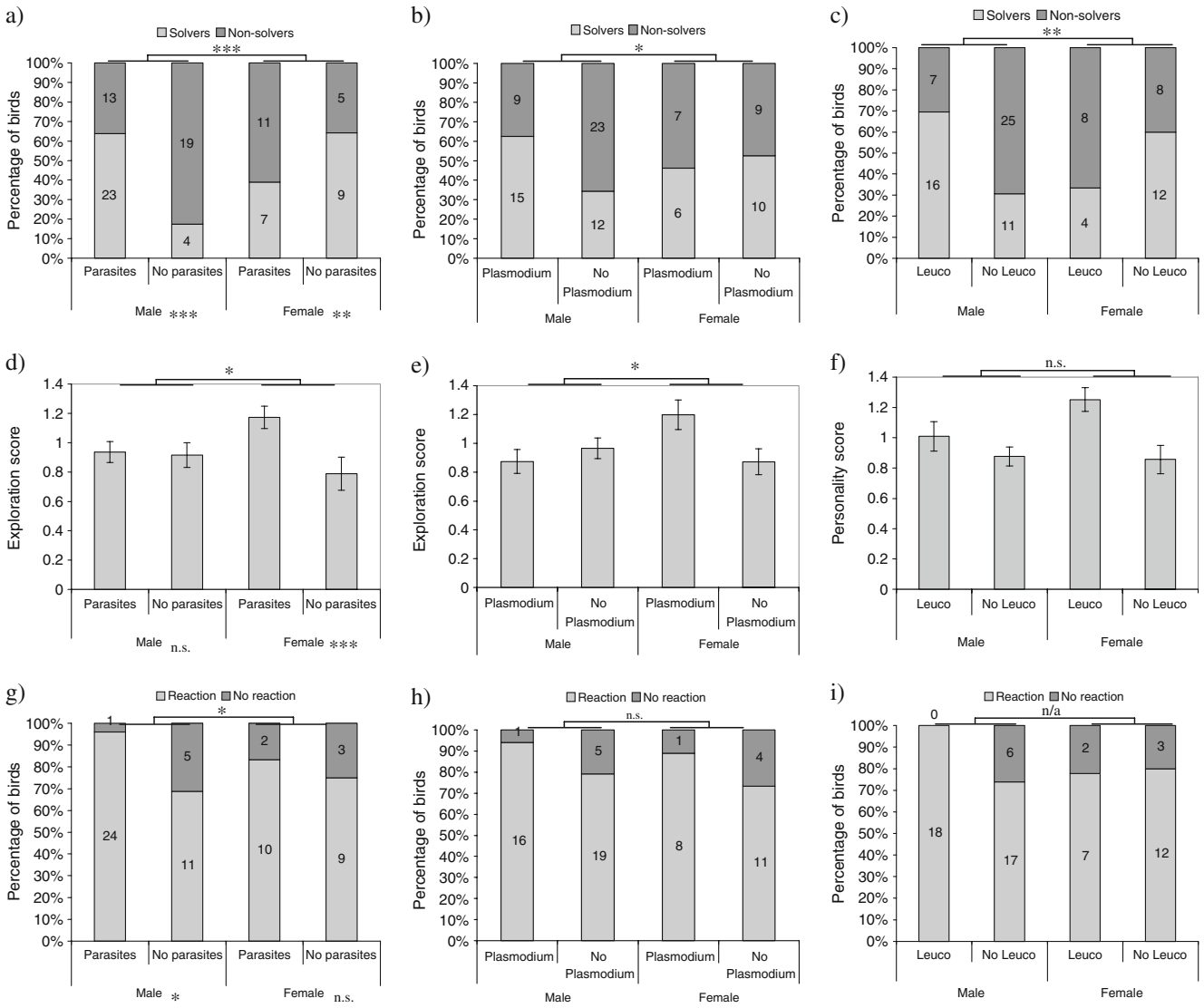


Fig. 1 Associations between **a**–**c** problem-solving performance, **d**–**f** exploration behaviour and **g**–**i** startle response and **a**, **d** and **g** infection by either parasite family, **b**, **e** and **h** infection by *Plasmodium* spp. and **c**, **f** and **i** infection by *Leucocytozoon* spp. **a**–**c** and **g**–**i** *Bars* show percentage of total number of birds; *numbers in bars* show sample size. **d**–**f** *Bars* show mean±1 SE. *Lines above bars* represent significance levels for the sex×infection interaction; symbols by the sexes indicate behavioural associations with parasitism within each sex: *$p<0.05$; **$p<0.01$; ***$p<0.001$. Full results from statistical analyses for (**a**, **d** and **g**) are shown in Table 1; results of analyses for (**b**, **c**, **e**, **f**, **h** and **i**) are given in the Electronic supplementary material

2.03, $p=0.04$). The likelihood of a female reacting was not significantly associated with infection status (GLM, LRT= 0.03 $p=0.87$); however males were more likely to react if infected (GLM, $z_{1,\ 38}=2.46$, $p=0.01$; Fig. 1g). Whether a bird responded also varied with year (GLM, $z_{1,\ 60}=-2.86$, $p=0.004$), with more birds reacting in 2008 (97%) than in 2009 (74%), and with the distance of the bird from the startle stimulus (GLM, $z_{1,\ 61}=-2.39$, $p=0.02$); birds that did not react were on average further away from the startle stimulus than those that did (did react, 1.50±0.06 m and did not react, 1.72±0.06 m). Age was not significantly associated with the likelihood of reacting (GLM, LRT= 0.95, $p=0.33$), and there was no evidence of the effects for parasites differing with age (age×parasite, LRT=0.98, $p=$ 0.32), or between years (year×infection, LRT=0.60, $p=$ 0.44). Sex differences in associations were not found when examining associations with *Plasmodium* spp. (GLM, $z_{1,\ 85}=$ 0.38, $p=0.54$, Fig. 1h; for full model details see Table 1 and Online Appendix 1 in the Electronic supplementary material); associations with *Leucocytozoon* spp. could not be tested as the inclusion of the interaction term destabilised the model. An interaction between sex and the number of parasite infections also influenced the likelihood of birds responding to a startle stimulus (GLM, $Z_{1,\ 59}=2.18$, $p=$

Table 1 Full model results from general linear models analysing associations between parasite infection and each of problem-solving performance (PSP), exploration behaviour (EB) and startle response (SR) for all birds; males only and females only

Variable	Parasite infection						Males						Females					
	df	z/LRT	*F*	*p*	Estimate	SE	*df*	z/LRT	*F*	*p*	Estimate	SE	*df*	z/LRT	*F*	*p*	Estimate	SE
PSP																		
Sex (male)	1, 89	2.299		0.002	−2.587	0.851												
Parasites (yes)	1, 88	−3.041		0.046	−1.634	0.820	1, 57	3.273		0.001	2.129	0.650	1, 29	−3.121		0.002	−1.040	0.738
Year (2009)	1, 87	−2.648		0.008	−1.412	0.533	1	1.002		0.317			1, 20	−2.500		0.012	−1.887	0.790
Age	1	0.065		0.799			1	0.017		0.897			1	1.099		0.294		
Sex×parasites	1, 86	3.566		0.0004	4.024	1.128												
Year×parasites	1	0.054		0.816			1	1.268		0.260			1	0.001		0.999		
Age×parasites	1	0.011		0.915			1	0.001		0.999			1	0.001		0.999		
EB																		
Sex (male)	1, 85		0.631	0.429	0.183	0.131												
Parasites (yes)	1, 86		3.063	0.084	0.292	0.137	1		0.140	0.710			1, 29		6.183	0.019	0.284	0.114
Year (2009)	1		0.685	0.410			1, 54		4.105	0.048	−0.222	0.110	1		0.628	0.435		
Age (adult)	1, 84		8.888	0.004	0.247	0.095	1		0.553	0.460			1, 30		18.929	0.0002	0.433	0.120
Capture site (Great Wood)	2, 82		3.182	0.047	−0.278	0.127	2		0.335	0.717			2		0.242	0.786		
Capture site (Marley)					−0.192	0.154												
Sex×parasites	1, 81		4.156	0.045	−0.354	0.174												
Year×parasites	1		0.284	0.595			1		0.001	0.989			1		1.264	0.272		
Age×parasites	1		1.725	0.193			1		2.102	0.154			1		1.148	0.295		
SR																		
Sex (male)	1, 63	−1.170		0.242	−1.386	1.185												
Parasites (yes)	1, 62	0.120		0.904	0.153	0.153	1, 38	2.459		0.014	3.766	1.531	1	0.029		0.866		
Year (2009)	1, 60	−2.859		0.004	−3.824	1.337	1, 37	−2.009		0.045	−3.071	1.529	[b]					
Age	1	0.951		0.329			1	1.514		0.219			1	1.702		0.192		
Distance	1, 61	−2.386		0.017	−0.038	0.016	1, 39	−1.567		0.117[a]	−0.034	0.021	1	1.513		0.219		
Sex×parasites	1, 59	2.031		0.042	3.988	1.964												
Year×parasites	1	0.603		0.437			1	0.129		0.719			[b]					
Age×parasites	1	0.984		0.321			1	0.523		0.470			1	1.009		0.315		

Estimates±1 SE are presented for all terms remaining in the minimum adequate model (MAM); terms considered to significantly influence the response variable are highlighted. Statistics presented for non-significant terms are from model comparisons using either likelihood ratio tests (binomial) or *F* tests (Gaussian), depending on the error distribution of the model

[a] This term showed marginal significance in influencing the fit of the model (LRT_1=3.63, p=0.06) and thus remained in the MAM but is not considered to significantly influence the response variable

[b] The inclusion of this term and its interaction destabilised the model (probably due to all females reacting in 2008); thus, we had to omit this term from the maximal model and did not consider it any further

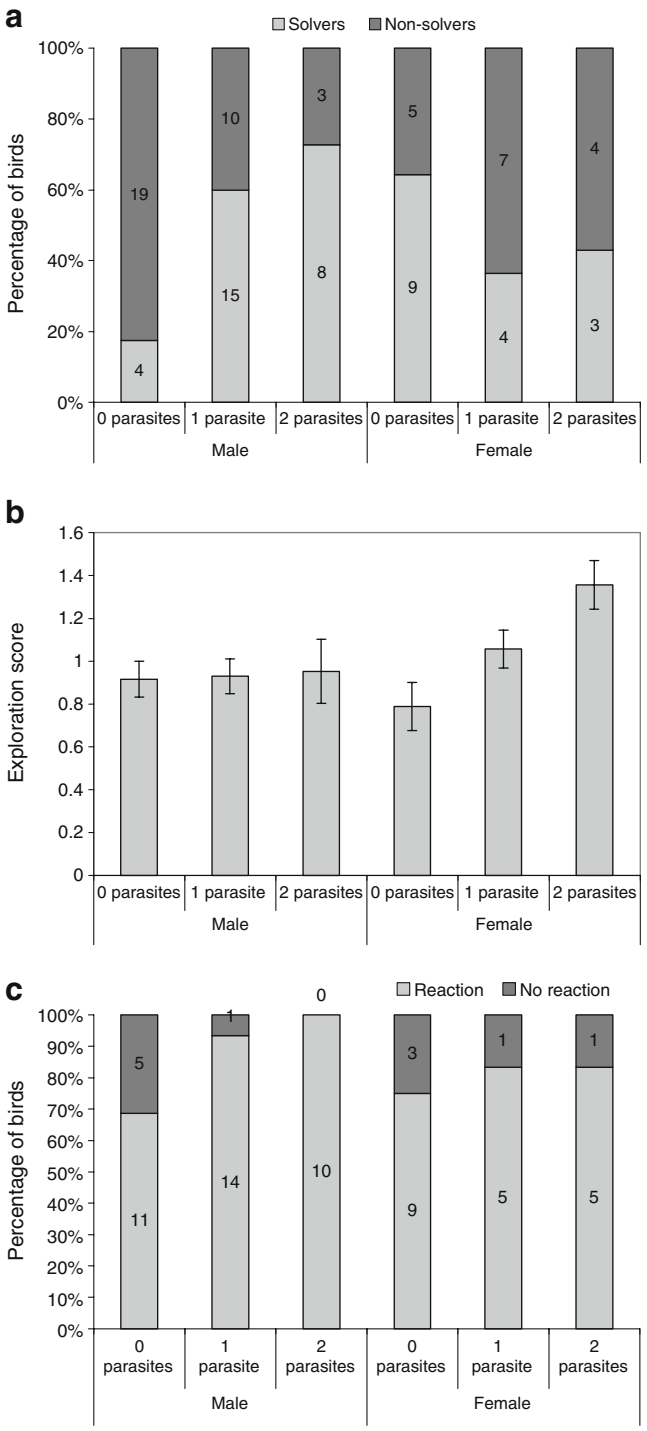


Fig. 2 Associations between the number of parasite infections and **a** problem-solving performance, **b** exploration behaviour and **c** startle response. **a**, **c** *Bars* show percentage of total number of birds; *numbers in bars* show sample size. **b** *Bars* show mean±1 SE. Full results for statistical analyses are shown in Table 2

0.03): males with one parasite were more likely to respond than uninfected birds and all males infected with two parasites reacted to the stimulus (Fig. 2c; full model details are given in Table 2).

Table 2 Full model results from general linear models analysing associations between the number of parasite infections and each of problem-solving performance (PSP), exploration behaviour (EB) and startle response (SR) for all birds

Variable	PSP					EB				SR			
	df	z/LRT	*p*	Estimate	SE	*df*	*F*	*p*	Estimate	SE	*df*	z/LRT	*p*	Estimate	SE
Sex (male)	1, 89	−2.68	0.007	−1.947	0.727	1, 85	0.504	0.480	0.173	0.124	1, 63	−1.254	0.210	−1.474	1.175
No. parasites	1, 88	−1.561	0.119	−0.795	0.509	1, 86	3.390	0.069	0.205	0.088	1, 62	−0.037	0.971	−0.030	0.811
Year (2009)	1, 87	−2.474	0.013	−1.238	0.501	1, 80	0.687	0.410			1, 60	−2.856	0.004	−3.832	1.342
Age	1, 89	0.024	0.876			1, 84	8.901	0.004	0.233	0.096	1, 59	1.257	0.262		
Capture site (Great Wood)	NA	NA	NA	NA	NA	2, 82	3.421	0.037	−0.301	0.126	NA	NA	NA	NA	NA
Capture site (Marley)	NA	NA	NA	NA	NA				−0.194	0.154	NA	NA	NA	NA	NA
Distance	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1, 61	−2.387	0.017	−0.038	0.016
Sex×no. parasites	1, 86	3.242	0.001	2.300	0.708	1, 81	4.390	0.039	−0.234	0.112	1, 59	2.179	0.029	3.746	1.719
Year×no. parasites	1, 84	2.698	0.101			1, 79	0.813	0.370			1, 57	0.598	0.439		
Age×no. parasites	1, 85	0.717	0.397			1, 78	0.738	0.393			1, 56	0.406	0.524		

NA refers to terms that were not included in the model

Discussion

We report several associations between three behavioural traits and infection by two avian malaria parasites. Elsewhere, we show that two of these behavioural traits, exploration behaviour (Quinn et al. 2009) and problem-solving performance (Cole et al. 2011), are repeatable or heritable, while variables similar to startle response are also known to be repeatable (van Oers et al. 2004). On average there was no difference in any of the behaviours or in infection rate between the sexes, but the association between behaviour and parasitism was strongly sex dependent.

Problem solving

Firstly, we found that malaria infection was associated with higher problem-solving performance in male great tits, agreeing with another study that found a positive relationship between avian malaria parasite prevalence and feeding innovations at the species level (Garamzegi et al. 2007). The effect reported in Garamzegi et al. (2007) is assumed to be behaviourally mediated because problem solvers often have more diverse foraging habits which should increase their exposure to parasites (Garamzegi et al. 2007). We speculate that this is also the case for male great tits because in our population problem solving amongst males is associated with a greater diet breadth (Cole et al., unpublished data). Furthermore, the sexes are also known to have different foraging strategies in winter when the majority of birds found turning over leaves in search of beechmast on the ground are male, while females are more commonly seen foraging for invertebrates in the trees. Sex differences in foraging strategies at times of the year when malaria vectors are active are also likely to occur (Gosler 1987). The association in males could be the result of adaptive parasite mediation but we are unaware of any examples involving a vector-transmitted parasite. In contrast to the pattern we found for males, avian malaria was associated with lower problem solving amongst female great tits. Kihara et al. (2006) found a negative association between malaria and cognition in humans but do not mention sex differences, and the directly transmitted protozoan parasite *Crithidia bombi* has also been linked to a parasite mediated reduction in spatial memory among female bumblebees (Gegear et al. 2006). Finally, we note that whilst there was no difference in either exploration behaviour or startle response between uninfected males and females, uninfected females were four times more likely to problem solve than uninfected males, a pattern that is only seen when infection status is taken into account. Thus, controlling for important sources of environmental variation, such as parasitism, may be crucial when exploring latent sex differences in behavioural variation (e.g. Healy et al. 2009).

Exploration behaviour

We found that female great tits with malaria infection were faster explorers than uninfected females. Associations between activity levels and parasitism are relatively widely reported across trophically, directly and vector-transmitted parasites (summarised in Table 3.7 of Moore 2002); however, the direction of the associations varies. The majority of parasites are associated with lethargy, probably due to parasite load or competition by the parasite for host resources (Edelaar et al. 2003), but some trophically transmitted parasites are associated with increased movement, for example rats infected by *Toxoplasma gondii* show increased activity, which improves the chance of the parasite being transmitted through predation of the intermediate host (Webster 1994). Wilson et al. (1993) suggested that differences in directly transmitted gut parasite fauna between bold and shy pumpkinseed sunfish *Lepomis gibbosus* were caused by differential habitat use by bold and shy personality types, that is, the associations were behaviourally rather than parasite mediated. More recent studies found positive associations between exploratory behaviour, or boldness, and directly transmitted parasites such as tick load or viral infection (Natoli et al. 2005; Easterbrook et al. 2007; Boyer et al. 2010), and Boyer et al. (2010) concluded that tick load resulted from space use. Boyer et al. (2010) also found sex differences in both parasite load and in exploratory behaviour, with adult males more active than both females and juveniles, and males having a higher parasite load. Similar to our results, Webster (1994) found female rats infected by congenitally acquired and trophically transmitted *Toxoplasmosis gondii* to be more active than uninfected females, but found no association in males (Webster 1994), though no explanation was offered for these sex differences. As the prevalence of infection varies on a large spatial scale at Wytham, (Wood et al. 2007) and the parasites in our system are vector transmitted, it seems plausible that this spatial variation, or perhaps variation at a finer micro-habitat scale, explains the association between higher exploration behaviour and malaria among female great tits in our study; territoriality restricting space use by males during the breeding season when vectors are more likely to cause infection may explain the lack of association seen in males.

To conclude this section, we note that exploration behaviour and other temperament traits are currently the focus of considerable attention among evolutionary ecologists because, amongst other reasons, they are easily measured under standardized conditions, making them ideal candidate behaviours for quantitative genetic studies.

Previous quantitative genetic analysis in our population showed that the 'permanent environment' component of variation was equally, if not more, important than additive genetic variance (Quinn et al. 2009). If the association we report here is parasite mediated, malaria may be an important contributor to these permanent environment effects.

Startle latency

We also found links between parasite infection and startle latency. Empirical data offer conflicting evidence for whether parasites have a negative or positive effect on anti-predation behaviour and predation risk, and to our knowledge no study has considered sex differences in these associations (Valkiunas 2005; Holmstad et al. 2006; Møller and Nielsen 2007; Médoc et al. 2009). Some trophically transmitted parasites influence host anti-predator behaviour, either to avoid falling prey to a non-host predator (Médoc et al. 2009) or to increase the likelihood of predation and transmission to the parasite's target host (Webster 1994). Avian malaria is not a trophically transmitted parasite and our finding that infected males were more likely to respond to startle latency supports the hypothesis of a parasite-mediated anti-predator response in order to increase transmission rate through continued exposure to vectors. However, comparative analyses suggest that species with higher vector-transmitted blood parasite prevalence have a higher risk of predation (Møller and Nielsen 2007). Two studies show that avian malaria parasites specifically are associated with a reduction in the likelihood of fleeing from a stimulus (Valkiunas 2005; Holmstad et al. 2006). However, interpreting the functional significance of fleeing versus the use of alternative anti-predation measures, for example crypsis, is fraught with difficulty and can depend on the predator species involved (Cresswell 1993) or on an individual's state (Cresswell 1994), a point that has previously been made in the context of personality (Quinn and Cresswell 2005). Previous studies have assumed that fleeing was the adaptive response stimulus (Valkiunas 2005; Holmstad et al. 2006) but freezing could be adaptive under some circumstances (Quinn and Cresswell 2005), and therefore the effect observed could feasibly be an adaptive parasite-mediated effect on the host.

Sex dependence

All of the associations we reported between behaviour and parasite infection were sex dependent. Sex differences in behavioural traits associated with latent toxoplasmosis in humans are thought to be mediated by hormone levels altering dopamine levels (Lindová et al. 2006; Flegr et al. 2008). In this case, female hormones protect the dopaminergic system, causing less severe, or even opposing behavioural effects among infected women when compared with those shown by infected men (Lindová et al. 2006). Sex-specific hormonal effects could be behind at least some of the sex differences that we observed. However, whether hormones play a role in the patterns observed says nothing about whether the associations are parasite or behaviourally mediated. Hormones are a likely cause of male biases in infection, as testosterone is known to decrease immune function (Oppliger et al. 2004), and birds with higher plasma testosterone levels tend to have a higher intensity of malaria infection (Saino et al. 1995). The intensity of infection could potentially indicate whether our associations are parasite mediated: other systems have demonstrated quantitative impacts of parasites upon behaviour (e.g. Lafferty and Morris 1996) with the more extreme behaviour observed when parasite load is at its highest and the parasite has reached its transmissible stage (Koella et al. 2002; Lacroix et al. 2005; Lefèvre and Thomas 2008; Parker et al. 2009) and in theory quantitative PCR methods could be used to investigate causality in our system. However, the intensity of avian malaria infection is also strongly dependent upon individual immune response (Zehtindjiev et al. 2008) and thus, prior knowledge of individual immune status, along with the relative status of infection within an individual would be required before this approach could allow inference into the direction of causality. This is also likely to be confounded by the strong association between physiological and behavioural traits (Koolhaas 2008; Coppens et al. 2010). Additionally, PCR does not allow discrimination between transmissible and non-transmissible stages of the parasite and thus cannot discriminate between stages that should be associated with behavioural response if the behavioural association is parasite mediated (Koella et al. 2002).

Multiple infections

We found associations between an increased number of infections and male (although not female) problem-solving performance, exploration behaviour in females, and startle response in males, with doubly infected birds exhibiting more extreme behaviour. Co-infection can have additive, synergistic or protective effects on hosts (Read and Taylor 2001; Pedersen and Fenton 2006; Helmby 2009) frequently through immunomodulated interactions within the host (Niikura et al. 2008; Putaporntip et al. 2010; van Duivenvoorde et al. 2010), although the impacts of co-infection on behavioural variation or parasite manipulation have seldom been explored (Thomas et al. 2002; Rigaud et al. 2010). A study in a similar system to ours suggested that the avian immune system promotes multiple infections within the same erythrocyte, providing a direct means for interaction of multiple parasites within the

same host cell (Martínez-de la Puente et al. 2007). Interestingly, Martínez-de la Puente et al. (2007) suggests that this effect is amplified in females due to increased levels of immunoglobulin. This warrants further investigation within our population as to whether parasites interact within a host to influence host behaviour or whether host behaviour influences the likelihood of multiple infections.

Morphological and life-history associations with parasitism can be host–parasite specific and differ between parasite species (e.g. Rätti et al. 1993). On the one hand, this suggests that the similarity in the effects of both parasites on our behavioural traits points to behaviourally mediated effects, especially since both are transmitted by blood-sucking dipterans (Valkiunas 2005). On the other hand, even if parasites do modify behaviour, then they are likely to initiate a feedback loop to increase the likelihood of transmission (e.g. Brown et al. 2002) or reciprocal effects may occur (Blanchet et al. 2009), and thus experimental work, or work involving the recapture and resampling of marked individuals (e.g. Beldomenico et al. 2009), may be the only way to clarify the causality of these relationships, although investigating correlations between the intensity of the infective stage of the parasite and behaviour of wild-caught individuals would complement this approach. An alternative explanation is that some of the patterns observed could arise because susceptibility to parasite-mediated mortality may vary between behavioural phenotypes (Barber and Dingemanse 2010) because of correlated differences, either in immunocompetence (Zehtindjiev et al. 2008; Réale et al. 2010), or in the ability to compensate for the negative effects of parasitism on behaviour through differing sensitivity to stress (Réale et al. 2010).

Conclusions

Our results provide evidence that avian malaria can be associated with multiple, repeatable and partially independent behavioural traits at the same time within individual hosts. Previous studies have tested for associations between parasite infection and multiple behavioural traits but in most cases the traits were similar to one another, or associations were found with a restricted number of behavioural traits (Boyer et al. 2010; Coats et al. 2010). Problem-solving performance (Keagy et al. 2009), exploration behaviour (Dingemanse et al. 2002; Both et al. 2005; Quinn et al. 2009) and startle latency (e.g. van Oers et al. 2004; Quinn and Cresswell 2006) are functionally significant traits and therefore the implications of the associations between avian malaria and behaviour are likely to be far reaching within our population. Elsewhere, it has been suggested that effect specificity might lead to the decoupling of correlations between behavioural traits if the selective consequences on behaviour as a result of parasitism are sufficiently strong (Barber and Dingemanse 2010). Our results emphasise an alternative process, which is that the selective consequences of parasitism might act on multiple behavioural traits independently of one another. Another conclusion from our results is that latent sexual differences in behavioural variation might be observed only after controlling for the effects of parasitism, as differences in problem-solving performance are only seen in uninfected birds where females were almost four times as likely to problem solve than uninfected males. Finally, although only an experimental approach can confirm the direction of causality, we suspect the associations are primarily behaviourally mediated in our population, given the likely link between at least two of these behavioural traits and exposure to vectors. If true, this highlights the importance of controlling for the effects of exposure to parasites in evolutionary ecological studies of behavioural variation, which could lead to complex effects when multiple behavioural traits are correlated within individuals (Sih et al. 2004a). Alternatively, if the effects prove to be primarily parasite mediated, traditional host–parasite studies in natural populations should consider that the effects of parasites on behaviour are potentially broader than might otherwise have been assumed.

Ethical standards

The authors declare that all work described in this manuscript complies with the laws of the UK. Behavioural assays and temporary maintenance of wild birds in captivity was carried out under licence from Natural England. Blood sampling was carried out under licence from the Home Office.

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Conflicts of interest The authors declare that they have no conflicts of interest.

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Appendix E

Cognitive ability influences reproductive life history variation in the wild

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Report

Cognitive Ability Influences Reproductive Life History Variation in the Wild

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Summary

Cognition has been studied intensively for several decades, but the evolutionary processes that shape individual variation in cognitive traits remain elusive [1–3]. For instance, the strength of selection on a cognitive trait has never been estimated in a natural population, and the possibility that positive links with life history variation [1–5] are mitigated by costs [6] or confounded by ecological factors remains unexplored in the wild. We assessed novel problem-solving performance in 468 wild great tits *Parus major* temporarily taken into captivity and subsequently followed up their reproductive performance in the wild. Problem-solver females produced larger clutches than nonsolvers. This benefit did not arise because solvers timed their breeding better, occupied better habitats, or compromised offspring quality or their own survival. Instead, foraging range size and day length were relatively small and short, respectively, for solvers, suggesting that they were more efficient at exploiting their environment. In contrast to the positive effect on clutch size, problem solvers deserted their nests more often, leading to little or no overall selection on problem-solving performance. Our results are consistent with the idea that variation in cognitive ability is shaped by contrasting effects on different life history traits directly linked to fitness [1, 3].

Results and Discussion

The ecological and evolutionary significance of cognition—defined as the mechanisms by which animals acquire, process, store, and act upon information from the environment [7]—is increasingly being studied in natural populations [4, 5, 8–10]. We used a wild population of great tits (*Parus major*) to examine life history correlates and the selective consequences of a simple cognitive trait, problem-solving performance (PSP, with two categories, "solver" and "nonsolver" [11]) (see Movies S1 and S2 available online). The great tit has long been an influential model species in the study of life history variation [12, 13]. Previously we demonstrated that individual great tits differ consistently in their propensity to solve novel, goal-oriented foraging problems, and that these differences persist for at least a year [11] and predict the efficiency with which similar problems are solved in the wild [14]. In our population, PSP is unrelated to a variety of motivation factors and personality traits, including hunger, neophobia, and exploration behavior [11]. Video analysis of problem-solving attempts suggests that the solution involves operant conditioning mediated by a perceptual-motor feedback (see also [15, 16]) and does not depend on feeding motivation or activity levels (see Supplemental Information and Movies S1 and S2). Furthermore, PSP is correlated with string-pulling success [11], a task involving trial-and-error learning [15, 17, 18]. Our measure of PSP is therefore likely to reflect operant conditioning ability, though we note that other non-mutually exclusive cognitive processes, such as inhibitory control [19] or unexamined personality traits such as persistence [16, 19], could also explain some of the observed interindividual variation in PSP. Additionally, PSP is likely to reflect intrinsic variation in innovativeness [20, 21] because the tasks that birds were presented with had never been encountered previously.

First we tested whether clutch size, a trait that is intensively studied in many taxa, was higher for solvers than for nonsolvers. Typically clutch size is under positive selection but is moderated by the ability to provision nestlings [22] and counterselection for offspring condition and adult survival [23, 24]. Female great tits that solved the novel problem in captivity laid significantly larger clutches than nonsolvers when they were subsequently found breeding in the wild ($F_{1, 231} = 4.47$, $p = 0.036$, mean difference ± SE = 0.40 ± 0.189 eggs; Tables 1 and S1). The effect did not arise because PSP covaried with other traits known to influence clutch size, including the timing of breeding and habitat quality [25] (oak trees within 75 m of nest box) (Tables 1, S1, and S3). A link between PSP and clutch size was also found in males: although the effect was weak among all males (Tables 1 and S2), clutch sizes were larger in nests where both parents were solvers than in nests that included nonsolver parents ($F_{2, 115} = 5.13$, $p = 0.007$; Figure 1A), possibly because male great tits feed their partners during egg laying [26, 27]. These results provide the first evidence for a positive link between a cognitive trait and clutch size, one of the most important determinants of fecundity and reproductive fitness in birds.

We then asked whether solvers also produce more offspring and examined the possibility that apparent benefits of higher cognitive ability are traded off against costs associated with other reproductive life history traits [6]. Among those individuals that successfully reared young to fledging age, solver females indeed fledged more young than nonsolvers ($F_{1, 182} = 4.10$, $p = 0.044$; Figure 1B; Tables 1 and S1), although there was no effect of male PSP on the number of fledglings (Tables 1 and S2), and the number of parents that were solvers also had no effect (parental PSP was not present in the final model and dropped out of the model at $F_{1, 96} = 0.93$, $p = 0.337$). The condition of the larger number of fledglings in nests with solver females was not compromised: average fledgling mass was similar among broods from solver and nonsolver females ($F_{1, 188} = 0.52$, $p = 0.473$; PSP dropped from model in Table S1), and therefore their viability in the post-fledging period was unlikely to have been compromised. Similarly, parental viability was unaffected, because neither breeding female nor breeding male body condition differed between all solvers and nonsolvers that bred (Table S4) and

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Table 1. The Link between Problem-Solving Performance and Reproductive Life History Variation in Great Tits

	Lay Date	Clutch Size	Nest Success (1/0)	Number of Fledglings	Average Fledging Mass (g)	Number of Recruits
Female	n = 373	n = 368	n = 368	n = 307	n = 307	n = 368
PSP[a]	ns	(+)*	(−)*	(+)*	ns	ns
Lay date	x	(−)***	ns	(−)***	(−)***	ns
Disparity	x	(−)*	ns	(−)***	(−)***	ns
Habitat quality	ns	ns	ns	ns	ns	ns
Brood size	x	x	(+)***	x	x	x
Age[b]	(−)***	ns	ns	ns	ns	ns
Male	n = 308	n = 308	n = 308	n = 273	n = 273	n = 308
PSP[a]	ns	ns[c]	ns	ns	ns	ns
Lay date	ns	(−)**	ns	(−)***	(−)*	(−)**
Disparity	ns	(−)*	ns	(−)**	(−)**	ns
Habitat quality	ns	ns	(+)**	ns	ns	ns
Brood size	x	x	(+)***	x	x	x
Age[b]	ns	ns	ns	ns	ns	ns

Separate statistical models are shown for each trait for females (top) and males (bottom). Initial models included all fixed effects: problem-solving performance (PSP) (solver/nonsolver), age (first year/older), lay date (date first egg laid), disparity (difference in days between peak caterpillar abundance and when nestlings were 9 days old), habitat quality (oak density within 75 m of nest), and brood size, unless indicated by "x" in the table. Note that PSP for both partners was known for too few nests to allow an analysis with both sexes simultaneously. All models include the random terms bird identity and year. Model results are from either GLMMs (for nest success, binary error structure; for number of recruits, Poisson error structure) or LMMs (all other life history traits). (+), positive coefficient; (−), negative coefficient; ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns, $p > 0.05$. See Tables S1 and S2 for full model outputs and Experimental Procedures and Supplemental Experimental Procedures for more details.

[a]Nonsolver set to zero.

[b]First-year breeder set to zero.

[c]Last term removed from the model with $p = 0.071$.

there was no difference in adult survival among all solvers and nonsolvers that bred (Table S5). Thus, there was no evidence that the higher reproductive success achieved by solvers was traded off against fledgling condition or adult viability.

However, there was evidence for a trade-off with total brood viability, because the probability of fledging any young at all was lower for solver females than for nonsolvers ($W_1 = 6.22$, $p = 0.013$, $n = 242$; Tables 1 and S1; Figure 1B). This lower nest success among solvers was not caused by higher adult mortality during reproduction, because the nest success effect remained in a second analysis where the data were restricted to nests in which both partners were still alive post-breeding ($W_1 = 4.36$, $p = 0.039$, $n = 134$). Thus, solvers exhibited both larger clutch size and a higher probability of nest desertion than nonsolvers. These contrasting links with different life history traits may explain why we detected little or no directional selection on PSP in either sex or in any of the four years (Table S6).

Next we examined possible mechanisms that could have led to the links between problem solving and the different life history traits. Cognitive processes are commonly hypothesized to improve fitness by increasing foraging efficiency or quality (e.g., [9, 27]), which we explored using a variety of approaches. First, automatic loggers (recording presence of parents) and cameras at the nest showed that when nestlings were 5 days old, working day length for solvers was shorter than for nonsolvers (mean difference ± SE = 13.40 ± 7.33 min; $F_{1, 38} = 5.54$, $p = 0.024$; Tables 2 and S7), not longer as might be expected given that solvers were provisioning more offspring. There was no significant difference in provisioning rate or the proportion of caterpillars provisioned (a measure of diet quality [28, 29]) between solvers and nonsolvers (Tables 2 and S7); similarly, there was no difference in amount of time spent provisioning, provisioning rate, or diet quality when nestlings were 10–11 days old (Tables 2 and S8). Finally, radio tracking showed that home ranges during provisioning were 65% smaller among solvers than among nonsolvers ($F_{1, 6} = 14.88$, $p = 0.010$; Figure 2). The smaller ranges were unlikely to be a result of gross differences in the quality of habitat used, because, in addition to the oak density analysis mentioned above, several measures of local habitat quality were similar for solvers and nonsolvers of both sexes (Table S3). Apparently problem solvers were able to produce more eggs and offspring without exhibiting higher provisioning rates, although the possibility remains that they foraged at higher rates on other days during the breeding period, or at times other than those when we recorded activity. For instance, the combined effect of male and female solving performance was more pronounced for clutch size than for fledgling number, so solvers may have had a behavioral advantage primarily during egg laying, when foraging conditions are much less favorable compared to the provisioning period [28, 29] and when foraging behavior is difficult to assess in the great tit. Alternatively, the shorter foraging distances and working days exhibited by solvers may have allowed solvers to be more nest attentive [30], helping them to optimize brood temperature especially in the morning and evening when temperatures are cold [31], to minimize predation risk through nest defense [32], and/or to reduce parasite load in chicks [33].

In birds, nest desertion is a common adaptive response to declining environmental conditions [34, 35]. Sixteen percent of nests were abandoned between the parent trapping (when nestlings were one week old) and when nestlings reached fledging weight (14 days old). Experimental data suggest that the majority of these desertions were likely to be a response to trapping. Trapping adults at the nest when nestlings were 7 days old caused higher desertion rates than postponing adult catching until nestlings were 10 days old ($Z = 2.837$, $p = 0.005$, $n = 132$; nests were assigned randomly to 7- or 10-day-old treatment groups; see Supplemental Experimental Procedures for further details). Until recently, adults were trapped when nestlings were 7 days old, but an increase in the

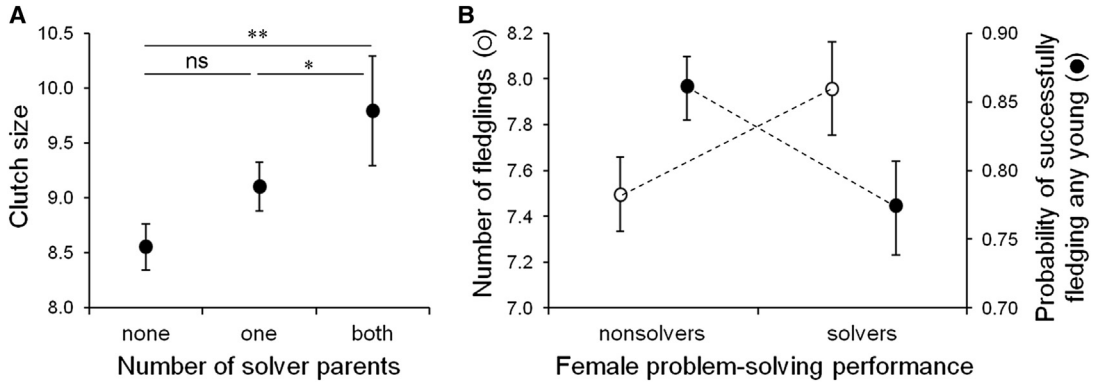


Figure 1. Problem-Solving Performance and Reproductive Performance in the Great Tit

(A) Clutch size varied with the number of solver parents at the nest. Analysis was restricted to nests where the problem-solving performance (PSP) of both parents was known (n = 136 pairs; both parents nonsolvers, n = 49; one solver parent, n = 65 [male only, n = 33; female only, n = 32]; two solver parents, n = 22). Clutch size was averaged across multiple individual breeding attempts for illustration. **$p < 0.01$; *$p < 0.05$; ns, $p > 0.05$.

(B) Number of fledglings and probability of fledging any offspring varied between solver and nonsolver females. Open circles indicate the average number of fledglings produced by nonsolver and solver females, based on nests where at least one nestling fledged (n = 214 individuals; nonsolvers, n = 132; solvers, n = 82). Where a female bred in successive years, fledgling number was averaged across breeding attempts for the sake of illustration. Black circles indicate the probability of fledging any young successfully from the nest. Plotted success data are back-transformed mean effects from a GLMM with a binomial error structure (n = 382 breeding attempts for 246 individuals; nonsolvers, n = 147; solvers, n = 99).

Error bars represent SEM.

population size in recent years has led to increased density-dependent desertion, and consequently adults are now trapped when nestlings are 10 days old (see Supplemental Experimental Procedures). Desertion following trapping and handling of birds is likely to mimic adaptive desertion following exposure to a natural predator [34, 35]. Previously we showed that the startle response, an antipredation behavior, tends to be more pronounced in solvers than in nonsolvers [36]. Problem solvers may generally be more sensitive to disturbance at the nest, and predation risk, than nonsolvers, though whether they have a stronger response to natural predation attempts remains to be tested.

Experiments on captive insect populations [2, 3] and common garden experiments [9, 10] suggest that adaptation to local environmental conditions can influence cognitive ability. Pioneering work on bumblebees (*Bombus terrestris*) [4] revealed a positive correlation between learning ability and a proxy for fitness, foraging efficiency among free-ranging colonies, and a study on male bowerbirds (*Ptilonorhynchus violaceus*) reported a correlation between problem-solving ability at the bower and mating success [5]. The results presented in this paper advance the field substantially for several reasons. First, they represent the first explicit investigation of links between cognitive ability and multiple life history traits determining reproductive fitness in a natural population; the selection coefficients presented are also the first estimates of natural selection for any cognitive trait in the wild. Second, the analyses control for the major ecological determinants of life history variation in the great tit, which has not been attempted previously. However, the possibility that unexamined correlates of PSP underlie the observed relationships remains until these links are assessed experimentally. Third, the higher desertion probability among solvers represents the first evidence from the wild for reproductive costs of elevated cognitive performance [6]. Previously we showed that problem solvers were less competitive at artificial feeders than nonsolvers [37]; though direct links to survival fitness were not tested, this illustrates that trade-offs with other unexplored traits may also be important, as emphasized by the concept of behavioral syndromes [38]. Contrasting effects on fecundity and desertion highlight the importance of considering potential life history trade-offs when examining selection for cognition in natural environments. Ultimately, they offer a potential explanation for why variation in cognitive ability occurs within populations.

Experimental Procedures

Data Collection

Standardized assays of PSP were conducted on individually marked birds temporarily taken into captivity during winter (November to March) from Wytham Woods (51°46'N, 1°20'W), Oxfordshire UK, between 2007 and 2010. Birds were housed singly in wire cages (45 × 45 × 68 cm) and presented with a simple task, where a lever had to be removed from a device in order to obtain a food reward. Individuals were given three hours to solve this task and were classified as "solvers" or "nonsolvers" based on their performance (see [11] for full details). After being assayed, all individuals were subsequently released back into the wild, at the site of catching. In addition to these individuals, a further sample of birds was taken into captivity from February 27 to March 9, 2012, in order to examine the proximate mechanisms underlying individual variation in PSP. Specifically, we examined the hypothesis that the solution involves operant conditioning mediated through a perceptual-motor feedback. Videos of solving assays were analyzed to quantify feeding motivation and contacts with functional and nonfunctional parts of the problem-solving device (see Supplemental Experimental Procedures for full details). The protocols outlined were all subject to ethical review by the Department of Zoology (Oxford) ethical committee.

Over the four breeding seasons (2007–2010), 247 females and 221 males of known PSP bred in Wytham (n = 382 and n = 316 breeding attempts, respectively, including 152 breeding attempts where the PSP of both parents was known). Breeding attempts of all great tits in Wytham were monitored as part of a long-term study using 1,020 nest boxes (see [39]). Parents were trapped and identified at the nest when nestlings were approximately 7 days old. Laying date of the first egg, clutch size, brood size (number of young observed in the nest), fledgling number, fledgling mass, and nest success (failure or success, where a nest was classified as successful when at least one chick fledged successfully) were recorded during visits to nest boxes between April and June. Recruitment from each nesting attempt was established by recording how many fledglings bred in Wytham the following year (see [22]).

Table 2. Relationship between Problem-Solving Performance and Parental Provisioning Behavior in the Great Tit

	Working Day Length (Hours)	Provisioning Rate (Feedings/Hour, ln Transformed)	Proportion of Prey Items = Caterpillars
5 Days	n = 44	n = 42	n = 42
PSP[a]	(−)*	ns	ns
Sex[b]	ns	(+)***	ns
Age[c]	ns	ns	(+)***
Lay date	ns	ns	(+)***
Disparity	ns	ns	ns
Habitat quality	ns	ns	ns
Brood size	ns	ns	ns
10–11 Days	n = 128	n = 106	n = 123
PSP[a]	ns	ns	ns
Sex[b]	(−)***	ns	(+)***
Age[c]	ns	ns	ns
Lay date	(+)**	(−)***	(+)*
Disparity	ns	(+)***	(−)***
Habitat quality	ns	ns	ns
Brood size	(+)*	ns	ns
Year[d]	(+)**	ns	ns

Relationship between parental provisioning behavior and parental PSP when nestling great tits were 5 days old during 2010 (top) and 10–11 days old during 2009 and 2010 (bottom). Separate statistical models are shown for each of the three provisioning variables. Each column represents a separate model; the final model included only significant terms. Fixed-effects definitions are as in Table 1; 10–11 day models also included year; nest identity was included as a random effect in all models. (+), positive coefficient; (−), negative coefficient; ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns, $p > 0.05$. See Tables S7 and S8 for full model outputs and Experimental Procedures and Supplemental Experimental Procedures for further information.

[a]Nonsolver set to zero.

[b]Female set to zero.

[c]First-year breeder set to zero.

[d]2009 set to zero.

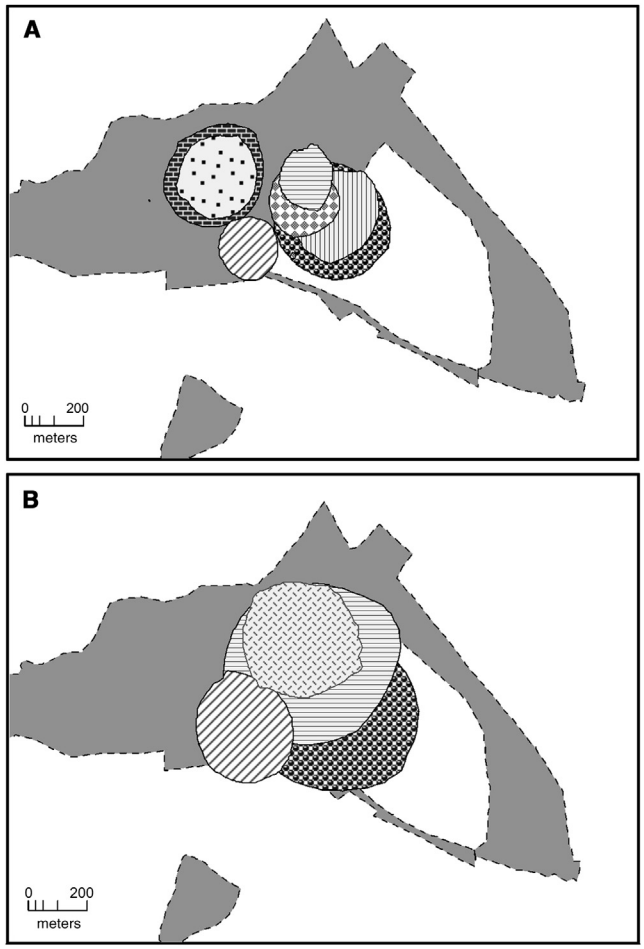


Figure 2. Home Range Sizes of Individual Great Tits When Provisioning Offspring

Harmonic mean-centered contour home ranges within part of Wytham Wood (gray area enclosed by dashed line). Individual nests within each panel are indicated by different patterns; nests in which both parents were tracked (n = 3 nests) are indicated by the same pattern across panels. White areas are farmland. Data are from n = 11 individuals from n = 8 nests.

(A) Solver great tits.

(B) Nonsolver great tits.

Individual provisioning behavior was recorded for birds of known PSP (usually only one parent per nest) using a combination of uniquely identifiable passive integrated transponder (PIT) tags detectable at nest boxes using PIT tag loggers, and video cameras (Handykam) attached to nest boxes during the 2009 and 2010 breeding seasons. Provisioning rate was estimated from video using the number of food items successfully delivered to the nest, divided by sample duration (1.5–3 hr). Video footage was also used to establish the proportion of caterpillars provisioned; caterpillars are a high-quality and preferred food source of *Parus* species [28, 29]. Working day length was calculated by subtracting, from 24 hr, the time elapsed between the last provisioning visit in the evening and the first feeding the following morning. In 2009, 11 adults for which PSP assays had previously been conducted were also radio tracked over 3 to 6 days (mean duration ± SD = 235 ± 61 min; range = 135–335 min) when nestlings were 8–13 days old in order to estimate home range size (see Supplemental Experimental Procedures for more details).

The hypothesis that the trapping protocol used in our population resulted in significant nest desertion was experimentally tested during the 2011 breeding season. This was done by comparing the rate of nest failure where adults were trapped using the normal trapping procedure to that where adults were not trapped until later in the nestling period, when increased brood value is likely to result in lower desertion rates. Nests were randomly assigned to one of two treatments, normal trapping (adults trapped when nestlings were 7 days old) or late trapping (adults trapped when nestlings were 10 days old). All broods were subsequently visited when 14 days old to determine whether the nest had failed, with failure being defined as no live nestlings remaining in the nest. "Late trapping" nests were also visited when nestlings were 7 days old, so that brood survival between 7 and 14 days old could be compared between treatments, and "normal trapping" nests were also visited at 10 days so that the total number of visits was equivalent for both treatments. The potential ethical issue associated with trapping became apparent only immediately before the 2011 breeding season; the experiment was conducted to test causality, and the trapping protocol has since been altered accordingly.

Data Analysis

Relationships between PSP and life history traits were tested using linear mixed models (LMMs) or generalized linear mixed models (GLMMs) containing the random factors year and bird identity (to account for multiple breeding attempts per individual), with males and females analyzed separately. The relationships between PSP and provisioning variables were analyzed using LMMs and GLMMs controlling for appropriate fixed and random effects (see Supplemental Experimental Procedures for more details). All final models were formed by backward stepwise removal of nonsignificant terms. Standardized directional selection coefficients (following methods from [40]) were estimated for fecundity (total number of young that fledged successfully) and recruitment. All analyses were carried out with GenStat v13.1 [41].

Supplemental Information

Supplemental Information includes eight tables, Supplemental Experimental Procedures, and two movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.07.051.

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