



Sources of variability in heterospecific social information use for breeding habitat selection: role of genetics and personality in collared flycatchers

Jennifer Morinay

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Jennifer Morinay

Sources of variability in heterospecific social information
use for breeding habitat selection:
Role of genetics and personality in collared flycatchers

Devant le jury composé de :

Dr. Desouhant Emmanuel, Pr., Université Claude Bernard Lyon 1	Président
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Dr. Aplin, Lucy, Max Planck Institute for Ornithology	Examinatrice
Dr. Doligez, Blandine, CR, CNRS UMR 5558 LBBE	Co-directrice de thèse
Dr. Gustafsson, Lars, Pr., Uppsala University	Co-directeur de thèse
Dr., Forsman, Jukka, Oulu University	Co-encadrant



Thèse réalisée au Laboratoire de Biométrie et Biologie Evolutive, UMR 5558 CNRS
Université Claude Bernard Lyon 1 - Bât. Grégor Mendel
43 bd du 11 novembre 1918
69622 VILLEURBANNE cedex

et au Department of Ecology and Genetics, Animal Ecology
Evolutionary Biology Center - Uppsala University
Norbyvägen 18D
75236 Uppsala

Sous la direction de Dr. Blandine Doligez
Prof. Lars Gustafsson

Co-encadrement Dr. Jukka Forsman

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Abstract in English

All their life, individuals have to make decisions that may strongly affect their fitness. To optimize their decisions, they can use personally acquired information but also information obtained from observing other individuals (“social information”). The propensity to gather and use social information and the information meaning might depend on both individual and environmental factors. Studying what drives within- and between-individual differences in social information use should help us understand the evolutionary potential of this supposedly adaptive behaviour. The aim of my PhD was to empirically investigate sources of variability in heterospecific social information use for breeding habitat selection. I worked on a natural population of collared flycatchers (*Ficedula albicollis*, Gotland Island, Sweden), a passerine species shown to cue on the presence, density, reproductive investment and nest site preference of dominant titmice for settlement decisions. Using both long term and experimental data, I showed that the use of heterospecific social information, measured as the probability to copy tit nest preference, is not heritable but depends on male age and aggressiveness and on tit apparent breeding investment at the time of flycatcher settlement. Using a playback experiment, I also showed that female flycatchers can fine-tune nest site choice according to (i) song features supposedly reflecting great tit (*Parus major*) quality and (ii) their own aggressiveness level. This thesis highlights the importance of personality in the use of heterospecific social information for breeding site selection in this population, and broadens the traditionally known sources of heterospecific information to fine song characteristics reflecting heterospecifics’ quality. To fully understand the evolutionary mechanisms and consequences of heterospecific social information use, genetically based plasticity and fitness consequences remain to be explored.

Keywords: Heterospecific social information, personality, aggressiveness, nest site choice, within- and between-individual variability, quantitative genetics, experimental approaches in the wild, collared flycatchers

Sammanfattning på svenska

Hos de flesta fågelarter påverkas den individuella reproduktionsframgången till stor del av den tidsmässiga och rumsliga variationen av lämplig häckningsbiotop. Därför kommer ett starkt selektionstryck främja beteendestrategier som gör det möjligt för individer att optimera beslutsfattandet för val av häckningsplats. I synnerhet kan individer samla in och använda information om kvaliteten på häckningsplatser för att välja mellan dem. Två huvudtyper av information kan urskiljas : (i) Upplysningar som förvärvats genom individens personliga erfarenhet när de interagerar med sin miljö (personlig information, t.ex. reproduktiv framgång) och (ii) information som erhållits från observationer av andra individer och deras interaktioner med miljön (social information, t ex närvaro och / eller reproduktiv framgång hos individer av den egna arten eller andra närbesläktade arter). Användningen av social information har visat sig förekomma i olika sammanhang, inklusive val av häckningsplatser vid olika rumsliga skalor. Men innebörden av social information kan bero på både enskilda faktorer (t ex konkurrenskraft, ålder, erfarenhet) och miljöfaktorer (t ex datum, årstid). Därför kommer individernas fenotyp och omgivande förhållanden sannolikt att påverka informationsanvändningen starkt. Informationsanvändningen är delvis beroende på miljöförhållandena, och vi förväntar oss att individer konsekvent skiljer sig från varandra i hur de använder sig av social information över tid och i olika sammanhang. Dessa konsekventa skillnader kan vara ärftliga, beroende av tidigare individuell erfarenhet, och stå i relation till olika personligheter, vilket tidigare visats i andra sammanhang. Dessutom kan informationsanvändning mellan olika arter leda till en ökning av nischöverlapp, vilket leder till en avvägning mellan fördelarna med att använda informationen och kostnader som orsakas av mellanartskonkurrens. Från informationsmottagarnas perspektiv kan vi förvänta oss evolution av informationsinsamlingsstrategier som möjliggör välinformerade beslut, utan nära och därmed potentiellt kostsamma interaktioner med konkurrenskraftiga informationsleverantörer. Tjuvlyssning och spaning på sexuellt selekterade karaktärer har visat sig användas av bo-parasiter (t ex gökar) för att uppskatta fosterföräldrarnas kvalitet. Bland de sexuellt selekterade karaktärerna är akustiska parningssignar lättillgängliga och är pålitliga indikatorer av individernas kvalitet.

Målet med mina doktorandstudier var att empiriskt undersöka dessa frågor i en naturlig population av halsbandsflugsnappare (*Ficedula albicollis*) på Gotland, som lever i samma områden som populationer av talgoxe (*Parus major*) och blåmes (*Parus caeruleus*).

leus). Flera tidigare empiriska och experimentella studier i denna och andra populationer har visat att individer av alla arterna använder social information (närvaro och reproduktionsframgång) från både deras egen art och en annan art på ett komplicerat sätt för att justera besluten om val av häckningsplats i olika rumsliga skalor (plats eller område). Det finns emellertid stor variation mellan individer i användningen av dessa informationskällor och det återstår att förklara detta.

Syftet med min doktorsavhandling var mer specifikt trefaldigt. För det första ville vi veta om användningen av social information skulle kunna vara ett ärftligt beteende och / eller om det berodde på tidigare erfarenheter och kunskaper om miljön (kapitel 3). Jag genomförde kvantitativa genetisk analyser ("animal models") med hjälp av både långtidsdata (1980-2016) för att bygga en stamtavla (pedigree) av populationen och data från ett 5-årigt experiment (2012-2016) som testade om flugsnapparna kopierade mesarnas häckningsplatspreferenser. Experimentet bestod i att skapa en uppenbar preferens hos talgoxe och blåmesar för en särskild fågelholk och undersöka om flugsnapparna, just när de anlänt tillbaka efter flyttningen från sina övervintringsområden i Afrika, kopierade eller inte kopierade mesarnas preferenser för en särskild fågelholk. Liknande experiment har utförts framgångsrikt i samma och andra populationer av flugsnappare (kapitel 2), men vanligtvis vid kortare tidsmässiga och mindre rumsliga skalor. Genom att genomföra detta experiment flera år kunde vi (i) genomföra kvantitativ genetisk analys över flera generationer, (ii) testa effekten av tidigare erfarenheter (tidigare kopieringsbeteende men även tidigare reproduktiv framgång) och (iii) testa effekten av kunskapen hos olika typer av individer (åldersgrupper, återvändare och invandrare skiljer sig åt i deras erfarenhet av den lokala miljön). Vi upptäckte att tidigare erfarenheter påverkade flugsnapparnas kopieringsbeteende, och att detta beteende inte var ärftligt. Mer specifikt påverkar hanliga erfarenheter det gemensamma beslutet att kopiera mesarnas val av fågelholk.

För det andra verkar vissa personlighetsdrag påverka inhämtningen och användningen av social information, och vi ville testa om personlighetsskillnader kan förklara en del av skillnaderna i social information som används för att välja häckningsplats. Med hjälp av data som tidigare samlats in mellan 2011 och 2013 extraherade jag uppskattningar av aggressivitet, djärvhet och neofobi hos häckande hanar och honor, uppskattade repeterbarheten av dessa beteenden mellan år och fenotyp samt mellan-individuella korrelationer för att se om de bildade beteendesyndrom (Kapitel 4). Med hjälp av både data från experimentet med den sociala informationen, som användes i kapitel 3, och personlighetsbedömningarna som härleddes i kapitel 4 (för 2012 och 2013), undersökte jag sambandet mellan varje personlighetskategori och sannolikheten för flugsnapparna att kopiera mesarnas preferenser (Kapitel 5). Aggressivitet, som var repeterbart men inte ärftligt, påverkade kopieringsbeteendet på olika sätt beroende på flugsnapparnas kön och på hur långt i häckningen mesarna (informationsleverantörerna) hade kommit. Användningen av mellanartsspecifik social information, mätt som sannolikheten för kopiering eller förkastning

av mesarnas val av fågelholk, beror inte på (i) hanarnas ålder och aggressivitet, (ii) eller mesarnas investering i reproduktionen vid tidpunkten för flugsnapparnas val av häckningsplats. Andra personlighetsdrag som djärvhet och neofobia, påverkade inte sannolikheten för att kopiera eller förkasta mesarnas fågelholkspreferens.

För det tredje ville jag utöka omfattningen av de traditionellt kända källorna till social information och testa huruvida andra lättillgängliga indikatorer på informationsleverantörernas (mesarnas) kvalitet, det vill säga en förmodligen mer noggrann information än mesarnas närvaro eller holk/områdespreferens, skulle kunna användas av flugsnapparna. Vi vet att flugsnapparna använder mesarnas kullstorlek eller antal ungar som en källa till social information för sina beslut om av var de skall häcka. Flugsnapparnas kan dock också drabbas av höga kostnader om de bosätter sig i mesholkar (de kan bli dödade). Därför ville jag undersöka om halsbandsflugsnapparna kan använda mesarnas sång, för att informera sig om mesarnas kvalitet, vilket går lätt att tjuvlyssna lyssna på, som en källa till social information (Kapitel 6). Vi utförde ett uppspelningsexperiment och som spelades upp under flugsnapparnas hela etableringsfas, antingen sång som liknar en högkvalitativ talgoxe, en lågkvalitativ talgoxe eller kontroll-sång. Vi registrerade hur flugsnapparna valde fågelholkar nära våra uppspelningsplatser och uppskattade deras aggressivitet (eftersom detta kan påverka deras konkurrenskraft och därmed deras beslut att bosätta sig nära en dominerande konkurrent, Kapitel 6). Bland de äldre honorna föredrog de aggressiva att etablera sig i närheten av uppspelningar av högkvalitativ talgoxe-sång och undvek uppspelningar av sång av låg kvalitet, medan mindre aggressiva äldre honor föredrog att bosätta sig i närheten av uppspelningar av låg kvalitet. Hanarnas personlighet eller ålder påverkade inte beslutsfattandet. Våra resultat visar att halsbandsflugsnapparhonor använder talgoxarnas sångkvalitetsegenskaper som information för avgörande beslut vid val av område och fågelholk, men olika beroende på deras egen konkurrenskraft och / eller tidigare erfarenhet av talgoxarnas sång.

Denna avhandling belyser betydelsen av personlighet i den sammanhangsberoende användningen av mellanartsspecifika sociala informationer för val av boplats i denna population och breddar de traditionellt kända källorna till mellanartsspecifik information till subtila sångegenskaper som återspeglar mellanartsspecifika kvaliteter. Omvänt spelade genetiken ingen direkt roll för att forma användningen av mellanartsspecifik social information, men genetiskt baserad plasticitet i detta beteende återstår att undersöka. Särskild uppmärksamhet bör också ges till vilka konsekvenser på individernas fitness detta beteende kan ha för att fullt ut förstå dess evolutionära mekanismer och konsekvenser.

Översättning av /translation by Lars Gustafsson

Résumé en français

Au cours de leur vie, les individus doivent constamment prendre des décisions qui peuvent fortement affecter leur valeur sélective. Pour optimiser leur prise de décisions, ces individus peuvent utiliser des informations soit issues de leurs propres interactions avec l'environnement (informations personnelles), soit issues de l'observation d'autres individus (informations sociales). D'après des études empiriques, la propension à utiliser des informations sociales et leur signification dépend probablement de paramètres individuels et environnementaux. Pour comprendre le potentiel évolutif de ce comportement à priori adaptatif, il est nécessaire de déterminer les causes de ces variations inter- et intra-individuelles. Ainsi, le but de cette thèse était donc de déterminer les sources de variations individuelles dans l'utilisation d'information sociales hétérospécifiques pour le choix d'habitat de reproduction, chez le gobe-mouche à collier (*Ficedula albicollis*). A partir de données à long terme et d'expérimentations en nature dans la population de Gotland (Suède), j'ai montré que l'utilisation d'informations sociales n'est pas héritable dans cette population, mais dépend de l'âge et de l'agressivité des mâles, ainsi que de la taille de ponte des compétiteurs au moment où les gobe-mouches font leur choix de nid. A partir d'une expérience de repasse, j'ai également montré que les femelles peuvent ajuster, en fonction de leur propre niveau d'agressivité, leur choix de site de nidification en fonction de caractéristiques de chants liés à la qualité des mésanges charbonnières (*Parus major*). Cette thèse souligne l'importance de la personnalité dans l'utilisation d'informations sociales hétérospécifiques pour la sélection d'habitat de reproduction, et montre que des caractéristiques fines de signaux à l'intention de congénères peuvent être utilisées par d'autres espèces. Pour pleinement comprendre les mécanismes évolutifs et les conséquences de l'utilisation d'informations sociales hétérospécifiques, il faudrait maintenant explorer les conséquences de ce comportement sur la valeur sélective ainsi que les bases génétiques de la plasticité comportementale associée.

Mots clés : information sociale hétérospécifique, personnalité, agressivité, variabilité inter- et intra-individuelle, choix d'habitat de reproduction, génétique quantitative, expérience en nature, gobe-mouche à collier

Résumé détaillé en français

La qualité de l'habitat de reproduction influence fortement le succès reproducteur chez de nombreuses espèces. La sélection naturelle doit donc favoriser des stratégies permettant aux individus d'optimiser leurs prises de décision pour le choix de l'habitat de reproduction. Les individus peuvent notamment utiliser différentes sources d'informations disponibles dans l'environnement, reflétant la qualité des différents sites de reproduction, leur permettant de choisir entre les sites disponibles de façon optimale. Deux types d'informations peuvent être distinguées : l'information acquise à partir de la propre expérience de l'individu dans l'environnement (information personnelle, par exemple le succès reproducteur de l'année précédente), et l'information acquise par l'observation des autres individus dans l'environnement (information sociale, par exemple la présence ou le succès reproducteur de compétiteurs, ou des signaux interceptés de voisins).

Il a été montré, au sein de plusieurs taxons, que les individus peuvent récolter et utiliser de l'information sociale de congénères mais aussi d'individus d'autres espèces. Si ces études ont mis en évidence une tendance globale d'utilisation d'informations sociales à l'échelle de la population, elles ont aussi montré que tous les individus ne les utilisent pas de la même façon. Cette utilisation peut dépendre de facteurs individuels comme l'âge et l'acquisition d'expérience par exemple. On peut s'attendre à ce que les individus diffèrent de façon consistante dans leur utilisation d'information, et que ce comportement, au même titre que d'autres comportements liés et déjà étudiés, soit héritable, c.-à-d. transmis génétiquement de parents à enfants. La variabilité d'utilisation d'informations sociales pourrait également tenir au fait qu'il existe plusieurs types d'informations disponibles, et que selon leur facilité d'accès et leur importance, certains individus utilisent préférentiellement un type d'information, et d'autres un autre type. La récolte d'informations auprès

de congénères, voire de compétiteurs d'une autre espèce, peuvent avoir des risques et engendrer des coûts (nécessité de fuite, blessures, voire mortalité). Ainsi, seuls les individus suffisamment compétitifs pourraient avoir accès à certaines informations (comme le nombre de petits produits, qu'il faut aller voir directement dans le terrier ou le nid par exemple), les individus moins compétitifs devant utiliser des informations récoltées plus à distance. Certaines études ont montré un lien entre les traits de personnalité (niveau d'agressivité, de témérité, d'exploration, ...) et le niveau de réaction aux congénères, ce qui peut suggérer que certains individus accorderaient plus d'attention aux congénères, et collecteraient potentiellement plus d'informations sociales.

Mon projet de thèse, dirigé par Dr. B. Doligez (Université de Lyon, France), Prof. L. Gustafsson (Université d'Uppsala, Suède), et co-encadré par Dr. J.T. Forsman (Université d'Oulu, Finlande), a pour but d'explorer l'origine des différences inter-individuelles d'utilisation d'informations sociales, et notamment de voir si ces différences sont dues à l'expérience passée des individus et à leur patrimoine génétique (Chapitre 3), à leurs traits de personnalité (Chapitres 4-6), et/ou au fait qu'ils utilisent d'autres informations confondantes que l'on ne soupçonnait pas jusqu'alors (Chapitre 6).

Pour répondre à ces questions, je me suis basée sur les données d'une population de gobe-mouches à collier (*Ficedula albicollis*). Le gobe-mouche à collier est un petit passereau migrateur, et représente aujourd'hui une espèce modèle dans l'étude des passereaux et des oiseaux en général, de par l'important jeu de données récolté chaque année depuis 1980 sur l'île de Gotland en Suède. Les gobe-mouches utilisent volontiers des nichoirs artificiels pour construire leur nid, ce qui facilite la mise en place de protocoles expérimentaux et le suivi de la reproduction. De nombreuses études ont mis en évidence que les gobe-mouches utilisent des informations sociales récoltées auprès d'autres gobe-mouches mais aussi de mésanges charbonnières (*Parus major*), espèce compétitrice, pour leur choix d'habitat de reproduction. Les mésanges partagent en effet les mêmes besoins en habitat et nourriture, et sont présentes sur le site de reproduction avant les gobe-mouches. Les conséquences (bonnes ou mauvaises) de leurs décisions sont donc facilement observables lorsque les gobe-mouches s'installent à leur retour de migration. Les gobe-mouches utilisent notamment

la présence, le succès reproducteur, l'investissement primaire dans la reproduction, et les préférences de site de leurs compétiteurs tels que les mésanges comme indice de la qualité de l'habitat.

Les données empiriques sur le gobe-mouche à collier sont nombreuses, mais j'ai aussi eu accès à des données expérimentales d'utilisation d'informations sociales. En effet, entre 2012 et 2016, nous avons mené une expérience pendant laquelle nous mimions une préférence de type de site par des mésanges et nous laissions aux gobe-mouches la possibilité de s'installer dans des nichoirs identiques à la préférence des mésanges, ou des nichoirs différents (test de copiage). Comme nous avions ces données pour plusieurs années, nous avons récolté plus de 1500 choix en tout. Le gobe-mouche se reproduisant tous les ans pendant environ 5-6 ans, et 30% de la progéniture revenant sur son site de naissance, nous avions à la fois des décisions des parents, mais aussi de la progéniture revenue se reproduire. Avec des modèles statistiques bayésiens de génétique quantitative, j'ai pu ainsi montrer que ce comportement n'est pas transmis entre parents et enfants, et ce en utilisant une approche statistique très novatrice permettant d'estimer l'héritabilité de décisions conjointes mâle-femelle. De plus, mes résultats ont permis de mettre en avant que cela dépendait de l'expérience passée des individus, les couples avec un jeune mâle ayant respectivement plus de chances de copier le choix des mésanges que les autres couples (Chapitre 3, article publié dans *Frontiers in Ecology and Evolution*). Pour ces mêmes individus expérimentaux, j'ai estimé leur degré d'agressivité, de témérité, et de néophobie (peur de la nouveauté) via des tests comportementaux. Nous avons montré que ces trois traits sont répétables, constituant donc des traits de personnalité (Chapitre 4), et qu'il affecte le comportement de copiage (Chapitre 5). La probabilité de copier était en effet dépendante de l'agressivité des mâles de plus de un an, la témérité et la néophobie n'ayant alors aucun effet (Chapitre 5). Mes résultats témoignent d'un accès et d'une utilisation différentielle de l'utilisation d'informations sociales selon le statut (sexe, âge, personnalité), et expliquent le maintien des différentes stratégies (copier ou ne pas copier les compétiteurs) au sein de la population. Ces effets âge- et sexe- spécifiques devraient structurer de façon importante le réseau social et l'assemblage spatial des populations.

J'ai également conduit un autre protocole expérimental en 2017 pour tester si les gobe-mouches utilisent les caractéristiques de chant des mésanges, représentatifs de la compétitivité, pour choisir leur habitat. En effet, la qualité intrinsèque des individus peut représenter une information témoignant de la qualité de l'habitat occupé. Les individus peuvent être en bonne condition car vivant dans un habitat riche, ou bien les individus de « bonne qualité », via leur plus forte compétitivité, peuvent avoir accès à de meilleurs habitats. Des pressions de sélection devraient donc favoriser des stratégies limitant les interactions avec les compétiteurs, mais qui permettraient à l'individu collectant l'information d'estimer soit la qualité des individus informatifs soit leur valeur sélective dans l'habitat. Les signaux acoustiques par exemple sont facilement accessibles, et constituent donc des informations peu coûteuses à récolter. Ils représentent de façon fiable la qualité de l'individu produisant le signal du fait de fortes pressions de sélection sexuelle. Nous pouvons donc nous demander si ces signaux fiables et peu coûteux pourraient être utilisés comme information sociale témoignant de la qualité individuelle. Il existe plusieurs études portant sur l'attraction conspécifique due à de la repasse de chants de congénères, mais les exemples à l'échelle hétérospécifique sont plus rares. Certains parasites de ponte par exemple se basent sur des traits sélectionnés sexuellement pour estimer la qualité des parents adoptifs.

L'objectif de ce projet était de tester expérimentalement si les gobe-mouches à collier utilisent l'information de qualité individuelle contenue dans les chants des mésanges charbonnières, pour choisir leur habitat de reproduction. Les gobe-mouches à collier partagent en partie leur niche écologique avec les mésanges charbonnières. Des études empiriques et expérimentales ont mis en évidence que les gobe-mouches à collier et les gobe-mouches noirs, une espèce proche, utilisent de l'information sociale à la fois conspécifique et hétérospécifique (présence et performances reproductives) de façon complexe pour ajuster leurs décisions de choix d'habitat de reproduction, et ce, à différentes échelles spatiales (à l'échelle du site local, ou de la forêt). On peut donc s'attendre à ce que les gobe-mouches se basent également sur d'autres indices de la qualité des mésanges ou de leur habitat, indices qui seraient moins coûteux à récolter, comme des traits phénotypiques (par exemple

la taille), ou des traits sexuels secondaires (par exemple la coloration ou les caractéristiques de chant). Les traits sexuels secondaires acoustiques tels que la taille de répertoire de chant, ou la longueur de strophes sont liées à la qualité des mésanges charbonnières (leur succès reproducteur au cours de la vie ou leur dominance, et donc par extension leur capacité à s'installer dans de bons habitats).

Ce projet visait à expérimentalement tester si les gobe-mouches utilisent les signaux acoustiques des mésanges pour leur choix d'habitat de reproduction à petite échelle. J'ai tout d'abord testé s'il y avait une attraction hétérospécifique du simple fait de la diffusion de chants de mésanges au moment de la prospection et de l'installation des gobe-mouches. J'ai également testé si les gobe-mouches discriminaient des chants de mésanges à partir des caractéristiques de taille de répertoire et de longueur de strophes, en s'installant préférentiellement à proximité de mésanges charbonnières qui seraient de meilleure qualité. Afin de tester ces hypothèses, pendant la période d'installation des gobe-mouches (du 25 avril au 20 mai environ), nous avons diffusé dans de petites zones expérimentales (i) soit des chants de mésange charbonnière présentant les caractéristiques d'une mésange de bonne qualité (grand répertoire et strophes longues : « mésange compétitive »), (ii) soit des chants de mésange charbonnière présentant les caractéristiques d'une mésange de moins bonne qualité (petit répertoire et strophes courtes : « mésange non compétitive »), (iii) soit comme contrôle des chants de pinson des arbres *Fringilla coelebs*, espèce avec laquelle les gobe-mouches ne partagent pas leur niche écologique mais qui ne leur est pas étrangère pour autant. Nous avons ensuite observé les dynamiques d'installation dans les nichoirs alentours, puis nous avons réalisé des tests comportementaux afin de mesurer l'agressivité des gobe-mouches s'étant installé. Enfin, nous les avons capturés pour le suivi à long terme de la population. Encore une fois, mes résultats ont permis de mettre en évidence que le niveau d'agressivité de l'individu influençait le choix d'habitat ici, mais chez les vieilles femelles cette fois : les plus agressives préférant s'installer près des mésanges les moins compétitive. Cette expérience est la première mise en évidence que des individus d'une espèce peuvent utiliser l'information de qualité contenu dans le chant d'une autre espèce, alors que cette information est destinée initialement au choix

de partenaire et à la compétition intra-sexuelle (Chapitre 5).

Pour conclure, mes résultats de thèse démontrent que l'utilisation d'informations provenant des mésanges n'est pas génétiquement déterminée, mais dépend bien de l'expérience (Chapitre 3). Il dépend aussi de l'âge, et de la personnalité des individus (Chapitre 4-6).

Nous savons que les autres individus alentours, même s'ils ne sont qu'observés, ont une grande importance dans les décisions individuelles. Ceci doit donc structurer spatialement les communautés d'oiseaux, et comme j'espère le montrer très prochainement, les individus pourraient se répartir suivant leurs niveaux d'agressivité, celui de leurs voisins, les chants qu'ils entendent etc. La mise en évidence d'une structuration non aléatoire des communautés d'oiseaux serait un grand pas en avant dans la compréhension des mécanismes de sélection d'habitat. Or, les critères de sélection d'habitat sont des paramètres cruciaux dont on doit tenir compte lors de la mise en place de protocoles de réintroduction d'espèces ou de restauration d'écosystèmes, sans quoi les individus risquent tout simplement de ne pas s'installer dans les habitats proposés. La composante liée à l'environnement social est très peu présente encore dans ces protocoles, car cela implique des processus complexes et très dépendants des caractéristiques individuelles, et surtout parce que jusqu'alors on sous-estimait leur importance. Mes projets de recherche permettront je l'espère d'améliorer la conduite de protocoles de conservation d'oiseaux, mais aussi plus généralement de toute espèce pouvant glaner de l'information de compétiteurs.

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Affiliations of co-authors

DANIEL, Grégory

Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Univ Lyon - Université Claude Bernard Lyon 1, Villeurbanne, France

Department of Ecology and Evolution, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

DOLIGEZ, Blandine

Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Univ Lyon - Université Claude Bernard Lyon 1, Villeurbanne, France

FORSMAN, Jukka

Department of Ecology and Genetics, University of Oulu, Oulu, Finland

GERMAIN, Marion

Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Univ Lyon - Université Claude Bernard Lyon 1, Villeurbanne, France

Department of Ecology and Evolution, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

Centre d'Étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, Canada

GUSTAFSSON, Lars

Department of Ecology and Evolution, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

KIVELÄ, Sami

Department of Ecology and Genetics, University of Oulu, Oulu, Finland

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Chapter 1

General introduction



1.1 Social information use: a strategy used in various contexts

1.1.1 Defining social and personal information

Throughout their life, individuals have to make decisions, such as where to forage, where to breed, with whom to mate, whether to fight or retreat. As resource availability and quality vary in time and space, such decisions may have major consequences on individual fitness. Therefore, strong selective pressures must promote the use of strategies that will enable individuals to adaptively choose among the possible options. One strategy is the use of information; indeed, making informed decision enables individuals to better cope with environmental uncertainty (Schmidt et al. 2010).

Defining biological **information** is not an easy task. One can define information as anything that reduces uncertainty (Danchin et al. 2004), but this definition lacks generality and applicability in some contexts (Dall 2005). For “anything” to be defined as information, it needs to be somehow useful, processed, and change the state of the receiver (Jablonka 2002, Dall 2005, Dall et al. 2005). Therefore we can distinguish “potential information” (detectable facts) from “realized information” (detected, processed, and used “factors that can affect the phenotype in ways that may influence fitness” (Wagner and Danchin 2010). Realized information can be divided into two categories: (1) information derived from the individual’s own experience in the environment (**personal information**, e.g. previous foraging or reproductive success), and (2) information obtained by observing other individuals’ actions, decisions, and performances in the environment (**social information**, Danchin et al. 2004, Dall et al. 2005).

The concept of social information encompasses a variety of information types (Figure 1.1), and are either signals, i.e. information intentionally produced (e.g. calls, songs, ornaments), or inadvertently produced (e.g. presence, reproductive success). We further distinguish **performance cues**, i.e. social information on individual’s success, quality,

or performance in the environment (e.g. feeding rate or breeding success of competitors), from other **social cues**, i.e. qualitative information such as the presence of others or the flight behaviours of conspecifics under threat (Danchin et al. 2004, Dall et al. 2005). The term **public information** formerly referred to performance cues (Danchin et al. 2004), but was later redefined as any social information available to others, as opposed to **private information** (Wagner and Danchin 2010). Given the discrepancies in the literature in the use of the term “public information”, one can also simply use the terms “private” and “non-private” information (Figure 1.1).

Several processes originate from social information use. **Social attraction** for example, refers to the attraction of conspecifics or heterospecifics to the mere presence of others. **Social learning** is another well-studied process, both in human and non-human behavioural studies, and refers to learning from the observation of - or interaction with- other individuals or their product (e.g. scent; Heyes 1994); it typically encompasses learning the location of a resource (through “local enhancement”) or how to obtain it. **Social eavesdropping** refers to the extraction of quality information by observing the interactions between several individuals (e.g. observing the outcome of male-male fight for mate choice, or of cleaning interactions). This fairly restrictive definition is sometimes broadened and refers merely to the fact that some individuals look at other’s (extended) phenotype (e.g. also their nest, their offspring). **Copying** (e.g. mate copying, habitat copying) is well used also in the literature and can be viewed as the process of copying others (e.g. choosing the same mate), as well as the social learning process leading to this decision.

From the variety of these terms, it is clear how broad and inter-disciplinary is the study of social information use, bridging behavioural ecology, ethology, evolutionary biology, communication, or even, when referring to humans, sociology and anthropology.

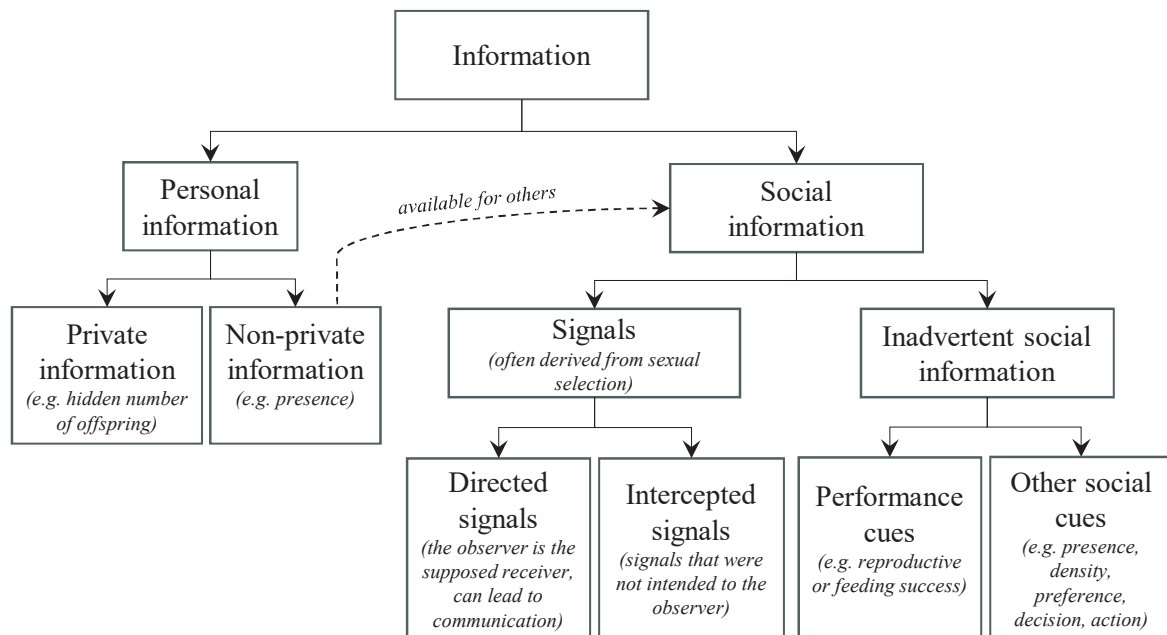


Figure 1.1: *Distinctions and links between the different types of information that are considered in the literature. Adapted and modified from Danchin (2004) and Dall (2005).*

1.1.2 The use of social information: a widespread strategy

The use of social information in decision-making plays a key role in ecology and evolution, driving complex species assemblage, aggregation, coloniality and to an extreme point, cultural evolution (Danchin et al. 2004). This behaviour occurs in various taxa (e.g. in birds, Doligez et al. 1999; fish, van Bergen et al. 2004; reptiles, Cote and Clobert 2007; insects, Loyau et al. 2012; mammals, Vale et al. 2014) and various contexts: foraging strategies (e.g. Templeton and Giraldeau 1995, Coolen et al. 2005), mate choice (e.g. Galef and White 1998, Doutrelant and McGregor 2000, Loyau et al. 2012), assessing opponent abilities (e.g. Oliveira et al. 1998), danger detection (e.g. Karban et al. 2003, Ridley et al. 2014), cleaning interaction (e.g. Bshary and Grutter 2006) and breeding habitat selection (Doligez et al. 2002, Boulinier et al. 2008). Several reviews described this variety in great details (Valone and Templeton 2002, Danchin et al. 2004, Laland 2004, Dall et al. 2005, Valone 2007, Bonnie and Earley 2007). Here I will only present a few examples to provide a good appreciation of the variety of social information use in nature, and start introducing the differences posed by short- and long-term decisions (e.g. foraging and fleeing from predators, vs. mate choice for mate-faithful species and breeding site selection).

Using information for foraging decisions

While foraging, individuals can use the presence of other individuals to assess the location of food patches (local enhancement), but could also use the feeding success of competitors to assess the quality of the food patch and its depletion (Valone and Templeton 2002, Valone 2007). One of the early experimental studies on that topic revealed that starlings (*Sturnus vulgaris*) use the successful and unsuccessful foraging activities of others for their own departure patch decisions (Templeton and Giraldeau 1995, 1996). Fairly recently, technological advances enabled fine scale study of social foraging. In tit species (*Paridae*) for example, the use of RFID-antennas on feeders (spread in forests to detect the identity

of foraging birds equipped with Passive Integrated Transponder, PIT tags), combined with recently developed social network analytical tools, revealed that social connectivity within a population affect individuals' ability to find and use new food patches (likely through an increased access to social information with increasing network centrality, Ap-
lin et al. 2012). Another technology-based example comes from central place foragers: based on GPS data, dive recorders, and behavioural observations, Guanay cormorants (*Phalacrocorax bougainvillii*) were shown to use the position of "compass rafts" (aggregation of conspecifics on the sea, off the colony) as an indication of food patch location (Weimerskirch et al. 2010). Indeed, these sea birds move between breeding and foraging grounds in large columns, and the position of the rafts of sea birds passively, but constantly aligns with the bearing (to the island) from the largest group coming back from foraging ground towards the colony. The position of the raft thus provides information on the direction to be taken to reach the most recent food patch foraged by conspecifics (Weimerskirch et al. 2010).

With the many more example on (novel) food consumption (e.g. Carter et al. 2014), tool use copying (Loukola et al. 2017), and local enhancement (e.g. Thiebault et al. 2014), it appears that the use of social information plays an important role in foraging decisions, with short-term payoffs allowing a rapid assessment of the benefits to rely on social information.

Assessing other individuals' quality (mate, rival, cooperative partner)

Eavesdropping on others' interactions or signalling may provide information on their quality or performances, a strategy used for example in mate choice, rival assessment, and fish cleaning interactions (Valone and Templeton 2002, Valone 2007, Bonnie and Earley 2007). Regarding mate choice, an individual could prefer to mate with a partner seen mating or preferred by others (e.g. in guppies *Poecilia reticulata*, Dugatkin and Godin 1993, in Japanese quails *Coturnix japonica*, Galef and White 1998) or on the contrary to avoid already mated partners (e.g. in fruit flies *Drosophila melanogaster*, Loyau et al. 2012).

One may also prefer a partner that won a competitive interaction (e.g. in fighting fish *Betta splendens*, Doutrelant and McGregor 2000) or lost it (e.g. in Japanese quails, where mating with aggressive males implies injuries, Ophir and Galef 2003). If mate choice will allow securing a proper partner and optimizing reproduction, it may also be crucial to discriminate who one should not interact with, like a rival competing over resources (e.g. food, partner). Eavesdropping on contests between rivals, to assess rival's competitive abilities and adjust subsequent behaviour has been well studied for example in birds and fish (Oliveira et al. 1998, Valone and Templeton 2002, Valone 2007, Bonnie and Earley 2007). This type of social information seems fairly complex, implying a substantial period of learning. But an interesting experiment on barn owls nestlings (*Tyto alba*) showed that eavesdropping can occur at a very early stage: the nestlings eavesdropped on the calling behaviour of their siblings in the nest, and used this information to assess the dominance of their "nestmates" (among two other owlets) and adjust their own begging behaviour accordingly (when interacting with one owlet at least, Dreiss et al. 2013). A substantial body of work, both in the field and experimentally, focused on understanding the evolution of cleaning mutualism, i.e. cooperation between cleaner and client fish, and revealed the importance of social information use, both from the client and the cleaner perspective, for the maintenance of this system. Indeed, cleaner fish (*Labroides dimidiatus*) prefer to feed on client's mucus rather than client's ectoparasites, i.e. they prefer to cheat (Grutter and Bshary 2003). Client fish may eavesdrop on the interaction between cleaner fish and other clients: eavesdropper clients have been shown to avoid interacting with cleaner fish they have seen cheating and prefer interacting with cooperative ones (Bshary 2002, Bshary and Grutter 2006). Cleaner fish constantly adjust their cooperative/cheating behaviour depending on the presence of another bystander client ("audience effect", Bshary and Grutter 2006), and on the client size and species (Bshary 2002). The coexistence of cheating and cooperating behaviour is thus highly driven by social information use, but was also later found to partly originate from personality differences between cleaner fish (Wilson et al. 2014). In summary, assessing the quality of required resource, whether it is a food item, a food patch, or a partner to mate or cooperate with, may provide valuable

information to fine-tune and optimize short- and long-term decision making.

Using information to avoid risks

It is not surprising that when facing “the ultimate” risk, i.e. death, individuals may rely on social information, or more specifically on the behaviour of individuals sharing the same predators. Mixed bird communities exemplify this well with their heterospecific mobbing behaviour against common predators (reviewed in Magrath et al. 2015). Some species not only use social information for direct response to predation risk, but may also adjust their behaviour when living with other species sharing the same predators (Magrath et al. 2015): Scimitarbill (*Rhinopomastus cyanomelas*) for example, a solitary species, expands its foraging range to more open areas in the presence of pied babblers (*Turdoides bicolor*), a social species sharing the same predators and presenting a sentinel system (presence of babblers mimicked with playback, Ridley et al. 2014). Moving away from the classical behavioural ecology research, eavesdropping on alarm signals has also been shown in plants: a plant partially eaten by herbivores may release chemicals that are detected by neighbouring plants (not necessarily of the same species), which, in turn, increase their chemical defences against predators (e.g. sagebrush *Artemisia tridentata* and tobacco pants *Nicotiana attenuata*; Karban et al. 2003). Social information is thus an important component of danger detection for many species.

Using information for breeding habitat selection

The choice of a breeding site is a crucial decision in an individual’s life, as it determines what the adults and offspring will have to face during the reproductive period in terms of abiotic factors (e.g., temperature, humidity), food, parasites, competitors and predators. Species selecting an all-purpose breeding territory constitutes an extreme case, as the breeding habitat is where they will perform courtship, mate, breed, forage, for sometimes a long period relative to an individual’s lifespan. Thus, all the cases reviewed above where

the use of social information occurs, might occur for breeding site selection too, but with an additional temporal effect as a breeding event lasts much longer than a foraging trip for example (but choosing a partner for life has also long term fitness consequences).

Most examples of social information use for breeding site selection come from birds (but not exclusively, see for example Deutsch and Nefdt 1992 for evidence in antelopes, or Cote and Clobert 2007 in lizards). This may originate from the greater prospecting and moving abilities of birds, from the great number of migratory species that may lack up-to-date information on habitat quality when arriving in their breeding or wintering grounds, or from the global greater interest they have received in behavioural ecology compared to other taxa (even more particularly on passeriformes, Rosenthal et al. 2017). Birds have been shown to cue on the presence of other breeding individuals to choose their own breeding site (social attraction; e.g. Hahn and Silverman 2006, Ward et al. 2010, Szymkowiak et al. 2017). For instance, migratory passerines were found to be attracted to breeding sites by the songs of conspecific and heterospecific competitors (Szymkowiak et al. 2017). This has even been used as a management strategy for conservation: decoys or playbacks of conspecific placed on empty breeding sites may attract new individuals (e.g. in *Vireo atricapilla*, Ward and Schlossberg 2004). But the mere presence of conspecifics may poorly inform on the real habitat quality: if all individuals settle because of others' presence, it will not inform on the actual habitat quality (individuals may saturate the environment, and suffer large costs due to increased competition, whereas other habitat patches are available for settlement). Another strategy that should inform more accurately on habitat quality consists in cueing on other's reproductive success at the end of their reproductive season. However, if individuals are single-brooded and/or highly synchronous, the reproductive success of competitors can only be used as information source after a long time-lag, i.e. only for the next breeding attempt. This strategy would thus only be beneficial if habitat quality is sufficiently predictable in time (Boulinier and Danchin 1997, Doligez et al. 2003). Cueing on other's reproductive success is thought to be one cause of the emergence of coloniality (process coined performance-related conspecific attraction, Danchin et al. 1998, 2004).

A long-studied example comes from black-legged kittiwakes (*Rissa tridactyla*), a colonial seabird that has been shown to prospect late in the breeding season (prospecting peaks at chick rearing and early fledging, Boulinier et al. 1996), and to use the breeding success of the breeding patch (here, cliff) to make dispersal decisions in the following year (Danchin et al. 1998, Boulinier et al. 2008). Successful breeders were shown to be site faithful between years irrespective of the patch reproductive success, while failed breeders dispersed to other breeding patches when the reproductive success of their patch was low (Danchin et al. 1998, Boulinier et al. 2008). Other well-studied avian examples come from the hole-nesting and/or migratory passerine guild. For example, Doligez et al. (2002) manipulated the patch reproductive success in a patchy population of collared flycatchers (*Ficedula albicollis*), and found that this affected the immigration and emigration decisions the following year (see Chapter 2 for more details).

The use of social information for breeding site selection is thus also a widespread strategy, but imposes different time (and probably energy and cognitive) constraints than in the foraging context.

1.2 The adaptive use of social information

1.2.1 Value, costs, and benefits of information use

For the use of social information to be adaptive, it should increase the fitness of the information users. More generally, the value of information can be measured as the difference in fitness while making an informed vs. an uninformed decision (Gould 1974). Gathering personal information, by **trial-and-error** tactics, is time and energy consuming, especially when considering reproductive decisions for which a trial is made over an entire breeding season, or when considering predator avoidance for which a trial might lead to immediate death. Conversely, personal information, which directly reflects the interactions of the individual's own genotype or phenotype with the environment, may be more reliable than social information.

As gathering social information can be less costly than personal information, social information usually appears beneficial, but this is not always the case (Kendal et al. 2005, 2009, Laland 2004, Duboscq et al. 2016). First, gathering social information involves direct costs: for example prospection requires energy, but can also be risky (increased predation risks and interactions). Second, if the acquisition of social information cannot coincide with other activities such as foraging or acquiring personal information, it may also involve costs (e.g. waste of time, energy, and opportunities). Third, copying others or using the same information as others may increase competition costs (at the conspecific level: Barta and Giraldeau 1998, Lee et al. 2016, and through an increase in niche overlap when copying heterospecifics, Seppänen et al. 2007, Loukola et al. 2013).

There is thus a trade-off between acquiring and using reliable but costly personal information, and cheap (or cheaper) but not as reliable social information. This trade-off is also mediated by the accuracy of each information type, for example how up to date they are regarding the resource quality or position, and thus may depend on the delay between information gathering and use. For the use of social information to be adaptive, it should thus be flexible and context-dependent (Laland 2004). Effectively, individuals can altern-

actively use personal or social information depending on the reliability and availability of these information (Templeton and Giraldeau 1996, Kendal et al. 2004, 2005, van Bergen et al. 2004, Coolen et al. 2005). Different strategies were described, regarding **when** to use social vs. personal information, and **from whom** to collect information (Kendal et al. 2005, 2009, Laland 2004).

1.2.2 When to use social information, and from whom?

Theoretical studies, supported by empirical and experimental evidence (reviewed in Kendal et al. 2005, 2009, Laland 2004), described that social information should be favoured:

- when the individual is uncertain because it has no personal information (young, unexperienced, immigrant individuals) or its information is outdated or unreliable
- when it is more costly to use personal than social information
- when the fitness outcome of the previous decisions (based on other information) was null or detrimental (i.e. when dissatisfied)

Different social learning strategies are also distinguished depending on who is the information provider (“who strategies”; reviewed in Kendal et al. 2005, 2009, Laland 2004):

- copy the majority: positive frequency-dependent behaviour; the probability to copy increases with the proportion of demonstrators (information providers), the most common behaviour is adopted
- copy if rare: negative-frequency-dependent behaviour; the least common behaviour is adopted, occurs in particular if innovation provides fitness benefits
- copy individuals that are successful, dominant, older, more experienced, or good social learners
- copy kin or friends, with whom altruistic behaviours are more likely to occur

At the population level, the use of social information for social learning can be viewed as a producer-scrouter game, where asocial learners (i.e. individuals using personal information) are producers, and social learners (i.e. using social information) are scroungers. Within the framework of game theory, a stable equilibrium is reached for a mixture of producers and scroungers in the population (Barnard and Sibly 1981). Otherwise, if most individuals use only social information (e.g. most individual copy the breeding or foraging preference of others), the information (e.g. others presence) no longer reflects the habitat quality, leading sometimes to maladaptive decisions (Giraldeau et al. 2002, Rieucou and Giraldeau 2011). The benefits arising from copying the majority thus likely depend on the actual proportion of the population following a scrounging strategy (Giraldeau et al. 2002, Rieucou and Giraldeau 2011).

1.2.3 Heterospecifics as information providers

All these strategies (copying the majority, the successful, the dominant ...) are not limited to conspecific demonstrators. Indeed, the use of social information gathered from heterospecific individuals has been shown to occur for foraging decisions, breeding site selection, predator avoidance... (reviewed in Seppänen et al. 2007, Goodale et al. 2010, Avarguès-Weber et al. 2013). If another species partly shares the same needs or the same predators, it may provide information as useful and valuable as information obtained from conspecifics. If the ecological niche does not fully overlap between species (e.g. they share the same predators but not the same food resources), using social information from heterospecifics may even be more valuable than from conspecifics, as the competitive costs of copying heterospecifics should be lower than copying conspecifics (Seppänen et al. 2007). Besides, heterospecific individuals may be better at sampling the environment and/or may provide different information than conspecifics (e.g. more difficult to obtain; Goodale et al. 2010). Seppänen et al. (2007) suggested that there is an optimal ecological distance between the information provider and receiver, and that heterospecific social information, acquired at the proper distance, should be more valuable than conspecific

information.

In the context of breeding site selection, heterospecific social information is thought to be particularly reliable and valuable for migratory species, which are highly timely constrained in their reproduction, and should thus rapidly decide where to breed. Resident species, which experienced the environmental conditions all winter long, might have a better knowledge of habitat quality. They are supposedly less constrained in their reproductive timing and had time to thoroughly assess habitat quality before choosing a specific breeding site. Besides, if residents are present and breeding, this should reliably inform on the local absence of predators (Mönkkönen and Forsman 2002). Moreover, when the first migrants arrive on breeding grounds, only heterospecific individuals are present, there is no conspecific information available. For all these reasons, migratory species, especially early individuals, may use information provided by resident species in order to assess habitat quality. Of course, this is conditioned by the costs induced by heterospecific competitors (Mönkkönen and Forsman 2002). A well-studied example of migratory species using information from resident ones are forest bird communities at rather high latitudes (i.e. where the proportion of migratory species is the largest and seasonality is the strongest, putting even stronger time-constraints on the reproduction; reviewed in Mönkkönen and Forsman 2002). In Chapter 2, I further develop examples showing the use of social information from tit species by flycatchers in boreal forests, a typical example of resident-migrant information system.

1.3 A variable use of social information

Social information use is a usually beneficial and widespread strategy. However, the empirical studies conducted so far also showed that the use of social information may differ among species, populations and individuals. Such differences may arise because this behaviour is flexible in time and between contexts, or because individuals consistently differ from each other in their propensity to gather and use social information (because of physical attributes, or consistent behavioural response for instance). I hereafter describe some within- and between- individual causes of variability in social information use.

1.3.1 Sources of within-individual variability

The amount of personal information an individual acquired, as well as the reliability of both personal and social information, plays an important role in the individual propensity to use both types of information. If an individual has no prior experience (i.e. no personal information, e.g. a young individual), it is more likely to use social information (reviewed in Kendal et al. 2005). In collared flycatchers, a migratory passerine, yearling males were shown to rely more on social information for dispersal decisions than old successful breeders, likely because yearlings had less personal information (Doligez et al. 1999). In the same species, the use of social information for nest site selection has also been shown to depend on prior knowledge on the environment (dispersal status and age, yearlings and immigrants having presumably less knowledge of the local habitat quality, Kivelä et al. 2014, see Chapter 2 for further details).

When both personal and social information are available, they can be differently weighed depending on their reliability. The flexible use of personal and social information has been particularly studied in fish with experiments showing that the use of social over personal information depends (i) on the reliability of personal information but also (ii) on the risk to use personal over social information. Indeed, the preference of personal over social information use decreased with the reliability of the personally-acquired knowledge on food

patch richness, and decreased with increasing time since personal information acquisition (in nine-spined sticklebacks *Pungitius pungitius*, van Bergen et al. 2004). Guppies have been shown to prefer using social information rather than their own reliable personal information regarding food patch location, but only when using personal information meant losing visual contact with the shoal, a situation that should be risky in the presence of predators (Kendal et al. 2004). In such a situation, it is clear that the use of social information will be flexible depending also on the ecological context.

Some personally acquired information may also increase the motivation to use social information. Failed breeders for example could have a greater motivation than successful breeders to gather reliable information for future decisions, besides having more time to collect them (unsuccessful kittiwakes disperse when the cliff reproductive success is low, Danchin et al. 1998, Boulinier et al. 2008; unsuccessful collared flycatcher males disperse to patches with lower competition, Doligez et al. 1999).

The use of social information is thus surely flexible depending on the context and changing throughout an individual's lifetime, but there is also some evidence showing that individuals may be constrained in their access to information, their interpretation of it, and their resulting decision.

1.3.2 Sources of between-individual variability

To better understand how some individuals may be more likely to use social information than others, we can think about the use of social information as a 5-steps process: (1) the event occurring (e.g. a competitor feeding in a patch), (2) the observation of this event (or information gathering), (3) the cognitive processing of the information, (4) the resulting decision and (5) the consequences of this decision (usually the only step, with the event, that scientists can observe, especially when conducting experiments in the wild). Individuals can consistently differ in their likelihood to observe an event, in their cognitive abilities, and in their decisions given the information they acquired. These consistent differences may originate from physical, physiological, or behavioural attributes. An ex-

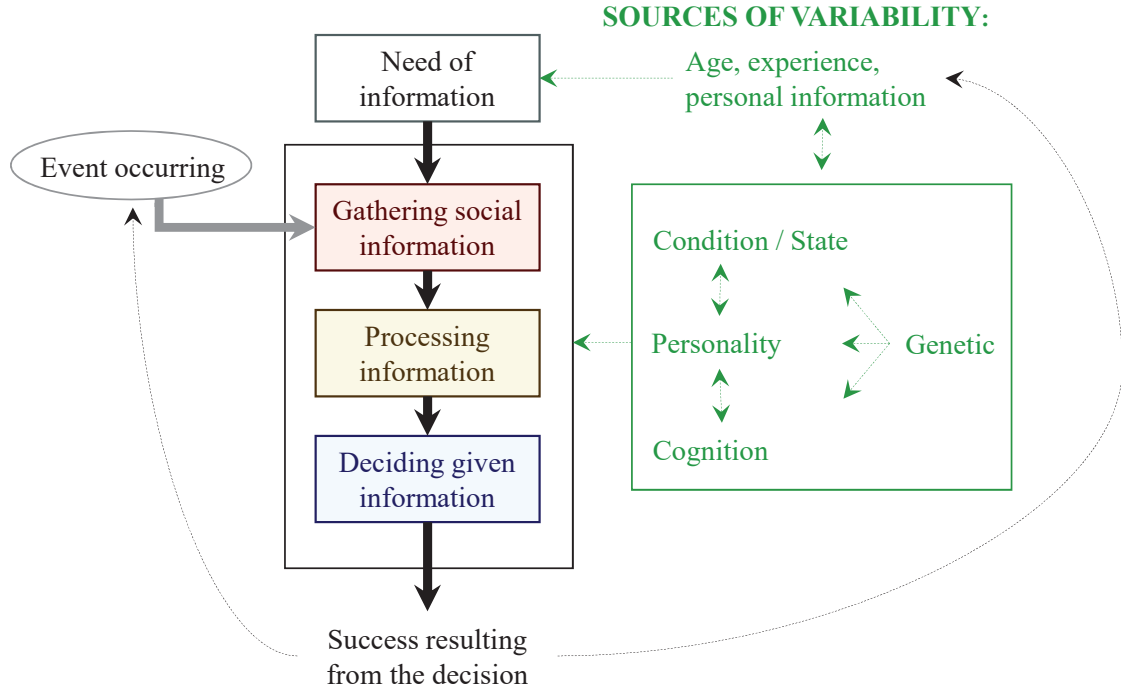


Figure 1.2: *Flowchart of the various individual parameters (in green), either consistent or flexible throughout an individual lifetime, are expected to affect the different steps of social information use. This graph is a raw and non-exhaustive illustration of possible pathways of variability.*

tensive body of literature investigated the link between the use of social information and consistent behavioural differences (so-called “personality traits”). Because this has been one of the main focus of my PhD, I provide more details on it in the next section. But before going further into personality studies, I provide here general but non-exhaustive food-for-thought regarding consistency in information access, information process, and the resulting decisions (summarized in Figure 1.2). Note that all mentioned factors participating in between-individual differences in social information use may change over time as individuals age for example, and thus may also participate in within-individual variability.

Consistent between-individual differences in information access

Physical and physiological states are likely to affect individuals’ ability to find and interact with others. Depending on their body condition, early-life environment, consistent exploration tendency, wing or leg length etc.), individuals may differ in their prospection

behaviour or in their ability to detect others based on chemical, acoustic, or visual cues for example.

Among factors affecting the access to information, the social connectivity between individuals, i.e. how likely are individuals to be close to each other or interact, certainly plays its role in between-individual variation in social information use. Information can be transmitted in a population through so-called social network (i.e. social connections between individuals through which information or diseases for example can be transmitted). How well an individual is connected in a social network (1) could be quite consistent over time, depending on an individual global ability to establish social links, and (2) should directly affect how much information an individual has access to. These hypotheses has been studied in Great tits (*Parus major*) for example. In winter, great tits form loose fission-fusion foraging flocks which composition varies within minutes. A population of great tits (in Wytham woods, Oxfordshire, UK) has been monitored since 1947, and all captured individuals have been identified with a PIT tag (attached on a plastic ring) since 2007 (over 90% of the population is pit-tagged). Using RFID-antennas at the entrance of feeders allowed to collect large scale-high quality data on social network during winter (a social bound reflecting the probability of two birds to be detected as part of the same foraging flock). It has been shown that, more central individuals within the social network are more likely to find new food patches, probably because of a greater access to social information (Aplin et al. 2012). Importantly, the position within social network was repeatable over time (Aplin et al. 2015). The between-individual differences in position within social network could thus participate in between-individual differences in social information access.

Constraints in information processing

Once viewed, smelled or perceived, information should be processed, interpreted, deciphered and compared to other information to lead to an optimal decision. Learning, memorizing, processing and storing information are costly processes part of cognition (Shettleworth 2010). Coming back to the specific case of breeding site selection, (hetero-

specific) social information use certainly engages complex cognitive abilities such as long-term learning and memory (from one breeding season to the next) and species recognition (Avarguès-Weber et al. 2013). If cognitive abilities are likely changing over an individual lifetime (throughout the development, and at senescence for instance), they have also been shown to be repeatable (meta-analysis showing repeatability estimates between 0.15 and 0.28; Cauchoux et al. 2018) and correlated with personality traits (eventough not in the same direction depending on the studies; meta-analysis by Dougherty et al. 2018). It is thus likely that individuals differ in their overall social information use because of different cognitive abilities. However, this requires further investigation, especially in wild populations.

Constrained final decisions

Once information is gathered and processed, the resulting decision an individual will make might again be context-dependent, but might also depend on particular traits of the individual. Coming back to the example showing that guppies change their use of personal vs. social information depending on predation risks (induced by foraging far from the shoal, Kendal et al. 2004), some individuals may also be consistently more prone to take risk or to use personal rather than social information. Highly social females (a repeatable behaviour in this species) were shown to follow the decision of the shoal when this decision conflicted with personal information (Trompf and Brown 2014). Conversely, highly social females favoured personal over social information when other fish were present but not feeding at a specific site; less social females on the contrary did not show this plasticity (Trompf and Brown 2014).

Copying the foraging or breeding site of competitors should increase social interactions and thereby competition costs. Some individuals, characterized by physical, physiological, or behavioural traits might be consistently more able to cope with the increased competitive costs resulting from copying competitors. It is thus possible that only the more competitive individuals (maybe dominant, larger and more aggressive for example) will either dare or manage to successfully copy competitor's decisions. In practice, it is

difficult to assess whether individuals do not copy because they do not have information, or do not copy because based on their information, they preferred not to copy. To address this issue, we need first to make sure that all individuals accessed and processed the information (two preceding steps), which could be quite complicated, especially when conducted experiments in wild populations. Second, whether individuals chose not to copy competitors or failed after trying to copy them is an important distinction, but is, again, not so easily observable in the wild. It is possible to address such question using a 2-options trials (often used in laboratory studies). Keeping the example of guppies studied in lab conditions, non-neophobic females (that spent more times near novel objects, again a repeatable behaviour here, correlated with body length) were found to avoid feeding sites of conspecifics, whether the conspecific feeding site coincided or conflicted with the female personal information (Trompf and Brown 2014). In the wild, Forsman J.T. and his collaborators conducted a series of experiments testing copying and rejection of breeding habitat preferences in collared flycatchers: individuals always had both choices available, copy or reject competitor choices, and did not suffer fitness costs for their choice (see Chapter 2 for a review of these experiments; e.g. Seppänen and Forsman 2007, Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013, Forsman et al. 2014, Jaakkonen et al. 2015). Whether the individuals that copied or rejected the tit preference differed consistently in some phenotypic or behavioural traits remained to explore and was the main focus of two chapters of this thesis (Chapters 3 and 5).

1.3.3 Role of genes in maintaining the variability

One fascinating question in evolution is why are the observed differences maintained? What are the evolutionary driving forces behind the maintenance of such different strategies? Why do not all individuals use social information if it is (usually) beneficial? Some answers are found within the game theory framework, which should favour a mixture of producer and scrounger strategy within a population. Combined with the above mentioned individual constraints in social information, consistent rather than flexible producer/scrounger strategies could arise. Of course, the variability in external conditions could also favour

sometimes some social information use strategies and sometimes others, or may favour individual plasticity (further discussed in Chapter 7).

Genetic constraints could play a role in the maintenance of within- and between individual differences in social information use. If the propensity to use social information is genetically transmitted, and the selective pressure favours different strategies in different contexts (season, presence of predators, etc.), it would explain the observed maintenance of between-individual variability in social information use. Similarly, if the plasticity of social information use is itself heritable, we would observe high within- and between-individual variability at the population level. There are so far very few direct evidence of a genetically determined use of social information. Some laboratory experiments showed that the genetic polymorphism at one foraging locus was associated with strong differences in the predominant use of social information in *Drosophila*, both for spatial learning (Foucaud et al. 2013) and in social aggregation (Philippe et al. 2016).

Either directly or through correlations with other genetically based traits (e.g. personality, dispersal), the propensity to use social information could be heritable, thus constraining its flexibility at the individual level. If studies on the genetic determinism of such behaviour are still scarce, the link between social information use and personality, and the heritability of personality traits have received much more attention (see next section and van Oers and Sinn 2013).

Understanding whether the use of social information is highly plastic, partly genetically determined, or part of a larger correlate of various traits will help us understand its evolutionary potential, and was the main purpose of this thesis. To clarify the concepts adopted, in the next section, I start by defining personality. Then I will shortly review the links between social information use and personality.

1.4 Personality differences as an importance source of variability in social information use

In the past two decades, personality, and as a forthcoming its link with social information use, have received great attention. In this section, I first define personality in more details, second explain the theoretical expectations regarding the link between specific personality traits and social information use, and third review the empirical evidence for such links.

1.4.1 Defining personality

For a long time, consistent behavioural differences between individuals were considered as non-adaptive noise around the population adaptive mean (Wilson 1998). In the past two decades, these differences have received considerable attention in behavioural and evolutionary ecology studies (e.g. Dingemanse et al. 2003, Sih et al. 2004b, 2004a, 2012, Dingemanse and Réale 2005, Bell 2007, Réale et al. 2007, Sih and Bell 2008, Bell et al. 2009, Carere and Maestripieri 2013, Dochtermann and Dingemanse 2013, Niemelä et al. 2013, Araya-Ajoy and Dingemanse 2014). Such between-individual differences in behaviour, if they are consistent over time and between contexts, are broadly referred to as **personality, coping style, or temperament**. In other words, when estimating a personality trait in 2 contexts (or over 2 time periods), individuals may show variability in their behaviour (plasticity), but the differences between individuals will be overall maintained (Figure 1.3).

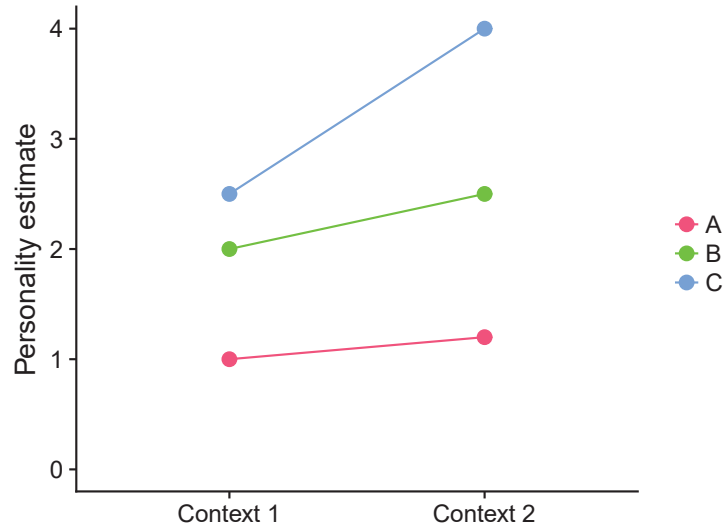


Figure 1.3: *Illustration of the concept of personality trait: the ranking of individuals A, B, and C along the personality axis is consistent between contexts 1 and 2. However, the three individuals show different plasticity level (different slopes).*

In order to provide a common framework for non-human animal personality studies, Réale et al. (2007) proposed to categorize personality along five axes, based on the five axes used to describe human personality (the Big-Five: agreeableness, extraversion, openness to experience, conscientiousness, neurotism; reviewed in Digman 1990):

- **Aggressiveness:** agonistic reaction towards conspecifics
- **Sociality:** non-agonistic reaction towards the presence (or absence) of conspecifics
- **Activity:** general activity in a non-risky known environment
- **Exploration-avoidance:** reaction towards novelty (either novel food, novel environment, novel object, i.e. include neophobia)
- **Boldness-shyness:** reaction in a risky situation, such as the presence of predators or humans (sometimes called ‘docility’, ‘tameness’, ‘fearfulness’)

This discrimination into 5 categories is maybe too restrictive because a set of behaviours measured in very different contexts cannot always be align along a 2D axis (Greenberg

and Mettke-Hofmann 2001, Bell 2017). However, this discrimination presents the advantage to cover many ecological situations and define many behaviours measured so far. Besides, this categorisation enables easy comparisons between studies via meta-analysis, thus providing interesting knowledge on the evolution of such traits (as long as these traits were really collinear, otherwise, complex trend may disappear when projecting on a fictive axis). Rather than a strict guidelines, this 5-axis discrimination could thus be seen as a global framework, open to refinement and adjustment depending on the ecology of the species under study (see comments in Bell 2017).

Throughout this thesis, I used the above definitions with an extension of aggressiveness to the heterospecific level. The use of the term “neophobia” to describe personality differences along the exploration-avoidance axis is usually avoided (except for a pure methodological description) as it refers to the mechanism involved (reaction to a novel object) rather than the underlying process of interest (avoidance of novelty, non-exploration). I acknowledge this subtlety, however, I use, in the next chapters the concept of “neophobia” rather than “exploration-avoidance”, because, reactions towards novel object can be a mixture of fear and curiosity and may not always (negatively) correlate with other exploration tests (Carter et al. 2013a, Greggor et al. 2015). As I did not conduct formal tests of exploration, I hereby preferred, for caution, to use the more precise term of neophobia.

1.4.2 How personality can shape social information gathering and use

As I shortly described in section 3.2, personality likely affects both the access to social information, through prospection and social interactions, and the resulting decision for breeding habitat selection. More specifically, regarding information gathering, we may expect that: (1) more explorative and more active individuals will have access to more information in general, both personal and social, or at a larger spatial scale than others, (2) more sociable individuals may be more prone to observe others and gather social in-

formation and be more attracted to conspecifics (this latter characteristics derives purely from the definition of sociability), and (3) if some information are costly to obtain because of predation risks or competition, bolder and more aggressive individuals may be more able to cope with such constraints and thus gather more information than shy and non-aggressive ones (Figure 1.4). Indeed, copying competitors should also increase the niche overlap with competitors (Loukola et al. 2013, Parejo and Avilés 2016). We may thus expect individuals to modulate their copying behaviour depending on their own competitive abilities (aggressiveness) and that of their competitors.

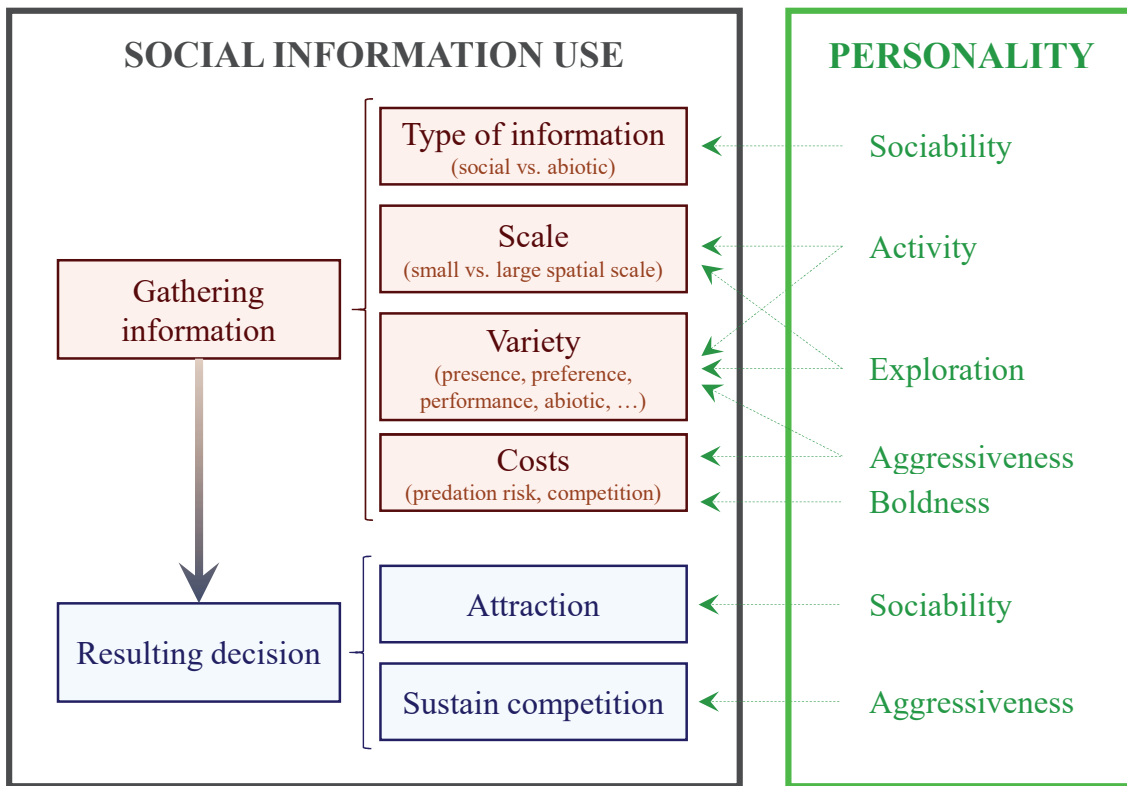


Figure 1.4: Theoretical links between personality and social information use.

1.4.3 Empirical and experimental evidence of links between personality and social information use

At least 22 studies on 4 species of birds, 2 of mammals, and 5 of fish (described in more details in Table 1.1) highlighted a link between one or several personality traits and the use of social information in foraging and shoaling contexts (i.e. predator avoidance

in fish). These studies used very different approaches to study social information use, testing social attraction, local enhancement, scrounging, shoaling or flocking, comparison between social and personal information use, novel food consumption, or task-handling. The majority of these studies looked at the link between exploration and social information use (19 correlations: 11 with a novel object test, “Neophobia” in the table, and 8 with an exploration test). Boldness was also well studied (8 correlation estimates, incl. 5 in fish), but sociability and activity much less (3 and 2 correlation estimates respectively), while aggressiveness was not directly studied.

Personality traits are often correlated (Sih et al. 2004a, Garamszegi et al. 2012) along a proactive-reactive or slow-fast continuum (Koolhaas et al. 1999, Groothuis and Carere 2005), forming so-called behavioural syndrome, i.e. correlated behavioural differences (Sih et al. 2004b). Bold, aggressive, explorative, active, non-neophobic, and less social individuals can be considered as “fast” or “proactive”, and shy, non-aggressive, non-explorative, non-active, neophobic, and social individuals can be considered as “slow” or “reactive”. When projecting the links found for the different personality traits on a slow-fast axis, 12 correlation estimates suggest that slow individuals are more prone to use social information (in light green on Table 1.1), and 6 correlation estimates suggest the opposite (in light orange on Table 1.1).

A corpus of studies on social network offers also additional evidence that personality, social interactions, and social information use may interact: at least 8 additional studies looked at the link between personality traits and position within social network or information transmission through social network (Table 1.2). One common finding among some of these social-network studies is that slow explorer or shy individuals tend to have few but strong and long-lasting social bonds, while fast explorer and bold individuals have numerous but weak social bonds (Pike et al. 2008, Schürch et al. 2010 in agonistic network but the opposite in affiliative network, Aplin et al. 2013a, Snijders et al. 2014 to some extent; but see Croft et al. 2009). In great tits, individuals with a central position within the social network (numerous but possibly weak bonds) are also fast explorers (Aplin et al. 2014, Snijders et al. 2014), and have a greater access to social information

than less central individuals (Aplin et al. 2012). These results would thus be in favour of the hypothesis that fast individuals use more social information than slow ones.

But despite the commonly assumed position of each personality trait along a slow-fast continuum, the correlation with social information remains unclear and may be trait- or species-specific (e.g. different selective pressures acting on migrant vs. resident species, as mentioned previously), or context-dependent (e.g. number or position of conspecifics present, as further explored by Kurvers et al. 2011, 2012). Investigating the link between several personality traits and the use of various types of social information is a challenging task, especially in wild populations, i.e. where selection occurs. When looking at personality traits in a “pace-of-life syndrome” context (fast or proactive individuals having also fast life-history traits), we may wonder whether a given individual will gather and weight similarly social information for foraging, breeding or predator avoidance for example. So far, most of the studies were interested in the foraging context. But as I mentioned previously, the costs and benefits of using social information can greatly differ between foraging decisions and breeding site choice. The selective pressures acting on both contexts may differently shape the relation between personality and social information use. Further empirical and experimental studies on other species, in other contexts, possibly in the wild, should greatly improve our understanding of the mechanisms in social information gathering, processing, and decision making.

Table 1.1: Description of the 22 studies looking at the link between personality and social information use (whether it has been found positive “+”, negative “-”, or non-significant “NS”), sorted by taxa and species. “Pop.” refers to the conditions in which the population was studied (“c” for captivity, “w” for wild, “wc” for wild population brought back in captivity for the study). N is the sample size. We also describe the context in which the use of social information has been studied (“F” for foraging, “S” for social context, e.g. shoaling). Links in light green suggest that reactive/slow individuals use more social information. Links in light orange suggest that proactive/fast individuals use more social information.

Taxa & Species	Pop	N	Context	Social information	Perso. trait	Link	Details	Reference	Ref.
Aves									
<i>Branta leucopsis</i>	c	28	F	Feeding site of conspecifics	Neophobia	+	Neophobic individuals join conspecifics at feeding site	Kurvers et al., 2010a	[1]
<i>Branta leucopsis</i>	c	12	F	Sites with higher conspecific feeding rate	Neophobia	+	Neophobic individuals join conspecifics feeding at higher rate	Kurvers et al., 2010b	[2]
<i>Branta leucopsis</i>	c	28	S	Following tutors through a maze towards aviary	Neophobia	+	Neophobic individuals followed demonstrator in a maze, rather than lead (only when 1 demonstrator, no personality effect when 3)	Kurvers et al. 2011	[3]
<i>Corvus frugilegus</i>	wc	19	F	Scrounging for feeding site	Neophobia	-	Less neophobic individuals did not produce more (foraging context), but scrounged more than neophobic ones.	Jolles et al. 2013	[4]
<i>Parus major</i>	c	14	F	Copying tutors feeding site	Exploration	+	Explorers copy tutors feeding site	Marchetti & Drent, 2000	[5]
<i>Parus major</i>	w	152	F	Discovering new food patch while foraging in flocks	Sociability		Individuals with a higher centrality had more chance to discover new food patch, likely due to a greater access to social information	Aplin et al. 2012	[6]
<i>Parus major</i>	w	134	F	Flocking behaviour during foraging	Exploration	-	Slow explorers were more socially attracted and choose foraging sites with high conspecific density	Aplin et al. 2014	[7]
<i>Parus major</i>	c	36	S	Conspecific attraction (mimicking social defeat or mate choice decisions)	Neophobia	+	Neophobic individuals were more attracted to conspecifics	Snijders et al., 2017	[8]
					Exploration	NS	No effect of exploration on social attraction		
<i>Taeniopygia guttata</i>	c	24	F	Scrounging for feeding site	Exploration	NS	No effect of exploration on scrounging success	David et al., 2011	[9]

[1] Kurvers et al. (2010b); [2] Kurvers et al. (2010a) ; [3] Kurvers et al. (2011); [4] Jolles et al. (2013); [5] Marchetti & Drent (2000); [6] Aplin et al. (2012); [7] Aplin et al. (2014); [8] Snijders et al. (2017); [9] David et al. (2011)

Table 1.1. (Continued)

Taxa & Species	Pop	N	Context	Social information	Perso. trait	Link	Details	Reference	Ref.
Mammalia									
<i>Ovis aries</i>	d	40	S	Group dynamic	Neophobia	+	Groups of neophobic individuals tended to be more cohesive (split less)	Michelena et al. 2009	[10]
<i>Ovis aries</i>	d	20	F	Flocking behaviour, with or without human disturbance	Exploration	-	Slow explorers aggregated more to conspecifics, especially when disturbed	Sibbald et al. 2009	[11]
<i>Papio ursinus</i>	wc	55	F	Scrounging for feeding site	Neophobia	+	In natural conditions, no effect of personality of joining conspecifics. In manipulated conditions, when patch quality could not be seen from far, neophobic individuals tend to join conspecifics.	Carter et al. 2013	[12]
					Boldness	NS	No effect of boldness.		
<i>Papio ursinus</i>	wc	32-36	F	Social learning (novel food)	Neophobia	-	Less neophobic and shy individuals handled the novel food longer after observing a demonstrator	Carter et al. 2014	[13]
					Boldness	+	Bold (less "anxious") individuals payed more attention to demonstrators		
<i>Papio ursinus</i>	wc	33-41	F	Social learning (solving task for food)	Neophobia	NS	No effect of personality on the propensity to observe demonstrator, or to handle longer the task after observing demonstrator	Carter et al. 2014	[13]
					Boldness	NS			
<i>Papio ursinus</i>	wc	94	F	Scrounging for feeding site	Neophobia	NS	No effect of personality on the observation of others or on entering feeding patch newly discovered by others	Carter et al. 2016	[14]

[10] Michelena et al. (2009); [11] Sibbald et al. (2009); [12] Carter et al. (2013b); [13] Carter et al. (2014); [14] Alecia et al. (2016)

Table 1.1. (Continued)

Taxa & Species	Pop	N	Context	Social information	Perso. trait	Link	Details	Reference	Ref.
Pisces									
<i>Gasterosteus aculeatus</i>	wc	60	S	Schooling tendency	Boldness	-	Shy individuals tended to school more	Ward et al. 2004	[15]
<i>Gasterosteus aculeatus</i>	wc	30	F	Sites with higher conspecific feeding rate	Exploration	NS	No effect of exploration on public information use	Webster et al. 2007	[16]
<i>Gasterosteus aculeatus</i>	wc		F	Following demonstrators in maze to feeding site	Exploration	+	Explorers follow conspecifics	Nomakuchi et al., 2009	[17]
<i>Gasterosteus</i>	wc	43	F	Joining 2 vs. 6 conspecifics. Joining conspecifics feeding vs. not feeding	Boldness	NS	No effect of boldness, but shy individuals took more time to decide.	Harcourt et al. 2010	[18]
				Joining conspecifics feeding at a high vs. low rate	Boldness	NS			
<i>Poecilia reticulata</i>	wc	136	F	Scrounging for feeding site	Boldness	-	In mixed group, female shy individuals follow bold ones	Dyer et al. 2008	[19]
<i>Poecilia reticulata</i>	wc	49	F	Use public over personal information	Neophobia	+	Neophobic individuals tend to scrounge. Less neophobic individuals tended to avoid conspecifics, maybe to avoid depleted patch	Trompf & Brown, 2014	[20]
					Sociability	+	Social individuals are attracted by conspecifics, and favor social over personal information		
<i>Pungitius</i>	wc	60	F	Public information	Exploration Sociability	NS NS	Personality traits did not affect the probability to use public information about patch quality	Webster et al. 2015	[21]
<i>Symphodus tinca</i>	w	25	S	Schooling tendency	Activity	+	Active <i>S. tinca</i> school more	Budaev et al. 1998	[22]
<i>Symphodus ocellatus</i>	w	23	S	Schooling tendency	Activity	NS	No correlation in <i>S. ocellatus</i>	Budaev et al. 1998	[22]

[15] Ward et al. (2004); [16] Webster et al. (2007); [17] Nomakuchi et al. (2009); [18] Harcourt et al. (2010); [19] Dyer et al. (2008); [20] Trompf & Brown 2014 (2014); [21] Webster et al. (2015); [22] Budaev & Zworykin (1998).

Table 1.2: Description of the 8 studies looking at the link between personality and position within social network, sorted by taxa and species. “Pop.” refers to the conditions in which the population was studied (c for captivity, “w” for wild, “wc” for wild population brought back in captivity for the study). N is the sample size.

Species	Pop.	N	Social information	Perso. trait	Details	Ref.
Amphibia						
<i>Tiliqua rugosa</i>	w	23	Social network position for 81 days (mating, foraging)	Aggressiveness / Boldness	Less aggressive / shy individuals interacted more with females within the network	[1]
Aves						
<i>Parus major</i>	w	90	Social networking during foraging	Exploration	Fast Explorers had numerous but weaker and less persistent social bonds within social network	[2]
<i>Parus major</i>	w	13	Social networking during breeding season	Exploration	Slow explorers males had a less central spatial position within the social network	[3]
<i>Parus major</i>	w	775	Social networking during foraging	Sociability	Individuals are repeatable in their social position within foraging social networks, implying constraints on the access and use of social information	[4]
<i>Poecile atricapillus</i>	w	68	Diffusion of social information through network (NDBA analysis) during	Exploration	No effect of exploration on diffusion of social information	[5]
Pisces						
<i>Gasterosteus aculeatus</i>	wc	120	Social networking in shoal	Boldness	Shy individuals formed long-lasting bonds with few individuals.	[6]
<i>Neolamprologus pulcher</i>	n/a	215	Social networking during group settlement in this	Exploration Neophobia Aggressiveness	Large less explorative, less aggressive, and neophobic tended to have more affiliative connections. Large explorative, aggressive, neophilic individuals tended to be more central in agonistic network. None robust trends.	[7]
<i>Poecilia reticulata</i>	w	72	Social networking in shoal	Boldness Sociability	Shyer individuals, with a higher tendency to shoal (sociable), have more and stronger social bonds	[8]

[1] Godfrey et al. (2012); [2] Aplin et al. (2013); [3] Snijders et al. (2014); [4] Aplin et al. (2015); [5] Jones et al. (2017); [6] Pike et al. (2008); [7] Schürch et al. (2010); [8] Croft et al. (2009).

1.5 Aims of the thesis

From the above introduction, it clearly appears that the use of social information is a complex behaviour, both plastic over an individual's lifetime, and constrained by intrinsic factors such as personality traits, at least in the foraging and flocking/shoaling contexts. Besides, individuals likely use various sources of (social or personal) information depending on the context, their current state, their amount of information, how up to date are their information etc. They may even use sources of information that we do not know about yet. Between-individual differences are the material on which selection can act, provided that the traits are heritable and linked to fitness. Between individual differences might be the result of contrasting selection pressures in time and space, or selection for a mixture of behaviours at the population level similarly to a producer-scrounger game in which an optimal number of scroungers should be selected for (Barnard and Sibly 1981). Understanding what drives the differences between individuals will help understand first, the evolution and the mechanisms behind this behaviour, and second whether and how the population (and this behaviour) might evolve under changing conditions.

During my PhD, I aimed to explain the observed between-individual variability in social information use for breeding habitat selection. Focusing on breeding site selection is particularly interesting because, as explained before, the selective pressures for breeding-related decisions might be different from foraging or predator avoidance decisions. Besides, even though the use of social information for breeding site has been also well documented, explaining the observed variability in this behaviour is still in its premises, contrary to the foraging context.

I used both long term and experimental data from a wild population of collared flycatchers (*Ficedula albicollis*), as collared and pied flycatchers (*F. hypoleuca*, a sister species) have repeatedly been shown to use social information from other hole-nesting competitors, either conspecifics or resident heterospecifics (tit species), for nest site and dispersal decisions (Doligez et al. 1999, 2002, Seppänen and Forsman 2007, Forsman and Seppänen 2011, Jaakkonen et al. 2013, Kivelä et al. 2014, Samplonius and Both 2017). In particular,

they have been shown to use conspecific and heterospecific social information at different spatial and temporal scales and differently depending on individual characteristics (see Chapter 2 for an exhaustive review of the literature on the use of social information by flycatchers). Besides, flycatcher show fitness benefits and great tits suffer fitness costs from this use of social information (for this reason coined information parasitism; Forsman et al. 2002, 2007). If using social information from tit species is beneficial, we may wonder (i) why not all flycatchers use them, (ii) what are the hidden costs of copying tits and (iii) whether the subset of flycatchers successfully using social information from tits is random or reflect common characteristics. This migrant-resident system, already well studied and documented (see Chapter 2) makes collared flycatchers an ideal model species to understand the evolutionary potential and evolutionary constraints of (heterospecific) social information use for breeding site selection.

The aims of my PhD were more specifically three-fold. First, we wanted to know whether the use of social information could be an inherited behaviour and/or whether it depended on the past experience and knowledge of the environment (Chapter 3). I conducted quantitative genetic analysis (“animal models”; Wilson et al. 2010), using both long-term data to construct a pedigree of the population and data from a 5-years experiment (2012-2016, started before the start of my PhD) testing whether flycatchers copied the nest site preferences of tits. The experiment consisted in creating an apparent preference of great tits and blue tits for a specific nest box feature and monitor whether flycatchers, just coming back from migration, copied or not this preference in their nest site choice. Fairly similar experiments were successfully performed in the same and other populations of flycatchers (see Chapter 2), but usually at shorter temporal and smaller spatial scales. Conducting this experiment several years allowed us (i) to conduct quantitative genetic analysis on these multi-generational data, (ii) to test the effect of past experience (past copying behaviour but also past reproductive success associated) and (iii) to test the effect of the knowledge of the individuals (yearling, philopatric, and immigrants differ in their experience with the local habitat).

Second, as shown in other contexts and reviewed earlier, some personality traits seem

to influence the gathering and use of social information, and we wanted to test whether personality differences might explain part of the differences in social information use for breeding habitat selection. Using data previously collected between 2011 and 2013, I extracted estimates of aggressiveness, boldness, and neophobia of male and female breeding flycatchers, estimated the repeatability of these behaviours between years and their phenotypic and between-individual correlations to see if they formed behavioural syndromes (Chapter 4). Using both the data from the social information use experiment already used in Chapter 3, and the personality estimates derived in Chapter 4 (for 2012 and 2013), I looked at the link between each personality trait and the probability of flycatchers to copy tit preferences (Chapter 5). I also studied whether this link depended on other individual parameters, namely sex and age (Chapter 5).

Third, I wanted to expand the scope of the traditionally known sources of social information, and test whether some easily accessible indicators of demonstrators' quality, i.e. a presumably more accurate information than tit's presence or site preference, could be used by flycatchers. We know that flycatchers use tit clutch or brood size as a source of social information for their settlement decisions (Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013). However, flycatchers might also suffer high costs when entering tit nest boxes (they might get killed, Merilä and Wiggins 1995, Forsman et al. 2018). Therefore I wanted to test whether collared flycatchers may use tit song characteristics, supposed to inform on tit quality and easily eavesdropped on, as a source of social information (Chapter 6). We conducted a playback experiment, and broadcasted throughout the period of flycatcher settlement either songs mimicking a high quality great tit, a low quality great tit, or control songs. We monitored the settlement of flycatchers near our playback treatments, and estimated their aggressiveness (as this might influence their competitive abilities and as a consequence their decision to settle near a dominant competitor; Chapter 6).

Finally, I generally discuss the results of this thesis, how they help better understand the use of social information in a migrant-resident system, some methodological perspectives regarding the personality analyses, and further research perspectives (Chapter 7).

This thesis is composed of 7 chapters. Chapter 1 (general introduction), chapter 2 (methods), and Chapter 7 (general discussion) are unpublished work. Chapter 3 has been published in open access in 'Frontiers in Ecology and Evolution', and has been reproduced in the thesis with the authors' copyrights. Chapter 4 is currently submitted to 'Animal behaviour'. Chapter 5 and 6 are manuscripts in preparation for future publication.

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Chapter 2

Some Methodological Considerations



2.1 Study species & site

Distribution

The collared flycatcher (*Ficedula albicollis* - *Muscicapidae* family) is a small migratory passerine wintering in sub-Saharan Africa and breeding in central and Eastern Europe (Figure 2.1). The northern most breeding populations of collared flycatchers are on the Swedish islands of Gotland (57°10' N, 18°20' E) and Öland, in the Baltic Sea (Figure 2.1). There, and throughout most of its range, the collared flycatcher live in sympatry with the pied flycatcher *F. hypoleuca*, a sister species (hybrid zone, Figure 2.1). Collared flycatchers colonized Gotland island approximately 160 years ago, and Öland island 50-60 years ago, while pied flycatchers were already present; the collared flycatchers, outcompeting the pied flycatchers, quickly displaced them from preferred habitats (reviewed in Qvarnström et al. 2010).

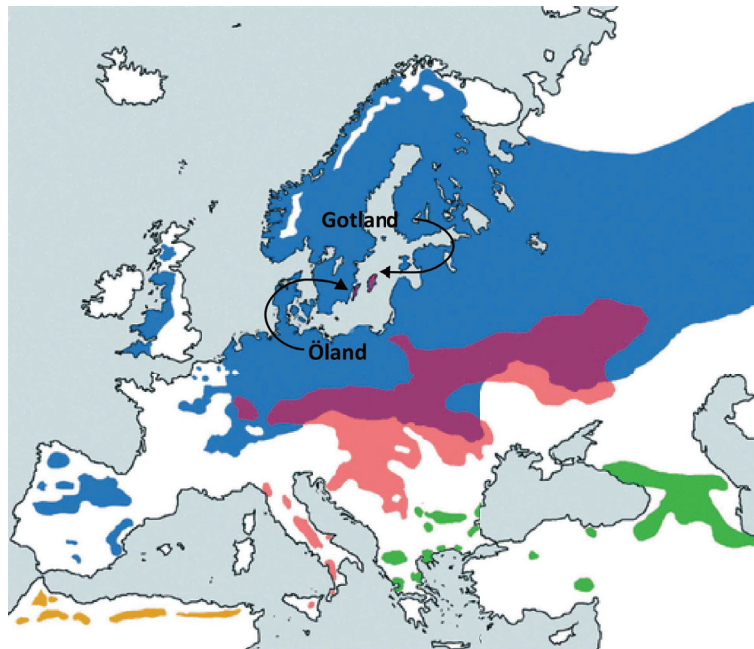


Figure 2.1: Breeding distribution of the collared flycatcher *Ficedula albicollis* (red), compared to the pied flycatcher *F. hypoleuca* (blue), the Atlas flycatcher *F. speculigera* (yellow), and semi-collared flycatcher *F. semitorquata* (green). Collared and pied flycatchers overlap in most of the collared flycatcher breeding range (overlapping regions, constituting hybrid zones, in purple). Modified map from Sætre and Sæther (2010), reprinted with permission.

Breeding habitat

Collared flycatchers breed in tree cavities, but are conveniently prone to use nest boxes as well. This insectivorous passerine bird breed in mixed deciduous forests, forested pastures typical from Gotland agro-pastoral landscape (*Änge*), and gardens. Gotland landscape remains fragmented, suitable habitats for collared flycatchers being separated by cropped fields, unplanted pastures, and alvars (limestone formations covered with a thin soil and sparse grassland vegetation). The monitored population is located at the southern isthmus of Gotland (4 km wide, 10 km long; Figure 2.2). This field site houses a very large nest-box population of flycatchers (currently around 1800 nest boxes, i.e. 500 to 700 collared flycatcher pairs each year) that has been intensively monitored since the early 80's.

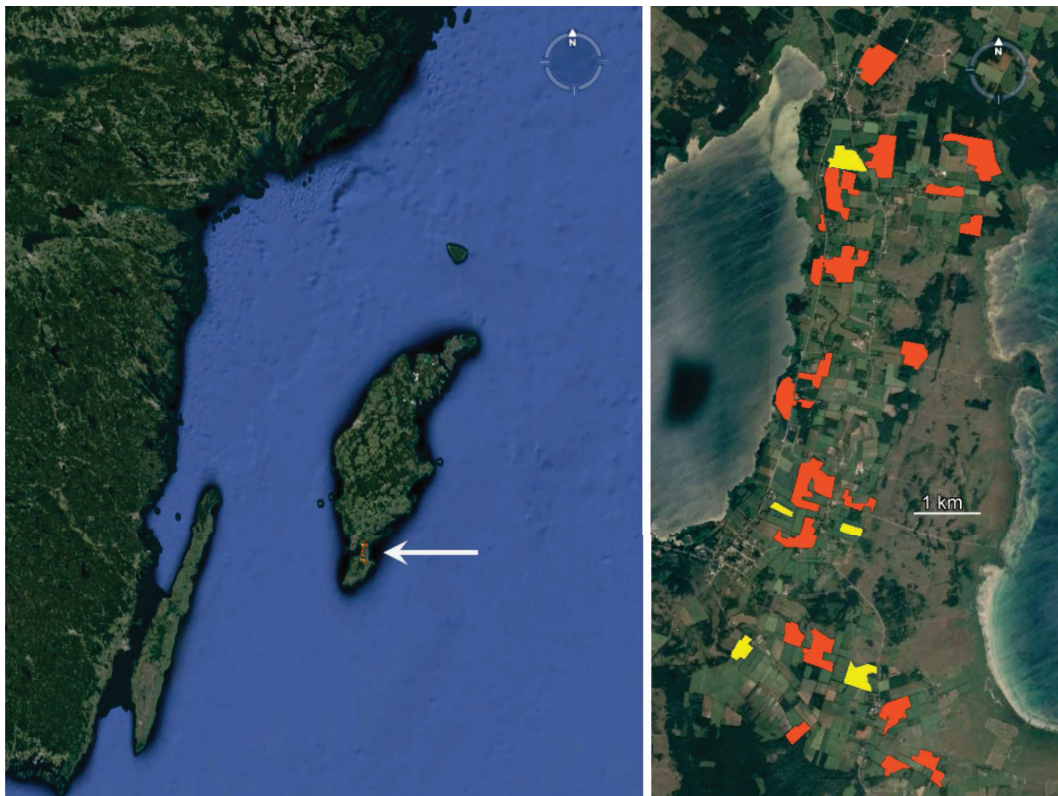


Figure 2.2: *Location of the long-term monitored breeding population of collared flycatchers in Southern Gotland (Left). Monitored forest patches are indicated in colours on the right panel. Patches in orange were used in the experimental protocols of this thesis, patches in yellow were only part of the long-term monitoring protocol.*

In this population, collared flycatchers live in sympatry with other resident, cavity-nester, passerine birds: great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), coal tits (*Periparus ater*), nuthatch (*Sitta europaea europaea*), sparrows (*Passer domesticus* and *P. montanus*). Flycatchers and titmice partially overlap in their ecological niche: they share the same predators, compete for nest sites and partly for food resources. Predation pressure is quite low on Gotland given the absence of mustelids. Clutch can still be depredated by Eurasian red squirrels (*Sciurus vulgaris*) and great spotted woodpeckers (*Dendrocopos major*; Figure 2.3). Adult predation by domestic cat (*Felis catus*) also occurs in specific areas.



Figure 2.3: *Red squirrel and great spotted woodpeckers regularly seen at the vicinity of (or inside!) nest boxes. The red squirrels are in a nest box with an enlarged entrance, in a private garden.*

Morphology and sexual dimorphism

Collared flycatcher weighs approx. 13g (measured during nestling feeding stage), but female weighs approx. 15-16g at incubation. In winter, both males and females have a

cryptic brown plumage. During the breeding season however, males are black above and white below, with white patches on the wings, the forehead, and the rump; they also have a white collar, characteristic of that species (Figure 2.4; Svensson 1992). Collared flycatchers can be aged based on plumage criteria: yearling males still have brown primaries during their first breeding season (Figure 2.4), are therefore very easily aged, even from a distance. For females, the difference is more difficult to detect, but one criteria is the more pointy cover feathers on the wing in yearling females compared to old ones (Figure 2.4).

Breeding

Collared flycatchers arrive on breeding grounds between late-April and early May. Males arrive slightly before females, and old individuals arrive before younger ones (Part and Gustafsson 1989). Males display in front of several nest boxes, and females choose their mate based on the territory quality (Alatalo et al. 1986 on pied flycatchers) and secondary sexual traits such as the forehead patch size (Gustafsson et al. 1995, Pärt and Qvarnström 1997, Qvarnström et al. 2000).

Flycatcher nests are composed of dry grass. Nest building duration is highly variable and decreases as season progress. Females lay 3 to 9 eggs mid-May to early June, one egg per day, with most of the clutches having 5 to 7 eggs. Incubation lasts around 14 days (can be extended under cold conditions), and is exclusively performed by the female (see Figure 2.5 for pictures from each breeding stage, and Figure 2.6 for the summarized breeding cycle).

This short-lived species breed from 1 to 8 times in its life, with an average number of recorded breeding of 1.6 ± 0.7 (between 1980 and 2011). Collared flycatchers are mostly monogamous, with a very low between-year partner fidelity (less than 2%), but are also facultative polygynous. Around 9% of males attract a secondary female (Gustafsson and Qvarnström 2006, 5% more did not attend their females, and were thus not captured). Taking into account early breeding failures and the nests with uncaptured males, polygynous rate should thus be around 15%. Besides, 15% of the chicks, from 33% of the

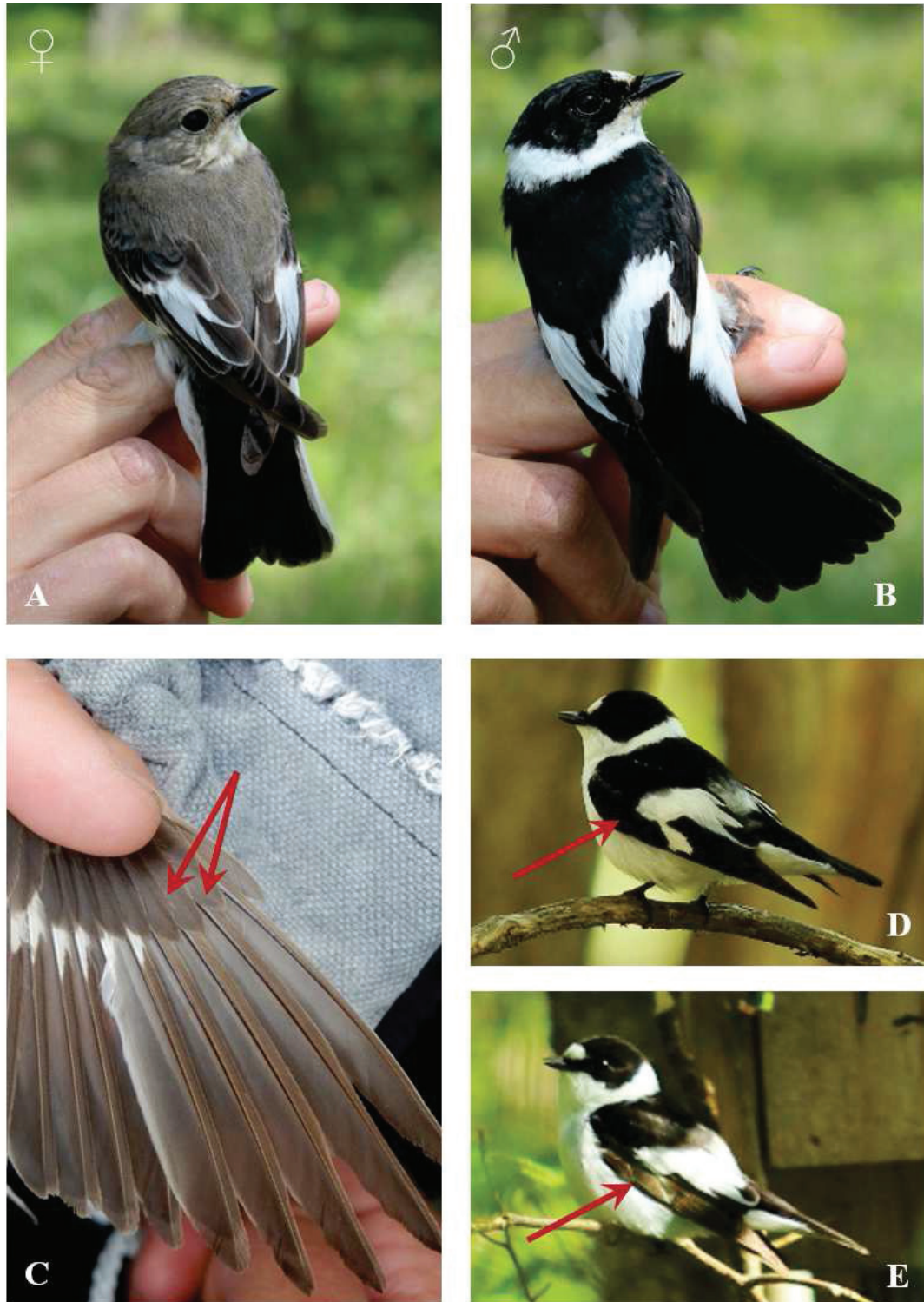


Figure 2.4: Female (A) and male (B) collared flycatcher plumage dichromatism. Yearling female collared flycatchers are characterised by pointy cover feathers (C) instead of round ones for older females, and yearling males (E) are characterised by brown primaries instead of black ones for older males (D).

broods, come from extra-pair copulations (Sheldon and Ellegren 1999).

2.2 Social information use in collared and pied flycatchers

Since the late 90's, the use of social information for breeding site selection has been one important focus on pied and collared flycatchers research. Flycatchers are known to prospect (in the forests and inside nest boxes) at the beginning and at the end of the breeding season, presumably to collect social information for their settlement decisions (Pärt and Doligez 2003, Doligez et al. 2004a, Forsman and Thomson 2008, Ponchon et al. 2013, Forsman et al. 2018).

Evidence of conspecific social information use

Collared flycatchers have been shown to adjust their dispersal decisions on year T depending (1) on their own reproductive success in year T-1, (2) on the conspecific reproductive success as well as (3) the conspecific density in their breeding patch on year T-1 (Doligez et al. 1999, 2004b). Females and unsuccessful males dispersed more the following year. Besides, yearling males and unsuccessful males dispersed more if the conspecific reproductive success in their breeding patch was high, likely to reduce competition costs, while it was the opposite for females (Doligez et al. 1999). Adult male flycatchers dispersed more if their breeding patch was densely populated, while yearling males and adult females dispersed more when conspecific density was low (Doligez et al. 1999). Based on a chick translocation experiment, adult immigration increased in forest patch with numerous chicks the year before (not dependent on the chick quality), while adult emigration increased when the quantity and/or the quality of the chicks in the breeding patch decreased (Doligez et al. 2002). These results were confirmed with a correlative study using the long-term database of the population showing that adult, but not yearling, flycatchers were attracted by forest patches with higher fledgling number the year before (Doligez et al. 2004b). Yearlings were however more attracted to patches



Figure 2.5: Pictures of the different stages in flycatcher breeding. (A) Nests are built mostly by the female, early to late May. (B) The first egg is laid around mid-May depending on the seasons. (C) Collared flycatchers lay 3 to 8 eggs, the usual clutch size on Gotland being 5-7eggs. (D) Female flycatchers incubate eggs for 14 days on average (12 to 16 days) (E; credits: Laure Cauchard). (F) Nestlings develop a cryptic spotted plumage, and fledge at 16 days.

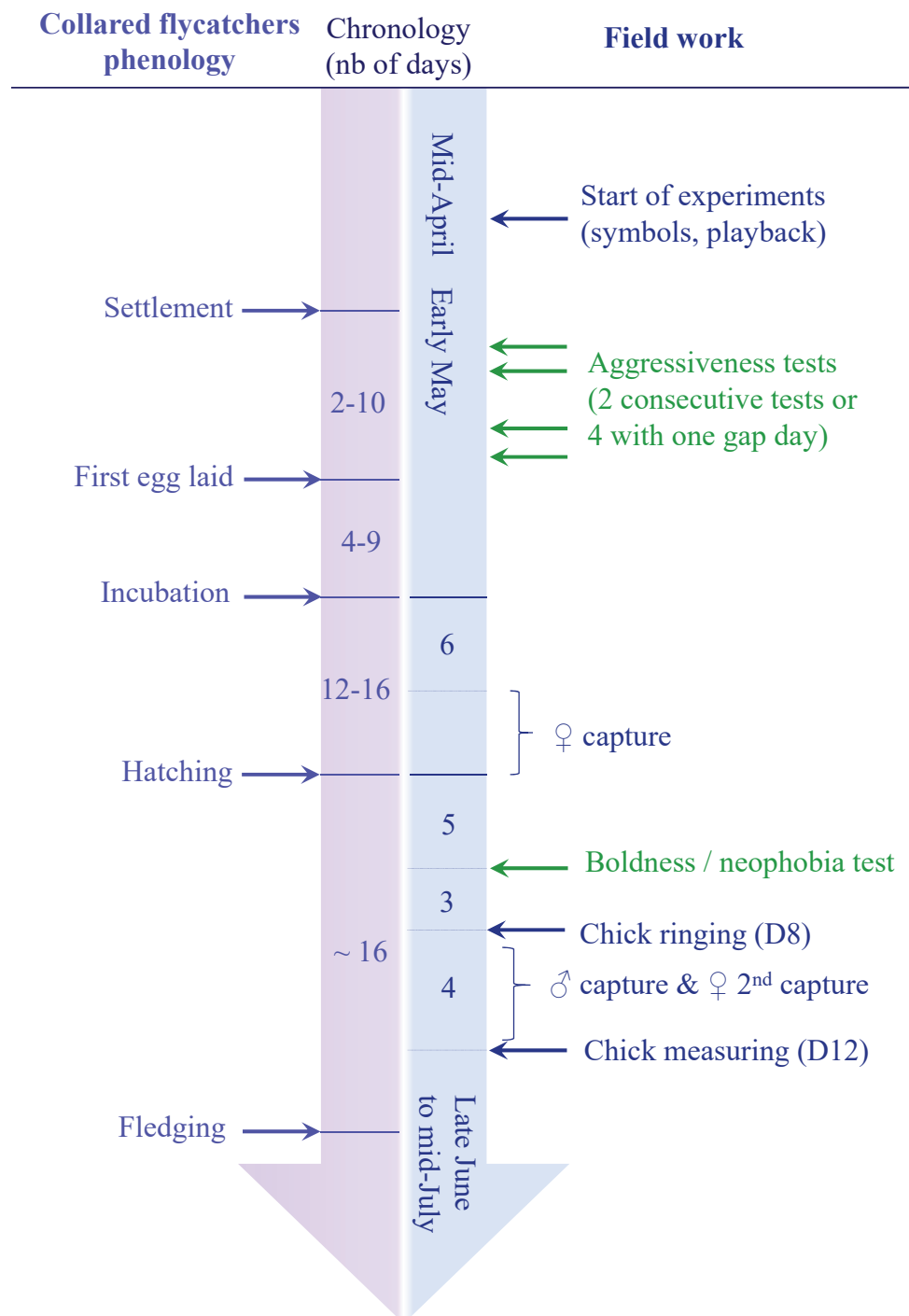


Figure 2.6: Chronology of the flycatcher breeding season (purple) and of the population monitoring (blue), including the behavioural tests (green).

with high (resp. low) fledgling condition when the patch density was low (resp. high) the previous year (Doligez et al. 2004b). Both yearling and older individuals were attracted to breeding patches with formerly a high conspecific density, but there was less yearlings (in proportion) in forest patches that had a high patch reproductive success the year before (Doligez et al. 2004b). Overall, dispersal decisions seemed to depend on various conspecific social information, and individual flycatchers respond to these cues according to their own needs/competitive abilities.

At a smaller spatial scale, collared flycatchers prefer settling in nest boxes occupied by flycatchers the year before (especially pairs of philopatric individuals, Kivelä et al. 2014). Note that flycatchers only very rarely breed in the same nest box from one year to the other (6.7 % in the restricted dataset used in Chapter 4). Pied flycatchers have also been shown to copy (more than at random) the evolutionary neutral artificial preference of conspecifics for specific types of nest boxes (Jaakkonen et al. 2013; Figure 2.7). Indeed, when experimentally creating an apparent preference of early flycatchers for a specific type of nest boxes (i.e. by attaching white plastic symbol at the entrance of boxes, Figure 2.7), 60% of the later arriving pied flycatchers have been shown to copy this apparent preference, independently from their age or dispersal status (Jaakkonen et al. 2013).

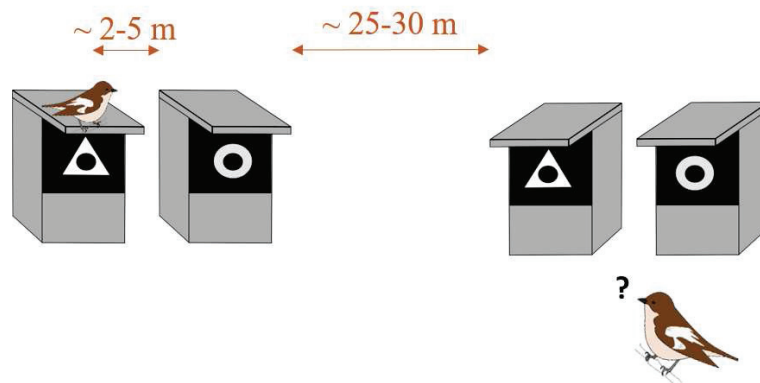


Figure 2.7: *Experimental protocol used by Jaakkonen et al. (2013) to test the conspecific copying behaviour of pied flycatchers. When one pied flycatcher pair settled in a nest box, 3 more nest boxes were set-up to create two neighbouring pairs of boxes. Two types of white plastic symbol were attached on the boxes to test for the copying behaviour of subsequently arriving flycatchers. Similar experiments at the heterospecific level (with tits as tutors instead of early flycatchers) had previously been conducted (e.g. Seppänen and Forsman 2007, Seppänen et al. 2011).*

Evidence of heterospecific social information use

Using social information from heterospecifics partly sharing the same ecological niche might decrease the competition costs compared to using information from conspecifics, while still providing useful information to detect predators, find resource, settle in good quality habitat, etc. (Seppänen et al. 2007). Great tits (the main tit species in the studied populations, but there are also blue tits) and flycatchers are both cavity nesters, feed their young nestlings with caterpillars, and share the same predators (and to a lower extent parasites); at the adult and old nestling stages, flycatchers and tit diets overlap less than at the young nestling stage, as flycatchers also feed on flying preys (Slagsvold 1975, Lundberg and Alatalo 1992). Using information from the resident sympatric species should thus increase the fitness of the flycatchers, but only if the associated competition costs do not exceed the potential information benefits.

Several studies investigated the costs and benefits for flycatchers of breeding in close vicinity of tits, or in areas with high/low tit density. In Gotland population, flycatchers have been shown to have a higher reproductive success when breeding with tits showing a natural density rather than an increased density (Gustafsson 1987). Conversely, in northern Finland, flycatchers settled slightly earlier and had more nestlings but not more fledglings in patches with increased compared to decreased tit density (Forsman et al. 2002). However, when flycatchers had the choice to breed either close (25m) or far (50m) from breeding tits, they showed a clear preference for breeding close to tits (Forsman et al. 2002). Another study based on the long-term dataset of the Gotland population revealed that collared flycatchers settle preferably at the closest vicinity from tit nests (rather than further away, Kivelä et al. 2014). Flycatcher nestlings reared close to tits were besides heavier and had longer wings than nestlings reared further away from tits (Forsman et al. 2002). Results from Gustafsson (1987) and Forsman et al. (2002) seem to contradict themselves. Later, Forsman et al. (2008) found that actually, flycatchers prefer to settle -and have an increased fitness- in forest patches with intermediate tit density. By creating a gradient of tit density among the Gotland forest patches (from 0 to 4 pairs/ha with

0–8 boxes available for tits/ha), Forsman et al. (2008) showed that flycatchers had an earlier onset of laying and a larger clutch size at intermediate tit density (marginal clutch size effect when controlled for laying date). Besides, females in patches with intermediate density produced more male than female offspring (60%) (Forsman et al. 2008), males being the philopatric sex in this species. When pied flycatchers and great tits were forced to breed either as neighbours or alone, great tits seemed to bear all the competitive costs: results varied between years but overall either the number, quality, wing length, or survival of tit offspring decreased for tits breeding near flycatchers (Forsman et al. 2007). Conversely, flycatcher nestlings had either longer wings or longer tarsi when breeding near tits than alone (again depending on the year, Forsman et al. 2007).

Overall, flycatchers seemed to be attracted to tit presence and to cue on tit density to adjust their own reproductive investment, while benefitting (or not suffering) from competition costs, as long as the tit density is not too high. Tits on the contrary suffered from flycatcher's proximity, but tolerate more the proximity of breeding flycatchers than other tits (Doligez, pers. comm.). However, one should note that flycatchers may suffer a high risk by prospecting in tit nest boxes (mostly flycatcher males found injured or killed in tit nest boxes, Merilä and Wiggins 1995, Forsman et al. 2018).

Besides the density and nearby presence of tits, flycatchers have also been shown to cue on the artificial nest site preference, early reproductive investment and phenology of tits. Using “double-box symbol experiments” (Figure 2.7) but attributing a specific “preferred” symbol to settled tits (rather than settled flycatchers as illustrated in Figure 2.7), pied and collared flycatchers have been shown to copy more than at random the apparent tit preference, especially late arriving (presumably younger) individuals (Seppänen and Forsman 2007). This copying behaviour has later been shown to actually depend on the number of eggs or offspring in the tit nest at the time flycatchers settled: flycatchers copied the artificial preference of tits when tits exhibited high clutch size, but rejected it and chose the nest box with the opposite, “non-preferred”, symbol when tit showed a small reproductive investment (Seppänen et al. 2011). This effect was also later shown to be mediated by the cover the tit put on top of their clutch during egg laying: the effect

remained when the tit clutch was uncovered, but not when it was covered (Loukola et al. 2013). In a similar “double-box symbol experiment” but when the tit nest appeared deserted (i.e. when no tit was around to protect it), most flycatchers bred on top of the deserted tit nest directly, while the other flycatchers, settling in boxes further away, chose in higher proportion the box with the same symbol as the tit apparent preference (Forsman and Seppänen 2011).

Both the flycatcher copying behaviour and the flycatcher investment differed according to the tit clutch size. Indeed, when flycatchers settled near a tit nest with either 4 or 13 eggs, the reproductive investment of the female flycatchers differed: females produced more and heavier eggs and clutches when breeding near a tit nest with a large rather than a small clutch (at least old females, Forsman et al. 2012). This confirmed that flycatchers may adjust their reproductive behaviour according to social information gathered from tits (as shown in Forsman et al. 2008). Finally, a recent experiment manipulating the advance in tit phenology between forest patches showed that female (but not male) pied flycatchers preferred settling in forest patches that showed an advanced tit phenology rather than a delayed one (Samplonius and Both 2017), confirming former findings that flycatchers benefit from a short difference in onset of breeding between themselves and tits (Slagsvold 1975).

When conspecific and heterospecific social information conflict

Flycatchers seem to use social information from conspecific for settlement decisions the following spring, and social information from tits for the current spring. However, when conspecific and heterospecific information conflict, either the previous or the current year, interesting trends arise.

Using a double-box symbol experiment in which several pairs of boxes (not only 2 pairs) were spread in forest patches (at 25m distance), Jaakkonen et al. (2015) attributed to all the nest boxes occupied by tits a specific symbol (e.g. circle), and to all the nest boxes occupied by flycatchers another symbol (e.g. triangle, Figure 2.8). If a new tit or flycatcher pair settled in the empty boxes, the symbols could be swapped according to the

attributed patch-scale preference. Early settling flycatchers (that had only few flycatcher tutors to gather information from) copied more the heterospecific preference, while later arriving flycatchers copied more the conspecific preference (Jaakkonen et al. 2015). This suggest that flycatchers favour conspecific over heterospecific information, even in the current year, when available.

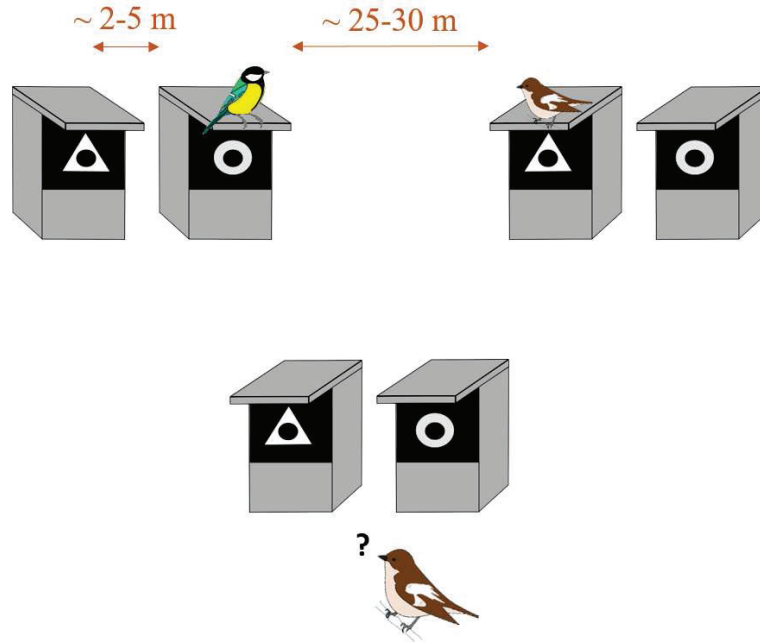


Figure 2.8: *Experimental protocol used by Jaakkonen et al (2015) to test the copying behaviour of flycatchers for their current settlement decision when con- and heterospecific social information conflict.*

To test which type of information (conspecific or heterospecific) flycatchers would use for settlement decisions from one season to the next, Forsman et al. (2014) used the nest boxes from Gotland island (not set-up in pairs but regularly spread within forest patches) and attributed one symbol (e.g. triangle) to all the nest boxes occupied by tits, a second symbol to all the nest boxes occupied by flycatchers (e.g. square), and a third symbol to all the nest boxes that remained empty (e.g. a rectangle). In the Gotland population, approx. 1/3 of the nest boxes are occupied by tits, 1/3 by collared flycatchers, and 1/3 remain empty; each symbol was thus equally represented. The following year, all types of symbols were available in equal proportion on all the empty boxes and the choices of settling tits and flycatchers were recorded. Right after a settlement was detected (nest material), the symbol on the box was removed to ensure that only information from the

previous year will be available to subsequently arriving birds. Flycatchers did not prefer a specific type of symbol the following year, but great tits preferred symbols associated to an empty nest box, which suggest an active avoidance of competition and/or parasites by great tits (the latter being maybe less likely as but the old nests were removed, Forsman et al. 2014).

Summary of the use of social information by flycatchers

The number of studies conducted on that topic since the late 90's reveals how intriguing this behaviour is, and how much is still to be investigated. Currently, we know that flycatchers (I combine here pied and collared flycatchers) use the presence, density, and reproductive success/investment of both conspecifics (with a one year delay) and heterospecific dominant competitors (for current year decisions, at least when conspecific information is unavailable). Flycatchers gain benefits from using social information from tits, and seem to adjust their own reproductive decisions and investment according to the apparent quality of the habitat, as demonstrated by the preference and density of tits.

However, what these studies also show is that these copying/rejecting behaviours are not adopted by all flycatchers within a population. Such behavioural differences could reflect underlying constraints or plasticity, could be adaptive, or could be maintained by differential selection across breeding seasons. The goal of my thesis is to help understand why these differences are maintained, by studying which individual parameters shape the heterospecific copying behaviour of flycatchers (gene, age, experience, personality), and which other types of social information might be used and that we did not discover yet.

2.3 Data recording

Population monitoring

Nest boxes were monitored every 1 to 5 days (depending on the ongoing experiments)

until incubation. Females were captured after 5-6 days of incubation. After 12 days of incubation, we monitored the nest every late afternoon until hatching, to record a precise hatching date. Chicks were ringed on day 8 and measured on day 12. Males (and females) were (re)captured using traps inside the nest box from the 8th day after hatching until successful capture (attempts every two days approx.). The chronology of a field season is summarized in Figure 2.6, with the key breeding periods and the corresponding monitoring tasks in parallel.

Social information use experiments

To study heterospecific social information use for nest site choices in the collared flycatchers, I used experimental data collected between late-April and early June, i.e. over the entire settlement period of flycatchers.

First, I used data from an experiment started in 2012, and that I contributed to in 2015 and 2016 (“symbol experiment”, Chapter 3 & 5, Table 2.1). The experiment resemble that of Forsman and collaborators (e.g. Seppänen and Forsman 2007, Forsman et al. 2014) and experimentally tested whether flycatchers copy or reject a preference of tits for a specific type of nest sites. At the patch scale, we created an apparent preference of tits for a specific symbol attached around the entrance of their box (either a circle or a triangle). In the other (empty) nest boxes we attached either the same symbol or another one. When the flycatchers arrived from migration, they thus had the choice to settle in nest boxes looking similar to the apparent preference of tits (i.e. with the same symbol), or looking dissimilar (i.e. with the other symbol). We monitored the choice of nesting flycatchers and regularly withdrew the symbol on the nest boxes chosen by flycatcher to avoid conspecific information. In parallel of flycatcher settlement, we constantly adjust the proportion of each symbol type in the empty boxes, to ensure that in the case of a random choice, each symbol could be chosen with the same probability. Mid-June we withdrew the symbol on all the remaining boxes (empty ones and the ones occupied by tits) to avoid fledglings to gather social information regarding the tit symbol preference. The data acquired for 5 years with this experiment allowed for quantitative

genetic analyses of the copying behaviour, and between-year comparisons of the copying behaviour (Chapters 3 & 5). The experimental protocol is further detailed in Chapter 3.

Second, I implemented a playback experiment (in 2017, Table 2.1) to test whether flycatchers would use song characteristics supposed to reveal great tit quality (repertoire size and song rate, known to be positively related to the fitness of great tits) as a source of information for their settlement decision (see details in Chapter 6). In forest areas composed of 5 neighbouring nest boxes, we broadcasted one type of songs during the entire flycatcher settlement period, among three possible treatments: (1) songs mimicking a high quality great tit, (2) songs mimicking a low quality great tit, (3) songs of chaffinch (*Fringilla coelebs*). We daily monitored the settlement of flycatchers in the experimental areas. The experimental protocol and the results are further detailed in Chapter 6.

Behavioural data

To test whether the use of heterospecific social information depended on individual personality traits, we estimated the aggressiveness, boldness, and neophobia scores of the breeding flycatchers for several years (Table 2.1). In 2017, for the playback experiment, we also recorded the aggressiveness scores of the focal breeding pairs. Two to four aggressiveness tests were conducted during nest building, and one combined boldness/neophobia test was conducted during nestling feeding (green arrows on Figure 2.6). Aggressiveness reaction was elicited by attaching dummy (conspecific or heterospecific) competitors on the flycatchers nest boxes and monitoring the reaction of the flycatcher pairs (every moves around the box, every attack or stationary fight in front of a dummy; Figure 2.9). Boldness and neophobic reactions were measured as the reaction towards the intrusion of a human near the nest box and towards a novel object attached near the entrance of the nest box, respectively. These behavioural tests are described in more details in Chapter 4, but you can look at an example of aggressive and non-neophobic reaction by following the link or scanning the codes provided in Figure 2.9).



Figure 2.9: Pictures of the behavioural tests. On the left (aggressiveness test), you can see the dummy flycatchers and tits attached on the box, and the camouflaged loudspeaker attached below the box. On the right (boldness/Neophobia test), you can see the novel object attached near the entrance of the nest box. Scan the QR codes or follow this link *"Personality videos"* to watch short videos of each test.

Table 2.1: Overlap in the records of the different data used in this thesis. Boldness and Neophobia were also measured in 2014 and 2015 in a subset of nests, but the data are still in the process of being extracted. The playback experiment (Chapter 6) was preceded by a pilot study in other forest patches north of the core study area.

2011	2012	2013	2014	2015	2016	2017	2018
Aggressiveness						Aggr.	
Boldness / Neophobia							
« Symbol » experiment							
					Pilot	Playback	
			PhD thesis				

2.4 References

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Chapter 3

Role of Genes and Experience in Heterospecific Social Information Use for Breeding Site Selection



Heterospecific nest site copying behavior in a wild bird: assessing the influence of genetics and past experience on a joint breeding phenotype

Jennifer Morinay, Jukka Forsman, Sami Kivelä, Lars Gustafsson, Blandine Doligez

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Keywords: social information, breeding site selection, collared flycatcher, *Ficedula albicollis*, heritability, indirect genetic effects, quantitative genetics, past experience

Abstract

Breeding site selection is often a joint decision of pair members in species with biparental care and the experience of both pair members may influence the use of information for site selection. Nevertheless, quantitative genetics of joint information use for site selection remains unexplored so far. We used an experimental approach to quantify the relative importance of genetics (heritability) and past experience (age, familiarity with the environment, previous breeding success, previous information use) in heterospecific social information use for nest site selection in wild collared flycatchers (*Ficedula albicollis*). Flycatchers collect social information from resident tits for nest site selection. We created an apparent preference of tits for a novel nest site feature and recorded choices of flycatchers (copying or rejecting the tit preference). Copying behavior was stronger for naive individuals but also differed between years, which could be explained by contrasting seasonality in the demonstrator species. Past experience as reflected by age affected subsequent use of social information: pairs with a yearling male were more likely to copy the heterospecific preference than pairs with older immigrant males. There was no general pattern in successive individual choices over the years. Accordingly, individual repeatability in copying tit preference was very low. At the pair level, we estimated sex-specific direct and indirect genetic effects on the joint nest site decision and found no sex-specific heritability and no cross-sex genetic correlation. Our results confirm the importance of past experience for social information use and suggest that social information use is highly plastic and most likely not genetically inherited in collared flycatchers. Whether individuals use social information should be related to environmentally-induced changes in the quality of information and thus be context-dependent. Selection may therefore act on the ability to optimally use social information in varying environments and on the processes underlying such adjustment, such as learning, rather than the use of information itself.

3.1 Introduction

In species with biparental care, many breeding traits can be considered as joint (or interacting) phenotypic traits (Moore et al. 1997) because both partners may influence reproductive behaviors such as egg laying, territory defense, breeding site selection, etc. (e.g. Brommer and Rattiste 2008; Hall et al. 2013). In particular, the choice of a breeding site is likely to be a joint phenotypic decision made by both the male and the female (Loukola et al. 2012), and it will strongly affect pair reproductive success (Danchin et al. 2008; Doligez and Boulinier 2008). In spatio-temporally varying environments, this joint decision may involve the use of social information, that is, information derived from the presence, performance, or actions of other individuals, to reduce the uncertainty about habitat quality (Danchin et al. 2004; Dall et al. 2005). Because breeding constraints (on e.g. extra-pair or mating opportunities, intra-sexual competition) often differ between sexes (Trivers 1972; Arnqvist and Rowe 2005), males and females may use different social information sources or use the same information differently when decisions are made independently (e.g. for dispersal decisions Doligez et al. 1999; for mate-choice Kniel et al. 2015). Nevertheless, male and female information use may interact to produce a joint breeding site decision. If the use of social information is heritable, through e.g. the influence of genes on behaviors shaping information gathering and use (e.g. Fidler et al. 2007 for exploration behaviour; Foucaud et al. 2013 for information use in spatial learning), the choice of a breeding site can be seen as the result of the interaction between male and female genotypes. However, very little is known about the relative phenotypic and genetic contribution of the male and the female in a breeding pair to the use of social information for breeding site choice.

The massive evidence for social information use in breeding site selection (reviewed by Seppänen et al. 2007; Valone 2007; Avarguès-Weber et al. 2013) suggests that this behavior is often favored by natural selection, but very little is known about its genetic basis. The only study (to our knowledge) that provided evidence for the role of genetics in social information use was conducted in a laboratory population of *Drosophila melanogaster* and

involved genetic polymorphism at one locus (Foucaud et al. 2013). Yet, understanding the genetic architecture of social information use for breeding site selection requires assessing its heritability in wild populations. Importantly, social information use is often context-dependent and may depend on age (e.g. Dugatkin and Godin 1993), sex (e.g. Kniel et al. 2015), personality (e.g. Marchetti and Drent 2000; Kurvers et al. 2010) or individual's personal experience (e.g. Danchin et al. 1998; Kendal et al. 2004; van Bergen et al. 2004; and see Valone 2007). The benefits of social information use may indeed change over a lifetime, as individuals gather more experience and thus personal information (reviewed in Kendal et al. 2005; and Valone 2007). A strong contribution of individual experience to social information use can therefore be expected for breeding site selection, and both partners' experience may interact when the breeding site choice represents a joint decision.

Reproductive decisions are thought to be highly plastic in response to environmental variations (Lynch and Walsh 1998; Meffert et al. 2002; Stirling et al. 2002). Consequently, heritability estimates of behaviors linked to reproduction are usually relatively low to moderate (on average 0.3; Stirling et al. 2002). Besides strong phenotypic plasticity, low heritability estimates in reproductive behaviors can be due to strong directional selection on traits tightly linked to fitness, depleting additive genetic variance (Gustafsson 1986; Roff 1997; Merilä and Sheldon 1999) and/or to the presence of non-additive genetic effects masking additive genetic effects (Meffert et al. 2002). Such non-additive genetic effects arise when (1) the phenotype of a focal individual is affected by interactions with other individuals and (2) this effect is heritable. This defines so-called indirect genetic effects, that are effects of genotypes of other individuals on the phenotype of the focal individual (reviewed by Moore et al. 1997; Bijma 2014). Among indirect genetic effects are the well-studied maternal effects, i.e. the effects of the mother's genotype on the phenotype of its offspring (McAdam et al. 2014).

Indirect genetic effects are often overlooked in quantitative genetics studies in the wild, but ignoring these effects can result in over- or under-estimating heritability estimates and can therefore impact predictions about the micro-evolutionary potential of the trait

considered (Wolf et al. 1998; Bijma 2014; McAdam et al. 2014; Wolak and Keller 2014). Indirect genetic effects may particularly be expected for joint phenotype as they are likely affected by the genotypes of both pair members. For example, in *Larus canus* (common gulls), laying date depended on direct female but also indirect male genetic effects. Male genes could influence the female laying date through genetically determined pre-copulatory behaviors such as mate guarding or feeding for example (Brommer and Rattiste 2008). Importantly, direct female and indirect male genetic effects interacted negatively, resulting in a negative cross-sex genetic correlation that could be due to pleiotropy: genes promoting earlier laying in females probably promoted delayed laying of partners when expressed in males (Brommer and Rattiste 2008). This result revealed a reproductive conflict between sexes at the genetic level, which maintained phenotypic variation in laying date in the population and constrained evolution towards earlier laying date, despite strong selection for this trait in this species (Brommer and Rattiste 2008).

Here, we estimated the phenotypic (in terms of overall individual experience) and genetic contributions of males and females to the use of social information for joint nest site selection in a patchy population of collared flycatchers *Ficedula albicollis*. Social information has been shown to play a critical role for habitat quality assessment and settlement decisions in the *Ficedula* species. Flycatchers use both conspecific and heterospecific density, reproductive investment, or success for breeding habitat selection and adjustment of reproductive effort (Doligez et al. 1999, 2002, 2004a, Forsman et al. 2008, 2012), which results in fitness benefits (Forsman et al. 2002). Experiments have also shown that flycatchers copy the (apparent) nest site preference of their main heterospecific competitors, great tits *Parus major* and blue tits *Cyanistes caeruleus* (Seppänen and Forsman 2007; Seppänen et al. 2011). Nevertheless, these studies also report high among-individual variability in the use of social information (Jaakkonen et al. 2013). The use of different sources of social information in the collared flycatcher and its among-individual variation previously described thus make this species a highly suitable model to assess the repeatability, heritability, and the importance of personal experience in breeding habitat selection decisions based on social information.

Over five years, we experimentally provided individuals with a source of social information independent from actual site quality using an artificial nest site feature design previously successfully used in this system (Seppänen and Forsman 2007; Seppänen et al. 2011; Jaakkonen et al. 2013, 2015; Forsman et al. 2014). Using a quantitative genetic approach (Wilson et al. 2010), we simultaneously explored the relative contribution of female and male (i) overall experience (age, familiarity with the environment, previous experience with the experimental design, and previous breeding success) and (ii) direct and indirect additive genetic effects on the joint decision to use the manipulated information source for nest site choice. Individuals with low personal information are expected to rely more on social information for decision-making, provided that such information is available to them, compared to individuals with high personal information (Reed et al. 1999; Danchin et al. 2001; Valone 2007; Doligez and Boulinier 2008). Therefore, pairs with young and/or naive individuals are expected to show higher propensity to use our manipulated social information than pairs with older individuals and/or individuals more familiar with the environment or with the experimental design, because our experimental social information was provided for all individuals at the time of settlement. Among individuals tested over several years, past reproductive success and past use of the manipulated information may have interactive effects on subsequent nest site decisions. Finally, in line with previous studies showing highly context-dependent social information use (reviewed in Kendal et al. 2005; e.g. Forsman and Seppänen 2011), we expect that the use of social information for nest site selection would show relatively low individual repeatability and joint heritability.

3.2 Material and Methods

Study System and Population Monitoring

We conducted the nest site choice experiment from spring 2012 to 2016 on a population of collared flycatchers breeding on the island of Gotland (Sweden, 57°03' N, 18°18' E). Flycatchers are cavity nesters and readily accept to breed in artificial nest boxes, allowing detailed breeding data and identity of breeders to be collected on a large number of nests. Nest boxes have been provided in 18 forest patches separated by habitat unsuitable for breeding in this species, with inter-patch distances spanning from several hundreds of meters up to 12 km. The experiment was performed in 12 patches in 2012, 17 patches in 2013, 2014 and 2015, and 16 patches in 2016. Forest patches varied in size and included between 29 and 106 nest boxes each, with an average nest box density of 5 boxes/ha. During the breeding season, approximately 1/3 of the boxes are occupied by flycatchers, 1/3 by tits (of which 3/4 are great tits and 1/4 blue tits) and 1/3 remains empty.

Flycatchers have been found to use conspecific cues from the previous year (presence and/or reproductive success) for departure (Doligez et al. 1999, 2002) and settlement decisions both at large (Alatalo et al. 1982; Doligez et al. 2002, 2004a) and small spatial scales (Jaakkonen et al. 2013; Kivelä et al. 2014). In addition, flycatchers are migratory and arrive on the breeding grounds from late April to late May, when most tits have already started laying or incubating. Flycatchers use information on the presence and reproductive investment of their main competitors, resident tit species, collected at the beginning of the breeding season to adjust settlement and reproductive decisions (Seppänen and Forsman 2007; Forsman et al. 2008, 2012; Kivelä et al. 2014). All flycatchers breeding in nest boxes in the study area were captured inside boxes, either at mid-incubation (females) or at mid- to late chick rearing period (males). Because of early brood failure, adult capture rate was thus sex-biased (approx. 90% of females vs. 70% of males caught in boxes every year). Caught individuals were identified or ringed if previously unringed (approx. 40% of breeders every year), weighed, measured, and aged

in the field based on plumage criteria (yearlings vs. older individuals; Svensson 1992). All nestlings in nest boxes were ringed during the rearing period. This information, as part of the long-term monitoring of the population since 1980, allowed the construction of a social pedigree of the flycatcher population (see below in the statistical analysis section).

Nest Box Choice Experiment

The experiment was conducted from early April (i.e. just before tit settlement) to early June (i.e. after the settlement of the last flycatcher pairs). We manipulated a source of heterospecific social information available to collared flycatchers by creating an apparent preference of tits for a novel nest site feature. This artificial feature was a white geometric symbol, either a triangle or a circle, attached around the entrance hole of the nest box. To create an apparent preference of tits at the patch scale, the same symbol was systematically attached to all boxes occupied by great and blue tits in a given patch (Figure 3.1). All empty boxes were randomly attributed to one or the other of the symbols (Figure 3.1). Systematically associating a given symbol to each nest box occupied by a tit pair should thus give, to a newly arrived flycatcher, the artificial information that all tits within a patch have preferred nest boxes with the same symbol. We subsequently monitored nest box choice of newly settling collared flycatcher pairs with respect to the symbol present on the chosen box to determine whether flycatchers copied or rejected the apparent preference of tits. We systematically withdrew symbols from boxes occupied by flycatchers to avoid conspecific information, and in parallel we adjusted the proportion of triangles and circles on remaining empty nest boxes in the patch. We recorded 1497 symbol choices by flycatchers over the 5 years of the experiment, among which 1005 for which both male and female were identified, and thus used in the quantitative genetic analyses. A detailed description of the protocol can be found in Appendix A1.

The symbol associated with tit nests in a given patch was alternated in space among patches so that tit nests were associated to a circle in half of the patches and to a triangle in the other half without creating larger-scale apparent preference (see Appendix A1 for the map of the attribution of the symbol associated with tit nests for each patch in 2014).

We also switched the symbol associated with tit nests in each patch each year to avoid symbol information reinforcement across years for individuals that returned to the same patch from one year to the next (i.e. philopatric individuals, approx. 70% of breeding adults in the study population; Doligez et al. 1999).

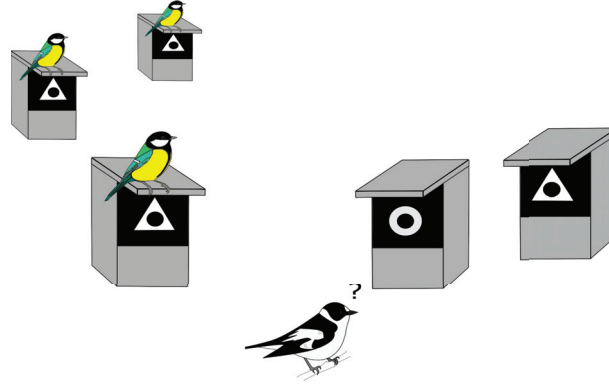


Figure 3.1: *Experimental design used between 2012 and 2016. All nest boxes occupied by great and blue tits were attributed a similar symbol (here a triangle as an example). All other nest boxes available for the flycatchers settlement were attributed either the same symbol as the nest boxes occupied by tits, or the other symbol, in equal proportion. We subsequently monitored the choice of arriving flycatchers (matching or opposing the tit apparent preference). The tit apparent preference for triangle or circle was randomized between patches, and systematically changed from one breeding season to the next. The front of all boxes had previously been painted black to increase the contrast with the white symbol.*

Statistical Analyses

We conducted all analyses within the Bayesian framework by using the R function *MCMCglmm* (“MCMCglmm” R package; Hadfield 2010) in R version 3.3.2 (R Development Core Team 2011). Our response variable was the probability that flycatchers choose a nest box presenting the same symbol as the one associated to tit nests in the same patch, thereafter called “probability to copy” (binary variable: 1 if choosing a box with the symbol associated with tit nests, i.e. copying the apparent tit preference, and 0 otherwise, i.e. rejecting the apparent tit preference). First, we estimated the repeatability estimate of the probability to copy. The repeatability estimate for a trait provides a

maximal value for its heritability (Lynch and Walsh 1998; but see Dohm 2002), therefore informing about the possible heritability estimate. However, because of high mortality and breeding dispersal rates in our population, individuals very rarely mate with the same partner over several years (less than 2% in our sample), and thus we could not estimate the repeatability of the probability to copy at the pair level, but estimated it first only at the individual level. Second, we used a quantitative genetic mixed effects models (“animal model”; Kruuk 2004; Charmantier et al. 2014) to estimate simultaneously the importance of overall experience (age, familiarity with the environment, and previous experience with the experimental design) on, and quantitative genetic parameters of, the probability to copy at the pair level. Third, we restricted the data to individuals that made multiple nest box choices over the course of the experiment, and explored whether subsequent choices (i.e. excluding the first choice of each individual) depended on personal information previously acquired with respect to the symbols.

Repeatability at the Individual Level

We estimated individual repeatability in the probability to copy by fitting two binomial generalized linear mixed-effects models (one for males and one for females to avoid pseudoreplication of nest box choice) with the probit link function, including only individual identity as a random effect, and no fixed effect. Repeatability was estimated as the ratio between the individual variance and the total variance plus 1 for the probit link function (Nakagawa and Schielzeth 2010). Using a similar approach, we also estimated individual repeatability in the probability to choose a specific symbol (either circle or triangle), to test for a potential innate preference for a natural round shape (Forsman et al. 2014).

Animal Model at the Pair Level: Specification and Variance Partitioning

We used an animal model at the pair level to separate different sources of phenotypic variance in the probability of flycatchers to copy. Animal models allow controlling for fixed effects while partitioning the total phenotypic variance into genetic and non-genetic components by considering all relatedness links between individuals obtained from the

pedigree (Wilson et al. 2010). The presence of fixed effects in animal models may increase heritability estimates in particular by decreasing the residual variance (reviewed in Wilson 2008). We found no quantitative change in variance component estimates between models without and with selected fixed effects (results not shown).

We included in our animal models different fixed effects that may have affected nest box choice with respect to symbols in flycatchers (Table 3.1). First, because of higher familiarity with their environment (Pärt 1995), philopatric adults (i.e. individuals that bred in the same patch the previous year) may rely less on social information for habitat quality assessment than newly arrived individuals in the patch, including both young individuals and immigrant adults (Kivelä et al. 2014). Indeed, newly arrived individuals lack personal breeding information on the local patch (i.e. here, information gained through their own breeding experience; Danchin et al. 2004; Dall 2005). Young, less competitive individuals can also be expected to rely differently on social information for breeding decisions (Doligez et al. 2004a). Therefore, we included in the models a sex-specific three-class status variable to account for the individual's expected level of breeding experience in the patch (Kivelä et al. 2014): (i) yearlings, (ii) older (two years or older) immigrant individuals, and (iii) older philopatric individuals. Immigrants in a patch were all individuals new to this patch, i.e. comprised both previously unringed adults and dispersers (i.e. individuals that changed breeding patch between years). Second, individuals that were involved in the experiment for several years and made a symbol choice prior to the current choice may be expected to rely on their past experience with symbols and therefore be less likely to copy. Therefore, we included in the models a fixed effect to account for pair members' previous experience with symbols. Preliminary analyses revealed no interaction between the female and male previous experience with symbols on the probability to copy. Therefore, we implemented a joint three-level variable: (i) both pair members were naive to the symbol experiment, (ii) both had already experienced the symbol experiment, and (iii) one pair member was naive and the other one experienced, irrespective of their sex. Separating the latter "mixed" pairs according to the sex of the naive individual did not qualitatively change the results (results not shown). In addition to factors related to individuals' over-

all experience, we included as fixed effects in the models (i) the symbol type (triangle or circle) chosen by the pair to control for a potential innate symbol preference; (ii) the date of nest box choice (continuous variable, 1 = 1st of April) and its square value, because late birds tended to copy more in previous experiments, probably as a result of a lack of time to collect personal information (Seppänen and Forsman 2007), and this effect may be non-linear; (iii) whether or not a flycatcher pair bred in the chosen nest box the year before (binary variable), because collared flycatchers are more likely to select nest boxes occupied by conspecifics in the previous year (Kivelä et al. 2014); (iv) the proportion of nest boxes occupied by tits on the day of choice out of the total number of boxes per patch, because information strength is likely to depend on the proportion of demonstrators in the patch (here tit pairs). Furthermore, the proportion of empty nest boxes with each symbol in each patch was not always exactly equal; this was particularly noticeable when the number of empty boxes was small (i.e. in the smallest patches towards the end of the settlement period). Therefore, we tested whether the probability to copy the apparent symbol preference of tits differed from random by adding the deviation from 0.5 of the proportion of the symbol associated to tit nests on empty boxes (i.e. $[\text{number of empty boxes presenting the symbol associated with tits on the day of choice}] / [\text{total number of empty boxes in the patch on the day of choice}] - 0.5$) as a covariate in the model. The time needed to withdraw symbol on boxes newly occupied by flycatchers could also vary because it was not always easy to classify a small amount of nest material as a proper start of nest (in which case the symbol could be withdrawn only when the nest reached a later stage) and also because the speed of nest building varies between birds. To control for the resulting variation in individuals' exposure to conspecific information among newly settled flycatchers, we added as a covariate the ratio of nest boxes occupied by conspecifics (i.e. with at least 0.5 cm of dry grass) that presented the symbol associated to tit nests over all boxes occupied by flycatchers with either symbol in the same patch two days before settlement (i.e. on the last check before the settlement was detected).

Table 3.1: *Summary of the fixed effects included in the full animal model fitting the probability to copy tit preference.*

Variable	Number of levels or range	Definition
Categorical fixed effects		
<i>Symbol</i>	<i>circle, triangle</i>	Symbol chosen: circle or triangle
<i>Pair.symbol.exp</i>	<i>experienced, mixed, naive</i>	Whether both pair members experienced the symbol choice the year before, none of them, or only one of them
<i>Status</i> ♀	<i>Y, I, P</i>	Female age and dispersal status: yearling, older immigrant, or older philopatric
<i>Status</i> ♂	<i>Y, I, P</i>	Male age and dispersal status: yearling, older immigrant, or older philopatric
<i>Flycatcher[y-1]</i>	<i>yes, no</i>	Absence or presence of a flycatcher pair breeding in the same nestbox the year before
Continuous fixed effects		
<i>Day</i>	[28 ; 67]	Day of choice, counted from the 1st of April
<i>Day</i> ²	[784 ; 4489]	Square the day of choice
<i>Dev.symbol</i>	[-0.25 ; 0.50]	Nb of empty boxes with the tit symbol / Total nb of empty boxes - 0.50, on the day of choice
<i>Prop.tit</i>	[0.03 ; 0.73]	Nb of tit breeding in the plot on the day of choice / Total nb of boxes in the patch
<i>Prop.flycatcher</i>	[0.00 ; 1.00]	Nb of boxes with the tit symbol occupied by flycatcher / Nb of boxes with any symbol occupied by flycatcher, before the day of choice

Regarding the quantitative genetic estimates, the animal models disentangled sex-specific additive and non-additive genetic effects to estimate as accurately as possible the additive genetic variance V_A . The models therefore included sex-specific dominance and maternal effects (McAdam et al. 2002; Wilson et al. 2010; Wolak and Keller 2014) as random effects. Because we had several nest box choices for a fraction of individuals over the years, we accounted for a permanent environment effect by including the identities of the male and female as random effects. Because of the low inter-annual pair fidelity in our population (see above), we did not control for pair identity in our models. Finally, we also included year and nest box identity as random effects to account for spatio-temporal environmental variability. Including the patch instead of the nest box or including the year as a fixed effect instead of a random effect did not qualitatively change the results (results not detailed). Model specification is detailed in Appendix A2.

We partitioned the phenotypic variance as follows:

$$V_P = V_{A\text{♀}} + V_{A\text{♂}} + 2Cov_{A\text{♀}\text{♂}} \times 2k_{mean} + V_{D\text{♀}} + V_{D\text{♂}} + V_{M\text{♀}} + V_{M\text{♂}} + V_{PE\text{♀}} + V_{PE\text{♂}} + V_Y + V_N + V_R$$

(Bijma et al. 2007a, b) where V_A and V_A are sex-specific additive genetic variances, Cov_A is the cross-sex additive genetic covariance, $2k_{mean}$ is the mean female-male relatedness across breeding pairs, estimated from the pedigree (twice the mean pairwise coefficient of kinship; Bijma et al. 2007a, b; Bouwman et al. 2010; Germain et al. 2016); V_D and V_D are the sex-specific dominance variances; V_M and V_M are the sex-specific maternal identity variances; V_{PE} and V_{PE} are the sex-specific variances associated to the permanent environment effect (individual identities); V_Y is the variance associated to the year; V_N is the variance associated to the nest box; and V_R is the residual variance, which has to be fixed in the case of a binomial response variable (see Nakagawa and Schielzeth 2010). Sex-specific narrow-sense heritability estimates and were computed as the ratio of the sex-specific additive genetic variance over the total phenotypic variance $V_P + 1$ (the addition of 1 accounting for the probit link function; see Nakagawa and Schielzeth 2010). The proportion of phenotypic variance explained by the total additive genetic variance, T^2 , was computed as the ratio of the total additive genetic variance to $V_P + 1$ (Bijma et al. 2007a,b; Bouwman et al. 2010) as follows:

$$T^2 = \frac{V_A}{V_P + 1} = \frac{V_{A\text{♀}} + V_{A\text{♂}} + 2Cov_{A\text{♀}\text{♂}}}{V_P + 1}$$

Probability to copy in subsequent years

We explored whether the individual probability to copy was affected by previous personal information about symbols at the individual (and not pair) level by restricting the data to the 2nd and subsequent (up to 5th) individual choices ($N = 354$ choices made by 276 females, and 243 choices made by 187 males). We fitted separate models for males and females to avoid pseudoreplication in nest choice and included as fixed effects: whether the

individual copied the year before (copied vs. rejected), the age the year before (yearling vs. older), the individual's reproductive success the year before (success vs. failure; considering the continuous variable of the number of fledged youngs instead gave similar results) and its interaction with the past copying behavior. We also controlled for the deviation to the equal proportion of symbols on the day of choice (*Dev.symbol*, see Table 3.1) and whether the individual was tested for the 2nd, 3rd, 4th, or 5th time. Philopatric individuals always experienced opposite tit preferences in successive years (see Methods) but immigrants (in this case, all dispersers with known previous breeding patch) may experience either the same or the opposite symbol preference depending on their previous breeding patch. However, because breeding dispersal is very low in flycatcher males, only 4 male choices out of 243 were made while exposed to the same tit preference in two successive years; therefore, we tested this in females only. We included as fixed effects the dispersal status (philopatric vs. immigrant) and the variation experienced in the symbol associated to tits between successive years (i.e. apparent preference for the same vs. the opposite symbol), along with its interaction with past copying behavior, in the female model only. As random effect, we included the year, the forest patch, and the individual identity (i.e. no genetic random effects) in both models.

Implementation of models

We fitted our binary response variable (copy vs. reject) with the ordinal family. We used parameter expanded χ^2 distributions with 1 degree of freedom for the prior distributions of our variances (de Villemereuil et al. 2013; Hadfield 2014). We fixed the residual variance to 10 here instead of the value of 1 usually used for a binary response variable to improve the mixing of the Markov chain Monte-Carlo (MCMC) chains (Hadfield 2014). Indeed, preliminary analyses showed that estimated variances were expected to be small here. For the fixed effects, we used the classical diffused centered normal distribution with large variance ($V=10^8$; Hadfield 2014). Heritability estimates are given on the liability scale (i.e. taking into account the variance associated to the link function; see Nakagawa and Schielzeth 2010; de Villemereuil et al. 2013, 2016). All other posterior modes and

95% credible intervals (CI) presented are given on the latent (link) scale in the text and the tables, and on the original scale in the figures.

For the implementation of animal models, the social pedigree was prepared using the function *fixPedigree* (“pedantics” R package; Morrissey and Wilson 2010). As in many other passerine populations, 15% of all nestlings are extra-pair (Sheldon and Ellegren 1999). Such a relatively low extra-pair paternity rate should allow us to estimate quantitative genetic effects accurately enough from social pedigree (Charmantier and Réale 2005). The number of individuals was large in our quantitative genetic analyses (from 141 up to 311 complete breeding pairs per year over 5 years), with a pedigree depth of 15 years (Quinn et al. 2006). To optimize model computation, the pedigree was pruned using function *prunePed* from the “MCMCglmm” R package (Hadfield 2010) and the dominance genetic relatedness matrix was derived from this pruned pedigree using function *makeD* (“nadiv” R package; Wolak 2012). The pruned pedigree comprised 2623 individuals with a mean female-male relatedness across breeding pairs of 0.001 (see Appendix A3 for details on the pedigree characteristics).

We ran the MCMC chains for 600 000 iterations, using a burn-in period of 10 000 iterations and a thinning interval of 150 (except mentioned otherwise in some sensitivity analyses, see Appendix A4). Our effective sample size was approximately 3000 for each parameter, autocorrelations of the posterior samples being always below 0.1. The convergence of the MCMC chains was assessed visually and by using the Heidelberg stationary test on the random factors (*heidel.diag* function, “MCMCglmm” R package; Hadfield 2010). We removed the genetic correlation effect from the full model as its Heidelberg stationary and half-width tests showed conflicting outcomes despite a high number of retained iterations, suggesting a variance of zero. We then selected fixed effects by hierarchically removing the effects whose 95% CI encompassed zero, starting with the effects with a posterior mode closer to zero. Because this stepwise method may increase the risk of type-I error (Mundry and Nunn 2009; Forstmeier et al. 2016), we compared the 95% CI in the selected fixed structure to those obtained from the full models, but retained estimates from the selected models. Removing the genetic correlation effect after selecting

the fixed effects did not change the results (results not detailed, but see Appendix A5 for the full model output). Finally, for the animal models, we checked the sensitivity of the results to (1) the prior chosen, (2) the years included in the dataset, (3) the value chosen for V_R , and (4) the presence of the dominance or maternal identity effects (see Appendix A4).

3.3 Results

The probability to copy was significantly higher than random (i.e. copying tit preference) in 2012 (the only year where all individuals were naive with respect to the symbols; = 6.28, p-value = 0.012, Table 3.2). The probability to copy did not differ from random in 2014, 2015, or 2016 (Table 3.2). When restricting the data to naive pairs over the years, the probability to copy was significantly lower than random in 2013 (i.e. rejecting tit preference; = 4.36, p-value = 0.037, Table 3.2). Overall, the proportion of nest boxes chosen that presented the symbol associated to tit nests was not different from random (50.6%, = 0.19, p-value = 0.660, Table 3.2), which was likely due to opposing patterns of copying in 2012 and 2013 combined with the absence of copying on average from 2014 onwards. Flycatchers arrived later on average in 2013 and 2015 compared to other years (Table 3.2). Nevertheless, the day of choice (95% CI = [-0.517; 0.576]) did not explain the probability to copy (Appendix A5). Similarly, the proportion of boxes occupied by tits on the day of choice was greater in 2012, but this variable did not affect the probability to copy (95% CI = [-3.687; 3.419], Appendix A5). As could be expected, when a symbol was overrepresented on the empty boxes in a given patch, the probability to choose a box with this symbol was higher than random (95% CI = [3.725; 20.103], Table 3.3).

Repeatability estimates

Repeatability estimates for the probability to copy, estimated as the proportion of variance attributable to individual identity (compared to residual variance V_{R+1} ; Nakagawa and Schielzeth 2010) did not differ from zero for either sex (95% CI = [0; 0.087] for fe-

males, $N = 1368$; $[0; 0.086]$ for males, $N = 1014$). Similarly, repeatability estimates for the probability to settle in a box with a circle (i.e. “prefer” a circle over a triangle) did not differ from zero for either sex (95% CI = $[0; 0.094]$ for females, $[0; 0.108]$ for males).

Table 3.2: *Annual variations in the copying behavior, number of choices and flycatcher and great tit phenology. Proportion estimates in bold are significantly different from random (χ^2 test; p -value < 0.05). Sample sizes are given in parentheses (they include here choices made by unidentified individuals, i.e. those not caught during breeding later on). The day of choice and the average laying dates are given from the first of April (\pm SD).*

	2012	2013	2014	2015	2016	Overall
<i>Copying in % (N)</i>						
All pairs	59.2 (184)	46.8 (378)	51.8 (423)	49.7 (312)	48.5 (200)	50.6 (1497)
Pairs naive to the symbols	59.9 (137)	41.9 (167)	57.6 (144)	49.3 (69)	48.3 (58)	51.7 (575)
Pairs with a yearling male	66.7 (30)	52.2 (69)	61.8 (68)	46.4 (28)	47.6 (21)	56.0 (216)
Pairs with an older male	57.7 (116)	38.6 (166)	50.0(230)	48.1 (156)	48.5 (130)	48.1 (798)
<i>Flycatcher phenology</i>						
Day of choice	39.5 ± 3.9	42.2 ± 3.9	39.9 ± 5.7	45.9 ± 6.1	39.3 ± 5.3	
Laying date	47.8 ± 3.1	50.8 ± 2.7	48.8 ± 3.3	53.1 ± 5.0	45.8 ± 4.2	
<i>Tit phenology</i>						
Laying date	29.8 ± 4.9	42.3 ± 3.9	29.6 ± 5.4	31.6 ± 4.5	26.6 ± 6.9	
Prop.tit (%)	49.1	27.1	35.2	32.2	41.6	
<i>Number of days between flycatchers and tit laying dates</i>						
	18.0	8.5	19.2	21.5	19.2	

Age, experience, and environmental effects

Based on the animal model output, pairs including a yearling male were more likely to copy compared to pairs including an older immigrant male (56.0% of copying over the years, against 47.3% for pairs with an old immigrant male; 95% CI = $[0.145; 1.746]$, Tables 3.2, 3.3, Figure 3.2). Pair experience with symbols, defined as whether both or one partner was naive or had experience with symbol choice had no effect on the probability to copy, even though we got a slight trend for mixed pair to reject tit preference (95% CI = $[-2.064; 0.174]$, Appendix A5). The deviation to the proportion of empty boxes with the symbol associated with the tit preference had the strongest effect on the probability to copy (Table 3.3), but the distribution of this deviation was highly condensed around

zero (Figure 3.2). The day of choice, its quadratic effect, the symbol chosen (triangle or circle), the proportion of tutors in the patch and the proportion of informative flycatchers did not explain the probability to copy (Appendix A5).

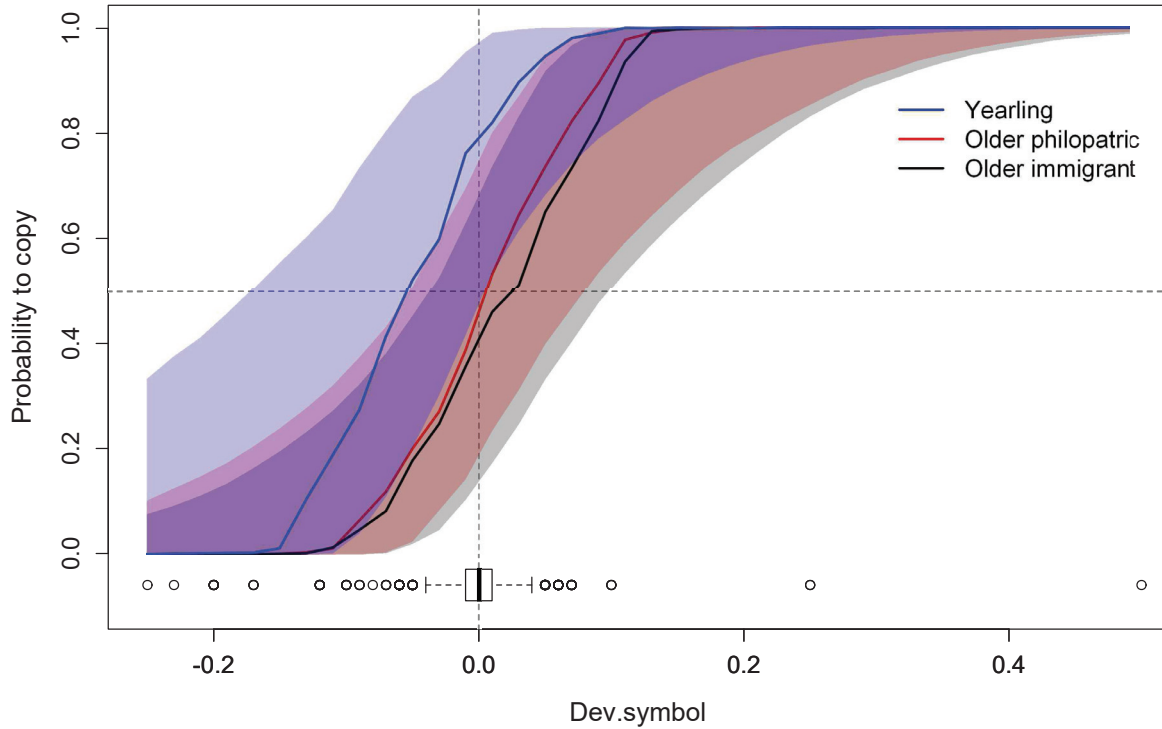


Figure 3.2: Relationship between the probability to copy and the deviation to an equal proportion of symbols on empty boxes (*Dev.symbol*, see Table 3.1) for the different male age and dispersal status (yearling/older immigrant/older philopatric). Positive values of *Dev.symbol* indicate a prevalence of empty nest boxes with the same symbol as the tit apparent preference. The posterior modes (solid lines) and their 95% Credible Intervals (shades) are given on the original scale, for pairs with a yearling male (in blue), an older philopatric male (in red), or an older immigrant male (in black). The vertical dashed line corresponds to an even proportion of triangles and circles on empty boxes on the day of flycatcher choice. The horizontal dashed line corresponds to a random choice (probability = 0.5). The boxplot represents the distribution of *Dev.symbol*. There was no interaction between *Dev.symbol* and the male experience status.

Quantitative genetics of the probability to copy

There was no cross-sex additive genetic covariance in the probability to copy (95% CI = [-0.024; 0.029] in the full model). Therefore, we removed this covariance from our

models. The proportion of phenotypic variance explained by the total additive genetic effects, T^2 , was thus calculated as the sum of both sex-specific heritabilities. The posterior modes of all additive genetic variances and heritability estimates were below 0.01 (Table 3.3). The posterior distributions of all variances and heritability estimates were condensed close to zero (Appendix A4). The above figures were obtained when using $V_R = 10$ but when increasing V_R , the posterior distributions for the sex-specific heritabilities and T^2 shifted even further towards 0 (Appendix A4). Overall, the results strongly suggest that the additive genetic variance components (as well as non-genetic components) and heritability estimates were not different from 0.

Probability to copy in subsequent years

In males, none of the variables explained the probability to copy the subsequent year (Table 3.4). Females tended to reject if they had copied in the previous year, but only if they were again exposed to the same apparent tit preference as in the previous year (89.6% out of 22 female choices copied on average, Figure 3.3, Table 3.4). On the contrary, when females were exposed to the opposite apparent tit preference, their copying behavior did not depend on whether they had copied or not in the previous year (Figure 3.3, Table 3.4).

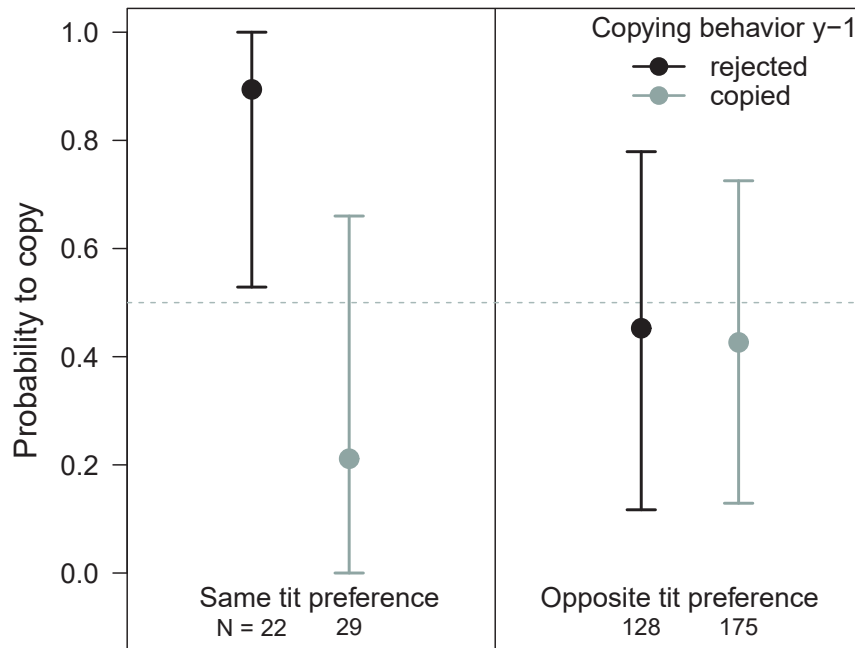


Figure 3.3: *Female probability to copy in subsequent nest site choices, given previous copying behavior and the difference in exposure to the apparent tit preference compared to the previous year. Females were either exposed to the same (Left) or opposite (Right) apparent tit preference than the year before. Females that rejected (did not copy) the tit preference the year before are represented in black, and females that copied are represented in light gray. Posterior means and 95% CI are given on the original scale. The horizontal dashed line corresponds to a random choice (probability = 0.5). Sample sizes are given at the bottom of each panel. Sample sizes are higher for females exposed to the opposite tit preference because this situation corresponds to both the philopatric females and the females that dispersed to a patch with the opposite symbol.*

Table 3.3: *Posterior modes and credible intervals of the final animal model fitting the probability to copy the tit preference. Estimates for the selected fixed and random effects are given on the latent scale with the residual variance V_R set to 10. See Table 3.1 for a detailed description of the fixed effects. For the male categorical status variable (Status), older immigrant males are considered as the group of reference.*

	Posterior mode	CI (95%)	Effective sample size
Fixed effects			
Intercept	-0.252	[-1.066 ; 0.497]	3934
Status ♂			
older philopatric	0.159	[-0.576 ; 0.722]	3934
yearling	0.837	[0.145 ; 1.746]	3934
Dev.symbol	11.194	[3.725 ; 20.103]	3934
Random effects			
$V_{A♀}$	0.007	[0 ; 1.024]	3934
$V_{A♂}$	0.008	[0 ; 1.262]	3934
$V_{D♀}$	0.009	[0 ; 1.240]	3934
$V_{D♂}$	0.009	[0 ; 1.226]	3934
$V_{M♀}$	0.009	[0 ; 2.157]	3934
$V_{M♂}$	0.006	[0 ; 2.737]	3934
$V_{PE♀}$	0.010	[0 ; 1.352]	3934
$V_{PE♂}$	0.006	[0 ; 1.192]	3495
V_Y	0.077	[0 ; 1.703]	3934
V_N	0.006	[0 ; 1.672]	3934
V_R	10.000	[10 ; 10]	0
Derived estimates			
$h^2_{♀}$	0.0003	[0 ; 0.065]	3934
$h^2_{♂}$	0.0003	[0 ; 0.080]	3934
T^2	0.0016	[0 ; 0.112]	3934

$V_{A♀}$ and $V_{A♂}$: sex-specific additive genetic variances; $V_{D♀}$ and $V_{D♂}$: sex-specific dominance variances; $V_{M♀}$ and $V_{M♂}$: sex-specific maternal identity variances; $V_{PE♀}$ and $V_{PE♂}$: sex-specific variances associated to the permanent environment effect (individual identities); V_Y : variance associated to the year; V_N : variance associated to the nest box; V_R : residual variance. $h^2_{♀}$ and $h^2_{♂}$: sex-specific narrow-sense heritability estimates; T^2 : proportion of phenotypic variance explained by the total sex-specific additive genetic effects.

Table 3.4: Posterior modes and credible intervals of the model explaining the probability to copy in subsequent years. Estimates for the selected fixed and random effects are presented for the male and female full models, and for the selected model for females. All estimates are given on the latent scale with the residual variance V_R set to 10. In restricted dataset used for this model, all males were philopatric, the apparent tit preference was consequently always “opposite” compared to the previous year. For categorical variables, estimates are given for the category between parentheses, the category of reference being part of the intercept estimate.

	Male full model		Female full model		Female final model	
	Post mode	CI (95%)	Post mode	CI (95%)	Post mode	CI (95%)
Fixed effects						
intercept	0.632	[-2.789 ; 4.671]	-3.148	[-6.048 ; 1.196]	-0.036	[-1.099 ; 0.847]
breeding success y-1 (success)	-0.277	[-3.115 ; 3.007]	1.453	[-0.488 ; 4.025]		
age y-1 (yearling)	0.381	[-0.948 ; 1.786]	0.642	[-0.513 ; 1.868]		
choice y-1 (copying)	0.430	[-3.204 ; 3.948]	0.455	[-2.573 ; 2.871]	0.124	[-1.265 ; 0.881]
tit preference than y-1 (same)			1.517	[-0.835 ; 4.699]	1.745	[-0.183 ; 4.199]
dispersal status (philopatric)			-0.819	[-2.506 ; 1.075]		
dev.symbol (c.f. Table 1)	9.786	[-7.544 ; 34.650]	5.971	[-9.868 ; 22.977]		
number of past symbol experience	-0.285	[-1.299 ; 0.770]	0.324	[-0.287 ; 1.517]		
choice : tit preference y-1 (copying : same)			-3.545	[-6.087 ; -0.281]	-2.594	[-5.853 ; -0.152]
choice * success y-1 (copying * success)	-0.476	[-4.459 ; 3.072]	-0.153	[-3.406 ; 2.248]		
Random effects						
V_{PE}	0.008	[0 ; 2.098]	0.055	[0 ; 7.261]	0.017	[0 ; 5.356]
V_Y	0.001	[0 ; 1.198]	0.004	[0 ; 1.362]	0.002	[0 ; 0.968]
V_{patch}	0.006	[0 ; 1.215]	0.009	[0 ; 1.089]	0.007	[0 ; 0.851]
V_R	10.000	[10 ; 10]	10.000	[10 ; 10]	10.000	[10 ; 10]
Effective sample size:		>3560		>3642		>3070

Success y-1, breeding success vs. failure the previous year; age y-1, age the previous year, yearling vs. older; choice y-1, previous copying behavior, copying vs. rejecting; tit preference y-1, whether the individual was confronted to the same apparent tit preference or the opposite than the previous year; dispersal status, philopatric vs. immigrant; dev.symbol, deviance to the equal proportion of triangles and circles on empty boxes on the day of choice (see Table 1); number of past symbol experience, whether it is the 2nd, 3rd, 4th, and 5th choice, continuous variable; V_{PE} : variance associated to the permanent environment effect (individual identity); V_Y : variance associated to the year; V_{patch} : variance associated to the forest patch; V_R : residual variance, set to 10.

3.4 Discussion

In this study, we investigated the influence of genotypic and phenotypic variation on social information use for habitat selection by experimentally manipulating a source of heterospecific (tit) social information in a wild flycatcher population. We estimated (1) repeatability in information use for nest site selection (at the individual level) as well as (2) the effect of individual overall experience as measured by age, familiarity with the environment, previous experience with the experimental design, and previous breeding success, and (3) female and male direct and indirect genetic effects on information use for the joint nest site selection (at the pair level). The probability to copy apparent tit nest site choices showed variation among years: flycatchers tended to copy apparent tit choices in the first year of the experiment (2012) but reject it the following year. Flycatcher pairs where the male was a yearling were more likely to copy the apparent tit choice than pairs with an older immigrant male (but not pairs with an older philopatric male), indirectly suggesting a sex-specific difference in social information use in nest site selection. Individual repeatability in the probability to copy apparent tit choices, as well as the sex-specific estimates of additive genetic variance and heritability, were null. Thus direct and indirect genetic effects explained no part of the variance in the probability to copy apparent tit choices. These results are in line with large environmental variances observed in other behavioral studies (Stirling et al. 2002; Bell et al. 2009; Doctermann et al. 2015) and potentially reflect that social information use in nest site selection is most importantly affected by environmental factors, including the availability and reliability of the information obtained from tits. The ability to perceive and use social information may, however, have a genetic basis and respond to selection, even though we did not find genetic variation in the use of a specific, experimentally provided, source of social information.

The role of experience in social information use

As expected, individual overall experience partly affected the probability to copy tit choices in this study. Regarding the effect of age and familiarity with the environment, a previous study in the same population showed that pairs where both partners were old and philopatric were more likely to settle in nest boxes occupied by conspecifics in the previous year, than pairs where at least one member was a yearling or an immigrant (Kivelä et al. 2014). Because this source of social information (i.e. conspecific presence in the previous year) was probably not (or little) available for yearlings and immigrants, this suggests that the use of social information depends on its availability to individuals. Here, the higher probability to copy tit choices in pairs with yearling males compared to pairs with older immigrant males suggests that, in collared flycatchers, this heterospecific social information in the current year may be used for nest site selection in particular by late arriving, less competitive individuals (Doligez et al. 2004a). We could not detect a difference in the probability to copy between pairs with a yearling or an older philopatric male, but this might only be due to a lack of power. Indeed, Figure 3.2 suggests that the probability to copy was similar between pairs with older philopatric and immigrant males. Our results are thus in accordance with previous results on heterospecific nest site copying behavior in collared and pied flycatchers using the same experimental design showing higher probability to copy tit choices for late arriving, thus presumably young individuals (Seppänen and Forsman 2007). The age-related difference in the probability to copy apparent tit preference for nest site selection suggests that the use of this heterospecific source of information is more advantageous for yearlings. More work would be needed to determine whether this results from their lower level of personal information or from a temporal change in the reliability or value of this information source along the season.

Males may have a preponderant influence on nest site selection, as illustrated by the absence of effect from female age and dispersal status on the joint nest site selection phenotype (Jaakkonen et al. 2013). The low female contribution to the joint phenotype observed here contrasts with another recent experimental study in the pied flycatcher,

where only females used tit phenology as a source of social information for breeding site selection (Samplonius and Both 2017). Even though our study is not directly comparable with that of Samplonius and Both (2017), both report differences between sexes in social information use for breeding site selection, and our results also suggest a differential effect of individual experience as reflected by age and dispersal status between sexes. Such between-sex differences may result from sex-specific information gathering processes (Reed et al. 1999; Doligez et al. 2004b), in relation to sex-specific fitness benefits associated with breeding system and dispersal processes (Greenwood 1980). In birds, males are expected to benefit from fine-scale knowledge of their environment, which can be achieved by philopatry and fine-scale prospecting within the natal habitat and allows them to select and defend high-quality territories where to attract females (Greenwood 1980; Doligez et al. 2004b). Conversely, females benefit from larger-scale knowledge of the environment and thus larger-scale prospecting, leading to longer dispersal distances, allowing them to select the best males or territories (Greenwood 1980; Arlt and Pärt 2008). These sex-specific selective pressures acting on the knowledge of the environment and information gathering may translate into the use of different information sources (including social information) between sexes and/or differential use of the same information depending on individual experience, as suggested here. Both our results and previous results (Samplonius and Both 2017) are coherent with a preponderant use of fine-scale social information by males and large-scale social information by females.

Overall, previous pair experience with symbols had no effect on the probability to copy apparent tit choices. Nevertheless, individuals were more likely to copy tit choices in the first year of the experiment, when they were all naive to the experimental setup. Previous experiments in this system using a similar experimental design have been conducted only for one year in most cases, thus including only naive individuals (Seppänen and Forsman 2007; Seppänen et al. 2011; Jaakkonen et al. 2013). This could explain the contrast between our overall results, including individuals experienced with the symbols, and former studies. However, when excluding the first symbol choice (i.e. by naive individuals), experienced females tended to copy tit choice when they had rejected it

the year before and were again exposed to the same apparent tit preference. Those females were all dispersing individuals, but not all dispersers were exposed to the same apparent preference depending on the patch they dispersed to. This switching behavior did not depend on the individual's past reproductive success, even though past success affected dispersal decisions in the same population (Doligez et al. 1999), but at a much larger spatial scale (patch vs nest site here). Importantly, our experimental set-up *de facto* disconnected the use of heterospecific social information for nest site selection from its fitness pay-offs. This may have led part of the individuals that failed in breeding to learn and use other information sources in subsequent nest-site choices. To what extent such learning processes are under genetic determinism and thus interfere when estimating heritability of information use in wild populations, remains unknown. Specific caution should be taken in this respect when designing long-term experiments where the association between manipulated information and fitness payoff is altered.

High environmental variances: the role of between-species synchrony

Most of the variance in the use of apparent tit nest site choice was here due to environmental factors. One of the main factors that may affect the probability for flycatchers to copy apparent heterospecific (tit) nest site choice was the temporal delay between tit reproduction and flycatcher arrival. The usual time interval between average tit and flycatcher laying date is two to three weeks on Gotland but it may strongly vary among years (Table 3.2). When tit reproduction is delayed, the number of tit demonstrators upon flycatcher arrival from wintering grounds, and thus the strength and possibly the reliability of heterospecific information, may decrease, due in particular to environmental stochasticity (see also Parejo 2016 for a discussion on information mismatching). Interestingly, female pied flycatchers have been shown to prefer settling in forest patches where tit phenology is early (Samplonius and Both 2017). Here, we found no effect of the date of choice by flycatchers or the proportion of nest boxes occupied by tit pairs in the patch, which suggests that the number of tit demonstrators may not have strongly

affected inter-individual variation in copying behavior here (Jaakkonen et al. 2013). Nevertheless, between-species temporal delay may explain variation in copying behavior at the inter- rather than intra-annual scale. In 2013, tit pairs settled much later than in other years, leading to the lowest proportion of tit demonstrators settled (Table 3.2), but also to apparently small tit clutches upon flycatcher's arrival, because tits were still settling or laying. This could explain why flycatchers, especially pairs with old males that arrive first, did not just choose at random but actually rejected tit choices in 2013, in line with previous results (Seppänen et al. 2011; Loukola et al. 2013). In contrast, 2012 was the year with the higher proportion of tit demonstrators upon flycatcher settlement. This could contribute to explain the higher probability to copy in 2012 compared to other experimental years.

The high residual variance in the probability to copy may also partly be due to the experimental design used here. In many of the former experiments based on symbol choice in the tit-flycatcher system, each nest box was paired with another one at a distance of ca. 2 meters and the two boxes received different symbols. This allowed settling flycatchers to choose between symbols independently from other characteristics of the microhabitat (Seppänen and Forsman 2007; Seppänen et al. 2011; Loukola et al. 2012; Forsman et al. 2014). Here, we used a single-box design to be able to conduct our experiment over large spatial and temporal scales, but the choice of a nest box could in this case be associated not only with the symbol but also with other microhabitat characteristics around the box. Consistent differences in preference for nest boxes (measured by the probability and date of occupancy) over years have been found in this population, and they were suggested to relate to local microhabitat quality (Pärt 1995). Here, by including nest box as a random factor, we aimed at controlling for such small-scale habitat characteristics. Nevertheless, microhabitat quality around a box (including the inter- and intra-specific social neighborhood) is likely to remain an important source of residual variance in the probability to copy. Other environmental factors could also participate in the high residual variance but they remain to be identified.

No additive genetic variance

We found no additive genetic variance for the probability to use our experimentally provided heterospecific social information for nest site choice. Other quantitative genetic studies also found low or null estimates of additive genetic variance in joint breeding phenotypes. For example, considering sex-specific additive genetic variances as we did here, breeding time was found not to be heritable in female red-billed gulls (*Larus novaehollandiae scopulinus*, Teplitsky et al. 2010) or in male blue tits (Caro et al. 2009). From an evolutionary point of view, low or null estimates of additive genetic variances may reflect either a high degree of phenotypic plasticity, an erosion of additive genetic variance through selection, and/or an absence of genetic basis of social information use. In the context of breeding site selection, social information use is expected to be highly beneficial, because acquiring the same information by direct sampling of the environment can entail high costs in terms of time, energy, and missed opportunities, especially in short-lived species (Doligez and Boulinier 2008), and the use of social information for breeding site selection has indeed been experimentally demonstrated in different species (Doligez et al. 2002; Boulinier et al. 2008). In the flycatchers-tits system, pied flycatchers have been shown to gain fitness benefits when breeding in proximity to great tits (by achieving earlier breeding, and heavier and larger broods; Forsman et al. 2002). Flycatchers have also been observed actively prospecting inside great tit nest boxes (Forsman and Thomson 2008; Forsman et al. 2018) despite a high risk of being killed (Merilä and Wiggins 1995). Altogether, these results suggest strong benefits of heterospecific information use that should exceed the costs of interspecific competition and information acquisition. Thus, heterospecific social information use for nest site selection may often be adaptive and should be favored but whether individuals actually use it in the context of our study (i.e. copying vs. rejecting tit choice) seemed highly plastic, which could be related to spatio-temporal changes in the quality (i.e. availability and reliability) of information.

Our results are in line with the idea that stochastic environmental variation should strongly affect social information use strategies by shaping the quality of information (e.g.

Doligez et al. 2003). In our study, the quality of heterospecific information could have been in particular dependent on the synchrony between the information provider and user. Its use therefore appeared plastic and not genetically inherited. However, what could be genetically based and should be under strong selective pressures could be the ability to use the specific sources of information (among social, personal, and environmental cues) that provide the highest quality information depending on spatio-temporally changing environmental conditions rather than the use of a given source of information itself. Such adjustment of information use could in particular result from learning. While learning has been found to be heritable in captive populations (e.g. Mery and Kawecki 2002), no estimation of the heritability of learning and its genetic covariance with social information use is available in the wild so far. More generally, estimating the genetic basis of optimally adjusting social information use would require testing the use of different information sources in different environmental conditions. For example, both social information (e.g. the tit apparent preference for an artificial nest site feature) and the quality of information providers (e.g. tit clutch size) could be manipulated simultaneously in a crossed design (see Forsman and Seppänen 2011) to explore the phenotypic and genetic contribution to the probability to make the apparently optimal decision (here, copying the choice of high quality individuals with large clutches, and rejecting the choice of low quality individuals with small clutches). Such experiment would have to be conducted over many years to account for possibly strong environmental variability, as observed here. Thus, testing this hypothesis in the wild remains a challenging task and more work on the quantitative genetics of social information use is needed to understand its evolution.

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Authors contribution

JM, JTF, SMK, and BD designed the study; JM, JTF, SMK, BD and many assistants carried out the fieldwork; JM analyzed the data; JM, JTF, SMK, LG, and BD drafted and critically revised the manuscript.

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3.6 Appendix

Appendix A1. Detailed protocol of the symbol experiment

The experiment was conducted from early April (i.e. just before tit settlement) to early June (i.e. after the settlement of the last flycatcher pairs). In early April, either a triangle or a circle was randomly attached to each nest box so that the two symbols were present in equal proportion over all boxes within a patch. Until early June, all nest boxes were visited every second day and symbols were adjusted where needed as follows: (1) if a nest box was newly occupied by a great or blue tit pair, the symbol was checked and changed if it did not correspond to the symbol associated with a tit nest in the patch in question; (2) if a nest box was newly occupied by a flycatcher pair, the symbol present on the box was recorded and removed from the box; finally, (3) the number of empty nest boxes with each symbol in the patch was counted and if needed, symbols were changed on randomly chosen empty nest boxes until an equal proportion of both symbols was restored on empty boxes. Nest boxes were considered occupied by tits only when a large amount of nest material (mainly moss, c.a. 5cm deep) was detected in the box, that is, when nest building was at a late stage. This was because tits often initiate several nests before settling in a nest box, especially early in the season (pers. obs.). Thus, by adjusting the symbol only for advanced tit nests, we kept only tit pairs actively building nests in the pool of information providers. For this reason, we also emptied nest boxes from inactive nests (i.e. nests whose building did not proceed further after 6 to 8 days) and randomly reassigned one of the symbols to the corresponding nest box. Conversely, nest boxes were considered occupied by flycatchers when a small amount of nest material (0.5-2 cm of dry grass) was detected in the nest box, because flycatchers do usually not start building additional nests so that each start of nest corresponds to an active pair (pers. obs.). We removed the symbol on boxes newly occupied by flycatchers so that social information with respect to the symbols would not be provided to later arriving flycatchers by conspecifics, but only by tits. On the last visit early June, all symbols were

removed from both nest boxes occupied by tits and empty nest boxes so that individuals prospecting for social information late in the season (breeders and fledglings; Doligez et al., 2004; Ponchon et al., 2013) would get no information with respect to the symbols to be used in the next year.



Figure A.3.1: Map of the experimental plots with the corresponding symbol associated to tit nests in 2014.

Appendix A2: Animal model specification

The animal model was specified as follows:

$$y \sim X\beta + Z_1a_{\text{♀}} + Z_2a_{\text{♂}} + Z_3d_{\text{♀}} + Z_4d_{\text{♂}} + Z_5m_{\text{♀}} + Z_6m_{\text{♂}} + Z_7p_{\text{♀}} \\ + Z_8p_{\text{♂}} + Z_9t + Z_{10}n + e$$

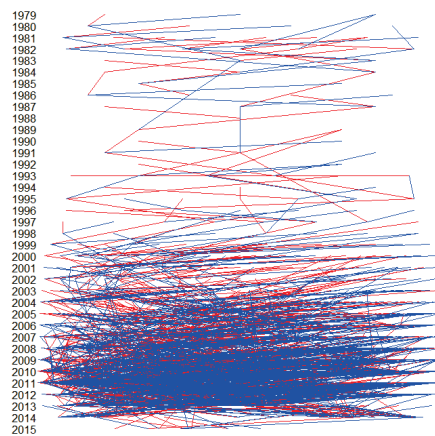
where y is the vector of binary responses (copying/rejecting for a given pair a given year), and β is a vector of fixed effects (see below). a , a , d , d , m , m , p , p are sex-specific vectors of random additive, dominance, maternal identity, and permanent environment (i.e. individual identity) effects, respectively. Vectors t and n include random effects associated with year and nest box identity. Vector e includes residuals. X and Z_i ($i = 1, 2, \dots, 10$) are design matrices associated with the fixed and random effects for each pair, respectively. We assumed that female and male additive genetic effects $a = [a_{\text{♀}}^T, a_{\text{♂}}^T]$ (T denotes transpose) follow a joint multivariate normal (MVN) distribution $\text{MVN}(0, G \otimes A)$, where A is the additive genetic relationship matrix derived from the pedigree, \otimes denotes the Kronecker product, and the variance-covariance matrix G is estimated by the model as follows:

$$G = \begin{bmatrix} V_{A\text{♀}} & \text{Cov}_{A\text{♀♂}} \\ \text{Cov}_{A\text{♀♂}} & V_{A\text{♂}} \end{bmatrix}$$

where V_A and V_A are sex-specific additive genetic variances and Cov_A is the cross-sex additive genetic covariance.

Appendix A3. Representation of the pruned pedigree by cohort along with pedigree statistics

Red and blue lines respectively represent maternities and paternities. Cohort attribution is either the birth year or, if the birth year is unknown, one year before first capture for yearlings and two years before first capture for older birds. The graph and the pedigree statistics were obtained using *drawPedigree* and *pedigreeStats* respectively, from the “pedantics” R package (Morrissey and Wilson, 2010).



Pedigree statistics	
Records	2628
Founders	1627
Maternities	987
Paternities	919
Full sibs	156
Maternal sibs	297
Maternal half sibs	141
Paternal sibs	268
Paternal half sibs	112
Maternal grandmothers	315
Maternal grandfathers	291
Paternal grandmothers	363
Paternal grandfathers	327
Maximum pedigree depth	16
Mean Relatedness	1.11×10^{-3}

Appendix A4. Sensitivity analysis for the animal model

We conducted several sensitivity analyses on our animal model fitting the probability to copy the apparent tit preference.

1. Sensitivity to priors

We checked the sensitivity of the results to the choice of prior by testing all combinations of parameter expanded priors with ν and $\alpha.V_R$ set to 1 or 1000. See Table A.3.1.

2. Sensitivity to temporal variation (years)

Because of natural annual variations (breeding synchrony between tits and flycatchers, weather, etc.), we tested the robustness of the results to the year effect by running the final model with fixed effects while removing the data from a given year at a time. Heritability estimates were not qualitatively affected by the years of data included in the analysis. See Table A.3.2.

3. Sensitivity to the value of the residual variance V_R (fixed arbitrarily)

We tested the sensitivity of our final model to the value chosen for V_R . See Table A.3.3 and Figure A.3.2.

4. Estimate of dominance and maternal identity variances

When datasets encompass too few relatedness links outside the nuclear family (e.g. contain mostly parent-offspring links), dominance and maternal identity variances may not be accurately and independently estimated (Wolak and Keller, 2014). Therefore, we checked that dominance and maternal identity variances were well estimated by comparing their estimates and 95% CI, as well as the estimates of sex-specific additive genetic variances and their 95% CIs, between models including both the sex-specific dominance and maternal identity effects and those including only one of them. See Table A.3.4.

Table A.3.1: *Posterior modes and 95% CI of the variances, sex-specific heritabilities, and T^2 for the model without fixed effects and additive genetic covariance, given three different expanded prior distribution types for the random terms. We fixed nu and $alpha.V$ to either 1 or 1000, V to 1, and $alpha.mu$ to 0. Other parameters used in the MCMCglmm model are indicated at the bottom of the table.*

	<i>nu = 1000, alpha.V = 1</i>		<i>nu = 1, alpha.V = 1</i>		<i>nu = 1, alpha.V = 1000</i>	
	Post mode	CI (95%)	Post mode	CI (95%)	Post mode	CI (95%)
$V_{A\text{♀}}$	0.005	[0 ; 1.008]	0.001	[0 ; 0.915]	0.008	[0 ; 1.439]
$V_{A\text{♂}}$	0.003	[0 ; 1.152]	0.002	[0 ; 1.093]	0.012	[0 ; 1.640]
$V_{D\text{♀}}$	0.010	[0 ; 1.206]	0.002	[0 ; 1.231]	0.006	[0 ; 1.973]
$V_{D\text{♂}}$	0.009	[0 ; 1.162]	0.002	[0 ; 1.100]	0.003	[0 ; 1.669]
$V_{M\text{♀}}$	0.010	[0 ; 2.214]	0.007	[0 ; 2.703]	0.019	[0 ; 4.876]
$V_{M\text{♂}}$	0.018	[0 ; 2.357]	0.007	[0 ; 2.633]	0.029	[0 ; 4.679]
$V_{PE\text{♀}}$	0.012	[0 ; 1.289]	0.006	[0 ; 1.270]	0.009	[0 ; 2.137]
$V_{PE\text{♂}}$	0.002	[0 ; 1.100]	0.004	[0 ; 1.087]	0.012	[0 ; 1.586]
V_Y	0.053	[0 ; 1.450]	0.071	[0 ; 1.519]	0.243	[0 ; 3.411]
V_N	0.009	[0 ; 1.516]	0.010	[0 ; 1.515]	0.012	[0 ; 2.566]
$h^2_{\text{♀}}$	0.0002	[0 ; 0.0643]	0.0004	[0 ; 0.0596]	0.0002	[0 ; 0.0749]
$h^2_{\text{♂}}$	0.0002	[0 ; 0.0725]	0.0004	[0 ; 0.0704]	0.0006	[0 ; 0.0850]
T^2	0.0014	[0 ; 0.1046]	0.0026	[0 ; 0.0987]	0.0105	[0 ; 0.1278]
Effective sample size	>3251		>3253		>3675	
	<i>Family = ordinal,</i> <i>nb.iter=6 x 10⁵,</i> <i>burn-in=10⁴,</i> <i>thin interval=150</i>		<i>Family = ordinal,</i> <i>nb.iter=15 x 10⁵,</i> <i>burn-in=3 x 10⁴,</i> <i>thin interval=400</i>		<i>Family = ordinal,</i> <i>nb.iter=15 x 10⁵,</i> <i>burn-in=3 x 10⁴,</i> <i>thin interval=400</i>	

$V_{A\text{♀}}$ and $V_{A\text{♂}}$: sex-specific additive genetic variances; $V_{D\text{♀}}$ and $V_{D\text{♂}}$: sex-specific dominance variances; $V_{M\text{♀}}$ and $V_{M\text{♂}}$: sex-specific maternal identity variances; $V_{PE\text{♀}}$ and $V_{PE\text{♂}}$: sex-specific variances associated to the permanent environment effect; V_Y : variance associated to the year; V_N : variance associated to the nest box; V_R : residual variance. $h^2_{\text{♀}}$ and $h^2_{\text{♂}}$: sex-specific narrow-sense heritability estimates; T^2 : proportion of phenotypic variance explained by the total sex-specific additive genetic effects.

Table A.3.2: Posterior modes and 95% CI of the variances, sex-specific heritabilities and T^2 for the final models (i.e. with selected fixed and random effects), with data from one year removed at a time (indicated as column head). V_R was set to 10 (see text).

	-2012		-2013		-2014		-2015		-2016	
	Post mode	CI (95%)	Post mode	CI (95%)	Post mode	CI (95%)	Post mode	CI (95%)	Post mode	CI (95%)
$V_{A\text{♀}}$	0.003	[0 ; 1.680]	0.008	[0 ; 2.327]	0.021	[0 ; 2.419]	0.011	[0 ; 1.298]	0.006	[0 ; 1.062]
$V_{A\text{♂}}$	0.005	[0 ; 1.342]	0.011	[0 ; 2.197]	0.013	[0 ; 1.607]	0.004	[0 ; 1.901]	0.007	[0 ; 2.011]
$V_{D\text{♀}}$	0.009	[0 ; 1.929]	0.016	[0 ; 2.488]	0.005	[0 ; 2.356]	0.005	[0 ; 1.542]	0.010	[0 ; 1.408]
$V_{D\text{♂}}$	0.008	[0 ; 1.255]	0.005	[0 ; 2.386]	0.004	[0 ; 1.683]	0.008	[0 ; 2.133]	0.017	[0 ; 2.321]
$V_{M\text{♀}}$	0.019	[0 ; 3.567]	0.020	[0 ; 2.410]	0.005	[0 ; 2.759]	0.008	[0 ; 2.641]	0.011	[0 ; 1.834]
$V_{M\text{♂}}$	0.019	[0 ; 2.884]	0.025	[0 ; 3.761]	0.006	[0 ; 2.467]	0.012	[0 ; 2.794]	0.017	[0 ; 4.078]
$V_{PE\text{♀}}$	0.010	[0 ; 2.016]	0.004	[0 ; 2.659]	0.019	[0 ; 2.454]	0.009	[0 ; 1.692]	0.006	[0 ; 1.479]
$V_{PE\text{♂}}$	0.003	[0 ; 1.211]	0.008	[0 ; 2.175]	0.003	[0 ; 1.658]	0.018	[0 ; 2.068]	0.017	[0 ; 2.133]
V_Y	0.016	[0 ; 1.355]	0.019	[0 ; 1.959]	0.290	[0 ; 2.590]	0.332	[0 ; 2.628]	0.285	[0 ; 2.556]
V_N	0.014	[0 ; 1.994]	0.004	[0 ; 1.822]	0.012	[0 ; 2.416]	0.007	[0 ; 2.418]	0.008	[0 ; 2.352]
$h^2_{\text{♀}}$	0.0005	[0 ; 0.0963]	0.0006	[0 ; 0.1231]	0.0008	[0 ; 0.1285]	0.0004	[0 ; 0.0735]	0.0002	[0 ; 0.0590]
$h^2_{\text{♂}}$	0.0003	[0 ; 0.0790]	0.0007	[0 ; 0.1159]	0.0008	[0 ; 0.0897]	0.0004	[0 ; 0.1058]	0.0007	[0 ; 0.1092]
T^2	0.0021	[0 ; 0.1353]	0.0112	[0 ; 0.1800]	0.0028	[0 ; 0.1682]	0.0042	[0 ; 0.1368]	0.0015	[0 ; 0.1320]
Effective sample size	>3714		>3559		>3557		>3350		>3860	

$V_{A\text{♀}}$ and $V_{A\text{♂}}$: sex-specific additive genetic variances; $V_{D\text{♀}}$ and $V_{D\text{♂}}$: sex-specific dominance variances; $V_{M\text{♀}}$ and $V_{M\text{♂}}$: sex-specific maternal identity variances; $V_{PE\text{♀}}$ and $V_{PE\text{♂}}$: sex-specific variances associated to the permanent environment effect (individual identities); V_Y : variance associated to the year; V_N : variance associated to the nest box; V_R : residual variance. $h^2_{\text{♀}}$ and $h^2_{\text{♂}}$: sex-specific narrow-sense heritability estimates; T^2 : proportion of phenotypic variance explained by the total sex-specific additive genetic effects.

Table A.3.3: *Posterior modes and 95% CI of the variances, sex-specific heritabilities, and T^2 for the final model, i.e. with selected fixed and random effects, with V_R set to 1, 50 and 100. The model with V_R set to 1 had 22×10^5 iterations and a thinning interval of 700. The other models had 6×10^5 iterations, and a thinning interval of 150. The burn-in was set to 10 000 for all models.*

	<i>Model with $V_R = 1$</i>		<i>Model with $V_R = 50$</i>		<i>Model with $V_R = 100$</i>	
	Post mode	CI (95%)	Post mode	CI (95%)	Post mode	CI (95%)
$V_{A\text{♀}}$	0.002	[0 ; 0.267]	0.006	[0 ; 2.433]	0.011	[0 ; 2.808]
$V_{A\text{♂}}$	0.002	[0 ; 0.327]	0.021	[0 ; 2.619]	0.025	[0 ; 3.125]
$V_{D\text{♀}}$	0.001	[0 ; 0.329]	0.008	[0 ; 2.694]	0.011	[0 ; 2.923]
$V_{D\text{♂}}$	0.002	[0 ; 0.322]	0.019	[0 ; 2.601]	0.024	[0 ; 3.491]
$V_{M\text{♀}}$	0.004	[0 ; 0.737]	0.026	[0 ; 3.447]	0.018	[0 ; 3.624]
$V_{M\text{♂}}$	0.003	[0 ; 0.896]	0.022	[0 ; 4.002]	0.016	[0 ; 4.236]
$V_{PE\text{♀}}$	0.003	[0 ; 0.354]	0.017	[0 ; 2.665]	0.012	[0 ; 3.213]
$V_{PE\text{♂}}$	0.001	[0 ; 0.320]	0.013	[0 ; 2.503]	0.014	[0 ; 3.145]
V_Y	0.043	[0 ; 0.556]	0.025	[0 ; 3.255]	0.036	[0 ; 4.083]
V_N	0.003	[0 ; 0.484]	0.020	[0 ; 3.138]	0.012	[0 ; 3.782]
$h^2_{\text{♀}}$	0.0007	[0 ; 0.0756]	0.0002	[0 ; 0.0396]	0.0001	[0 ; 0.0253]
$h^2_{\text{♂}}$	0.0004	[0 ; 0.0949]	0.0003	[0 ; 0.0433]	0.0002	[0 ; 0.0278]
T^2	0.0025	[0 ; 0.1320]	0.0025	[0 ; 0.0643]	0.0017	[0 ; 0.0418]
Effective sample size	>2968		>3734		>3558	

$V_{A\text{♀}}$ and $V_{A\text{♂}}$: sex-specific additive genetic variances; $V_{D\text{♀}}$ and $V_{D\text{♂}}$: sex-specific dominance variances; $V_{M\text{♀}}$ and $V_{M\text{♂}}$: sex-specific maternal identity variances; $V_{PE\text{♀}}$ and $V_{PE\text{♂}}$: sex-specific variances associated to the permanent environment effect; V_Y : variance associated to the year; V_N : variance associated to the nest box; V_R : residual variance. $h^2_{\text{♀}}$ and $h^2_{\text{♂}}$: sex-specific narrow-sense heritability estimates; T^2 : proportion of phenotypic variance explained by the total sex-specific additive genetic effects.

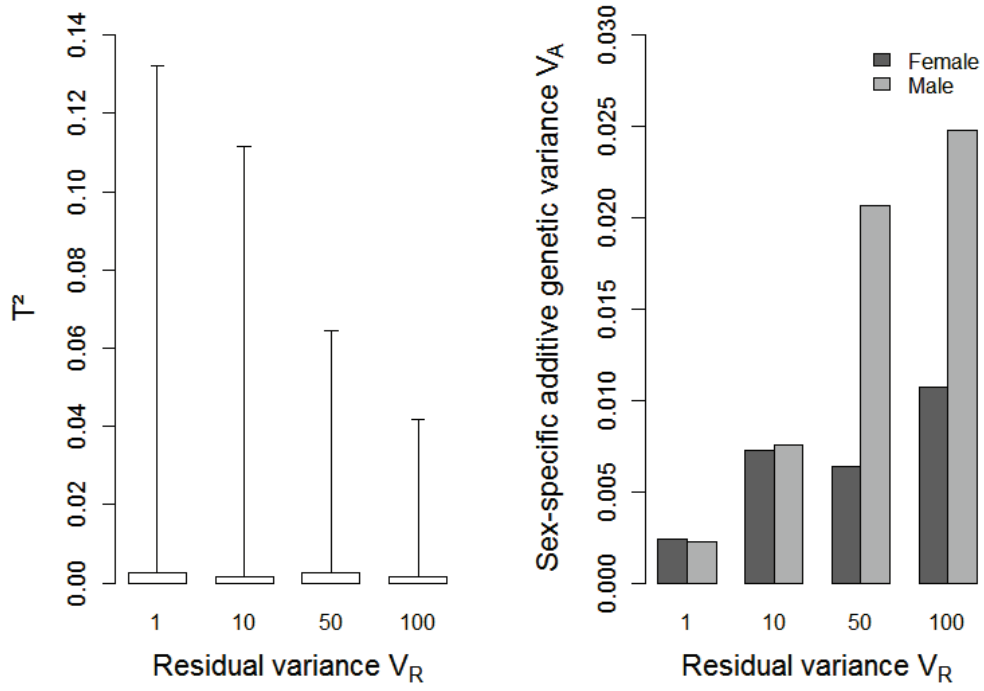


Figure A.3.2: Quantitative genetic estimates for the different, arbitrarily chosen values of residual variance. Posterior modes and corresponding upper 95% Credibility Interval limit for T^2 (the total proportion of additive genetic variance in the phenotypic variance; left) and the sex-specific additive genetic variances modes (right) for the final models with the selected fixed effects and residual variances V_R set to 1, 10, 50 and 100. The female and male additive genetic variance are respectively in dark and light grey (right panel).

Table A.3.4: *Posterior modes and 95% CI of the variances, sex-specific heritabilities, and T^2 for the final model, with selected fixed and random effects, and with or without the sex-specific dominance and maternal identities effects. D is for sex-specific dominance effects, M is sex-specific maternal identities effects. V_R was set to 10.*

	<i>With D only</i>		<i>With M only</i>		<i>Without D nor M</i>	
	Post mode	CI (95%)	Post mode	CI (95%)	Post mode	CI (95%)
$V_{A♀}$	0.002	[0 ; 1.179]	0.004	[0 ; 1.087]	0.007	[0 ; 1.069]
$V_{A♂}$	0.008	[0 ; 1.413]	0.011	[0 ; 1.293]	0.008	[0 ; 1.376]
$V_{D♀}$	0.010	[0 ; 1.466]				
$V_{D♂}$	0.004	[0 ; 1.388]				
$V_{M♀}$			0.012	[0 ; 2.311]		
$V_{M♂}$			0.007	[0 ; 2.911]		
$V_{PE♀}$	0.006	[0 ; 1.457]	0.008	[0 ; 1.437]	0.010	[0 ; 1.504]
$V_{PE♂}$	0.006	[0 ; 1.354]	0.004	[0 ; 1.301]	0.005	[0 ; 1.336]
V_Y	0.226	[0 ; 1.793]	0.159	[0 ; 1.775]	0.136	[0 ; 1.830]
V_N	0.006	[0 ; 1.554]	0.008	[0 ; 1.495]	0.009	[0 ; 1.522]
$h^2_{♀}$	0.0004	[0 ; 0.0777]	0.0002	[0 ; 0.0701]	0.0002	[0 ; 0.0758]
$h^2_{♂}$	0.0003	[0 ; 0.0928]	0.0004	[0 ; 0.0841]	0.0007	[0 ; 0.0970]
T^2	0.0044	[0 ; 0.1267]	0.0026	[0 ; 0.1149]	0.0012	[0 ; 0.1314]
<i>Effective sample size</i>	>3731		>3710		>3934	

$V_{A♀}$ and $V_{A♂}$: sex-specific additive genetic variances; $V_{D♀}$ and $V_{D♂}$: sex-specific dominance variances; $V_{M♀}$ and $V_{M♂}$: sex-specific maternal identity variances; $V_{PE♀}$ and $V_{PE♂}$: sex-specific variances associated to the permanent environment effect (individual identities); V_Y : variance associated to the year; V_N : variance associated to the nest box; V_R : residual variance. $h^2_{♀}$ and $h^2_{♂}$: sex-specific narrow-sense heritability estimates; T^2 : proportion of phenotypic variance explained by the total sex-specific additive genetic effects.

Appendix A5. Output of the full animal model

Table A.3.5: *Posterior modes, 95% CI, and effective sample size for the full model fitting the probability to copy. See Table 3.1 for a description of the fixed effects. Values in bold indicate effects retained in the final model.*

	Posterior mode	CI (95%)	Effective sample size
Fixed effects			
<i>Intercept</i>	0.491	[-11.573 ; 12.359]	3934
<i>Symbol</i>			
<i>Triangle</i>	-0.130	[-0.721 ; 0.513]	3934
<i>Day</i>	0.029	[-0.517 ; 0.576]	3756
<i>Day</i> ²	0.000	[-0.006 ; 0.006]	3934
<i>Pair.symbol.exp</i>			
<i>Mixed pair</i>	-0.815	[-2.064 ; 0.174]	3934
<i>Naive pair</i>	-0.720	[-1.771 ; 0.778]	3934
<i>Status</i> ♀			
<i>older philopatric</i>	-0.038	[-0.755 ; 0.773]	3730
<i>yearling</i>	-0.105	[-0.931 ; 0.661]	3817
<i>Status</i> ♂			
<i>older philopatric</i>	0.018	[-0.772 ; 0.772]	3934
<i>yearling</i>	0.931	[-0.013 ; 1.729]	3934
<i>Dev.symbol</i>	12.842	[5.159 ; 22.762]	3934
<i>Prop.tit</i>	-0.116	[-3.687 ; 3.419]	3934
<i>Prop.flycatcher</i>	-0.169	[-2.358 ; 1.505]	3934
Random effects			
$V_{A♀}$	0.011	[7.507×10^{-8} ; 1.381]	3934
$V_{A♂}$	0.008	[2.658×10^{-7} ; 1.616]	3934
$COV_{A♀♂}$	0.0000	[-0.024 ; 0.029]	3934
$V_{D♀}$	0.006	[1.375×10^{-7} ; 1.663]	3934
$V_{D♂}$	0.008	[6.378×10^{-9} ; 1.604]	3934
$V_{M♀}$	0.008	[2.271×10^{-7} ; 2.272]	3934
$V_{M♂}$	0.018	[3.553×10^{-8} ; 3.386]	3934
$V_{PE♀}$	0.016	[7.654×10^{-8} ; 1.834]	3934
$V_{PE♂}$	0.008	[2.835×10^{-10} ; 1.568]	3934
V_Y	0.270	[5.612×10^{-7} ; 2.304]	3934
V_N	0.009	[2.086×10^{-8} ; 2.010]	3934
V_R	10.000	[10 ; 10]	3934

$V_{A♀}$ and $V_{A♂}$: sex-specific additive genetic variances; $V_{D♀}$ and $V_{D♂}$: sex-specific dominance variances; $V_{M♀}$ and $V_{M♂}$: sex-specific maternal identity variances; $V_{PE♀}$ and $V_{PE♂}$: sex-specific variances associated to the permanent environment effect (individual identities); V_Y : variance associated to the year; V_N : variance associated to the nest box; V_R : residual variance, set to 10.

Chapter 4

Personality traits in flycatchers: Definition, Repeatability, and Correlations



No evidence for behavioural syndrome and genetic basis for three personality traits in a wild bird population

Jennifer Morinay, Gregory Daniel, Lars Gustafsson, Blandine Doligez

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Abstract

Personality traits can strongly affect individual life-history strategies. When personality traits show between-individual correlations, they constitute behavioural syndromes that can facilitate evolutionary responses to environmental variation but may strongly differ between ecological contexts. Understanding the genetic and ecological determinants of personality traits and how they form behavioural syndromes in the wild is thus needed to shed light on their evolutionary potential. However, because this requires large numbers of behavioural observations on many individuals of known relatedness level, studies on wild populations sometimes make the assumptions that (i) phenotypic (co)variances reliably inform on underlying genetic (co)variances and (ii) within-individual correlations reliably inform on between-individual correlations (i.e. behavioural syndromes). We tested the validity of these assumptions using three years of behavioural data collected on a long-term monitored breeding population of collared flycatchers (*Ficedula albicollis*). We estimated the repeatability and heritability of aggressiveness, boldness and neophobia, and their between-individual correlations. All three traits were repeatable between years, and thus corresponded to personality traits, but none were heritable. Permanent environment effects explained 16% of the phenotypic variance in aggressiveness, and maternal effects explained 28% of the phenotypic variance in neophobia. These effects are in line with other studies in the wild showing that permanent and maternal effects may shape personality traits. The three traits showed phenotypic within-individual, but not between-individual, correlations. Thus, our results did not support the assumptions that phenotypic covariances reveal genetic covariances and that within-individual correlations reveal between-individual correlations. We discuss the reasons for the absence of heritability for these three personality traits and the absence of behavioural syndrome between them in light of the possible selective pressures acting on this population.

4.1 Introduction

Behavioural differences between individuals have long been considered as noise around the population adaptive mean (Wilson 1998). Interestingly, many studies have shown that some of these differences can be consistent between individuals over time and contexts, constituting personality traits (Réale et al. 2007). Over the past two decades, these personality traits have received increasing attention in animal behavioural and evolutionary ecology studies (Sih et al. 2004a, b; Dingemanse and Réale 2005; Bell 2007; Réale et al. 2007; Bell et al. 2009; Carere and Maestripieri 2013), with the characterization of five main personality axes linked to the behaviour of individuals when interacting with their environment (activity, exploration, boldness) and with others (aggressiveness, sociality; Réale et al. 2007). In many studies, personality traits have been shown to depend on ecological parameters (Réale et al. 2007; Sih et al. 2012), to be heritable (van Oers et al. 2005; van Oers and Sinn 2013), to be linked to life-history traits or fitness (Dingemanse et al. 2004; Smith and Blumstein 2008; Duckworth and Kruuk 2009; Réale et al. 2010) and, overall, to be under natural (Dingemanse and Réale 2005, 2013) and sexual selection (Schuett et al. 2010). Altogether, these results reveal the crucial role that personality traits may play in shaping evolutionary processes in wild populations (e.g. Dingemanse et al. 2004; Duckworth and Badyaev 2007; Niemelä et al. 2015; Karlsson Green et al. 2015) and call for a deeper understanding of the mechanisms generating and maintaining these between-individual differences in behaviour along with their consequences.

In particular, personality traits are often found to correlate with each other (Sih et al. 2004a; Garamszegi et al. 2012a; van Oers and Sinn 2013) and such phenotypic correlations result from the addition of between-individual and residual correlations. Significant between-individual correlations among personality and other behavioural traits define behavioural syndromes (Dingemanse et al. 2010; Brommer 2013; Dingemanse and Réale 2013) that may have major evolutionary consequences in the wild. Behavioural syndromes may result from the functional integration of traits favoured by selection because the interaction between these traits increases individuals' fitness in given environmental

conditions. Such functional integration at the individual level may lead to genetic correlations between traits at the population level. Alternatively, behavioural syndromes may also result from ontogenetic and physiological constraints linked to pleiotropic effects. In both cases, these processes can then constrain the independent evolution of the concerned traits depending on environmental variations (Sih et al. 2004a). Identifying the processes underlying the patterns of associations among personality traits is thus key to understanding the evolution of complex behavioural syndromes in changing environments.

Yet, testing whether observed phenotypic correlations between personality traits reflect between-individual correlations, i.e. behavioural syndromes, and whether these correlations are genetically based, is a challenging task in the wild. Reliably quantifying the relative contribution of between-individual and residual correlation components requires collecting multiple measurements of several personality traits on a large number of individuals; quantifying genetic covariance between these traits further requires pedigree information on these individuals. Because such data is rarely available, it is often assumed that (1) a phenotypic correlation observed between personality traits reflects an underlying between-individual correlation, i.e. the residual correlation is negligible (the so-called “individual gambit”; van Oers et al. 2005) and (2) observed phenotypic (co)variance reflects underlying genetic (co)variance (the so-called “phenotypic gambit”; Grafen 1984, Hadfield et al. 2007, Dochtermann 2011, Brommer 2013). Recent meta-analyses including > 30 studies, among which 25 from wild populations, confirmed the overall validity of these assumptions (Dochtermann 2011; Dochtermann et al. 2015; Brommer and Class 2017). Nevertheless, the level of correlations among personality traits can be affected by individual and environmental factors (reviewed in Réale et al. 2007), such as predation risk (e.g. Bell 2005; Dingemanse et al. 2007), individual’s sex (e.g. Fresneau et al. 2014) or age (e.g. Class and Brommer 2015). Such effects may thus invalidate the assumptions of a negligible residual correlation or a genetic covariance at the origin of the phenotypic covariance. To draw inferences about the mechanisms underlying correlations among personality traits, it is thus necessary to account for potential individual and environmental confounding factors while partitioning the observed phenotypic (co)variances

into between-individual (genetic and non-genetic) and residual components.

In this study, we investigated whether three behavioural traits, aggressiveness, boldness and neophobia, were repeatable (i.e. defined personality traits) and were phenotypically correlated in a natural population of a small passerine bird, the collared flycatcher *Ficedula albicollis*. We then tested whether (i) phenotypic correlations between these three traits resulted from between-individual correlations (i.e. defined behavioural syndromes) and (ii) their phenotypic (co)variance resulted from additive genetic, maternal or permanent environment effects, while accounting for fixed individual (sex, age) and environmental covariates. During three consecutive years, we measured (i) aggressiveness (as the agonistic reaction to simulated intrusions by intra- and inter-specific competitors), (ii) boldness (as the latency to return to the nest after human disturbance) and (iii) neophobia (as the reaction towards a novel object in a familiar environment; Réale et al. 2007), for several hundreds of breeding pairs in the wild. Based on smaller data in another population of collared flycatchers, male aggressiveness and boldness, but not neophobia, were found to be repeatable (Garamszegi et al. 2012b, 2015) and, in some years, phenotypically correlated (Garamszegi et al. 2009, 2015). However, between-individual correlations as well as genetic covariance between these traits remain unexplored in our study population thus far. Based on the many previous studies on similar traits in small passerine populations (e.g. Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004b; Duckworth and Badyaev 2007), we expected aggressiveness, boldness and neophobia to constitute personality traits, i.e. be repeatable, and to be heritable. Furthermore, because individual fitness may be affected by interactions among these three behavioural traits or between these traits and others (e.g. dispersal, Cote et al. 2010), we can expect them to show functional integration, and thus (possibly genetically-based) between-individual correlations, defining behavioural syndromes.

4.2 Material and Methods

Study species and population monitoring

Collared flycatchers are migratory cavity nesters and readily breed in artificial nest boxes, providing easy access to parents' identity and breeding data. Between 2011 and 2013, we conducted the behavioural tests (see below) on 1131 pairs breeding in nest boxes spread over 14 to 22 forest patches in our study population located on the island of Gotland (Sweden, Baltic Sea). Each year since 1980, nests in boxes have been monitored at least weekly from late April until early July, allowing recording major breeding variables (laying and hatching dates; clutch size; nestling number, condition and fledging success). Parents have also been captured, identified and ringed if previously unringed; females were caught during incubation and males while feeding nestlings. The clear sexual dimorphism in plumage colouration in this species allows an easy discrimination of adult males (black and white plumage with a white forehead patch) from females (brown plumage; Svensson 1992), even from several meters away during behavioural tests. Upon capture, we measured and weighed all adults and aged them (yearlings vs. adults, based on plumage criteria; Svensson 1992). We ringed chicks between day 8 and day 13 after hatching; fledging typically occurs 16 days after hatching. Adult and chick identification every year combined with a high return rate of both adults (approx. 40%) and juveniles (approx. 10%) allowed establishing a high-quality social pedigree of the population that has previously been used in several quantitative genetic studies (Merilä and Sheldon 2000; Sheldon et al. 2003; Evans and Gustafsson 2017). In this population, approx. 15% of all nestlings are extra-pair (Sheldon and Ellegren 1999), a percentage considered low enough for quantitative genetic models to yield accurate estimates from the social pedigree (Charmantier and Réale 2005).

Aggressiveness score

We measured the level of aggressiveness of breeding flycatchers soon after settlement, during nest building or early laying, i.e. when the risk of losing a nest box to a competitor is highest in this single-clutch species. During the breeding season, collared flycatchers are competing for nest sites with conspecifics but also with great tits (*Parus major*), the second most abundant species breeding in nest boxes in the study area (Gustafsson 1987). Aggressiveness towards conspecific intruders was shown to decrease after the start of incubation (Král and Bíčík 1989) even though aggressiveness towards great tit intruders remained high throughout the breeding cycle (Král and Bíčík 1992). To elicit an aggressive response from a focal flycatcher pair, we simulated the intrusion of competitors at the nest of the pair by attaching to its nest box clay decoys mimicking either a flycatcher pair or a single (male) great tit. We used a pair (one male and one female) for flycatcher decoys to elicit and measure an aggressive response by both pair members, i.e. avoid sex-specific response towards this intra-specific stimulus, while the response to the inter-specific stimulus (great tit decoy) was not expected to differ between male and female flycatchers. In addition, we simultaneously broadcasted male song corresponding to the decoy(s) species with a loudspeaker placed just under the nest box. To avoid pseudo replication, we randomly used one of 10 different sets of decoys and one of 5 different song tracks per species for each test. After attaching the decoys to the nest box and the loudspeaker under the box, the observer sat under a camouflage net approx. 8-10 meters away from the nest box and recorded the following behaviours for each pair member: (i) movements between perches and perching position (within 2 meters, between 2 and 5 meters, or between 5 and 10 meters away from the nest box), (ii) agonistic behaviours towards a decoy (attacks and stationary flights in front of the decoy) and (iii) chases towards living birds attracted by the stimulus. A behavioural test started with an observation period of 15 minutes but we lengthened the test for up to 5 minutes when an individual arrived between 10 and 15 minutes after the start of the test, and up to 5 additional minutes if its partner arrived during this extra time, so that we could

observe the behavioural response of each pair member for at least 5 minutes. Each test thus lasted between 15 and 25 minutes. If an individual was observed during less than 5 minutes before the end of the test, it was discarded from the analyses.

The number of each behavioural response (movements, agonistic behaviours and chases) was standardized by the time interval between the first observation of the individual and the end of the test, rescaled to 15 minutes. Aggressiveness level was measured as the sum of the number of movements within 2 m of the nest box, attacks, stationary flights and chases. Using alternative scores did however not change the results (see Appendix A1 and Table S.4.1). We conducted aggressiveness tests two to four times per focal pair over a five day-interval, with maximum one test per day and tests during maximum two days in a row. The stimulus used (intra- / interspecific decoys) was alternated between tests after a random assignment for the first test. An aggressiveness score was computed for each individual for each test. We obtained 1079 (respectively 1076) breeding pairs where the female (respectively the male) responded more than 5 minutes to at least one aggressiveness test. Among those, 602 females and 535 males were later captured and identified. We obtained repeated aggressiveness estimates for 501 females and 519 males within years, and for 107 females and 111 males between years.

Boldness and neophobia scores

During nestling rearing, we estimated (1) boldness score by measuring the individual reaction towards the presence of a human observer near the nest box and (2) neophobia score by measuring the reaction towards the presence of a novel object on the nest box (i.e. in a familiar environment). We conducted one combined boldness / neophobia test per breeding pair when the chicks were 5 days old, i.e. at the beginning of the period of highest provisioning by parents (and before parents' capture on nestlings to avoid any behavioural interference). A test consisted of two consecutive periods of approx. one hour each: the behaviour of the parents was recorded first without any change in the surroundings of the nest box, i.e. without the novel object, and second with a novel object (here a coloured figurine approx. 7 cm high) attached near the entrance hole of

the nest box. Both periods were video-recorded from a distance (6-8m). At the beginning of each period, the observer checked the camouflaged video recorder, walked to the nest box, opened it to check nestling satiety, closed it, and then left the area. The test was abandoned if nestlings were very hungry to avoid nestling starvation risk if parents are too disturbed by the test.

We estimated boldness score as the latency to enter the nest box after the departure of the observer in the first period (i.e. without the novel object). Reaction to disturbance by humans has previously been used in boldness tests in this species (e.g. Garamszegi et al. 2009). We log-transformed and inversed our boldness estimate to normalize the data and ease interpretation (i.e. higher values of boldness score corresponding to higher level of boldness). We estimated neophobia score as the ratio of the latency to enter the box after the departure of the observer in the second period (i.e. in presence of the novel object) over the latency in the first period (i.e. in the absence of the object), to control for disturbance by the observer (see Garamszegi et al. 2009). Individuals who did not enter the nest box during the first period of the test were discarded (187 out of 1251 observations, i.e. 15%). Individuals who entered the nest box during the first but not the second part of the test (401 out of 1064 observations, i.e. 39%) were considered as the most neophobic ones but could not be attributed a latency ratio. To include them in the analyses, we discretized the neophobia score into 5 categories of increasing latency ratio (see Appendix A1 for the boundaries used for each category, based on the observed distribution of values of latency ratio) and added a 6th category including individuals who did not enter in the second part of the test. Using alternative scores for boldness and neophobia did not qualitatively change the results (except for the sex effect in boldness, Tables S.4.2 and S.4.3). We extracted boldness and neophobia scores from 626 tests, from which 432 females and 371 males who entered the nest box in the first part of the test were identified. We obtained repeated boldness and neophobia scores (i.e. several years in a row) for 69 females and 74 males.

Repeatability and heritability of aggressiveness, boldness and neophobia

To assess whether aggressiveness, boldness and neophobia represented personality traits in our study population, we estimated their repeatability as well as their heritability by fitting three separate univariate animal models. The models included the following random effects: individual identity for the repeated measures per individual (permanent environment effect) and additive genetic effect (associated to the pedigree), as well as maternal identity, forest patch, observer identity (for the boldness and neophobia test, it was the person extracting latencies from the video recording). The model of the aggressiveness score also included the broadcasted song track and decoy set identifiers. In addition, the models included the following fixed effects, to control for potential confounding factors: sex, age (yearling vs. older) and their interaction, day of the test (because the risk of losing a nest box due to competition is likely to vary along the season), time of the day and its squared value (because bird activity strongly varies within a day), mean temperature on the day of the test (obtained from the Swedish Meteorological and Hydrological Institute), and year (categorical: 2011, 2012, or 2013). The aggressiveness model also included general weather (sunny, cloudy or rainy), wind conditions (absent, weak, moderate or strong wind), stimulus type (flycatcher vs. great tit decoys, in interaction with sex and age), the presence of the partner during the test (binary variable: yes / no; in interaction with the sex of the focal individual) and the presence of other live flycatchers or great tits (binary variable: yes / no). The boldness and neophobia models included the number of ringed chicks as a proxy of the motivation to enter the nest box to feed nestlings (in interaction with sex). All continuous fixed terms were centred and standardized prior analysis to allow comparisons between effects.

Model selection was performed using a step-wise approach (see below). Repeatabilities (R) were estimated from the final model including only the retained fixed effects as the ratio of the sum of the additive genetic (V_A), permanent environment (V_{PE}), and maternal identity variances (V_M) over the total phenotypic variance (V_P , sum of all vari-

ances, Falconer and Mackay 1996; Wilson et al. 2010). Narrow-sense heritabilities (h^2) were estimated from the same model as the ratio of the additive variance V_A over the phenotypic variance V_P . Adjusted repeatabilities and heritabilities estimated from models with fixed effects may be over- or underestimated (Nakagawa and Schielzeth 2010); therefore, we also estimated them from models with no fixed effect, and the results remained qualitatively unchanged (see Tables S.4.1, S.4.2, S.4.3). For aggressiveness, we also estimated within-year repeatability by replacing the additive genetic and permanent environment effects by a unique identifier per individual per breeding season. Finally, to test for possible sex-differences in repeatability and heritability for all three traits, and for differences between competitive contexts (decoy type) in repeatability and heritability for aggressiveness, we fitted additional models including the random-slope sex or decoy type effects respectively. There were no quantitative differences between sexes or competitive contexts (see Appendix A2 for a complete description of the results).

Correlations between aggressiveness, boldness and neophobia scores

We estimated the correlations between aggressiveness, boldness and neophobia scores by fitting a trivariate mixed effects model (Dingemanse and Dochtermann 2013), including sex and year as fixed effects and ring number as a random effect. The phenotypic correlation between two traits A and B, $r_{P.A,P.B}$, and the between-individual correlation between the traits A and B, $r_{ind.A,ind.B}$, were estimated as follows (Snijders and Bosker 1999):

$$r_{P.A,P.B} = \frac{Cov_{ind.A,ind.B} + Cov_{\varepsilon.A,\varepsilon.B}}{\sqrt{V_{P.A} \times V_{P.B}}}$$

$$r_{ind.A,ind.B} = \frac{Cov_{ind.A,ind.B}}{\sqrt{V_{ind.A} \times V_{ind.B}}}$$

$Cov_{ind.A,ind.B}$ and $Cov_{\varepsilon.A,\varepsilon.B}$ being the between-individual and the residual covariances between traits A and B, and $V_{P.A \text{ or } B}$ being the total phenotypic variance (sum of the

individual and residual variances) associated to trait A or B. Combining aggressiveness, boldness and neophobia score data for a given individual in a given year, we obtained a total sample size of 838 observations to fit our trivariate model. Among those, we obtained 111 and 100 repeated measures from 52 males and 49 females, respectively. We also estimated sex-specific correlations but found no major difference between sexes in correlation levels (see Appendix A2 and Table S.4.4 for the results on sex-specific correlations).

Implementation of Bayesian models

All statistical analyses were performed within the Bayesian framework in R v.3.3.2 (R Core Team 2015). Both univariate and trivariate models were fitted using the function *MCMCglmm* (“MCMCglmm” R package, Hadfield 2010). The pedigree was prepared using the function *fixPedigree* (“pedantics” R package, Morrissey and Wilson 2010) and pruned using the function *prunePed* (“nadiv” R package, Wolak 2012; see Table S.4.5 for a description of the pedigree). Aggressiveness scores were fitted with a Poisson family (logit link), boldness scores with a Gaussian family (after log and inverse transformations) and neophobia scores with a Threshold family with variance fixed to 10 (instead of the usual value of 1, to improve the mixing of the chains for low variances, which were expected from preliminary analyses; Hadfield 2016). We used wide Normally distributed priors for fixed effects (large variance $V=108$; Hadfield 2016) and parameter expanded χ^2 distributed priors with 1 degree of freedom for random effects. For the univariate models, we adjusted the number of iterations, burn-in and thinning interval for each model so as to obtain an effective sample size over 1,500 (see Appendix A1) and autocorrelations of posterior samples below 0.1 in all cases. For the trivariate model, we used 3×10^6 iterations, a burn-in of 10^5 and a thinning interval of 1,200 to reach the same criteria. We visually assessed the convergence of the MCMC chains, and, for univariate models, successively removed the fixed effects whose 95% Credible Intervals (CI) encompassed zero (but see Tables S.4.1, S.4.2, S.4.3, for the outputs of the full univariate models and univariate models without interactions, to check for the absence of type I error in using this stepwise selection

approach; Mundry and Nunn 2009; Forstmeier et al. 2017); the trivariate model only contained sex and year as fixed effects, thus no model selection was performed. We kept all random effects to control for pseudo replication. Following Nakagawa and Schielzeth (2010), we retained in our univariate models data from individuals tested only once. Estimates are presented as posterior modes. To estimate repeatability and heritability of aggressiveness, log-transformed boldness and neophobia scores on the observed scale (R_{obs} , h^2_{obs}), we used the *QGparams* function (“QGglmm” R package, de Villemereuil et al. 2015; de Villemereuil 2018). For the repeatability and heritability of neophobia scores, which yields one value per score level on the observed scale, we present only the range of estimates.

4.3 Results

Repeatability and heritability estimates of behavioural scores

Aggressiveness, boldness and neophobia scores all showed a low to moderate level of repeatability between years (0.20, 0.14 and 0.42 respectively; Table 4.1). In addition, aggressiveness score was repeatable within years ($R=0.24$, 95% CI = [0.19; 0.29]). None of the three behavioural traits were however heritable (all 95% CI for V_A values included zero and posterior modes for h^2 very close to zero; Table 4.1). Permanent-environment effects explained 16% of the phenotypic variance in aggressiveness score (95% CI of V_{PE} = [0.15; 0.72]) and maternal identity explained 28.1% of the phenotypic variance in neophobia score (95% CI of V_M = [1.75; 10.63]). Observer identity explained 8.6% of the phenotypic variance for aggressiveness (95% CI of $V_{Observer}$ = [0.15; 0.62]). All other variances were low (less than 6 % of the phenotypic variance) or not different from zero (Tables S.4.1, S.4.2, S.4.3).

Phenotypic, between-individual and additive genetic correlations between behavioural scores

Aggressiveness and neophobia scores were phenotypically correlated: more aggressive individuals were less neophobic ($r_P = -0.20$, 95% CI = [-0.29; -0.14], Table 4.2). There was no phenotypic correlation between boldness and aggressiveness (95% CI = [-0.05; 0.10]) or neophobia scores (95% CI = [-0.06; 0.09], Table 4.2; see Table S.4.6 for the full model output). However, when excluding from the sample the individuals that did not enter the nest box in presence of the novel object, i.e. the most neophobic ones (highest neophobia category; $N = 315$ observations withdrawn out of a total of 838 observations), boldness and neophobia scores showed a strongly positive correlation ($r_P = 0.56$, 95% CI = [0.48; 0.61], Table 4.2, Figure 4.1); the negative correlation between aggressiveness and neophobia scores was reduced but remained with this restricted dataset ($r_P = -0.09$, 95% CI = [-0.21; -0.03]). Results remained qualitatively unchanged when controlling the boldness score by the feeding rate (i.e. dividing the latency to enter the nest box in the

period without the object by the subsequent mean between-feeding interval, restricted to individuals feeding at least twice in the first period, $N=567$ observations): no phenotypic correlation between new boldness score and aggressiveness (95% CI = [-0.13; 0.05]) or neophobia scores (95% CI = [-0.01; 0.17]).

None of the phenotypic correlations between the behavioural traits reflected a behavioural syndrome, because none of the between-individual covariances differed from zero (Table 4.2). Because additive genetic variance did not differ from zero for any of the three behavioural traits under investigation, we did not estimate their additive genetic correlations.

Influence of individual and environmental fixed effects on behavioural scores

Males were more aggressive than females, especially among yearlings (interaction sex by age, with yearling males as reference: 95% CI = [0.02, 0.61], Figure 4.2a). In addition, males were shyer (longer latency to enter in the absence of a novel object) and less neophobic (shorter latency in the presence of a novel object) than females (Figure 4.2b, with male as a reference 95% CI = [-0.40; -0.17] and [-2.75; -1.54] respectively), and this did not depend on age (see Tables S.4.2 and S.4.3 for sex by age interactions). These differences were not the result of sex differences in feeding behaviour, because males and females still differed when controlling boldness score for the feeding rate in absence of the novel object (i.e. dividing the latency to enter the nest box by the mean feeding interval during the remaining time of the first part of the test; Table S.4.2). In addition, individuals with larger broods were bolder (95% CI = [0.03; 0.14], Table S.4.2), less neophobic (95% CI = [-0.96; -0.36], Table S.4.3), independently of sex (interactions sex by brood size: S.4.2 and S.4.3).

Regarding environmental effects, aggressiveness, boldness and neophobia scores depended on the year: individuals were less aggressive in 2011 compared to 2012 (Table

S.4.1), shy in 2011 compared to 2013 (Table S.4.2), and less neophobic in 2011 compared to 2012 and 2013 (Table S.4.3). In addition, individuals were more aggressive when it was cloudy compared to when raining, in the presence of their partner or neighbouring tits attracted by the stimulus, early in the day, and during the first tests of the sequence (Table S.4.1); finally, females were less aggressive towards conspecific than heterospecific (great tit) decoys while it was the opposite for males (Figure A.4.3 and Table S.4.1). Other effects did not influence behavioural scores (Tables S1-S3).

Table 4.1: *Between-year repeatability estimates (R) and heritability estimates (h^2) for aggressiveness, boldness and neophobia scores. Repeatabilities are given on the latent scale (R_{latent} , posterior mode and 95% Credible Interval), and on the observed scale (R_{obs}). Stars indicate estimates whose 95% CI does not encompass zero. For aggressiveness, estimates are given both using all tests in all years (first line) and using a mean value of aggressiveness score per individual per year (second line). For neophobia, we provide the range of repeatability values on the observed scale (one value per neophobia score: 0 to 5, i.e. 6 repeatability values in total).*

	R_{latent}		R_{obs}	h^2	
	Post. mode	95% CI	estimate	Post. mode	95% CI
Aggressiveness (all tests)	0.20 *	[0.16; 0.26]	0.03	0.001	[0.00; 0.13]
Aggressiveness (mean value / year)	0.23 *	[0.08 ; 0.39]	0.08	0.000	[0.00; 0.14]
Boldness	0.14 *	[0.03 ; 0.26]	0.09	0.001	[0.00; 0.17]
Neophobia	0.42 *	[0.25 ; 0.55]	0.00 - 0.21	0.001	[0.00; 0.14]

Table 4.2: Phenotypic, between-individual and residual correlations between aggressiveness, boldness, and neophobia scores (posterior mode and 95% CI). Stars indicate estimates whose 95% CI does not encompass zero.

Correlations:	Phenotypic		Between-individual		Residual	
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI
Aggressiveness - Boldness	0.02	[-0.05 ; 0.10]	0.00	[-0.06 ; 0.06]	0.03	[-0.05 ; 0.12]
Aggressiveness - Neophobia	-0.20 *	[-0.29 ; -0.14]	-0.01	[-0.06 ; 0.07]	-0.26 *	[-0.37 ; -0.17]
Aggressiveness - Neophobia†	-0.09 *	[-0.21 ; -0.03]	0.01	[-0.07 ; 0.06]	-0.15 *	[-0.27 ; -0.02]
Boldness - Neophobia	0.02	[-0.06 ; 0.09]	0.00	[-0.07 ; 0.06]	0.03	[-0.09 ; 0.11]
Boldness - Neophobia†	0.56 *	[0.48 ; 0.61]	-0.01	[-0.06 ; 0.06]	0.65 *	[0.55 ; 0.75]

† Correlations estimated on a restricted sample, when removing the last category (5) of the neophobia score, i.e. individuals which did not enter the nest box in the presence of a novel object (c.f. Figure 4.1).

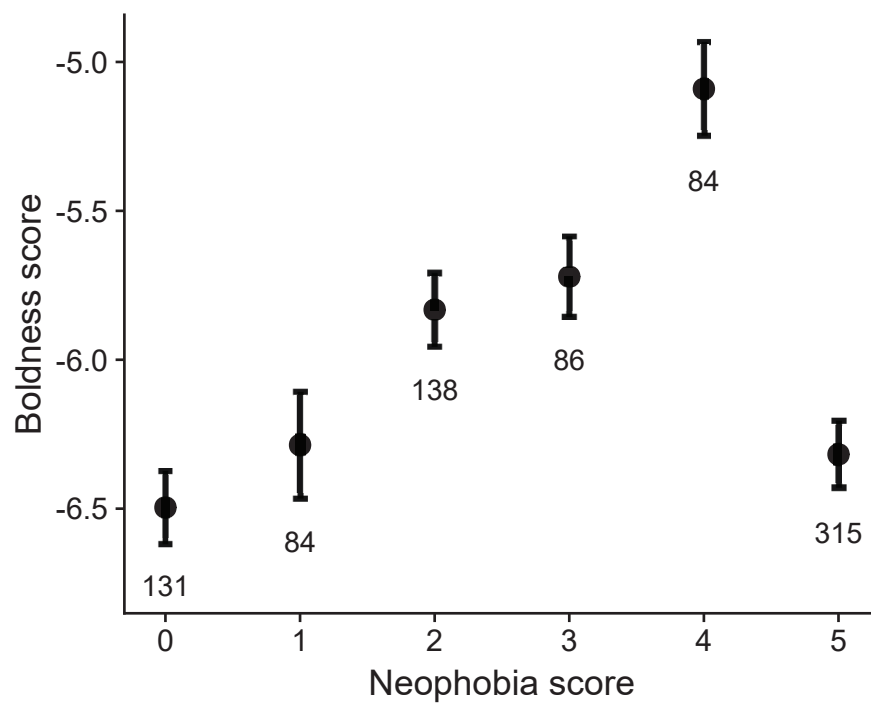


Figure 4.1: *Boldness score depending on the neophobia score (means \pm 95% confidence interval). Numbers indicate sample sizes. See text for definitions of the boldness and neophobia scores. The boldness score was log-transformed and inversed to ease computation and interpretation (increasing score with increasing boldness).*

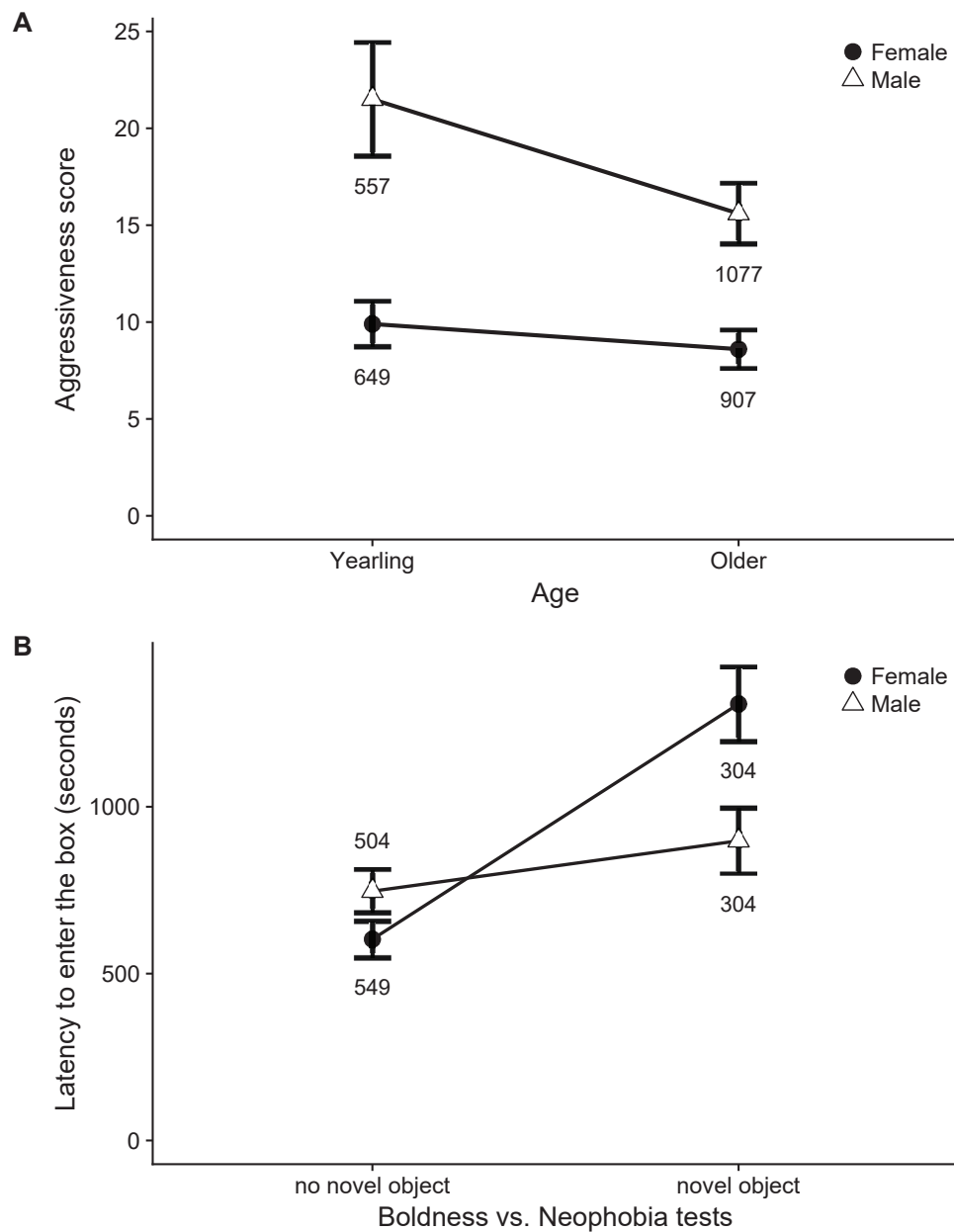


Figure 4.2: Sex differences in aggressiveness, boldness and neophobia scores (means \pm 95% confidence interval). (A) Differences in aggressiveness score between sexes depending on age (yearling vs. older). (B) Differences in the latency to return after human disturbance for the period without object, as a proxy of boldness, and for the period with the novel object (neophobia was estimated as the ratio between the latencies with and without object). Number of observations are indicated near each estimate

4.4 Discussion

In this study, we tested whether three behavioural traits (aggressiveness, boldness and neophobia) were personality traits, formed behavioural syndromes during breeding, and had a genetic basis in a wild population of collared flycatchers, to shed light on their possible evolutionary consequences. We found that the three traits were repeatable between years and showed some phenotypic correlations in the population. However, none were heritable, and none showed between-individual covariance. Thus, these traits are indeed personality traits but do not form behavioural syndromes, and have no genetic basis in our population. The between-individual variance originated mainly from permanent environment effects for aggressiveness and from maternal identity for neophobia. The absence of behavioural syndrome involving these personality traits suggests that interactions between them lead to no systematic fitness benefits, thus no functional integration of these traits at the individual level and genetic correlations at the population level.

Aggressiveness, boldness and neophobia: personality traits with no genetic basis

Aggressiveness, boldness and neophobia scores all being repeatable, the three traits constitute personality traits in our population of collared flycatchers. This result is in line with the many studies that described these between-individual behavioural differences as personality traits in many animal species (reviews in Bell et al. 2009; Brommer and Class 2017). Yet, the levels of repeatability, estimated both within and between years for aggressiveness score, and between years for boldness and neophobia scores, were lower than usually reported for such behaviours: around 50% for aggressiveness and exploration, and around 40% for anti-predator behaviours (Bell et al. 2009). Interestingly, the repeatability level estimated here for aggressiveness score was similar within and between years, contrary to the usual decrease observed when the time interval between recordings increases (Bell et al. 2009, Chervet et al. 2011, Dingemanse et al. 2012, Wuerz and Krüger

2015, Garamszegi et al. 2015, but see David et al. 2012 for differences between traits). In another population of collared flycatchers, aggressiveness and boldness were repeatable within years, but not between years, and neophobia was only weakly repeatable in one year (Garamszegi et al. 2015). We may have detected between-year repeatability here thanks to our larger sample sizes. These differences between flycatcher populations could also be due to the different statistical scales considered, in relation to the distributions used for the variables (latent scale here, observed scale in Garamszegi et al. 2015). When comparing estimates on the observed scale, our results did indeed not quantitatively differ from Garamszegi et al. (2015). Overall, our lower levels of repeatability compared to studies on other species suggest higher within-individual behavioural flexibility, both within and between years.

Accordingly, we found no genetic basis for our three personality traits. A meta-analysis on personality traits in wild animal populations estimated an average heritability level of 0.28 for aggressiveness, 0.31 for boldness and 0.58 for exploration-avoidance (including estimates from novel environment and novel object tests; van Oers and Sinn 2013). Based on associations found between personality traits and genetic (SNP) polymorphism in the DrD4 gene, coding for a dopamine receptor involved in different cognitive processes, previous studies on different bird and mammal species, including the collared flycatcher, underlined the possible role of genetic processes in shaping personality (e.g. Fidler et al. 2007; Hejjas et al. 2007; Korsten et al. 2010; Ninomiya et al. 2013; Garamszegi et al. 2014). The absence of heritability for our personality traits here was likely the result of (1) very low additive genetic variance and (2) large environmental variance as illustrated for instance by between-year differences in behavioural scores, which reflected large variations in environmental conditions among the three years of our study (see Chapter 3 for differences between 2012 and 2013). In general, measuring behavioural scores in nature most probably leads to higher variance due to environmental variations compared to measures obtained in controlled captive conditions. Yet, conducting behavioural tests in natural settings has the advantage of minimizing disturbance and thereby eliciting the natural behaviours on which selection may act, i.e. avoiding the alteration of behaviours via e.g.

stress, as already described in collared flycatchers (Garamszegi et al. 2009). Furthermore, because between-year fidelity to the nest box and/or partner is very low in this population (approx. 6.7 % over 240 individuals bred in the same nest box several years and 1.0 % over 214 identified pairs were faithful over several years), individuals were tested in different environments (including the social context) in different years, again possibly increasing residual variance. This however limits the risk of pseudo-replication (Niemelä and Dingemanse 2017). Finally, we estimated boldness and neophobia scores only once per year, which again possibly increased residual variance. However, aggressiveness score was estimated several times per year and was less repeatable than neophobia (while it was as repeatable within as between years). The absence of heritability for our three personality traits here should therefore reliably reflect the absence of a genetic basis for these traits in our study population.

Factors at the origin of behavioural trait repeatability

The observed repeatability in aggressiveness score resulted mostly from permanent environment effects. These effects explained 16% of the phenotypic variance and 80% of the repeatability in aggressiveness score. Here, because we controlled for the identity of the mother, permanent environment effects could be linked for example to differences in individual condition or experience. The measures of personality traits have indeed been found to depend on individual condition or experience in previous studies (reviewed in Stamps and Groothuis 2010). In our population, condition and experience also affect breeding habitat choice depending on social cues (e.g. Doligez et al. 1999, 2004; Kivelä et al. 2014), which could shape individuals' response to the risk of competition for nest sites. Permanent environment effects may also include a dominance effect (Kruuk and Hadfield 2007; Wilson et al. 2010), which could not be directly modelled here because full- and half-sibs links were relatively rare in our pruned pedigree (Wilson et al. 2010). Dominance effects remain poorly investigated in studies of personality traits, particularly in the wild (see van Oers et al. 2004c for great tits fast and slow lines selected in captivity), and further work is thus needed to assess their role in shaping between-individual

differences, especially on heritable traits.

In turn, the observed repeatability in neophobia resulted mostly from maternal identity, which accounted for 28% of the phenotypic variance and 74% of the between-individual variance. Both pre- and post-natal maternal effects have been found to affect exploration and neophobia behavioural responses later in life (see review in Groothuis and Maestri-pieri 2013). In particular, the levels of maternal hormones early in life have been shown to affect neophobia at the adult stage (e.g. Spencer and Verhulst 2007). Food provisioning at the nestling stage has also been experimentally found to have long-lasting effects on exploration in birds (Carere et al. 2005). Maternal effects also affect other personality traits (e.g. aggressiveness: Eising et al. 2006; review in Groothuis and Maestri-pieri 2013). However, maternal identity did not explain between-individual differences in aggressive-ness and boldness here, which may depend more on individual or local environmental conditions, in particular individual competitive ability and neighbour presence or density, at the time of the measure(s). Further work is needed to assess the relative contribution of early-life conditions (brood size, fledging body condition) and short-term individual and environmental factors (habitat quality, density of intra- and interspecific competitors) on different personality traits at the adult stage in collared flycatchers, which goes beyond the scope of our study here.

No personality syndrome: no functional integration of personality traits?

The personality traits investigated here did not form behavioural syndromes, but phenotypic correlations were nevertheless observed: more neophobic individuals were found to be less aggressive (and bolder but only when excluding individuals in the last category of neophobia scores, which could be a methodological artefact). The absence of correlation between aggressiveness and boldness partly contrasts with previous results reporting more aggressive individuals to be bolder, as part of the proactive-reactive axis, in different species (Koolhaas et al. 1999; Sih et al. 2004a) including the collared flycatcher (Garamszegi et al. 2015). Bolder individuals are also usually reported to be more explorative in a novel

environment (or less neophobic in a novel object test; e.g. van Oers et al. 2004a; Garamszegi et al. 2009), which was not found here. Because many studies (but see Garamszegi et al. 2015) did not partition phenotypic correlation into between-individual and residual correlation, it is difficult to know whether the difference in patterns between our study and others are due to different selection regimes favouring behavioural syndromes in other populations.

The observed phenotypic correlations resulted solely from correlated changes in behaviours between measurements for the same individuals, i.e. residual correlations. Residual correlations could be due (but not exclusively) to micro-environmental effects (e.g. nest box location), individual effects (long-term between-year plasticity but short-term within-year behavioural constraints, for instance due to experience) or from correlated measurement errors (Dingemanse and Dochtermann 2013). Error correlation is however more likely to occur between boldness and neophobia scores, which were extracted from the same test, than between aggressiveness and neophobia scores, which were measured several days apart by different persons. To tease these sources of residual correlations apart, aggressiveness, boldness and neophobia scores need to be estimated several times during the same breeding season and possibly at the same phases of the reproductive cycle. The limited number of individuals measured several times here (211 observations of 101 individuals) may be one reason why we did not detect between-individual covariance (Garamszegi and Herczeg 2012; Dingemanse and Dochtermann 2013 recommended sample size of indeed at least 200 individuals tested twice).

The absence of behavioural syndrome in our population suggests that selective pressures did not yield or maintain a functional integration between the personality traits investigated here. Plasticity in the association between personality traits could be selected for if the fitness costs and benefits of expressing each trait relative to the others depend on the environmental (including social) context (e.g. competition level or predation risk). Collared flycatchers are migratory and during the breeding season, they may suffer from strong competition with dominant resident tits upon arrival on the breeding grounds and also with conspecifics later on. In our population, nest sites have been provided in excess

in the study forest patches since the early 80's and do not represent a limiting resource anymore. The availability of high quality nest sites may in particular have released joint selective pressures on exploration (mirrored here by neophobia) to find suitable nest sites and aggressiveness to acquire and defend this resource against competitors in a natural context. In turn, providing nest boxes likely increased local breeding densities and thereby competition for food resources during the nestling period, especially in a highly synchronous species such as the collared flycatcher. Furthermore, our population suffers from very low nest predation rates, due to the absence of mustelid species on Gotland (Doligez and Clobert 2003) and the high level of protection provided by nest boxes. Selective pressures may thus also have been released on boldness through the decrease in the need to defend the brood. In addition, birds may habituate to the disturbance due to the presence of humans because of the regular nest box visits throughout the season (as reflected by behavioural differences between birds breeding in forests and gardens; pers. obs.). Overall, these relatively recent changes in environmental breeding conditions that operated in our study population may have strongly modified the selective regime for personality traits and for a functional integration between them if costly. Testing whether changes in breeding conditions, in particular in nest box-based populations, yield to changes in the selective regime for functional integration of different personality traits is a challenging question. To address it and understand why we found no between-individual covariance between the three personality traits (i.e. no behavioural syndrome) here, a first step could be to investigate the fitness benefits associated with each trait and their interaction depending on, in particular, local intra- and interspecific density and/or nest predation risk.

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Authiors contribution

GD and BD designed the study. GD and BD conducted field work, LG provided data. JM, GD, and many students extracted behavioural. JM conducted the analyses, drafted the manuscript. JM and BD critically revised the manuscript.

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4.6 Appendix

Appendix A1. Alternative behavioural score estimates and model parametrisation

Aggressiveness score

We estimated aggressiveness score using the following alternative measures and modelled them using the parameters given in parentheses:

1. number of aggressive behaviours (movements $< 2\text{m}$ from the nest box, stationary flights and attacks towards the decoys, chases of live birds) standardized per 15 minutes (Poisson family; number of iterations $\text{nit} = 10^6$; burn-in $= 10^4$; thinning interval $\text{thin} = 400$);
2. first axis of the PCA presented below (Table A.4.1; Gaussian family; number of iterations $\text{nit} = 6 \times 10^5$; burn-in $= 10^4$; thinning interval $\text{thin} = 200$);
3. discrete score (Threshold family, residual variance $V_R = 10$; $\text{nit} = 101 \times 10^4$; burn-in $= 8 \times 10^4$; $\text{thin} = 400$). This score was based on the distinction between activity (number of movements, including stationary flights) performed far ($> 2\text{ m}$) and close ($< 2\text{ m}$) away from the nest box, and on attacks, subdivided into 6 categories (Fig. A.4.1):
 - 0: individuals who performed no movements (either far or close to the nest box).
 - 1: individuals who performed no attack or movements close to the nest box, and performed less than 0.444 movements per min far ($> 5\text{ m}$) away from the nest box.
 - 2: individuals who performed no attack or movements close to the nest box, and performed more than 0.444 movements per min far ($> 5\text{ m}$) away from the nest box.
 - 3: individuals who performed no attacks and less than 0.283 movements per min close ($< 2\text{ m}$) to the nest box.
 - 4: individuals who performed no attacks and between 0.283 and 0.785 movements per min close ($< 2\text{ m}$) to the nest box.
 - 5: individuals who performed no attacks and above 0.785 movements per min close ($< 2\text{ m}$) to the nest box.
 - 6: individuals who performed attacks towards decoys(s).

The thresholds were chosen so as to distribute individuals equally among categories for scores 1 and 2 on the one hand and scores 3, 4 and 5 on the other hand.

Boldness score

We estimated boldness score using the following alternative measures and modelled them using the parameters given in parentheses:

1. inverse logarithmic latency to enter the nest box after human departure (Gaussian family; nit = 25×10^4 ; burn-in = 10^4 ; thin = 100);
2. inverse logarithmic ratio of the latency to enter the nest box after human departure divided by the feeding rate for the remaining time after the first entrance in the nest box (Gaussian family; nit = 25×10^4 ; burn-in = 10^4 ; thin = 100);
3. discrete score (Threshold family, $V_R = 10$; nit = 3×10^6 ; burn-in = 2×10^5 ; thin = 1000). The score was based on entrance in the nest box during the first part of the boldness-neophobia test (no novel object) and latency to enter after human disturbance; individuals that did not enter were given a score of 0, and individuals that entered the nest box were given a score of 1 to 4 based on quartiles of latency to enter (Fig. A.4.1).

Neophobia score

We estimated neophobia score using the following alternative measures and modelled them using the parameters given in parentheses:

1. discrete score based on the ratio of the latency to enter the box in the presence of a novel object over the same latency without a novel object L , discretized as shown on Fig. A.4.2 (Threshold family; $V_R = 10$; nit = 13×10^5 ; burn-in = 13×10^4 ; thin = 400);
2. composite variables including a binary variable separating individuals who did and did not enter during the second period of the test (Threshold family; $V_R = 10$; nit = 18×10^5 ; burn-in = 2×10^5 ; thin = 700) and the continuous ratio of the latencies (as in 1) but only for individuals that entered during the second period (Logarithm transformation; Gaussian family; nit = 15×10^5 ; burn-in = 2×10^5 ; thin = 500).

Results obtained for these alternative scores for the three behavioural traits are given in Tables S1 to S3, in comparison to the scores retained for general analyses.

Table A.4.1: *Output of a Principle Component Analysis of behaviours recorded during the aggressiveness assays. We used the function “PCA” from the “FactoMineR” R package (Lê et al. 2008).*

	Corrdinates		Contribution	
	PC1	PC2	PC1	PC2
Moves < 2m from the nest box	0.83	-0.06	37.56	0.26
Stationary flights towards the decoy	0.72	-0.19	28.16	3.15
Attacks towards the decoy	0.66	-0.27	23.69	6.11
Moves between 2 and 5 m from the nest box	0.37	0.65	7.31	35.34
Moves between 5 and 10 m from the nest box	-0.07	0.46	0.27	17.43
Chases of living birds	0.24	0.67	3.01	37.73

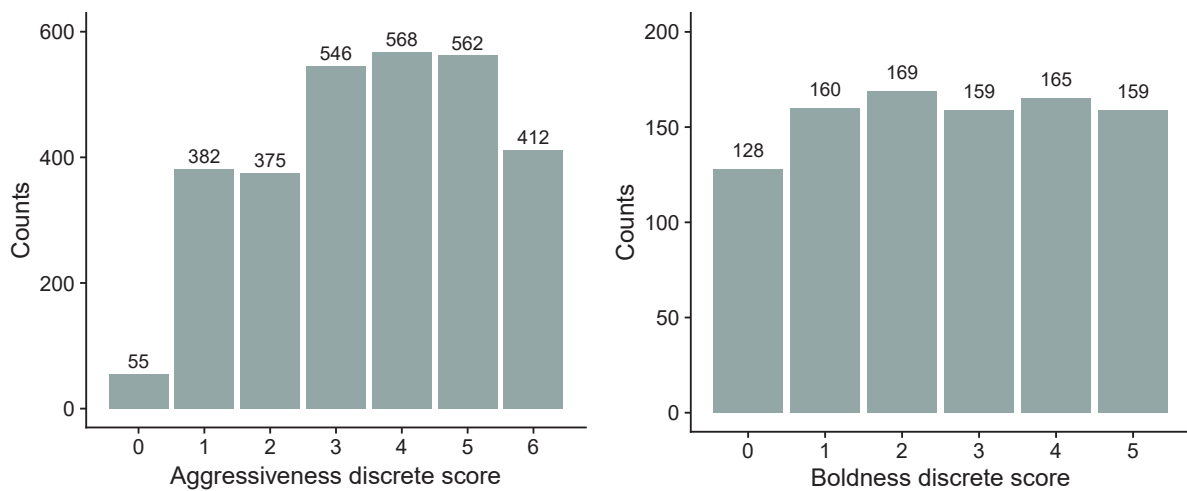


Figure A.4.1: *Distribution of the discrete score for aggressiveness (left) and boldness (right).*

Table A.4.2: Neophobia score based on δL (see above). Individuals with δL below 1 entered faster in presence of the novel object compared to in absence of the novel object. Individuals that entered the nest box in absence but not in presence of the novel object were attributed the maximal score of 5.

	Neophobia score	Sample size
Ratio of the latencies to enter δL		
$\delta L \leq 1$	0	188
$1 < \delta L \leq 1.6$	1	121
$1.6 < \delta L \leq 3.4$	2	210
$3.4 < \delta L \leq 6.4$	3	134
$6.4 < \delta L$	4	129
No entrance	5	455

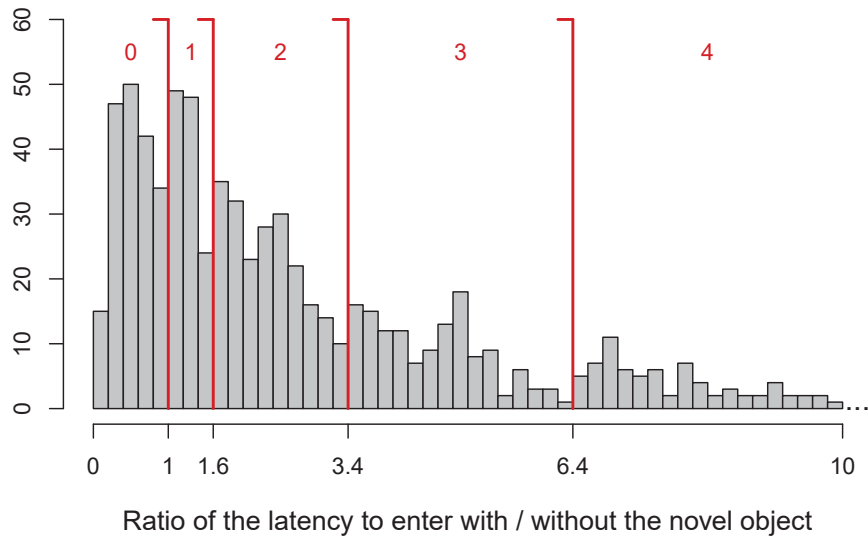


Figure A.4.2: Distribution of δL , ratio of the latency to enter the nest box in presence of a novel object (2nd part of the assay) over the latency in absence of the novel object (1st part of the assay). Red lines indicate the thresholds for discretizing the ratio to create a neophobia score. Red numbers indicate the neophobia score category. Category '4' encompasses all individuals showing a ratio above 6.4 (up to 68) but because individuals with ratios over 10 are scarce, we did not show them here.

Appendix A2. Differences in variance estimates between sexes and, for aggressiveness, competitive context

(Co)Variance differences between sexes

Because evolutionary pressures acting on behavioural traits and their possible interactions may differ between females and males in this species (e.g. due to facultative polygyny thus higher competition level in the access to mates for males compared to females), we expected sex differences in the behavioural traits considered and their repeatability, as reported in other bird species (Schuett and Dall 2009). To test for possible sex differences in trait repeatability and heritability, we estimated sex-specific additive genetic, maternal and permanent environment variances by fitting a random slope sex effect to the associated random effects, in the univariate models for each of the three behavioural traits. We also estimated sex-specific correlations between traits by fitting two separate trivariate models, one for females and one for males (rather than a random slope sex effect on the ring identity and the residuals, because a random slope model would have estimated covariances between male and female traits, which was not our goal here). Both univariate and trivariate models were fitted using the function *MCMCglmm* (c.f. main text) and random slope effects were fitted using the *idh* function (Hadfield 2010).

Results

Females and males showed similar level of repeatability for the aggressiveness ($R = 0.22$, 95% CI = [0.16; 0.30]; $R = 0.21$, 95% CI = [0.14; 0.27]) and boldness scores ($R = 0.21$, 95% CI = [0.11; 0.36]; $R = 0.13$, 95% CI = [0.004; 0.25]), while females were less repeatable than males for the neophobia score ($R = 0.27$, 95% CI = [0.12; 0.51]; $R = 0.60$, 95% CI = [0.41; 0.74]). Neither male nor female heritability estimates differed from zero (results not shown). When separating females from males, the sign of the phenotypic correlation between aggressiveness and neophobia were the same in both cases, but males showed a stronger phenotypic correlation than females (posterior mode for males = -0.20, 95% CI = [-0.30; -0.09]; for females = -0.11, 95% CI = [-0.21; 0.01]; Table S.4.4). In all cases, between-individual correlations did not differ from zero.

Discussion

The observed sex differences in levels and repeatability of personality traits might be explained by differential selective pressures acting on males and females. Regarding aggressiveness, both pair members are at risk of losing their nest box to con- and heterospecifics (great and blue tits) upon settlement. Former studies showed that collared flycatcher females exhibit aggressive behaviour towards conspecifics to defend their nest box while males exhibit aggressive behaviour towards both con- and heterospecifics (Gustafsson

1987; Král and Bíčík 1992, 1994; Král 1996). Accordingly, we found here that males and females had similar (low) repeatability in their overall aggressiveness score.

Regarding boldness, females were bolder and tended to be slightly more repeatable than males. This could be explained by the higher investment in parental care by females compared to males, even though the between-sex difference in feeding rate in this species is not high (Sheldon et al. 1997); in females, constancy in feeding behaviour but also risk-taking in nest defence should be selected for. Conversely, in males, a more plastic parental care can be expected because of (i) extra-pair paternity risk (Sheldon and Ellegren 1999) and (ii) facultative polygyny (14% of males acquire a secondary female in this population; Gustafsson and Qvarnström 2006).

Finally, regarding neophobia, males were more repeatable than females. This is in accordance with a common assumption that females should select males that are repeatable in their behaviours, as shown in zebra finches (Schuett and Dall 2009). It would be interesting to test this assumption by looking at the plasticity itself, its heritability and fitness consequences in collared flycatcher males and females.

Variance differences between competitive contexts

Because evolutionary pressures acting on aggressiveness towards conspecifics and heterospecifics may differ, we tested for differences in repeatability and heritability between the intraspecific (flycatcher decoys) and interspecific (great tit decoy) contexts of the aggressiveness test. As described above for sex differences, we fitted a random slope context effect on the genetic additive, maternal and permanent environment random effects.

Results and discussion

Aggressiveness scores were slightly more repeatable in response to intraspecific ($R = 0.27$, 95% CI = [0.21; 0.35]) compared to interspecific stimulus ($R = 0.16$, 95% CI = [0.09; 0.26]). Flycatchers were thus more plastic in their response towards dominant, heterospecific competitors. Besides, males and females differed greatly in their aggressiveness towards conspecific decoys (males being more aggressive) but barely differed in their aggressiveness towards the heterospecific decoy (FigureA.4.2). This suggests that in the intraspecific context, male reaction is driven by intrasexual competition (e.g. to avoid losing its mate too), while in the heterospecific context, both sexes respond to a risk of losing the nesting site.

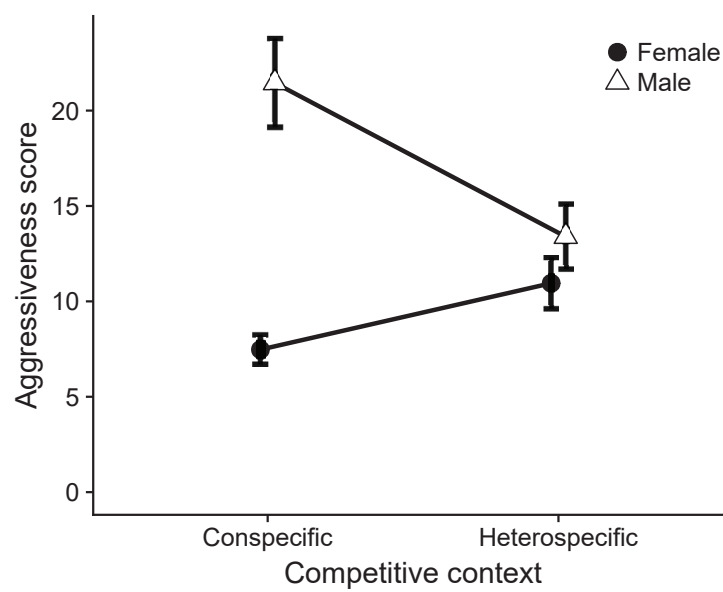


Figure A.4.3: *Aggressiveness scores (mean \pm 95%CI) of female and male flycatchers depending on the competitive context of the aggressiveness test.*

4.7 Supplementary data

In the following 3 tables, stars indicate estimates which 95% CI does not encompass zero. For categorical variables, estimates refer to the category indicated in parentheses. V_A , V_{PE} , V_M , and V_ϵ respectively refer to the additive genetic, permanent environment, maternal, and residual variances. V_{plot} , V_{obs} , V_{decoy} , V_{song} respectively refer to the variances associated to the plot and observer identities, the decoy set used, and the played song track used for the test. N is the sample size of the data set used in the model.

Table S.4.1: **Output of the univariate models fitting aggressiveness score.**(1) to (4): models for the general aggressiveness score, based on the number of aggressive behaviours standardized per 15 minutes: (1) model with no fixed effects, (2) model with only the retained fixed effects, (3) model with all fixed effects and only the retained interactions, and (4) model with all fixed effects and interactions. We also present the results of models for alternative aggressiveness scores (see above): (5) model for the first axis of the PCA and (6) model for the discrete score (see Appendix A1).

Table S1	Number of aggressive behaviours / 15 minutes			
	(1) No fixed effect		(2) Selected model	
	Post. mode	95% CI	Post. mode	95% CI
Fixed effects				
intercept	1.26 *	[0.93 ; 1.48]	0.06	[-0.47 ; 0.49]
sex (<i>male</i>)			0.20	[-0.01 ; 0.43]
age (<i>young</i>)			0.23	[0.00 ; 0.42]
weather (<i>rain</i>)			-0.36 *	[-0.69 ; -0.04]
(<i>sunny</i>)			0.12	[0.00 ; 0.25]
wind				
mean temperature				
presence of tits (<i>present</i>)			0.36 *	[0.21 ; 0.51]
presence of flycatchers (<i>present</i>)				
presence of the partner (<i>present</i>)			0.56 *	[0.42 ; 0.78]
hour of the day			-0.06 *	[-0.13 ; 0.00]
hour of the day ²				
number of test			-0.20 *	[-0.27 ; -0.15]
dummy type (<i>flycatcher</i>)			-0.31 *	[-0.65 ; -0.02]
nest stage				
year (<i>2012</i>)			0.43 *	[0.05 ; 0.82]
(<i>2013</i>)			0.31	[-0.06 ; 0.68]
day in the season				
sex : age (<i>male : young</i>)			0.29 *	[0.02 ; 0.61]
sex : presence of the partner (<i>male : present</i>)				
sex : dummy type (<i>male : flycatcher</i>)			0.74 *	[0.55 ; 0.99]
age : dummy type (<i>young : flycatcher</i>)				
Random effects				
V _A	0.00	[0.00 ; 0.32]	0.00	[0.00 ; 0.41]
V _{PE}	0.62 *	[0.27 ; 0.79]	0.51 *	[0.15 ; 0.72]
V _M	0.00	[0.00 ; 0.22]	0.00	[0.00 ; 0.19]
V _{plot}	0.06 *	[0.02 ; 0.15]	0.06 *	[0.01 ; 0.14]
V _{decoy}	0.00	[0.00 ; 0.04]	0.00	[0.00 ; 0.03]
V _{song}	0.02	[0.00 ; 0.09]	0.01	[0.00 ; 0.10]
V _{obs}	0.26 *	[0.14 ; 0.54]	0.26 *	[0.15 ; 0.62]
V _ε	2.57 *	[2.42 ; 2.76]	2.03 *	[1.19 ; 2.22]
Derived estimates				
R	0.20 *	[0.15 ; 0.24]	0.20 *	[0.16 ; 0.26]
h ²	0.00	[0.00 ; 0.09]	0.00	[0.00 ; 0.13]
N	4 680		2 900	
Effective sample size	> 2 336		> 2 322	

Table S1 (continued)	Number of aggressive behaviours / 15 minutes			
	(3) Not all interactions		(4) All interactions	
	Post. mode	95% CI	Post. mode	95% CI
Fixed effects				
intercept	-0.14	[-0.67 ; 0.42]	-0.29	[-0.79 ; 0.47]
sex (<i>male</i>)	0.12	[-0.03 ; 0.43]	0.35	[-0.18 ; 0.66]
age (<i>young</i>)	0.26 *	[0.01 ; 0.44]	0.10	[-0.08 ; 0.41]
weather (<i>rain</i>)	-0.44 *	[-0.77 ; -0.12]	-0.39 *	[-0.81 ; -0.15]
(<i>sunny</i>)	0.16 *	[0.02 ; 0.29]	0.18 *	[0.03 ; 0.31]
wind	0.04	[-0.02 ; 0.11]	0.03	[-0.03 ; 0.11]
mean temperature	-0.05	[-0.13 ; 0.02]	-0.05	[-0.13 ; 0.02]
presence of tits (<i>present</i>)	0.36 *	[0.19 ; 0.50]	0.34 *	[0.19 ; 0.50]
presence of flycatchers (<i>present</i>)	0.23	[-0.10 ; 0.51]	0.12	[-0.09 ; 0.50]
presence of the partner (<i>present</i>)	0.62 *	[0.43 ; 0.79]	0.67 *	[0.35 ; 1.00]
hour of the day	-0.08 *	[-0.14 ; -0.01]	-0.15	[-0.69 ; 0.26]
hour of the day ²			0.13	[-0.35 ; 0.60]
number of test	-0.21 *	[-0.27 ; -0.13]	-0.19 *	[-0.27 ; -0.13]
dummy type (<i>flycatcher</i>)	-0.39 *	[-0.71 ; -0.07]	-0.39 *	[-0.77 ; -0.08]
nest stage	0.01	[-0.06 ; 0.09]	0.02	[-0.06 ; 0.09]
year (<i>2012</i>)	0.45	[-0.01 ; 0.77]	0.41	[0.00 ; 0.79]
(<i>2013</i>)	0.49 *	[0.12 ; 0.90]	0.45 *	[0.08 ; 0.88]
day in the season	-0.04	[-0.16 ; 0.06]	-0.05	[-0.16 ; 0.06]
sex : age (<i>male : young</i>)	0.34 *	[0.06 ; 0.66]	0.33 *	[0.02 ; 0.62]
sex : presence of the partner (<i>male : present</i>)			-0.07	[-0.48 ; 0.30]
sex : dummy type (<i>male : flycatcher</i>)	0.80 *	[0.58 ; 1.06]	0.87 *	[0.57 ; 1.07]
age : dummy type (<i>young : flycatcher</i>)			0.11	[-0.11 ; 0.38]
Random effects				
V _A	0.00	[0.00 ; 0.39]	0.00	[0.00 ; 0.37]
V _{PE}	0.54 *	[0.11 ; 0.69]	0.52 *	[0.13 ; 0.69]
V _M	0.00	[0.00 ; 0.14]	0.00	[0.00 ; 0.12]
V _{plot}	0.04	[0.00 ; 0.14]	0.04	[0.00 ; 0.14]
V _{decoy}	0.00	[0.00 ; 0.04]	0.00	[0.00 ; 0.03]
V _{song}	0.02	[0.00 ; 0.09]	0.02	[0.00 ; 0.09]
V _{obs}	0.33 *	[0.15 ; 0.63]	0.28 *	[0.16 ; 0.63]
V _ε	2.03 *	[1.87 ; 2.24]	2.09 *	[1.88 ; 2.24]
Derived estimates				
R	0.19 *	[0.14 ; 0.24]	0.20 *	[0.14 ; 0.24]
h ²	0.00	[0.00 ; 0.12]	0.00	[0.00 ; 0.12]
N	2 900		2 900	
Effective sample size	> 2 112		> 2 070	

Table S1 (continued)	(5) PC1		(6) Categories	
	Post. mode	95% CI	Post. mode	95% CI
Fixed effects				
intercept	-0.78 *	[-1.22 ; -0.44]	5.62 *	[4.49 ; 6.61]
sex (<i>male</i>)	0.14	[-0.03 ; 0.32]	0.24	[-0.30 ; 0.64]
age (<i>young</i>)	0.12	[-0.05 ; 0.26]	0.29	[-0.11 ; 0.73]
weather (<i>rain</i>)	-0.20	[-0.42 ; 0.07]	-1.02 *	[-1.68 ; -0.36]
(<i>sunny</i>)	0.05	[-0.03 ; 0.18]	0.39	[0.11 ; 0.65]
wind	0.06	[0.00 ; 0.11]	0.05	[-0.10 ; 0.18]
mean temperature	-0.05	[-0.11 ; 0.01]	-0.08	[-0.22 ; 0.08]
presence of tits (<i>present</i>)	0.05	[-0.07 ; 0.16]	0.42 *	[0.12 ; 0.73]
presence of flycatchers (<i>present</i>)	0.27 *	[0.04 ; 0.51]	0.57	[-0.16 ; 1.08]
presence of the partner (<i>present</i>)	0.34 *	[0.20 ; 0.47]	1.08 *	[0.77 ; 1.48]
hour of the day	-0.07 *	[-0.12 ; -0.02]	-0.20 *	[-0.33 ; -0.06]
hour of the day ²				
number of test	-0.15 *	[-0.20 ; -0.09]	-0.25 *	[-0.40 ; -0.11]
dummy type (<i>flycatcher</i>)	-0.19	[-0.44 ; 0.04]	-0.53 *	[-1.16 ; 0.00]
nest stage	-0.01	[-0.07 ; 0.05]	-0.03	[-0.17 ; 0.15]
year (<i>2012</i>)	0.20	[-0.08 ; 0.49]	0.03	[-0.54 ; 0.99]
(<i>2013</i>)	0.30 *	[0.00 ; 0.57]	0.61 *	[0.02 ; 1.45]
day in the season	-0.01	[-0.09 ; 0.07]	-0.17	[-0.38 ; 0.08]
sex : age (<i>male : young</i>)	0.33 *	[0.08 ; 0.54]	0.93 *	[0.26 ; 1.53]
sex : presence of the partner (<i>male : present</i>)				
sex : dummy type (<i>male : flycatcher</i>)	0.78 *	[0.57 ; 0.94]	1.63 *	[1.20 ; 2.19]
age : dummy type (<i>young : flycatcher</i>)				
Random effects				
V _A	0.00	[0.00 ; 0.11]	0.01	[0.00 ; 1.46]
V _{PE}	0.23 *	[0.10 ; 0.33]	1.91 *	[0.69 ; 2.98]
V _M	0.00	[0.00 ; 0.21]	0.00	[0.00 ; 0.72]
V _{plot}	0.01	[0.00 ; 0.04]	0.11	[0.00 ; 0.38]
V _{decoy}	0.00	[0.00 ; 0.04]	0.04	[0.00 ; 0.26]
V _{song}	0.01	[0.00 ; 0.05]	0.00	[0.00 ; 0.18]
V _{obs}	0.09 *	[0.02 ; 0.17]	0.68 *	[0.29 ; 1.40]
V _ε	1.57 *	[1.47 ; 1.66]	10.00	[10.00 ; 10.00]
Derived estimates				
R	0.17 *	[0.12 ; 0.22]	0.19 *	[0.14 ; 0.24]
h ²	0.00	[0.00 ; 0.06]	0.00	[0.00 ; 0.11]
N	2 900		2 900	
Effective sample size	> 2 717		> 1 546	

Table S.4.2: **Output of the models fitting boldness scores.** (1) to (4): models for the general boldness score, based on the transformed and inversed latency to enter the nest box after human disturbance: (1) model with no fixed effects, (2) model with only the retained fixed effects, (3) model with all fixed effects and only the retained interactions, and (4) model with all fixed effects and interactions tested. We also present the results of models for alternative boldness scores: (5) model for the transformed and inversed latency to enter the nest box after human disturbance divided by the feeding rate during the time remaining, and (6) model for the discrete score (see Text S1).

Table S2	Latency to feed after human disturbance					
	(1) No fixed effect		(2) Selected model		(3) Without interactions	
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI
Fixed effects						
intercept	-6.09 *	[-6.17 ; -5.97]	-5.99 *	[-6.14 ; -5.85]	-5.91 *	[-6.12 ; -5.77]
sex (male)			-0.31 *	[-0.40 ; -0.17]	-0.30 *	[-0.43 ; -0.16]
age (young)					-0.07	[-0.19 ; 0.08]
year (2012)			-0.09	[-0.23 ; 0.09]	-0.07	[-0.27 ; 0.14]
(2013)			0.24 *	[0.10 ; 0.45]	0.22 *	[0.03 ; 0.43]
temperature					0.03	[-0.05 ; 0.10]
hour of the day					0.00	[-0.08 ; 0.05]
hour of the day ²						
nb. chicks			0.08 *	[0.03 ; 0.14]	0.09 *	[0.001 ; 0.13]
day					0.02	[-0.03 ; 0.08]
sex : age (male : young)						
sex : nb. chicks (male)						
Random effects						
V _A	0.00	[0.00 ; 0.17]	0.00	[0.00 ; 0.16]	0.00	[0.00 ; 0.22]
V _{PE}	0.00	[0.00 ; 0.17]	0.00	[0.00 ; 0.16]	0.00	[0.00 ; 0.22]
V _M	0.00	[0.00 ; 0.07]	0.00	[0.00 ; 0.07]	0.00	[0.00 ; 0.08]
V _{plot}	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.03]	0.00	[0.00 ; 0.02]
V _{obs}	0.02	[0.00 ; 0.07]	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.03]
V _ε	0.81 *	[0.67 ; 0.92]	0.73 *	[0.66 ; 0.88]	0.70 *	[0.56 ; 0.84]
Derived estimates						
R	0.14 *	[0.02 ; 0.25]	0.14 *	[0.03 ; 0.26]	0.20 *	[0.05 ; 0.36]
h ²	0.00	[0.00 ; 0.17]	0.00	[0.00 ; 0.17]	0.00	[0.00 ; 0.25]
N	1251		1046		812	
Effective sample size	> 2224		> 2126		> 2170	

Table S2 (Continued)	Latency to feed		(5) Latency / feeding rate		(6) Score	
	(4) With all interactions					
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI
Fixed effects						
intercept	-5.95 *	[-6.10 ; -5.74]	0.04 *	[-0.32 ; 0.36]	5.33 *	[4.18 ; 6.45]
sex (<i>male</i>)	-0.35 *	[-0.52 ; -0.19]	-0.69 *	[-0.87 ; -0.51]	-1.19 *	[-2.00 ; -0.78]
age (<i>young</i>)	-0.19	[-0.33 ; 0.04]	-0.02	[-0.21 ; 0.19]	-0.25	[-0.84 ; 0.27]
year (<i>2012</i>)	-0.08	[-0.25 ; 0.15]	-0.12	[-0.50 ; 0.24]	-0.64	[-1.42 ; 0.34]
(<i>2013</i>)	0.26 *	[0.02 ; 0.42]	0.15	[-0.19 ; 0.53]	1.42 *	[0.43 ; 2.33]
temperature	0.04	[-0.05 ; 0.10]	0.04	[-0.09 ; 0.15]	0.03	[-0.36 ; 0.29]
hour of the day	0.23	[-0.20 ; 0.74]	-0.02	[-0.11 ; 0.08]	-0.15	[-0.37 ; 0.17]
hour of the day ²	-0.22	[-0.72 ; 0.22]				
nb. chicks	0.04	[-0.05 ; 0.12]	-0.12 *	[-0.23 ; -0.03]	0.35 *	[0.05 ; 0.59]
day	0.02	[-0.03 ; 0.08]	0.00	[-0.06 ; 0.07]	0.19	[-0.11 ; 0.45]
sex : age (<i>male : young</i>)	0.20	[-0.10 ; 0.43]				
sex : nb. chicks (<i>male</i>)	0.09	[-0.04 ; 0.22]				
Random effects						
V _A	0.00	[0.00 ; 0.21]	0.00	[0.00 ; 0.21]	0.05	[0.00 ; 7.59]
V _{PE}	0.00	[0.00 ; 0.23]	0.00	[0.00 ; 0.20]	0.02	[0.00 ; 7.18]
V _M	0.00	[0.00 ; 0.08]	0.00	[0.00 ; 0.09]	0.01	[0.00 ; 1.60]
V _{plot}	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.08]	0.20	[0.00 ; 0.95]
V _{obs}	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.05]	0.00	[0.00 ; 0.76]
V	0.67 *	[0.56 ; 0.85]	1.07 *	[0.81 ; 1.23]	10.00	[10.00 ; 10.00]
Derived estimates						
R	0.22 *	[0.06 ; 0.36]	0.06 *	[0.001 ; 0.26]	0.39 *	[0.18 ; 0.53]
h ²	0.00	[0.00 ; 0.24]	0.00	[0.00 ; 0.17]	0.00	[0.00 ; 0.39]
<i>N</i>	812		524		940	
<i>Effective sample size</i>	> 2041		>1937		>2800	

Table S.4.3: **Output of the models fitting neophobia scores.** (1) to (4): models for the general neophobia score, based on the ratio of latency to enter the nest box in presence of the novel object divided by latency to enter in absence of the novel object: (1) model with no fixed effects, (2) model with only the retained fixed effects, (3) model with all fixed effects and only the retained interactions, and (4) model with all fixed effects and interactions tested. We also present the result of models for alternative neophobia scores: (5) model for a binary variable (individual entered vs. did not enter in the presence of the novel object) and (6) model for a continuous variable L , for individuals which entered in the presence of the novel object (see Text S1).

Table S3	Score based on δ_L (main text)					
	(1) No fixed effect		(2) Selected model		(3) Without interactions	
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI
Fixed effects						
intercept	3.70 *	[3.30 ; 4.63]	4.97 *	[3.66 ; 5.96]	5.04 *	[3.50 ; 6.23]
sex (male)			-2.11 *	[-2.75 ; -1.54]	-2.20 *	[-2.81 ; -1.46]
age (young)			-0.65 *	[-1.21 ; -0.05]	-0.23	[-1.04 ; 0.23]
year (2012)			1.92 *	[0.91 ; 2.78]	2.40 *	[1.09 ; 3.61]
(2013)			1.19	[-0.06 ; 1.99]	1.33 *	[0.18 ; 2.71]
temperature					0.11	[-0.21 ; 0.53]
hour of the day					0.05	[-0.21 ; 0.41]
hour of the day ²						
nb. chicks			-0.69 *	[-0.96 ; -0.36]	-0.81 *	[-1.13 ; -0.45]
day					-0.19	[-0.39 ; 0.05]
sex : age (male : young)						
sex : nb. chicks (male)						
Random effects						
V_A	0.02	[0.00 ; 2.32]	0.01	[0.00 ; 3.01]	0.03	[0.00 ; 5.64]
V_{PE}	0.01	[0.00 ; 2.32]	0.03	[0.00 ; 3.98]	0.02	[0.00 ; 5.52]
V_M	4.97 *	[1.22 ; 8.75]	5.76 *	[1.75 ; 10.63]	6.31 *	[2.69 ; 13.99]
V_{plot}	0.68 *	[0.23 ; 2.22]	1.14 *	[0.32 ; 2.86]	0.94 *	[0.32 ; 3.32]
V_{obs}	0.19	[0.00 ; 0.84]	0.30	[0.00 ; 0.95]	0.35	[0.00 ; 1.69]
V_E	10.00	[10.00 ; 10.00]	10.00	[10.00 ; 10.00]	10.00	[10.00 ; 10.00]
Derived estimates						
R	0.34 *	[0.18 ; 0.50]	0.42 *	[0.25 ; 0.55]	0.48 *	[0.32 ; 0.63]
h^2	0.00	[0.00 ; 0.12]	0.00	[0.00 ; 0.14]	0.00	[0.00 ; 0.21]
N	1251		914		812	
Effective sample size	>2599		>2365		>1800	

Table S3 (Continued)	Score based on L		(5) Binary		(6) Continuous log(L)	
	(4) With all interactions					
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI
Fixed effects						
intercept	4.65 *	[3.37 ; 6.14]	-2.98 *	[-4.50 ; -0.93]	0.22	[-0.02 ; 0.47]
sex (<i>male</i>)	-1.54 *	[-2.67 ; -1.05]	-1.50 *	[-2.63 ; -0.60]	-0.69 *	[-0.88 ; -0.55]
age (<i>young</i>)	0.32	[-0.90 ; 0.97]	-0.45	[-1.23 ; 0.59]	-0.10	[-0.27 ; 0.08]
year (<i>2012</i>)	2.28 *	[1.08 ; 3.73]	1.93 *	[0.25 ; 3.97]	0.43 *	[0.08 ; 0.62]
(<i>2013</i>)	1.46 *	[0.15 ; 2.79]	1.82 *	[0.02 ; 3.91]	0.27	[-0.03 ; 0.53]
temperature	0.11	[-0.24 ; 0.53]	0.20	[-0.43 ; 0.57]	0.05	[-0.03 ; 0.17]
hour of the day	-0.34	[-2.13 ; 2.36]	0.36	[-0.08 ; 0.82]	-0.08	[-0.15 ; 0.03]
hour of the day ²	0.18	[-2.15 ; 2.33]				
nb. chicks	-0.72 *	[-1.16 ; -0.26]	-0.80 *	[-1.27 ; -0.31]	-0.07	[-0.16 ; 0.03]
day	-0.12	[-0.38 ; 0.09]	-0.45	[-1.98 ; 0.13]	0.01	[-0.06 ; 0.04]
sex : age (<i>male</i> : <i>young</i>)	-1.45	[-2.40 ; 0.26]				
sex : nb. chicks (<i>male</i>)	-0.21	[-0.90 ; 0.42]				
Random effects						
V _A	0.03	[0.00 ; 6.64]	0.16	[0.00 ; 19.91]	0.00	[0.00 ; 0.23]
V _{PE}	0.04	[0.00 ; 6.55]	0.06	[0.00 ; 19.48]	0.00	[0.00 ; 0.23]
V _M	6.13 *	[2.47 ; 14.82]	0.11	[0.00 ; 27.50]	0.00	[0.00 ; 0.28]
V _{plot}	1.21 *	[0.37 ; 3.36]	0.52	[0.00 ; 4.45]	0.05 *	[0.01 ; 0.14]
V _{obs}	0.40	[0.00 ; 1.80]	0.82 *	[0.17 ; 4.56]	0.00	[0.00 ; 0.05]
V	10.00	[10.00 ; 10.00]	10.00	[10.00 ; 10.00]	0.64	[0.47 ; 0.84]
Derived estimates						
R	0.49 *	[0.35 ; 0.65]	0.63 *	[0.38 ; 0.80]	0.26 *	[0.06 ; 0.45]
h ²	0.00	[0.00 ; 0.24]	0.00	[0.00 ; 0.45]	0.00	[0.00 ; 0.24]
N	812		940		491	
Effective sample size	>2208		>1732		>2335	

Table S.4.4: Phenotypic, between-individual and residual correlations between aggressiveness, boldness and neophobia estimates for females and males separately. Stars indicate estimates whose 95% CI does not encompass zero.

	Phenotypic		Between-individual		Residual	
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI
Among females						
Aggressiveness - Boldness	0.02	[-0.06 ; 0.14]	0.01	[-0.06 ; 0.06]	0.03	[-0.08 ; 0.17]
Aggressiveness - Neophobia	-0.11	[-0.21 ; 0.01]	-0.02	[-0.07 ; 0.06]	-0.16	[-0.31 ; 0.01]
Aggressiveness - Neophobia	0.01	[-0.13 ; 0.14]	0.00	[-0.07 ; 0.06]	0.01	[-0.16 ; 0.21]
Boldness - Neophobia	0.02	[-0.05 ; 0.14]	0.00	[-0.07 ; 0.06]	0.07	[-0.09 ; 0.22]
Boldness - Neophobia†	0.59 *	[0.49 ; 0.66]	0.00	[-0.06 ; 0.07]	0.75 *	[0.61 ; 0.85]
Among males						
Aggressiveness - Boldness	0.03	[-0.05 ; 0.15]	0.00	[-0.07 ; 0.06]	0.03	[-0.05 ; 0.19]
Aggressiveness - Neophobia	-0.20 *	[-0.30 ; -0.09]	0.00	[-0.07 ; 0.06]	-0.25 *	[-0.38 ; -0.10]
Aggressiveness - Neophobia	-0.06	[-0.17 ; 0.08]	0.00	[-0.05 ; 0.07]	-0.06	[-0.25 ; 0.09]
Boldness - Neophobia	-0.03	[-0.11 ; 0.10]	0.01	[-0.06 ; 0.06]	-0.03	[-0.15 ; 0.12]
Boldness - Neophobia†	0.52 *	[0.39 ; 0.58]	0.01	[-0.06 ; 0.06]	0.57 *	[0.44 ; 0.71]

Table S.4.5: *Detailed description of the collared flycatcher pedigree from the Gotland Island population. The pedigree statistics were obtained from all identified individuals involved in either aggressiveness, boldness or neophobia assays, and were extracted using the pedigreeStats and pedStatSummary functions from pedantics R package (Morrissey and Wilson 2010).*

Pedigree statistics	
Records	2 218
Founders	1423
Maternities	728
Paternities	781
Full sibs	130
Maternal sibs	222
Maternal half sibs	92
Paternal sibs	230
Paternal half sibs	100
Maternal grandmothers	249
Maternal grandfathers	268
Paternal grandmothers	220
Paternal grandfathers	236
Maximum pedigree depth	15
Mean Relatedness	5.29×10^{-4}

Table S.4.6: *Result of the trivariate model fitting aggressiveness, boldness and neophobia scores. V stands for variance terms, and Cov for covariance terms (posterior mode and 95% CI). “ind” and “ε” stand for between-individual and residual terms respectively. The residual variance for neophobia score was fixed to 1 (see text for the distributions used for the three scores). Stars indicate estimates whose 95% CI does not encompass zero.*

	Post. mode	95% CI
Fixed effects		
aggressiveness	1.85 *	[1.68 ; 1.94]
boldness	-6.10 *	[-6.22 ; -6.03]
neophobia	1.12 *	[0.95 ; 1.35]
sex (<i>male</i>)	-0.15 *	[-0.23 ; -0.04]
year (<i>2012</i>)	0.10	[-0.01 ; 0.19]
(<i>2013</i>)	0.26 *	[0.14 ; 0.37]
Random effects		
V _{ind, aggressiveness}	0.00	[0.00 ; 0.71]
V _{ind, boldness}	0.13	[0.00 ; 0.26]
V _{ind, neophobia}	0.35	[0.00 ; 0.65]
V _{ε, aggressiveness}	1.48 *	[1.10 ; 1.93]
V _{ε, boldness}	0.71 *	[0.59 ; 0.89]
V _{ε, neophobia}	1.00 *	[1.00 ; 1.00]
Cov _{ind, aggressiveness-neophobia}	0.00	[-0.02 ; 0.02]
Cov _{ind, aggressiveness-boldness}	0.00	[-0.01 ; 0.01]
Cov _{ind, boldness-neophobia}	0.00	[-0.01 ; 0.01]
Cov _{ε, aggressiveness-neophobia}	-0.32 *	[-0.46 ; -0.21]
Cov _{ε, aggressiveness-boldness}	0.04	[-0.05 ; 0.13]
Cov _{ε, boldness-neophobia}	0.02	[-0.07 ; 0.10]
<i>N</i>		838
<i>Effective sample size:</i>		>1967

Chapter 5

Linking heterospecific social information use and personality for breeding site selection



Male aggressiveness predicts heterospecific social information use for breeding site selection: experimental evidence from a wild bird population

Jennifer Morinay, Jukka Forsman, Marion Germain, Gregory Daniel, Blandine Doligez

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Keywords: copying, personality, boldness, aggressiveness, neophobia, collared flycatcher, *Ficedula albicollis*

Abstract

Social information is commonly used for optimizing decision-making. However, personality can constrain individuals' ability to gather social information (through activity, exploration, or boldness) or to cope with the increased competition due to similar decisions by different individuals based on the same information (through aggressiveness, sociality). Links between personality traits and social information use remain poorly understood so far, in particular in the breeding habitat selection context. We experimentally tested whether three personality traits (aggressiveness, boldness, neophobia) affected the use of heterospecific social information for nest site selection in a natural population of collared flycatchers *Ficedula albicollis*. We manipulated the apparent preference of tits (the main competitors of flycatchers in our population) for a nest site feature and recorded whether flycatchers copied or rejected this preference (i.e. preferred nest boxes with the same or a different feature). Male aggressiveness affected the probability to copy tit apparent preference in interaction with tit local presence (density) and early reproductive investment (clutch / brood size at the time of flycatcher settlement). Only more aggressive males rejected tit preference when local tit clutch / brood size was small, and only less aggressive males copied tit preference when local tit density was high. Male neophobia and boldness, as well as female personality traits did not affect the probability to copy tit apparent preference. In addition, yearling (inexperienced) males were more likely to copy tit preference, and only older males adjusted their copying behaviour depending on tit clutch / brood size. Aggressiveness may allow males to access more information or information at a larger scale; alternatively, it may affect males' interactions with dominant tits when selecting a breeding site. Our study highlights the role of aggressiveness in shaping between-individual variation in social information use for breeding habitat selection and calls for further work to explore the underlying mechanisms.

5.1 Introduction

To optimize decision-making, individuals can use information to reduce environmental uncertainty (Schmidt et al. 2010). Information can be derived either from the individual's own interactions with the environment (personal information) or from the observation of other individuals' actions and the result of these actions (Danchin et al. 2004, Dall et al. 2005). Individuals have been found to flexibly use personal and/or social information depending on the relative reliability and availability of these information sources (Templeton and Giraldeau 1996, Kendal et al. 2004, 2005, van Bergen et al. 2004, Coolen et al. 2005), which can depend on environmental conditions (e.g. population size, spatio-temporal predictability) but also on individual factors (Dugatkin and Godin 1993, Doligez et al. 1999, 2002, 2003, Valone 2007).

Among individual factors, personality traits in particular may constrain the flexibility in using social information, either by affecting the propensity to acquire and use information or by restraining the decisions made once information is acquired. Personality traits are between-individual behavioural differences consistent over time and contexts (Groothuis and Carere 2005). Such differences are widespread in the animal kingdom and have been classified into five major axes linked to behavioural responses to the environment itself (activity, exploration/neophobia, boldness) or to other individuals, including both con- and heterospecifics (Réale et al. 2007). Activity, boldness and exploration may shape individual's prospecting behaviour and affect overall knowledge of the environment, especially at large spatial scales. Aggressiveness and sociability may more specifically affect interactions with others and thus access to social information. Thus far, 22 published animal studies (to our knowledge) have investigated the links between social information use and personality traits, mostly in the context of foraging decision-making (reviewed in Table 5.1; see Table 1.1 in Chapter 1 for full details). Among these studies, the investigation of the exploration / neophobia axis (Réale et al. 2007) was largely predominant (17 over 22 studies, i.e. 77%). Higher neophobia level was frequently associated to higher use of social information (Table 5.1); conversely, no clear pattern was found in the links

between social information use and other personality traits (Table 5.1), either because of mostly non-significant relations (for exploration and boldness) or because very few studies investigated these links (for activity, sociability and more specifically aggressiveness, whose direct links with social information use have not been investigated so far; Table 5.1, Table 1.1 in Chapter 1). Furthermore, testing the causality of links between personality traits and social information use requires experimentally manipulating information sources. Yet, such manipulations have only been conducted in captivity, where behaviours may be altered by stress (for wild animals tested in captivity) or artificial selection (for long-term captive populations). Therefore, to which extent different personality traits may favour or constrain the use of social information for decision-making in the wild, depending on environmental conditions, remains poorly understood.

Despite the large body of work on social information use in the context of breeding habitat selection, on the one hand (Doligez et al. 1999, Seppänen and Forsman 2007, Loukola et al. 2013, Forsman et al. 2014, Szymkowiak et al. 2017), and on dispersal syndromes involving personality traits, on the other hand (Dingemanse et al. 2003, Duckworth and Badyaev 2007, Cote et al. 2010), no study investigated the influence of personality traits on social information use for breeding site choice (Table 1.1 in Chapter 1). Yet, prospecting to gather information on potential breeding sites can be costly especially in terms of time and energy spent as well as increased agonistic interactions with competitors (Forsman and Thomson 2008, Kingma et al. 2016). Therefore, more aggressive, bold and/or explorative individuals may have access to more information sources or information at larger spatial scales. Social information use itself may also increase intra- (and inter-) specific competition by individuals choosing the same sites/territories, and thus spatially aggregating, based on the same use of information (Doligez et al. 2003, Loukola et al. 2013, Parejo and Avilés 2016). Therefore, the realised breeding site choices may depend on aggressiveness allowing individuals to acquire and defend the chosen site/territory against competitors. Assessing to what extent personality traits shape social information use for the optimal choice of a breeding site is needed to understand how selective pressures act on personality over different decision-making contexts along an individual's lifetime.

Here, we tested whether individuals differed in their propensity to use an experimentally manipulated source of social information for nest site selection according to three personality traits (aggressiveness, boldness and neophobia) in a natural population of a small passerine bird, the collared flycatcher *Ficedula albicollis*. Collared and pied flycatchers (*F. hypoleuca*, a sister species) have been repeatedly shown to use social information from con- and heterospecific (titmice) competitors at various spatial scales when choosing a breeding site (Doligez et al. 1999, 2002, Seppänen and Forsman 2007, Forsman and Seppänen 2011, Jaakkonen et al. 2013, Kivelä et al. 2014, Samplonius and Both 2017). Flycatchers have been found to prospect all along the breeding season to collect social information for their settlement decisions in the same or the next year (Doligez et al. 2002, 2004, Pärt and Doligez 2003, Forsman and Thomson 2008, Ponchon et al. 2013). However, social information use shows high between-individual variability in this system, only partly explained by sex, age or dispersal status (Doligez et al. 1999, 2002, Kivelä et al. 2014). We tested whether personality could explain this variability by using an experimental design already successfully implemented in this species, to create an apparent local preference of dominant tutors (here tits) for a specific nest box feature observable from a distance (Seppänen and Forsman 2007, Seppänen et al. 2011, Loukola et al. 2012). We then recorded whether flycatchers copied or rejected this preference by settling in nest boxes displaying the same feature. After settlement, we measured levels of aggressiveness, boldness and neophobia of the experimental birds to test the link between these personality traits and the probability to copy tit apparent preference. Neophobia could restrain access to other information sources besides tit apparent preference, and thus more neophobic individuals could be expected to be more likely to copy tutors' preference than less neophobic ones. Furthermore, due to potential risks of collecting data at the vicinity of tit territories and increased costs of competition due to niche overlap after settlement, we expected aggressive individuals to be more likely to copy tutors' preference than less aggressive ones. Finally, boldness could decrease the potential anti-predator benefits of copying tutors' preference for flycatchers, and thus bolder individuals (i.e. individuals more prone to take risks) could be expected to be less likely to copy tutors' preference

than shy individuals. We also tested whether the effects of personality traits might depend (1) on environmental conditions (here tit density and early reproductive investment), which could modulate the value of our information source compared to other sources (e.g. Forsman et al. 2008, Seppänen et al. 2011), and (2) on age, because young individuals are also more prone to use social information than older, more experienced, ones (Valone 2007).

Table 5.1: *Summary of the results of studies investigating relations between personality traits and social information use: for each personality trait, number of studies that found a positive (+), negative (-), or non-significant (NS) relation. Full details on each study and measured traits are given in Table 1.1 in Chapter 1. Note that neophobia and exploration were often referred to as ‘boldness’ in articles, but we follow here the definitions from Réale et al. (2007) and refer to boldness as the reaction in a risky situation (presence of potential predators, including humans).*

Personality trait	Definitions	Nb. and signs of the links with social information use			Ref.
		-	0	+	
Activity	Reaction in a known environment	0	1	1	[1]
Aggressiveness	Agonistic reaction towards others	0	0	0	
Boldness	Reaction in a risky situation	2	5	1	[2-6]
Exploration	Reaction in a novel environment	2	4	2	[7-14]
Neophobia	Reaction towards a novel object	2	2	7	[4, 5, 14-21]
Sociability	Non-agonistic reaction towards others	0	1	2	[13, 20, 22]

[1] Budaev and Zworykin (1998); [2] Ward et al. (2004); [3] Dyer et al. (2008); [4] Carter et al. (2013); [5] Carter et al. (2014); [6] Harcourt et al. (2010); [7] Marchetti and Drent (2000); [8] Webster et al. (2007); [9] Nomakuchi et al. (2009), [10] Sibbald et al. (2009); [11] David et al. (2011); [12] Aplin et al. (2014); [13] Webster and Laland (2015); [14] Snijders et al. (2017); [15] Michelenia et al. (2009); [16] Kurvers et al. (2010a); [17] Kurvers et al. (2010b); [18] Kurvers et al. (2011); [19] Jolles et al. (2013); [20] Trompf and Brown (2014); [21] Carter et al. (2016); [22] Aplin et al. (2012).

5.2 Material and Methods

Species and study site

The experiment was conducted in spring 2012 and 2013 on a breeding population of collared flycatchers (*Ficedula albicollis*) on the island of Gotland (Baltic Sea, Sweden). Collared flycatchers are sexually dimorphic migratory hole-nesting passerine birds that readily breed in artificial nest boxes provided in the forest patches of the study area. Collared flycatchers typically arrive on breeding grounds between late April and late May. Flycatchers compete for nest boxes with great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*), which are resident passerine species, are dominant over flycatchers and typically start laying on average 2 weeks before flycatchers' arrival (but see Chapter 3 and Table 5.2 for between-year variation in this time interval). Breeding flycatchers were captured in nest boxes (during incubation for females and chick rearing for males) as part of the long-term monitoring of the population (e.g. Gustafsson 1990). Caught individuals were measured and aged based on plumage criteria (yearling vs. older individuals; Svensson 1992). See Pärt and Gustafsson (1989) or Doligez et al. (Doligez et al. 2009) for more information about study area and population monitoring procedures.

Heterospecific preference copying experimental design

To create an apparent preference of tits for a specific nest box feature and measure flycatchers' subsequent copying behaviour, we attached around the entrance of nest boxes different geometric symbols (white plastic shapes) depending on the species occupying the nest box (same protocol as presented in Chapters 3). Before flycatchers' arrival (i.e. beginning to mid-April), we attached on all boxes occupied by great and blue tits in a given patch either a triangle or a circle. At the same time, we attached a triangle on half of the remaining (empty) nest boxes, i.e. nest boxes available for newcomers' settlement, and a circle on the other half. Therefore, when flycatchers arrived from migration (late

April to mid-May), they had the choice between settling in a box with the same symbol as tit boxes, thus matching tit apparent preference (i.e. copy), or in a box with the opposite symbol (i.e. reject tit preference). When a flycatcher pair had settled in a nest box, as shown by the presence of new nest material in the box, we removed the symbol on this box. This avoided providing conspecific information via the symbol chosen to later arriving flycatchers. We checked empty nest boxes every second day to detect newly started nest building and remove (for new flycatcher nests) or change if needed (for new tit nests) the symbol accordingly. At the same time, we adjusted the number of triangles and circles on empty boxes within a forest patch to keep an equal proportion of available nest boxes presenting each symbol, and thus an equal probability for newcomers to choose a symbol at random. Because this equal proportion between symbols could not always be verified (e.g. when an odd number of empty boxes remained in a patch), we controlled for the deviation from 0.5 of the actual proportion of empty boxes matching the tit apparent preference within a plot on the day of choice for each flycatcher pair. The symbol associated with tits was randomised among experimental forest patches (12 patches in 2012, 10 in 2013), and alternated between 2012 and 2013 in each patch. Switching the symbol associated with tits between years for a given patch allowed us to control for potential across-year learning effects (Forsman et al. 2014). Indeed, even though we retained only individuals whose symbol choice was naive (i.e. first choice) in 2013 (see below), we could not exclude a potential influence of individuals' experience with symbols if they were not captured in the first year of the study (2012), e.g. if they failed breeding before capture.

Measuring personality traits

Personality traits were measured exactly as described in Chapters 4. Aggressiveness was measured through the agonistic response to a simulated intrusion by conspecific and heterospecific (great tit) competitors on the nest box of a focal pair during the nest building stage, i.e. when the risk of losing a nest box to a competitor is highest. We used both a conspecific and heterospecific decoys (but only one stimuli type per test) because

Table 5.2: *Differences between the two years of the study (2012 and 2013) in flycatcher heterospecific copying behaviour, and in flycatcher and tit breeding variables. Estimates are means \pm SD.*

	2012	2013
% of flycatcher pairs copying tit apparent preference	59.1 %	39.3 %
Flycatcher settlement day	May 10 th \pm 4.0 days	May 14 th \pm 4.4 days
Great tit laying date	May 2 nd \pm 9.1 days	May 13 th \pm 5.5 days
Overall great tit density per the forest plots (proportion of boxes where great tits layed eggs, even if they subsequently deserted or failed)	0.44 \pm 0.11	0.27 \pm 0.06
Great tit density in the forest patch at the time of flycatcher settlement	0.35 \pm 0.10	0.24 \pm 0.06
Average complete great tit clutch size	8.5 \pm 2.2	8.1 \pm 2.0
Great tit clutch/brood size in the forest patch at the time of flycatcher settlement	7.1 \pm 1.5	2.9 \pm 2.8
Great tit adult body mass	18.2 \pm 0.99 g	18.3 \pm 1.03 g
Great tit adult body condition (body mass / tarsus length)	0.80 \pm 0.04 g. mm ⁻¹	0.80 \pm 0.04 g. mm ⁻¹

flycatchers compete for nest sites with both other flycatchers and great tits, and respond aggressively to both species (Gustafsson 1988, Král 1990, Král and Bíčík 1992). At the start of a test, an observer attached on the box decoys of either a flycatcher pair (rather than a single individual, to avoid sex-specific responses) or a male great tit, randomly chosen among 10 different sets for each species, as well as a loudspeaker broadcasting songs of the same species as the decoy(s), randomly chosen among 5 different song tracks per species. The observer then hid under a camouflage net approx. 8-10 meters away from the box, and recorded all behaviours performed by each member of the focal pair during 15 to 25 minutes: movements and distance from the nest box, flights and attacks towards the decoys or other live birds attracted by the stimulus. A total of 2 to 4 tests were conducted for each focal pair (1 to 2 tests per stimuli species), with one test maximum per day, 2 days maximum in a row, to avoid habituation. The decoy species was randomized for the first test and alternated between subsequent tests. To account for differences in

the duration of response between individuals (depending on when individuals started to respond), each behavioural variable was divided by the time interval between the first observation of the individual during the test and the end of the test, and standardized to 15 minutes, the typical length of a test. An aggressiveness score was estimated for each individual for each test as the sum of the standardized number of movements within 2 meters from the nest box, including landings on the nest box plus the number of attacks or stationary flights towards a decoy, and chases towards live intruders.

Boldness was measured through the reaction towards the presence of a human observer near the nest box and neophobia through the reaction towards the presence of a novel object on the box (i.e. in a familiar environment). We conducted one combined boldness / neophobia test per breeding pair per year, when the chicks were 5 days old, i.e. during the period of highest provisioning by parents (nestlings fledge approx. 19 days post-hatching). The test consisted of two consecutive periods lasting one hour each, during which the provisioning behaviour of both parents was recorded from a distance (6-8m). In the first period, an observer settled a camera and approached the nest box to check chick satiety, before leaving the area; this first period thus involved no change in the surroundings of the nest box. In the second period, the observer came back to the nest box, checked chick satiety again, attached a novel object (here a coloured figurine approx. 7 cm-high) near the entrance of the nest box and left again for one hour. Boldness score was estimated for each pair member as the latency to enter the nest box after the departure of the observer in the first period of the test. Neophobia score was estimated for each pair member as the ratio of the latency to enter the nest box after the departure of the observer in the second period of the test, i.e. in the presence of the novel object, divided by the latency to enter in the first period. Overall, 39% out of 241 tested individuals entered the nest box during the first but not the second period of the test. To include these very neophobic individuals in the analyses, we discretized the continuous neophobia score into 5 categories of increasing latency ratio (levels 0 to 4, based on the distribution of the variable, see supplementary material in Chapter 4) and added a 6th category (level 5) for individuals who entered the nest box in the first period of the test but not in the second.

Individuals who entered the nest box as fast or faster in the second period compared to the first were attributed a score of 0, and individuals who entered but took more than approx. 7 times longer to enter in the second period compared to the first were attributed a score of 4.

Aggressiveness, boldness and neophobia scores have been shown to be repeatable between years, i.e. define personality traits, in collared flycatchers (Chapter 4). See Chapter 4 for more details on the experimental protocols used to measure these three personality traits.

Statistical Analyses

We analysed the probability for collared flycatcher pairs to copy the apparent preference of tits (binary response variable: copy vs. reject). In the second year of the experiment (2013), we retained only the choices of naive individuals, i.e. individuals who did not take part in the experiment in 2012 (but including all choices in 2013 did not change the main results). We also excluded the few secondary nests of polygynous males (3 in total). Because nest site choice is a joint decision by both pair members, the most appropriate model to estimate the effect of individual personality on the joint copying behaviour would include both male and female personality traits simultaneously. However, this would have strongly reduced our sample size because the data included 121 choices by naive males and 138 by naive females separately, but only 89 by naive pairs (i.e. both pair members naive together). The lower number of males in the sample was due to early breeding failures (before the boldness/neophobia test and/or male capture and identification) or the absence of some males during behavioural tests. Therefore, we fitted sex-specific models including as fixed effects individual's aggressiveness, boldness and neophobia scores, as well as age (yearling vs. older) and the deviance to equal proportion in symbols on empty nest boxes within the forest patch on the day of flycatcher choice, which was the only environmental variable shown to influence the probability of copying tit apparent preference in this experimental set-up in this population (Chapter 3). We also included all two-way interactions between age and each personality trait. Finally, we included the

forest patch as a random factor to control for potential spatial effects on social information use. We also fitted the sex-specific models without boldness and neophobia scores (and the corresponding interactions) because 57% out of 452 individuals could be measured for aggressiveness but not boldness and neophobia due to early breeding failure, absence during the first period of the boldness/neophobia test or time constraints in the field. Prior to analyses, boldness score was log-transformed and inversed, to ease interpretation (i.e. match higher score values with lower latencies), and both aggressiveness and boldness were standardized and centred on zero to ease comparison between effects. Neophobia score, with integer values between 0 and 5, was kept untransformed and considered as a continuous variable.

Preliminary models including year (2012 or 2013) as an additional fixed effect revealed that the probability to copy tit apparent preference strongly depended on year (see also Chapter 3). Collared flycatchers were more likely to copy tit apparent preference in 2012 and to reject it in 2013 (Table 5.2). To account for this difference, we included as fixed effects variables measuring the great tit presence and early reproductive investment at the time of flycatcher settlement, because they are known to be used as social information sources by flycatchers in settlement decisions (Forsman et al. 2008, Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013) and they markedly differed between the two years of the study. Great tit density was higher in 2012 than in 2013, and the number of eggs or chicks present in great tit nests when flycatchers chose their nest sites (later referred to as “tit clutch / brood size”) was much lower in 2013 than 2012 (Table 5.2). There was no overall difference in final great tit reproductive investment (clutch size) between 2012 and 2013, but great tits started breeding later than usual in 2013, leading to a small apparent average clutch size when flycatchers settled (Table 5.2). For each flycatcher pair, tit density was estimated here as the proportion of nest boxes occupied by great tits (i.e. with tit nest material) on the day of flycatcher nest box choice, because nest box density was fairly similar between forest patches (distributed approx. every 20 to 30 m). Tit clutch / brood size was averaged within the forest patch on the day of flycatcher nest box choice. Year was also included as a random effect to control for other

possible sources of difference between years that we could not control for.

Models were fitted within the Bayesian framework in R (R Core Team 2015) with the *MCMCglmm* function (“MCMCglmm” R package, Hadfield 2016). The probability to copy tit apparent preference (i.e. copy vs. reject) was fitted with a threshold family, setting the residual variance to 10 instead of the usual value 1 to ease the mixing of the MCMC chains (Hadfield 2016). Wide Normally distributed priors were used for fixed effects (large variance $V=10^8$; Hadfield 2016) and parameter expanded χ^2 distributed priors with 1 degree of freedom for random effects. We used 150 000 iterations, with a burn-in of 1 000 and a thinning interval of 60, to obtain final effective sample sizes greater than 1 800. We checked for the absence of autocorrelation, and visually controlled the convergence of the chains. Fixed effects with a 95% Credible Interval (CI) not encompassing zero were successively removed (starting with effects whose 95% CI was most centred around zero). To detect potential type I errors, which are more likely to occur when using such a stepwise method (Mundry and Nunn 2009, Forstmeier et al. 2017), we compared the final models to the full models, as well as to the ‘best’ models based on a DIC comparison, using the relative importance (RI) of each variable assessed with the *model.avg* function (“MuMIn” R package, Barton 2016) over the set of ‘best’ models (i.e. whose DIC value was less than 2 above the model with the lowest DIC value). See Tables A.5.1 and A.5.2 for the full results of the different model selection procedures.

5.3 Results

Male personality traits and probability to copy tit apparent preference

In males, the probability to copy tit apparent preference was affected by both tit clutch / brood size and density, but these effects were modulated by male aggressiveness score (significant interactions with aggressiveness score; Table 5.3). Males were more likely to

copy tit preference when tit clutch / brood size was high (Table 5.3), but only aggressive males rejected tit preference when clutch size was low (Table 5.3; Figure 5.1a). In addition, only less aggressive males showed an increased probability to copy tit apparent preference when tit density was high (Table 5.3, Figure 5.1b); there was no overall effect of tit density (Table 5.3). Male neophobia and boldness scores did not affect the probability to copy tit apparent preference (Table A.5.1, 95%CI = [-8.99; 2.11] and [-3.97; 0.33] respectively). When restricting the personality traits investigated to aggressiveness score alone (see Methods), the probability to copy tit apparent preference increased with increasing tit clutch / brood size only in older males (Table A.5.1, Figure A.5.1) and with male aggressiveness (Table A.5.1). Overall, yearlings were more likely to copy tit preference than older males (Table A.5.1). Forest patch and year had no effect on male probability to copy tit preference (random term variances not different from zero; Table 5.3 and Table A.5.1 for the full model outputs).

Female personality traits and probability to copy tit apparent preference

In females, only tit clutch / brood size affected the probability to copy tit apparent preference (positive effect similar to the model for males; 95% CI = [0.15; 0.68]; Table A.5.2). None of the three personality traits (aggressiveness, boldness and neophobia scores) affected the probability to copy tit preference in females (Table A.5.2). As for males, forest patch and year did not explain any part of the variance of the probability to copy tit preference (Tables A.5.2).

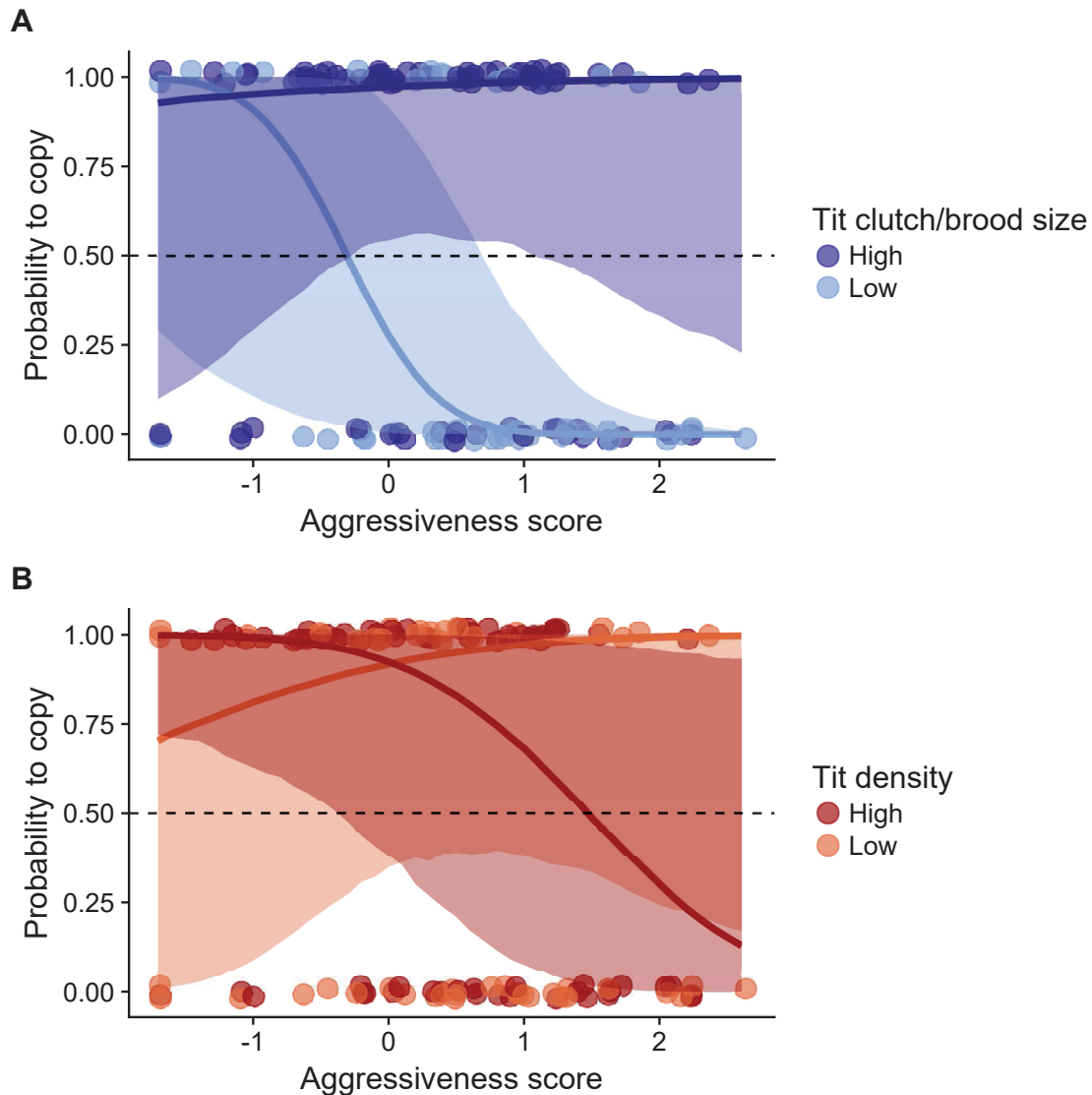


Figure 5.1: *Posterior probability for flycatchers to copy tit apparent preference depending on male aggressiveness score and (A) tit clutch/brood size and (B) tit density in the forest patch at the time of flycatcher settlement. Data points show actual choices (copy = 1 / reject = 0); lines show posterior means of estimates and areas around the lines show the corresponding 95% CI, derived from the final selected model (Table 5.3). (A) Low and high tit clutch/brood size correspond to the 1st and 3rd quartile values respectively (the illustration is for an average tit density, i.e. 0.3). (B) Low and high tit density correspond to the 1st and 3rd quartile values respectively (the illustration is for an average tit clutch/brood size, i.e. ~6.7). See Figure A.5.2 for illustration of the model outputs for other combinations of tit density and clutch / brood size values.*

Table 5.3: *Influence of male aggressiveness score, tit clutch / brood size (c/b) and tit density on the probability to copy tit apparent preference of nest box artificial features. Stars indicate the variables which 95% CI does not encompass zero. We provide the minimum effective sample size of the posterior distributions and the sample size of the raw data (N).*

	Model with male personality	
	Post. mode	95% CI
Fixed effects		
Intercept	-1.39	[-5.39 ; 1.94]
male aggressiveness	0.37	[-1.88 ; 3.56]
tit clutch/brood (c/b) size	0.46	[0.11 ; 0.81] *
tit density	0.80	[-10.03 ; 11.90]
male aggressiveness : tit c/b size	0.39	[0.09 ; 0.73] *
male aggressiveness : tit density	-11.59	[-21.84 ; -2.61] *
Random effects		
forest patch	0.01	[0.00 ; 2.41]
year	0.01	[0.00 ; 2.88]
<i>Effective sample size</i>		> 2 483
<i>N</i>		121

5.4 Discussion

We have experimentally shown in a wild bird population that the use of heterospecific social information for nest site selection (measured here as the propensity to copy an apparent preference of heterospecific competitors for a nest site feature) depended on both individual factors, here male personality (aggressiveness) as well as male age, and on environmental factors, here the density and early reproductive investment of the heterospecific tutors. Overall, flycatchers were more likely to copy tit apparent preference when average tit clutch / brood size in the patch at the time of nest site choice, reflecting tit early reproductive investment, was high. This is in line with previous results (Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013) and suggests that flycatchers adjusted the use of this heterospecific social information source depending on tit tutors' fitness prospects or timing of reproduction. Nevertheless, this effect was modulated by male aggressiveness score, because only aggressive males rejected tit apparent preference when tit clutch / brood size was small. In addition, less aggressive males were more likely to copy tit apparent preference when tit density was high in the patch at the time of nest site choice. Finally, yearling males were more likely to copy tit preference and did not adjust their behaviour depending on the tit clutch / brood size, compared to older ones. This could reflect their more limited personal information, in line with female age differences in copying behaviour reported in pied flycatchers (Forsman et al. 2012). Conversely, female personality did not affect the probability to copy tit apparent preference. In terms of personality traits, the joint copying behaviour of the pair was therefore affected only by male aggressiveness, and this effect might result from its effect on information availability and/or on the competition costs associated with the decision to copy or reject tit preference once information has been acquired.

Copying behaviour depending on male aggressiveness

Our results provide clear evidence that aggressiveness, i.e. the agonistic reaction towards competitors, can shape the use of heterospecific social information. Overall, increasing male aggressiveness is associated with increasing rejection of tit apparent preference. Aggressive individuals may be more prone to engage in agonistic interactions with other individuals, including heterospecifics, and this may affect the ability to acquire social information. In particular, the physical proximity to the source of social information likely increases the quality of information gathered in most cases but it also increases the risk of agonistic interactions. For migratory flycatchers, the density and reproductive investment of resident tits are sources of information for breeding habitat selection (e.g. Seppänen and Forsman 2007, Forsman et al. 2009, Loukola et al. 2013, Kivelä et al. 2014) but acquiring information about clutch size in tit nests poses a mortal risk (Merilä and Wiggins 1995, Forsman and Thomson 2008, Forsman et al. 2018). Only more aggressive males may be willing to engage in such risky behaviours and thus may have access to information on tit clutch / brood size, leading to their adjustment of copying behaviour according to tit reproductive investment. In contrast, less aggressive individuals may avoid interactions with tits, and rather adjust their decision depending on cues that can be acquired from a distance, such as tit density. Compared to other information sources such as tit reproductive investment, the symbol associated with nest box occupied by tits can be observed from a distance, thereby minimizing the risks of agonistic interactions with tits, and could for this reason be preferred by less aggressive individuals, especially when associated with high tit density. Overall, aggressiveness could affect both the quantity and quality of social information available to individuals for decision-making.

An alternative (but not mutually exclusive) explanation could be that the negative effect of aggressiveness on the probability to copy tit preference resulted from differential decision-making according to aggressiveness level once information has been gathered. Using the same source of social information may lead individuals (here flycatchers) to make similar choices and thus increase intraspecific competition. Copying tit preference

may also result in increased interspecific competition through possible niche overlap. The relative costs of both intra- and interspecific competition may differ according to aggressiveness level, such that more aggressive individuals might pay higher relative costs and therefore try and avoid these costs by rejecting tit preference more often. Although this may seem counterintuitive in the first place, more aggressive individuals may engage more often into agonistic interactions and thereby pay a larger cost compared to non-aggressive individuals. This situation would be in line with previous results reporting great tits to avoid niche overlap with flycatchers even though they are dominant over flycatchers (Forsman et al. 2014).

No influence of other male personality traits

Boldness did not seem to influence the probability to copy tit apparent preference here. Former studies on the link between boldness and social information use reported highly contrasted results (Tables 5.1, and 1.1 in Chapter 1). In guppies and sticklebacks, shy individuals were more likely to shoal and follow others (Ward et al. 2004, Dyer et al. 2008, Croft et al. 2009), which was suggested to be the result of higher attention paid to, and higher probability to rely on, others' decisions. Another study on sticklebacks however found no support for boldness to affect the propensity to use three different types of social information, even though shy individuals took more time to make decisions than bold ones, presumably weighing information differently (Harcourt et al. 2010). In chacma baboons (*Papio ursinus*), bold individuals paid more attention to others, but shy ones handled novel food items (previously handled by conspecifics) for longer (Carter et al. 2014). The effect of boldness on social information use may be strongly dependent on the context and in particular on social organisation. Here, because the risks associated to heterospecific social information gathering and use were mostly due to agonistic reactions from con- and/or heterospecifics, boldness may not be involved in this process.

More surprisingly given the many studies in different taxa reporting higher social information use for more neophobic and less explorative individuals (Tables 5.1 and 1.1),

we also found here no effect of male neophobia on the probability to copy tit apparent preference. Flycatchers are known to prospect information all along the breeding season (Pärt and Doligez 2003, Doligez et al. 2004, Forsman and Thomson 2008), and larger prospecting area has previously been suggested to favour longer dispersal distances because of a better knowledge and easier comparison of alternative breeding sites (Badyaev et al. 1996). Thus increased exploration, which could be reflected here in decreased neophobia (Réale et al. 2007), could be expected to favour the use of large-scale social information as here. The absence of effect of neophobia on the probability to copy tit preference suggests that neophobia does not shape the ability of individuals to collect social information in our population. Testing this hypothesis would require directly assessing prospecting behaviour according to exploration / neophobia level.

No influence of female personality traits

Here, only male aggressiveness affected the probability to copy tit preference for nest site selection, i.e. a joint behaviour by both pair members: none of the female personality traits influenced copying probability. This could suggest that males play a predominant role in the nest site choice of the pair at a small scale, which would be in line with the idea that males gather and use information at smaller scales compared to females in this species (see Discussion in Chapter 3). Importantly, we estimated here aggressiveness, boldness and neophobia scores of both pair members simultaneously at their nest box. The design of our behavioural tests thus implied that both pair members could see each other, interact directly during the tests and adjust their own behaviour depending on the behaviour of their mate. In line with this, we showed in a previous study that flycatchers were more aggressive when their mate was also present around the box during the aggressiveness test (but not testable for boldness and neophobia, see Chapter 4). Another study also reported that an individual's behavioural response towards a neighbouring fish could be affected by the neighbour's personality (Jolles et al. 2015). Such a mutual influence from breeding partners or neighbouring individuals could lead to trait enhancement or in-

hibition depending on whether individuals distribute themselves heterogeneously in space according to their personality traits (e.g. in great tits, Johnson et al. 2017). Future work is needed to understand the influence of other individuals' (including mates) behavioural responses on the measure of personality traits and their role in social information use for breeding site selection.

Modulation of heterospecific social information using tutors' investment and quality

The increase in the probability to copy tit preference with increasing local tit clutch / brood size suggests that flycatchers can estimate average tit reproductive investment at the patch scale at the time when they settle and use it for modulating nest site choice according to tit apparent preference. This is in line with former experimental results at a smaller scale, showing that pied flycatchers use tit clutch size as social information to choose between two close-by nest boxes according to the symbol associated to tit nest (Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013) but also to adjust breeding investment later on (Forsman et al. 2012). Another study showed that pied flycatcher females preferably settled in forest patches where tit phenology had been experimentally advanced compared to delayed (Samplonius and Both 2017). Because variation in tit phenology could have been reflected in tit reproductive investment (clutch / brood size) at the time when flycatchers arrive from migration, pied flycatcher females may have used tit clutch size as the proximate information source in this study. In our population, the difference between the two years of the study in the overall probability to copy could be explained by the difference in tit phenology between years (Table 5.2): due to very cold temperatures in March 2013 compared to 2012 (mean daily temperature \pm SD: $-3.1^{\circ}\text{C} \pm 2.7$ in 2013, $3.1^{\circ}\text{C} \pm 3.4$ in 2012), tit laying date in spring 2013 was so late that arriving flycatchers perceived low clutch size in most tit nests, leading to an overall rejection of tit preference as a result of low performance (Chapter 3). Flycatchers

may also have used other sources of information, such as tit quality or body condition, even though the cold weather in 2013 affected neither the final average tit clutch size (Table 5.2) nor tit body mass or condition (Table 5.2). Overall, our results provide clear evidence that flycatchers modulated their use of heterospecific social information obtained from tit apparent preference for nest site features with other information sources (here tit density and early reproductive investment), and that this modulation could depend on their personality traits (here male aggressiveness). More work is needed to understand the mechanisms underlying the effect of personality on the relative use of different social information sources.

Our study extends the importance of personality traits in shaping the availability and use of social information reported in previous studies to the context of breeding habitat selection in the wild, using a powerful experimental manipulation of social information. The joint copying behaviour of the pair was most likely constrained by the intra- and interspecific competitive costs related to social information use, explaining the role of male aggressiveness. Further studies will be needed to (i) test whether male personality influences nest site selection by constraining information availability to the pair and/or shaping the decisions made based on similar information, (ii) assess the relative importance of both processes and (iii) test whether they can be modulated by other information sources such as tutors' reproductive investment. This would help understanding the selective pressures acting on personality in relation to breeding habitat selection.

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Authors contribution

BD and JTF designed the study; GD, MG, BD and many assistants carried out the fieldwork; JM analysed the data, and drafted the manuscript. JM, JTF, and BD critically revised the manuscript.

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5.6 Appendix

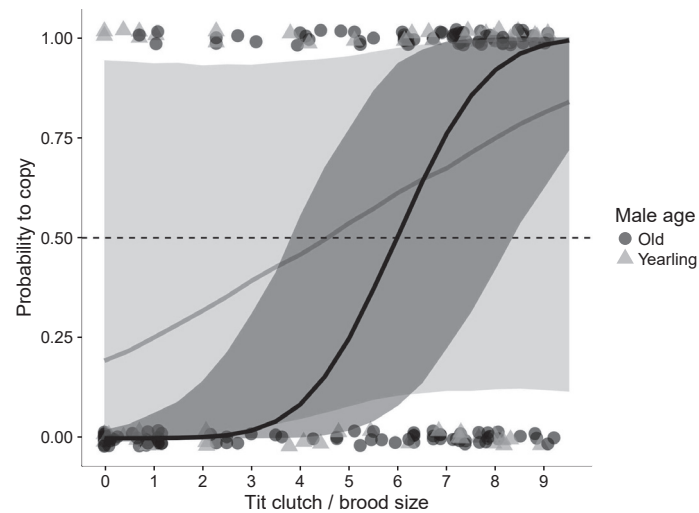


Figure A.5.1: *Posterior probability for flycatchers to copy tit apparent preference given tit clutch/brood size within the forest patch and male age (Yearling vs. older). We provide the posterior mean (line) and 95%CI (shades) of the posterior distribution.*

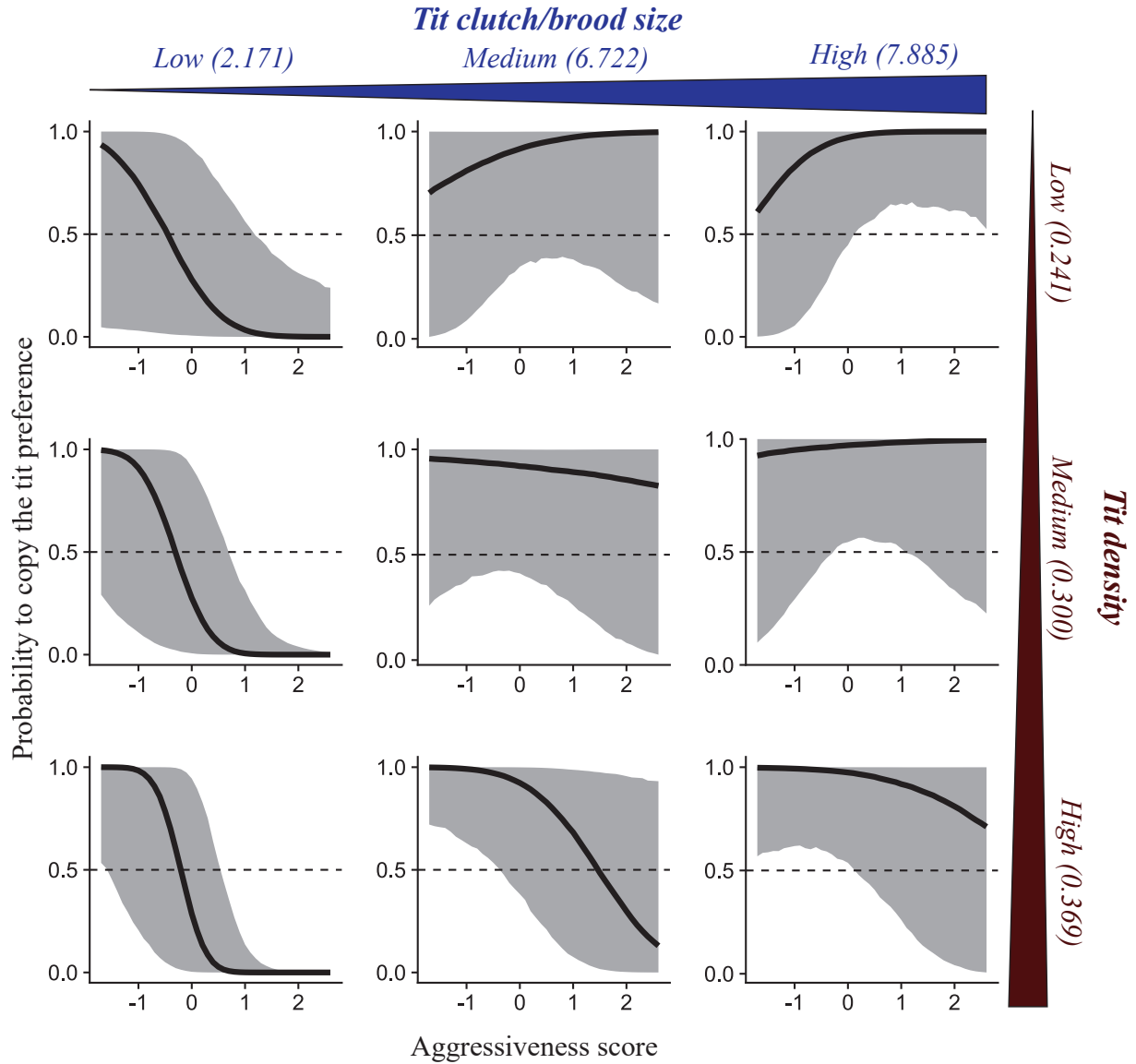


Figure A.5.2: *Posterior probability for flycatchers to copy tit apparent preference given male aggressiveness score for different levels of tit clutch/brood size and density in the patch at the time of flycatcher settlement. We provide the posterior mean (line) and 95%CI (shades) of the posterior distribution for each 0.025, 0.5, and 0.975 quantile of tit clutch/brood size (in blue, respectively 2.171, 6.722 and 7.885 eggs/chicks) and of tit density (in red, respectively 0.241, 0.300 and 0.369 % of nest boxes occupied by tits).*

Table A.5.1: Results (posterior mode and 95% CI) of the models exploring the influence of **male** personality traits, tit clutch/brood size (c/b), tit density and other factors on the probability to copy tit apparent preference. For the age effect, the estimate is given for the yearling category compared to older. The residual variance was set to 10. Values in bold indicate estimates which 95% CI does not encompass zero. † among 14 models with DIC < 2 compared to the model with the lowest DIC, computed using the dredge and model.avg functions (“MuMIn” R package, Barton 2016)

	Final selected model		Full model		Only aggressiveness		DIC comparison
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI	Relative importance†
Fixed effects							
Intercept	-1.39	[-5.39 ; 1.94]	3.11	[-7.63 ; 13.76]	-3.94	[-5.85 ; -1.71]	
age (yearling)			-0.27	[-9.64 ; 8.29]	2.87	[0.72 ; 6.05]	0.92
aggressiveness	0.37	[-1.88 ; 3.56]	-3.98	[-8.06 ; 1.71]	-1.42	[-3.00 ; -0.31]	1.00
boldness			-3.64	[-8.99 ; 2.11]			0.04
neophobia			-1.55	[-3.97 ; 0.33]			0.21
tit c/b	0.46	[0.11 ; 0.81]	0.57	[-0.40 ; 1.35]	0.59	[0.35 ; 0.94]	1.00
tit density	0.80	[-10.03 ; 11.90]	-9.13	[-36.11 ; 9.00]			1.00
dev.symbol			3.97	[-16.53 ; 15.84]			0.05
age : aggressiveness			1.97	[-0.69 ; 4.66]			0.41
age : boldness			3.29	[-0.99 ; 5.41]			
age : neophobia			-0.58	[-1.97 ; 0.50]			
aggressiveness : boldness			-0.16	[-2.03 ; 1.65]			
aggressiveness : neophobia			0.51	[-0.01 ; 1.13]			0.04
boldness : neophobia			0.23	[-0.38 ; 0.98]			
age : tit c/b			-1.11	[-1.84 ; -0.06]	-0.49	[-0.97 ; -0.08]	0.70
age : tit density			24.20	[-8.98 ; 56.08]			0.46
aggressiveness : tit c/b	0.39	[0.09 ; 0.73]	0.89	[0.36 ; 1.37]	0.25	[0.02 ; 0.45]	1.00
boldness : tit c/b			-0.02	[-0.64 ; 0.44]			
neophobia : tit c/b			0.07	[-0.15 ; 0.30]			
aggressiveness : tit density	-11.59	[-21.84 ; -2.61]	-14.53	[-27.79 ; -2.64]			1.00
boldness : tit density			9.61	[-6.38 ; 19.22]			
neophobia : tit density			4.46	[-1.51 ; 10.02]			
Random effects							
forest patch	0.01	[0.00 ; 2.41]	0.01	[0.00 ; 3.01]	0.01	[0.00 ; 1.03]	
year	0.01	[0.00 ; 2.88]	0.02	[0.00 ; 3.17]	0.01	[0.00 ; 2.63]	
Effective sample size	> 2 483		> 1 926		> 1 937		
N	121		121		205		121

Table A.5.2: *Results (posterior mode and 95% CI) of the models exploring the influence of **female** personality traits, tit clutch/brood size (“tit c/b”), tit density, and other factors on the probability to copy tit apparent preference. The estimate is given for the yearling category for the age effect. The residual variance was set to 10. Values in bold indicate estimates which 95% CI does not encompass zero. † among 46 models with DIC < 2 compared to the model with the lowest DIC, computed using the dredge and model.avg functions (“MuMIn” R package, Barton 2016)*

	Final selected model		Full model		Only aggressiveness		DIC comparison
	Post. mode	95% CI	Post. mode	95% CI	Post. mode	95% CI	Relative importance†
Fixed effects							
Intercept	-2.05	[-4.27 ; -0.30]	-4.26	[-19.30 ; 6.64]	-1.46	[-3.29 ; 0.14]	
age (yearling)			4.67	[-2.62 ; 11.79]	0.37	[-0.70 ; 1.35]	0.98
aggressiveness			3.86	[0.02 ; 7.71]			1.00
boldness			0.26	[-4.24 ; 3.15]			0.28
neophobia			-1.68	[-3.67 ; 0.21]			1.00
tit c/b	0.35	[0.15 ; 0.68]	1.14	[0.34 ; 2.07]	0.23	[0.06 ; 0.47]	1.00
tit density			-24.35	[-56.55 ; -1.82]			1.00
dev.symbol			15.14	[-1.98 ; 35.57]			0.72
age : aggressiveness			1.00	[-0.92 ; 2.64]			0.22
age : boldness			0.16	[-0.96 ; 2.41]			
age : neophobia			0.09	[-0.99 ; 1.16]			0.02
aggressiveness : boldness			-0.21	[-1.17 ; 0.56]			
aggressiveness : neophobia			-0.30	[-0.83 ; 0.15]			0.74
boldness : neophobia			0.51	[-0.16 ; 1.01]			0.14
age : tit c/b			-0.52	[-1.14 ; 0.10]			0.25
age : tit density			-1.99	[-16.94 ; 18.34]			0.02
aggressiveness : tit c/b			-0.18	[-0.50 ; 0.12]			0.09
boldness : tit c/b			-0.06	[-0.35 ; 0.22]			
neophobia : tit c/b			-0.10	[-0.34 ; 0.07]			0.68
aggressiveness : tit density			-10.63	[-17.60 ; 0.29]			0.95
boldness : tit density			-1.04	[-10.22 ; 6.30]			
neophobia : tit density			6.90	[1.85 ; 13.93]			
Random effects							
forest patch	0.00	[0.00 ; 1.02]	0.01	[0.00 ; 3.27]	0.00	[0.00 ; 0.78]	
year	0.01	[0.00 ; 2.57]	0.01	[0.00 ; 4.09]	0.01	[0.00 ; 2.77]	
Effective sample size	> 2 483		> 2 204		> 1 804		
N	138		138		247		138

Chapter 6

Great tit song: another source of social information for flycatchers



Song traits associated to singer quality as heterospecific social information for nest site selection

Jennifer Morinay, Jukka Forsman, Blandine Doligez

Article in preparation

Keywords: social information, signal, eavesdropping, bird song, heterospecific competition, individual quality, personality, aggressiveness, collared flycatcher, great tit

Abstract

Assessing local habitat quality via social cues provided by con- or heterospecific individuals sharing the same needs is a widespread strategy of social information use for breeding habitat selection. However, gathering information about the competitors may involve agonistic costs. The use of cues allowing individuals to predict local success in the short-term from a distance, such as acoustic cues, should therefore be favoured. Bird songs are conspicuous signals commonly assumed to reliably reflect producer quality, and thereby local site quality. Birds of different species have been shown to be attracted to breeding sites by heterospecific songs, but it is unknown whether they can use heterospecific song fine features as information on the producer- (and by extension habitat-) quality. Using a playback experiment in a wild population of collared flycatchers (*Ficedula albicollis*), a species known to eavesdrop on dominant great tit (*Parus major*) presence and performance, we tested whether flycatchers preferred to settle near broadcasts mimicking the presence of a high quality great tit (songs with large repertoire size, long strophes, high song rate), a low quality great tit or a chaffinch (control). Among old females, aggressive ones preferred to settle near broadcasts of high quality tit song and avoided broadcasts of low quality tit song, while less aggressive old females preferred to settle near broadcasts of low quality tit song. Male personality or age did not influence settlement decisions. Our results show that collared flycatcher females use great tit song quality-features as information for settlement decisions, but differently depending on their own competitive ability and/or previous experience with great tit songs. Our study therefore enlightens the complex condition-dependent use of heterospecific social information for breeding habitat selection.

6.1 Introduction

When habitat quality varies in time and space, choosing where to breed might have crucial consequences for individual fitness. Hence, strong selective pressures must promote behavioural strategies allowing individuals to optimize habitat selection decisions. In particular, individuals can collect and use information about habitat quality to choose among alternative breeding sites or patches (Danchin et al. 2004, Dall et al. 2005). Such information can be acquired from the individual's own interactions with its environment, i.e. its personal experience ('personal information', e.g. its own reproductive success, Switzer 1997). Alternatively, information can be acquired from observing other individuals interacting with the environment and the result of their actions, either inadvertently or when they intentionally communicate with others ("social information", e.g. Coolen et al. 2005; Danchin et al. 2004, Dall et al. 2005).

When cueing on others, individuals can rely on the mere presence of con- or heterospecifics (patch / site occupancy or density, Thiebault et al. 2014), an information that can be easily accessible but does not directly inform on the fitness correlates of others' actions. Individuals can also use the performance of others, i.e. the success obtained after making a decision, an information that can be more difficult to access but is supposed to better inform about the fitness correlates of the decision. Yet, if this information is available, it can be used only after a delay, which in the context of breeding habitat selection, can be a whole breeding season (Boulinier et al. 2008). When breeding synchrony with individuals sharing similar needs (either con- or heterospecific competitors) is low, eavesdropping on the reproductive investment of early competitors could inform on habitat quality for decisions later in the same season (e.g. clutch size in birds, Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013). However, assessing competitors' performance can in particular involve gathering information close to their breeding sites and can therefore increase the risk of agonistic interactions, especially in territorial species (e.g. Merilä and Wiggins 1995, Forsman et al. 2018). Individuals thus have to trade information accuracy and reliability in predicting future fitness against information availability and

the costs associated to information gathering. Consequently, selective pressures should favour the use of cues reflecting the performance of others that can be obtained to a lower cost than a direct assessment, such as cues obtained from a distance.

Among such cues, acoustic signals have been shown to be an information source easily eavesdropped on, even from a long distance (e.g. anti-predatory strategies involving eavesdropping on conspecific and heterospecific alarm calls; reviewed in Magrath et al. 2015). Experimental studies have clearly shown that calls and, in birds, songs can, on their own, induce conspecific (Hahn and Silverman 2006) and heterospecific attraction (Fletcher 2008, Szymkowiak et al. 2017) to otherwise empty breeding sites, a property often used in reintroduction programmes to enhance local settlement of released animals (e.g. in Black capped vireo, Ward and Schlossberg 2004). Importantly, signals used in sexual communication, which include acoustic signals, should be selected (1) to be conspicuous, allowing emitters to be detected by the highest possible number of potential partners (in intersexual communication) and/or competitors (in intrasexual communication), and (2) to reliably reflect individual quality (e.g. in terms of health, competitive ability, etc.; Andersson 1994, Catchpole and Slater 2008). Female birds have for example been shown to eavesdrop on males singing contests and adjust mate choice and reproductive behaviour accordingly (Otter et al. 1999, Mennill et al. 2002). Therefore, acoustic signals could provide social information on individual quality and both past and current condition (Møller 1991, e.g. Buchanan and Catchpole 2000, Bischoff et al. 2009), indirectly informing on habitat / territory quality in terms of predator risks or parasitic load for example. This more specific type of eavesdropping behaviour could occur not only within species, but also between species, which has not been explored yet.

Using a playback experiment in a wild population of collared flycatchers *Ficedula albicollis*, we experimentally tested whether individuals use songs from heterospecific competitors as a source of information for nest site selection and whether they modulate the use of this cue depending on song features, reflecting the quality of its emitter. Migratory flycatchers are known to use different heterospecific social information from their main competitor, the resident great tit *Parus major*, for nest site selection (tit presence: Kivelä

et al. 2014; tit density: Forsman et al. 2008; tit early reproductive investment: Seppänen et al. 2011, Loukola et al. 2013; Chapter 1). Prospecting tit nests to gather information on tit presence or reproductive investment may nevertheless be risky (Merilä and Wiggins 1995, Forsman and Thomson 2008, Forsman et al. 2018). Therefore, flycatchers could be expected to rely also on less costly cues, such as great tit songs, which can be heard from a distance and whose characteristics (repertoire size and strophe length) have been shown to correlate with great tit quality (McGregor et al. 1981, Lambrechts and Dhondt 1986). Upon flycatchers' arrival from migration, we broadcasted artificially created great tit songs of either high quality (large repertoire, long strophes, high song rate) or low quality (small repertoire, short strophes, lower song rate) in experimental zones with available nest boxes and monitored flycatchers' settlement in these zones. If flycatchers are attracted by great tits songs when choosing where to breed, they should settle preferentially in patches with broadcasted songs; in addition, if flycatchers use information about great tit quality contained in song, they should settle preferentially in patches where we broadcasted high quality tit songs, i.e. presumably in 'high quality habitat'. We also tested whether the nest site choice near a specific song treatment depended on flycatchers' age and aggressiveness, which may affect their previous experience with great tit songs and their ability to sustain competitive costs with great tits, respectively. Finally, we tested whether flycatchers adjusted early reproductive investment according to the experimental treatment, as previously found in this population (in reaction to tit density, Forsman et al. 2008).

6.2 Material and Methods

Study area and population monitoring

The experiment was conducted in spring 2017, in a patchy population of collared flycatchers breeding on the island of Gotland (Sweden, Baltic Sea). In this population, collared flycatchers, dominant great tits and blue tits (*Cyanestes caeruleus*) partly share

the same ecological niche, and breed in tree cavities or, in the study area, nest boxes provided in excess for these hole-nesting species. Collared flycatchers start arriving from migration on the breeding grounds late April-early May, *c.a.* 2 weeks on average after the beginning of tit settlement. Every year, approx. 1/3 of the nest boxes available in the population are occupied by collared flycatchers, 1/3 by tits (among which 3/4 are great tits) and 1/3 remain empty. In all occupied nest boxes, we captured flycatcher females during incubation and males during the chick rearing period. All captured individuals were identified (or ringed if previously unringed), measured, weighed and aged based on plumage criteria (yearlings vs. older adults; Svensson 1992). Nest boxes were then visited throughout the breeding season to record the main breeding variables for each breeding pair: laying date, clutch size, number of hatchlings, and number of fledglings.

Playback experimental design

Within 13 forest patches, which contained 47 to 182 nest boxes each, we established experimental zones composed of 5 neighbouring nest boxes spread in a circular area of approx. 50m diameter and separated from each other by at least 30 m (i.e. each zone was surrounded by at least one row of non-experimental nest boxes). Each forest patch contained 3 to 9 experimental zones, for a total of 58 experimental zones. We conducted the playback experiment between the 29th of April and the 27th of May, i.e. during the whole period of flycatcher settlement. During these 29 days, we broadcasted at the centre of each experimental zone either (i) a great tit song track with song features of high quality individuals (i.e. large repertoire and high strophe rate, McGregor et al. 1981, Lambrechts and Dhondt 1986, Rivera-Gutierrez et al. 2010), (ii) a great tit song track with song features of low quality individuals (i.e. with a small repertoire size and short strophe length) or (iii) a song track from a species with no a priori influence on flycatcher settlement decisions (the chaffinch, *Fringilla coelebs*), as a control. For each experimental zone, the treatment (i.e. nature of the song track broadcasted) remained unchanged during the whole broadcasting period.

Song tracks were broadcasted from dawn (1 hour before sunrise) for a duration of 17

hours. Along the broadcasting period, the starting hour of the broadcast was adjusted (15 minutes earlier every 10 days) to match the seasonal change of dawn hour, but the length of the track remained unchanged, thus the playback gradually stopped earlier over the period (at dusk late April, and up to 1h30 before dusk late May). Tracks were broadcasted at ~85-95dB, i.e. close to the natural sound amplitude of great tit songs (McGregor and Horn 1992; sound amplitude checked at 1m with a sound level meter “Dr. Meter MS10”). In each experimental zone, song track was broadcasted from a camouflaged Loudspeaker (Zealot S1) attached 1.5-2 m above ground on a tree next to the central nest box of the zone.

Playback song structure

To create the broadcasted sound tracks while avoiding pseudoreplication, we used songs from 4 different great tits to mimic songs of high quality tits, from 4 others to mimic songs of low quality tits and from 4 different chaffinches for controls. Great tit songs had been recorded in the same population in 2016, at dawn chorus, with a SENNHEISER MKH70 microphone and a ZOOM H4N recorder. Chaffinch songs had been recorded on Gotland in 2016 (1 individual) and on the Swedish mainland and available on-line (Xeno Canto on-line database, www.xeno-canto.org, accessed in April 2017; recordings ID: XC84011, XC196974, and XC27602). A sound track was composed of songs originating from only one individual to mimic the presence of a single individual in each experimental zone and avoid mixing signals in case flycatchers were able to individually recognize songs. All recordings were in .wav format to ensure sufficient sound quality and had a sample frequency of 44.1 kHz and a resolution of 16 bit. Using Audacity software (v. 2.1.0, <http://audacity.sourceforge.net/>), original recordings were high-pass filtered with a threshold below the song minimum frequency (2 kHz), modified to create the song bouts (see below) and amplified to reach 80-95dB at one meter distance from the loud speakers. We amplified whole song bouts (see below) but kept natural variations in amplitude within bouts, to mimic bird movement while singing.

To match the natural singing activity of great tits, we broadcasted 10 minute-long song

periods every 30 minutes from dawn to 3 hours after dawn, and then every hour till the end of the sequence (around dusk, see above; Figure 6.1a), similarly to Krebs et al. (1978). A song period was composed of successive song bouts. A great tit song bout was defined as a succession of strophes, all of which composed here of a unique syllable type, thus defining a song type. Depending on the great tit consistency in singing, the syllables within a strophe slightly varied in rhythm, amplitude, and, before transformation, in length. To change strophe length, we duplicated or deleted syllables. Song tracks mimicking songs of high quality tits had a large repertoire (i.e. a high number of song types, here 5 song types; colour shades in Figure 6.1b), long strophes (4 seconds), produced at a high rate (one strophe every 8 seconds; Figure 6.1b). Tracks mimicking songs of low quality tits had a small repertoire (2 song types colour shades in Figure 6.1c), short strophes (2 seconds), produced at a low rate (one strophe every 11 seconds; Figure 6.1c). A chaffinch song bout was defined as a succession of strophes with the same rate (one strophe every 11 seconds; two different strophes recorded per individual) than low quality great tit songs, and composed of a fixed syllable structure that could vary between individuals but was quite conserved within individuals.

Controlling for neighbouring live great tits

To keep nest boxes in the experimental zones available to flycatchers and avoid songs from live great tits to interfere with our broadcasted songs, we prevented great tits (but not blue tits) to settle in our experimental zones early April by narrowing nest box entrance hole of each nest box in an experimental zone to 28mm diameter. We did not block the nest box completely to let the blue tit choose freely, as part of another experiment. At the beginning of the broadcasting period, i.e. on the 29th of April, we expanded again the nest box entrance hole to 32mm diameter (preferred size of for flycatchers, Prof. Lars Gustafsson pers. comm.). As a consequence, blue tits and late great tits could settle in the experimental zones. In that case, to ensure that the first flycatchers in each zone always had 5 available nest boxes near the loudspeakers, we readjusted whenever possible the position of our experimental zones by relocating the entire zone 1 nest box away, and

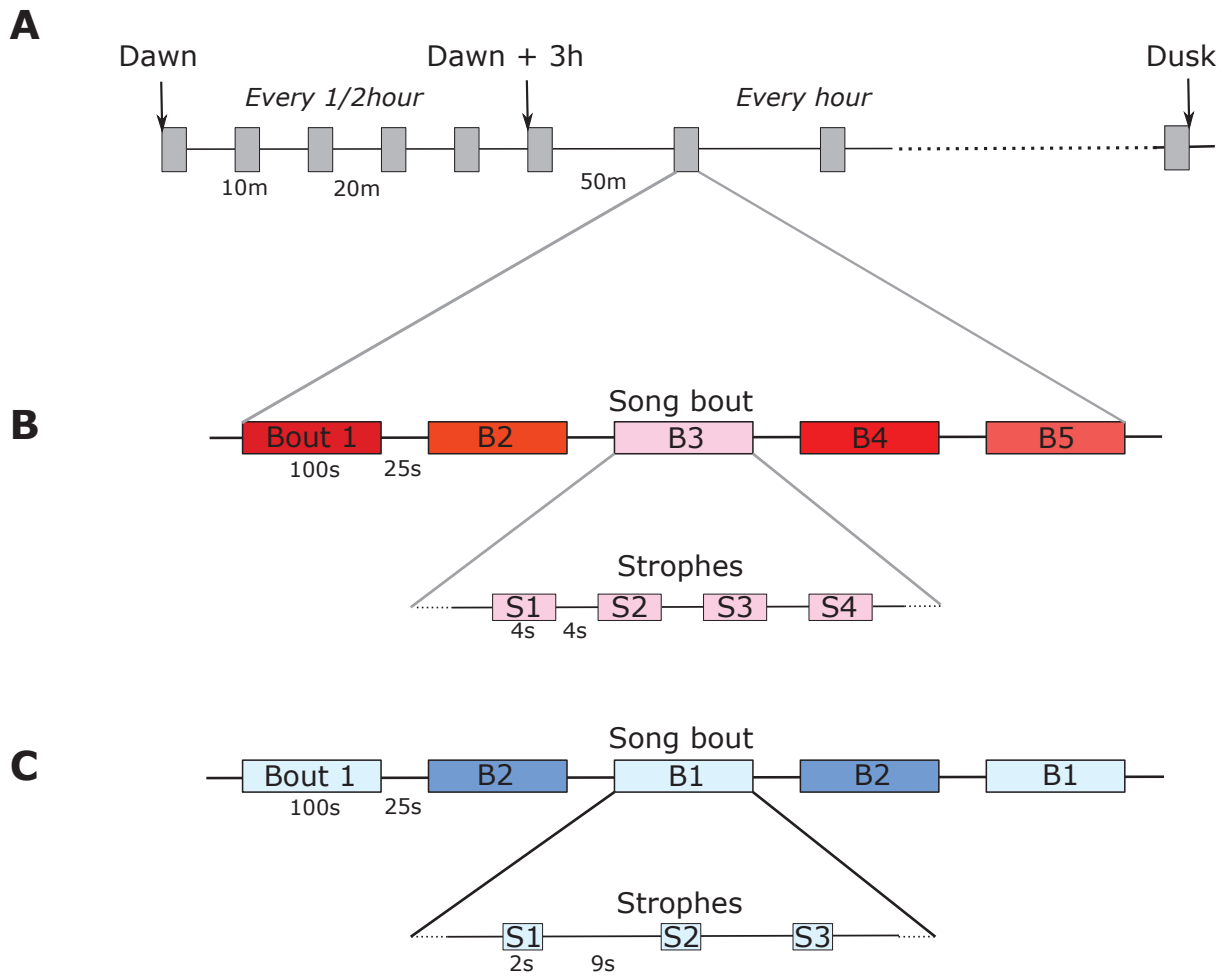


Figure 6.1: Structure of a song track (**A**), composed of a succession of 10 minute-long song periods (**B & C**). Song periods are composed of song bouts (B1, B2...), which are composed of strophes (S1, S2...). All strophes in the same song bout were composed of the same type of syllable, but could slightly differ in the rhythm, or the amplitude of the syllables. Playback tracks mimicking a good quality great tit song had a repertoire size of 5 song bout types (bouts B1-B5 in **B**, different colour shades), composed of 4 second-long strophes separated by 4 seconds of silence. Playback tracks mimicking a low quality song had a repertoire size of 2 song bout types (B1 & B2 in **C**, different colour shades), composed of 2 second-long strophes separated by 9 seconds of silence. The order of song bouts within a song period, and of strophes within song bouts (S1, S2, S3, etc.), were alternated between song periods and song bouts to avoid habituation. Chaffinch song track followed the same temporal pattern as presented in **C**, as it matches better their natural singing behaviour.

thus readjusting the position of the loud speaker accordingly. As the season progressed, it was not always possible to relocate the experimental zones.

We expected neighbouring great tits to sing in the vicinity of the experimental zones, especially when stimulated by broadcasted songs. Therefore, we monitored the number of singing great tits that could be heard from the loudspeaker in each experimental zone (20 times per zone over the broadcasting period), during 10 minutes picked at random before 10am in between two broadcasted songs. We also recorded the approximate distance at which these great tits were heard (on a 3-distance class scale: close, medium distance, far away). Due to time constraints, we did not have time yet to implement these data in the models to control for the natural singing activity in the vicinity of the experimental zones.

Aggressiveness test

We estimated the aggressiveness level of each flycatcher settling in the experimental zones during nest building or early egg laying stage. We followed the protocol detailed in Chapter 4. In short, at the beginning of the test, an observer attached (i) to the nest box of the focal pair clay decoys representing either a flycatcher pair or a male great tit and (ii) below the nest box, a loudspeaker broadcasting songs of the corresponding species. The observer then sat camouflaged 8-10 meters away and described all the behaviours of both the male and the female flycatchers for 15 minutes (if both individuals were seen at least 5 minutes), or up to 25 minutes to maximise the chance to describe the flycatchers behaviour for at least 5 minutes. We conducted one test with flycatcher decoys and one with great tit decoy. However, if one individual was not seen during either test, we conducted more tests (up to 5), with a day break between two consecutive tests. To avoid pseudoreplication, we used 10 sets of flycatcher decoys, 10 sets of great tit decoys, 5 different song tracks per species, and we randomized the song track used with a given decoy set. Aggressiveness score was then later estimated as the number of moves within 2 m away from the nest box (between branches or to the box, attacks on decoys) plus the number of chases performed against live intruders, even far from the nest box, standardized per 15 minutes (Chapter

4).

Statistical analyses

Comparison of occupancy pattern between treatments

We first tested whether flycatchers preferred settling in experimental zones with broadcasted (high quality) great tit songs by analysing the occupancy pattern in space (between treatments) and time using Cox proportional hazard models ("survival analysis", survival being equivalent, for a nest box, to remain unoccupied; Cox and Oakes 1984, Therneau and Grambsch 2000). After preliminary model diagnosis (checking for proportional hazards, and absence of influential observations and non-linearity), we included several variables as stratified effects (i.e. factors likely to influence the 'survival', but not matching the proportional hazard): the position of the nest box with respect to the loudspeaker (binary variable, i.e. the box beside the loudspeaker or not), the number of great tits settled in the experimental zone and the average number of great tit eggs (time-dependent variables, known to be used by flycatcher as a source of social information). We also included playback track and forest plot as random effects. To detect a potential effect of the presence of great tits in the experimental zone, we separated analyses for experimental zones where at least one great tit pair settled (with the associated stratified effects of tit presence and number of eggs) and those where no great tit pair settled (without the corresponding stratified effects of tit presence and egg number). To run the Cox models, we used the R packages "survival" (Therneau and Grambsch 2000, Therneau 2015) and "coxme" (Therneau 2018).

Factors influencing the choice of an experimental zone

We tested whether the probability for flycatchers to settle in an experimental zone according to the treatment (type of broadcasted song: high quality great tit song, low quality great tit song, chaffinch song) depended on individual parameters (age, personality) and environmental variables (weather, presence of live great tits) using multinomial mixed

effects models implemented in the Bayesian framework with the *MCMCglmm* function (“MCMCglmm” R package, Hadfield 2010). We fitted a model with the treatment of the zone (3 modalities) chosen by each flycatcher pair as the response variable and included as fixed effects male and female age and aggressiveness scores, the lowest temperature on the day before settlement (i.e. the day before the first record of nest material in the nest box), settlement date, the number of great tit nests and the number of empty nest boxes in the experimental zone on the day of choice, as well as the two-way interaction between with age and aggressiveness scores. Age and settlement date were included because late arriving birds, which are usually mainly yearlings, have been found to rely more on social information from great tits compared to early arriving ones (Seppänen and Forsman 2007). We included the forest patch as a random effect, but not the playback track because of model convergence issues. We selected fixed effects by comparing models based on DIC criteria with the *dredge* and *MuMIn* functions (“MuMIn” R package, Barton 2016); models with a DIC value less than 2 above the model with the lowest DIC were retained and the relative importance of each effect that appeared in these models was retrieved using the *model.avg* function (“MuMIn” R package, Barton 2016). The final model contained all variables of relative importance above 0.8. All models were implemented using the ‘categorical’ family, a burn-in of 10^4 , a thinning-interval of 1,500 initially (600 for the final model, which converged without autocorrelation with lower values of thinning-interval and iteration number) and 3×10^6 iterations (10^6 for the final model), which resulted in autocorrelation levels below 0.1 and effective sample sizes above 2,000 for all models. We fixed the variance-covariance residual matrix to 2/3 for the diagonal terms (variance) and 1/3 for all the off-diagonal terms (covariance; Hadfield 2016). We used the classical inverse-gamma priors for the random terms, without treatment-specific structure as we did not expect the variance associated to the forest patch to differ between treatments.

Factors influencing reproductive investment in the experimental zones

We tested whether flycatcher early reproductive investment, measured here by settlement day, the delay between settlement and laying, and clutch size, depended on ex-

perimental treatment (3 modalities), controlling for the same individual parameters and environmental variables as above using mixed effects Bayesian models with the *MCMCglmm* function (Hadfield 2010). For the models for the delay between settlement and laying and clutch size only, we also included settlement day as a fixed effect. We implemented the model for settlement day with the Gaussian family (12×10^4 iterations, burn-in = 6,000, thinning interval = 50) and the other two models with the Poisson family (for the delay and the clutch size respectively: 12 and 15×10^5 iterations, burn-in = 500, thinning interval = 10^4). Autocorrelation scores were below 0.1 and effective sample sizes above 2,000 for all three models. We choose a normal prior with mean 0 and a large variance (10^8) for fixed effects and inverse-Gamma priors for the residual and random variances.

6.3 Results

Occupancy pattern

The probability for a nest box to be chosen by collared flycatchers did not differ between treatments: the total number of settled pairs was 33 in the high quality great tit song treatment, 27 in the low quality tit song treatment and 40 in the chaffinch song (control) treatment ($\chi^2(2) = 2.54$, p-value > 0.28). The flycatcher occupancy pattern did not differ between treatments (p-values > 0.25 , Table A2; Figure 6.2b); it did not depend on the presence of live great tits in the experimental zone either (p-values > 0.59 with great tits and > 0.11 without great tits, see Table A2 for the complete outcome of the cox models).

Effect of individual and environmental variables on the choice of an experimental zone

Based on the DIC model comparison for the models fitting the probability to choose an experimental zone according to the song treatment, the interaction between female age

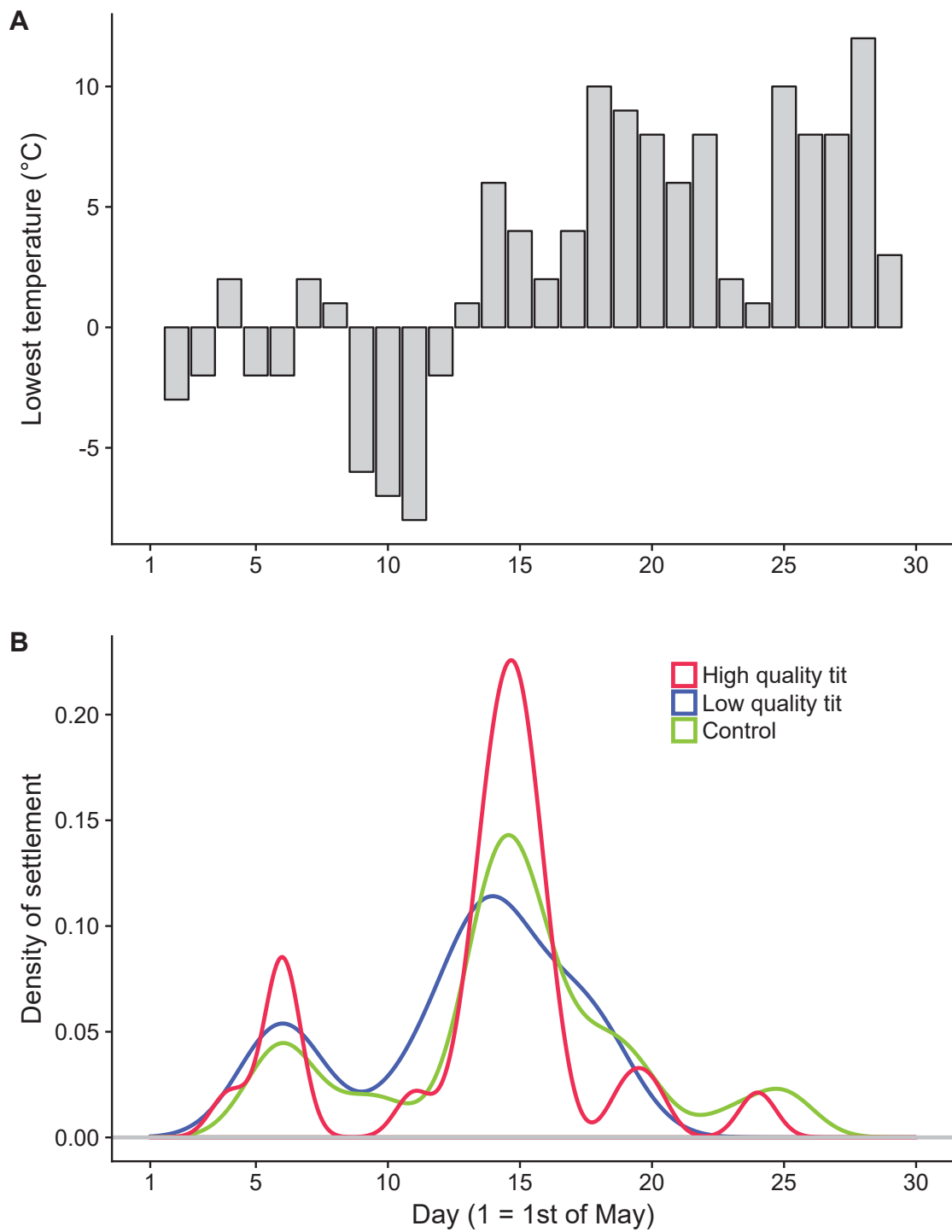


Figure 6.2: *Evolution of the lowest daily temperature (A) and flycatcher settlement in experimental zones of each treatment (B).*

and female aggressiveness score, the number of great tit pairs settled in the experimental zone, as well as the lowest temperature on the day before settlement, were present in the 8 best models (i.e. models with the lowest DIC values, relative importance = 1.00; Table 6.1). Other variables (male age and aggressiveness, settlement date, number of flycatcher pairs settled in the experimental zone) did not affect the probability to choose a zone according to song treatment (relative importance < 0.8; Table 6.1).

Table 6.1: *Importance of individual and environmental parameters for the probability to settle in each treatment: composition of the 8 best multinomial models. ‘+’ indicates the presence of the variable in the model. ‘trait’ is a function-specific notation referring to the 3 playback treatments (high and low quality tit and control; can be thought as a treatment-specific intercept). All other variables were also estimated per treatment. ‘aggr’ refers to aggressiveness score, low T° to the lowest temperature on the day before, nb.empty and nb.gt to the number of nest boxes in the experimental zones that were empty or occupied by tits (gt) on the day of flycatchers settlement (day).*

Presence of each variable in the 8 'best' models												
Models	DIC	Δ DIC	trait	age♀	age♂	aggr♀	aggr♂	low T°	nb.empty	nb.gt	day	age x aggr♀ age x aggr♂
1	115.497	0.000	+	+		+	+	+	+	+		+
2	115.504	0.008	+	+		+	+	+		+		+
3	115.725	0.229	+	+		+	+	+	+	+	+	+
4	116.682	1.186	+	+		+		+	+	+		+
5	117.167	1.670	+	+		+		+		+		+
6	117.329	1.832	+	+	+	+	+	+	+	+		+
7	117.427	1.930	+	+	+	+	+	+		+		+
8	117.478	1.981	+	+		+		+	+	+	+	+
Relative importance			1.00	1.00	0.16	1.00	0.73	1.00	0.64	1.00	0.25	1.00 0.00

The probability to choose an experimental zone according to the song playback treatment depended on female aggressiveness score in old females only, while no effect was found in yearling females, thus leading to an interaction between female age and female aggressiveness score (Table 6.2). Among old females, more aggressive females were more likely to settle in a high quality great tit song treatment zone while less aggressive ones did not choose this treatment more than random (Figure 6.3a, Table 6.2); in addition, less aggressive females were more likely to settle in a low quality tit song zone while more aggressive ones were more likely to avoid this treatment compared to random (Figure 6.3b, Table 6.2). Yearling females tended to settle more in the control zones than in the great tit song treatment zones (54% of yearling females were found in the control zones, 21% in low quality great tit song zones and 25% in high quality song zones; 95% CI for

any tit song treatment vs. control = [-2.92; 0.28]; Figure 6.3c).

Besides the female age by aggressiveness score interaction, the probability for flycatchers to choose an experimental zone according to the treatment depended on the number of great tits pairs settled in the zone: flycatchers were more likely to settle in a great tit song (either high or low quality) treatment when the number of great tit pairs settled increased (Table 6.2).

When considering only the choices made in the absence of tits in the zone, the effect of the interaction between female aggressiveness and the playback treatment remained (low quality vs. control: 95% CI = [-3.79; -0.51]; high quality vs. control: marginal trend 95%CI = [-0.17; 1.84]).

Finally, the probability to settle in the low quality song treatment decreased with increasing temperature the day before settlement (Table 6.2).

Table 6.2: *Effect of individual and environmental variables on the probability for flycatchers to settle in experimental zones of the low / high quality great tit song vs. the control treatment (taken as reference here). We derived level specific estimates (posterior means and 95% Credible Intervals) for the intercept and female aggressiveness score for each age category (yearling females vs. older females). Forest patch (random effect) had a variance of 0.27 [0.00; 1.2]. The residual treatment-specific variances were fixed to 2/3 and the covariance to 1/3. Stars indicate estimates for which 95% CI do not encompass zero. ‘aggr’ refers to aggressiveness score, low T° to the lowest temperature on the day before, nb.gt to the number of nest boxes in the experimental zones that were occupied by tits at the time the flycatchers settled.*

	Low quality tit vs. Control		High quality tit vs. Control	
	Post. mean	95% CI	Post. mean	95% CI
Intercept (yearling ♀)	-0.66	[-1.88 ; 0.57]	-0.72	[-1.92 ; 0.48]
Intercept (old ♀)	-0.88	[-2.15 ; 0.38]	0.29	[-0.60 ; 1.33]
low T°	-0.95	[-1.80 ; -0.16] *	-0.02	[-0.63 ; 0.75]
nb.tit	0.88	[0.02 ; 1.82] *	1.28	[0.40 ; 2.17] *
aggr ♀ (yearling)	0.08	[-1.12 ; 1.21]	0.21	[-0.76 ; 1.15]
aggr ♀ (old)	-2.24	[-4.01 ; -0.61] *	0.92	[0.02 ; 2.00] *

Effect of treatment, individual and environmental variables on early reproductive investment

We found no difference between treatments in settlement date, delay between settlement and laying, and clutch size (all 95%CI encompassing zero, Table A3). Fitting the models without interactions gave the same results (not shown), except that yearling females were found to settle later in the season than older females (95% CI = [0.06; 4.73]). Aggressiveness scores and male age had no effect on early reproductive investment (all 95%CI for main effects and two-way interactions encompassing zero, Tables A3).

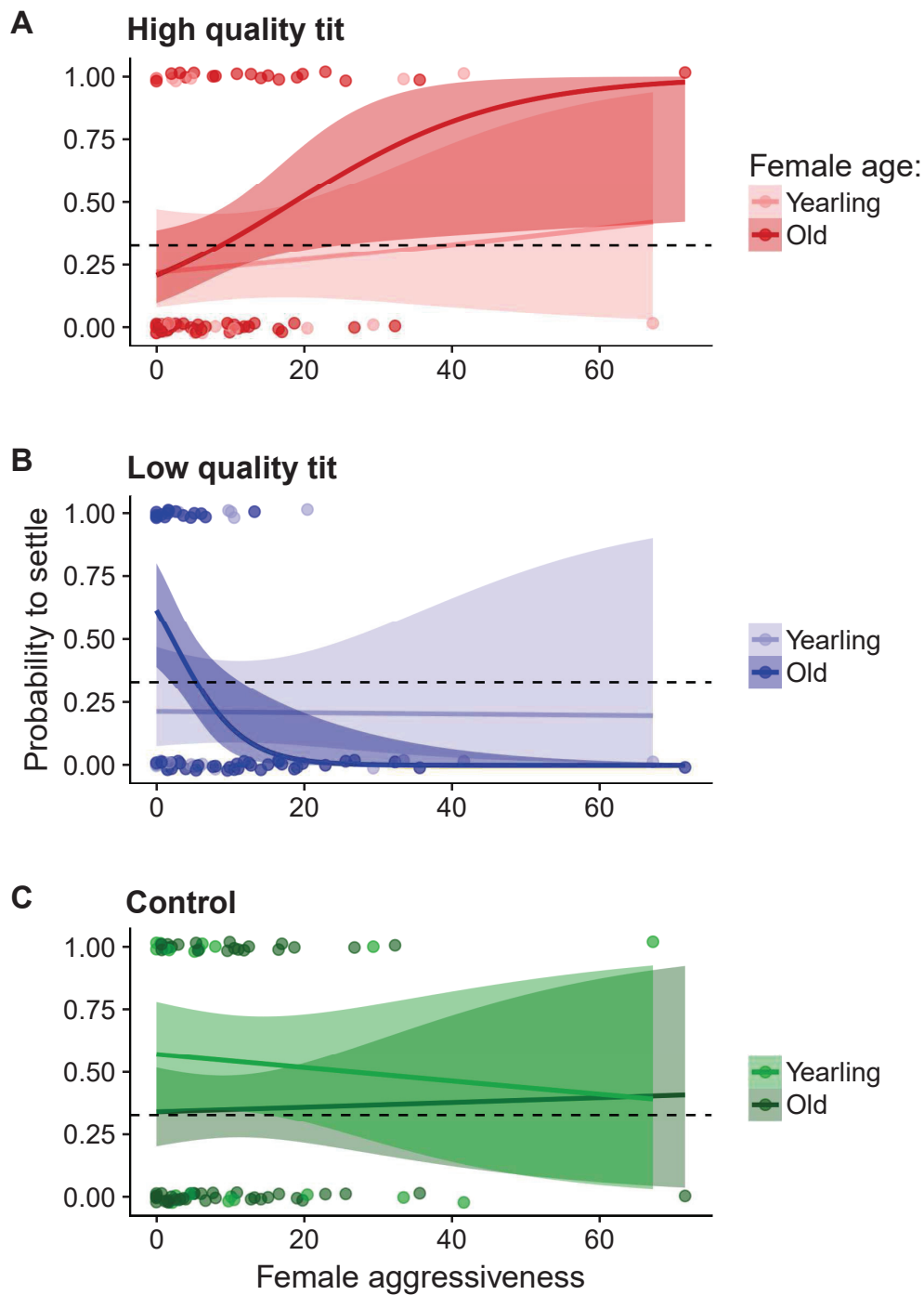


Figure 6.3: Probability for flycatchers to choose an experimental zone according to the playback treatment (3 modalities), depending on female aggressiveness score and female age (older female in dark colours, yearling females in light colours). For illustration, the settlement probability was derived here from models with binomial distributions (1 = settlement in a zone of the song treatment considered, 0 = settlement in a zone of another song treatment). The horizontal dashed line represents the probability to choose at random the song treatment considered (i.e. 0.33).

6.4 Discussion

In this study, we investigated the role of heterospecific song features as social information for settlement decisions in wild collared flycatchers. Using a playback experimental approach, we tested whether flycatcher settlement differed in zones where high quality great tit songs, low quality great tit songs or chaffinch songs (as a control) were broadcasted early in the season. The settlement behaviour of pairs with old females in experimental zones with great tit song broadcasts strongly depended on their aggressiveness level: pairs with more aggressive old females settled preferentially in the high quality tit song zones while pairs with less aggressive old ones settled preferentially in low quality tit song zones. Pairs with yearling females tended to prefer to settle in control zone, but this trend was not significant. These results provide the first evidence for eavesdropping on heterospecific song features related to quality in addition to song or call presence. The use of this source of social information did however affected neither the timing of flycatcher settlement nor their early reproductive investment (laying date, clutch size), suggesting that different information sources are used for different breeding decisions, and calling for a finer understanding of the specific fitness benefits of using each information source.

Why and when using great tit song features for settlement decisions? Benefits and constraints

When individuals do not have direct or easy access to information about breeding habitat quality, they can rely on social information from con- or heterospecifics sharing similar needs during breeding but with different constraints (Seppänen et al. 2007). In particular, migratory flycatchers have been shown to rely on resident, already settled, great tit presence and early reproductive investment for their own settlement decisions under strong time constraints when returning from migration (e.g. Forsman and Seppänen 2011, Kivelä et al. 2014). They have been found to benefit from settling near great tits (Forsman et al. 2002), showing that heterospecific cues can inform flycatchers about optimal breeding

sites (at various spatial scales) and thereby allow them to secure future breeding success. Such benefits can be achieved via the direct assessment of local habitat quality upon settlement or via indirect effects through enhanced access to food during provisioning and/or social benefits such as protection against nest predators (Forsman et al. 2002). Great tit density is likely easily assessable from a distance, in particular through acoustic cues (songs but also alarm calls), but information about early reproductive investment might be more difficult and costly to gather (Merilä and Wiggins 1995, Forsman et al. 2018).

Song production is overall costly (in terms of time, energy, or risk of predation and agonistic reactions by competitors) and should thus be selected to honestly inform on the producer quality (Gil and Gahr 2002), for example reflecting its past (Bischoff et al. 2009) or present parasitic load (Møller 1991, Buchanan and Catchpole 2000). Song features in great tit males have been shown to inform on male survival and reproductive success (repertoire size, strophe length, drift; McGregor et al. 1981, Lambrechts and Dhondt 1986, Rivera-Gutierrez et al. 2010), on mate quality during escalating song contests (Otter et al. 1999), and on rival competitive abilities at the conspecific level (Peake et al. 2005). Great tit song features have not directly been related to territory quality (but see Hoi-Leitner et al. 1995, Manica et al. 2014 in other species), but great tit males singing longer strophes were found to be dominant at feeders (Lambrechts and Dhondt 1986) and more willing to engage in territorial defence (McGregor and Horn 1992). Dominance may also positively correlate with social learning abilities (e.g. in blue tits, Aplin et al. 2013), which in turn may improve foraging efficiency (Aplin et al. 2012). Great tits cognitive abilities have been shown to positively correlate with their reproductive investments (number of nestlings, Cole et al. 2012) and their reproductive success (Cauchard et al. 2013). Overall, these studies suggest that high quality great tit individuals, assessable from their song features, are likely to be better in acquiring and defending a high quality territory when facing intraspecific competition compared to low quality individuals, but also better exploit their habitat during nestling provisioning and better defend their nests against predators via increased vigilance and risk-taking (Krams 1998). Thus, cueing on great tit song features may be a relatively cost-free

proximate mechanism for flycatchers to identify and select high quality individuals close to which it can be beneficial to settle. Our experimental results confirmed the direct use of this cue in small-scale settlement decisions by flycatchers because we used broadcasted songs alone, i.e. in absence of the actual presence of settled great tit pairs. This did not preclude flycatchers to simultaneously use the presence of great tit pairs in addition to the broadcasted songs, as reflected by higher settlement probability when the number of great tit pairs settled increased. However the presence of great tits pairs did not overcome the effect of song broadcasts, showing that information obtained from alive birds was maybe not given more weight compared to information derived from songs.

Nevertheless, the availability of great tit songs to newly arrived flycatchers may vary both within and between years. When flycatchers arrive on the breeding grounds, a large part of great tit females can have initiated incubation and thus great tit males singing activity can be largely reduced (Mace 1987, Amrhein et al. 2008). The time delay between great tit settlement and flycatcher arrival, as well as the time interval between the arrival of the first and last flycatchers, may strongly constrain the possibility for flycatchers to eavesdrop on great tit song. The timing of great tit reproduction but also the synchrony of flycatcher arrival shows high variability between years in this population (Chapter 3; BD pers. obs.), affecting the availability of cues linked to great tit presence and reproductive activity upon flycatcher arrival. Thus selective pressures should favour high flexibility in the use of the different heterospecific cues in response to environmental variation. The use of cost-free great tit song characteristics by flycatchers for settlement decisions may be selected for in years when tits are late and in early arriving flycatchers, while other information about tit quality and reproductive investment (e.g. clutch size, Seppänen et al. 2011, tit incubating, Samplonius and Both 2017; or provisioning activity) or conspecific social information should be favoured in other cases. In 2017, when we conducted our experiment, tit laying date was intermediate compared to other years (2012-2016, see Table 2 in Chapter 3; in 2017, the average great tit laying date was day 34.8 ± 7.8 (SD), counted from the 1st of April). This may explain why we did observe relatively small differences, between treatments.

Old and yearling females cue differently on great tit songs: role of experience and competitive ability

Old flycatcher females were able to use the information provided by both the presence and quality of great tit individuals through their songs to select a breeding site. Conversely, yearling females showed no discrimination between high and low quality great tit songs. They nevertheless tended to avoid zones with great tit song broadcasts, suggesting that they only relied on the presence information contents of songs. The difference between yearling and older females may result from different past experience with great tit songs. Among songbirds, the response to songs is usually shaped by imprinting in the intraspecific (Kroodsma 1982, Catchpole and Slater 2008), but also heterospecific context (Hansen and Slagsvold 2003). Because flycatchers breed a couple of weeks later than great tits, just fledged flycatchers are usually not much exposed to great tit songs before leaving on migration mid-August (second broods remain infrequent in this great tit population and when they occur, they rarely involve new pair formation; BD pers. obs.). Therefore, cueing on great tit song features may require experience obtained only during the first breeding season for flycatchers. Yet, in the pied flycatcher, a sister species, yearling females seemed to adjust their settlement behaviour in response to great tit cues: later arriving (mostly yearling) females copied great tit tutors more often than early arriving (mostly older) females (Seppänen and Forsman 2007), and yearling females avoided copying great tit tutors when great tits had small clutches (Loukola et al. 2013). Yearling females therefore could use other information sources than song to assess great tit presence and reproductive investment. Here, yearling females may have avoided settling in experimental zones with great tit song broadcasts because competition with (supposedly late) breeding great tits could be higher compared to control zones. Such age difference in social information use in relation to the lower competitive ability of yearling individuals has already been suggested in males in this population (Doligez et al. 1999). Because the difference in settlement probability between treatments in yearling females was only a trend here, more work would however be needed to confirm these interpretations.

Among older females, the settlement behaviour with respect to great tit song features depended on aggressiveness level. This relation could be explained by two processes. First, flycatcher females may adjust their settlement decisions depending on the balance between benefits in terms of habitat quality and costs in terms of competition level: more aggressive females settled in the apparently most favourable habitats (as reflected by song of higher quality great tit) where they could cope with potentially higher competition level; less aggressive females still preferred settling near great tits, i.e. in habitats of supposedly higher quality than control (chaffinch song) zones, but they avoided zones where competition with great tits was highest. This would be consistent with intraspecific results showing higher settlement of great tits near broadcasts of great tit songs with smaller repertoires, i.e. reflecting potentially lower quality individuals (Krebs et al. 1978): later-settling individuals could indeed be low competitive individuals more prone to avoid potential competitive costs. Because the timing of settlement was similar between great tit song broadcast treatments and independent from female aggressiveness score, it is unlikely that less aggressive females had been expelled from the high song quality zones by already settled aggressive conspecifics.

Alternatively, flycatcher females may have adjusted their response to our aggressiveness test after settlement depending on the apparent competitive level of neighbouring great tits. Indeed, we measured aggressiveness during nest building, at a time when playback songs were still broadcasted (or two days after the end of the broadcasting period for the last tests), and higher singing performance was suggested to induce social aggression, at least at the intra-specific level (Gil and Gahr 2002). Thus females settled near apparently high quality great tits may have shown a higher aggressive response to intruders in response to such increased heterospecific social stimulation. In our population, aggressiveness score was weakly repeatable (~ 0.2 , Chapter 4); thus this personality trait shows relatively high variability allowing for behavioural adjustment depending in particular on the context. Whether females adjust settlement choice according to their aggressiveness level or aggressiveness response according to songs of surrounding tits, both explanations involve female ability to discriminate low and high quality great tit songs, and adjust

behaviour accordingly.

Sex difference in the use of heterospecific songs

Interestingly, male traits (age, aggressiveness score) did not influence pair settlement with respect to the heterospecific song treatment. Even though nest site selection is a joint behaviour by both pair members, this could suggest that only female flycatchers were capable of adjusting their behaviour in response to great tit songs, which could reflect in particular a higher ability to discriminate fine song features compared to males. Selective pressures may be higher in flycatcher females compared to males for the use of songs in the context of species recognition (in our population, hybridization occurs with sympatric pied flycatchers, but females do not sing; Veen et al. 2001) and/or mate selection (facultative polygyny imposes higher constraints on females than males; Gustafsson 1989). Former studies have shown differential auditory processes between sexes (Williams 1985, Negro et al. 2000), upon which selection could act differently. Alternatively, males could discriminate fine song features just as well as females (as suggested by widespread ‘dear enemy’ effects; Moser-Purdy and Mennill 2016), but may be less prone to use this information for settlement decisions if others are more relevant at the spatial scale of male choice. Among most bird species, males are thought to benefit more from small-scale knowledge of the environment to select high-quality habitat to attract females, resulting in philopatry and small-scale prospecting behaviour, as shown in particular in our population (Greenwood 1980, Doligez et al. 2004). Conversely, females are thought to benefit more from large-scale knowledge of the environment allowing them to optimize male and/or territory choice, resulting in longer dispersal distances and large-scale prospecting behaviour (Greenwood 1980, Arlt and Pärt 2008). Males may thus use social cues providing information at smaller spatial scales compared to females (see Discussion in Chapter 3 and Samplonius and Both 2017). Because great tit songs can be heard from potentially long distances (up to 100 m in our forests), they may thus constitute social information available at a large scale, and consequently used mostly by females. Further work would be needed to assess whether flycatcher males can discriminate great tit song

features and in this case which other information sources would be more valuable to them compared to females.

In general, our results shed lights on the complexity of social information use with the first evidence for access to and use of refined heterospecific information sources such as the performance/quality-related information contained in heterospecific acoustic signals for settlement decisions, with potential implications for songbird community dynamics. Further work is needed to assess how and when different information sources are used for different breeding decisions (see e.g. Doligez et al. 2008) depending on individual and environmental conditions, including the quantification of fitness benefits of using each information source in a given context.

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Authors contribution

JM, JTF, and BD designed the experiment. JM collected and analysed the data, and drafted the manuscript. JM and BD critically revised the current version of the manuscript.

6.5 Reference

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6.6 Appendix

Table A.6.1: *Cox proportional hazard mixed models, depending on whether there was great tit settling in the experimental zone or not. ‘treatment’ = high quality great tit song, low quality great tit song, control (chaffinch song); the control treatment is taken as the reference here). ‘nb.GT’ and ‘eggs.GT’ are the number of great tits present and the average number of eggs in the experimental zone each on the given day (time-dependent variables). ‘position’ = whether the nest box of interest was the one near the loud speaker (binary variable: yes; no); ‘playback’ = playback song track number; ‘forest’ = forest patch.*

Cox proportional hazards mixed regression models						
	Fixed terms				Random terms	
	coef	exp(coef)	se(coef)	z value	p-value	variance
<i>All data (925 events among 4833 daily-nest box data):</i>						
<i>Occupancy ~ treatement + strata(nb.GT) + strata(eggs.GT) + strata(position) + (1 playback) + (1 forest)</i>						
Low quality tit vs. Control	-0.379	0.684	0.327	-1.16	0.25	
High quality tit vs. Control	-0.244	0.784	0.325	-0.75	0.45	
Playback song track						0.196
Forest						0.794
<i>Great tit present (309 events among 1743 daily-nest box data):</i>						
<i>Occupancy ~ treatement + strata(nb.GT) + strata(eggs.GT) + strata(position) + (1 playback) + (1 forest)</i>						
Low quality tit vs. Control	0.181	1.198	0.884	0.20	0.84	
High quality tit vs. Control	0.612	1.843	0.898	0.68	0.50	
Playback song track						1.113
Forest						3.736
<i>Great tit absent (616 events among 3090 daily-nest box data):</i>						
<i>Occupancy ~ treatement + strata(position) + (1 playback) + (1 forest)</i>						
Low quality tit vs. Control	-0.471	0.624	0.296	-1.59	0.11	
High quality tit vs. Control	-0.466	0.627	0.285	-1.63	0.10	
Playback song track						0.130
Forest						0.506

Table A.6.2: *Linear mixed effect model for (i) the day of settlement, (ii) the delay (in days) between the day of settlement and the day of the first egg laid, and (iii) the clutch size of collared flycatcher pairs. For categorical variable (age and treatment) the estimates are given with ‘old’ and ‘control’ as the reference categories. Stars indicate variables which 95% CI does not overlap zero. N=58.*

	Settlement day		Delay (laying - settlement days)		Clutch size	
	Post. mean	95% CI	Post. mean	95% CI	Post. mean	95% CI
Fixed terms						
Intercept	8.74	[6.60 ; 10.78] *	2.82	[2.53 ; 3.10] *	1.87	[1.47 ; 2.21] *
treatment						
(Low quality tit)	3.10	[-1.62 ; 8.62]	-0.04	[-0.53 ; 0.41]	-0.01	[-0.59 ; 0.56]
(High quality tit)	0.93	[-1.96 ; 3.82]	-0.01	[-0.28 ; 0.27]	0.00	[-0.31 ; 0.34]
aggr ♀	-0.65	[-2.85 ; 2.03]	-0.02	[-0.25 ; 0.22]	0.01	[-0.28 ; 0.27]
age ♀	3.29	[-0.49 ; 6.68]	0.01	[-0.35 ; 0.36]	-0.02	[-0.44 ; 0.37]
aggr ♂	0.95	[-0.65 ; 2.59]	-0.05	[-0.22 ; 0.14]	0.02	[-0.16 ; 0.20]
age ♂	-0.66	[-4.77 ; 2.66]	0.00	[-0.35 ; 0.37]	-0.06	[-0.47 ; 0.36]
low T°	2.38	[1.10 ; 3.68] *	-0.01	[-0.16 ; 0.14]	-0.01	[-0.17 ; 0.16]
nb.tit	0.18	[-1.29 ; 1.52]	-0.02	[-0.16 ; 0.11]	0.00	[-0.15 ; 0.16]
age x aggr ♀	-0.30	[-2.76 ; 2.37]	0.03	[-0.20 ; 0.27]	-0.03	[-0.30 ; 0.26]
age x aggr ♂	-0.12	[-3.03 ; 2.93]	0.05	[-0.29 ; 0.34]	-0.07	[-0.42 ; 0.24]
treatment x age ♀						
(Low quality tit)	-2.74	[-11.06 ; 5.19]	0.02	[-0.82 ; 0.76]	0.05	[-0.88 ; 0.94]
(High quality tit)	-1.27	[-7.61 ; 4.88]	0.03	[-0.59 ; 0.65]	-0.17	[-0.89 ; 0.51]
treatment x aggr ♀						
(Low quality tit)	2.53	[-5.96 ; 10.38]	-0.02	[-0.82 ; 0.73]	-0.06	[-0.91 ; 0.87]
(High quality tit)	-0.02	[-3.11 ; 2.79]	0.05	[-0.23 ; 0.34]	0.03	[-0.31 ; 0.36]
treatment x age ♂						
(Low quality tit)	-3.68	[-10.91 ; 2.71]	0.12	[-0.46 ; 0.75]	-0.10	[-0.82 ; 0.72]
(High quality tit)	2.02	[-5.91 ; 10.06]	-0.13	[-0.90 ; 0.65]	0.09	[-0.79 ; 0.97]
treatment x aggr ♂						
(Low quality tit)	-1.07	[-3.89 ; 1.85]	0.07	[-0.22 ; 0.36]	-0.07	[-0.40 ; 0.23]
(High quality tit)	1.08	[-2.72 ; 4.98]	0.10	[-0.25 ; 0.49]	-0.03	[-0.44 ; 0.41]
settlement day	.	.	-0.07	[-0.09 ; -0.04] *	0.00	[-0.04 ; 0.03]
Random terms						
Forest patch	0.43	[0.00 ; 2.19]	0.01	[0.00 ; 0.02]	0.01	[0.00 ; 0.02]
Residual variance	13.57	[8.21 ; 19.97]	0.00	[0.00 ; 0.01]	0.01	[0.00 ; 0.02]

Chapter 7

General Discussion



7.1 Summary of the results and aims of this general discussion

The use of social information is a widespread strategy, both in terms of taxa and contexts, and is usually beneficial, as long as it is used in a discriminative way (i.e. that the observed individuals are reliable informers and are not randomly chosen, Laland 2004). Using social information instead of directly sampling the environment oneself can save time, energy, and may increase fitness (see Chapter 1). More specifically, heterospecific social information use is an expanding field of research since the last 20 years (Forsman et al. 1998, Mönkkönen et al. 1999, Coolen et al. 2003). Heterospecifics have been suggested to provide more diverse, valuable and up-to-date information, or inducing less competitive costs than when using social information from conspecifics (Seppänen et al. 2007). This strategy can however lead to increased niche overlap with competitors, with consequences on individual fitness (e.g. great tits may have a lower reproductive success when breeding near flycatchers, Forsman et al. 2007), but also on community structure (reviewed in Goodale et al. 2010). With environmental stochasticity, the benefits to use one or another type of information may vary between and within seasons or between contexts, which could have dramatic fitness effects especially in short-lived species. To better understand the evolutionary potential, determinism and plasticity of social information use, it is necessary to determine the causes of variations in this behaviour at various scales. In this thesis, I presented my results on between-individual variability in heterospecific social information use for breeding site selection in a migrant short-lived passerine bird, the collared flycatcher.

In chapter 3, we showed that the use of heterospecific social information in collared flycatchers, measured as a binary “copy/reject the competitor preference” behaviour, was not heritable in this population, and was greater in pairs with a yearling male than in pairs with an old immigrant male. We also showed that the probability to copy tits depended on the apparent reproductive investment of local tits at the time flycatchers

settled, and on male flycatcher aggressiveness, but not on female or male boldness and neophobia (Chapter 5). These three personality traits, aggressiveness, boldness, and neophobia, were found repeatable between years but not heritable (Chapter 4). Similarly to former studies on pied flycatchers (Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013), collared flycatchers copied the tit preference when tits had large clutch / brood size, and rejected it when tits had small clutch / brood size at the time of flycatchers' settlement, especially when the flycatcher male was aggressive. Pairs with less aggressive males copied tits tutors when tit density was high (Chapter 5). Finally, in Chapter 6, we showed that female flycatchers can cue on fine acoustic features from great tit songs for their settlement decision. Again, aggressiveness and age affected the use of this social information, with more aggressive old females settling preferentially near tits that "sounded" of good quality (large repertoire size, high strong rate and longer strophes) and, on the contrary, less aggressive old females settling near tits that "sounded" of low quality.

Combined, these chapters showed that individual differences in age and personality traits, but not in genetics, influence the propensity to use information obtained from heterospecifics (summarized in Figure 7.1). What first appeared to be an overall absence of effect (no overall copying between 2012 and 2016 in Chapter 3, no overall treatment preference in Chapter 6), were actually complex year-, sex-, age- and aggressiveness-dependent patterns. It would be interesting to know to what extent an absence of effect found in (possibly unpublished) behavioural ecology studies could be explained by different individual strategies or constraints. It is interesting to note that here, boldness and neophobia did not influence this behaviour. Heterospecific social information use will likely increase the niche overlap with dominant competitors, and it was influenced by a very relevant trait for this decision, that is, the agonistic reaction towards competitors. Of course, we did not measure activity, sociability, exploration *per se*, so this assertion has to be taken with caution.

From the Figure 7.1, we can see that several questions still need to be addressed, such as the links with cognition and fitness, or the different processes in the social information

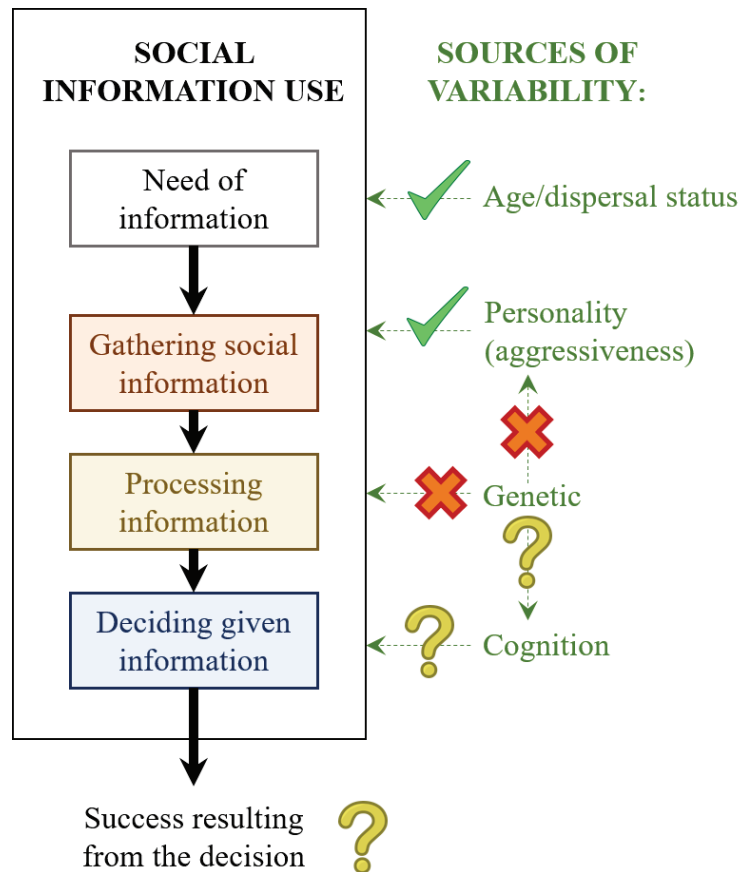


Figure 7.1: Adapted diagram from Chapter 1, with the final results from the thesis: we showed an effect of age/dispersal status and aggressiveness (but not boldness or neophobia), and no genetic inheritance in the use of heterospecific information.

use “black box”. Indeed, when measuring social information use, we often face the same problem: did the individual access the information? Did the individual decide not to use the information? It is very difficult to differentiate what is really a non-use of social information, a non-motivation to use, a use but to do something else (e.g. reject the tit preference here). With new technologies, both in the lab and in the wild, we are now able to track very precisely individuals, their contact with others, or even head directions. This should thus lead to promising future studies decoupling the access to information and the resulting decision.

The aim of this general discussion is not to mention what has already been discussed in the manuscripts but rather to bring the results together and discuss them in a broader perspective, and to discuss some methodological and conceptual aspects that were not addressed in the manuscripts.

In the first part of this discussion, I come back to recent opinions regarding the interpretation of results from the so-called “symbol” experiments. I explain the divergence of ideas, and show how my results can help improve our understanding of the processes behind the copying/rejecting pattern we observe in flycatchers. I also propose a complementary hypothesis to explain how flycatchers copy tits with an apparent large clutch size. In a second part, I address some methodological points regarding our personality estimates and explain additional analyses and data that will help addressing these issues in the future. In a third part, I propose some research perspectives to continue the investigation on the evolution of social information use for breeding site selection.

7.2 What do we really measure with the ‘symbol experiments’?

From the previous chapters and the body of literature on social information use in flycatchers, we might be quite convinced that flycatchers use social information obtained through the observation of great tits, and adjust their decisions depending on great tit quality or reproductive investment. However, recent criticism highlighted that this may not be so obvious and needs further investigations. Here, I will shortly review the former and the newly proposed hypotheses explaining the observed results. Even though the exposed criticisms and hypotheses, I believe this was a good time, 10 years after the first “symbol-experiment” to clarify and put together the current knowledge on the fascinating tit-flycatcher system. In particular, one overlooked but important aspect in this system is the behaviour of the information providers, the tits (but see Forsman et al. 2014).

7.2.1 The Selective Interspecific Information Use: hypothesis and evidence

The original hypothesis emerging from the “symbol” experiment has been coined Selective Interspecific Information Use (SIIU, Forsman et al. 2018), and states that flycatchers tend to copy the nest site choices of titmice, but only when tits show a high reproductive investment at the time of flycatchers settlement (and reject the tit preference otherwise). The assumed benefits for flycatchers to use information from tits have been detailed in Chapter 2 and encompass the fact that tits are supposedly more knowledgeable and share the same predators, parasites, nest sites, and food requirements.

The SIIU hypothesis is supported by three experiments conducted on pied flycatchers and varying slightly in their ecological context (illustrated in Figure 7.2; Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013). All three experiments tested

flycatchers' nest site choice between two types of symbols on boxes, given (1) the apparent preference of tits for a specific symbol (triangle in the example on Figure 7.2), and (2) tit clutch / brood size at the time of flycatchers settlement. These experiments differed from the one I used during my PhD (Chapter 3 and 5) because nest boxes were spatially paired: in one pair of boxes, separated by 2-5 meters, there was one tit nest. Further away (25-30m), another pair of nest boxes was set-up, allowing flycatcher pairs to settle. Indeed, tits tolerate the presence of breeding flycatchers at such a close vicinity from their own nest site, while they would be more territorial against other tits (Campbell 1968; Doligez, pers. comm.). As an example, in private gardens on Gotland, we find great tits and flycatchers nesting only 5-10 meters apart.

Seppänen et al. (2011), conducted their experiment in Latvia, central Finland, and northern Finland and found that flycatchers copy the tit apparent preference when tits exhibit a large clutch / brood size at the time of flycatcher settlement. However, when tits exhibit low clutch / brood size, flycatchers tend to reject their preference (no data for the Latvian population which had only high tit clutch size when flycatchers settled).

Forsman & Seppänen (2011) conducted their experiment in northern Finland, and tested the copying behaviour of pied flycatchers when artificial tit nests containing either 4 or 13 fake eggs were placed in boxes bearing a specific symbol (while the adjacent box and the further paired nest boxes remained empty). They showed that most flycatchers preferred to settle on top of the fake tit nest (64%), and therefore brought less nest material themselves (40% less material), but did not change the onset of laying. Only one flycatcher pair (among 58) settled in the box adjacent to the one with the fake tit nest. Among the flycatchers that settled in the boxes 25-30m away from the tit nest, flycatchers tended to copy the apparent tit preference for high tit clutch size (13 eggs), but reject it for low tit clutch size (4 eggs). In the absence of tits protecting the nest, flycatchers thus prefer to take over tit nests, probably to save time and energy of nest building, as shown by the lower amount of nest material brought to the box, and maybe also to gain some protection against parasites with the moss (Doligez pers. comm.).

To test what was the preferred choice of flycatchers when tits were protecting their

nest (i.e. active nests, contrary to the experiment described above), Loukola et al. (2013) manipulated the clutch size of already settled tits in the Latvian and northern Finnish populations, to create tit nests with either 5 or 13 eggs (Figure 7.2). They daily recorded whether the tit clutches were covered by nest material or uncovered (i.e. clutch size presumably visible or invisible to intruders), and monitored the settlement and symbol choice of flycatchers in the nearby paired boxes. They found that when the tit clutch was uncovered, the copying behaviour of the flycatchers matched the one observed in Seppänen et al (2011): flycatchers copied when tit clutch size was high, and rejected it when tit clutch size was low. However, when the tit clutch was covered, the opposite pattern was observed: flycatchers rejected the tit choice when tits had large covered clutch (see Loukola et al. 2013).

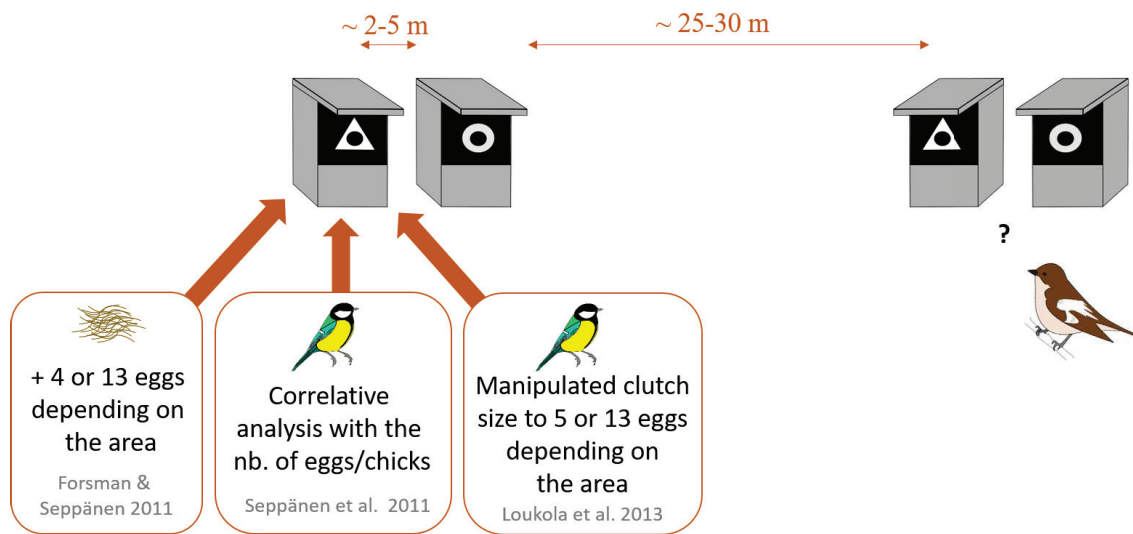


Figure 7.2: Schematic representation of the three experiments (each orange block) testing the copying and rejection behaviour of pied flycatchers depending on the tit reproductive investment (clutch / brood size). Within a pair of nest boxes, both symbols were represented. One of the four boxes contained a tit nest, the other 3 boxes were empty before flycatchers' arrival. Replicates of these 4-boxes areas were spread at least 1km apart.

7.2.2 Doubts formulated by Slagsvold & Wiebe (2017)

In their recent point-of-view article, Slagsvold & Wiebe (2017) do not question the fact that flycatchers use heterospecific social information, but rather criticize the hypothesis and mechanisms proposed by Forsman and collaborators to explain that flycatchers are found to copy (resp. reject) the tit apparent preference when tits show high (resp. low) clutch size (later referred as the “copy/reject pattern”). I summarize here their main criticisms (Slagsvold and Wiebe 2017, 2018), the replies (Forsman et al. 2018, Samplonius 2018), and personal comments.

In particular, Slagsvold & Wiebe (2017) argued that (in *italic*):

- a. *Flycatchers have no apparent reason to prefer an external nest box feature based on tit choice.*
- b. *These experiments do not reflect natural conditions (cavities varying in quality, depth, etc.) therefore it is unlikely that such a copying behaviour would have been selected for.*

The fact that choosing a symbol on a box is not a natural setting and do not bring any benefit, is the core principle of the experiments, and support the hypothesis that flycatchers follow a “copy the successful” (conversely “reject the unsuccessful”) strategy (Laland 2004). This strategy may have been selected for in other contexts and still apply in this simple 2-choices experiment (Forsman et al. 2018). As Forsman et al. (2018) explained, the strategy would be to copy good quality tits (expected to be better foragers, make better decisions), and not necessarily copy the territory, which should not greatly differ at such a small spatial scale (2-5 meters separating the paired boxes). My results from Chapter 6 support this view, as I showed that old aggressive female flycatchers preferred to settle near greats tits of apparently good quality based solely on song features.

- c. *There is no evidence that flycatchers really prospect in boxes occupied by tits (especially) during incubation when the tit clutch is uncovered.*

Flycatchers do prospect in tit nest boxes (Forsman and Thomson 2008, Forsman et al. 2018), but indeed, not often at incubation (at least in the years and populations that were video recorded). In their second reply, Slagsvold & Wiebe (2018) take this as a concrete evidence that SUII should be dismissed. As pinpointed by Slagsvold & Wiebe, tits show aggressiveness and territoriality, and this may prevent the flycatchers to access nest boxes at incubation stage (especially if the female great tit is inside). However, I suggest that flycatchers could use other cues (e.g. the behavioural response of the tits, the presence of the tits inside the box, the alarm calls or songs of tits) as indication of tit quality. If some of these other cues reflect the tit reproductive investment, we would observe the similar trend of “copying only when tit clutch size is high”. This hypothesis is further developed in section 7.2.6. The synchrony between tits and flycatchers is besides highly variable between years (see Chapter 3). Prospecting in tit nest boxes during egg laying could be possible in years when tits are late. To provide more thorough evidence of flycatchers’ prospecting behaviours, we would ideally have to re-iterate video recordings but from the outside of the nest box (or direct observations), several years, both during egg-laying and incubation, and, whenever possible, in different populations. This kind of data is highly time-consuming to extract but alternative methods may be used (see section 7.2.7).

- d. *If flycatchers are really cueing on tit clutch size, they would have to wait for the clutch to be uncovered, at incubation, and then wait for the tit female to leave her eggs (quite short periods). Besides, if flycatchers compare the ‘observed’ clutch size to the population mean, they should globally reject the choice of tits that are still at the laying stage.*

Delaying reproduction after arrival on breeding grounds is highly costly (Lundberg and Alatalo 1992). Therefore, flycatchers are unlikely to “wait” for the tits to complete their clutch, as Slagsvold & Wiebe suggest. Eggs are not always very well covered during egg laying, thus flycatchers may have access to this information (see section 7.2.6 for further developments). It is also probably unlikely that they compare tit clutch size observed in boxes with the mean clutch size of the population. They would more likely acquire the knowledge of the mean tit clutch size with experience, by prospecting in numerous nests and making a relative comparison of clutch sizes among tit nests or even with their own clutch size from the year before (Forsman et al. 2018). This would be in accordance with the fact that young (less experienced) individuals do not show such a copy/reject pattern (Loukola et al. 2013; also suggested in Chapter 5 for males, and in Chapter 6 for females).

The rejection pattern of tits preference when tit were still laying eggs was observed in 2013 (Chapter 5). Besides, female pied flycatchers prefer to settle in forest patches where tits show an advanced phenology rather than a delay one (Samplonius and Both 2017). It is possible that flycatchers do not (only) use information on tit clutch size, but rather use information on tit advances in the reproduction at the time flycatchers arrive. The clutch size could then be only one cue, among others, used to assess tit reproductive advances. Early settled and paired tits are probably of higher quality, acquire better territory. A non-mutually exclusive (but probably a bit more speculative) hypothesis is that flycatchers copy early breeding tits to minimize their overlap in food requirements later in the season. This has been suggested but not much developed by Samplonius & Both (2017). Flycatchers and tits feed their nestlings with caterpillars, and tits adjust their breeding phenology according to environmental cues, to synchronize with the expected caterpillar peak (Lundberg and Alatalo 1992, Noordwijk et al. 1995, Naef-Daenzer and Keller 1999, Wilkin et al. 2009). Over the course of the breeding season, flycatchers shift their prey item from soft, highly digestible and available preys for young nestlings (*Lepidoptera* larvae) to harder but larger prey for older nestlings (Meidell 1961, Slagsvold 1975, Lundberg and Alatalo 1992, benefits for young nestlings reviewed in Slagsvold and Wiebe 2007; pers. obs.). Copying early breeding tits would thus maximise the availability

of caterpillars for nestlings. This remained to be tested but the higher survival of young nestlings for flycatchers breeding early (or well synchronized with tits) could have selected for a short time-lag between flycatchers and tits laying dates (Slagsvold 1975), and thus for a preference of flycatchers to copy early tits.

- e. *Flycatchers are unlikely to see eggs in dark tit nest boxes. But if flycatchers really “count” (or assess the relative quantity) of eggs, more than visually, it should be by touching eggs with the brood patch. Yet, only females have a brood patch and it seems that mostly males prospect in tit nest boxes (during laying).*

Flycatchers should be able, whether seeing or touching the eggs, to evaluate their relative quantity. Indeed, counting abilities has been shown in other species (briefly reviewed in Samplonius 2018), and flycatchers have also been shown to adjust their dispersal decisions depending on conspecific reproductive success (number of nestlings, Doligez et al. 1999, but they might also cue on the parents provisioning behaviour or the nestling calls rather than the number of nestlings per se). Regarding the flycatcher vision in the dark, Forsman et al. (2018) objected that birds see egg shell or faecal bags in nest, so they should be able to see eggs, which appear bright with their UV colouration. I would add that, in passerines such as blue tits, great tits and pied flycatchers, their greater-than-expected eye size compared to body size gives them a very efficient vision, also in the dark (Thomas et al. 2002, Gomez et al. 2014). Whether flycatchers would detect the proportion of white/UV in the nest cup, count the eggs, or feel the eggs (e.g. with the brood patch), remain of course to be experimentally tested.

7.2.3 The Owner Aggressiveness Hypothesis

When conducting experiments on social information use in the wild, we often only observe the resulting decision from the focal individuals, we do not have access to their prior

experience (except if controlled for), we do not know what they perceive and how they interpret the received information. Therefore, it is always valuable and interesting to explore several hypotheses regarding the mechanisms behind the observed behaviours. With their opinion article, Slagsvold & Wiebe (2017) helped rethinking the observed trends, called for further experiments, and proposed themselves another alternative explanation coined the Owner Aggressiveness Hypothesis (OAH).

The main assumptions behind the OAH are that (i) individuals should prefer settling in a site that limit predation risk, (ii) because of search-image strategies used by predators, it is risky to settle in boxes similar to the one used before or similar to the one from depredated competitors, and (iii) tits should defend extra nest boxes during breeding season, to facilitate re-nesting in case of breeding failure. According to the OAH, tits should invest more time and energy in protecting extra nest boxes that look different from their own current nest box. Another major assumption of the OAH is that flycatchers should prefer settling in nest boxes with the opposite symbol as the tit apparent preference, because tits and flycatchers share the same predators. Choosing a nest box with the opposite symbol would then be less risky in case of depredation of tits and search-image strategy of predators (I will come back to this hypothesis later on). Because tits would aggressively secure the nest boxes with the opposite symbol (e.g. circle) compared to their own current box, flycatchers would not be able to settle in the boxes with the opposite symbol and would, by default, settle in the nest box with the symbol matching the tit apparent preference (e.g. triangle).

Slagsvold & Wiebe (2017) also hypothesised that male great tits should be more aggressive during incubation because they are free from mate-guarding activities, and that “good quality tits”, with a large clutch size, presumable older, in better condition, and motivated for a second clutch, should defend more their territory and other boxes. Flycatchers would be able to settle in their presumably ‘preferred’ box (with the opposite symbol) when the tits are still laying or are of bad quality (have a small clutch), and would otherwise only be able to settle in boxes with the same symbol as tits.

To explain the observed temporality in copying behaviour (late birds copying more),

Slagsvold & Wiebe (2017) argue that late flycatchers are more time-constrained, and do not invest in fights for the opposite symbol boxes, and thus, take more willingly boxes with the same symbol as the tit choice. This would be amplified by the fact that (1) later in the season, most tits are incubating, and then male tits have more time to invest in protecting opposite-symbol boxes, and (2) late breeding tits, with a small clutch at the time of late flycatchers settlement, have less time to protect other boxes.

In summary, the OAH states that flycatchers do not copy tits based on their clutch size, but rather are not able to settle in nest boxes with the opposite symbol as the tit apparent preference, because tits would agonistically protect these “opposite” nest box, especially when they are incubating (i.e. have a large clutch size).

7.2.4 Why isn’t the OAH likely?

The comments from Slagsvold & Wiebe (2017, 2018) raised awareness on the fact that some more justifications and experiments are needed to validate one hypothesis or another. However, there are also several inconsistencies, and rather speculative arguments in the OAH formulation. Most of them have been addressed in replies (Forsman et al. 2018, Samplonius 2018); here I will summarize and comment myself some (not all) of these points.

It is unlikely that flycatchers would prefer boxes with the opposite symbol

At the time of flycatcher settlement, the demonstrator tits are well alive, not depredated (Seppänen et al. 2011, Loukola et al. 2013). Their presence should thus attest of the non-predation of the nest and should constitute a valuable information (as mentioned by Slagsvold and Wiebe themselves, 2018). When tits are absent (e.g. deserted nests), flycatchers prefer to settle on top of their nest than in an adjacent nest bearing the opposite symbol, or 25 meters away in boxes with either symbol (Forsman and Seppänen 2011); we would not observe this trend if flycatchers were following an anti-searching-image predator strategy. However, predation on eggs or on adults (as it would be simulated in Forsman and Seppänen 2011) are two very different processes, so this justification has to be taken

with caution as well.

Ecological context favouring the OAH: low density and high nest predation risk

In the Finnish and Latvian populations, nest box densities reflect the natural occurrence of tree holes. In the Gotland and Dutch studied populations, nest boxes are provided largely in excess. Interestingly, only the Swedish population is rather free from nest predator: there are no mustelids on Gotland, the nest boxes are well maintained, and their entrances are protected in areas where woodpeckers are nesting nearby or where farm cats are hunting (usually specific restricted areas). Nest predation is thus very limited on Gotland. Slagsvold & Wiebe (2017) suggested that, if the OAH is true, the copying-rejection pattern should be stronger in areas with few nest holes (so that the tits are more territorial), and in areas with high predation risks. However, on Gotland we observe the same copying-rejection pattern (Chapter 5) than in areas with low density and high predation risks. Of course, due to our slightly different experimental design testing flycatcher copying behaviour (unpaired nest boxes, Chapter 3), our results are not fully comparable to the ones from Forsman and collaborators (e.g. Seppänen and Forsman 2007, Seppänen et al. 2011, Forsman and Seppänen 2011, Loukola et al. 2013). At least our results show that the observed patterns are quite robust to the ecological context. This is in favour of the “copy-the-successful” or SIU hypotheses.

Very selective territoriality of tits

Tit aggressiveness and territoriality around secondary nest boxes should be highly costly and remains to be tested. Nevertheless, there are several reasons to be sceptical regarding the fact that tits would defend more a box with the opposite symbol than a box with the same symbol as on their own current box. First, nest boxes are only separated by 2-5 meters within a pair of boxes (see the design described in Figure 7.2). Therefore, if tits protect one nest box, they are likely to protect the other one as well, or their aggressive behaviour is likely to deter intruders in both of them. Second, predators are likely to

prospect nest boxes that are only few meters away from each other (they usually predate an whole area, Samplonius 2018). Then, choosing an opposite symbol would not bring any fitness benefits against predators.

As well pointed out by Samplonius (2017), the symbols on the tit nest box were attached only after the settlement of tits: they did not choose to settle in a box with one symbol or the other. Choosing additional nest boxes according to a feature that one did not choose makes it a rather complex assumption. However, this is not so unrealistic because, as Slagsvold & Wiebe (2017) argued, tits have been shown to remember apparent symbol preference of their own species and other species (flycatchers), and use this information for their nest box choice the following year: they preferred to settle in nest boxes with the symbol associated to empty nest boxes the year before (Forsman et al. 2014).

Tits are probably less aggressive against flycatchers during incubation

The temporal variation of tit aggressiveness towards flycatchers along the season need to be tested, but at the conspecific level, great tits have been shown to be less aggressive during incubation than earlier on (Araya-Ajoy and Dingemanse 2014). Conspecific agonistic reaction may however originate from different motivation rules than heterospecific aggressiveness (avoiding paternity loss namely, Araya-Ajoy and Dingemanse 2014).

We don’t observe dead flycatchers in empty boxes

All dead flycatchers were found in active tit nests, not in empty adjacent nest boxes (Forsman et al. 2018). How can we explain that tits would kill flycatchers in their own nest but not when found in the nest they actively protect for future breeding? Slagsvold & Wiebe argue that tits probably do not risk injuries from fights in confined boxes, and cannot waste energy to kill prospecting flycatchers from nest box that they protect for future breeding; chasing and calling would certainly be enough to deter flycatchers (Slagsvold & Wiebe 2017). Their argument is rather speculative, but is useful to highlight that, if calling, chasing, or even hissing (from the incubating female) are enough to deter prospecting flycatchers, then they are likely to be often deterred from active primary tit

nests as well, explaining the absence of prospecting inside tit nest boxes at incubation. Even more convincingly, if great tits only chase/call to flycatchers prospecting in the further pair of boxes, being chased by tits when prospecting in the box with the opposite symbol would likely not make flycatchers settle in the other box two meters away either. Then, if tit aggressiveness at the further boxes occurred, flycatchers would not settle at all.

7.2.5 Do the results of this thesis help understand what is going on?

The main results of Chapters 3 and 5 are summarized in Table 7.1 and interpreted from the SIIU (like in my manuscripts) and the OAH perspectives.

Table 7.1: *Mains results of the thesis interpreted from the SIIU or the OAH perspectives.*

Copy/reject behaviour	SIIU	OAH
Pairs with young males copy more than pairs with old ones (Ch 3 & 5)	Young males copy more because inexperienced (“copy if uninformed”)	Young males, due to their inexperience, may be more likely to be deterred by tits at nest boxes with the opposite symbol. Most of them choose by default the other “matching” symbol.
Pairs with more aggressive old males reject more when tit clutch/brood size is small (Ch 5)	They have access to the information regarding the clutch size so they are the one rejecting when tit clutch size is low (“reject the unsuccessful”).	They are able to take over the tit preferred secondary boxes (opposite symbol), even more so when competition is low (during egg laying according to the OAH), so they choose the boxes with the opposite symbol.
Pairs with less aggressive old males are more likely to copy when tit density is high (Ch 5)	They have mostly access to the symbol information, maybe not many other information (like clutch size); at high density, the symbol signal is stronger, they are more likely to copy. Pairs with more aggressive males will on the contrary base their choice on multiple information, incl. tit clutch size.	They cannot take over the tit preferred secondary boxes (opposite symbol), even less so when competition is high, so they choose the boxes with the matching symbol.

At first, things do not seem much clearer when considering my results from Chapters 3 and 5 (Table 7.1). However, the interpretations I provide given the OAH, are based on one assumption: there is a gradient of competitiveness, yearling flycatchers assumed to be less competitive than non-aggressive adults, themselves less competitive than more aggressive old males. Therefore, young rarely take over the preferred “opposite” symbol boxes, old non-aggressive males may do so a bit more often, especially when tit clutch size is small, i.e. when tits are too busy mate-guarding to protect extra boxes. More aggressive old males would be more likely to settle in boxes with the opposite symbol. However, we showed that young males were more aggressive than old ones (Figure 4.2a in Chapter 4). Of course, before going any further in the assumptions, we should test whether aggressiveness of flycatchers against tits reflects truly their competitive abilities.

Results from the playback experiment (Chapter 6) are interesting to consider here as well: we showed that female flycatchers cue on acoustic features supposed to inform on tit quality, and adjust their decision depending on their own aggressiveness and age. These results remained the same whether some tits settled in the experimental zone or not. Therefore, without any other clue than tit songs, females adjusted their settlement choice according to the tit apparent quality. This could be considered as a “copy the successful (or dominant) if you can” strategy, supporting more the SIIU than the OAH.

7.2.6 Another complementary explanation

The initial questioning of the SIIU by Slagsvold & Wiebe probably comes from the fact that (1) prospecting in tit nests is highly risky, (2) tits would certainly protect their nest box, preventing flycatchers from entering and “counting” the eggs, and (3) when Slagsvold & Wiebe video recorded tit nest boxes in their Norwegian population, they did not observe flycatcher prospecting in tit nests (Wiebe pers. comm., no information on the sampling effort). Even though the OAH seems to present some inconsistencies and lack parcimony, I agree with them on the points that prospecting rate seems quite low, and that tit aggressiveness certainly plays an important role in this system and should be

further investigated.

I propose a hypothesis complementary to the SIIU, based on a multi-information approach. From this thesis and former studies (see Chapter 2), we know that flycatchers use multiple cues from great tits for their settlement decision (presence, density, phenology, reproductive investment and song features revealing their quality). In that respect, it is possible that flycatchers also use the behaviour of tits as a source of information. We could assume that more aggressive or more present tits are more likely to deter prospecting flycatchers around their nest box. In that case, **during egg laying**, flycatchers would be more able to access tit nests because tits are less present around their nest box. Then, they could use the clutch size as a source of information. The cover on the top of the clutch is highly variable, going from an opaque layer of wool and fur to a single small feather. As large clutch tend to be less covered than small clutch (pers. obs.), the visibility of eggs should still reflect the size of the clutch. Loukola et al. (2014) showed that (a) 24 hours after withdrawing the cover from tit nest, the clutch was again covered at 70-87%, and (b) when broadcasting songs of flycatchers at their vicinity of the box, tits covered their eggs with 41% more hair and 17% more carefully (clutch coverage) than in response to a waxwing playback. In normal conditions (a), if flycatchers only prospect but do not display near the nest box, 13-30% of the clutch should still be visible despite the cover.

In Seppänen and Forsman (2011), most tits were incubating, but flycatchers' probability to copy depended on the tit clutch size at the time of flycatcher settlement. How can flycatchers cue on the tit reproductive investment if they cannot enter the nest box? As the presence of tits in or around their nest box increases **at incubation**, the simple presence of tits should indicate to flycatchers that the nest is active. Flycatchers could also use other information such as great tits songs, alarm calls, aggressive behaviour, hissing calls from the female inside the box, great tit body mass, colouration, etc.. These cues could indicate to flycatchers that tits are highly competitive, dominant, motivated to keep their nest, or overall of good quality, and therefore presumably defending a high quality territory, likely to deter predator, or more prone to make good choices (great tits

with greater cognitive abilities lay larger clutches, Cole et al. 2012, and have a higher reproductive success, Cauchard et al. 2013). If the intensity and/or occurrence of these tit behaviours covary with the tit reproductive investment, it would explain the greater copying behaviour when (incubating) tits have a large clutch size.

One enigma remains: how to explain that flycatchers copied more in the presence of 5 covered than 13 covered tit eggs in Loukola et al. experiment (2013)? The authors argued that this unexpected result might come from a change in tit (aggressive) behaviour after clutch manipulation.

7.2.7 Further testing

Further experiments and rethinking the observed copy-reject pattern should help our understanding of the underlying processes involved. Lots of questions still need to be addressed, for example: Can flycatchers count? How often do the flycatchers prospect around (and not necessarily in) tit nest boxes? How often do they try to enter? Does the behaviour of the tits affect the copying behaviour of the flycatchers?

Despite several experiments to test heterospecific social information use in flycatchers, we still lack evidence of the mechanisms behind this behaviour, for the obvious reason that it can be difficult to measure in the wild. Here are some first easy steps to at least refute hypotheses: Slagsvold & Wiebe (2017) proposed to test the aggressiveness of tits at different distances from their nest with an alive caged flycatcher; Forsman et al. (2018) suggested to conduct another symbol experiment, during which eggs would be completely covered during egg laying, and the choice of flycatchers monitored. If the probability to copy still increase with the number of eggs laid, then either the OAH or the multi-information hypothesis I proposed would be more likely than the pure SIIU. Another promising study is on-going in southern Finland: pied flycatchers have been PIT tagged for several years near Turku and their prospecting behaviour in boxes was recorded (Ratnayake, Thompson, Laaksonen, unpubl.). Ideally, measuring the aggressiveness of these PIT-tagged flycatchers would allow answering the assumption we made in Chapter 5: do

the more aggressive males prospect more inside tit nest boxes? In parallel, measuring the aggressiveness of the breeding tits would allow answering whether flycatchers prospect less in nest boxes with more aggressive tits. To gather more data on prospecting behaviour, we could use laser detection at the entrance of nest boxes (Dutour pers. comm). This method does not allow identifying the species entering the nest box, but easily provide a large amount of data on visitation rate. RFID and laser methods allow automatic detection which ease data analyses but do not inform at all on the behaviours of birds outside the nest boxes, which could be very important in the tit-flycatchers system. Direct observations have the advantage of detecting birds in a wider spatial range than using cameras. In populations with low nest box density (to increase the chances of prospecting event), we could conduct an experiment using available nest boxes to compare the visitation rate (with RFID or laser method) or the approach and behaviour of prospecting flycatchers (with direct observations or video-recordings). By manipulating the content of the available nest boxes, we could record the prospecting behaviour (1) in completely empty nest boxes, (2) in boxes with a tit nest added, (3) in boxes with a tit nest added and playback of tit songs, or (4) in boxes with a tit nest added, tit playback, and a tit decoy on the nest box.

Better understanding the mechanisms behind heterospecific social information use should increase our understanding of the evolution of this behaviour. The various experiments highlighted how complex this flycatcher-tit system is. The fact that great tits cover more their eggs after hearing a flycatcher singing nearby suggest that there is an arm-race between the two species. Very rarely, flycatchers have also been seen withdrawing wool and fur from tit nest boxes (Loukola et al. 2014). Explanations for these complex patterns can be quite simple, with a ‘copy-the-successful’ strategy weighed given one’s competitive ability, but it is of course only one side of the story. The contrasting populations from Sweden, Finland, Norway, the Netherlands and Latvia provide a great opportunity to study whether the driving forces behind such a complex system are common or on the contrary differ between ecological contexts (e.g. predation and parasite load, onset of tit and flycatcher breeding). This decade of research on the flycatcher-tit information

system broadened our view of heterospecific social information use, social learning, and signal eavesdropping. Many more experiments could (or should) be conducted to fully understand these complex copying behaviours.

7.3 What do we really measure with our personality assays?

When estimating behavioural traits, it is always difficult to be sure that what we are observing and what we are analysing match what we are interpreting. As mentioned in the introduction for example, I was reluctant to use the term “exploration” to refer to the reaction of the flycatchers to a novel object. Several studies showed that responses to novel objects and in novel environments do not always correlate (reviewed in Carter et al. 2013), but of course, this problem is not restricted to this specific test. There are indeed different ways to measure personality traits falling under the same umbrella term: for example boldness can be measured as the reaction to humans (flight initiation distance is often used), to predators (dummy predators, or predator cues), as struggle while handling at capture (even though some categorise it as aggressiveness, it seems rather a response to risks). To ensure that I reliably estimated aggressiveness, boldness, and neophobia, we should have measured it in different ways, with different tests. If the different measures of the supposedly same trait do not correlate, then we should consider which one better translates the biological reaction we wanted to measure.

Aggressiveness can be tricky to measure with different tests because to measure agonistic reaction towards competitors, one has to present competitors (or associated cues) to elicit a response. The aggressiveness towards flycatchers vs. great tits can be considered as aggressiveness response in two different contexts. The responses to these contexts were more correlated among females than among males (Chapter 4). I extracted aggressiveness

scores with different methods, which allowed me to be rather confident that at least the statistical computation of the aggressiveness scores did not impact the results. Besides, the number of moves close to the box and the number of attacks toward the dummies are rather intuitive measures of aggressiveness (even though the fact that alive birds intruding during the tests might have biased the response of some individuals). One concern regarding our aggressiveness test is the variance associated to the observer identity: either some people detected better birds in the vegetation, or the relative distance estimate (2-5-10 meters from the boxes) differed greatly between observers, or some observers were noisier than others. An alternative set up would have been to video-record the tests, but this represents a much greater time investment for subsequent data extractions. Another alternative was of course to capture the birds and estimate their aggressiveness in a control room, but is not really possible with breeding flycatchers without greatly impacting their already time-constrained reproduction (if we had to keep them several days to repeat the behavioural tests). Besides, without the nest box to protect, flycatchers would probably have shown more fear than aggressive response. Finally, by testing the birds in control rooms, we would not have been able to test that many individuals, a trade-off between quantity and accuracy that we had to make for such a large scale experiment.

Regarding boldness, other alternative methods, more independent from the neophobia test, were used but are not analysed yet. In particular, we wanted to estimate the reaction of the birds (1) towards a stuffed predator, (2) while handling (struggle, alarm), or (3) when releasing after capture (we released incubating females inside their box and monitored the time it took them to leave the box). It will be very interesting to compare the response of the birds in the four types of tests. I actually expect the correlation between tests to differ between males and females. Females suffer a greater predation risk than males at incubation. Besides, we can imagine that in such a long-term monitored population, in which we capture females during incubation since the 80's, we might have selected females that are quite tolerant to human handling and disturbance. Therefore, compared to males, females might be less disturbed by humans (as observed in Chapter 4) but more disturbed by predators.

As for neophobia, it would have been interesting to measure the reaction in a novel environment (exploration) and/or the reaction towards different objects, at different breeding stages (nest building, incubation, chick rearing). In 2015, I conducted neophobia tests twice in the season on approx. 80 flycatcher pairs: once during nest building (with a pink clothespin) and once during chick provisioning (with the plastic toy). We did not randomly assign the object to be used in the tests, to keep the same protocol across years for the test during chick provisioning. Unfortunately, the data are also still in the process of being extracted. Given the high between-year repeatability of neophobia in our population, I expect the within-year repeatability to be either (1) as high if this behaviour shows generally a low plasticity or if it strongly depends on physiological states specific to the breeding status for example, or (2) much lower if the response is stage-specific, for example if the motivation and stress during chick provisioning is greater than during nest building. In this latter case, estimating neophobia and boldness only at chick rearing would have biased our sample towards individuals that successfully reached the chick provisioning stage. Estimating neophobia and boldness at an early and a late breeding stage will bring interesting new insights in that respect.

Further work is needed to assess whether we reliably estimated boldness, neophobia and aggressiveness, or whether we measured context-specific behaviours for which sexes respond differently, as it seems to be the case for aggressiveness in the conspecific and heterospecific contexts.

Conducting the behavioural assays in controlled environments, i.e. capture the individuals and perform behavioural tests in aviaries or control rooms, instead of on site, would likely have reduced the observed environmental variances. Conducting the behavioural tests on site, however, presents the ethical and methodological advantages to (1) minimize the disturbance of breeding birds, (2) to elicit natural behaviours on which selection may operate, and not behaviours altered by stress (as it has been already described in collared flycatchers, Gáramszegi et al. 2009), and (3) to avoid sampling bias when captured individuals are not a random sample of personality phenotypes (Biro and

Dingemanse 2009, Garamszegi et al. 2009). By measuring aggressiveness on site, near the nest boxes, we estimated so-called “pseudo-repeatabilities”, as each pair was tested in the same particular environment during the same year (Westneat et al. 2011, Niemelä et al. 2015). As such, our repeatability estimates might be overestimated (Dingemanse and Dochtermann 2013), even though we controlled for several environmental and methodological factors. However, as explained in Chapter 4, only very few flycatcher pairs rebounded or bred in the same nest box several years, individuals were thus tested in different social and physical environments between years which should limit the risk of pseudo-replication (Niemelä and Dingemanse 2017). Therefore, we hope to have avoided such issues, while estimating more accurately the natural response of the birds. Of course, it also leads to greater methodological residual variances : not always the same weather, light or noise, not always alive intruders during the aggressiveness test. By improving and standardising the methods, and keeping the ecological relevance of each measure for each species, we can probably gain a lot from measuring personality traits on site.

7.4 The evolution of social information use: some research perspectives

The flycatcher-tit system is a convenient model to study social information use, representing the migrant in need of quickly acquired information and the knowledgeable resident species. The findings on this system could be extended to other migrant species, but also to other central-place foragers, and in general to other species using social information (for breeding site selection or more generally). One frustration posed by studying collared or pied flycatchers is that we cannot observe or sample them on their wintering grounds (despite some –failed– attempts on pied flycatchers by colleagues from Uppsala!). But before wondering how the flycatcher behaviour might differ between breeding and non-

breeding season, there are still many more questions we can attempt to answer with data collected during breeding. The results of this thesis help to better understand why individuals differ in their use of (heterospecific) social information. However, some more questions should be addressed to get a better insight on the evolutionary potential of this behaviour. In this section, I aim to provide some perspectives for future research.

7.4.1 Inheritance of social information use: truly absent?

Similarly to a correlative study on the same population (Tolvanen et al., in prep), I did not find any inheritance for social information use in collared flycatchers. Based on 6 years of breeding data on flycatchers and tits (2004-2010), Tolvanen et al. estimated the additive genetic variance of nest site choice according to the social environment around the chosen nest box. This social environment was either the abundance or success of other flycatchers and tits, in the same forest patch, in the year before or the current year. The use of all these sources of information were repeatable in males (and marginally so in females), but were non heritable. However, Tolvanen et al.'s and my own results should be taken with caution and might greatly be due to high environmental variance in our measurements of social information use.

One of the next steps that could be taken based on these data is to try disentangling genetic from cultural inheritance from the parents. With the large number of cross-fostering experiments that have been conducted on the Gotland population since the late 80's, we could combine both the pedigree based on the original parents (as in Chapter 3 and in Tolvanen et al.) and the pedigree based on the foster parents, to estimate the genetic and social heritability of the use of various social information studied in Tolvanen et al. (the “double pedigree” approach, Danchin et al. 2013).

Another approach would be to focus on the plasticity in the use of various types of information. As discussed in the thesis manuscripts, the “asynchrony” (time interval between the onsets of breeding) between flycatchers and tits is so variable between years that we could imagine flycatchers to plastically use one or another source of information

depending on this synchrony, and depending on their own competitive abilities. The plasticity in social information use could be repeatable, heritable and selected for if it provides fitness benefits (see e.g. Brommer et al. 2008 on the repeatability and heritability of plasticity in laying date depending the temperature, or Araya-Ajoy and Dingemanse 2017 on the repeatability and non-heritability of between-year plasticity in great tit aggressiveness). In practice, estimating the repeatability and heritability of social information use might be complicated to implement because what we measure as a use of information is a nest site choice (n=1 observation per year) characterised either by the symbol on it (binary choice, see Chapter 3, experiment between 2012 and 2016), or by the social environment around the chosen nest box. In this latter case, the choice of an individual is characterised by a variable (e.g. average number of tit eggs in boxes surrounding the flycatcher nest) that depends itself on the asynchrony between tits and flycatchers (Figure 7.3). In a given year, if tits start to breed early, then all the flycatchers will have a relatively high number of tit eggs in the boxes surrounding their own nest. If on the contrary tits start breeding late, there will be no egg in the tit nests at the time of flycatcher settlement; then we will record that “flycatchers chose to settle in an area with an average number of eggs of 0.00”... But did they really choose their nest box based on that (absence of) information? The availability of options for flycatchers’ settlement (represented by the black funnels in Figure 7.3) is *de facto* limited by the asynchrony between tits and flycatchers.

Besides, flycatchers are short-lived, and the age of flycatchers (among other individual factors) affects their use of social information. As one year represent one “context”, not all individuals will be sampled in the same contexts, at the same age. With the missing observations we have some years, and the overlapping and short generations in this species, our dataset does not seem ideal for that kind of analyses (Figure 7.3). Another difficulty with our study-system is the variety of social information used. The simplified example represented in Figure 7.3. does not account for the multiple sources of information which may be used differently depending on the season, or on the aggressiveness and sex of the flycatchers. I am not an expert in the field of behavioural plasticity, so I am not sure whether studying the plasticity in social information use for breeding site selection

would be possible with our dataset. Because breeding site choice is a rather rare event, studying a long-lived species (e.g. kittiwakes) should ease investigations of plasticity in social information use. Whether the use of social information would be more or less plastic in long-lived than in short-lived species is another issue. Another interesting and easier perspective would be to estimate the repeatability and heritability of social information use (and its plasticity) in the foraging context (e.g. on fish, lizards). We could also subsequently compare the use of social information across contexts (foraging vs. breeding site choice).

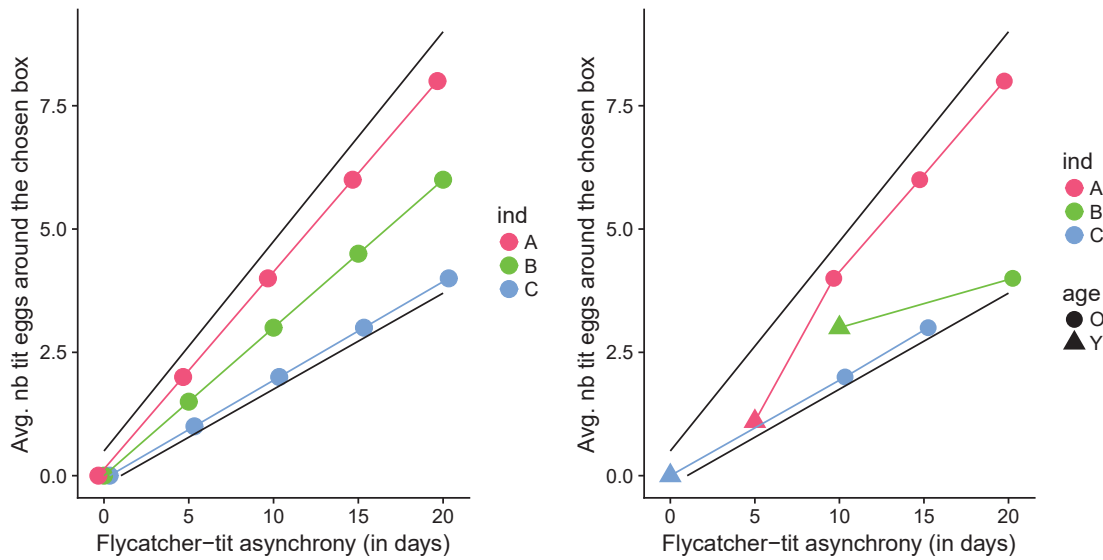


Figure 7.3: Representation of the reaction norms in social information use for three hypothetical individuals (A, B, C), given the flycatcher-tit asynchrony. The asynchrony is characterised per breeding season and refers to the time-lag in onset of breeding between flycatchers and tits. The use of social information here is measured as the average number of eggs in tit nests surrounding the chosen nest box (y axis). Black lines show the funnel of actual possibilities of settlement for flycatchers (i.e. minimum and maximum average number of tit eggs around any available nest box). On the left panel is an ideal situation where all individuals are sampled in the same context (x axis). On the right panel, individuals are not always sampled in each context, and the slopes may differ depending on the individuals age.

7.4.2 Estimating the fitness outcome of social information use

To better understand the selective pressures acting on the use of (heterospecific) social information for breeding site selection and the maintenance of variability in this behaviour at the population level, it is of tremendous interest to estimate the fitness consequences of the resulting decisions. In our particular case, it would be interesting to evaluate the lifetime reproductive success (number of fledglings and recruits) and the survival of the flycatchers depending on their personality scores and on their use of social information. Interestingly, it has already been demonstrated that flycatchers gain fitness benefits from settling near great tits (more and heavier flycatcher nestlings when reared close to tit nests, Forsman et al. 2002; even when this settlement is experimentally forced, flycatchers nestlings had either longer wings or tarsi when reared near a tit nest, Forsman et al. 2007).

We showed that aggressiveness plays an important role in shaping heterospecific social information use among old individuals. Given the potential energetic costs associated with aggressiveness, aggressive individuals could have a lower survival, but may protect their nest / brood more efficiently, and thus have a higher reproductive success. Preliminary analyses revealed that it is not the case: the number of fledging did not increase with aggressiveness of the parent. However, further analyses, in particular of the failure probability, the number of recruits and the parent survival would help determine whether the maintenance of aggressiveness (and social information use) variability in this population is due to different life-history strategies.

In conclusion, the results of this thesis highlight the importance of personality differences in shaping the use of heterospecific social information in the context of breeding site selection. This thesis also broadens the currently known sources of social information to heterospecific sexual signals. In the context of climate change, the advanced onset of laying observed in several bird species to match the earlier peak of food abundance, could disturb the information transfer between species (reviewed in Parejo 2016). The flycatcher-tit system for example is highly dependent on the 'asynchrony' between the species. On Öland (south-west of Gotland), collared flycatchers, similarly to tits, have been shown to better adjust their onset of breeding in response to climate change than pied flycatchers (Sirkiä et al. 2018, see also Burger et al. 2012). A change in the timing between flycatchers and tits could lead to information mismatch, with potential consequences on individual fitness (Parejo 2016). Better understanding the observed differences in social information use and personality should help us predict the evolution of this behaviour and more globally of community shaped by heterospecific information use.

7.5 References

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