

Université de Montréal

**VARIATIONS INTERINDIVIDUELLES DES PERFORMANCES COGNITIVES ET
CONSÉQUENCES ÉVOLUTIVES CHEZ UNE POPULATION NATURELLE DE MÉSANGE
CHARBONNIÈRE (*PARUS MAJOR*)**

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RÉSUMÉ

Les animaux font face à des changements environnementaux brutaux dus aux modifications de milieux liés à l'activité humaine et aux changements climatiques, et doivent s'ajuster rapidement à leur nouvel environnement. Certains processus cognitifs comme l'innovation et l'apprentissage permettent aux animaux d'intégrer de nouveaux comportements à leur répertoire comportemental (flexibilité comportementale), leur donnant l'opportunité d'intégrer un comportement plus optimal pour s'ajuster. Les performances cognitives varient entre espèces et les individus d'une même population et bien que des études récentes se soient intéressées aux causes des variations interindividuelles des performances cognitives, les conséquences restent peu explorées. Dans cette thèse, les questions des pressions de sélection s'exerçant sur les capacités cognitives sont abordées afin de mieux comprendre l'évolution de ces traits au sein d'une population naturelle de mésange charbonnière *Parus major*. Un nouveau test de résolution de problème a tout d'abord été présenté à des couples reproducteurs directement en milieu naturel. Les résultats ont montré que les couples les plus performants à résoudre la tâche surpassaient les couples les moins performants sur plusieurs mesures de succès reproducteur. Afin de vérifier que la motivation à nourrir les poussins ne biaisait pas cette relation, la taille de nichée a ensuite été manipulée, ce qui n'a pas affecté la performance subséquente des parents. Les couples innovateurs démontraient un meilleur succès reproducteur quel que soit le changement de la taille de nichée subit, ce qui suggère que cette performance influence bien le succès de reproduction, et non l'inverse. De plus, les couples innovateurs approvisionnaient leurs poussins plus souvent que les couples non innovateurs, suggérant que les innovateurs pourraient exploiter leur habitat de façon plus optimale. Dans un troisième temps, plusieurs caractéristiques morphologiques, dont la coloration des plumes, ont été reliées aux performances de résolution de problème et d'apprentissage. Ces liens, bien que complexes et condition-dépendants, pourraient indiquer un rôle de ces performances lors de la sélection sexuelle. Enfin, afin de tester l'effet du parasite sanguin du paludisme sur les traits comportementaux, un médicament contre le paludisme a été injecté à des femelles reproductrices. Cette injection n'a pas modifié leurs performances cognitives mais a augmenté leur niveau d'activité et d'exploration du nichoir en réponse à la tâche de résolution de problème. Ce parasite sanguin, très présent chez les populations de

passereaux, pourrait donc expliquer les variations interindividuelles et interpopulationnelles de certains traits comportementaux en milieu naturel, au même titre que dans nombreux autres systèmes hôte-parasites étudiés. Les travaux présentés dans cette thèse ont permis de détailler pour la première fois la relation entre une performance cognitive et le succès reproducteur chez une population aviaire naturelle, une relation robuste et non influencée par la motivation à nourrir la couvée. Cette performance cognitive est reliée à plusieurs traits morphologiques, mais non à la charge parasitaire. Une meilleure exploitation de l'habitat et habileté à s'occuper des poussins pourrait expliquer cette relation.

Mots clefs : cognition, résolution de problème, apprentissage, sélection naturelle, succès reproducteur, nourrissage, sélection sexuelle, coloration des plumes, parasitisme

ABSTRACT

Animals face a rapidly changing world due to anthropogenic habitat destruction and climate change, forcing them to quickly adjust their behaviour to new environmental conditions. Cognitive processes such as innovation and learning can allow animals to incorporate novel behaviours into their behavioural repertoires and facilitate optimal responses to environmental change. Cognitive performances vary between and within species and although several studies have recently addressed the causes of inter-individual variations in cognitive performance, the fitness consequences of this variation remain poorly explored in natural populations. In my PhD thesis, I investigated different selective pressures acting on innovation and learning performance to better understand the evolution of these traits in a natural population of great tits *Parus major*. Firstly, I designed a novel problem-solving task that involved opening a trap door to access chicks, and presented it to breeding great tit pairs in their natural habitat. I found that the most efficient birds at solving this task performed better at multiple measures of reproductive success than the less efficient. Secondly, to test whether chick provisioning motivation confounded this relationship, I manipulated brood size and recorded whether this affected the problem-solving performance of the parents. My results showed that this was not the case. Instead, solvers had higher reproductive success whatever the brood size manipulation experienced, supporting the hypothesis that this cognitive performance drives reproductive success rather than the opposite. Problem-solving performance correlates positively with reproductive success both at the early stages of breeding (i.e. number of eggs laid and hatched) and during the nestling rearing period (i.e. number and condition of fledged young). Moreover, solvers seem to provision their young at a higher rate than non-solvers, suggesting that solvers exploit their breeding habitat more efficiently than non-solvers. Thirdly, I found multiple links between morphological traits, among which feather colouration, and problem-solving and learning performances. Although complex and condition-dependent, these links suggest that cognitive performances may be under sexual selective pressures, since they can be signaled by morphological traits shown to be important in great tit mate choice. Finally, injecting breeding females with an anti-malaria drug did not affect their cognitive performances, but increased their level of activity and exploration when presented with the novel problem-solving task. This suggests that the presence of these blood parasites, which are frequent in passerine populations, could partly explain between-individual and

between-population variation in certain behavioural traits in natural populations, as previously described in many other host-parasite study systems. In summary, my thesis provides the first detailed analysis of the relationship between cognitive performance and reproductive success in a wild bird population. My studies show that this relationship is robust and not confounded by parents' motivation to provision their young. This problem-solving performance is also correlated with various morphological traits, but not with parasite load. The relationship between cognitive performance and reproductive success might be mediated through habitat exploitation and chick provisioning skills, but requires further investigation.

Key words: cognition, problem-solving task, learning, natural and sexual selection, reproductive success, provisioning, feather colouration, parasitism

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*« Par moments, j'entrevois brièvement l'harmonie de la nature,
la façon dont un élément s'imbrique dans l'autre,
tels les rouages d'une machine compliquée. »*

Alexander Graham Bell

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INTRODUCTION GÉNÉRALE

La cognition est définie, au sens large, comme « l'ensemble des mécanismes qui permettent aux animaux d'acquérir des informations sur leur environnement, de les traiter et de les mémoriser pour pouvoir décider ensuite de leurs actes » (Shettleworth 2001). La perception, l'apprentissage, la mémoire, l'innovation (apparition d'un comportement nouveau) ou encore la prise de décision, jouent un rôle important lors de processus tels que la communication, le choix du partenaire, ou encore l'approvisionnement (Dukas 2004, Shettleworth 2009). Certains de ces comportements, bien qu'ils soient « pré programmés » depuis la naissance, peuvent laisser place à une certaine flexibilité quant à l'issue du processus (par exemple l'apprentissage du chant chez les oiseaux par les juvéniles; Tencate *et al.* 1993, Bolhuis et Honey 1998). D'autres peuvent même se révéler entièrement nouveaux et s'ils confèrent un avantage à l'auteur, être intégrés à son répertoire comportemental (Sasvari 1979). Un exemple connu est celui d'Imo, une jeune femelle de Macaque japonais (*Macaca fuscata*), qui fut observée en 1953 lavant des patates douces dans l'eau avant de les manger (Kawai 1965). En peu de temps, ce comportement se multiplia au sein de la troupe et devint partie intégrante du répertoire comportemental de cette population. Bien que de nombreuses études se soient intéressées aux variations de l'apparition de ces comportements nouveaux ainsi qu'à leurs causes (Kummer et Goodall 1985, Gajdon *et al.* 2006, Range *et al.* 2006, Boogert *et al.* 2010, Cole *et al.* 2011, Overington *et al.* 2011a, Benson-Amram et Holekamp 2012, Sol *et al.* 2012, Thornton et Lukas 2012), les conséquences évolutives de ces variations restent peu explorées, en particulier au niveau intraspécifique (Dukas et Duan 2000, Grieco *et al.* 2002, Thornton et Lukas 2012, Dukas 2013, Jaumann *et al.* 2013). Pourtant, placés dans un contexte écologique dans lequel de tels comportements seraient sélectionnés, ces nouveaux comportements pourraient influencer notre futur environnement (Cantalapiedra *et al.* 2014). Dans un monde sans cesse modifié majoritairement par l'activité humaine, des espèces capables d'ajuster rapidement leurs décisions et comportements face à ces changements pourraient affecter les pressions de sélection présentes et « diriger » la biodiversité de demain (Wyles *et al.* 1983, Dukas 2004, Aplin *et al.* 2013, Sih 2013).

L'apparition de nouveaux comportements

La plasticité phénotypique est la capacité d'un organisme à exprimer différents phénotypes au cours de son développement à partir d'un génotype donné selon les conditions biotiques et/ou abiotiques environnementales. La plasticité définit la qualité de ce qui est modifiable et qui peut prendre diverses formes, depuis la modulation de l'activité des gènes, en passant par la physiologie jusqu'au comportement. La plasticité comportementale est donc la capacité d'un organisme à modifier ses comportements, sous la forme d'apprentissage, d'autres processus cognitifs et/ou d'ajustements rapides aux nouvelles conditions en réponse aux variations de son environnement (Sol et Lefebvre 2000). Contrairement à d'autres formes de plasticité phénotypique qui ne sont pas réversibles, celle-ci peut être rapide et réversible, permettant de s'ajuster au fait qu'une information/situation peut varier avec le temps. On parle alors de flexibilité comportementale, qui représente une réponse adaptative importante (Wyles *et al.* 1983, Sih 2013). Via leurs capacités cognitives ('the cognitive buffer hypothesis'; Sol 2009), les individus pourraient par exemple développer de nouvelles stratégies anti-prédatrices (Lima 2009) ou modifier ou étendre leur niche écologique lorsque leurs ressources diminuent (Overington *et al.* 2011b). Cette flexibilité comportementale peut apparaître sous la forme d'innovation lorsqu'un individu invente un nouveau comportement ou à travers l'apprentissage social lorsqu'un individu adopte le nouveau comportement d'un autre (Reader et Laland 2003, Tebbich *et al.* 2010). L'innovation et l'apprentissage font appel à des réponses uniques face à des informations nouvelles et bien que ces deux processus soient différents, ils peuvent agir conjointement dans la diffusion au sein d'une population d'un nouveau comportement avantageux (Lefebvre 1995, Galef 2003, Aplin *et al.* 2013): pendant que certains individus seront plus aptes à innover, d'autres apprendront d'eux, facilitant la diffusion du nouveau comportement (ou transmission culturelle) (Boogert *et al.* 2010, Cadieu *et al.* 2010).

Le concept même de l'innovation est récent et fait encore partie de nombreuses discussions et divergences d'opinions quant à la définition et aux processus impliqués dans ce mécanisme (Reader et Laland 2003, Ramsey *et al.* 2007). En somme, l'innovation est définie généralement comme tout processus qui consiste à inventer un nouveau comportement ou à en modifier un préexistant de manière appropriée face à une nouvelle situation (Reader et Laland 2003). L'innovation peut être considérée comme le produit final de ce processus, ou comme le processus en soi. Elle ne doit pas être le simple produit du hasard ou d'un comportement

accidentel, mais être la démonstration d'un processus cognitif, qui peut faire appel à plusieurs autres processus tels que la réponse à la nouveauté (soit l'attraction ou la répulsion à un nouvel item ou une nouvelle situation), l'apprentissage individuel (c'est à dire la compréhension d'un problème ou d'une situation par essai / erreur), ou encore la perspicacité (c'est à dire la compréhension d'un problème sans avoir recours à l'essai / erreur) (Ramsey *et al.* 2007). Les cas d'innovations alimentaires sont fréquents dans l'ensemble du règne animal (comme un nouveau type de nourriture ou une nouvelle technique de recherche de nourriture; Overington *et al.* 2009b). Les exemples vont de l'ingestion d'un nouveau type d'aliment (Estók *et al.* 2010) à l'invention de nouvelles techniques permettant l'accès à la nourriture (Kummer et Goodall 1985) en passant par l'utilisation d'outils (Hunt 2000, Patterson et Mann 2011). Cependant, les innovations peuvent aussi concerner d'autres comportements, comme un signal de communication observé pour la première fois dans un groupe, ou bien l'utilisation d'un signal connu mais dans un nouveau contexte (Kummer et Goodall 1985).

L'apprentissage est le processus par lequel le comportement d'un individu est modifié par des informations acquises par expérience (Dukas 2004, Shettleworth 2009). Les processus de base de l'apprentissage sont très répandus et surviennent à chaque instant de la vie des animaux. L'habituation par exemple est la diminution graduelle de l'intensité ou de la fréquence d'apparition d'une réponse suite à la présentation répétée ou prolongée du stimulus l'ayant déclenchée (Thompson et Spencer 1966). Le conditionnement classique (c'est à dire apprentissage dû à l'association entre un stimulus de l'environnement et une réponse automatique de l'organisme; Pavlov 1927) et instrumental (c'est à dire apprentissage dû à l'association d'un renforcement positif ou négatif suivant une action, soit l'essai - erreur; Skinner 1938) sont souvent considérés comme les maillons de base d'une chaîne dont l'ensemble formerait des comportements plus complexes. Des associations entre ces différentes formes d'apprentissage simple peuvent donner naissance à des processus plus complexes. L'apprentissage peut être préprogrammé depuis la naissance, comme le processus de l'empreinte permet aux oisillons d'apprendre le chant des mâles de leur espèce pendant une période précise du développement (Tencate *et al.* 1993). Cependant, des changements imprévisibles de l'environnement ne peuvent être « anticipés » par ces formes d'apprentissage préprogrammé et dans certains cas, les animaux doivent se fonder sur leur propre expérience, leur propre capacité à modifier leur comportement pour s'adapter à ces nouvelles conditions. Par exemple, beaucoup d'espèces sont capables d'apprendre en observant ou en interagissant avec d'autres conspécifiques ou même avec des individus d'une autre espèce, une capacité définie

comme l'apprentissage social (Galef et Laland 2005, Aplin *et al.* 2013). Ils peuvent par exemple obtenir des informations sur des territoires potentiels afin de choisir le meilleur pour s'y reproduire (Doligez *et al.* 2002).

Variabilité inter et intraspécifique

Chez les humains, le quotient intellectuel (ou QI) est un test basé à la fois sur des mesures psychologiques et cognitives dont le but est de fournir une valeur quantitative standardisée de l'«intelligence» d'une personne (Sternberg 1985). Très critiqué, car ces tests seraient restreints et ne permettraient pas d'évaluer toutes les compétences associées à l'intelligence (Gould 1996, Neisser *et al.* 1996, Neisser 1997), cette mesure reste largement utilisée bien que la notion même d'intelligence soit constamment discutée (pour certains, l'intelligence serait la capacité à faire face à une nouvelle situation, pour d'autres, l'intelligence serait reflétée par la capacité à penser de façon abstraite, etc.). Chez les animaux (non humains) également, le concept même d'« intelligence » et sa définition ne font pas encore consensus au sein de la communauté scientifique (Thorndike 1898, Jerison et Barlow 1985, Shettleworth 2001). Comparer les performances cognitives entre des espèces ainsi qu'entre les individus d'une même espèce est une tâche particulièrement délicate (Boesch 2007).

En tant qu'organe « responsable » de la cognition, la taille relative du cerveau a été proposée comme mesure opérationnelle des capacités cognitives (Jerison et Barlow 1985). Chez les oiseaux, les variations de la taille du cerveau ou de certaines structures du cerveau ont été largement utilisées comme des corrélats de la capacité cognitive, comme l'hippocampe pour la mémoire spatiale (Sherry *et al.* 1992) ou le mesopallium et nidopallium pour les performances innovatrices (Timmermans *et al.* 2000). La taille du cerveau est positivement reliée à la quantité de neurones présents (Bottjer *et al.* 1986, Roth et Dicke 2005), et la lésion spécifique de ces structures peut affecter les capacités cognitives associées (Nottebohm *et al.* 1976, Bingman et Jones 1994, Hampton et Shettleworth 1996). De plus, certains processus cognitifs complexes pouvant faire appel à plusieurs régions différentes du cerveau (Chiappe et MacDonald 2005), la taille relative du cerveau est donc un solide candidat pour étudier les variations des performances cognitives entre les espèces. Bien que cette mesure soit également largement discutée (Healy et

Rowe 2007, Thornton et Lukas 2012, Willemet 2012), très peu d'alternatives ont été proposées à ce jour (Auersperg *et al.* 2012). En ce qui concerne la capacité d'innovation, le taux d'innovation (corrige par de nombreuses variables de confusion comme la phylogénie ou l'effort d'observation; Lefebvre *et al.* 1997, Nicolakakis et Lefebvre 2000) mesure le nombre d'innovations par espèce. Corrélié positivement à la taille relative du cerveau (Lefebvre *et al.* 1997, Reader et Laland 2002), le taux d'innovation a été utilisé à la fois chez les oiseaux (Lefebvre *et al.* 1997, Nicolakakis et Lefebvre 2000) et les primates (Reader et Laland 2002) pour quantifier les variations des performances innovatrices entre les espèces.

Au niveau interindividuel, résoudre des problèmes ou apprendre à exécuter des tâches sont classiquement utilisées en laboratoire pour mesurer les performances cognitives telles que les capacités d'innovation ou d'apprentissage. L'apprentissage animal est un domaine très étudié depuis de nombreuses années notamment suite aux travaux de Pavlov sur le conditionnement (Pavlov 1927). Une littérature abondante est disponible sur des expériences de conditionnement classique et instrumental ou d'apprentissage inversé (test consistant à inverser la règle d'apprentissage afin de regarder le temps que mets un individu à comprendre que la règle a changé), notamment chez les rats et les pigeons, mais aussi chez plusieurs autres espèces (revue dans Shettleworth 2009). En ce qui concerne l'innovation, bien que les recherches soient plus récentes, qu'il s'agisse de tâches d'enlèvement d'obstacle, de tirage de ficelle, d'inhibition de réflexe, d'utilisation d'outil, des tests de résolution de problème sont effectués dans le but de quantifier leur capacité à résoudre le nouveau problème, ou à adopter une nouvelle technique ou solution face à un problème connu (Webster et Lefebvre 2001, Seibt et Wickler 2006, Overington *et al.* 2011a, Cole *et al.* 2011, Auersperg *et al.* 2012). Ces tâches sont adaptées aux caractéristiques morphologiques de l'espèce étudiée (Laland et Reader 1999, Biondi *et al.* 2008, Boogert *et al.* 2010, Leal et Powell 2011, Benson-Amram et Holekamp 2012; mais voir Auersperg *et al.* 2012 pour une critique de la diversification des tâches utilisées) et utilisent la satiété afin de motiver les individus testés à interagir avec la tâche: les individus sont mis à jeun avant le test et une récompense alimentaire est proposée afin de motiver les individus à résoudre le problème.

Cependant, la capture et le maintien d'animaux sauvages en captivité pour la réalisation de tests comportementaux peuvent altérer la capacité de ces derniers à répondre à ces tests. On mesure alors la capacité des animaux à répondre à la captivité et non la variation qu'ils expriment

sur le terrain en ce qui a trait au comportement qui nous intéresse. Bien que dans la majorité de ces études, les performances cognitives soient corrigées par les variations interindividuelles dans les traits par exemple de réponse à la nouveauté (telle que la néophobie, soit la peur d'un nouvel objet ou d'une nouvelle situation; Greenberg 2003), des tests comportementaux réalisés directement en milieu naturel sont nécessaires afin de confirmer les résultats obtenus en laboratoire. Mais les ressources alimentaires, utilisées par exemple comme source de motivation pour réaliser des tests de résolution de problème, d'apprentissage ou de néophobie, sont très difficiles à contrôler lors d'expériences réalisées sur le terrain directement, le niveau de satiété des individus testés et la disponibilité de la nourriture dans la nature variant dans le temps et l'espace. L'utilisation de sources de motivation alternatives, comme l'attrait ou la répulsion d'un objet ou d'une couleur (Keagy *et al.* 2011), ou la motivation à nourrir sa progéniture (comme la tâche de résolution de problème utilisée tout au long de ce doctorat) offre de nouvelles opportunités pour caractériser les performances cognitives en milieux naturels.

L'ensemble de ces méthodes ont permis une accumulation récente d'études examinant les causes des variations interindividuelles dans les performances cognitives. Cependant, les conclusions ne sont pas unanimes et les résultats varient selon l'espèce ou le protocole utilisé. Certaines études montrent par exemple que la performance de résolution de problème pourrait être considérée comme un trait comportemental, c'est à dire comme une tendance intrinsèque affectant les réponses comportementales d'un organisme dans différents contextes, de manière constante au cours du temps : individu plus « intelligent » ou « créatif » (Pfeffer *et al.* 2002, Funk et Matteson 2004, Cole *et al.* 2011). D'autres études évoquent un état motivationnel : la performance serait dépendante par exemple de l'état de satiété, du statut social ou du genre (Kummer et Goodall 1985, Laland et Reader 1999, Bókony *et al.* 2013). Enfin, la performance pourrait être le résultat d'une exposition à un stimulus particulier, comme un changement dans l'environnement (Reader et Macdonald 2003; Schuck-Paim *et al.* 2008). Bien que les hypothèses varient, il en ressort que les performances cognitives peuvent être influencées (mais pas systématiquement) par l'âge (Cole *et al.* 2011, Aplin *et al.* 2013), le sexe (Range *et al.* 2006, Aplin *et al.* 2013), les conditions d'élevage (comme un stress subi par l'individu lors des premiers stades de son développement : hypothèse du stress développemental; Spencer *et al.* 2003, Pfaff *et al.* 2007) ou l'expérience antérieure des individus (Seibt et Wickler 2006, von Bayern *et al.* 2009, Thornton et Lukas 2012). Les traits de personnalité liés à la réponse à la nouveauté tels que l'exploration ou la néophobie sont

généralement liés à la performance d'innovation (Seferta *et al.* 2001, Biondi *et al.* 2010, Overington *et al.* 2011a), bien que ces liens varient d'une espèce à l'autre et selon la tâche utilisée. Chez les espèces vivant en groupe, la compétition (Carlier et Lefebvre 1996, Overington *et al.* 2009a), le statut de dominance (Boogert *et al.* 2006, Cadieu *et al.* 2010, Aplin *et al.* 2013) et le niveau d'agressivité des individus (Boogert *et al.* 2010, Cadieu *et al.* 2010) sont aussi des facteurs influençant l'apparition et/ou l'intensité des performances (mais voir Griffin *et al.* 2013).

Coûts et bénéfices des performances d'innovation et d'apprentissage

Lorsque des animaux présentent à la fois une fréquence d'innovation élevée couplée à un apprentissage social rapide, les nouveaux comportements peuvent apparaître et s'étendre rapidement à toute la population (transfert horizontal entre individus du même âge, et vertical entre générations), ainsi que modifier potentiellement les pressions de sélection s'exerçant originellement sur cette population et, à terme, la fréquence de spéciation (« the Behavioural Drive Hypothesis »; Wyles *et al.* 1983, Sol *et al.* 2005b).

Selon l'hypothèse de « l'intelligence sociale », l'évolution des groupes d'animaux vers la vie en société aurait nécessité des niveaux de cognition plus ou moins évolués selon la complexité des relations sociales mises en jeu (Byrne et Whiten 1988, Dunbar 1998). Ainsi, les capacités cognitives auraient permis aux individus les plus performants d'accéder à des ressources augmentant leur survie et/ou leur reproduction. Les capacités cognitives pourraient permettre par exemple de se remémorer des liens de parenté ou des rangs de dominance lors d'une rencontre avec un congénère (Wilkinson 1984), ou de manipuler ses rivaux pour cacher ou accéder à des ressources (Emery *et al.* 2004). Cette hypothèse a également reçu le support de plusieurs études démontrant une corrélation positive entre des mesures opérationnelles de la complexité sociale et de la capacité cognitive. Chez les primates et les oiseaux, des études comparatives ont montré que la taille relative du cerveau était corrélée positivement avec la taille du groupe (Dunbar 1995) et l'utilisation de tactiques de vie en société (Byrne & Corp 2004; Clayton *et al.* 2007). Chez les oiseaux, bien que les liens sociaux soient différents de ceux des primates, la cognition aussi pourrait jouer un rôle dans les relations sociales (Bond *et al.* 2003, Emery *et al.* 2007, Overington *et al.* 2009a).

Une autre hypothèse majeure de l'évolution de la cognition met quant à elle en jeu le rôle des facteurs écologiques comme pression de sélection. Selon l'hypothèse de « l'intelligence écologique », les capacités cognitives pourraient permettre aux animaux d'exploiter de nouvelles ressources, ou des ressources existantes mais à moindres coûts, ou encore de localiser de nouvelles ressources (Eisenberg et Don 1978, Sol 2009, Cantalapiedra *et al.* 2014). Un exemple classique est celui des mésanges (*Parus*) en Grande-Bretagne dans les années 50, chez lesquelles apparut le nouveau comportement alimentaire de perforer les couvercles en aluminium des bouteilles de lait afin d'en récolter la crème, très bonne source de nutriments (Fisher et Hinde 1949). Ce comportement s'est rapidement transmis à toute la population et a exposé les mésanges à de nouvelles pressions de sélection, favorisant par exemple certaines mésanges ayant la capacité biochimique de digérer le lactose présent dans le lait. Il a été proposé que l'innovation pourrait atténuer les effets des changements environnementaux en permettant de s'ajuster aux milieux complexes changeants (à fortes variations de température ou l'apparition de milieux urbanisés par exemple) (Godfrey-Smith 2002, Liker et Bokony 2009, Møller 2009, Cantalapiedra *et al.* 2014). Cette capacité pourrait également faciliter l'introduction dans un nouvel environnement (Lee 1991, Sol et Lefebvre 2000, Sol *et al.* 2008, Sutter et Kawecki 2009), voire dans certains cas favoriser le phénomène de spéciation (Sol *et al.* 2005b, Sol et Price 2008, Cantalapiedra *et al.* 2014), ou pousser vers le généralisme d'habitat (Overington *et al.* 2011b). Les capacités d'apprentissage présenteraient aussi des bénéfices (revue dans Dukas *et al.* 2013). Chez la mésange bleue (*Parus caeruleus*), les femelles utilisent leurs expériences de nidifications passées pour synchroniser leur reproduction avec les conditions actuelles de l'environnement (Grieco *et al.* 2002). Les Gobe-mouches à collier (*Ficedula albicollis*) apprennent de la réussite, ou de l'échec, de la reproduction d'une autre espèce d'oiseau nicheur afin de choisir leur site de reproduction (Doligez *et al.* 1999, Doligez *et al.* 2002). Bien qu'uniquement chez les insectes à ce jour, il a été montré que l'apprentissage pourrait même affecter la dynamique de population prédateur-proie (Ishii et Shimada 2012).

Cependant, d'autres études suggèrent aussi que les capacités cognitives auraient également un coût (Dukas 1999, Jaumann *et al.* 2013). Chez les insectes, et plus particulièrement les drosophiles (*Drosophila melanogaster*), des lignées artificiellement sélectionnées pour augmenter leurs performances d'apprentissage et de mémoire présenteraient également une baisse d'aptitude phénotypique (Mery et Kawecki 2003, 2005). Chez les oiseaux et les primates, les capacités

cognitives comme l'innovation et l'apprentissage sont associées à une taille relative du cerveau plus grande (Lefebvre *et al.* 1997, Timmermans *et al.* 2000, Reader et Laland 2002), or avoir un cerveau volumineux est très coûteux en énergie (Laughlin *et al.* 1998, Isler et van Schaik 2006). Un cerveau plus volumineux va également nécessiter un développement plus long, allongeant par la même occasion une période très sensible pour la survie des juvéniles (Nicolakakis et Lefebvre 2000) et très coûteuse pour les parents. De plus, Garamszegi *et al.* (2007) ont récemment découvert qu'un taux élevé d'innovation serait associé à une pression parasitaire également plus forte.

Variations interindividuelles des performances cognitives et conséquences évolutives chez une population naturelle de mésange charbonnière (*Parus major*)

Afin de mieux comprendre les pressions de sélection influençant l'évolution des capacités cognitives, il est apparu nécessaire d'en étudier les mécanismes à l'échelle de l'individu, là où la sélection s'exerce. Les traits comportementaux, au même titre que de nombreux autres caractères phénotypiques tels que la taille et la forme du bec chez les pinsons de Darwin (Grant et Grant 1996), peuvent être le résultat d'une longue histoire évolutive à travers le processus de sélection naturelle. Les caractéristiques individuelles sont les bases à partir de laquelle la sélection naturelle peut opérer et il a été montré que les variations entre les individus pour certains traits comportementaux affectent de multiples manières la survie et la reproduction des individus (personnalité : Dingemanse *et al.* 2004, Hollander *et al.* 2008 ; sociabilité : Cote *et al.* 2008 ; dispersion : Doligez et Pärt 2008, Pärt *et al.* 2011). Pour qu'il puisse y avoir évolution sur un trait, trois conditions sont nécessaires : (i) il doit exister une variation entre les individus pour ce trait, (ii) la variation sur ce trait doit jouer un rôle sur la survie et/ou la reproduction des individus, et (iii) ces variations doivent être transmises de génération en génération. Dans cette thèse, nous nous focaliserons sur l'hypothèse de l'intelligence écologique et nous intéresserons aux variations interindividuelles des performances de résolution de problème et d'apprentissage et leurs conséquences sur les traits d'histoire de vie des individus afin d'explorer le rôle des pressions de sélection sur la variation de ces performances.

Le modèle écologique choisi, la mésange charbonnière *Parus major*, est un petit passereau reconnu pour ses performances cognitives (Overington *et al.* 2009b). Monogame, et nichant dans des cavités, cette espèce accepte très facilement de se reproduire dans des nichoirs artificiels, ce

qui en facilite le suivi lors de la reproduction (Gosler 1993). Peu farouche, la mésange est un modèle de choix pour des tests comportementaux à la fois en captivité, car elle s'habitue facilement aux conditions (Cole *et al.* 2011), ainsi qu'en milieu naturel où elle est facile à capturer et à identifier.

Variations interindividuelles des performances cognitives et succès de reproduction

Afin d'évaluer si des forces sélectives s'exercent sur les capacités cognitives, les conséquences en termes de survie et/ou de succès de reproduction associées aux variations interindividuelles des performances cognitives doivent être mesurées. On s'intéresse alors à la valeur sélective d'un individu, c'est-à-dire à la capacité d'un phénotype à produire des descendants matures relativement aux autres phénotypes de la même population à un moment donné. Dans le cadre de l'approvisionnement, résoudre un nouveau problème ou apprendre une nouvelle technique de recherche de nourriture pourrait permettre aux individus d'utiliser de nouvelles stratégies alimentaires (Eisenberg et Don 1978, Godfrey-Smith 2002, Overington *et al.* 2008, Zrelec *et al.* 2013), leur permettant de faire face aux difficultés rencontrées dans un environnement variable lorsque les sources de nourriture habituelles diminuent rapidement et que la compétition augmente alors pour ces ressources. Lors de la reproduction, lorsque l'approvisionnement du parent sert à maximiser les gains de la couvée et que la compétition pour les ressources est très forte, découvrir une nouvelle source de nourriture ou apprendre une technique d'approvisionnement plus efficace pourrait être susceptible d'influencer directement le succès de reproduction, ou de permettre aux individus reproducteurs de maintenir une bonne condition corporelle avant et après l'effort de reproduction. Keagy et collaborateurs (Keagy *et al.* 2009, 2011) sont les premiers à s'être intéressés au rôle de telles capacités cognitives dans la reproduction en montrant que chez le Jardinier satiné (*Ptilonorhynchus violaceus*), les mâles les plus performants à résoudre différents tests cognitifs (dont la résolution de problème et l'apprentissage) obtenaient le plus grand nombre de copulations avec des femelles, une mesure du succès reproducteur chez cette espèce (Keagy *et al.* 2009, 2011; mais voir Isden *et al.* 2013). Cependant, un lien direct entre la performance de résolution de problème et le succès de reproduction restait à mettre en évidence.

Le **chapitre 1** de ce doctorat a pour but de vérifier l'hypothèse que la performance d'innovation d'un individu peut influencer son succès de reproduction. Chez une population naturelle de mésanges charbonnières, des couples reproducteurs ont été suivis tout au long de la reproduction afin de relever les différentes variables relatives au succès de reproduction (date de ponte, taille de couvée, nombre de poussins à l'envol, etc.). Les couples ont ensuite été soumis à un test de résolution de problème directement en milieu naturel, puis l'échec ou la réussite ainsi que la vitesse de résolution du problème ont été mesurés.

Une corrélation positive entre le succès de reproduction et la performance de résolution de problème cependant peut être le résultat de plusieurs mécanismes :

(1) les performances cognitives pourraient influencer directement la reproduction : chez une espèce monogame, un partenaire plus performant serait par exemple plus efficace à utiliser son habitat et donc mieux à même de nourrir sa progéniture (Cole *et al.* 2012). Si on présume que les performances cognitives en question sont héréditaires, les performances cognitives pourraient également agir comme des indicateurs honnêtes de la qualité génétique d'un partenaire (Airey et DeVoogd 2000) : un partenaire plus performant produirait une progéniture de meilleure qualité (par exemple ayant une meilleure condition corporelle et/ou en plus grand nombre: Airey *et al.* 2000; Spencer et MacDougall-Shackleton 2011). Enfin, les performances cognitives pourraient n'avoir aucune influence sur le succès reproducteur, mais les individus pourraient utiliser leurs propres capacités pour influencer et attirer le choix des partenaires potentiels afin d'augmenter leur propre succès reproducteur.

(2) à l'inverse, la reproduction elle-même pourrait influencer les performances cognitives : un nombre plus important de jeunes nécessiterait un approvisionnement au nid plus important et les parents pourraient être 'contraints' à chercher de nouvelles solutions pour augmenter la capacité de nourrissage.

Le but du **chapitre 2** de ce doctorat est de tester le lien causal sous-jacent impliqué dans la corrélation positive entre la performance de résolution de problème et le succès de reproduction. Durant deux saisons de reproduction consécutives, le succès reproducteur de couples de mésanges charbonnières a été manipulé (ajouts ou retraits de poussins après éclosion), puis les couples ont été soumis au test de résolution de problème afin de vérifier expérimentalement le lien de causalité

entre le succès reproducteur des parents et leurs performances de résolution de problème. Si la performance des parents influence le succès de reproduction, alors il ne devrait pas y avoir de différence entre les couples dont la couvée a été diminuée et les couples dont la couvée a été augmentée. Par contre, si le succès reproducteur influence les performances cognitives, alors les couples dont la couvée a été augmentée devraient être plus performants.

Variations interindividuelles des performances cognitives et sélection sexuelle

Si les performances cognitives comme la résolution de problème ou l'apprentissage peuvent influencer le succès de reproduction chez certaines espèces, il est possible que ces capacités cognitives puissent jouer un rôle important lors du choix du partenaire. Évaluer directement les performances cognitives d'un partenaire potentiel pourrait s'avérer être une tâche difficile, de par la nature de la performance elle-même. En l'absence d'une évaluation directe des performances de résolution de problème ou d'apprentissage des mâles (Snowberg et Benkman 2009), des caractères sexuels secondaires associés à ces performances, comme des traits phénotypiques dépendant du régime alimentaire, pourraient être associés à ces performances et jouer un rôle lors de la sélection sexuelle (revue dans Boogert *et al.* 2011b).

La complexité du chant est un caractère sexuel secondaire bien connu chez les oiseaux. La complexité du chant, mesurée communément par le nombre de chants, syllabes ou éléments différents produits par un individu (Devoogd *et al.* 1993, Airey et DeVoogd 2000, Pfaff *et al.* 2007) est associée avec une structure bien précise du cerveau chez les oiseaux, le HVC (« High Vocal Center »; Airey et DeVoogd 2000). Cette structure étant très vulnérable au stress lors de son développement (par exemple, le manque de nourriture ou une infection parasitaire; Spencer *et al.* 2003, 2005), son développement reflète donc la qualité d'un individu et sa capacité à faire face aux défis de l'environnement (Nowicki et Searcy 2005, Spencer et MacDougall-Shackleton 2011). Ainsi, la complexité du chant, corrélée positivement avec un noyau de contrôle du chant bien développé et dont le volume est héritable (Airey *et al.* 2000), pourrait être utilisée par les femelles lors du choix de partenaire afin de choisir un mâle de meilleure qualité (évidences revues dans Nowicki *et al.* 2002). De par son association avec une structure du cerveau, la complexité du chant serait également un candidat de choix pour indiquer les performances cognitives d'un individu

(Nowicki et Searcy 2011, Spencer et MacDougall-Shackleton 2011). Boogert et collaborateurs (2008) ont été les premiers à tester cette hypothèse en montrant que chez le mâle Diamant mandarin (*Taeniopygia guttata*) élevé en captivité, le temps nécessaire pour apprendre à résoudre une tâche alimentaire était corrélé négativement avec la complexité du chant. Ainsi, chez cette espèce, la complexité du chant pourrait être utilisée par les femelles pour évaluer les performances d'apprentissage de partenaires potentiels. Chez une autre espèce cependant, le bruant chanteur (*Melospiza melodia*), la complexité du chant des mâles serait cette fois-ci corrélée positivement à une tâche d'inhibition de réflexe, mais négativement avec une tâche d'apprentissage inversée (Boogert *et al.* 2011a), et la taille du répertoire de chant serait corrélée négativement avec une tâche d'apprentissage spatial (Sewall *et al.* 2013). Les performances cognitives telles que l'innovation, l'apprentissage du chant ou l'apprentissage spatial étant associées à différentes structures dans le cerveau dont l'espace est limité (c'est à dire mésopallium et nidopallium, noyau de contrôle du chant et hippocampe respectivement), la taille de chacune est un compromis avec celle des autres structures, rendant les liens entre chant et performances cognitives complexes.

Un second candidat potentiel à jouer le rôle d'indice indirect de la performance cognitive est la coloration. Chez les oiseaux, trois mécanismes sont à l'origine de la coloration des plumes : les pigments de type caroténoïdes (responsables des couleurs jaune, orange ou rouge), mélaniques (responsable des couleurs noire et marron) et les plumes structurelles (responsable des colorations non-iridescentes et iridescentes bleue et verte des UV) (Hill et McGraw 2006). Les caroténoïdes sont des pigments qui ne sont pas synthétisés directement par les animaux, mais uniquement assimilables via l'alimentation (c'est à dire qu'ils sont produits par les algues, plantes vertes, certains champignons et bactéries; Partali *et al.* 1987, Moller *et al.* 2000). Le rôle que jouent les caroténoïdes à maintenir une bonne santé et à signaler la qualité de l'individu a été étudié depuis de nombreuses années (revue dans Moller *et al.* 2000) et, bien que complexe (Svensson et Wong 2011), le rôle des caroténoïdes dans la sélection sexuelle est largement reconnu. À l'inverse, la mélanine est synthétisée par l'individu même (McGraw 2006). Bien que traditionnellement, les pigments mélaniques soient reconnus pour jouer un rôle moindre dans la sélection sexuelle car moins sensibles aux variations de l'environnement, de plus en plus d'études récentes semblent indiquer des liens avec la qualité des individus (revue dans Roulin 2004a). La coloration des plumes structurelles est produite par les différentes réflexions et réfractions des composants nanostructurels de ces plumes (Prum 2006). Le mécanisme et les fonctions de cette coloration ont

reçu un intérêt récent (Doucet et Meadows 2009) et les premières études semblent indiquer un lien avec la condition corporelle des individus (Doucet 2002, Doucet et Montgomerie 2003, Hegyi *et al.* 2007) et un rôle dans la sélection sexuelle (Andersson *et al.* 1998, Siitari *et al.* 2002, Henderson *et al.* 2013). Apprendre une nouvelle technique de recherche de nourriture ou découvrir de nouvelles ressources pouvant permettre aux individus d'accéder à des ressources plus riches ou en plus grande quantité, la coloration pourrait être utilisée par les animaux pour signaler la capacité d'un individu à trouver de la nourriture (Roulin *et al.* 2008, Slagsvold et Lifjeld 1985, Senar *et al.* 2002, 2008, Jacquin *et al.* 2012), signalant ainsi une bonne santé et/ou la capacité de nourrir des jeunes (Saetre *et al.* 1995, Senar *et al.* 2002). Cette hypothèse a d'abord été testée chez une espèce de poisson, les guppys (*Poecilia reticulata*) (Shohet et Watt 2009). Dans cette étude, les auteurs ont soumis des mâles à un labyrinthe au bout duquel une récompense alimentaire était proposée et ont ensuite soumis ces mâles à un test de choix de partenaire. Bien que les mâles les plus rapides à apprendre le bon chemin fussent préférés par les femelles, performance également corrélée à la couleur orange présente sur leur corps, la couleur elle-même ne faisait pas l'objet de la préférence des femelles (Shohet et Watt 2009). Chez les oiseaux, une seule étude a été réalisée et a montré que les mâles Tarin des aulnes (*Carduelis spinus*) les plus rapides à résoudre une tâche de résolution de problème présentaient une tache alaire jaune plus longue, un caractère sexuel secondaire reconnu pour être favorisé par les femelles de cette espèce lors du choix de partenaire (Mateos-Gonzalez *et al.* 2011). Cependant, chez cette espèce, un lien direct avec le choix de partenaire et le succès de reproduction en lien avec les performances cognitives n'a jamais été mis en évidence. De plus, une tache de couleur peut véhiculer plusieurs types d'informations (comme la longueur de la tache de couleur, mais aussi sa surface totale, sa brillance, la longueur d'onde ou encore l'intensité de la couleur), et des informations supplémentaires sont nécessaires afin de mieux comprendre le rôle de la coloration des plumes dans la signalisation de la performance de résolution de problème chez cette espèce.

Dans les chapitres précédents, nous avons examiné le lien entre les variations interindividuelles de performance de résolution de problème et le succès de reproduction au sein d'une population de mésange charbonnière sur l'île de Gotland (Suède). Cette espèce présente une coloration jaune sur les flancs, ainsi qu'une bande noire ventrale (plus large chez le mâle) et une calotte noire (présentant des reflets irisés chez le mâle), ce qui en fait un modèle idéal pour examiner le rôle de la coloration dans la signalisation des performances cognitives individuelles.

Dans le **chapitre 3** de ce doctorat, la coloration des plumes et les performances de résolution de problème et d'apprentissage ont été comparées en utilisant des plumes récoltées sur des individus testés pour leurs performances cognitives. Le but est d'examiner les liens entre les performances cognitives et les caractéristiques phénotypiques afin d'identifier quelles caractéristiques pourraient être utilisées pour signaler les performances cognitives.

Variations interindividuelles des performances cognitives et parasitisme

Chez les humains, une très vaste littérature est disponible concernant les effets néfastes du parasitisme sur les performances cognitives (Nokes *et al.* 1992, Kihara *et al.* 2006). Dans le cas du paludisme (*Plasmodium falciparum*), une infection, même aux premiers stades, peut affecter l'attention, la mémoire, le langage, les capacités cognitives spatiales ou encore la coordination (revue dans Kihara *et al.* 2006). Chez les animaux (non humains) aussi, le parasitisme peut affecter les performances cognitives (Kershaw *et al.* 1959) comme l'apprentissage (Stretch *et al.* 1960, Kavaliers *et al.* 1995), la résolution de problème (Olson et Rose 1966) ou la prise de décision (Milinski *et al.* 1990). Cependant, ces travaux ont été menés principalement chez les rongeurs. Le paludisme est présent aussi chez les oiseaux (Molyneux *et al.* 1983), et des études récentes ont montré que la présence de ce parasite, quel que soit le nombre de lignées différentes infectant l'animal (Marzal *et al.* 2008), peut avoir des conséquences négatives sur la condition corporelle, la reproduction et la survie (Allander 1997, Merino *et al.* 2000, Marzal *et al.* 2005, 2008). Une seule étude à ce jour s'est intéressée aux effets du paludisme sur les traits comportementaux d'une population naturelle de mésange charbonnière, et a révélé des effets complexes et opposés selon le sexe: en ce qui concerne la performance de résolution de problème par exemple, les mâles les plus performants sont également les plus parasités mais chez les femelles, la relation est inversée (Dunn *et al.* 2011). Bien que cette étude corrélative ne permette pas de démêler les causes des conséquences, que les parasites affectent le comportement de leur hôte (effets néfastes des parasites sur les performances cognitives) ou parce que les comportements en question augmentent les risques d'être exposé à des parasites (coût des performances cognitives : collecter des informations sur l'environnement, explorer de nouveaux environnements ou apprendre de nouvelles techniques de recherche de nourriture pourraient par exemple exposer les individus à de nouvelles pressions

parasitaires; Barber et Dingemanse 2010; Boyer *et al.* 2010), le parasitisme semble jouer un rôle important dans l'évolution des capacités cognitives.

L'objectif du **chapitre 4** de ce doctorat est d'examiner le lien sous-jacent reliant le paludisme aux traits comportementaux des hôtes. Durant deux saisons de reproduction successives, des femelles de mésange charbonnière ont été capturées tôt dans la saison de reproduction afin de recevoir soit une injection de médicament anti-paludisme (Primaquine), soit une solution saline contrôle. Ces femelles ont été soumises quelques jours plus tard au même test de résolution de problème utilisé dans les précédents chapitres afin de mesurer leurs réponses comportementales (performance de résolution de problème, apprentissage, néophobie, exploration, activité). Si les comportements mesurés bénéficient des injections de Primaquine, cela confirmera un effet néfaste de la charge parasitaire sur le comportement des individus infectés. Au contraire, si les comportements mesurés ne varient pas entre les deux groupes, il est possible que ces comportements soient à l'origine de la variation de la charge parasitaire : explorer ou apprendre de nouveaux comportements par exemple exposerait les individus à des pressions parasitaires plus fortes.

Contribution des co-auteurs :

Laure Cauchard, Blandine Doligez et Louis Lefebvre ont formulé l'hypothèse de travail et planifié les expériences. Laure Cauchard a mené les expériences sur le terrain. Laure Cauchard, Blandine Doligez et Louis Lefebvre ont effectué les analyses. Laure Cauchard a rédigé la première version du manuscrit et tous les co-auteurs ont participé à son amélioration.

CHAPITRE 1 :

PROBLEM-SOLVING PERFORMANCE IS CORRELATED WITH REPRODUCTIVE SUCCESS IN A WILD BIRD POPULATION

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(Modifié pour les besoins de la présente thèse)

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Abstract

Although interindividual variation in problem-solving ability is well documented, its relation to variation in fitness in the wild remains unclear. We investigated the relationship between performance on a problem-solving task and measures of reproductive success in a wild population of great tits, *Parus major*. We presented breeding pairs during the nestling provisioning period with a novel string-pulling task requiring the parents to remove an obstacle with their leg that temporarily blocked access to their nestbox. We found that nests where at least one parent solved the task had higher nestling survival until fledging than nests where both parents were non-solvers. Furthermore, clutch size, hatching success and fledgling number were positively correlated with speed in solving the task. Our study suggests that natural selection may directly act on interindividual variation in problem-solving performance. In light of these results, the mechanisms maintaining between-individual variation in problem-solving performance in natural populations need further investigation.

Introduction

An animal's habitat varies in time and space, whether this happens more or less predictably from one season to the next, unpredictably during environmental perturbations, or gradually as a result of climate change. As a consequence, animals are sometimes faced with situations in which they have to deviate from their normal behavioural repertoire to solve unexpected problems. Differences among species and individuals in the ability to solve such problems can be experimentally assessed with novel tasks conducted in captivity (Overington *et al.* 2009a) and in the field (Morand-Ferron *et al.* 2011). These tasks routinely involve obstacle removal (Keagy *et al.* 2011), detouring (Boogert *et al.* 2011a) or string pulling (Seibt and Wickler 2006; Cole *et al.* 2011). Such tests are assumed to operationalize innovativeness (Webster and Lefebvre 2001), defined as the propensity to invent a new behaviour or to flexibly adjust established behaviours to solve new problems (Reader and Laland 2003).

Although innovativeness is widespread in humans, many other animals, including nonhuman primates (Kummer and Goodall 1985) and other mammals (Patterson and Mann 2011), fish (Laland and Reader 1999) and birds (Sol *et al.* 2005a), are also known to innovate when faced with new situations. In birds, comparative studies have shown that innovation rate, measured for a large number of species (Lefebvre *et al.* 1997; Lefebvre 2011), is positively correlated with species introduction success (Sol *et al.* 2002), habitat generalism (Overington *et al.* 2011b), urbanization (Liker and Bokony 2009; Sol *et al.* 2011) and species richness (Nicolakakis *et al.* 2003; Sol *et al.* 2005b).

At the within-species level, differences among individuals in innovativeness, measured using problem-solving performance, have been well documented in a variety of avian taxa, such as Psittacidae (Funk and Matteson 2004), Falconidae (Biondi *et al.* 2008), Corvidae (Bluff *et al.* 2010) and Paridae (Cole *et al.* 2011), both in captivity (Boogert *et al.* 2008; Overington *et al.* 2011a) and in the field (Gajdon *et al.* 2006; Keagy *et al.* 2009; Morand-Ferron *et al.* 2011). Whereas the benefits of innovativeness have been well investigated at the species level, few studies have examined its fitness consequences at the individual level. Only four recent studies provide evidence for an indirect link between mating success and problem-solving ability (but see Boogert *et al.* 2011b for a review of sexual selection acting on other cognitive abilities). In the satin bowerbird, *Ptilonorhynchus violaceus*, males with better problem-solving ability in the field obtained more

populations (Keagy *et al.* 2009, 2011). In the siskin, *Carduelis spinus*, males with long yellow wing stripes, a secondary sexual trait used by females in mate selection, were faster problem solvers in captivity than males with shorter stripes (Mateos-Gonzalez *et al.* 2011). In captive zebra finches, *Taeniopygia guttata*, males that sang more complex songs, and thus, that were preferred by females, were faster in learning how to solve a novel foraging task (Boogert *et al.* 2008). Finally, in song sparrows, *Melospiza melodia*, males with larger song repertoires, which have higher lifetime reproductive success in the field (Reid *et al.* 2005), required fewer trials to solve a detour-reaching task in captivity (Boogert *et al.* 2011a). Yet only one recent study has provided direct evidence for a positive link between problem-solving performance and reproductive output: in great tits, *Parus major*, females that solved a novel foraging task in captivity produced larger clutches and fledged more young in the wild than did non-solvers (Cole *et al.* 2012). However, solvers were also more likely to desert their nests upon capture by experimenters than non-solvers, suggesting a trade-off between the fitness benefits and costs of problem-solving performance (Cole *et al.* 2012).

In this study, we explored the potential correlation between individual performance on a novel nonforaging task and reproductive success in a natural great tit population. The great tit is known for its innovativeness, as reflected in particular by its many feeding innovations reported in nature (Overington *et al.* 2009b), its ability to take advantage of anthropogenic food sources in urban environments (Fisher and Hinde 1949) and its broad diet (Gosler 1993). The ability to solve problems might benefit individuals in several ways, for example by escaping new (e.g. invasive) predator species, adjusting to new constraints in changing habitats (e.g. limited nest site availability due to urbanization) or finding new food resources when the usual ones are scarce. Food availability is particularly important for many passerine birds in temperate regions, where rapid nestling growth involves high-protein food demands and reproductive output therefore strongly depends on food resources with limited availability (van Noordwijk *et al.* 1995; Naef-Daenzer and Keller 1999; Cresswell and McCleery 2003). Survival of young until recruitment is strongly associated with growth and body mass at fledging (e.g. Tinbergen and Boerlijst 1990; Linden *et al.* 1992; Monrós *et al.* 2002), and thus depends on parental foraging performance during the nestling period (e.g. Ens *et al.* 1992; Barba *et al.* 1995; Naef-Daenzer and Keller 1999; Schwagmeyer and Mock 2008). Better problem-solving abilities might allow individuals to reduce the risk of starvation for their young and maintain optimal body condition before, during and/or after the reproductive effort. We

thus predicted that individuals showing better problem-solving performance should achieve higher reproductive success. Contrary to most previous problem-solving tests that use food as the source of motivation (but see Keagy *et al.* 2009, 2011), we assessed problem-solving performance during the nestling period in the field, using a string-pulling task that blocked access to the nest for 1 h during parental provisioning visits to the young. We measured reproductive success during one breeding season using several standard breeding parameters (laying date, clutch size, hatching and fledging probability, brood size), as well as motivation (Keagy *et al.* 2009) and neophobia (Webster and Lefebvre 2001; Bouchard *et al.* 2007), which could potentially confound our measure of problem-solving performance (Greenberg 2003; Sol *et al.* 2011).

Material and Methods

Study site, population monitoring and measures of reproductive success

We carried out the study in a breeding population of great tits monitored on the island of Gotland, Sweden, between April and June 2010. Great tits are small, socially monogamous passerines that readily breed in nestboxes. The female incubates alone, but both sexes care for the brood (Smith *et al.* 1988; Gosler 1993). We visited nestboxes at least every 2 days from the beginning of the breeding season onwards to determine the following measures of reproductive success: laying date, clutch size (from 6 to 12 eggs), hatching proportion (i.e. number of hatched young/number of eggs laid), brood size at day 14 and fledging proportion (i.e. number of fledged young/number of hatched young). We ringed young at day 9 after hatching and measured their tarsus length (to the nearest 0.1 mm) and body mass (to the nearest 0.1 g) at day 14. When chicks were 6 - 12 days old, we caught adults in the nestbox using a swing-door trap, ringed them if they were unringed, sexed them according to plumage characteristics (i.e. the male is generally the brightest and shows a large belly stripe whereas females are duller and their stripe is discontinuous on the belly; Svensson 1992) and measured their mass and tarsus length. Birds were caught, handled and ringed under a licence from the Stockholm Museum Ringing Center (license number 644:M03) and behavioural tests were conducted under a general licence from the Swedish Committee for Experiments on Animals for all experiments on the site (license number C 108/7).

Previous studies in different great tit populations revealed no brood parasitism and only a small percentage of extrapair young (3.5 - 8.6%; Verboven and Mateman 1997; Lubjuhn *et al.*

1999; Griffith *et al.* 2002). We therefore consider offspring number and body condition to be reliable measures of both male and female reproductive success in our study population.

Measurement of Problem-solving Performance

So far, most problem-solving tasks presented to birds have been motivated by food: to encourage participation in the test, the experimenter withholds food before testing or offers a preferred food item as a reward. In the wild, however, adult satiation cannot easily be manipulated. Using a food-motivated task could thus lead to low levels of response if natural food is abundant elsewhere in the environment or, if food is rare, it could affect offspring condition and/or survival depending on parental problem-solving success. Here, we measured problem-solving performance by developing a novel string-pulling task motivated by accessing the young during the peak of nestling food demand. This task featured a door placed in front of the entrance hole of the nestbox (Fig. 1.1). The door was by default closed, preventing the birds from entering and reaching their chicks. It could be opened by pulling a string placed below the door, and, once opened, birds could slip their body under the door to access their young. The door then closed behind them, but the birds could get out of the box by simply pushing the door open (Fig. 1.1). In this species, pulling behaviour can frequently be observed during foraging (e.g. lifting leaves or twigs) and nest building (e.g. collecting moss and hair material). However, great tits mainly pull using their beak, and very rarely pull using their legs only. Furthermore, the presence of an obstacle that would naturally and suddenly block the entrance of the nest cavity (e.g. following the fall of a branch) is an extremely unlikely event in this population. Over the past 10 years, no such natural blocking has been observed at the approximately 1500 boxes monitored each year, even though most of the forest study plots are unmanaged, with the presence of a lot of dead and broken trees and branches. Therefore, the novelty of the situation presented to great tits (removing an obstacle in front of the nestbox entrance) and the necessity to use a rarely used behaviour (pulling with a leg) to deal with

it, make our task a good problem-solving task that requires innovative behaviour to be solved (Reader and Laland 2003).

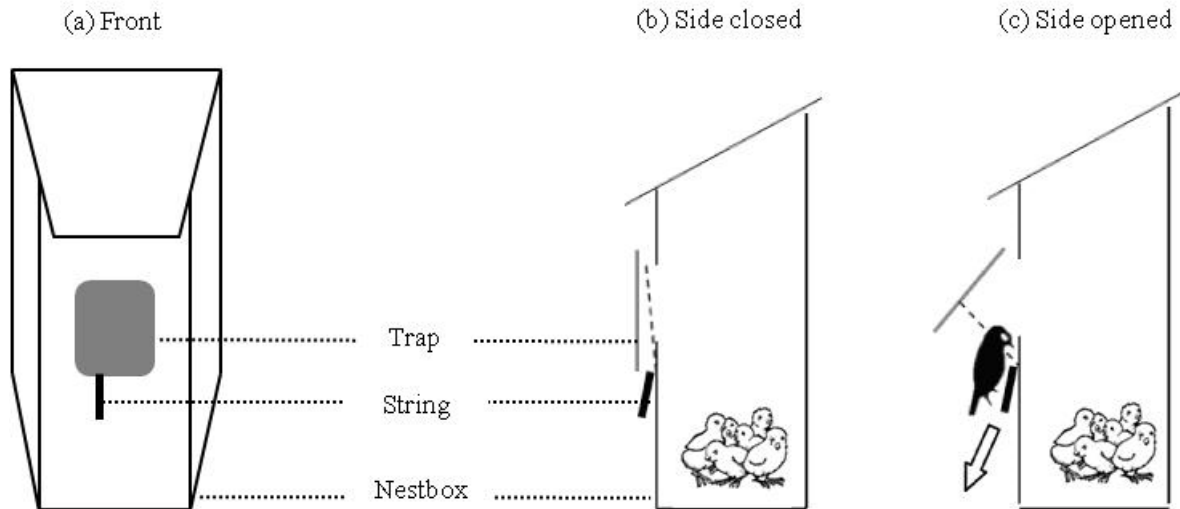


Figure 1.1. Views of the task used to measure problem-solving performance in great tits based on opening a door blocking the entrance to the nestbox. Birds had to pull the string to open the door and be able to slip under the door to enter the nestbox. The door then closed behind them. (a) Front view, door closed, (b) side view, door closed and (c) side view, door opened.

Our task was performed during a period when, and involved a problem for which, the effects of parental performance on offspring survival and condition are likely to be crucial. To ensure maximal participation of parents, we carried out the problem-solving test during the peak of nestling food demand and parental visiting rate (i.e. when chicks were 6 - 10 days old and between 8.00 and 16.00 hours; Gosler 1993). We conducted the test only when chicks were satiated (e.g. not begging) at the beginning of the test, and the test lasted for 1 h only, to avoid possible direct negative effects of the test itself on chicks if parents were not able to solve the task (e.g. starvation). In this population, parents are often observed to take 1 h breaks in chick provisioning when food is abundant and chicks are satiated before resuming provisioning (B. Doligez, personal observation). We randomly selected breeding pairs to be tested and avoided any bias due to sampling since parents were caught after we measured their problem-solving performance (Biro and Dingemanse 2009). Great tits are highly territorial and aggressive towards conspecifics during reproduction (Gosler 1993), which therefore ensured that only the breeding pair of the focal nest tested tried to solve the task and enter the nestbox. To ensure that problem-solving trials were

independent and to avoid social learning between tested pairs, we carried out the test on nests separated by at least 200 m from their nearest neighbours (Both and Visser 2000; Leal and Powell 2011). Just before attaching the task to the nestbox entrance, we installed a camouflaged video recorder at a distance of approximately 6 m in front of the nestbox and recorded the parents' behaviour for 60 min. When neither parent was seen during this period, the trial was cancelled and carried out once again on the next day. All the movements and interactions of each parent (sexes are distinguished using plumage and size differences that can be observed on videos) with the nestbox and the task were subsequently scored from video recordings by a single observer who was blind to the measures of reproductive success. We observed no desertion or total reproductive failure after the test was conducted.

For each tested parent, we first recorded whether the individual succeeded in solving the task (i.e. opened the door and entered into the nestbox at least up to its shoulders; results were unchanged when we used other parts of the body, such as head only or entire body, to define when the task was solved). Birds that failed to enter were considered non-solvers. For birds that succeeded in solving the task (i.e. entering the nestbox), we recorded the latency to enter into the nestbox as the time elapsed between the first contact of the bird with the string (i.e. that caused a movement of the door) and the bird's entry into the nestbox. Results were qualitatively similar when measuring latency as the time elapsed from the first contact with the task instead of the string. When individuals left the box after contacting the string and then returned within the same trial, we excluded the time spent away from the box from this latency (i.e. the latency only accounted for the time spent trying to enter the nestbox).

Neophobia and Motivation Levels

Personality traits can interfere with the process of innovation (Greenberg 2003). For instance, animals that avoid novel stimuli have been found to show longer problem-solving latencies than less neophobic ones (Bouchard *et al.* 2007; Sol *et al.* 2011). This potentially confounding effect on problem-solving performance should therefore be controlled for. Because the door and string were novel on the day of the test, we used the time between landing on the nestbox and first contact with

the door or string as a measure of neophobia for each individual, including the time away from the nestbox after first landing.

Problem-solving performance measured as the latency to remove an obstacle in front of the nestbox entrance could reflect a difference in motivation to access the young, for example, associated with the number of chicks in the nestbox (Smith *et al.* 1988). We controlled for the effect of this potentially confounding variable in two ways. First, when chicks were 5 days old, we recorded chick provisioning rates of the pair as the total number of visits to the nest during 1 h between 6.00 and 11.00 hours. Because provisioning rate depends on brood size, it should represent the motivation of the parents to enter the nest, and thus to solve the problem. Second, we also computed the number of times each parent contacted the two task areas directly relevant to solving the problem (i.e. the trapdoor and the string, Fig. 1.1) divided by the total number of times other areas (top, front, corners and sides of the box) were contacted during the problem-solving test. This measure should reflect the persistence of the parent in trying to solve the problem (Overington *et al.* 2011a), and thus its motivation.

Statistical Analyses

Because we could not measure latency for non-solvers, we used the performance of the solver as the performance of the pair composed of one solver and one non-solver. For the pairs where both parents were solvers, we considered the solving latency of the fastest parent only. In both cases, this relies on the assumption that the most successful parent drives the success of the pair. However, to test for the robustness of our results with respect to the measure for pairs with two solvers, we repeated the analyses considering the pairs that had two solving parents in alternative ways: (1) we excluded these pairs, keeping only the single-solver pairs, (2) we used the average latency of the two parents, and (3) we used the latency of the first parent that solved the task, instead of the fastest, to avoid possible social learning from the partner (see Supplementary Material in Appendix 1 of this thesis).

We analysed the relationship between problem-solving performance and reproductive success at the nest level. Because problem-solving latency could not be determined for the eight non-solver pairs, we conducted two different statistical analyses. First, we compared measures of

breeding success between nests where at least one parent solved the task and those where both parents were non-solvers. Then we tested for a relation between measures of breeding success and problem-solving latencies in nests where at least one parent solved the task. We analysed binary variables (hatching and fledging probability) using generalized linear models (GLM) with binomial error and logit link function (χ^2 tests). We analysed continuous variables (laying date, clutch size, fledgling number, provisioning rate) using linear models and, for offspring body mass, a linear mixed model including brood identity as a random factor to account for common rearing environment and parental effects on siblings (F tests).

All initial models included as explanatory variables the measure of the problem-solving performance of the pair (either a binary variable: solver versus non-solver pairs, or a continuous variable: latency to enter). Because breeding success can be measured at different stages throughout the breeding process, and each measure at a given stage depends on the preceding measure (i.e. clutch size depends on laying date: Perrins and McCleery 1989; brood size depends on clutch size, etc.), we used a sequential approach to investigate the influence of problem-solving performance on success at each breeding stage independently from preceding ones. To do so, we included some of the dependent variables as covariates in the models analysing subsequent independent variables: (1) laying date when analysing clutch size (or hatching date when analysing offspring body mass) and (2) clutch size when analysing brood size (or brood size at day 14 when analysing offspring body mass). This allowed us to characterize the cumulative relations between problem-solving performance and measures of breeding success over stage. In addition, we included as covariates (3) the body condition of both parents (defined as the ratio of body mass to tarsus length) in all analyses, (4) the tarsus length when analysing offspring body mass and (5) provisioning rate when analysing measures of reproductive success after day 5. The age of the parents (yearling versus older), which is known to affect breeding success, was not included in the models because age assessment was uncertain in the field. Given that age is highly correlated with laying date in this population (B. Doligez, unpublished data), as well as in other populations (Perrins and McCleery 1985), we included laying date as a covariate in all models to partially control for age effects. Including the sex of the parent with the highest problem-solving performance (or highest activity around the nestbox if both parents were non-solvers) as a covariate showed that sex had no influence on the results; we therefore did not retain this factor in the analyses. Sample sizes varied among analyses because one female could not be captured and feeding rate was not available for

four nests. We did not test for interactions between explanatory variables because of our small sample size and the fact that we had no a priori hypotheses to justify them.

We tested whether interindividual variation in the degree of neophobia could influence the variation of problem-solving performance by examining the relationship between these two variables at the individual level. We first compared neophobia between solvers and non-solvers. In a second analysis, we tested for a relation between neophobia and latency to open in solvers only. For both analyses we used linear mixed models with neophobia as the dependent variable and nest as a random factor to control for the nonindependence of the two pair members. The models also included the sex of the individual, its interaction with the measure of individual problem-solving performance and the age of the brood when measuring neophobia and performance. Again, sample sizes varied among analyses because the measure of neophobia was missing for three of the non-solvers.

Finally, we investigated the potentially confounding effect of motivation by testing whether parental provisioning rate per nest was related to between-pair variation in problem-solving performance (either as a binary factor: solving versus nonsolving pairs, or as a continuous variable: latency among solving pairs), using parental provisioning rate as the dependent variable and including laying date, clutch size and the body condition of both parents as covariates. We also tested whether the persistence score was related to interindividual variation in problem-solving performance, using persistence score as the dependent variable, the age of the brood on the day of the test as a covariate and nest as a random factor when comparing solvers versus non-solvers, to account for the nonindependence of both parents (this did not apply to the latency since only one parent was a solver in most pairs).

We performed all analyses using SAS version 9.1 (SAS Institute, Cary, NC, U.S.A.). We removed nonsignificant variables using a stepwise backward selection procedure (with a threshold at 0.05). We tested the residuals of linear models for normality and homoscedasticity. Overdispersion was checked for generalized linear models and we corrected chi-square tests into F tests (and corresponding *P* values) when (small) overdispersion occurred, which is why we report sometimes chi-square tests and sometimes F tests for our GLMs. All tests were two tailed.

Results

Eighteen out of 26 tested pairs solved the task, and among these solver pairs, only one parent succeeded in 16 pairs, while both parents did in the remaining two pairs. Of the 45 individuals that were tested, 44.4% were successful solvers ($N = 20$), including 50% of each sex ($N = 10$ females and $N = 10$ males; $\chi^2 < 0.01$, $P > 0.99$). Furthermore, among solving individuals, the latency to solve did not differ between males and females ($F_{1,18} = 0.67$, $P = 0.51$; mean latency \pm SE: males: 205.10 ± 536.51 s; females: 89.80 ± 74.58 s).

Problem-solving Performance and Reproductive Success

Nests where at least one parent solved the task had a significantly higher proportion of chicks surviving until fledging than nests where both parents were non-solvers ($\chi^2 = 5.92$, $P = 0.015$; Fig. 1.2). This result accounted for the effect of clutch size as a covariate in the same model (fledging success decreased with increasing clutch size: $\chi^2 = 4.28$, $P = 0.038$).



Figure 1.2. Mean offspring survival until fledging \pm SE (adjusted for clutch size) depending on the problem-solving status of the pair: nests where both parents solved the task (two solvers), nests where one parent solved the task (one solver), and nests where no parent solved the task (non-solvers). Numbers above bars indicate sample sizes. Grouping the nests where both parents solved the task and those where only one parent solved the task did not significantly change the value of fledging success for the solving category.

No significant difference was observed between solvers and non-solvers for laying date ($F_{1,24} = 2.58, P = 0.12$), clutch size ($F_{1,24} = 1.46, P = 0.24$), proportion of eggs that hatched ($F_{1,23} = 0.06, P = 0.81$), fledging number ($F_{1,18} = 0.01, P = 0.91$, with clutch size, $F_{1,18} = 6.67, P = 0.019$, and provisioning rate, $F_{1,18} = 4.90, P = 0.040$, as significant covariates in the same model) and offspring body condition (i.e. body mass corrected for tarsus length, $F_{1,152} < 0.01, P = 0.96$, with brood size at day 14, $F_{1,152} = 5.31, P = 0.022$, as a significant covariate in the same model). The absence of a significant difference in clutch size, hatching rate and fledging number between solvers and non-solvers, despite higher nestling survival rate for solvers, was probably due to the low statistical power to detect differences because of the limited sample size. The difference in fledging number between solvers and non-solvers was indeed higher than the difference in clutch size (relative fledging number and clutch size for solvers compared to non-solvers: 1.18 ± 0.84 and 0.69 ± 0.58 , respectively), as expected from a higher nestling survival rate, but these differences remained non-significant due to large associated standard errors. Furthermore, because clutch size was accounted for in the analysis of fledging number, we compared fledging number between solvers and non-solvers independently from earlier breeding stages, and thus a higher nestling survival rate may not translate into a higher fledging number once clutch size is accounted for.

Among solvers pairs, the fastest pairs to solve the task laid significantly more eggs per clutch than the slowest solver pairs ($F_{1,15} = 5.21, P = 0.037$; Fig. 1.3a), with a trend in male body condition ($F_{1,15} = 3.91, P = 0.067$), which was thus included as a covariate in the same model: 100s increase in latency to solve corresponded to a decrease in clutch size of 1.1 ± 0.5 eggs. The fastest pairs also hatched a higher proportion of eggs ($F_{1,14} = 4.85, P = 0.045$; partial regression coefficient \pm SE: -0.011 ± 0.005 ; Fig. 1.3b), with female body condition as a significant covariate in the same model ($F_{1,14} = 5.85, P = 0.030$). Finally, fast problem-solvers fledged significantly more young than slow solvers ($F_{1,11} = 24.45, P < 0.001$; partial regression coefficient \pm SE: -0.017 ± 0.003 ; Fig. 1.3c), with clutch size ($F_{1,11} = 14.34, P = 0.003$) and parental provisioning rate ($F_{1,11} = 7.90, P = 0.017$) as significant covariates in the same model. The relationship between latency to solve and number of fledged chicks remained significant ($F_{1,16} = 6.93, P = 0.018$) when latency was the only predictor in the model (excluding clutch size and parental provisioning rate as covariates). Solving latency was not related to laying date ($F_{1,16} = 2.05, P = 0.17$) or offspring body condition (i.e. body mass corrected for tarsus length; $F_{1,109} = 0.24, P = 0.62$), with male body condition ($F_{1,109} = 6.48, P = 0.012$) and hatching date ($F_{1,109} = 8.02, P = 0.005$) as significant covariates in the same

model. The proportion of chicks that survived from hatching to fledging was not related to solving latency ($\chi^2_1 = 0.12$, $P = 0.73$).

Our results are robust to the measures used to assess the performance of the pair in the cases where the two parents were solvers: most results were unchanged when considering different measures for the two concerned pairs (see Supplementary Material in Appendix 1 of this thesis).

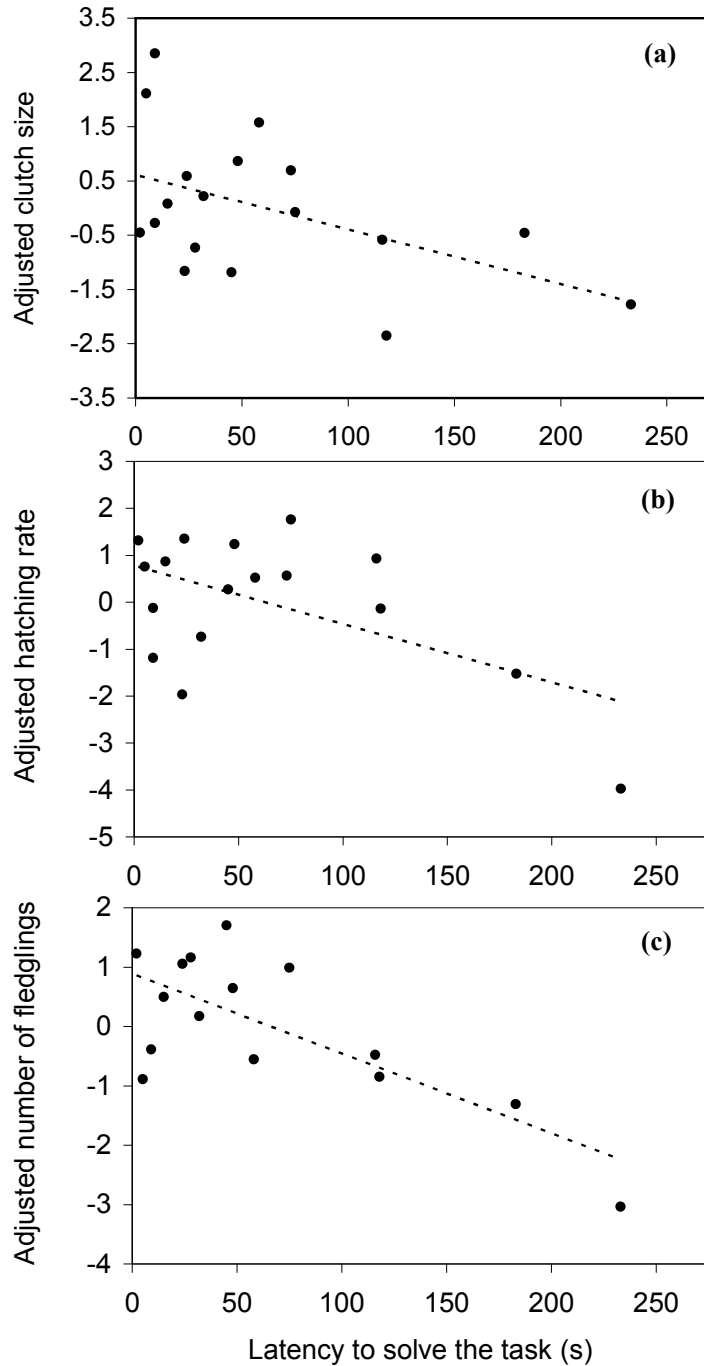


Figure 1.3. Measures of reproductive success depending on problem-solving latency (i.e. increasing latency to enter indicates worse performance) in nests where at least one parent solved the task: a) clutch size (adjusted for male body condition), b) hatching rate (adjusted for female body condition) and c) fledgling number (adjusted for clutch size and provisioning rate).

Problem-solving performance and levels of neophobia and motivation

The level of neophobia differed between solvers and non-solvers ($F_{1,15} = 5.22, P = 0.037$): solvers were less neophobic than non-solvers (mean level \pm SE: 9.80 ± 4.08 and 22.50 ± 3.92 for solvers and non-solvers respectively). The level of neophobia did not differ between fast and slow solvers, although there was a tendency for neophobia to decrease with increasing latency ($F_{1,17} = 3.91, P = 0.064$; partial regression coefficient \pm SE: -0.073 ± 0.037). Importantly, results remained qualitatively unchanged when the latency to solve the task was corrected for the level of neophobia (by including neophobia as an additional covariate in models exploring measures of reproductive success; results not detailed here).

Solvers showed a slightly higher provisioning rate than did non-solvers (29.7 ± 3.8 compared to 16.9 ± 5.5 feeds/hr), but this difference fell short of statistical significance ($F_{1,20} = 3.72, P = 0.068$). Among solvers, problem-solving latency was not related to parental provisioning rate ($F_{1,11} < 0.01, P = 0.972$, with clutch size as a covariate in the same model: $F_{1,12} = 4.58, P = 0.053$). After the first contact with the string, solvers also showed higher persistence than non-solvers ($F_{1,18} = 28.50, P < 0.0001$). However, latency to solve was not related to persistence ($F_{1,18} = 0.29, P = 0.271$).

Discussion

Our results suggest significant positive relationships between problem-solving performance and several measures of reproductive success in our study population of great tits, at least in the short term. Pairs where at least one parent solved the task fledged a higher proportion of their clutch than did pairs where no parent solved. Furthermore, nests where parents were faster at solving the task laid and hatched more eggs and fledged more offspring than nests where parents were slower. Because each measure of breeding success was analysed while accounting for preceding measures, our results suggest that the influence of problem-solving performance is cumulative over these different stages of the breeding event. Our study therefore supports the hypothesis that natural selection might be operating on problem-solving performance in great tits in the wild.

Although more relations involving solving latency for successful birds appeared significant than when distinguishing solvers from non-solvers, the differences between the two sets of analyses (binary vs. continuous measure of problem-solving performance) should be interpreted with caution. While the relationships between measures of breeding success and latency might be dependent on the few pairs that took longest to solve the problem, the ‘non-solver’ category may include both birds that tried but could not solve and birds that might eventually have solved had they tried harder, sooner or longer. Nevertheless, the fact that both the analyses of latencies and solver vs. non-solver categories showed a significant and positive relationship between problem-solving performance and different measures of reproductive success suggests that our findings are robust. Furthermore, the similarity between our results and those of Cole *et al.* (2012), while using different novel problems (opening a trap door vs. solving a foraging task) in different contexts (field vs. captivity, and spring vs. winter), further strengthens the evidence for a positive relationship between problem-solving performance and reproductive success in great tits.

Although it is tempting to conclude that better problem-solving performance causes higher reproductive success, we cannot exclude the possibility that the positive relationship between reproductive success and problem-solving performance might be a consequence, rather than a cause, of the higher motivation of parents to feed more successful and/or larger broods (Smith *et al.* 1988; Garcia-Navas and Sanz 2010). Parents with more chicks could have been more motivated to enter, and thus could have been more prone to contact the door and pulled the string harder. Pair provisioning rates and individual persistence scores in manipulating the task should reflect both chick demand and parental motivation to feed their chicks. Because problem-solving latency was not related to these two measures of motivation, and the relation between fledgling number and problem-solving latency remained significant even when provisioning rate was accounted for in the model, our results suggest that latency to solve reflects problem-solving performance rather than merely motivation. Furthermore, even though almost all birds succeeded to make the door move by pecking the string, not all of them persisted to peck or pull at the right place to finally open the door. Therefore, the parents’ motivation to feed the brood does not seem to have generated the observed relationship between problem-solving performance and breeding success. An experimental brood size manipulation is however needed to explicitly address this issue, i.e. to confirm the causality of the relation between parental problem-solving ability and breeding success. Furthermore, parents may trade the quantity and quality of food items brought to the

nestlings (Garcia-Navas and Sanz 2010). A recent study on house sparrows (*Passer domesticus*) showed that the size of the food items provided by parents was a better predictor of reproductive success than chick provisioning frequency (Schwagmeyer and Mock 2008). Moreover, males and females could differ in their provisioning strategies (Smith *et al.* 1988). In our study, we measured provisioning rate at the level of the pair, not the individual parent. Further studies should examine each parent's provisioning strategy in more detail to assess the link between an individual's problem-solving ability and the size or type of the food items it brings to feed chicks.

Finally, the potential role of stress as a mediator of the relationship between reproductive success and problem-solving ability needs to be explored. Parents showing a high level of stress in response to the presence of the novel task may have been unable to solve it and also achieved lower breeding success. However, the task itself is unlikely to have generated a sufficiently high level of stress to directly affect breeding success, because of its short duration over the course of the breeding cycle (one hour), and because problem-solving performance was also related to measures of breeding success before the test, namely clutch size and hatching success. Instead, the stress response to the task and the associated success (or failure) in solving may have revealed parental variation in the general ability to handle stressful situations, which is likely to have affected the final breeding success. Furthermore, because provisioning rate decreased during the test, chick begging intensity may have increased over the course of the test, eliciting an increasing stress response from the parents that may have been proportional to the number of chicks and thus have affected the chance to solve the task. Although this was not reflected in the parents' motivation to open the door (i.e. the individual persistence score), chick begging intensity, but also other factors known to affect parents' motivation to feed the chicks (i.e. plumage or beak coloration: Heeb *et al.* 2003; Tanner and Richner 2008), and parental stress hormone levels should be investigated to better understand the role of motivation and stress in the performance to solve the task. This however goes beyond the scope of the present study.

For natural selection on a trait to take place, three conditions are required: (1) there must be variation among individuals for the trait, (2) this variation must be linked to variation in individual fitness, and (3) this variation must be heritable (Fairbairn and Reeves 2001). Between-individual variation in innovative ability is well documented, while evidence for its association with fitness is limited to the current study and that of Cole *et al.* (2012) on great tits. Heritability

of many cognitive traits has been shown in non-human species, but evidence comes mainly from domesticated animals, mostly rodents, tested in captivity (Galsworthy *et al.* 2005), as well as from selection experiments in insects (Mery and Kawecki 2004). Exploration behaviour, a correlate of problem-solving in other birds (Carib Grackles: Overington *et al.* 2011a; Indian Mynahs: Sol *et al.* 2011), has been shown to be heritable in wild great tits (Dingemanse *et al.* 2002). In this species, boldness also correlates with the speed in searching for new food sources when familiar ones are experimentally decreased, which is a measure of feeding flexibility (van Overveld and Matthysen 2010). Investigating the heritability of innovative ability and cognition is an obvious next step.

If problem-solving performance is found to be heritable, and thus the three conditions for the evolution of innovative ability are met, the processes maintaining high levels of between-individual variation in this trait need to be explored, in particular the costs and benefits of increased innovative ability in relation to spatio-temporal variation of the environment. As far as costs are concerned, innovativeness at the interspecific level has been found to be associated with a bigger brain (Timmermans *et al.* 2000), increased vulnerability during the prolonged period of development associated with larger brains (Iwaniuk and Nelson 2003), and increased exposure to a wider variety of parasites and microbes (Garamszegi *et al.* 2007; Vas *et al.* 2011). At the intraspecific level, problem-solving performance can be associated with higher nest desertion following capture by experimenters (Cole *et al.* 2012), suggesting a potential link between innovativeness and sensitivity to nest disturbance and predation risk (Cole *et al.* 2012). Thus, although there is now evidence that problem-solving performance, a measure of innovativeness, is correlated with reproductive benefits, its potential costs remain to be investigated.

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Dans le chapitre 1, nous avons mis en évidence une corrélation positive entre la performance de résolution de problème et le succès de reproduction des individus. Le but du chapitre 2 est de tester la causalité liée à cette relation.

Contributions des co-auteurs :

Laure Cauchard et Blandine Doligez ont formulé l'hypothèse de départ. Laure Cauchard, Bernard Angers, Neeltje J. Boogert et Blandine Doligez ont planifié le terrain. Laure Cauchard et Mélissa Lenarth ont mené les expériences sur le terrain. Laure Cauchard a effectué les analyses, sous les conseils de tous les co-auteurs. Laure Cauchard a rédigé une première version du manuscrit et tous les co-auteurs ont contribué à son amélioration.

CHAPITRE 2 :

DOES PROBLEM-SOLVING PERFORMANCE DRIVE REPRODUCTIVE SUCCESS OR VICE VERSA? AN EXPERIMENTAL STUDY IN A NATURAL GREAT TIT POPULATION

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Abstract

The adaptive significance of cognitive performance remains unclear because of the difficulty to assess these performances and their fitness consequences in the wild. Recent studies have provided important first steps by showing a positive correlation between inter-individual variation in problem-solving performance (as a measure of cognitive ability) and reproductive success in a wild passerine bird, the great tit (*Parus major*). However, the causality of this relationship and the underlying mechanism are still unknown. We addressed this issue by experimentally manipulating the brood sizes of wild great tits in Sweden. We then presented the parents of these broods with a new problem-solving task to examine if their problem-solving performance was affected by experimental changes in brood size. Our results showed not only that brood size manipulation did not affect the probability to solve the task, but also that solver pairs fledged more young, accounting for brood size manipulation. Moreover, solver pairs showed higher chick provisioning rates than non-solver pairs, suggesting that the ability to solve novel problems might confer greater capacities to find food. Problem-solving performance thus appears to affect fitness through provisioning skills.

Introduction

Our understanding of inter-individual differences in cognitive performance has improved considerably in the last decade. Studies have shown that intrinsic traits such as gender (Jacobs *et al.* 1990, Range *et al.* 2006, Thornton and Samson 2012), age (Kummer and Goodall 1985, Cole *et al.* 2011, Thornton and Samson 2012), novelty responses (Overington *et al.* 2011a, Sol *et al.* 2011, Benson-Amram *et al.* 2013), stress (Bókony *et al.* 2013) and prior experience (Seibt and Wickler 2006), as well as external factors such as group size (Liker and Bokony 2009, Morand-Ferron and Quinn 2011), predation (Taylor *et al.* 2012), competition (Overington *et al.* 2009a) and dominance (Kummer and Goodall 1985, Thornton and Samson 2012), affect cognitive performance (Thornton and Lukas 2012). However, research on the question of the function of cognitive performance in non-human animals, in terms of its contribution to fitness in the wild, is still in its infancy.

To understand if and how selection acts on cognitive performance, field studies have to link inter-individual variations in these performances to their fitness consequences (Thornton and Lukas 2012). In birds, a pioneering study conducted in zebra finches (*Taeniopygia guttata*) showed that learning performance in males was correlated with their song complexity, a sexually selected trait in this species, possibly suggesting a link between cognitive performance and sexual selection (Boogert *et al.* 2008). This hypothesis was later supported by a study on satin bowerbirds (*Ptilonorhynchus violaceus*), which showed that males with higher overall scores on several cognitive tasks obtained more copulations (Keagy *et al.* 2009, 2011). However, these findings could not be replicated in other passerine species (Boogert *et al.* 2011a, Isden *et al.* 2013), where the cognitive performances measured were not significantly correlated with the proxy of mating success examined. Whether cognitive performance is under sexual selection in passerines thus remains unclear.

The first evidence for an association between cognitive performance and reproductive success in the wild was published two years ago, with two field studies conducted on two different populations of the same bird species, the great tit (*Parus major*) (Cole *et al.* 2012, Chapter 1). In these studies, innovative problem-solving performance measured either in captivity (stick-pulling task motivated by food; Cole *et al.* 2012) or in the field (string-pulling task motivated by nestling provisioning; Chapter 1), was linked to multiple measures of reproductive success. Nests where at

least one parent solved the novel task laid larger clutches (Cole *et al.* 2012, Chapter 1) and fledged more young (Chapter 1), despite the fact that this effect was counterbalanced by problem-solver females being more likely to desert their nest after experimenter manipulation in one of the studies (Cole *et al.* 2012).

Thus, cognitive performance might enable individuals to produce and raise more young. However, there are alternative explanations for the positive correlation between cognitive performance and reproductive success: for example, in our previous study (Chapter 1), birds with more young might have been more motivated to feed them and thus might have put more effort into solving the task. Therefore, an experimental manipulation is needed to determine the causal direction of the relationship found between problem-solving performance and reproductive success. Moreover, the mechanisms underlying potential reproductive benefits of problem-solving performance remain poorly explored. The main mechanism that has been suggested thus far is that parents with higher cognitive abilities may use their habitat more efficiently (Sutter and Kawecki 2009, Cole *et al.* 2012), allowing them to find more and/or higher quality food resources for nestling provisioning (Cole *et al.* 2012, Chapter 1).

We investigated the causal relationship between problem-solving performance and reproductive success in a natural population of great tits. Because manipulating problem-solving performance of individuals cannot be done easily in the short-term and without modifying other cognitive functions that can also influence reproductive success, we manipulated the number of young reared by parents. We thus experimentally increased or reduced parents' broods and recorded the parents' subsequent problem-solving performance on the same task used by in chapter 1 as well as chick provisioning rate. If the motivation to feed chicks drives parents' problem-solving performance, pairs with an increased brood size should show a higher probability to solve the task than pairs with a decreased brood size. Conversely, if higher problem-solving performance allows individuals to raise more young, our experimental brood size manipulation should not affect parents' probability to solve the task and the more efficient pairs should achieve a higher reproductive success beyond the brood size manipulation. Finally, if better problem-solvers are more efficient in exploiting their habitat, we predicted that pairs with better problem-solving performance should achieve a higher chick provisioning rate than pairs with lower problem-solving performance, beyond the brood size manipulation (Garcia-Navas and Sanz, 2010).

Material and methods

Study site, population monitoring and measures of reproductive success

Data were collected in a breeding population of great tits, on the island of Gotland, Sweden (57°10'N, 18°20'E), between April and June 2012 and 2013. Great tits are small, monogamous passerines that breed easily in nest boxes, allowing us to record each breeding pair's laying date, clutch size, number of hatchlings, brood size at day 14 and final number of fledglings. Chicks were ringed at day 9 and weighed and their tarsus length measured (to the nearest 0.1 mm) at day 14. Adults were caught within nest boxes between day 9 and day 14 after their chicks hatched, ringed if they were not, weighed and their tarsus length measured.

Brood size manipulation

In our great tit population, brood size ranges from 3 to 12 chicks, with an average of 8 chicks per brood (mean \pm SE = 8.06 \pm 0.13). We created enlarged, reduced and control broods by adding two chicks (i.e. an average 25% increase), removing two chicks (i.e. an average 25% decrease) or exchanging but not changing brood size. One day after hatching, nestlings were weighed to the nearest 0.01g to calculate the average nestling weight of the brood. Two days after hatching, nestlings were exchanged between broods that hatched on the same day and matched the same average weight (mean difference < 1g). Whenever possible, we used triplets of broods: four nestlings were transferred from a first nest (nest A) to a second nest (nest B), then four other nestlings from nest B to a third nest (nest C) and finally two other nestlings from nest C to nest A. We then reduced brood size by two nestlings in nest A, increased it by two nestlings in nest C and left it unchanged in nest B, which thus functioned as a control for having foreign chicks in the nest, without changing brood size. All broods thus contained either two (nest B) or four nestlings (nest A and C) coming from a different nest. When we could not match three broods we used duos by skipping the "control" nest B, and when more broods were available we used quadruplets by repeating the nest B treatment. We also excluded nests with extreme brood sizes (less than 5 or more than 10 hatchlings on day 2) and assigned treatment (reduced, control, or enlarged brood) randomly with respect to initial brood size.

Chick provisioning rate and problem-solving performance

In great tits, both parents feed their young (Gosler 1993). During the 2013 field season, nestling provisioning rate was recorded when chicks were 6 days old, using a camouflaged video recorder placed at a distance of approx. 6m from the nest box, during 90 min in the morning. Because distinguishing males from females on videos is difficult, we measured chick provisioning rate per breeding pair.

Problem-solving performance was measured using a string-pulling task that was used successfully previously in this population (Chapter 1). The task consisted of a door placed in front of the entrance of the nest box. To enter, parents had to pull a string placed below the door. The test was conducted in 2012 and 2013 during the peak of nestling food demand (i.e. when chicks were 7 to 10 days old, and between 6.00 and 16.00 hours), only when chicks were satiated (e.g. not begging at the beginning of the test) and was divided in two times 1 h (to avoid starvation of the chicks if parents were not able to solve the task) on two consecutive days. We installed a camouflaged video recorder at a distance of approx. 6m in front of the nest box to record parents' interactions with the task. All the movements and interactions of parents with the task were subsequently scored from video recordings by observers who were blind to brood size manipulation. Both pair members experienced the same brood size manipulation and reproductive success. We thus conducted the analyses of the relationships between problem-solving performance, experimental manipulation and reproductive success at the nest level. Thus, for each pair, we recorded it succeeded in solving the task (i.e. opened the door and entered the nest box at least up to the shoulders: solvers) or failed to do so (non-solvers).

Birds were caught, handled and ringed under a licence from the Stockholm Museum Ringing Center (license number 644:M03) and behavioural tests were conducted under a general licence from the Swedish Committee for Experiments on Animals for all experiments on the site (license number C 108/7).

Statistical analyses

We first checked that experimental nests in the different treatments did not differ in reproductive parameters prior to the brood size manipulation (i.e. clutch size, laying date and number of chicks at day 2) using a linear model (LM) with year, brood size treatment (reduced, control, or enlarged broods) and their pairwise interactions as fixed effects.

We then tested whether brood size manipulation affected problem-solving status using a generalized linear model (GLM) with binomial error and logit link function. We included also year, hatching date and all pairwise interactions with year as covariates to control for potential effects of the timing of the season and environmental variation between years.

Finally, we tested whether problem-solving performance affected measures of reproductive success subsequent to the brood size manipulation. The number of fledged chicks were analysed using LM, nestling survival probability from day 2 (i.e. after the brood size manipulation) until fledging using GLM, and chicks' body condition (body mass at day 14 accounting for tarsus length) using a linear mixed model (LMM) with nest as random factor (to account for the non-independence of nestlings within a brood). All models included also brood size treatment, year, hatching date, male and female body condition (i.e. ratio of body mass on tarsus length) and all pairwise interactions with year. In the LMM analysing chicks' body condition, we also added brood size at day 2 to control for the effect of brood size on the body mass of chicks from the same nest. Finally, we tested whether problem-solving performance affected parental provisioning rate using LM with brood size treatment, hatching date, male and female body condition and brood size after manipulation as covariates and the pairwise interaction between problem-solving status and brood size treatment.

Neophobia, the fear of novelty, can interfere with the process of innovation and should be taken into account in analyses. Although preliminary analyses of the 2013 data showed that solvers tended to be less neophobic (with neophobia measured as the time between landing on the nest box and first contact with the door or string; Chapter 1) than non-solvers, including this measure as a covariate did not quantitatively change our results (see Supplementary Material in Appendix 2 of this thesis). Similarly, adding the sex of the solving parent in the models did not qualitatively

change the results (see Supplementary Material in Appendix 2 of this thesis). Thus, we removed neophobia and sex from our models.

Sample sizes varied between models because of missing data. We removed from our analyses all pairs in which at least one parent was tested in both years ($N = 10$) to avoid any bias due to learning. Non-significant effects were backward eliminated from the initial full models. Over-dispersion was checked and we transformed chi-square test values into F test values (and corresponding P values) when (small) overdispersion occurred. All tests were two-tailed and analyses were performed with SPSS 18.0 (Chicago, SPSS Inc. 2009).

Results

Absence of bias in experimental nests and effect of the brood size manipulation

In total, 165 broods were experimentally reduced ($N = 60$), enlarged ($N = 65$) or partly exchanged with no change in brood size (control group: $N = 40$). There was no difference in clutch size ($F_{2, 160} = 0.13, P = 0.87$), hatching date ($F_{2, 161} = 0.40, P = 0.67$) or number of chicks at day 2 ($F_{2, 159} = 0.91, P = 0.40$) between treatments prior to brood size manipulation, accounting for an effect of the year on hatching date (i.e. later hatching dates in 2013 than 2012; $F_{1, 163} = 254.62, P < 0.001$). The manipulation had the expected effect on brood size, with larger broods in increased compared to control nests and in control compared to decreased nests at day 9 ($F_{2, 156} = 54.77, P < 0.001$, mean number of day 9 nestlings \pm SE = 6.08 ± 0.20 for reduced broods; 8.05 ± 0.24 in control broods; and 9.20 ± 0.24 in enlarged broods).

Effect of brood size manipulation on problem solving performance

Of the 165 pairs tested, 74 solved the task (44.8%). Brood size manipulation did not influence the probability to solve the task ($\chi^2_2 = 4.29, P = 0.12$), which only depended on the interaction between year and hatching date ($\chi^2_1 = 7.40, P = 0.007$): in 2012, the probability to solve the task decreased with hatching date ($\chi^2_1 = 5.73, P = 0.017$), while it tended to increase with hatching date in 2013 ($\chi^2_1 = 3.14, P = 0.076$).

Effect of problem-solving performance on final reproductive success beyond the brood size manipulation

Solver pairs fledged more young than non-solvers pairs ($F_{1, 155} = 4.58, P = 0.034$; mean \pm SE = 7.71 ± 0.47 and 6.91 ± 0.43 , respectively; Figure 2.1) and this effect did not depend on the brood size treatment (interaction between problem-solving status of the pair and treatment: $F_{2, 153} = 0.30, P = 0.74$). As expected, the manipulation also affected the number of fledged young, although the strength of the effect depended on year (interaction between year and treatment: $F_{2, 155} = 3.84, P = 0.024$, with a higher number of fledged young in increased broods and lower number in reduced broods in 2013 compared to 2012). The number of fledged young also increased with hatching date ($F_{1, 155} = 9.53, P = 0.002$; no interaction with year).

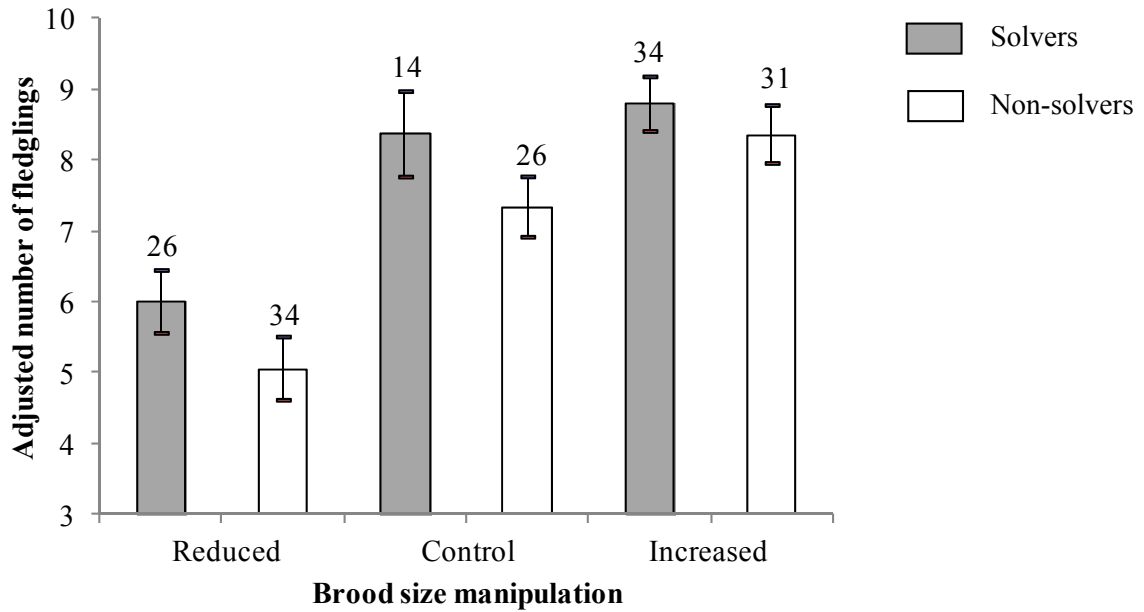


Figure 2.1. Mean number of offspring fledged \pm SE (adjusted for hatching date and the interaction between year and treatment) according to the problem-solving status of the pair and the brood size treatment (see text for the description of status and treatments). Numbers above bars indicate sample sizes.

Survival until fledging did not differ between solver and non-solver pairs ($F_{1, 156} = 0.18, P = 0.67$), but depended on the treatment ($F_{1, 157} = 10.59, P < 0.001$): nestlings from increased broods had a lower survival probability than nestlings from reduced broods, with intermediate control broods (adjusted survival probability (for other significant effects) \pm SE: -0.472 ± 0.275 for enlarged

broods, 0.351 ± 0.072 for reduced broods and 0.269 ± 0.142 for control broods). Nestling survival also increased with hatching date ($F_{1, 157} = 27.89$ $P < 0.001$). Finally, offspring body mass did not differ between solver and non-solver pairs ($F_{1, 132.2} = 2.46$ $P = 0.12$), nor between treatments ($F_{1, 132.2} = 2.48$, $P = 0.087$). Chicks were heavier in 2013 ($F_{1, 138.4} = 8.14$ $P = 0.005$), their body mass increased with tarsus length ($F_{1, 1033.4} = 732.25$, $P < 0.001$) and hatching date ($F_{1, 147.8} = 7.68$, $P = 0.006$), but decreased with brood size ($F_{1, 140.9} = 9.18$, $P = 0.003$).

Effect of problem-solving performance on feeding rate beyond the brood size manipulation

In 2013, solver pairs showed higher provisioning rates than non-solver pairs ($F_{1, 46} = 17.28$, $P < 0.001$), regardless of the brood size treatment (interaction between problem-solving status and treatment: $F_{2, 44} = 0.54$, $P = 0.58$; figure 2.2). In addition, the brood size manipulation affected parental provisioning rate ($F_{2, 46} = 3.66$, $P = 0.033$), with lower provisioning rates for reduced broods compared to control ($F_{1, 28} = 4.21$, $P = 0.050$) and enlarged broods ($F_{1, 29} = 6.87$, $P = 0.014$). Control and enlarged broods were provisioned equally ($F_{1, 34} = 0.21$, $P = 0.652$).

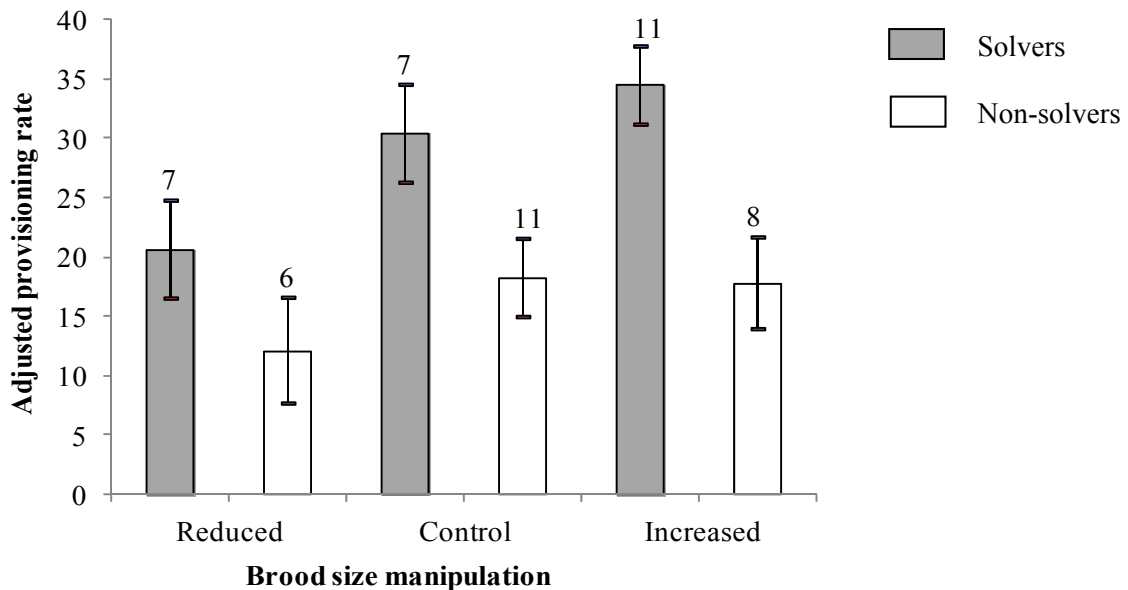


Figure 2.2. Mean feeding rate per hour of the pair \pm SE according to the problem-solving status of the pair and the brood size treatment. Numbers above bars indicate sample sizes.

Discussion

The first aim of this study was to test the causal link between problem-solving performance and reproductive success. The positive correlation between problem-solving performance and reproductive success previously observed in this study population (Chapter 1) could have arisen either from a direct effect (i.e. higher performance associated with a higher ability to provision chicks) or indirect effect (i.e. higher performance associated with a higher overall individual quality) of this performance on reproductive success, or, conversely, from a higher motivation of parents with more chicks to find the task solution and enter the nestbox. Our brood size manipulation resulted in adding or removing on average 25% of chicks (i.e. a difference between reduced and increased broods of nearly 50%), but our results show that this manipulation did not affect the probability of the parents to solve the task. Moreover, solver pairs fledged more young than non-solver pairs, beyond and independently from the brood size manipulation. These results suggest that we can reject the hypothesis that higher reproductive success leads to higher problem-solving performance of the pair because of a higher motivation to solve the task. Instead, our results strengthen support for the hypothesis that problem-solving performance may causally enhance reproductive success.

Our manipulation cannot however exclude the possibility that a third factor, such as parents' individual condition or quality, independently influenced both problem-solving performance and reproductive success. We partly controlled for this possibility by adding male and female body condition as covariates in our models analysing reproductive success. Because these variables were never significant, our results did not suggest such an influence of parental condition. Previous studies on this and other bird species (Cole *et al.* 2011, Mateos-Gonzalez *et al.* 2011, Overington *et al.* 2011a) also failed to find any effect of morphological traits such as body size or condition on innovativeness. However, other variables can reflect individual quality. In particular, physiological traits, such as stress level and immunity, which are known to affect the ability to raise many and/or high quality young in birds and other species (Lendvai *et al.* 2007, Bize *et al.* 2008, Stier *et al.* 2012), may also affect cognitive capacities (Lendvai *et al.* 2013) and thereby problem-solving performance (Bókony *et al.* 2013). Further studies should examine such effects while testing for relationships between cognitive performances and fitness.

The effect of problem-solving performance on reproductive success did not depend on brood size treatment. One could have expected problem-solving performance to affect the ability of the pair to cope with the manipulated reproductive effort differently depending on treatment. On the one hand, all pairs could have achieved a similar reproductive success when brood size was decreased, i.e. when reproductive effort was low, while only pairs with high problem-solving performance may have been able to efficiently face an increased brood size, i.e. high reproductive effort. On the other hand, pairs with high problem-solving performance may have been able to face reproductive effort more efficiently than pairs with low problem-solving performance when the effort was limited, i.e. when brood size was reduced, but may not have been able to do so when the effort was high, i.e. when brood size was increased, because of too high constraints. Here, there was no significant interaction between problem-solving status and brood size manipulation treatment, thus solvers consistently outperformed non-solvers whatever the level of reproductive effort imposed. This suggests that problem-solving performance may allow individuals to efficiently cope with reproductive effort over a large range of situations.

Interestingly, these results arise despite yearly variations in breeding conditions. In 2012 solver pairs started to reproduce earlier than non-solver pairs, but in 2013 the situation was reversed. Moreover, solver pairs fledged more young than non-solver pairs independently of a difference between years in the effect of the brood size manipulation, as revealed by the significant interaction between year and treatment. Thus, although environmental variations affect reproductive success (Charmantier *et al.* 2008), cognitive performances might influence reproductive success consistently across a large range of environmental conditions.

The second aim of this study was to investigate one possible mechanism underlying a causal link between problem-solving performance and reproductive success, via parental provisioning ability. Previous studies on great tits showed that solver pairs laid more eggs and had a higher hatching success than non-solvers pairs (Cole *et al.* 2012, Chapter 1), suggesting early effects of cognitive performance on reproduction. Breeding pairs with better problem-solving performance could be more efficient during the egg laying and incubation stage, or associated to a higher overall individual quality (i.e. genetic make-up or body condition) that in turn positively influences egg production. In our study, even though the problem-solving performance of the pair did not influence nestling survival probability until fledging or nestling body condition, solver pairs

showed a higher nestling provisioning rate than non-solver pairs, beyond the effect of the brood size manipulation. This result supports an effect of problem-solving performance during the rearing stage: the ability to innovate might allow parents to provision their young more efficiently, either through (i) choosing and/or securing a higher quality breeding territory, and/or (ii) finding and/or selecting higher quality and/or larger preys (Cole *et al.* 2012). More work is needed to investigate territory quality and provisioning strategies of solvers and non-solvers to improve our understanding of the behavioural mechanisms underlying the positive relationship between problem-solving performance and reproductive success, which may be mediated via resource availability and nestling provisioning.

To conclude, although we cannot exclude the possibility of a third factor affecting problem-solving performance and reproductive success simultaneously, our study indicates that an increased motivation to care for a larger number of nestlings does not lead to higher problem-solving performance, and clearly revealed individual fitness benefits of problem-solving performance in terms of yearly reproductive success over different environmental conditions.

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Dans les chapitres 1 et 2, nous avons mis en évidence l'influence de la performance de résolution de problème sur le succès reproducteur des individus. Le but du chapitre suivant est d'examiner s'il existe un lien entre les performances de résolution de problème et d'apprentissage avec des caractéristiques du plumage pouvant jouer un rôle lors du choix de partenaire.

Contributions des co-auteurs :

Laure Cauchard et Blandine Doligez ont formulé l'hypothèse de départ et planifié le terrain. Laure Cauchard a mené les expériences sur le terrain. Laure Cauchard et Stephanie Doucet ont effectué les analyses colorimétriques. Laure Cauchard a effectué les analyses, sous les conseils de tous les co-auteurs. Laure Cauchard a rédigé une première version du manuscrit et tous les co-auteurs ont contribué à son amélioration.

CHAPITRE 3 :

LOOK AT ME, I AM BRILLIANT: PROBLEM-SOLVING AND LEARNING PERFORMANCES CORRELATE WITH FEATHER COLORATION IN GREAT TITS *PARUS* *MAJOR*

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Abstract:

Recent findings suggest that natural selection might play a role in the evolution of cognitive abilities in the wild and individuals may benefit from selecting mates with enhanced cognitive abilities. However, assessing the cognitive performances of potential partners directly could be difficult. Instead, the use of indirect cues signalling cognitive performances, such as diet-dependent morphological traits, might be favored. We investigated whether individuals' problem-solving and learning performances on a novel non-foraging task correlated with plumage coloration in a natural population of great tits *Parus major*. We found multiple relationships between problem-solving and learning performances: solvers in 2010 and young learners had duller yellow breasts but showed higher UV reflectance, which might be used to indicate quality. Furthermore, solver males had darker crowns and both faster old solvers and learners had blue-black crowns that peaked more in the UV than in the blue as compared to slow individuals, which have been found to be favored during mate choice in other tits and bird species. Finally, fast learners had lighter stripe that might be associated with a larger width, a sexual secondary trait favored by females during mate choice. Together, these results suggest that feather colouration, and in particular UV reflectance, are associated with cognitive performances and might be used by higher efficient individuals during mate choice in a complex phenotype- and condition-dependent way.

Introduction

Cognition, broadly defined as « all ways in which animals take in information through the senses, process, retain and decide to act on it » (Shettleworth 2001), is crucial for many behaviours in the wild such as communication, mate and breeding site choice, foraging decisions and predator / parasite avoidance (Shettleworth 2009). For instance, cognitive abilities are involved in processing and using previous experience to determine egg-laying date (Grieco *et al.* 2002). Cognitive processes also underlie foraging behaviour, from simple processes such as using associative learning to choose food (Zrelec *et al.* 2013) through to complex foraging behaviours, such as using spatial memory to recover cached food (Sherry *et al.* 1992), or anti-pilfering strategies to outsmart thieving conspecifics (Preston and Jacobs 2001, Emery *et al.* 2004).

Cognitive performances vary both between (Lefebvre and Sol 2008, Healy *et al.* 2009, Reader *et al.* 2011) and within species (Funk and Matteson 2004, Cole *et al.* 2011, Benson-Amram and Holekamp 2012). Furthermore, cognitive performances have been shown to correlate with measures of reproductive success (Johnston *et al.* 1982; Keagy *et al.* 2009, Cole *et al.* 2012, Chapter 1, but see Isden *et al.* 2013) and sexually selected traits (reviewed in Boogert *et al.* 2011b, Mateos-Gonzalez *et al.* 2011). Although the heritability of cognitive abilities in non-human animals remains poorly investigated, these findings suggest that natural and sexual selection might play a role in the evolution of cognitive abilities in the wild (Thornton and Lukas 2012, Dukas 2013, Willemet 2013).

Selective pressures could act on cognitive abilities directly, for instance through a more efficient use of habitat by individuals with enhanced cognitive abilities (Overington *et al.* 2011b, Cole *et al.* 2012). This could possibly lead to more efficient foraging and thus, during breeding, higher offspring provisioning and survival. Furthermore, cognitive abilities could be an honest indicator of genetic quality (Airey and DeVoogd 2000). In this case, individuals with enhanced cognitive abilities might produce higher quality and/or more attractive offspring. Therefore, individuals may benefit both directly and indirectly from selecting mates with enhanced cognitive abilities.

However, individuals might not be able to easily assess the cognitive performances of potential partners directly. Indirect cues signalling cognitive performances, such as diet-dependent

morphological traits, may therefore be under strong selective pressures. For example, carotenoid pigments (i.e. yellow, orange or red colorations) are obtained exclusively from the diet and are limited in nature (Partali *et al.* 1987, Moller *et al.* 2000, McGraw 2006). This mechanism of feather coloration has been shown to be an honest signal of foraging abilities (Slagsvold and Lifjeld 1985, Senar *et al.* 2002, Senar *et al.* 2008), parental care (Hill 1991, Saetre *et al.* 1995) and health (Blount *et al.* 2003, McGraw and Ardia 2003, Senar *et al.* 2008, Helfenstein *et al.* 2010; but see Svensson and Wong 2011 for a review about the complexity of carotenoid-based signals). If individuals with higher problem-solving and/or learning abilities are able to find more or higher-quality carotenoid-rich food, such abilities could be signaled by the intensity of carotenoid-based secondary sexual coloration. In line with this hypothesis, Mateos-Gonzalez and colleagues (2011) found that in the siskin (*Carduelis spinus*), females choose their mate according to the length of the carotenoid-based yellow wing stripe, a secondary sexual trait that correlates positively with problem-solving performance in captivity.

The potential role of feather coloration as a signal of cognitive ability remains poorly studied, with only one avian study to date (Mateos-Gonzalez *et al.* 2011). In birds, feather coloration can be categorized into 3 main groups, which can act alone or together to produce the color: carotenoid pigments, melanin pigments, and structural coloration (Hill and McGraw 2006). All three have been shown to be related to health status, body condition, parental care and/or reproductive success (carotenoids: Hill 1991, Moller *et al.* 2000, Blount *et al.* 2003, McGraw and Ardia 2003, Senar *et al.* 2008, Helfenstein *et al.* 2010, melanin: Roulin 2004b, structural coloration: Doucet 2002, Doucet and Montgomerie 2003, Hegyi *et al.* 2007), even if mechanisms are complex and results are still controversial (Griffith *et al.* 2006, Svensson and Wong 2011). In this study, we investigated whether individuals' problem-solving and learning performances on a novel non-foraging task (Chapter 1) correlated with plumage coloration in a natural population of great tits *Parus major*. The great tit is a highly suitable model species to address this question, as i) it is known for its innovative problem-solving performance (Overington *et al.* 2009b, Cole *et al.* 2011), ii) problem-solving performance and reproductive success are positively correlated in this species (Chapter 1, Cole *et al.* 2012) and iii) great tits display carotenoid-based yellow breast coloration, as well as a melanin-based black ventral stripe and, in males, blue-black structural iridescence on the crown. These feather colouration are known to reflect body condition and/or mate quality

(Norris 1990, Hegyi *et al.* 2007, Senar *et al.* 2008, Remeš and Matysioková 2013). Here, we explore whether these feather colorations may signal cognitive abilities in great tits.

Material and methods

Study site, population monitoring and morphological data

We carried out the study in a breeding population of great tits monitored on the island of Gotland, Sweden (57°10' N, 18 ° 20' E) between April and June 2010 and 2011. Great tit readily breed in nest boxes, thereby providing researchers easy access to nests. Nest boxes were visited regularly from the beginning of the breeding season to record standard breeding data. When chicks were 9 to 14 days old, we caught both adults (with clap-traps or mist nests), ringed them (if they were unringed), aged (first-year vs older) and sexed them according to plumage characteristics (Svensson 1992). We also weighed them (to the nearest 0.1 g) and measured tarsus lengths (to the nearest 0.1 mm). We collected approximately 10 feathers from a standard position on the yellow breast for both males and females and on the black ventral stripe and blue-black crown for males, since these plumage areas are involved in sexual selection by females in this species (Hegyi *et al.* 2007). We stored feathers in envelopes in the dark for later spectral measurements in the laboratory. Feather samples are widely used to quantify plumage coloration and provide highly representative measurements of colour values (Quesada and Senar 2006).

Problem-solving and learning performances

To measure problem-solving and learning performances, we used a task based on parents' drive to access their young during nestling rearing (Chapter 1). A door was placed in front of the entrance hole of the nest box, preventing the birds from entering. To solve the task (i.e. open the door and enter), parents had to pull a string placed below the door and slip their body under the door (more details in Chapter 1). The test was conducted during the peak of nestling food demand (i.e. when chicks were 6 to 10 days old and between 8AM and 4PM), only when chicks were not starved (e.g. not begging at the beginning of the test). The test lasted for 1 h only, to avoid chick starvation if parents were not able to solve the task. In 2010, each pair was tested once. In 2011, we tried to

increase parents' participation by presenting the test twice on two consecutive days. We randomly selected pairs to be tested and recorded the parents' behaviour during the test using a camouflaged video recorder placed at a distance of approx. 6m in front of the nest box just before the test.

Using video recordings, we first assessed the problem-solving status of the parents. Parents who succeeded in solving the task were considered to be solvers, and those who contacted the nest box but failed to enter were considered to be non-solvers (i.e. problem-solving status). For solvers, we recorded their latency to enter the nest box as the time elapsed between the first contact of the bird with the string that caused a movement of the door and the bird's entry into the nest box, excluding the time spent away from the nest box (i.e. solving latency, Chapter 1). Second, we examined the subsequent task interactions to determine parent's learning status and their speed of learning. Individuals that solved the task twice or more and showed a decrease in solving latency across solving events were considered learners, while birds that failed to enter again or did not show learning upon trying were considered non-learners (learning status: learner vs. non-learner). For learners, we recorded the speed of learning as the mean of their successive latencies (excluding latencies once no further reduction in solving latency was apparent, i.e. when they solved the task three successive times with the same mean latency \pm 5 seconds). Neophobia can have a confounding effect on problem-solving performance (Chapter 1, Webster and Lefebvre 2001). We measured neophobia as the time between landing on the nest box and first contact with the task.

Birds were caught, handled and ringed under a licence from the Stockholm Museum Ringing Center (license number 644:M03) and behavioural tests were conducted under a general licence from the Swedish Committee for Experiments on Animals for all experiments on the site (license number C 108/7).

Spectral measurements of feathers

To measure plumage reflectance spectra, we taped together the 10 feathers from each body area taken from each individual on a matte black paper, overlapping the feathers to approximate their normal position on the bird's body. We used an Ocean Optics USB4000 spectrometer paired with a PX-2 light source to collect spectral readings. Using a bifurcated fibre optic probe, we collected five spectral readings per body area, lifting the probe away from the feathers between each reading.

The probe was tipped with a black rubber stopper which excluded external light and maintained the probe at a fixed 5 mm distance from, and perpendicular to, the feathers. All measurements were made relative to a white standard (WS-1), and were dark corrected. We visually examined all spectral files and omitted a few files from further analyses because they appeared abnormal due to measurement error (i.e. probe not fully centered on feathers, or measurement was saved before the reflectance curve had a chance to stabilize).

We calculated standard brightness, hue, and chroma colorimetric variables for each of the three body areas using CLR (Montgomerie 2006, 2008). Because the yellow breast of the great tit shows two peak reflectance values, in the UV (300-400nm) and in the yellow (400-700nm) regions, we calculated both UV chroma and carotenoid chroma for this body area. We calculated the UV chroma of the yellow breast as the proportion of reflectance between 300 and 400 nm relative to the reflectance across the entire bird-visible spectrum (i.e. between 300 and 700 nm). We calculated the carotenoid chroma of the yellow breast as the difference between the reflectance at 700 nm and the reflectance at 450 nm divided by the reflectance at 700 nm. We calculated the hue of the yellow breast as the wavelength at which the reflectance reached 50% of its maximum. We calculated the brightness of the yellow breast as the mean reflectance across the entire spectrum from 300 to 700 nm. For the blue-black crown, we calculated brightness and UV chroma as described above, blue chroma as the proportion of reflectance between 400 and 500 nm, and hue as the wavelength of maximum reflectance. For the achromatic black breast stripe, we calculated brightness as described above. Hue and chroma are typically irrelevant for achromatic plumage areas so we did not calculate these values in this case. The repeatability of individual measurements (Lessels and Boag 1987) was relatively high ($R = 0.78 \pm 0.06$ and $P < 0.001$ in all cases; see Supplementary Material in Appendix 3 of this thesis) and we used the mean of the five measurements in all subsequent analyses (Figure 3.1) (Andersson *et al.* 2006, Montgomerie 2006, 2008).

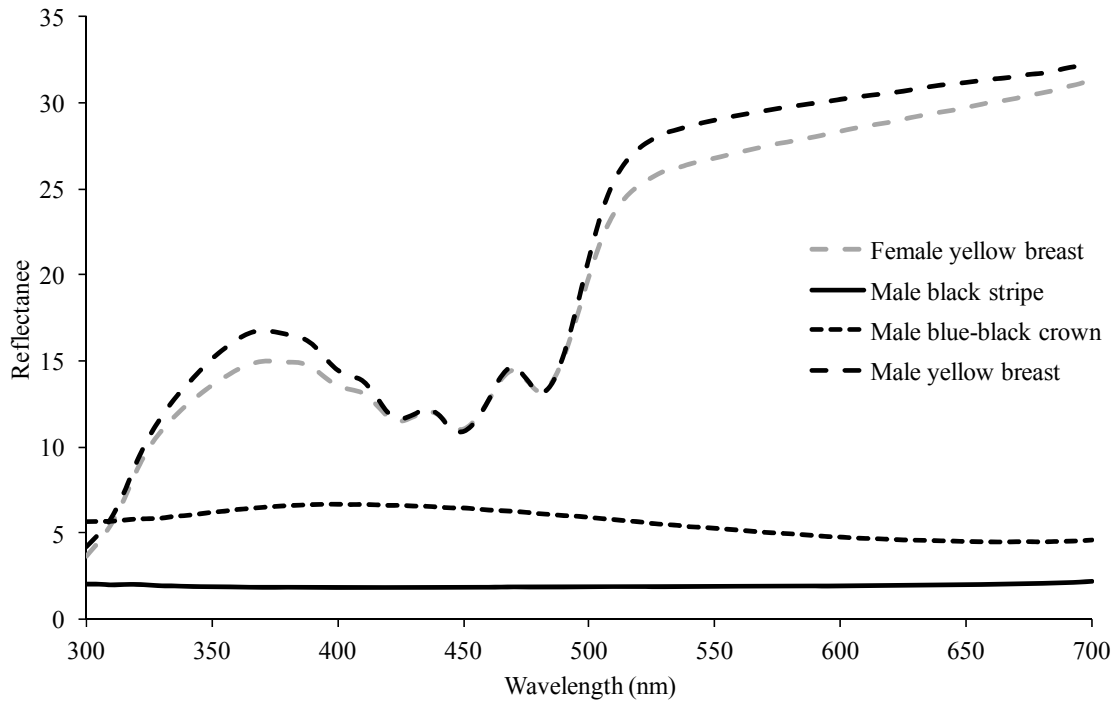


Figure 3.1. Spectral reflectance (mean) of the yellow breast feathers of both sexes and the blue-black crown and black stripe of males in our wild adult great tit population. Standard errors are not shown to keep the figure readable. N = 206 for yellow breast feathers, N = 97 for male blue-black crown and N = 100 for male black stripe.

Statistical analyses

We first ran Principal Component Analyses with Varimax rotation on feather colorimetric variables and kept the first two components extracted (i.e. with eigenvalues > 1), which explained 67% and 83% of the variation in the yellow breast and blue-black crown colour spectra respectively (see Supplementary Material in Appendix 3 of this thesis). For both body areas, the first principal component (PC1) summarizes the hue and chroma of the color. For the yellow breast, higher PC1 values correspond to longer-wavelength hues and lower UV chroma (i.e. yellower individuals), whereas lower PC1 values correspond to shorter-wavelength hues and higher UV chroma (i.e. high UV individuals). Similarly, for the blue-black crown, higher PC1 values correspond to longer-wavelength hues and lower UV chroma (i.e. bluer males), whereas lower PC1 values correspond

to shorter-wavelength hues and higher UV chroma (i.e. more UV males). Values of the second principal component (PC2) represent brightness, where higher PC2 values correspond to brighter (or lighter) color (see Supplementary Material in Appendix 3 of this thesis).

Second, we tested whether our four measures of problem-solving (i.e. problem-solving status and latency to solve the task) and learning performances (i.e. learning status and speed of learning) were correlated with each of the two plumage principal components. Since females may also signal their individual and maternal quality during mate choice and both males and females might be choosy (Clutton-Brock 2007, Kraaijeveld *et al.* 2007, Doutrelant *et al.* 2008, Henderson *et al.* 2013, Remeš and Matysioková 2013), we included both sexes in our analyses of the yellow breast coloration. We then used linear mixed models (LMM) with nest as a random effect to control for the non-independence of the mates when both parents were analysed. However, due to sample size constraints, we could use LMMs only in our models using problem-solving status. For models using problem-solving latency and learning performances, male and females were both measured in only a few nests (N = 13 for problem-solving latency and N = 3 for learning performances) and we repeated the analysis keeping either only the most efficient member of the pair, or the least efficient, or one at random. When only males were analysed, we use standard linear models.

The characteristics of feather colour spectra have been shown to be related to year and individual's sex, age and body condition (i.e. mass corrected for tarsus length) (Figuerola and Senar 2005, Evans *et al.* 2010). Therefore, the starting models included these variables as fixed effects in addition to the measure of problem-solving and learning performances considered, except for the analyses of the crown color and stripe brightness where sex was not included because only males were considered. The starting model included all pairwise interactions except (i) when analysing both parents, in which case year was nested within the random variable nest since, for a given nest, both parents were tested in the same year, and (ii) for models including learning performance, in which interactions with year were excluded because of a low sample size in 2010 (only one test was performed in that year and thus limited learning could be measured). Reproductive effort, especially nestling feeding, can increase the risk of damaging feathers (e.g. if parents lack time to take care of their plumage or if repeated entrances into the nest box damage feathers). We tested for the influence of brood size and its pairwise interaction with cognitive performance by including

it in our initial models; however, brood size was never significant and we removed this variable from our final models.

Preliminary analyses showed that solvers were less neophobic than non-solvers (Independent t-test: $t(147) = 1.986$, $P = 0.049$), even though neophobia was not related to the latency to solve the task (Pearson correlation test: $r = -0.169$, $n = 68$, $P = 0.168$). Neophobia was not related to learning performances (probability to learn: independent t-test: $t(41) = 0.611$, $P = 0.544$; speed of learning: Pearson correlation test: $r = 0.072$, $n = 33$, $P = 0.690$). Thus, only models with measures of problem-solving performance included neophobia as a fixed covariate.

We performed all analyses using SPSS 18.0 (Chicago, SPSS Inc. 2009). Non-significant variables and interactions were backward eliminated from the starting models, and we checked the normality and homoscedasticity of the residuals. Sample size varied between models because we were not able to assess some measures during a few trials due to technical problems. All tests were two-tailed.

Results

Out of the 152 individuals tested, 72 were able to solve the task (46.5 % in 2010, 47.7 % in 2011). The problem-solving performance of an individual was not related to the performance of his/her mate (Problem-solving status: chi-square test: $\chi^2_1 = 1.097$, $P = 0.29$; problem-solving latency: Pearson correlation test: $r = -0.286$, $N = 11$, $P = 0.39$). Of the 72 solvers, 43 returned and tried to enter again, of which 33 succeeded (i.e. learners; 71.4 % in 2010, and 77.8 % in 2011). We could not test for correlations between mates in learning performance because we only had 3 pairs with measures for both parents. Learners and non-learners did not differ in solving latency (Independent t-test: $t(40) = 0.913$, $P = 0.367$), but fast solvers were also fast learners (Pearson correlation test: $r = 0.407$, $N = 41$, $P = 0.023$).

Problem-solving performance and plumage coloration

The PC1 value of the yellow breast differed between solvers and non-solvers, but this difference depended on test year (interaction between problem-solving status and year: $F_{1,98.0} = 5.8$,

$P = 0.018$). In 2010, there was no difference between solvers and non-solvers ($F_{1,13} = 1.31$, $P = 0.27$), whereas in 2011, solvers tended to have lower PC1 yellow breast values than non-solvers ($F_{1,35} = 3.62$, $P = 0.065$; Figure 3.2). Thus, non-solvers in 2010 had breasts with shorter-wavelength hues, lower yellow chroma but higher UV chroma: they were duller, but showed higher UV reflectance. The PC1 value of the yellow breast also decreased with increasing tarsus length ($F_{1,93.4} = 15.8$, $P < 0.001$) and was higher in 2010 compared to 2011 in one-year old birds only (no difference for older birds; interaction between year and age: $F_{1,117.2} = 4.3$, $P = 0.040$). Among solvers, the PC1 value of yellow breast was not related to solving latency ($F_{1,62} = 1.1$, $P = 0.30$). The PC2 value of yellow breast (quantifying brightness) was related to neither problem-solving status ($F_{1,124.4} = 1.2$, $P = 0.27$) nor solving latency ($F_{1,61} = 1.1$, $P = 0.31$); it was higher in males compared to females in 2011 only (no difference between sexes in 2010; interaction between year and sex: $F_{1,73.2} = 17.9$, $P < 0.001$).

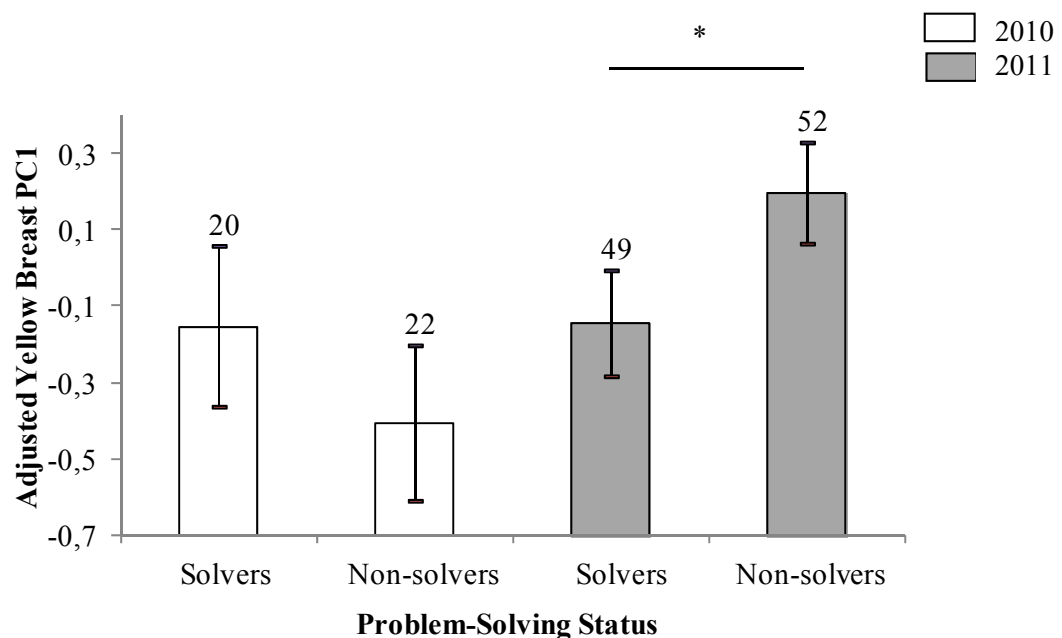


Figure 3.2. Mean yellow breast PC1 values \pm SE (adjusted for tarsus length and age by year interaction) for solvers and non-solvers for 2010 and 2011. Numbers above bars are sample sizes.

In males, the PC1 value of the crown did not differ between solvers and non-solvers ($F_{1,63} < 0.1$, $P = 0.87$) but increased with solving latency (i.e. decreased with rapidity) in two-year-old or older birds (interaction between problem-solving latency and age: $F_{1,24} = 5.5$, $P = 0.028$,

figure 3.3). Thus, among birds two years of age or older, fast solvers had crowns peaking at shorter wavelengths and with higher UV chroma and lower blue chroma. In addition, the PC2 value of the blue-black crown was lower in solvers compared to non-solvers ($F_{1,63} = 6.9, P = 0.011$, mean \pm SE = -0.26 ± 0.17 and mean \pm SE = 0.33 ± 0.15 respectively), but was not related to solving latency ($F_{1,26} < 0.1, P = 0.91$). Thus, solvers had darker crowns, which ranged more in the UV than in the blue coloration for faster old bird.

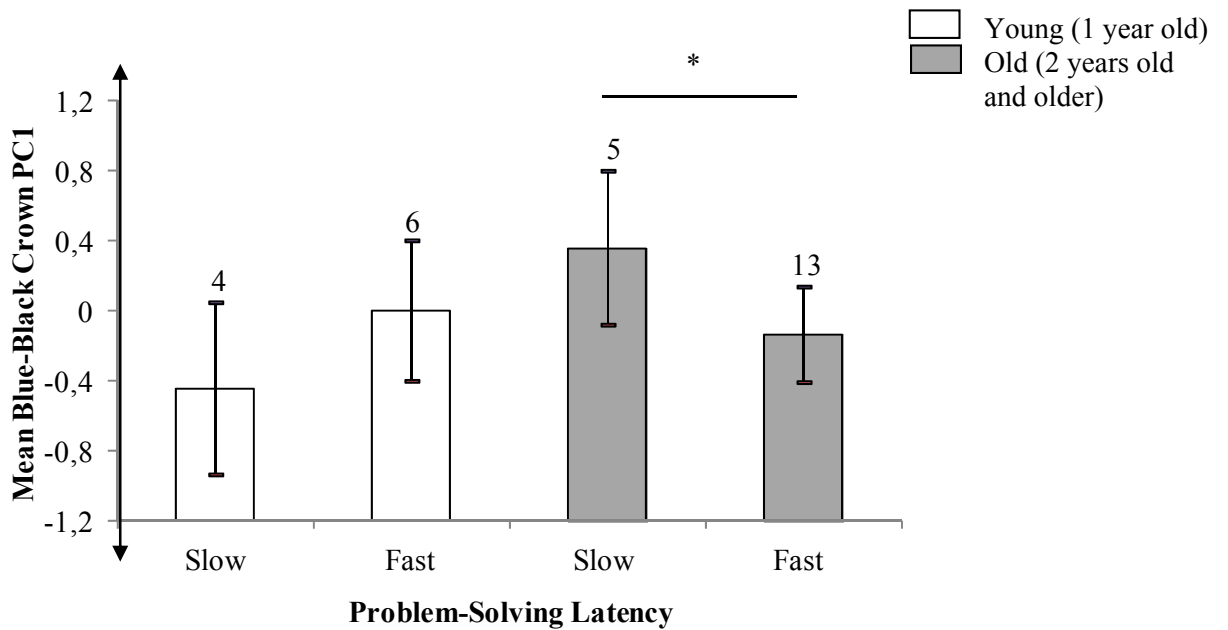


Figure 3.3. Mean blue-black crown PC1 values \pm SE for fast and slow solvers depending on age (one year old vs older adults). The categorisation of solvers as fast and slow (at the median value of the problem-solving latency distribution = 67s) is for the purpose of illustrating the age by latency interaction; the statistics in the text are based on latency as a continuous variable. Numbers above bars are sample sizes.

Finally, the brightness of the black stripe did not differ between solvers and non-solvers ($F_{1,67} = 0.2, P = 0.62$), but one-year-old males were lighter than older males ($F_{1,68} = 4.7, P = 0.033$). Among solvers, black stripe brightness also did not depend on solving latency ($F_{1,28} = 0.3, P = 0.61$).

Learning performance and plumage coloration

The PC1 value of the yellow breast differed between learners and non-learners, but only in one-year-old individuals (interaction between learning status and age: $F_{1,33} = 7.9$, $P = 0.008$): among one-year-old individuals, non-learners showed higher scores of yellow breast PC1 than learners (no difference in older individuals; Figure 3.4). Thus, young non-learners had breasts with shorter-wavelength hues and with lower yellow chroma but higher UV chroma: they were duller, but showed higher UV reflectance. This interaction was observed while accounting for effects of sex (higher values for females: $F_{1,33} = 14.0$, $P = 0.001$), body mass (decreasing values when increasing body mass: $F_{1,33} = 4.5$, $P = 0.041$) and tarsus length ($F_{1,33} = 7.6$, $P = 0.009$). The PC2 value of the yellow breast did not differ between learners and non-learners ($F_{1,35} = 2.5$, $P = 0.12$) and it was not related to the speed of learning ($F_{1,26} = 3.0$, $P = 0.095$), once effects of sex ($F_{1,36} = 8.0$, $P = 0.008$), tarsus length (increase in PC2 values with tarsus length: $F_{1,36} = 6.0$, $P = 0.020$) and body mass (increase in PC2 values with body mass: $F_{1,36} = 5.9$, $P = 0.020$) were accounted for.

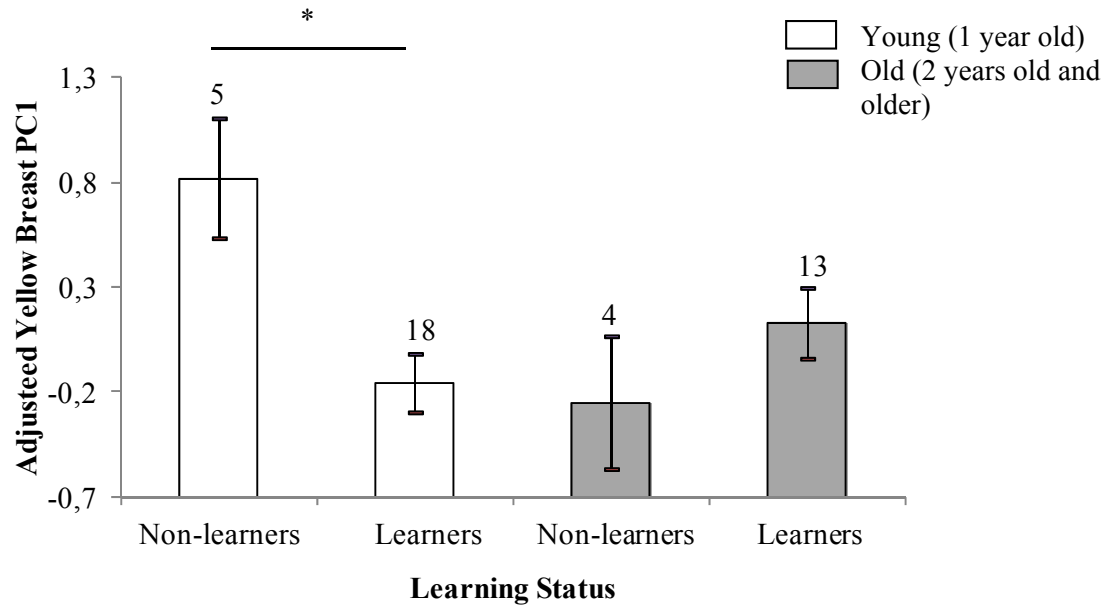


Figure 3.4. Mean yellow breast PC1 values \pm SE (adjusted for sex, body mass and tarsus length) for learners and non-learners depending on age (one year old vs older adults). Numbers above bars are sample sizes.

In males, the crown PC1 value did not differ between learners and non-learners ($F_{1,19} = 0.5, P = 0.482$), but among learners, the crown PC1 value increased with the speed of learning ($F_{1,14} = 4.7, P = 0.048$; regression coefficient \pm SE: 0.023 ± 0.010). Thus, fast learners had crown's colouration that ranged more in the UV than in the blue. The crown PC2 value was not related to learning status ($F_{1,19} = 1.8, P = 0.19$), nor to speed of learning ($F_{1,14} = 3.8, P = 0.07$).

Finally, the brightness of the ventral black stripe did not differ between learners and non-learners ($F_{1,20} = 0.9, P = 0.34$), but fast learners were brighter than slow learners ($F_{1,16} = 8.8, P = 0.009$; regression coefficient \pm SE: -0.017 ± 0.006).

Discussion

We found multiple relationships between problem-solving / learning performances and plumage colouration, suggesting that cognitive performances may be signalled by individuals, but in a complex phenotype- and condition-dependent way.

Relationships between cognitive performances and carotenoid-based coloration

The yellowness of the breast feathers was related to problem-solving status, but only in 2011. It was also related to learning status, but only for young individuals. In both cases, individuals with higher cognitive performances (solvers in 2011 and young learners) had breasts with shorter-wavelength hues and with lower yellow chroma but higher UV chroma than individuals with worse performances (non-solvers in 2011 and young non-learners). Thus, it is possible that individuals with higher cognitive performances trade-off the intensity of their yellow coloration against high UV reflectance. However, to date, a possible mechanism underlying this trade-off is unknown. It is also possible that individuals with higher cognitive performance, while using new resources and thereby increasing their diet diversity, used resources with decreased carotenoid availability compared to individuals sticking to resources rich in carotenoids but that could become scarce in the environment; therefore individuals with higher cognitive performances may become duller as the result of a trade-off between diet diversity and diet quality.

Despite the fact that a duller yellow plumage is traditionally thought to be sexually less attractive (Hill 1991, McGraw 2006, Svensson and Wong 2011), some recent studies have shown that the UV component of carotenoid color, influenced by the structural component of the feather (Shawkey and Hill 2005), can be positively associated with correlates of fitness (MacDougall *et al.* 2003, Doutrelant 2008) and thus should be favored during mate choice. Thus, even if dietary carotenoid availability might not have been associated in this case with cognitive performances, UV reflectance seems to be associated with better performance on the problem-solving task, and might be used by great tits when choosing mates.

Interestingly, these differences were phenotype- (age) or condition- (year) dependent in both cases. On the contrary to other passerine birds, great tits do not have pre-alternate moult before the mating season and only moult at the end of the summer or beginning of autumn (pre-basic moult; Jenni and Winkler 1994). In our study site, environmental conditions differed greatly between 2009 and 2010, the first being a very poor year for reproduction and the second far more favourable (pers. obs.). In 2009 environmental conditions had been so poor that solvers and non-solvers might have moulted in equally bad conditions, whereas in 2010 conditions were favorable and could allow solvers to increase the signalisation of their solving ability. Solvers might have allocated resources to feathers with higher UV rather than more intense coloration. Among solvers, young learners also had duller yellow breasts and higher UV reflectance than young non-learners, while no difference was observed between older individuals. This might indicate that, at a life stage where learning is likely to be very important because personal experience is lacking (i.e. for young individuals), learners also invested more resources in UV reflectance than in coloration.

Relationships between cognitive performances and structural-based coloration

In males, the blue-black crown coloration also varied with performances: solver males were darker than non-solver males, and faster two-year-old or older solvers and learners peaked more in the UV than in the blue as compared to slow individuals. In great tits and chickadees, previous studies have shown that a darker crown offers higher contrast against the yellow breast and white cheeks than a brighter crown, and males with darker and more UV crowns are dominant, in better condition, have higher reproductive success and are favoured by females (Mennill *et al.* 2003,

Doucet *et al.* 2005) than males with lighter crowns. Thus, our results show that males with higher performances had darker and UV-peaking crown, and thus might be favored during mate choice.

Relationships between cognitive performances and melanin-based coloration

The brightness of the breast stripe was negatively related to the speed of learning in males: fast learning males had a lighter stripe than slow learning males. This result apparently contradicts the relation found between problem-solving status and brightness of the crown, since solver males had darker crowns than non-solver males. However, it has been shown in great tit males that lighter breast stripe coloration, resulting from low barbule density, is associated with larger stripe (Galvan 2011). Great tit males with larger breast stripes are socially dominant, thus get better access to resources, defend their nest more vigorously and have higher body condition and reproductive success than males with thinner stripes (Jarvi and Bakken 1984, Norris 1990, Quesada and Senar 2007, Galvan 2010). Taken together, these results suggest that males might trade stripe brightness against stripe size. Fast learning males may signal this ability to females through a lighter but larger stripe. Stripe size was not measured in our study, but deserves further attention to test this signalling potential of cognitive capacities.

Conclusion

Overall, our results showed that individuals with high cognitive performances had reduced yellow breast and blue crown colorations but increased UV reflectance of feathers of the same areas, together with a darker crown and lighter but maybe larger black ventral stripe for males which are known to be favored during mate choice. Despite the fact that many studies in tit species have previously found the intensity of the yellow breast and dark crown colorations to be sexually selected traits, yet little is known about the role of UV reflectance in mate choice in tits and other species (Silitari *et al.* 2002, Kurvers *et al.* 2010a) and its possible interaction with the mechanism of colouration by pigments. Most of the relations with problem-solving or learning performances we found were phenotype- or condition-dependent. Even if some of the results have to be interpreted with caution due to the small sample size (e.g. results from male learning performance),

previous studies have shown that the links between plumage coloration and individual quality can be complex (Doutrelant *et al.* 2008, Parker *et al.* 2011). This is especially true for great tits, in which plumage coloration represents a complex, phenotype and/or condition-dependent signal (Hegyí *et al.* 2006, 2007, Galvan 2010). Nevertheless, our results suggest that cognitive capacities such as problem-solving and learning performances could be signalled through different phenotypic traits that have previously been shown to be under sexual selection and/or condition-dependent.

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Dans le chapitre précédent, nous avons exploré les liens entre des caractéristiques phénotypiques et les performances de résolution de problème et d'apprentissage afin de vérifier s'il pouvait exister un rôle de ces performances dans la sélection sexuelle. Le but de ce dernier chapitre est d'examiner le rôle de la pression parasitaire sur les réponses comportementales face à une tâche de résolution de problème.

Contributions de co-auteurs :

Laure Cauchard et Blandine Doligez ont formulé l'hypothèse de départ. Laure Cauchard, Anna Dubiec et Blandine Doligez ont planifié le terrain. Laure Cauchard et Anna Dubiec ont mené les expériences sur le terrain. Laure Cauchard a effectué les analyses, sous les conseils de tous les co-auteurs. Laure Cauchard a rédigé une première version du manuscrit et tous les co-auteurs ont contribué à son amélioration.

CHAPITRE 4 :

ANTI-MALARIA DRUG INJECTIONS AFFECT BEHAVIOURAL RESPONSES TO A NOVEL PROBLEM-SOLVING TASK IN GREAT TITS

Soumis à Biology Letters

(Modifié pour les besoins de la présente thèse)

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Abstract

Detrimental effects of malaria parasites on host behaviour, particularly on cognitive traits, and benefits of anti-malaria drugs have been well investigated in humans. Although malaria is ubiquitous in non-human animal populations, including passerines, experimental demonstration of such effects on host behaviour is currently lacking. Malaria parasites have been shown to decrease host fitness in several passerine species. In this study, we experimentally tested whether injection of an anti-malaria drug affected behavioural responses to a novel problem-solving task presented to females of a wild great tit (*Parus major*) population. We compared problem-solving and learning performances, neophobia, exploration and activity on the nestbox between females injected with an anti-malaria drug and control females. Females treated against malaria showed higher levels of exploration and activity than control females, while their problem-solving and learning performances were not affected. These results suggest that blood parasite load may help explain inter-individual as well as inter-population differences in behaviour in wild bird populations.

Introduction

Parasites are known to negatively affect cognitive performance and personality traits in animals (Kershaw *et al.* 1959, Olson and Rose 1966, Kavaliers *et al.* 1995, Moore 2002, Gegear *et al.* 2006, Poulin 2013). Malaria, one of the most common parasitic diseases of human populations in tropical regions, causes impaired cognitive functioning in terms of attention, memory and visuospatial performance (Bangirana *et al.* 2006, Kihara *et al.* 2006). Surprisingly, little is known concerning the direct effects of malaria-inducing parasites on animal behaviour, although malaria is widespread and harmful in many animal populations (Levine 1988).

In birds, malaria parasites (genera *Haemoproteus* and *Plasmodium*, sensu Perez-Tris *et al.* 2005) have been experimentally shown to decrease host reproductive success, body condition and survival (Merino *et al.* 2000, Marzal *et al.* 2005, Knowles *et al.* 2010). While the direct effects on health have been well investigated, the fact that malaria parasites can also affect avian host investment in behavioural traits, as found in other host-parasite systems, has been overlooked (Perez-Tris *et al.* 2005, Poulin 2013). If malaria parasite can influence behavioural traits, differences in malaria prevalence between populations may cause behavioural differences between them. Surprisingly, few studies have examined the effect of malaria parasites on behavioural performance. Examples include adult male canaries (*Serinus canaria*), in which early exposure to malaria parasites negatively affects the development of the high vocal centre (HVC) song nucleus in the brain and, as a consequence, song complexity (Spencer *et al.* 2005) and great tits (*Parus major*), in which infected females showed decreased problem-solving performance, and infected males took fewer risks, than non-infected individuals (Dunn *et al.* 2011). However, positive correlations between infection level and behavioural traits have also been found: in the same study on great tits, infected males showed better problem-solving performance and infected females were more explorative than non-infected individuals (Dunn *et al.* 2011). Moreover, at the interspecific level, innovation rate was positively associated with the size of immune defense organs, a proxy of infection level (Garamszegi *et al.* 2007). Such positive correlations may result from higher encounter and/or infection probability in hosts showing higher activity or propensity to explore new habitats (Barber and Dingemanse 2010). However, to make inferences about the causality of the relationships between malaria parasite infection and host behavioural traits, an

experimental approach is required that manipulates parasite pressure and examines subsequent behavioural responses.

We injected females of a wild great tit population at an early breeding stage with physiological salt either alone (control) or with an anti-malaria drug (primaquine) (Merino *et al.* 2000, Marzal *et al.* 2005, Martinez-de la Puente *et al.* 2010). We subsequently compared females' behavioural responses to a novel problem-solving task (neophobia, exploration, activity and cognitive traits: problem-solving and learning performances). If parasite infection has a detrimental effect on host behaviour, females treated with primaquine should be more explorative and active, and show enhanced problem-solving and learning performances, compared to control females.

Material and methods

Model system and anti-malaria drug injections

We carried out the study in a population of great tits breeding on the island of Gotland (Sweden) in spring 2011 and 2012. Only females were used since catching males early is difficult. Nestboxes were visited regularly from the beginning of the breeding season as part of the long-term monitoring of the population (see Chapter 1 for details).

During nest building, females were caught within nestboxes, ringed, aged, weighed and blood sampled. Females were randomly assigned to one of the two treatment groups and injected intraperitoneally with 0.1 ml of physiological salt (PBS) either alone (control; N = 27) or with 0.01 mg of primaquine (anti-malarial drug Aldrich; N = 30). Primaquine has been successfully used to reduce avian malaria infection in another close passerine species (Merino *et al.* 2000, Marzal *et al.* 2005, Martinez-de la Puente *et al.* 2010). Because over the course of the nesting cycle, infection intensity and/or the risk of acquiring novel infections increases (Atkinson and van Riper 1991), Primaquine administration is used to reduce parasite load and protect individuals against novel infections until the drug effect wears off (Merino *et al.* 2000, Marzal *et al.* 2005).

Blood samples revealed that, in our population, 87.6% females were infected with at least one malaria lineage. Results were unchanged when we removed the 3 uninfected females from analyses.

Problem-solving and learning performances

We used a problem-solving task consisting of a door blocking the nestbox entrance that could be opened by parents to access the young by pulling a string attached to the door (see Chapter 1). The tests were video-recorded, lasted 1 h to prevent nestling starvation if parents were unable to enter, and were conducted twice on two consecutive days during the peak of chick provisioning (i.e. on 7-9 days old chicks, 35.5 ± 2.9 days after injection), only if chicks were satiated (i.e. not begging when starting the test).

We determined from video recordings whether each female succeeded in solving the task (problem-solving status: solver vs. non-solver) and if so, the time elapsed between the first contact with the string that caused a movement of the door and the bird's entry into the nestbox, excluding the time spent away from the nestbox (latency to solve the task). We excluded females that did not really participate in the test, i.e. that were present during less than 50% of the fastest observed solving latency. To measure learning performance, we determined whether females that solved the task twice or more showed a decrease in latency (learning status: learner vs. non-learner) and if so, the mean of their successive latencies until no further reduction in latency could be seen, i.e. when they solved the task three successive times with the same latency ± 5 seconds (speed of learning).

Neophobia, exploration and activity measures

Neophobia, an animal's aversion to novelty, is traditionally measured by placing a novel object in a familiar environment (e.g. next to a familiar food source) and recording the increased latency to return to this environment (e.g. feed in the presence of the object) (Greenberg 2003, Reale *et al.* 2007). Here, because the problem-solving task was new to the bird, we considered it to be a 'novel object' in the bird's familiar breeding environment (nest box) (Chapter 1). We recorded the time between landing on the nestbox and first contact with the task as a measure of neophobia.

Exploration, a behaviour that allows animals to gather information about novel situations, is traditionally measured using an open field test (Verbeek *et al.* 1994). The avian version of this test consists of placing an individual in a room with artificial trees and recording the total number

of movements between different areas (Verbeek *et al.* 1994, Reale *et al.* 2007). Here, we measured the female's exploration score as the total number of different zones on the nestbox (see figure 1) that the bird contacted until solving the novel problem-solving task, or until the end of the test.

Finally, we measured activity during the problem-solving test as the total number of movements between the zones on the nestbox until solving the task or until the end of the test.

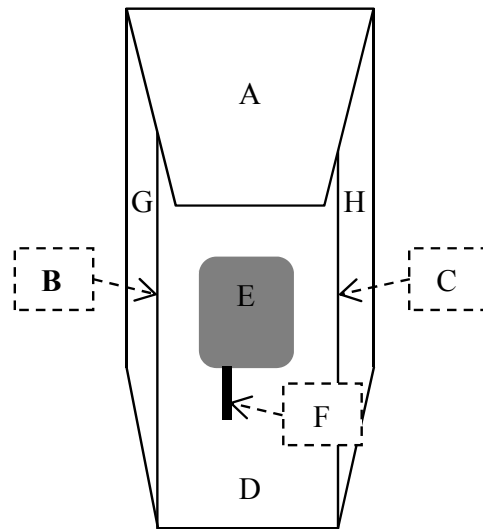


Figure 4.1. Nestbox exploration zones. A: roof, B and C: left and right corners, D: front, E: task door, F: task string, G and H: left and right sides.

Statistical analyses

We used generalized linear models (GLM) to examine how treatment affected females' problem-solving and learning status, with binomial error and logit link function, and linear models for continuous behavioural measures, in SPSS 18.0 (Chicago, SPSS Inc. 2009). Initial models included treatment, year, female age and all pairwise interactions. Because the number of different zones contacted during the test is likely to depend on the total number of movements a bird made (the more active a bird is, the more likely it is to explore different zones), exploration and activity scores can be expected to be correlated. Therefore, we included activity as a covariable when analysing exploration. Non-significant effects were backward eliminated and all tests were two-tailed.

Results

57 females were injected either with PBS alone (control; $N = 27$) or with Primaquine (Primaquine; $N = 30$) and successfully tested for behavioural performances.

Anti-malaria treatment affected neither problem-solving status ($\chi^2_1 = 0.09$, $P = 0.77$), latency to solve the task ($F_{1,31} = 1.08$, $P = 0.31$), learning status ($\chi^2_1 = 1.65$, $P = 0.20$) nor speed of learning ($F_{1,18} = 0.15$, $P = 0.71$). None of the other explanatory variables affected these cognitive measures (see Supplementary Material in Appendix 4 of this thesis).

Anti-malaria treatment did not affect neophobia ($F_{1,51} = 0.29$, $P = 0.59$). However, both exploration ($F_{1,55} = 4.57$, $P = 0.037$) and activity on the nest ($F_{1,55} = 8.59$, $P = 0.005$) differed between treatments (see Supplementary Material in Appendix 4 of this thesis). Females injected with primaquine were more explorative than control females (mean exploration score \pm SE = 5.37 ± 0.27 and 4.26 ± 0.23 respectively; figure 4.2), accounting for the effect of activity level on exploration score ($F_{1,55} = 20.05$, $P < 0.001$). Females injected with primaquine were also more active than control females (mean level of activity \pm SE = 44.60 ± 6.44 and 26.96 ± 4.14 respectively; figure 4.2). Activity also varied with year ($F_{1,55} = 5.28$, $P = 0.026$): females were more explorative in 2012 than in 2011.

Results were unchanged when we removed the 3 uninfected females from analyses.

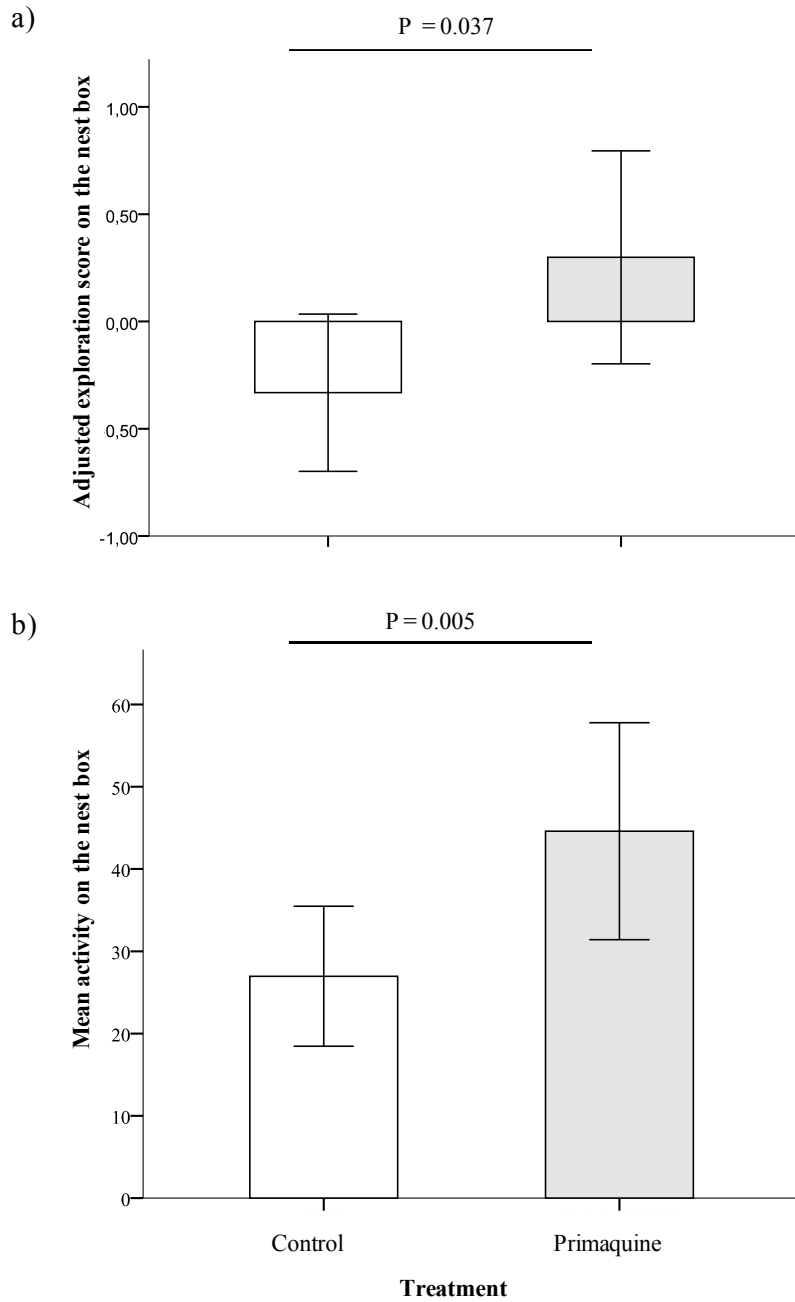


Figure 4.2. Mean adjusted exploration score (a) and activity level (b) on the nestbox for great tit females injected with 0.1 ml of physiological salt either alone (control) or with 0.01 mg of primaquine (primaquine).

Discussion

Our results show that injecting primaquine significantly increased females' exploration and activity around the nestbox. Previous studies have clearly shown that parasites can alter a broad range of phenotypic traits, including behaviour (Barber and Dingemanse 2010, Poulin 2013). Provided that Primaquine injection had successfully decreased parasite load, our study provides the first experimental support for the hypothesis that, besides ecological factors such as food availability and predation (Carere *et al.* 2005, Bell and Sih 2007), malaria parasites can be another factor causing variation in host behavioural traits in wild birds.

Interestingly, Primaquine injection did not improve female cognitive performance, which contrasts with previous results in the same species (Dunn *et al.* 2011). Although some behaviours might be affected by a short-term release from parasite pressure, changes in cognitive performance might require more time for the neural system to recover (Bangirana *et al.* 2006). Thus, we may not have detected an effect on cognitive performance because our problem-solving tests were performed only 5 weeks after the anti-parasite treatment. To test this hypothesis, using a longer anti-parasite treatment and measuring later cognitive performance would be needed. Furthermore, malaria parasite prevalence and community composition can vary between locations (Marzal *et al.* 2011, Szoellosi *et al.* 2011) and different populations might thus encounter different parasite pressures. Only 40% of great tit females in Whytam woods (UK) in the study by Dunn *et al.* (2011) were infected with malaria parasites, suggesting a lower parasite pressure than in our population, where over 85% of females were infected. Finally, contrasting results between studies can result from the reciprocity of effects between host and parasites (Blanchet *et al.* 2009). More innovative individuals could be more prone to explore new habitats, thus encounter parasites and get infected (i.e. a positive relationship), and these infections could then divert energy from other behaviours to immune defenses (i.e. a negative relationship). Parasite effects may then be blurred and difficult to detect between studies carried out at different stages.

Overall, our study confirms that injection of an anti-malaria drug can significantly affect some behavioural traits. This emphasises the role of parasites in explaining inter-individual and inter-population behavioural differences in the wild.

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DISCUSSION GÉNÉRALE

Tout au long de cette thèse, nous nous sommes intéressés aux conséquences sur les traits d'histoire de vie des variations interindividuelles des capacités de résolution de problème et d'apprentissage dans une population naturelle de mésanges charbonnières, un petit passereau reconnu pour ses performances cognitives en captivité mais aussi en milieu naturel (Overington *et al.* 2009b, Cole *et al.* 2011). Les travaux menés au cours de cette thèse ont permis de décrire pour la première fois (en même temps que Cole *et al.* 2012) une relation positive entre la performance de résolution de problème, une mesure opérationnelle de la capacité d'innovation, et le succès reproducteur annuel, utilisé comme un indicateur de l'aptitude phénotypique. Cette relation, robuste statistiquement et non générée par une plus grande motivation à nourrir une nichée plus importante, pourrait être expliquée par une meilleure exploitation de l'habitat et/ou capacité de s'occuper des poussins par les parents les plus performants dans la résolution de problème, ainsi que le suggère un taux de nourrissage plus important. Par ailleurs, nous avons exploré si certaines caractéristiques morphologiques (colorations du plumage), précédemment montrées comme impliquées dans la sélection sexuelle chez cette espèce et d'autres, pouvaient signaler les capacités de résolution de problème et d'apprentissage aux partenaires potentiels lors du choix de partenaire. Ceci suggérerait que ces capacités pourraient être soumises non seulement à la sélection naturelle, via le succès reproducteur, mais aussi à la sélection sexuelle. Enfin, nous avons testé expérimentalement l'effet de la pression parasitaire sur les variations interindividuelles des performances de résolution de problème et d'apprentissage ainsi que sur d'autres traits comportementaux, et montré que la réduction de la pression parasitaire à court terme jouait sur différents comportements mais pas les capacités de résolution de problème ni d'apprentissage.

La performance de résolution de problème comme facteur de variation du succès de reproduction

Chez les oiseaux, de nombreuses études ont pu mettre en évidence que le succès reproducteur dépend :

- de ses caractéristiques individuelles, comme l'âge (Forsslund et Pärt 1995), la condition corporelle (Blomqvist *et al.* 1997, Wendeln et Becker, 1999), le niveau de stress (Lendvai *et al.* 2007), l'immunité (Gustafsson *et al.* 1994), les traits de personnalité (Dingemanse *et al.* 2004, Quinn *et al.* 2009) ou la qualité génétique (Vonschantz *et al.* 1989, Sardel *et al.* 2014),

- des caractéristiques du couple, comme la coordination de la reproduction (Naef-Daenzer *et al.* 2001, Perrins et McCleery 1989, Verboven et Visser 1998, Verhulst et Tinbergen 1991), les performances de nourrissage (Naef-Daenzer et Keller 1999), de défense du nid (Montgomerie et Weatherhead 1988, Sergio et Bogliani 2001) ou de compétitivité (Ens *et al.* 1992, Both et Visser 2000),

- et des facteurs environnementaux, comme le degré de parasitisme (Fitze *et al.* 2004, Gustafsson *et al.* 1994, Marzal *et al.* 2005), la disponibilité en nourriture (Verhulst *et al.* 1995), la présence de prédateurs (Martin 1993) et le type / qualité d'habitat (Holmes *et al.* 1996).

De plus, tous les individus n'ayant pas la même capacité de répondre aux pressions imposées par les conditions environnementales, les interactions entre ces caractéristiques phénotypiques et les facteurs environnementaux, c'est à dire les interactions phénotype x environnement (par exemple, la réponse immunitaire à la présence de parasites ; la capacité à défendre un territoire de qualité élevée ; la capacité de se défendre contre les prédateurs) s'ajoutent également aux facteurs jouant sur les variations du succès reproducteur (Dingemanse *et al.*, 2004).

Le premier chapitre de cette thèse a permis de mettre en évidence pour la première fois un lien direct entre la performance de résolution de problème et le succès de reproduction chez les oiseaux, ajoutant ainsi cette performance cognitive à la liste des caractéristiques individuelles pouvant influencer le succès de reproduction. Cette étude a été réalisée simultanément avec une autre étude sur la même espèce, en Grande-Bretagne (Cole *et al.* 2012), qui conclut également à une relation positive de la capacité de résolution de problème avec le succès à l'envol, bien que le bénéfice net ne soit pas aussi clair que dans notre étude. En effet, dans l'étude de Cole *et al.* (2012), la probabilité d'échec (liée à une désertion suite à la capture) augmente avec la capacité de résolution de problème. De façon intéressante, ces deux études (Cole *et al.* 2012, chapitre 1) utilisent des tâches de résolution de problème différentes, impliquant des motivations différentes à résoudre la tâche : dans leur étude, Cole *et al.* (2012) maintiennent en captivité quelques jours des individus capturés en milieu naturel afin de les mettre à jeun et de leur soumettre une tâche de

résolution de problème de nature alimentaire (il s'agit de retirer un obstacle d'un distributeur pour faire tomber un ver). Au contraire, la tâche utilisée tout au long de cette thèse a été conçue pour être utilisée directement en milieu naturel, sans période de captivité préalable afin de ne pas influencer le succès reproducteur des individus testés. La nourriture étant disponible dans l'environnement de façon variable, nous avons utilisé la motivation des parents à rentrer au nid pour s'occuper des jeunes pour concevoir notre tâche, qui nécessite de tirer une ficelle pour soulever une trappe bloquant l'entrée au nid. De plus, ces deux études ont été réalisées à des périodes clés différentes : en hiver, pour l'étude de Cole *et al.* (2012) lorsque la nourriture nécessaire à la survie est la ressource limitante, et au printemps pour nos expériences, lorsque la reproduction et les soins parentaux (dont l'approvisionnement en nourriture) sont les facteurs principaux pour le succès de reproduction. Ainsi, bien que les performances intra-individuelles à différents tests cognitifs ne soient pas toujours corrélées (Boogert *et al.* 2011a, Isden *et al.* 2013, Keagy *et al.* 2011) et puissent varier dans le temps (Sherry et Hoshoooley 2009), les résultats de ces études se combinent et se renforcent pour constituer une première étape cruciale dans l'étude des conséquences évolutives des variations interindividuelles des performances cognitives en milieu naturel.

Comment la performance de résolution de problème peut-elle influencer le succès reproducteur ?

Dans le chapitre 2, nous avons testé la causalité de ce lien entre la performance de résolution de problème et le succès de reproduction, et exploré un mécanisme sous-jacent possible de ce lien. Manipuler la taille de la nichée n'a pas influencé la performance de résolution de problème du couple reproducteur, démontrant expérimentalement que la motivation, ici représentée par le nombre de jeunes à nourrir, n'influence pas la performance cognitive des parents. Ces résultats suggèrent donc que c'est bien la performance cognitive qui influence le succès de reproduction, et non une variation dans la motivation à résoudre la tâche qui influence sa réussite (Keagy *et al.* 2009, Sol *et al.* 2012). Cependant, une manipulation expérimentale des performances cognitives des parents serait nécessaire pour confirmer cette hypothèse : si les résultats d'une telle expérience montraient que les performances cognitives des parents influencent directement le succès de reproduction, alors la causalité de la relation serait confirmée. Si on observait au contraire une absence de lien entre les performances cognitives et le succès de reproduction, on pourrait

imaginer que le mécanisme sous-jacent générant la relation entre performance cognitive et succès reproducteur impliquerait un troisième facteur, lié à ces deux traits, de façon simultanée mais indépendamment l'un de l'autre, par exemple la condition ou qualité individuelle. Cependant, manipuler la performance de résolution de problème, ou plus généralement une capacité cognitive particulière, via par exemple une chirurgie ou des conditions de croissance, serait difficile à réaliser en nature sans risquer de modifier d'autres fonctions nécessaires à la survie et/ou à la reproduction.

Les résultats des chapitres 1 et 2 combinés montrent que les effets de la performance de résolution de problème pourraient avoir lieu à la fois au début de la période de reproduction (nombre d'œufs produits et de jeunes éclos), mais aussi pendant le nourrissage (nombre de jeunes envolés et soins parentaux). Un effet sur la taille de la couvée (Cole *et al.* 2012, chapitre 1) et le succès d'éclosion (chapitres 1 et 2) pourrait indiquer un avantage précoce, antérieur à et/ou durant la période de ponte. Par exemple, l'éclosion des œufs étant synchronisée chez la mésange charbonnière avec l'abondance maximale d'éclosion des larves dans l'environnement (Cresswell et McCleery 2003, van Noordwijk *et al.* 1995), la période de ponte a lieu bien avant (durée de l'incubation : de 12 à 16 jours), alors que la disponibilité en nourriture est plus faible, et seuls les individus les plus performants cognitivement pourraient être à même de trouver suffisamment de nourriture pour démarrer la reproduction dans de bonnes conditions (pour assurer par exemple la production coûteuse des œufs, Visser et Lessells 2001, Williams 2005). Des individus plus performants pourraient être également capables de choisir (par exemple via une meilleure utilisation de l'information, Doligez *et al.* 2004) et/ou de défendre (Cole et Quinn 2012) des territoires de reproduction de meilleure qualité, ayant par exemple une plus grande disponibilité en ressources alimentaires, une plus faible pression parasitaire et/ou un plus faible risque de prédation, permettant d'investir plus d'énergie dans la ponte. Les femelles montrant des capacités cognitives plus élevées pourraient également mieux gérer la période d'incubation en relation avec les variations de l'environnement (Charmantier *et al.* 2008), diminuant les risques de mortalité sur les œufs. Enfin, il est possible que les capacités cognitives soient associées à une meilleure qualité intrinsèque individuelle assurant une meilleure reproduction (par exemple une meilleure condition corporelle, réponse au stress ou bien réponse immunitaire).

La performance de résolution de problème pourrait également avoir un effet sur la reproduction pendant la période de nourrissage des jeunes. Les résultats du chapitre 2 suggèrent

que les couples innovateurs seraient plus efficaces à nourrir leurs poussins. Bien que les résultats d'une étude préliminaire réalisée sur un petit échantillon chez la mésange charbonnière (Cole *et al.* 2012) ne montraient pas de lien entre le nourrissage et la performance de résolution de problème (alors que les individus les plus performants fourragent effectivement sur un territoire plus petit), nos résultats montrent clairement un taux d'approvisionnement plus élevé pour les couples innovateurs et ce, quelle que soit la manipulation de la taille de nichée. Afin d'explorer cette hypothèse, des caméras miniatures ont été disposées à l'intérieur de 13 nichoirs pour enregistrer en détail l'approvisionnement des parents lors de la saison de reproduction 2013, dans le cadre d'une étude pilote (non présentée dans cette thèse). L'enregistrement via ces caméras miniatures de l'approvisionnement permet non seulement d'identifier précisément le sexe des parents à chaque visite (via le dimorphisme sexuel au niveau de la largeur de la bande noire ventrale mais aussi au niveau de la couleur du crâne), mais aussi le type (c'est à dire chenille vs autre type de proie, les chenilles étant les proies préférées, Gosler 1993) et la taille des proies apportées (c'est à dire plus grosses, de mêmes tailles ou plus petites que le bec). Les résultats, analysés donc au niveau individuel et non au niveau du couple, montrent que bien que la proportion de chenilles apportées ne différait pas selon la performance de résolution de problème, les individus innovateurs (c'est à dire ayant résolu la tâche) avaient une plus grande probabilité d'apporter des proies de plus grande taille, mais lorsque la nichée était réduite uniquement. Ces résultats pourraient indiquer un effet de la performance de résolution de problème sur les stratégies d'approvisionnement : les innovateurs seraient en mesure de choisir / apporter des proies plus grosses, donc plus nourrissantes (Schwagmeyer et Mock 2008), même si un compromis semble se dessiner entre stratégie d'approvisionnement et taille de la nichée, puisque dans les nichées augmentées, le nombre de poussin semble contraindre les parents à être moins sélectifs pour pouvoir nourrir l'ensemble des poussins. Il est également possible que nourrir les jeunes avec de la nourriture de meilleure qualité lorsque la nichée est petite soit favorisé afin d'assurer une meilleure survie aux poussins et de contrebalancer un faible nombre de poussins.

Existe-t-il des indices morphologiques signalant les performances cognitives individuelles ?

Que les performances cognitives soient des indicateurs honnêtes de la qualité génétique des individus, ou que ces performances puissent directement influencer le succès de reproduction via

une meilleure utilisation de l'habitat, les résultats des chapitres 1 et 2 indiquent qu'il devrait être bénéfique pour une mésange charbonnière de s'apparier avec un partenaire performant sur le plan cognitif.

L'hypothèse de l'optimisation individuelle de la taille de couvée (Pettifor *et al.* 1988) propose que les parents pondent le nombre d'œufs ajusté à la capacité de recrutement des jeunes (soit le nombre de jeunes qui survivent jusque l'âge adulte et deviennent reproducteurs dans la population). Or, nous avons vu précédemment que la performance de résolution de problème pourrait donner un avantage précoce aux parents performants, qui bénéficient d'une taille de nichée plus grande (Cole *et al.* 2012). Il est donc possible que cet ajustement se fasse par rapport aux performances cognitives des individus, et que la femelle se base sur ses propres performances, celles de son partenaire, ou les deux, pour évaluer les capacités du couple à élever un nombre donné de poussins. Dans ce cas, comment les individus peuvent-ils évaluer les performances cognitives de leur partenaire (revue dans Boogert *et al.* 2011b) ?

Dans le chapitre 3, nous avons montré que les performances de résolution de problème et d'apprentissage étaient corrélées avec plusieurs caractéristiques de la couleur des plumes dans notre population d'étude de mésanges charbonnières. En ce qui concerne les flancs, de couleur jaune, et associés aux pigments caroténoïdes d'origine exogène, les individus les plus performants, à la fois au niveau de la résolution de problème et au niveau de l'apprentissage, présentaient des plumes plus ternes (c'est à dire longueur d'onde plus courte et moins de caroténoïdes) mais dont la structure reflétait plus les UV que les individus moins performants. Chez les mâles, les plumes du crâne des innovateurs était plus foncé (c'est à dire moins brillants), et parmi ces innovateurs, les plus rapides à résoudre la tâche et à apprendre présentaient des plumes dont la coloration tirait plus dans les UV que vers le bleu. Les mâles les plus rapides à apprendre arboraient aussi une bande noire ventrale plus brillante, reflétant probablement une bande plus large (Galvan 2011). Ainsi, aussi bien pour les flancs jaunes associés aux pigments caroténoïdes que pour les plumes structurelles sur le crâne, les individus les plus performants cognitivement semblent avoir un plumage reflétant plus dans les UV que les individus moins performants. Des études récentes ont montré que la réflectance des plumes dans les UV, qui peuvent être détectés par les oiseaux (Hill et McGraw 2006), est reliée à différents indices de la qualité des individus comme la condition corporelle (Doucet 2002, Doucet et Montgomerie 2003) ou l'état de santé (Doucet et Montgomerie 2003, Hill *et al.* 2005), corrélée

positivement au succès reproducteur et à la survie (Doutrelant *et al.* 2008, Henderson *et al.* 2013) et serait donc favorisée par les femelles lors du choix de partenaire (Andersson *et al.* 1998, Siitari *et al.* 2002). Bien que certaines de ces relations soient phénotype- ou condition- dépendantes, ces résultats montrent que la coloration des plumes est associée aux performances cognitives, et pourrait donc être utilisée lors du choix de partenaire, à la fois chez les femelles et chez les mâles dans le contexte de la sélection sexuelle.

En ce qui concerne les mécanismes impliqués dans les relations entre les performances cognitives et la coloration des plumes, les hypothèses sont moins claires. Notre prédiction de départ proposait une relation entre les caractéristiques de coloration et les performances cognitives via le régime alimentaire : les individus les plus performants à résoudre et à apprendre une tâche seraient plus à même de mieux se nourrir et maintenir les fonctions corporelles (par exemple le système immunitaire), et seraient donc capables de signaler cette habileté via des caractéristiques morphologiques dépendantes de la condition, comme les caroténoïdes par exemple (Doutrelant *et al.* 2008). Cependant, nous avons trouvé que les innovateurs, ainsi que les individus qui apprennent à résoudre la tâche, montrent un plumage jaune plus terne que les individus moins performants, reflétant une quantité plus faible de caroténoïdes déposée dans les plumes (Saks *et al.* 2003). À l'inverse, les performances cognitives sont aussi positivement associées à un plus grand rayonnement dans les UV à la fois pour les plumes jaunes du ventre, mais aussi pour les plumes bleues-noires de la calotte pour lesquelles la couleur tire plus vers les UV que vers le bleu. Or, l'intensité de la couleur (Alonso-Alvarez *et al.* 2012) ainsi que les UV (Andersson *et al.* 1998, Saks *et al.* 2003; Siitari *et al.* 2002) sont tous deux des caractères sexuels secondaires préférés lors du choix de partenaire. Dans notre étude, un rayonnement UV est associé à un plumage plus terne, et cette dissociation pourrait indiquer un compromis entre la fabrication des plumes structurelles responsables de la coloration UV et le dépôt de pigments de couleur dans les plumes (Doucet et Meadows 2009), bien que le mécanisme physiologique impliqué dans ce compromis soit inconnu à ce jour. Alternativement, la préférence relative pour les UV et l'intensité de la couleur pourrait différer, et il est possible que les individus plus performants investissent plus dans les plumes structurelles (Shawkey *et al.* 2003) afin d'augmenter leur succès d'appariement (dans l'hypothèse où la réflectance dans les UV serait favorisée par rapport à l'intensité de la couleur par les individus chez cette espèce; Savard *et al.* 2011) et privilégient une coloration plus terne afin par exemple d'éviter la prédation. Les futures études s'intéressant au rôle de la sélection sexuelle sur les

performances cognitives devraient donc explorer le rôle des UV et du/des mécanisme(s) reliant les performances cognitives à la production des plumes structurelles.

Coûts potentiels des performances cognitives

Dans l'étude de Cole *et al.* (2012), bien que les femelles les plus performantes pondaient plus d'œufs, elles étaient également les plus susceptibles de désertir leur nid suite aux perturbations anthropiques résultantes du suivi des nids. Dans leur étude, cette désertion a diminué, voir annulé, l'effet positif de la sélection sur la performance de résolution de problème selon l'année. Ces résultats pourraient indiquer un potentiel coût des performances cognitives, et suggèrent que le maintien des variations interindividuelles dans les performances cognitives pourrait résulter d'effets contrastés des performances cognitives sur différents traits d'histoire de vie (et/ou de la variation spatio-temporelle de ces effets selon les conditions environnementales). Identifier et quantifier ces coûts potentiels apparaît donc primordial pour comprendre l'évolution de ces capacités en populations naturelles. Le test de résolution de problème utilisé tout au long de ce doctorat se déroulait lorsque les poussins avaient entre 6 et 9 jours et nous n'avons observé aucune désertion suite à nos tests (observation personnelle). Cependant, la méthode utilisée ne nous permettait pas de tester une relation entre les capacités cognitives et la probabilité de désertion avant le test de résolution de problème. Notre étude suggère simplement que, s'il existe une relation avec la probabilité de désertion dans notre population d'étude, elle n'est pas spécifiquement liée aux perturbations générées par les visites des nids engendrées par les tests et le suivi de la reproduction en eux-mêmes. Néanmoins, de nombreux autres coûts potentiels peuvent exister.

Dans l'étude de Dunn *et al.* (2011), les femelles les plus performantes à un test de résolution de problème étaient également les femelles les moins parasitées, suggérant un coût du paludisme sur cette performance. Dans le chapitre 4, nous nous sommes intéressés à l'effet de parasites responsables du paludisme (très fréquent chez les populations de passereaux) sur les différents comportements des mésanges face à un test de résolution de problème. Nous avons utilisé pour cette étude une approche expérimentale consistant à injecter un médicament contre le paludisme chez des femelles à un stade précoce de la reproduction (Marzal *et al.* 2005, Martínez-de la Puente 2010). Cette expérience nous a permis de montrer que l'injection de Primaquine

pouvait modifier des traits comportementaux tels que l'exploration et l'activité autour du nichoir en présence de la tâche. Si l'injection de Primaquine a bien diminué la pression parasitaire, cette augmentation de l'activité et de l'exploration pourrait suggérer par exemple un compromis entre l'énergie allouée au système immunitaire et aux activités comportementales (Eraud *et al.* 2005, Sheldon et Verhulst 1996). Bien que la manipulation du comportement d'un hôte par un parasite ait déjà été décrite dans de nombreux systèmes hôte-parasite (Moore 2002), notre étude est la première à tester l'effet d'un traitement anti-paludisme sur les variations interindividuelles de certains traits comportementaux des mésanges charbonnières en milieu naturel. Elle suggère aussi un rôle de ces parasites dans les variations inter-populationnelles de ces traits comportementaux : dans l'étude de Dunn *et al.* (2011), les femelles parasitées sont plus exploratrices ce qui va à l'encontre de nos résultats. Cependant, 40 % des individus de leur population étaient infectés par le paludisme, contre 85 % des individus dans notre population. La différence de pression parasitaire pourrait mener à des relations entre parasitisme et traits comportementaux différentes (bien que les tests comportementaux soient différents, ce qui pourrait aussi expliquer des résultats différents). Les études futures s'intéressant à l'origine des variations comportementales interindividuelles et inter populationnelles devraient donc prendre en compte les variations de la charge parasitaire du paludisme, mais aussi d'autres maladies.

Pour autant, l'injection du médicament anti-paludisme n'a pas eu d'effet sur les capacités cognitives mesurées dans notre étude, c'est-à-dire la résolution de problème et l'apprentissage. L'absence d'effet sur les capacités cognitives mesurées suggère que le parasitisme n'aurait pas d'effet néfaste sur les capacités cognitives et pourrait donc soutenir l'hypothèse alternative selon laquelle adopter des comportements nouveaux (innover ou apprendre) augmenterait les risques d'être exposé à des parasites, ce qui représenterait un coût des performances cognitives : collecter des informations sur l'environnement, explorer de nouveaux environnements ou apprendre de nouvelles techniques de recherche de nourriture pourraient augmenter la probabilité de rencontrer des parasites, nouveaux ou non, et exposer ainsi les individus à de plus fortes pressions parasitaires (Barber et Dingemanse 2010, Boyer *et al.* 2010). Cependant, ces résultats ne sont pas en accord avec ceux de Dunn *et al.* (2011), qui montre de façon corrélative, sur la même espèce, que les femelles infectées par le paludisme ont des performances de résolution de problème réduites par rapport aux femelles non infectées, indiquant un effet détrimental de ces parasites sur la performance de résolution de problème. Comme nous avons vu précédemment, plusieurs raisons

peuvent expliquer ces différences de résultats, comme des pressions parasitaires différentes subies par les deux populations d'étude et/ou des protocoles et tâches différents. Il est également possible que les capacités cognitives des individus testés dans notre population aient bénéficié d'un relâchement parasitaire, mais que ce processus pourrait nécessiter un temps plus long avant d'être effectif et donc observable (via un traitement antiparasitaire plus long suivi de tests cognitifs réalisés plus tardivement que dans notre étude). Comme dans le cas du chapitre 2, manipuler directement les performances cognitives des individus afin de tester par la suite leur exposition aux parasites, et donc leur degré d'infection, permettrait d'éclaircir ce mécanisme.

Perspectives

L'imprévisibilité de l'environnement et ses effets sur l'aptitude phénotypique des individus favorisent l'évolution de l'apprentissage, et plus généralement de l'adoption de comportements nouveaux (Shettleworth 2009). Pour qu'un trait puisse évoluer, trois conditions sont nécessaires : (i) il doit exister une variation entre les individus pour ce trait, (ii) la variation sur ce trait doit être soumise à sélection, et donc être liée à la survie et/ou la reproduction des individus, et (iii) les variations de ce trait doivent être transmises de génération en génération. À travers les 4 chapitres de cette thèse de doctorat, nous avons montré que les performances de résolution de problème et/ou d'apprentissage peuvent permettre aux individus d'obtenir un meilleur succès reproducteur, sont associées à des signaux pouvant être utilisés dans le cadre de la sélection sexuelle et suggéré qu'elles sont susceptibles d'influencer la pression parasitaire subie par les individus, dans une population naturelle de mésanges charbonnières. Afin de pouvoir conclure sur l'action globale de la sélection naturelle sur les performances cognitives, il serait important d'examiner l'effet des variations interindividuelles des performances cognitives sur la survie et à plus long terme, sur une mesure générale de l'aptitude phénotypique des individus (par exemple la production de recrues sur l'ensemble de la vie). Bien que Cole *et al.* (2012) n'ont mentionné aucun effet sur la survie, leur étude a été réalisée en utilisant le taux de retour et non le taux de survie basé sur des modèles de capture-recapture. Dans notre population, et probablement ailleurs également même si les chiffres peuvent varier sensiblement, on observe généralement 30% d'échecs de reproduction précoces, soit 30% de parents non identifiés car non capturés pendant le suivi de population. Une approche de

capture-recapture est nécessaire pour estimer la survie locale réelle et la séparer de la probabilité de recapture.

La question de l'héritabilité également est une prochaine étape importante. Chez les humains, de nombreuses études ont estimé l'héritabilité des performances cognitives générales, allant de 30 % à 80 % selon le stade de développement du sujet testé (revue dans Deary *et al.* 2009). Chez les autres groupes d'animaux, les études portant sur l'héritabilité des capacités cognitives, même en captivité, sont rares (Airey *et al.* 2000, Forstmeier *et al.* 2009, Galsworthy *et al.* 2005). De plus, le fait que pour être sélectionné, un trait nécessite une base génétique peut être remis en cause par la notion d' « évolution culturelle » (Tomasello *et al.* 1993). La culture représente l'ensemble des traditions comportementales d'une population acquises à partir des congénères soit par imprégnation, imitation ou apprentissage (Lefebvre 2013, Whiten *et al.* 1999). Lorsque les traits étudiés sont des traits comportementaux, l'« hérédité culturelle », c'est-à-dire la ressemblance entre parents et jeunes via la « transmission culturelle », devrait être prise en compte pour évaluer l'héritabilité des traits cognitifs (Danchin *et al.* 2011, Danchin *et al.* 2004, Tomasello *et al.* 1993).

Une hypothèse récurrente quant au mécanisme impliqué dans le lien positif entre performance de résolution de problème et succès de reproduction, et peut-être survie, serait que les individus présentant des capacités cognitives plus importantes obtiendraient un meilleur succès en raison d'une meilleure capacité à exploiter leur habitat de façon optimale (Cole *et al.* 2012). Cette meilleure exploitation pourrait reposer sur un meilleur traitement et une meilleure utilisation de l'information disponible sur la qualité de l'habitat. Chez la plupart des espèces, la qualité de l'habitat varie dans le temps et l'espace, et ces variations affectent fortement le succès reproducteur et/ou la survie des individus. Par conséquent, des pressions de sélection fortes devraient favoriser les stratégies permettant aux individus de choisir de façon optimale leur site de reproduction / habitat, comme la récolte et l'utilisation d'informations sur la qualité des habitats pour comparer des sites alternatifs (Dall *et al.* 2005, Danchin *et al.* 2004). L'utilisation d'informations en milieu naturel a récemment reçu un intérêt croissant, et les études aussi bien théoriques qu'empiriques ont souligné l'importance de la fiabilité des informations (c'est-à-dire l'efficacité avec laquelle les individus peuvent prédire leur succès attendu dans le site) ainsi que son accessibilité (c'est-à-dire le coût de sa récolte) dans l'évolution des stratégies d'utilisation de l'information (Dall *et al.* 2005, Doligez *et al.* 2003). Parmi les différentes sources d'information, les individus con- et hétérosécifiques

peuvent fournir des informations sociales, au travers de leur présence et/ou leur performance (Dall *et al.* 2005, Danchin *et al.* 2004, Doligez *et al.* 2002, Seppanen *et al.* 2007, Pärt *et al.* 2011). Cependant, la signification des informations sociales peut dépendre à la fois de facteurs individuels (par exemple la capacité compétitrice) et environnementaux (par exemple l'avancée de la saison), de telle sorte que les informations sociales pourraient devoir être utilisées d'une façon complexe, dépendant des conditions et du phénotype (Kurvers *et al.* 2010b, Loukola *et al.* 2012, Seppanen et Forsman 2007, Seppanen *et al.* 2011). De plus, en milieu naturel, de nombreuses sources d'informations peuvent être disponibles simultanément, avec des niveaux de fiabilité et d'accessibilité variés, et des contenus informatifs potentiellement contradictoires. Cette complexité suggère que les capacités cognitives individuelles pourraient jouer un rôle majeur dans la capacité à utiliser l'information de façon optimale lors de la prise de décision dans les populations naturelles. Ces capacités pourraient permettre aux individus de donner des priorités à différentes sources d'information en sélectionnant les plus fiables et/ou les moins coûteuses, de trier les informations les plus pertinentes, de collecter les informations aux meilleures échelles de temps et d'espace, de mettre à jour les informations et d'ajuster la signification des informations en fonction des conditions environnementales et du phénotype. Pour tester cette hypothèse, selon laquelle les performances cognitives permettraient de mieux utiliser les informations présentes dans l'environnement, une manipulation expérimentale d'une/des source(s) d'information sociale (Seppanen et Forsman 2007) serait nécessaire afin de vérifier si la capacité des individus à utiliser cette information dans le choix ultérieur de leur site de reproduction ou habitat est liée à leurs capacités cognitives. Une telle expérience serait une étape importante dans la compréhension des mécanismes qui sous-tendent la relation entre les capacités cognitives et succès de reproduction (et/ou de survie).

Enfin, les caractéristiques des espèces elles-mêmes pourraient façonner les variations interspécifiques des capacités cognitives. Chez le jardinier satiné (*Ptilonorhynchus violaceus*), les performances de résolution de problème sont positivement corrélées au succès d'appariement (Keagy *et al.* 2009, 2011). Mais chez une autre espèce très proche, le jardinier maculé (*Ptilonorhynchus maculatus*), les performances mesurées sur différentes tâches cognitives ne sont pas reliées au succès d'appariement (Isden *et al.* 2013). Bien que les tâches et protocoles utilisés diffèrent sensiblement entre les deux études, cette différence est surprenante : le jardinier maculé élabore des jardins et des parades plus complexes, et ces différences sont associées à une taille du

cerveau plus grande (Madden 2001); par conséquent on aurait pu prédire une relation plus forte entre les capacités cognitives et le succès d'appariement chez cette espèce par rapport au jardinier satiné. Or les résultats vont en sens inverse. De même, bien que les performances d'apprentissage soient reliées à la complexité du chant chez le diamant mandarin mâle (Boogert *et al.* 2008), seules les performances à une tâche d'inhibition de réflexe sont reliées au chant chez une autre espèce de passereau chanteur, le bruant chanteur (*Melospiza melodia*) (Boogert *et al.* 2011a). Pourquoi et comment les pressions de sélection sur les capacités cognitives varient-elles entre les espèces restent mal compris. Des études comparatives ont avancé des critères tels que le régime alimentaire (c'est à dire généraliste vs spécialiste; Overington *et al.* 2008, 2012), la propension à migrer (c'est à dire migrant vs résident; Mettke-Hofmann et Greenberg 2005, McGuire et Ratcliffe 2011) ou encore la socialité (par exemple la complexité des groupes sociaux; Reader et Laland 2002, Holekamp 2007, Emery *et al.* 2007) pour expliquer les variations interspécifiques des capacités cognitives (Shettleworth 2009). Il serait intéressant d'étudier les variations dans les pressions de sélection entre des espèces proches phylogénétiquement mais utilisant des niches écologiques différentes, ou entre des espèces différentes mais utilisant les mêmes niches écologiques, afin d'essayer d'identifier les facteurs responsables de la variation de la force de sélection et ainsi mieux comprendre le potentiel adaptatif, c.-à.-d la capacité à répondre aux pressions de sélection, des performances cognitives. « Ce n'est pas le plus fort de l'espèce qui survit, ni le plus intelligent. C'est celui qui sait le mieux s'adapter au changement », Charles Darwin (propos rapportés par Van Ommeren *et al.* 2009 dans *Collaboration in the cloud*, p. 67).

Une limite possible de ce travail consiste dans la méthode utilisée pour mesurer les performances cognitives. Les tests de résolution de problème, tels que la tâche utilisée tout au long de ce travail de doctorat, sont considérés comme des mesures opérationnelles de la capacité d'innovation (Auersperg *et al.* 2012, Webster et Lefebvre 2001). Cependant, comme ces tests diffèrent des tests cognitifs établis relevant du domaine de la psychologie, il a été avancé que les variations interindividuelles des performances de résolution de problème pourraient ne pas refléter des différences cognitives, mais plutôt être le résultat des différences physiques entre les individus, de variations au niveau de la motivation à résoudre la tâche ou d'autres comportements comme les réponses à la nouveauté. Bien que la majorité des études utilisent des tâches spécifiques adaptées aux capacités physiques des espèces étudiées, et que les variations phénotypiques mesurées alors soient corrigées par de nombreuses autres variables susceptibles d'interférer avec le processus

cognitif (comme la néophobie, la motivation etc.), on ne peut pas exclure la possibilité qu'un ou plusieurs autres facteurs inconnus viennent s'ajouter à la variation observée, comme pour tout autre comportement étudié. Puisqu'il n'a pas été démontré à ce jour que ces tests ne reflètent pas un processus cognitif, nos résultats restent un premier pas important dans la compréhension de l'évolution des performances cognitives au sein des populations naturelles. Développer des tests plus formels du point de vue du processus cognitif impliqué et applicables en milieu naturel sans que cela influence les traits d'histoire de vie mesurés est un défi pour les études futures (Auersperg *et al.* 2012).

Références bibliographiques :

- Airey, D. C., Castillo-Juarez, H., Casella, G., Pollak, E. J., DeVogd, T. J. (2000). Variation in the volume of zebra finch song control nuclei is heritable: developmental and evolutionary implications. *Proceedings of the Royal Society B-Biological Sciences*, 267(1457), 2099-2104.
- Airey, D. C., DeVogd, T. J. (2000). Greater song complexity is associated with augmented song system anatomy in zebra finches. *Neuroreport*, 11(10), 2339-2344. doi: 10.1097/00001756-200007140-00054
- Allander, K. (1997). Reproductive investment and parasite susceptibility in the great tit. *Functional Ecology*, 11(3), 358-364.
- Alonso-Alvarez, C., Perez-Rodriguez, L., Ester Ferrero, M., Garcia de-Blas, E., Casas, F., Mougeot, F. (2012). Adjustment of female reproductive investment according to male carotenoid-based ornamentation in a gallinaceous bird. *Behavioral Ecology and Sociobiology*, 66(5), 731-742. doi: 10.1007/s00265-012-1321-8
- Andersson, S., Ornborg, J., Andersson, M. (1998). Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society B-Biological Sciences*, 265(1395), 445-450.
- Andersson, S., Prager, M., Hill, G., McGraw, K. (2006). Quantifying colors (*Bird coloration* (Vol. 1, p. 41-89).
- Aplin, L. M., Sheldon, B. C., Morand-Ferron, J. (2013). Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, 85(6), 1225-1232. doi: <http://dx.doi.org/10.1016/j.anbehav.2013.03.009>
- Atkinson, C. T., van Riper III, C. (1991). Pathogenicity and epizootiology of avian haematozoa: Plasmodium, Leucocytozoon and Haemoproteus. *Bird-parasite interactions. Oxford University Press, Oxford*, 19-48.
- Auersperg, A. M. I., Gajdon, G. K., von Bayern, A. M. P. (2012). A new approach to comparing problem solving, flexibility and innovation. *Communicative and integrative biology*, 5(2), 140-145. doi: 10.4161/cib.18787
- Bangirana P., Idro R., John C.C., Boivin M.J. (2006). Rehabilitation for cognitive impairments after cerebral malaria in African children: strategies and limitations. *Tropical Medicine & International Health*, 11(9), 1341-1349. doi:10.1111/j.1365-3156.2006.01685.x

- Barba, E., Gildelgado, J. A., Monros, J. S. (1995). The Costs of Being Late - Consequences of Delaying Great Tit Parus-Major First Clutches. *Journal of Animal Ecology*, 64, 642-651.
- Barber, I., Dingemanse, N. J. (2010). Parasitism and the evolutionary ecology of animal personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4077-4088. doi: 10.1098/rstb.2010.0182
- Bell, A. M., Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10(9), 828-834. doi: 10.1111/j.1461-0248.2007.01081.x
- Benson-Amram, S., Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B-Biological Sciences*, 279(1744), 4087-4095. doi: 10.1098/rspb.2012.1450
- Benson-Amram, S., Weldele, M. L., Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour*, 85(2), 349-356. doi: 10.1016/j.anbehav.2012.11.003
- Bingman, V. P., Jones, T.-J. (1994). Sun compass-based spatial learning impaired in homing pigeons with hippocampal lesions. *The Journal of neuroscience*, 14(11), 6687-6694.
- Biondi, L. M., Bo, M. S., Vassallo, A. I. (2008). Experimental assessment of problem solving by *Milvago chimango* (Aves : Falconiformes). *Journal of Ethology*, 26(1), 113-118.
- Biondi, L. M., Bo, M. S., Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Animal Cognition*, 13(5), 701-710.
- Biro, P. A., Dingemanse, N. J. (2009). Sampling bias resulting from animal personality. *Trends in Ecology and Evolution*, 24, 66-67.
- Bize, P., Devevey, G., Monaghan, P., Doligez, B., Christophe, P. (2008). Fecundity and survival in relation to resistance to oxidative stress in a free-living bird. *Ecology*, 89(9), 2584-2593. doi: 10.1890/07-1135.1
- Blanchet, S., Thomas, F., Loot, G. (2009). Reciprocal effects between host phenotype and pathogens: new insights from an old problem. *Trends in Parasitology*, 25(8), 364-369. doi: 10.1016/j.pt.2009.05.005

- Blomqvist, D., Johansson, O. C., Gotmark, F. (1997). Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia*, 110(1), 18-24. doi: 10.1007/s004420050128
- Blount, J. D., Metcalfe, N. B., Birkhead, T. R., Surai, P. F. (2003). Carotenoid Modulation of Immune Function and Sexual Attractiveness in Zebra Finches. *Science*, 300(5616), 125-126. doi: 10.2307/3834315
- Bluff, L. A., Troscianko, J., Weir, A. A. S., Kacelnik, A., Rutz, C. (2010). Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society B-Biological Sciences*, 277, 1377-1385.
- Boesch, C. (2007). What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology*, 121(3), 227.
- Bókony, V., Lendvai, Á. Z., Vágási, C. I., Pătraș, L., Pap, P. L., Németh, J., . . . Seress, G. (2013). Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. *Behavioral Ecology*, art094.
- Bolhuis, J. J., Honey, R. C. (1998). Imprinting, learning and development: from behaviour to brain and back. *Trends in neurosciences*, 21(7), 306-311.
- Boogert, N. J., Anderson, R. C., Peters, S., Searcy, W. A., Nowicki, S. (2011a). Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. *Animal Behaviour*, 81(6), 1209-1216. doi: 10.1016/j.anbehav.2011.03.004
- Boogert, N. J., Fawcett, T. W., Lefebvre, L. (2011b). Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. *Behavioral Ecology*, 22(3), 447-459. doi: 10.1093/beheco/arq173
- Boogert, N. J., Giraldeau, L. A., Lefebvre, L. (2008). Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, 76, 1735-1741. doi: 10.1016/j.anbehav.2008.08.009
- Boogert, N. J., Monceau, K., Lefebvre, L. (2010). A field test of behavioural flexibility in *Zenaida* doves (*Zenaida aurita*). *Behavioural Processes*, 85(2), 135-141. doi: 10.1016/j.beproc.2010.06.020
- Boogert, N. J., Reader, S. M., Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, 72, 1229-1239. doi: 10.1016/j.anbehav.2006.02.021

- Both, C., Visser, M. E. (2000). Breeding territory size affects fitness: an experimental study on competition at the individual level. *Journal of Animal Ecology*, 69, 1021-1030.
- Bottjer, S. W., Miesner, E. A., Arnold, A. P. (1986). Changes in neuronal number, density and size account for increases in volume of song-control nuclei during song development in zebra finches. *Neuroscience Letters*, 67(3), 263-268. doi: [http://dx.doi.org/10.1016/0304-3940\(86\)90319-8](http://dx.doi.org/10.1016/0304-3940(86)90319-8)
- Bouchard, J., Goodyer, W., Lefebvre, L. (2007). Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, 10, 259-266.
- Boyer, N., Reale, D., Marmet, J., Pisanu, B., Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, 79(3), 538-547. doi: 10.1111/j.1365-2656.2010.01659.x
- Byrne, R. W., Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society B-Biological Sciences*, 271(1549), 1693-1699. doi: 10.1098/rspb.2004.2780
- Byrne, R., Whiten, A. (1989). *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford science publications.
- Cadiou, N., Fruchard, S., Cadiou, J. C. (2010). Innovative Individuals Are Not Always the Best Demonstrators: Feeding Innovation and Social Transmission in *Serinus canaria*. *Plos One*, 5(1). doi: 10.1371/journal.pone.0008841
- Cantalapiedra, J. L., FitzJohn, R. G., Kuhn, T. S., Fernández, M. H., DeMiguel, D., Azanza, B., . . . Mooers, A. Ø. (2014). Dietary innovations spurred the diversification of ruminants during the Caenozoic. *Proceedings of the Royal Society B: Biological Sciences*, 281(1776). doi: 10.1098/rspb.2013.2746
- Carere, C., Drent, P. J., Koolhaas, J. M., Ton, G. G. G. (2005). Epigenetic Effects on Personality Traits: Early Food Provisioning and Sibling Competition. *Behaviour*, 142(9/10), 1329-1355. doi: 10.2307/4536303
- Carlier, P., Lefebvre, L. (1996). Differences in individual learning between group-foraging and territorial *Zenaidura macroura* doves. *Behaviour*, 1197-1207.
- Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, 320(5877), 800-803. doi: 10.1126/science.1157174

- Chiappe, D., MacDonald, K. (2005). The Evolution of Domain-General Mechanisms in Intelligence and Learning. *The Journal of General Psychology*, 132(1), 5-40. doi: 10.3200/GENP.132.1.5-40
- Clayton, N. S., Dally, J. M., Emery, N. J. (2007). Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362(1480), 507-522. doi: 10.1098/rstb.2006.1992
- Clutton-Brock, T. (2007). Sexual Selection in Males and Females. *Science*, 318(5858), 1882-1885. doi: 10.1126/science.1133311
- Cole, E. F., Cram, D. L., Quinn, J. L. (2011). Individual variation in spontaneous problem-solving performance among wild great tits. *Animal Behaviour*, 81(2), 491-498. doi: 10.1016/j.anbehav.2010.11.025
- Cole, E. F., Morand-Ferron, J., Hinks, A. E., Quinn, J. L. (2012). Cognitive ability influences reproductive life history variation in the wild. *Current biology : CB*, 22(19), 1808-1812. doi: 10.1016/j.cub.2012.07.051
- Cole, E. F., Quinn, J. L. (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 279(1731), 1168-1175. doi: 10.1098/rspb.2011.1539
- Cote, J., Dreiss, A., Clobert, J. (2008). Social personality trait and fitness. *Proceedings of the Royal Society B: Biological Sciences*, 275(1653), 2851-2858.
- Cresswell, W., McCleery, R. (2003). How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology*, 72, 356-366.
- Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20(4), 187-193. doi: 10.1016/j.tree.2005.01.010
- Danchin, E., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B., Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics*, 12(7), 475-486. doi: 10.1038/nrg3028
- Danchin, E., Giraldeau, L. A., Valone, T. J., Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, 305(5683), 487-491. doi: 10.1126/science.1098254

- Deary, I. J., Johnson, W., Houlihan, L. M. (2009). Genetic foundations of human intelligence. *Human Genetics*, 126(1), 215-232. doi: 10.1007/s00439-009-0655-4
- Devoogd, T. J., Krebs, J. R., Healy, S. D., Purvis, A. (1993). Relations between Song Repertoire Size and the Volume of Brain Nuclei Related to Song: Comparative Evolutionary Analyses amongst Oscine Birds. *Proceedings: Biological Sciences*, 254(1340), 75-82. doi: 10.2307/49665
- Dingemanse, N. J., Both, C., Drent, P. J., Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271(1541), 847-852.
- Doligez, B., Cadet, C., Danchin, E., Boulinier, T. (2003). When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour*, 66, 973-988. doi: 10.1006/anbe.2002.2270
- Doligez, B., Danchin, E., Clobert, J. (2002). Public information and breeding habitat selection in a wild bird population. *Science*, 297(5584), 1168-1170. doi: 10.1126/science.1072838
- Doligez, B., Danchin, E., Clobert, J., Gustafsson, L. (1999). The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology*, 68(6), 1193-1206. doi: 10.1046/j.1365-2656.1999.00362.x
- Doligez, B., Pärt, T. (2008). Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *Journal of Animal Ecology*, 77(6), 1199-1211. doi: 10.1111/j.1365-2656.2008.01446.x
- Doligez, B., Pärt, T., Danchin, E. (2004). Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? *Animal Behaviour*, 67, 457-466. doi: 10.1016/j.anbehav.2003.03.010
- Doucet, S. M. (2002). Structural plumage coloration, male body size and condition in the Blue-Black Grassquit. *Condor*, 104(1), 30-38. doi: 10.1650/0010-5422(2002)104[0030:spcmbs]2.0.co;2
- Doucet, S. M., Meadows, M. G. (2009). Iridescence: a functional perspective. *Journal of the Royal Society Interface*, 6, S115-S132. doi: 10.1098/rsif.2008.0395.focus

- Doucet, S. M., Mennill, D. J., Montgomerie, R., Boag, P. T., Ratcliffe, L. M. (2005). Achromatic plumage reflectance predicts reproductive success in male black-capped chickadees. *Behavioral Ecology*, 16(1), 218-222. doi: 10.1093/beheco/arh154
- Doucet, S. M., Montgomerie, R. (2003). Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behavioral Ecology*, 14(4), 503-509. doi: 10.1093/beheco/arg035
- Doutrelant, C., Gregoire, A., Grnac, N., Gomez, D., Lambrechts, M. M., Perret, P. (2008). Female coloration indicates female reproductive capacity in blue tits. *Journal of Evolutionary Biology*, 21(1), 226-233. doi: 10.1111/j.1420-9101.2007.01451.x
- Dukas, R. (1999). Costs of memory: ideas and predictions. *Journal of Theoretical Biology*, 197, 41-50.
- Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution and Systematics*, 347-374.
- Dukas, R. (2013). Effects of learning on evolution: robustness, innovation and speciation. *Animal Behaviour*, 85(5), 1023-1030. doi: 10.1016/j.anbehav.2012.12.030
- Dukas, R., Duan, J. J. (2000). Potential fitness consequences of associative learning in a parasitoid wasp. *Behavioral Ecology*, 11(5), 536-543. doi: 10.1093/beheco/11.5.536
- Dunbar, R. I. M. (1995). Neocortex size and group-size in primates - a test of the hypothesis. *Journal of Human Evolution*, 28(3), 287-296. doi: 10.1006/jhev.1995.1021
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 6(5), 178-190. doi: 10.1002/(sici)1520-6505(1998)6:5<178::aid-evan5>3.0.co;2-8
- Dunn, J. C., Cole, E. F., Quinn, J. L. (2011). Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits. *Behavioral Ecology and Sociobiology*, 65(7), 1459-1471. doi: 10.1007/s00265-011-1156-8
- Eisenberg, J. F., Don, E. W. (1978). Relative Brain Size and Feeding Strategies in the Chiroptera. *Evolution*, 32(4), 740-751. doi: 10.2307/2407489
- Emery, N. J., Dally, J. M., Clayton, N. S. (2004). Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal cognition*, 7(1), 37-43.

- Emery, N. J., Seed, A. M., von Bayern, A. M. P., Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362(1480), 489-505. doi: 10.1098/rstb.2006.1991
- Ens, B. J., Kersten, M., Brenninkmeijer, A., Hulscher, J. B. (1992). Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, 61, 703-715.
- Eraud, C., Duriez, O., Chastel, O., Faivre, B. (2005). The energetic cost of humoral immunity in the Collared Dove, *Streptopelia decaocto*: is the magnitude sufficient to force energy-based trade-offs? *Functional Ecology*, 19(1), 110-118. doi: 10.1111/j.0269-8463.2005.00934.x
- Estók, P., Zsebök, S., Siemers, B. M. (2010). Great tits search for, capture, kill and eat hibernating bats. *Biology letters*, 6(1), 59-62.
- Evans, S. R., Hinks, A. E., Wilkin, T. A., Sheldon, B. C. (2010). Age, sex and beauty: methodological dependence of age- and sex-dichromatism in the great tit *Parus major*. *Biological Journal of the Linnean Society*, 101(4), 777-796. doi: 10.1111/j.1095-8312.2010.01548.x
- Fairbairn, D. J., Reeves, J. P. (2001). Natural selection. In: *Evolutionary Ecology* (Ed. by D. A. Roff and D. J. Fairbairn), pp. 29-43. Oxford: Oxford University Press.
- Figuerola, J., Senar, J. C. (2005). Seasonal changes in carotenoid- and melanin-based plumage coloration in the Great Tit *Parus major*. *Ibis*, 147(4), 797-802. doi: 10.1111/j.1474-919x.2005.00461.x
- Fisher, J., Hinde, R. (1949). The opening of milk bottles by birds. *British Birds* 42, 347-357.
- Fitze, P. S., Tschirren, B., Richner, H. (2004). Life history and fitness consequences of ectoparasites. *Journal of Animal Ecology*, 73(2), 216-226. doi: 10.1111/j.0021-8790.2004.00799.x
- Forslund, P., Pärt, T. (1995). Age and reproduction in birds - hypotheses and tests. *Trends in Ecology & Evolution*, 10(9), 374-378. doi: 10.1016/s0169-5347(00)89141-7
- Forstmeier, W., Burger, C., Temnow, K., Deregnaucourt, S. (2009). The genetic basis of Zebra Finch vocalizations. *Evolution*, 63(8), 2114-2130. doi: 10.1111/j.1558-5646.2009.00688.x
- Funk, M. S., Matteson, R. L. (2004). Stable individual differences on developmental tasks in young yellow-crowned parakeets, *Cyanoramphus auriceps*. *Learning and Behavior*, 32(4), 427-439.

- Gajdon, G. K., Fijn, N., Huber, L. (2006). Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Animal Cognition*, 9(3), 173-181.
- Galef, B. G. (2003). Social learning: promoter or inhibitor of innovation (*Animal innovation* (p. 137-152).
- Galef, B. G., Laland, K. N. (2005). Social Learning in Animals: Empirical Studies and Theoretical Models. *BioScience*, 55(6), 489-499. doi: 10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2
- Galsworthy, M. J., Paya-Cano, J. L., Liu, L., Monleon, S., Gregoryan, G., Fernandes, C., . . . Plomin, R. (2005). Assessing reliability, heritability and general cognitive ability in a battery of cognitive tasks for laboratory mice. *Behavior Genetics*, 35(5), 675-692. doi: 10.1007/s10519-005-3423-9
- Galvan, I. (2010). Plumage coloration can be perceived as a multiple condition-dependent signal by Great Tits *Parus major*. *Ibis*, 152(2), 359-367.
- Galvan, I. (2011). Feather microstructure predicts size and colour intensity of a melanin-based plumage signal. *Journal of Avian Biology*, 42(6), 473-479. doi: 10.1111/j.1600-048X.2011.05533.x
- Garamszegi, L. Z., Erritzoe, J., Møller, A. P. (2007). Feeding innovations and parasitism in birds. *Biological Journal of the Linnean Society*, 90, 441-455.
- Garcia-Navas, V., Sanz, J. J. (2010). Flexibility in the Foraging Behavior of Blue Tits in Response to Short-Term Manipulations of Brood Size. *Ethology*, 116, 744-754.
- Gegear, R. J., Otterstatter, M. C., Thomson, J. D. (2006). Bumble-bee foragers infected by a gut parasite have an impaired ability to utilize floral information. *Proceedings of the Royal Society B-Biological Sciences*, 273(1590), 1073-1078. doi: 10.1098/rspb.2005.3423 1471-2954
- Godfrey-Smith, P. (2002). Environmental complexity and the evolution of cognition. *The evolution of intelligence*, 233-249.
- Gosler, A. G. (1993). *The Great Tit*. Paul Hamlyn, London.
- Gould, S. J. (1996). *The mismeasure of man*. WW Norton and Company.
- Grant, B. R., Grant, P. R. (1996). High survival of Darwin's finch hybrids: Effects of beak morphology and diets. *Ecology*, 77(2), 500-509.

- Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. Dans S. M. Reader and K. N. Laland (dir.), *Animal innovation* (p. 175-196). New York, NY, US: Oxford University Press.
- Grieco, F., van Noordwijk, A. J., Visser, M. E. (2002). Evidence for the Effect of Learning on Timing of Reproduction in Blue Tits. *Science*, 296(5565), 136-138. doi: 10.1126/science.1068287
- Griffin, A. S., Lermite, F., Perea, M., Guez, D. (2013). To innovate or not: contrasting effects of social groupings on safe and risky foraging in Indian mynahs. *Animal Behaviour*(0). doi: <http://dx.doi.org/10.1016/j.anbehav.2013.09.035>
- Griffith, S. C., Parker, T. H., Olson, V. A. (2006). Melanin-versus carotenoid-based sexual signals: is the difference really so black and red? *Animal Behaviour*, 71(4), 749-763.
- Gustafsson, L., Nordling, D., andersson, M. S., Sheldon, B. C., Qvarnstrom, A. (1994). Infectious-diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 346(1317), 323-331. doi: 10.1098/rstb.1994.0149
- Hampton, R. R., Shettleworth, S. J. (1996). Hippocampal lesions impair memory for location but not color in passerine birds. *Behavioral neuroscience*, 110(4), 831.
- Healy, S. D., Bacon, I. E., Haggis, O., Harris, A. P., Kelley, L. A. (2009). Explanations for variation in cognitive ability: Behavioural ecology meets comparative cognition. *Behavioural Processes*, 80(3), 288-294.
- Healy, S. D., Rowe, C. (2007). A critique of comparative studies of brain size. *Proceedings of the Royal Society B-Biological Sciences*, 274(1609), 453-464.
- Heeb, P., Schwander, T., Faoro, S. (2003). Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Animal Behaviour*, 66, 637-642.
- Hegyí, G., Szigeti, B., Toeroek, J., Eens, M. (2007). Melanin, carotenoid and structural plumage ornaments: information content and role in great tits *Parus major*. *Journal of Avian Biology*, 38(6), 698-708. doi: 10.1111/j.2007.0908-8857.04075.x
- Hegyí, G., Torok, J., Toth, L., Garamszegi, L. Z., Rosivall, B. (2006). Rapid temporal change in the expression and age-related information content of a sexually selected trait. *Journal of Evolutionary Biology*, 19(1), 228-238. doi: 10.1111/j.1420-9101.2005.00970.x

- Helfenstein, F., Losdat, S., Møller, A. P., Blount, J. D., Richner, H. (2010). Sperm of colourful males are better protected against oxidative stress. *Ecology Letters*, *13*(2), 213-222. doi: 10.1111/j.1461-0248.2009.01419.x
- Henderson, L. J., Heidinger, B. J., Evans, N. P., Arnold, K. E. (2013). Ultraviolet crown coloration in female blue tits predicts reproductive success and baseline corticosterone. *Behavioral Ecology*. doi: 10.1093/beheco/art066
- Hill, G. E. (1991). Plumage coloration is a sexually selected indicator of male quality. *Nature*, *350*(6316), 337-339.
- Hill, G. E., Doucet, S. M., Buchholz, R. (2005). The effect of coccidial infection on iridescent plumage coloration in wild turkeys. *Animal Behaviour*, *69*, 387-394. doi: 10.1016/j.anbehav.2004.03.013
- Hill, G. E., McGraw, K. J. (2006). *Bird coloration: Mechanisms and measurements*. Cambridge, MA [etc.]: Harvard University Press.
- Holekamp, K. E. (2007). Questioning the social intelligence hypothesis. *Trends in Cognitive Sciences*, *11*(2), 65-69. doi: <http://dx.doi.org/10.1016/j.tics.2006.11.003>
- Hollander, F. A., Van Overveld, T., Tokka, I., Matthysen, E. (2008). Personality and nest defence in the great tit (*Parus major*). *Ethology*, *114*(4), 405-412.
- Holmes, R. T., Marra, P. P., Sherry, T. W. (1996). Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): Implications for population dynamics. *Journal of Animal Ecology*, *65*(2), 183-195. doi: 10.2307/5721
- Hunt, G. R. (2000). Tool use by the New Caledonian crow *Corvus moneduloides* to obtain *Cerambycidae* from dead wood. *Emu*, *100*, 109-114.
- Isden, J., Panayi, C., Dingle, C., Madden, J. (2013). Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. *Animal Behaviour*(0). doi: <http://dx.doi.org/10.1016/j.anbehav.2013.07.024>
- Ishii, Y., Shimada, M. (2012). Learning predator promotes coexistence of prey species in host-parasitoid systems. *Proceedings of the National Academy of Sciences*, *109*(13), 5116-5120. doi: 10.1073/pnas.1115133109
- Isler, K., van Schaik, C. (2006). Costs of encephalization: the energy trade-off hypothesis tested on birds. *Journal of Human Evolution*, *51*(3), 228-243.

- Iwaniuk, A. N., Nelson, J. E. (2003). Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 81, 1913-1928.
- Jacobs, L. F., Gaulin, S. J., Sherry, D. F., Hoffman, G. E. (1990). Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Sciences*, 87(16), 6349-6352. doi: 10.1073/pnas.87.16.6349
- Jacquín, L., Récapet, C., Bouche, P., Leboucher, G., Gasparini, J. (2012). Melanin-based coloration reflects alternative strategies to cope with food limitation in pigeons. *Behavioral Ecology*. doi: 10.1093/beheco/ars055
- Jarvi, T., Bakken, M. (1984). The function of the variation in the breast stripe of the great tit (*parus major*). *Animal Behaviour*, 32(MAY), 590-596. doi: 10.1016/s0003-3472(84)80296-1
- Jaumann, S., Scudelari, R., Naug, D. (2013). Energetic cost of learning and memory can cause cognitive impairment in honeybees. *Biology Letters*, 9(4). doi: 10.1098/rsbl.2013.0149
- Jenni, L., Winkler, R. (1994). Moults and ageing of European passerines. Academic Press, London.
- Jerison, H. J., Barlow, H. B. (1985). Animal Intelligence as Encephalization [and Discussion]. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 308(1135), 21-35. doi: 10.2307/2396281
- Johnston, T.D., Rosenblatt, J.S., Hinde, R., Beer, C., M-C, B. (1982). Selective Costs and Benefits in the Evolution of Learning, *Advances in the Study of Behavior*, Academic Press, pp. 65-106.
- Kavaliers, M., Colwell, D. D., Galea, L. A. M. (1995). Parasitic infection impairs spatial learning in mice. *Animal Behaviour*, 50(1), 223-229. doi: 10.1006/anbe.1995.0234
- Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, 6(1), 1-30.
- Keagy, J., Savard, J. F., Borgia, G. (2009). Male satin bowerbird problem-solving ability predicts mating success. *Animal Behaviour*, 78(4), 809-817.
- Keagy, J., Savard, J. F., Borgia, G. (2011). Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*. *Animal Behaviour*, 81(5), 1063-1070. doi: 10.1016/j.anbehav.2011.02.018
- Kershaw, W., Leytham, G., Dickerson, G. (1959). The effect of schistosomiasis on animal intelligence. *Annals of tropical medicine and parasitology*, 53, 504.

- Kihara, M., Carter, J. A., Newton, C. (2006). The effect of Plasmodium falciparum on cognition: a systematic review. *Tropical Medicine and International Health*, 11(4), 386-397. doi: 10.1111/j.1365-3156.2006.01579.x
- Knowles, S. C. L., Palinauskas, V., Sheldon, B. C. (2010). Chronic malaria infections increase family inequalities and reduce parental fitness: experimental evidence from a wild bird population. *Journal of Evolutionary Biology*, 23(3), 557-569. doi: 10.1111/j.1420-9101.2009.01920.x
- Kraaijeveld, K., Kraaijeveld-Smit, F. J. L., Komdeur, J. (2007). The evolution of mutual ornamentation. *Animal Behaviour*, 74(4), 657-677. doi: <http://dx.doi.org/10.1016/j.anbehav.2006.12.027>
- Kummer, H., Goodall, J. (1985). Conditions of Innovative Behavior in Primates. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 308(1135), 203-214.
- Kurvers, R. H. J. M., Delhey, K., Roberts, M.L., Peters, A. (2010a). No consistent female preference for higher crown UV reflectance in Blue Tits *Cyanistes caeruleus*: a mate choice experiment. *Ibis* 152, 393-396.
- Kurvers, R. H. J. M., van Oers, K., Nolet, B. A., Jonker, R. M., van Wieren, S. E., Prins, H. H. T., Ydenberg, R. C. (2010b). Personality predicts the use of social information. *Ecology Letters*, 13(7), 829-837. doi: 10.1111/j.1461-0248.2010.01473.x
- Laland, K. N., Reader, S. M. (1999). Foraging innovation in the guppy. *Animal Behaviour*, 57, 331-340.
- Laughlin, S. B., van Steveninck, R. R. d. R., Anderson, J. C. (1998). The metabolic cost of neural information. *Nature neuroscience*, 1(1), 36-41.
- Leal, M., Powell, B. J. (2011). Behavioural flexibility and problem-solving in a tropical lizard. *Biology Letters*, 8, 28-30. doi: 10.1098/rsbl.2011.0480
- Lee, P. C. (1991). Adaptations to environmental change: an evolutionary perspective (*Primate responses to environmental change* (p. 39-56): Springer.
- Lefebvre, L. (1995). Culturally-transmitted feeding behaviour in primates: evidence for accelerating learning rates. *Primates*, 36(2), 227-239.
- Lefebvre, L. (2011). Taxonomic counts of cognition in the wild. *Biology Letters*, 7, 631-633.

- Lefebvre, L. (2013). Brains, innovations, tools and cultural transmission in birds, non-human primates and fossil hominins. *Frontiers in Human Neuroscience*, 7. doi: 10.3389/fnhum.2013.00245
- Lefebvre, L., Sol, D. (2008). Brains, Lifestyles and Cognition: Are There General Trends? *Brain, Behavior and Evolution*, 72(2), 135-144.
- Lefebvre, L., Whittle, P., Lascaris, E., Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour*, 53, 549-560.
- Lendvai, Á. Z., Bókonyi, V., Angelier, F., Chastel, O., Sol, D. (2013). Do smart birds stress less? An interspecific relationship between brain size and corticosterone levels. *Proceedings of the Royal Society B: Biological Sciences*, 280(1770). doi: 10.1098/rspb.2013.1734
- Lendvai, A. Z., Giraudeau, M., Chastel, O. (2007). Reproduction and modulation of the stress response: an experimental test in the house sparrow. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 391-397. doi: 10.1098/rspb.2006.3735
- Lessels, C. M., Boag, P. T. (1987). Unrepeatable repeatabilities: a common mistake. *Auk*, 104, 116-121.
- Levine, N. D. (1988). *The protozoan phylum Apicomplexa. Volume I. Volume II*. CRC Press, Inc.
- Liker, A., Bokonyi, V. (2009). Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences of the United States of America*, 106(19), 7893-7898.
- Lima, S. L. (2009). Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, 84(3), 485-513.
- Linden, M., Gustafsson, L., Pärt, T. (1992). Selection on fledging mass in the Collared Flycatcher and the Great Tit. *Ecology*, 73(1), 336-343. doi: 10.2307/1938745
- Loukola, O. J., Seppanen, J.-T., Forsman, J. T. (2012). Intraspecific social information use in the selection of nest site characteristics. *Animal Behaviour*, 83(3), 629-633. doi: 10.1016/j.anbehav.2011.12.004
- Lubjuhn, T., Strohbach, S., Brun, J., Gerken, T., Epplen, J. T. (1999). Extra-pair paternity in great tits (*Parus major*) - A long term study. *Behaviour*, 136, 1157-1172.
- MacDougall, A., Montgomerie, R. (2003). Assortative mating by carotenoid-based plumage colour: a quality indicator in American goldfinches, *Carduelis tristis*. *Naturwissenschaften*, 90(10), 464-467. doi: 10.1007/s00114-003-0459-7

- Madden, J. (2001). Sex, bowers and brains. *Proceedings of the Royal Society B-Biological Sciences*, 268(1469), 833-838.
- Martin, T. E. (1995). Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, 65(1), 101-127. doi: 10.2307/2937160
- Martínez-de la Puente, J., Merino, S., Tomás, G., Moreno, J., Morales, J., Lobato, E., . . . Belda, E. J. (2010). The blood parasite *Haemoproteus* reduces survival in a wild bird: a medication experiment. *Biology Letters*, 6(5), 663-665. doi: 10.1098/rsbl.2010.0046
- Marzal, A., Bensch, S., Reviriego, M., Balbontin, J., De Lope, F. (2008). Effects of malaria double infection in birds: one plus one is not two. *Journal of evolutionary biology*, 21(4), 979-987.
- Marzal, A., De Lope, F., Navarro, C., Møller, A. P. (2005). Malarial parasites decrease reproductive success: an experimental study in a passerine bird. *Oecologia*, 142(4), 541-545. doi: 10.1007/s00442-004-1757-2
- Marzal A., Ricklefs R.E., Valkiunas G., Albayrak T., Arriero E., Bonneaud C., Czirjak G.A., Ewen J., Hellgren O., Horakova D., *et al.* (2011). Diversity, Loss and Gain of Malaria Parasites in a Globally Invasive Bird. *PLoS One* 6(7). doi:10.1371/journal.pone.0021905
- Mateos-Gonzalez, F., Quesada, J., Senar, J. C. (2011). Sexy birds are superior at solving a foraging problem. *Biology Letters*, 7(5), 668-669. doi: 10.1098/rsbl.2011.0163
- McGraw, K. J. (2006). Mechanics of Melanin-Based Coloration. *Bird Coloration: Function and evolution*, 2, 243.
- McGraw, K. J., Ardia, D. R. (2003). Carotenoids, Immunocompetence and the Information Content of Sexual Colors: An Experimental Test. *The American Naturalist*, 162(6), 704-712. doi: 10.1086/378904
- McGuire, L. P., Ratcliffe, J. M. (2011). Light enough to travel: migratory bats have smaller brains, but not larger hippocampi, than sedentary species. *Biology Letters*, 7(2), 233-236. doi: 10.1098/rsbl.2010.0744
- Mennill, D. J., Doucet, S. M., Montgomerie, R., Ratcliffe, L. M. (2003). Achromatic color variation in black-capped chickadees, *Poecile atricapilla*: black and white signals of sex and rank. *Behavioral Ecology and Sociobiology*, 53(6), 350-357. doi: 10.1007/s00265-003-0581-8
- Merino, S., Moreno, J., Sanz, J. J., Arriero, E. (2000). Are avian blood parasites pathogenic in the wild? A medication experiment in blue tits (*Parus caeruleus*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1461), 2507-2510. doi: 10.1098/rspb.2000.1312

- Mery, F., Kawecki, T.J. (2003). A fitness cost of learning ability in *Drosophila melanogaster*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 2465-2469.
- Mery, F., Kawecki, T. J. (2004). The effect of learning on experimental evolution of resource preference in *Drosophila melanogaster*. *Evolution*, 58, 757-767.
- Mery, F., Kawecki, T.J. (2005). A cost of long-term memory in *Drosophila*. *Science*, 308, 1148-1148.
- Mettke-Hofmann, C., Greenberg, R. (2005). Behavioral and cognitive adaptations to long-distance migration. *Birds of two worlds. Johns Hopkins University Press, Baltimore*, 114-123.
- Milinski, M., Barnard, C., Behnke, J. (1990). Parasites and host decision-making. *Parasitism and host behaviour*, 95-116.
- Møller, A. P. (2009). Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, 159(4), 849-858.
- Møller, A. P., Biard, C., Blount, J. D., Houston, D. C., Ninni, P., Saino, N., Surai, P. F. (2000). Carotenoid-dependent signals: Indicators of foraging efficiency, immunocompetence or detoxification ability? *Avian and Poultry Biology Reviews*, 11(3), 137-159.
- Molyneux, D., Cooper, J., Smith, W. (1983). Studies on the pathology of an avian trypanosome (*T. bouffardi*) infection in experimentally infected canaries. *Parasitology*, 87(01), 49-54.
- Monrós, J. S., Belda, E. J., Barba, E. (2002). Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos*, 99(3), 481-488.
- Montgomerie, R. (2006). Analyzing colors. *Bird coloration*, 1, 90-147.
- Montgomerie, R. (2008). CLR: colour analysis programs. v1: Kingston, ON, Queen's University, Canada.
- Montgomerie, R. D., Weatherhead, P. J. (1988). Risks and rewards of nest defense by parent birds. *Quarterly Review of Biology*, 63(2), 167-187. doi: 10.1086/415838
- Moore J. (2002). *Parasites and the behavior of animals*, Oxford University Press.
- Morand-Ferron, J., Cole, E. F., Rawles, J. E. C., Quinn, J. L. (2011). Who are the innovators? A field experiment with 2 passerine species. *Behavioral Ecology*, 22, 1241-1248.
- Morand-Ferron, J., Quinn, J. L. (2011). Larger groups of passerines are more efficient problem solvers in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, 108(38), 15898-15903. doi: 10.1073/pnas.1111560108

- Naef-Daenzer, B., Keller, L. F. (1999). The foraging performance of great and blue tits (*Parus major* and *P-caerulens*) in relation to caterpillar development and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology*, 68, 708-718.
- Naef-Daenzer, B., Widmer, F., Nuber, M. (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, 70(5), 730-738. doi: 10.1046/j.0021-8790.2001.00533.x
- Neisser, U. (1997). Rising Scores on Intelligence Tests Test scores are certainly going up all over the world, but whether intelligence itself has risen remains controversial. *American scientist*, 85(5), 440-447.
- Neisser, U., Boodoo, G., Bouchard Jr, T. J., Boykin, A. W., Brody, N., Ceci, S. J., . . . Sternberg, R. J. (1996). Intelligence: Knowns and unknowns. *American psychologist*, 51(2), 77.
- Nicolakakis, N., Lefebvre, L. (2000). Forebrain size and innovation rate in European birds: Feeding, nesting and confounding variables. *Behaviour*, 137, 1415-1429. doi: 10.1163/156853900502646
- Nicolakakis, N., Sol, D., Lefebvre, L. (2003). Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour*, 65, 445-452.
- Nokes, C., Grantham-McGregor, S. M., Sawyer, A., Cooper, E. S., Robinson, B. A., Bundy, D. A. (1992). Moderate to heavy infections of *Trichuris trichiura* affect cognitive function in Jamaican school children. *Parasitology*, 104(03), 539-547.
- Norris, K. (1990). Female choice and the quality of parental care in the great tit *Parus major*. *Behavioral Ecology and Sociobiology*, 27(4), 275-281.
- Nottebohm, F., Stokes, T. M., Leonard, C. M. (1976). Central control of song in the canary, *Serinus canarius*. *Journal of Comparative Neurology*, 165(4), 457-486.
- Nowicki, S., Searcy, W. A. (2005). Song and mate choice in birds: how the development of behavior helps us understand function. *The Auk*, 122(1), 1-14.
- Nowicki, S., Searcy, W. A. (2011). Are better singers smarter? *Behavioral Ecology*, 22(1), 10-11.
- Nowicki, S., Searcy, W. A., Peters, S. (2002). Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis". *Journal of Comparative Physiology A*, 188(11-12), 1003-1014.

- Olson, L. J., Rose, J. E. (1966). Effect of *Toxocara canis* infection on the ability of white rats to solve maze problems. *Experimental Parasitology*, 19(1), 77-84. doi: 10.1016/0014-4894(66)90055-5
- Overington, S. E., Cauchard, L., Cote, K.-A., Lefebvre, L. (2011a). Innovative foraging behaviour in birds: What characterizes an innovator? *Behavioural Processes*, 87(3), 274-285. doi: 10.1016/j.beproc.2011.06.002
- Overington, S. E., Cauchard, L., Morand-Ferron, J., Lefebvre, L. (2009a). Innovation in groups: does the proximity of others facilitate or inhibit performance? *Behaviour*, 146, 1543-1564.
- Overington, S. E., Dubois, F., Lefebvre, L. (2008). Food unpredictability drives both generalism and social foraging: a game theoretical model. *Behavioral Ecology*, 19(4), 836-841.
- Overington, S. E., Griffin, A. S., Sol, D., Lefebvre, L. (2011b). Are innovative species ecological generalists? A test in North American birds. *Behavioral Ecology*, 22(6), 1286-1293. doi: 10.1093/beheco/arr130
- Overington, S. E., Morand-Ferron, J., Boogert, N. J., Lefebvre, L. (2009b). Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour*, 78(4), 1001-1010. doi: 10.1016/j.anbehav.2009.06.033
- Parker, T., Wilkin, T., Barr, I., Sheldon, B., Rowe, L., Griffith, S. (2011). Fecundity selection on ornamental plumage colour differs between ages and sexes and varies over small spatial scales. *Journal of Evolutionary Biology*, 24(7), 1584-1597.
- Pärt, T., Arlt, D., Doligez, B., Low, M., Qvarnström, A. (2011). Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. *Journal of Animal Ecology*, 80(6), 1227-1235.
- Partali, V., Liaaenjensen, S., Slagsvold, T., Lifjeld, J. T. (1987). Carotenoids in food-chain studies. 2. The food-chain of *Parus* spp monitored by carotenoid analysis. *Comparative Biochemistry and Physiology B-Biochemistry and Molecular Biology*, 87(4), 885-888. doi: 10.1016/0305-0491(87)90408-1
- Patterson, E. M., Mann, J. (2011). The Ecological Conditions That Favor Tool Use and Innovation in Wild Bottlenose Dolphins (*Tursiops* sp.). *Plos One*, 6(7). doi: 10.1371/journal.pone.0022243
- Pavlov, I. P. (1927). *Conditioned reflexes*. DoverPublications. com.
- Perez-Tris J., Hasselquist D., Hellgren O., Krizanauskiene A., Waldenstrom J., Bensch S. (2005). What are malaria parasites? *Trends in Parasitology*, 21(5), 209-211. doi:10.1016/j.pt.2005.03.001

- Perrins, C. M., McCleery, R. H. (1985). The Effect of Age and Pair Bond on the Breeding Success of Great Tits *Parus-Major*. *Ibis*, 127 Conditions That Favor Tool Use and Innovation in Wild Bottlenose Dolphins (*Tursiops* sp.), 306-315.
- Perrins, C. M., McCleery, R. H. (1989). Laying Dates and Clutch Size in the Great Tit. *Wilson Bulletin*, 101, 236-253
- Pettifor, R. A., Perrins, C. M., McCleery, R. H. (1988). Individual Optimization of Clutch Size in Great Tits. *Nature*, 336, 160-162.
- Pfaff, J. A., Zanette, L., MacDougall-Shackleton, S. A., MacDougall-Shackleton, E. A. (2007). Song repertoire size varies with HVC volume and is indicative of male quality in song sparrows (*Melospiza melodia*). *Proceedings of the Royal Society B-Biological Sciences*, 274(1621), 2035-2040. doi: 10.1098/rspb.2007.0170
- Pfeffer, K., Fritz, J., Kotrschal, K. (2002). Hormonal correlates of being an innovative greylag goose, *Anser anser*. *Animal Behaviour*, 63(4), 687-695. doi: 10.1006/anbe.2001.1949
- Poulin R. (2013). Parasite manipulation of host personality and behavioural syndromes. *Journal of Experimental Biology*, 216(1), 18-26. doi:10.1242/jeb.073353
- Preston, S. D., Jacobs, L. F. (2001). Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. *Behavioral Ecology*, 12(5), 517-523.
- Prum, R. O. (2006). Anatomy, physics and evolution of structural colors. *Bird coloration*, 1, 295-353.
- Quesada, J., Senar, J. C. (2006). Comparing plumage colour measurements obtained directly from live birds and from collected feathers: the case of the great tit *Parus major*. *Journal of Avian Biology*, 37(6), 609-616. doi: 10.1111/j.0908-8857.2006.03636.x
- Quesada, J., Senar, J. C. (2007). The role of melanin- and carotenoid-based plumage coloration in nest defence in the Great Tit. *Ethology*, 113(7), 640-647. doi: 10.1111/j.1439-0310.2007.01364.x
- Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A., Sheldon, B. C. (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology*, 78(6), 1203-1215. doi: 10.1111/j.1365-2656.2009.01585.x
- Ramsey, G., Bastian, M. L., van Schaik, C. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, 30(04), 393-407.

- Range, F., Bugnyar, T., Schloegl, C., Kotrschal, K. (2006). Individual and sex differences in learning abilities of ravens. *Behavioural Processes*, 73(1), 100-106.
- Reader, S. M., Hager, Y., Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1017-1027.
- Reader, S. M., Laland, K. N. (2002). Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, 99(7), 4436-4441.
- Reader, S. M., Laland, K. N. (2003). *Animal innovation: An introduction*. Oxford University Press.
- Reader, S. M., MacDonald, K. (2003). Environmental variability and primate behavioural flexibility. Dans S. M. Reader & K. N. Laland (dir.), *Animal Innovation* (p. 83-116). Oxford: Oxford University Press.
- Reale, D., Reader, S. M., Sol, D., McDougall, P. T., Dingemans, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291-318.
- Reid, J. M., Arcese, P., Cassidy, A.L.E.V., Hiebert, S. M., Smith, J. N. M., Stoddard, P. K., Marr, A. B., Keller, L. F. (2005). Fitness correlates of song repertoire size in free-living song sparrows (*Melospiza melodia*). *The American Naturalist*, 165, 299-310.
- Remeš, V., Matysioková, B. (2013). More ornamented females produce higher-quality offspring in a socially monogamous bird: an experimental study in the great tit (*Parus major*). *Frontiers in zoology*, 10(1), 14.
- Roth, G., Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, 9(5), 250-257. doi: <http://dx.doi.org/10.1016/j.tics.2005.03.005>
- Roulin, A. (2004a). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews*, 79(4), 815-848. doi: 10.1017/s1464793104006487
- Roulin, A. (2004b). Proximate basis of the covariation between a melanin-based female ornament and offspring quality. *Oecologia*, 140(4), 668-675. doi: 10.1007/s00442-004-1636-x
- Roulin, A., Gasparini, J., Bize, P., Ritschard, M., Richner, H. (2008). Melanin-based colorations signal strategies to cope with poor and rich environments. *Behavioral Ecology and Sociobiology*, 62(4), 507-519. doi: 10.1007/s00265-007-0475-2
- Saetre, G.-P., Fossnes, T., Slagsvold, T. (1995). Food Provisioning in the Pied Flycatcher: Do Females Gain Direct Benefits from Choosing Bright-Coloured Males? *Journal of Animal Ecology*, 64(1), 21-30. doi: 10.2307/5824

- Saks, L., McGraw, K., Horak, P. (2003). How feather colour reflects its carotenoid content. *Functional Ecology*, 17(4), 555-561. doi: 10.1046/j.1365-2435.2003.00765.x
- Sardell, R. J., Kempenaers, B., Duval, E. H. (2014). Female mating preferences and offspring survival: testing hypotheses on the genetic basis of mate choice in a wild lekking bird. *Molecular Ecology*, 23(4), 933-946. doi: 10.1111/mec.12652
- Sasvari, L. (1979). Observational learning in Great, Blue and Marsh Tits. *Animal Behaviour*, 27(AUG), 767-and. doi: 10.1016/0003-3472(79)90012-5
- Savard, J. F., Keagy, J., Borgia, G. (2011). Blue, not UV, plumage color is important in satin bowerbird *Ptilonorhynchus violaceus* display. *Journal of Avian Biology*, 42(1), 80-84. doi: 10.1111/j.1600-048X.2010.05128.x
- Schuck-Paim, C., Alonso, W. J., Ottoni, E. B. (2008). Cognition in an ever-changing world: Climatic variability is associated with brain size in neotropical parrots. *Brain Behavior and Evolution*, 71(3), 200-215. doi: 10.1159/000119710
- Schwagmeyer, P. L., Mock, D. W. (2008). Parental provisioning and offspring fitness: size matters. *Animal Behaviour*, 75, 291-298.
- Seferta, A., Guay, P. J., Marzinotto, E., Lefebvre, L. (2001). Learning differences between feral pigeons and zenaida doves: the role of neophobia and human proximity. *Ethology*, 107(4), 281-293.
- Seibt, U., Wickler, W. (2006). Individuality in problem solving: String pulling in two *Carduelis* species (Aves : Passeriformes). *Ethology*, 112(5), 493-502.
- Senar, J. C., Figuerola, J., Pascual, J. (2002). Brighter yellow blue tits make better parents. *Proceedings of the Royal Society B-Biological Sciences*, 269(1488), 257-261. doi: 10.1098/rspb.2001.1882
- Senar, J. C., Negro, J. J., Quesada, J., Ruiz, I., Garrido, J. (2008). Two pieces of information in a single trait? The yellow breast of the great tit (*Parus major*) reflects both pigment acquisition and body condition. *Behaviour*, 145(9), 1195-1210. doi: 10.1163/156853908785387638
- Seppanen, J.-T., Forsman, J. T. (2007). Interspecific social learning: Novel preference can be acquired from a competing species. *Current Biology*, 17(14), 1248-1252. doi: 10.1016/j.cub.2007.06.034

- Seppanen, J.-T., Forsman, J. T., Monkkonen, M., Krams, I., Salmi, T. (2011). New behavioural trait adopted or rejected by observing heterospecific tutor fitness. *Proceedings of the Royal Society B-Biological Sciences*, 278(1712), 1736-1741. doi: 10.1098/rspb.2010.1610
- Seppanen, J.-T., Forsman, J. T., Monkkonen, M., Thomson, R. L. (2007). Social information use is a process across time, space and ecology, reaching heterospecifics. *Ecology*, 88(7), 1622-1633. doi: 10.1890/06-1757.1
- Sergio, F., Bogliani, G. R. (2001). Nest defense as parental care in the northern hobby (Falco subbuteo). *Auk*, 118(4), 1047-1052. doi: 10.1642/0004-8038(2001)118[1047:ndapci]2.0.co;2
- Sewall, K. B., Soha, J. A., Peters, S., Nowicki, S. (2013). Potential trade-off between vocal ornamentation and spatial ability in a songbird. *Biology letters*, 9(4).
- Shawkey, M. D., Estes, A. M., Siefferman, L. M., Hill, G. E. (2003). Nanostructure predicts intraspecific variation in ultraviolet-blue plumage colours. *Proceedings of the Royal Society B-Biological Sciences*, 270(1523), 1455-1460. doi: 10.1098/rspb.2003.2390
- Shawkey, M. D., Hill, G. E. (2005). Carotenoids need structural colours to shine. *Biology Letters*, 1(2), 121-124. doi: 10.1098/rsbl.2004.0289
- Sheldon, B. C., Verhulst, S. (1996). Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution*, 11(8), 317-321. doi: [http://dx.doi.org/10.1016/0169-5347\(96\)10039-2](http://dx.doi.org/10.1016/0169-5347(96)10039-2)
- Sherry, D. F., Hoshoooley, J. S. (2009). The seasonal hippocampus of food-storing birds. *Behavioural Processes*, 80(3), 334-338. doi: 10.1016/j.beproc.2008.12.012
- Sherry, D. F., Jacobs, L. F., Gaulin, S. J. (1992). Spatial memory and adaptive specialization of the hippocampus. *Trends in neurosciences*, 15(8), 298-303.
- Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal Behaviour*, 61, 277-286.
- Shettleworth, S. J. (2009). *Cognition, evolution and behavior*. Oxford University Press.
- Shohet, A. J., Watt, P. J. (2009). Female guppies *Poecilia reticulata* prefer males that can learn fast. *Journal of Fish Biology*, 75(6), 1323-1330. doi: 10.1111/j.1095-8649.2009.02366.x
- Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*.

- Siitari, H., Honkavaara, J., Huhta, E., Viitala, J. (2002). Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. *Animal Behaviour*, 63, 97-102. doi: 10.1006/anbe.2001.1870
- Skinner, B. F. (1938). The behavior of organisms: An experimental analysis.
- Slagsvold, T., Lifjeld, J. T. (1985). Variation in plumage color of the Great Tit *Parus major* in relation to habitat, season and food. *Journal of Zoology*, 206(JUL), 321-328.
- Smith, H. G., Kallander, H., Fontell, K., Ljungstrom, M. (1988). Feeding frequency and parental division of labor in the double-brooded Great Tit *Parus major* - effects of manipulating brood size. *Behavioral Ecology and Sociobiology*, 22, 447-453.
- Snowberg, L. K., Benkman, C. W. (2009). Mate choice based on a key ecological performance trait. *Journal of Evolutionary Biology*, 22(4), 762-769.
- Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, 5(1), 130-133. doi: 10.1098/rsbl.2008.0621
- Sol, D., Bacher, S., Reader, S. M., Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *the american naturalist*, 172(S1), S63-S71.
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., Lefebvre, L. (2005a). Big brains, enhanced cognition and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 5460-5465.
- Sol, D., Griffin, A. S., Bartomeus, I. (2012). Consumer and motor innovation in the common myna: the role of motivation and emotional responses. *Animal Behaviour*, 83(1), 179-188. doi: 10.1016/j.anbehav.2011.10.024
- Sol, D., Griffin, A. S., Bartomeus, I., Boyce, H. (2011). Exploring or Avoiding Novel Food Resources? The Novelty Conflict in an Invasive Bird. *PloS ONE*, 6.
- Sol, D., Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, 90(3), 599-605.
- Sol, D., Price, T. D. (2008). Brain size and the diversification of body size in birds. *American Naturalist*, 172(2), 170-177.
- Sol, D., Stirling, D. G., Lefebvre, L. (2005b). Behavioral drive or behavioral inhibition in evolution: Subspecific diversification in holarctic passerines. *Evolution*, 59(12), 2669-2677.
- Sol, D., Timmermans, S., Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds (vol 63, pg 495, 2002). *Animal Behaviour*, 64, 516-516.

- Spencer, K. A., Buchanan, K. L., Goldsmith, A. R., Catchpole, C. K. (2003). Song as an honest signal of developmental stress in the zebra finch (*Taeniopygia guttata*). *Hormones and Behavior*, 44(2), 132-139. doi: 10.1016/s0018-506x(03)00124-7
- Spencer, K. A., Buchanan, K. L., Leitner, S., Goldsmith, A. R., Catchpole, C. K. (2005). Parasites affect song complexity and neural development in a songbird. *Proceedings of the Royal Society B-Biological Sciences*, 272(1576), 2037-2043. doi: 10.1098/rspb.2005.3188
- Spencer, K. A., MacDougall-Shackleton, S. A. (2011). Indicators of development as sexually selected traits: the developmental stress hypothesis in context. *Behavioral Ecology*, 22(1), 1-9.
- Sternberg, R. J. (1985). *Beyond IQ: A triarchic theory of human intelligence*. CUP Archive.
- Stier, A., Reichert, S., Massemin, S., Bize, P., Criscuolo, F. (2012). Constraint and cost of oxidative stress on reproduction: correlative evidence in laboratory mice and review of the literature. *Frontiers in Zoology*, 9. doi: 10.1186/1742-9994-9-37
- Stretch, R., Leytham, G., Kershaw, W. (1960). The Effect of Acute Schistosomiasis upon Learning in Rats under Different Levels of Motivation. *Ann. Trop. Med. Parasit.*, 487-492.
- Sutter, M., Kawecki, T. J. (2009). Influence of learning on range expansion and adaptation to novel habitats. *Journal of Evolutionary Biology*, 22(11), 2201-2214. doi: 10.1111/j.1420-9101.2009.01836.x
- Svensson, L. (1992). *Identification guide to European passerines*. Thetford: British Trust for Ornithology.
- Svensson, P. A., Wong, B. B. M. (2011). Carotenoid-based signals in behavioural ecology: a review. *Behaviour*, 148(2), 131-189. doi: 10.1163/000579510x548673
- Szoellosi E., Cichon M., Eens M., Hasselquist D., Kempnaers B., Merino S., Nilsson J.A., Rosivall B., Rytkonen S., Toerek J., *et al.* (2011). Determinants of distribution and prevalence of avian malaria in blue tit populations across Europe: separating host and parasite effects. *Journal of Evolutionary Biology*, 24(9), 2014-2024. doi:10.1111/j.1420-9101.2011.02339.x
- Tanner, M., Richner, H. (2008). Ultraviolet reflectance of plumage for parent-offspring communication in the great tit (*Parus major*). *Behavioral Ecology*, 19, 369-373.
- Taylor, A. H., Hunt, G. R., Gray, R. D. (2012). Context-dependent tool use in New Caledonian crows. *Biology Letters*, 8(2), 205-207. doi: 10.1098/rsbl.2011.0782

- Tebbich, S., Sterelny, K., Teschke, I. (2010). The tale of the finch: adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1543), 1099-1109.
- Tencate, C., Vos, D. R., Mann, N. (1993). Sexual imprinting and song learning - 2 of one kind. *Netherlands Journal of Zoology*, 43(1-2), 34-45.
- Thompson, R. F., Spencer, W. A. (1966). Habituation: a model phenomenon for the study of neuronal substrates of behavior. *Psychological review*, 73(1), 16.
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Monographs: General and Applied*, 2(4), i-109.
- Thornton, A., Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 367(1603), 2773-2783. doi: 10.1098/rstb.2012.0214
- Thornton, A., Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, 83(6), 1459-1468. doi: 10.1016/j.anbehav.2012.03.018
- Timmermans, S., Lefebvre, L., Boire, D., Basu, P. (2000). Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. *Brain Behavior and Evolution*, 56(4), 196-203. doi: 10.1159/000047204
- Tinbergen, J. M., Boerlijst, M. C. (1990). Nestling Weight and Survival in Individual Great Tits (*Parus major*). *Journal of Animal Ecology*, 59(3), 1113-1127.
- Tomasello, M., Kruger, A. C., Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, 16(3), 495-511.
- van Noordwijk, A. J., McCleery, R. H., Perrins, C. M. (1995). Selection for the Timing of Great Tit Breeding in Relation to Caterpillar Growth and Temperature. *Journal of Animal Ecology*, 64, 451-458.
- van Overveld, T., Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, 6, 187-190.
- Vas, Z., Lefebvre, L., Johnson, K. P., Reiczigel, J., Rozsa, L. (2011). Clever birds are lousy: Covariation between avian innovation and the taxonomic richness of their amblyceran lice. *International Journal for Parasitology*, 41, 1295-1300.
- Verbeek, M. E. M., Drent, P. J., Wiepkema, P. R. (1994). Consistent Individual-Differences in Early Exploratory-Behavior of Male Great Tits. *Animal Behaviour*, 48(5), 1113-1121.

- Verboven, N., Mateman, A. C. (1997). Low frequency of extra-pair fertilizations in the Great Tit *Parus major* revealed by DNA fingerprinting. *Journal of Avian Biology*, 28, 231-239.
- Verboven, N., Visser, M. E. (1998). Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos*, 81(3), 511-524. doi: 10.2307/3546771
- Verhulst, S., Tinbergen, J. M. (1991). Experimental evidence for a causal relationship between timing and success of reproduction in the Great tit *Parus major*. *Journal of Animal Ecology*, 60(1), 269-282. doi: 10.2307/5459
- Verhulst, S., Vanbalen, J. H., Tinbergen, J. M. (1995). Seasonal Decline in Reproductive Success of the Great Tit - Variation in Time or Quality. *Ecology*, 76(8), 2392-2403.
- Visser, M. E., Lessells, C. M. (2001). The costs of egg production and incubation in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1473), 1271-1277. doi: 10.1098/rspb.2001.1661
- von Bayern, A. M. P., Heathcote, R. J. P., Rutz, C., Kacelnik, A. (2009). The Role of Experience in Problem Solving and Innovative Tool Use in Crows. *Current Biology*, 19(22), 1965-1968. doi: <http://dx.doi.org/10.1016/j.cub.2009.10.037>
- Vonschantz, T., Goransson, G., Andersson, G., Froberg, I., Grahn, M., Helgee, A., Wittzell, H. (1989). Female choice selects for a viability-based male trait in pheasants. *Nature*, 337(6203), 166-169. doi: 10.1038/337166a0
- Webster, S. J., Lefebvre, L. (2001). Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. *Animal Behaviour*, 62, 23-32.
- Wendeln, H., Becker, P. H. (1999). Effects of parental quality and effort on the reproduction of common terns. *Journal of Animal Ecology*, 68(1), 205-214. doi: 10.1046/j.1365-2656.1999.00276.x
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682-685. doi: 10.1038/21415
- Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, 308(5955), 181-184.
- Willemet, R. (2012). Understanding the Evolution of Mammalian Brain Structures; the Need for a (New) Cerebrotyping Approach. *Brain Sciences*, 2(2), 203-224.
- Willemet, R. (2013). Reconsidering the evolution of brain, cognition and behaviour in birds and mammals. *Frontiers in Psychology*, 4. doi: 10.3389/fpsyg.2013.00396

- Williams, T. D. (2005). Mechanisms Underlying the Costs of Egg Production. *BioScience*, 55(1), 39-48. doi: 10.1641/0006-3568(2005)055[0039:mutcoe]2.0.co;2
- Wyles, J. S., Kunkel, J. G., Wilson, A. C. (1983). Birds, Behavior and Anatomical Evolution. *Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences*, 80(14), 4394-4397.
- Zrelec, V., Zini, M., Guarino, S., Mermoud, J., Oppliger, J., Valtat, A., . . . Kawecki, T. J. (2013). *Drosophila* rely on learning while foraging under semi-natural conditions. *Ecology and Evolution*, 3(12), 4139-4148. doi: 10.1002/ece3.783

ANNEXE

Annexe 1: Robustness of the Relationship between Problem-solving Performance and reproductive Success

Among solver pairs where at least one parent succeeded in solving the task, we had two pairs in which both parents did. To test for the robustness of our results based on the solving latency of the fastest parent of the pair, we compared the results of the same analyses restricting the sample to the 16 pairs in which only one parent solved the task, and using the average latency of both parents of the pair or the latency of the first parent that solved the task.

When we excluded these two nests, the relationships observed with clutch size, hatching success and number of fledged chicks all remained significant (clutch size: $F_{1,13} = 5.89$, $P = 0.030$; hatching success: $\chi^2_1 = 4.05$, $P = 0.044$; brood size at day 14: $F_{1,9} = 15.14$, $P = 0.004$; Fig. 1). The relationships observed with clutch size and number of fledged chicks remained significant when we used the mean latency of the pair instead of the latency of the fastest parent to enter (clutch size: $F_{1,15} = 6.73$, $P = 0.020$; number of fledged chicks: $F_{1,11} = 11.45$, $P = 0.006$; Fig. 2a, c); the relationship with hatching success became marginally significant ($\chi^2_1 = 2.89$, $P = 0.089$; Fig. 2b). When we used the latency of the first parent to enter, the relationship for clutch size also remained significant ($F_{1,15} = 4.62$, $P = 0.048$; Fig. 3a), but the relationships with hatching success and number of fledged chicks became non significant (hatching success: $\chi^2_1 = 0.98$, $P = 0.321$; number of fledged chicks: $F_{1,11} = 2.78$, $P = 0.124$; Fig. 3b, c).

Overall, our results seem quite robust to the different ways in which we considered the two pairs for which both parents solved the task.

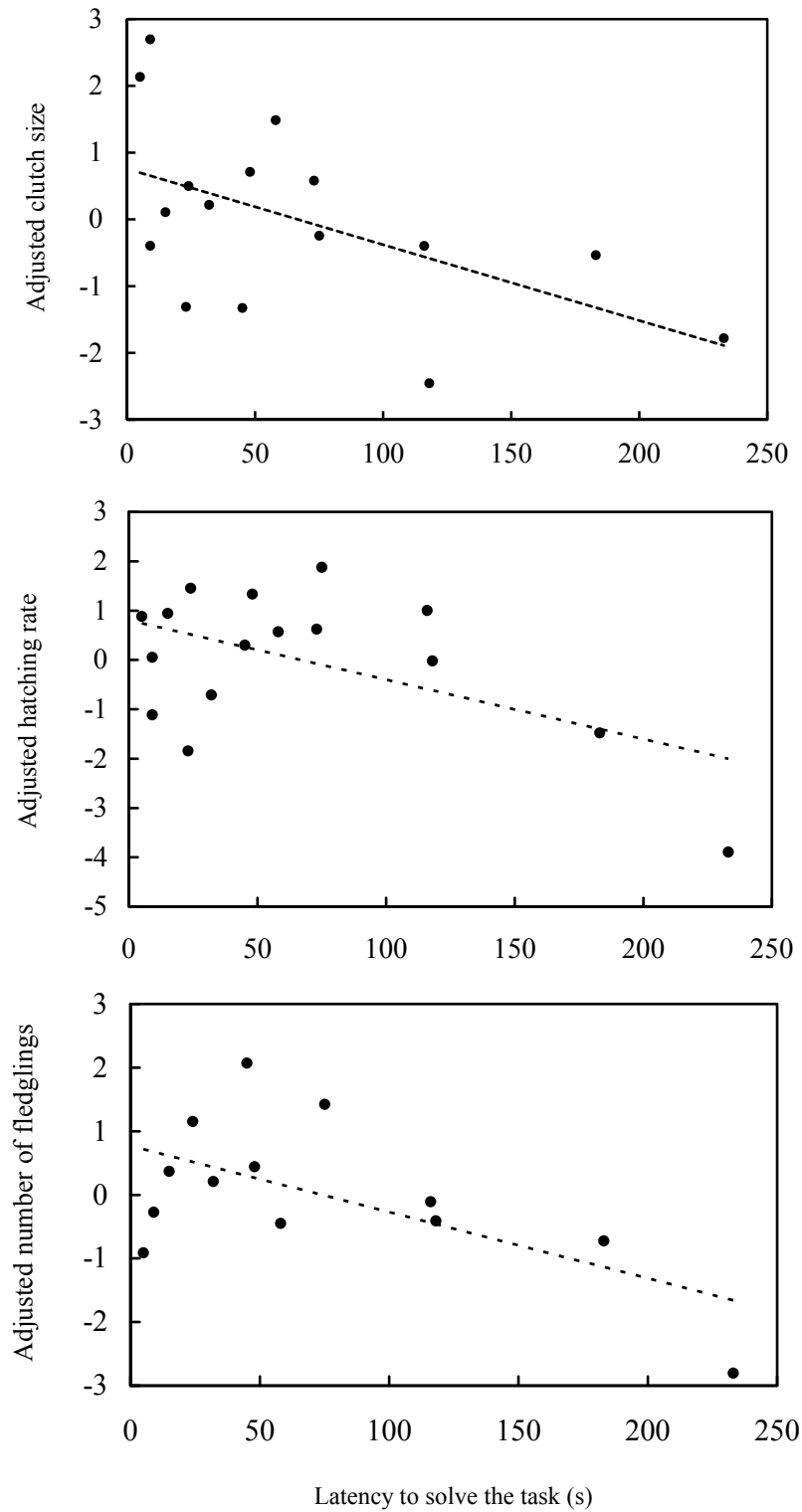


Figure A.1.1. Measures of reproductive success depending on problem-solving latency in nests where at least one parent solved the task: (a) clutch size (adjusted for male body condition), (b) hatching rate (adjusted for female body condition) and (c) fledgling number (adjusted for clutch size and provisioning rate). The two nests where both parents were solvers were excluded from the analyses.

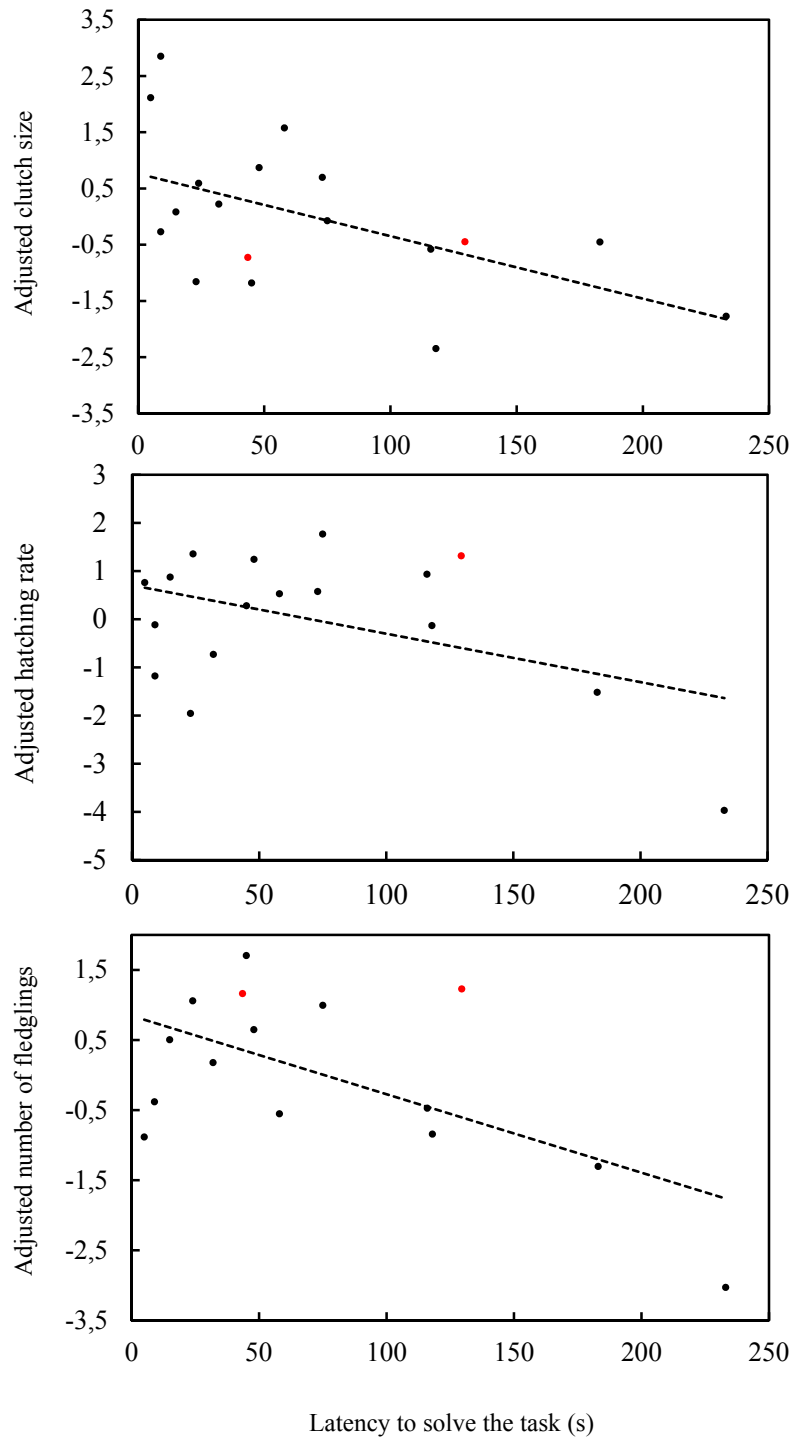


Figure A.1.2. Measures of reproductive success depending on problem-solving latency in nests where at least one parent solved the task: (a) clutch size (adjusted for male body condition), (b) hatching rate (adjusted for female body condition) and (c) fledgling number (adjusted for clutch size and provisioning rate). For the two nests where both parents were solvers, latency was measured as the average latency for both parents (red points on the graphs; for hatching rate, only one nest is shown since female condition was not known for the second nest); other latency values were unchanged.

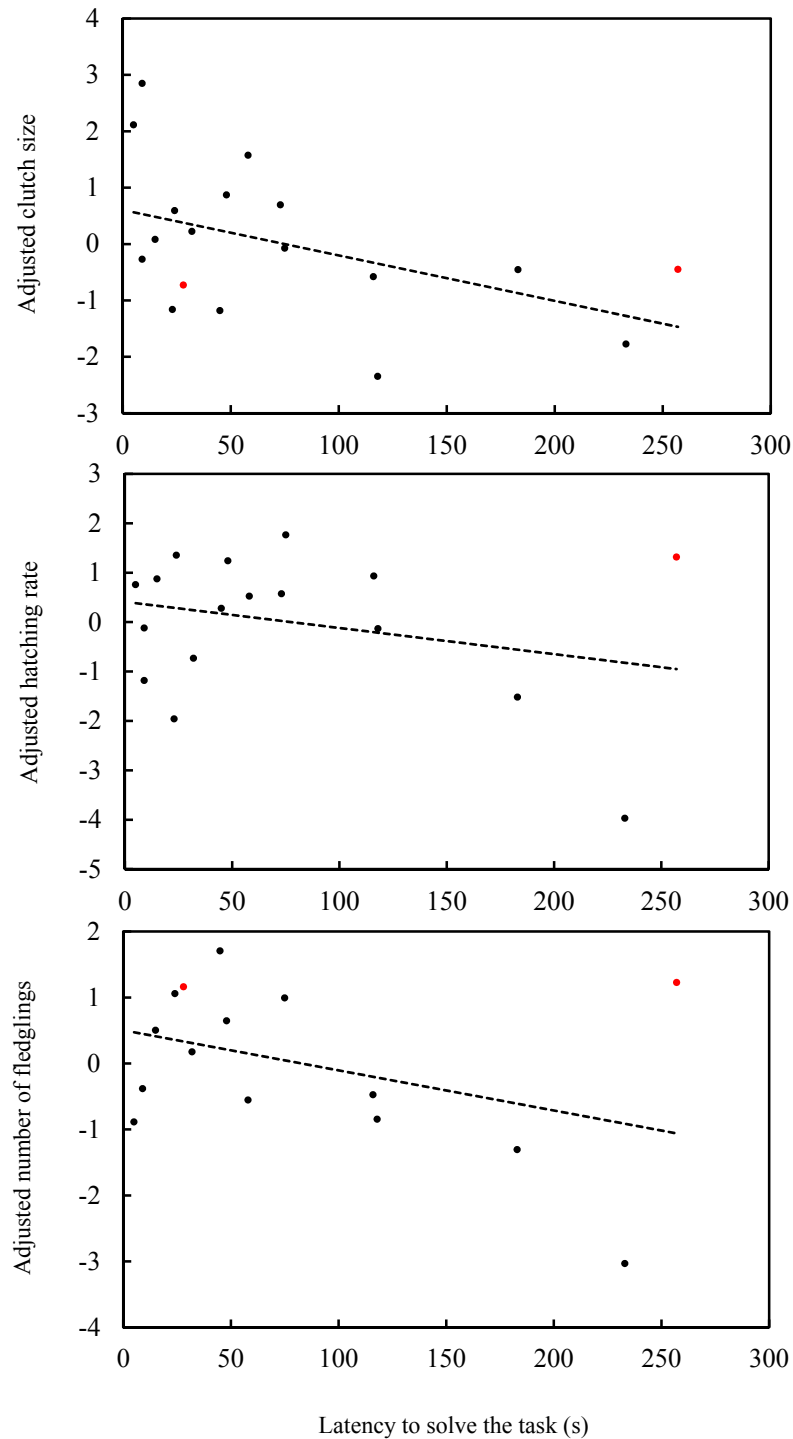


Figure A.1.3. Measures of reproductive success depending on problem-solving latency in nests where at least one parent solved the task: (a) clutch size (adjusted for male body condition), (b) hatching rate (adjusted for female body condition) and (c) fledgling number (adjusted for clutch size and provisioning rate). For the two nests where both parents were solvers, latency was here measured as the latency of the first parent to solve the task instead of the fastest parent (red points on the graphs; for hatching rate, only one nest is shown since female condition was not known for the second nest). For all other nests, latency was measured as the latency of the fastest parent. Only one latency value changed; for the other nest, the first parent was also the fastest.

Annexe 2 : Robustness of the relationships between brood size manipulation treatment, problem-solving performance and reproductive success of pairs to additional variables not included in the main analyses (neophobia and sex of the solvers).

Influence of neophobia level

Preliminary analyses on the 2013 data showed that the level of neophobia of an individual was not significantly related to problem-solving. We therefore did not include neophobia of the solver (in solver pairs where one individual solved the task), the neophobia of the fastest solver (in solver pairs where both parents solved the task), or the neophobia of the parent that participate the more in the task (in non-solver pairs), in the models. Nevertheless, solvers tended to be less neophobic than non-solvers ($F_{1,43} = 3.22, P = 0.079$). Because a significant relation between problem-solving performance and neophobia was previously found in this population (Chapitre 1), we tested the robustness of our results by repeating analyses including neophobia in the models as a covariable. These analyses were restricted to the 2013 data (neophobia measure currently unavailable for 2012).

- Effect of brood size manipulation treatment on problem-solving performance: when neophobia was included in the starting model, the treatment did not influence the probability to solve the task ($\chi^2_2 = 2.51, P = 0.28$); neophobia did not influence this probability either ($\chi^2_1 = 0.60, P = 0.44$).

- Effect of problem-solving performance on reproductive success: when neophobia was included in the starting model, solver pairs fledged more young than non-solver pairs ($F_{1,55} = 4.13, P = 0.047$) and this did not depend on brood size manipulation treatment (interaction between problem-solving status and treatment: $F_{2,55} = 0.38, P = 0.68$). As expected, the number of fledged young also varied among treatments ($F_{2,55} = 18.42, P < 0.001$). Neophobia did not influence the number of fledged young ($F_{1,55} = 0.33, P = 0.56$).

- Effect of problem-solving performance on feeding rate: when neophobia was included in the starting model, solver pairs had a higher provisioning rate than non-solver pairs ($F_{1,47} = 10.74, P = 0.002$), and this did not depend on brood size manipulation

treatment (interaction between problem-solving status and treatment: $F_{2,47} = 0.91$, $P = 0.41$; treatment alone: $F_{2,32} = 0.64$, $P = 0.53$). Neophobia did not influence provisioning rate ($F_{1,47} < 0.001$, $P = 0.99$).

Influence of sex

Results from a previous study using the same problem-solving task in the same population (Chapitre 1) showed that the sex of the solver (in solver pairs where one individual solved the task), the sex of the fastest solver (in solver pairs where both parents solved the task), or the sex of the parent that participate the more in the task (in non-solver pairs did not influence the relationship between the problem-solving performance and reproductive success of the pair. Therefore, we did not include sex in the models. Again, we tested the robustness of our results by repeating analyses including sex in the models as a cofactor. These analyses were again restricted to the 2013 data (sex of solvers currently unavailable for 2012).

- Effect of brood size manipulation treatment on problem-solving performance: when sex was included in the starting model, the treatment did not influence the probability to solve the task ($\chi^2_2 = 3.79$, $P = 0.15$); sex of the solver did not influence this probability either ($\chi^2_1 = 0.12$, $P = 0.72$).

- Effect of problem-solving performance on reproductive success: when sex was included in the starting model, solver pairs fledged more young than non-solver pairs ($F_{1,56} = 7.39$, $P = 0.008$) and this did not depend on brood size manipulation treatment (interaction between problem-solving status and treatment: $F_{2,56} = 0.54$, $P = 0.58$). As expected, the number of fledged young also varied among treatments ($F_{2,56} = 5.23$, $P < 0.001$). Sex did not influence the number of fledged young ($F_{1,56} = 0.53$, $P = 0.47$).

- Effect of problem-solving performance on feeding rate: when sex was included in the starting model, solver pairs had a higher provisioning rate than non-solver pairs ($F_{1,47} = 8.05$, $P = 0.006$), and this did not depend on brood size manipulation treatment ($F_{2,47} = 1.31$, $P = 0.28$). Sex did not influence provisioning rate ($F_{1,47} = 0.84$, $P = 0.36$).

In conclusion, our results remain qualitatively unchanged when a measure of neophobia and sex of the solver were included in the models and are therefore robust to the absence of these covariables.

Annexe 3 : Summary of the final statistical models used in chapter 3

Repeatability	Yellow Breast		Blue-black Crown		Black Ventral Stripe	
	R	F	R	F	R	F
UV Chroma	0.76	17.07	0.88	35.80	--	--
Chroma	0.77	18.38	0.69	11.37	--	--
Hue	0.79	19.56	0.82	23.20	--	--
Brightness	0.81	22.83	0.71	12.73	0.91	4.78

Table A.3.I. Repeatability of colorimetric variables for each of the three body areas

	Rotated Factor loadings	
	1	2
Black crown		
UV Chroma	-0.849	
Blue Chroma	0.796	
Hue	0.941	
Brightness		0.970
<i>Eigenvalues</i>	<i>2.241</i>	<i>1.071</i>
<i>% of variance</i>	<i>56.03</i>	<i>26.78</i>
Yellow Breast		
UV Chroma	-0.875	
Yellow Chroma	0.694	
Hue	0.636	
Brightness		0.889
<i>Eigenvalues</i>	<i>1.659</i>	<i>1.034</i>
<i>% of variance</i>	<i>41.49</i>	<i>25.85</i>

Table A.3.II. Summary of exploratory factor analysis results explaining variations in yellow breast and blue-black crown colour spectra (N = 206 et N = 96 respectively)

Annexe 4: Summary of the final statistical models used in chapter 4

PROBLEM-SOLVING			Status			Latency to solve		
Factor	Chi2	df	P	F	df	P		
Year	2.07	1	0.151	1.08	1	0.306		
Age	0.29	1	0.592	0.08	1	0.776		
Treatment (Primaquine vs PBS)	0.09	1	0.770	1.08	1	0.306		
Age * Treatment	2.45	1	0.117	0.19	1	0.665		
Year * Treatment	2.07	1	0.151	0.08	1	0.781		
Age * Year	2.99	1	0.084	< 0.01	1	0.965		

LEARNING			Learning Status			Speed of learning		
Factor	Chi2	df	P	F	df	P		
Year	1.49	1	0.222	0.02	1	0.898		
Age	0.14	1	0.712	0.81	1	0.380		
Treatment (Primaquine vs PBS)	1.65	1	0.199	0.15	1	0.706		
Age * Treatment	1.31	1	0.253	0.09	1	0.762		
Year * Treatment	0.41	1	0.523	0.33	1	0.576		
Age * Year	--	--	--	--	--	--		

Statistically significant factors are highlighted in bold.
 -- means that this factor was not included in the model.

Table A.4.I. Summary of statistical models exploring the link between cognitive performances and treatment.

BEHAVIOURAL TRAITS	Neophobia (N = 52)			Exploration (N = 57)			Activity (N = 57)		
	F	df	P	F	df	P	F	df	P
Year	2.07	1	0.157	0.81	1	0.372	5.28	1	0.026
Age	1.86	1	0.179	< 0.01	1	0.969	0.18	1	0.676
Treatment (Primaquine vs PBS)	0.29	1	0.593	4.57	1	0.037	8.59	1	0.005
Age * Treatment	< 0.01	1	0.993	1.14	1	0.290	< 0.01	1	0.969
Year * Treatment	0.25	1	0.618	0.05	1	0.830	1.52	1	0.223
Age * Year	0.30	1	0.585	0.36	1	0.551	3.24	1	0.078
Activity	--	--	--	20.05	1	< 0.001	--	--	--

Statistically significant factors are highlighted in bold.

Table A.4.II: Summary of statistical models exploring the link between behavioural traits and treatment.