Sources of variability in heterospecific social information use for breeding habitat selection: Role of genetics and personality in collared flycatchers
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The examination will be conducted in English. Faculty examiner: Dr. Rachel Kendal (Durham University, UK).

Abstract

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 albigilis, 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


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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 lämpligt 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) Uppläsningar 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 skalar. 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 årtliga, 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 parningssignal låttillgängliga 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 caeru-
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 skalar (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 skalar. 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 påverkade 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 extrahade jag uppskattningar av aggressivitet, djärvhet och neofobi hos häckande hanar och honor, uppskattade repeterbärheten 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 härsleds 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 mel lanartsspecific 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/områdes-preferens, 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 sångsegenskaper som återspeglar mellanartsspecifika kvaliteter. Omvänt spelade genetiken ingen direkt roll för att forma användningen av mellanartsspecifick 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 framtida dess evolutionära mekanismer och konsekvenser.

Översättning av /translation by Lars Gustafsson
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 nichoir. 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 évolutif 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
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
Résumé détaillé en français

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 répétibles, 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 vivants 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 couteuses 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 couteux 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 hétérospecifique 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 contenue dans le chant d’une autre espèce, alors que cette information est destinée initialement au choix
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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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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 broaden and refer 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.
Chapter 1 General introduction

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 Social information in various contexts

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
Chapter 1 General introduction

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” (aggreg-
atron 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 con-
stantly 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 qual-
ity or performances, a strategy used for example in mate choice, rival assessment, and fish
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 alter-
atively 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-scrounger 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, Rieucau 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, Rieucau 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 loosing visual contact with the shoal, a situation that should be risky if 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-
1.3 A variable use of social information

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; Cauchoix 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, physiolo-
gical, 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 constrains 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 constrains 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 favour 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).
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-
1.4 Personality differences: source of variability in social information use.

formations 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 that 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.](image)

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).

<table>
<thead>
<tr>
<th>Taxa &amp; Species</th>
<th>Pop.</th>
<th>N</th>
<th>Context</th>
<th>Social information</th>
<th>Perso. trait</th>
<th>Link</th>
<th>Details</th>
<th>Reference</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branta leucopsis</td>
<td>c</td>
<td>28</td>
<td>F</td>
<td>Neophobia +</td>
<td>Neophobic individuals join conspecifics at feeding site</td>
<td></td>
<td>Kurvers et al., 2010a [1]</td>
<td></td>
<td>1</td>
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</tr>
<tr>
<td></td>
<td>c</td>
<td>12</td>
<td>F</td>
<td>Neophobia +</td>
<td>Neophobic individuals join conspecifics feeding at higher rate</td>
<td></td>
<td>Kurvers et al., 2010b [2]</td>
<td></td>
<td>2</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>S</td>
<td>Neophobia + Neophobic individuals followed demonstrator in a maze, rather than lead (only when 1 demonstrator, no personality effect when 3)</td>
<td></td>
<td></td>
<td>Kurvers et al., 2011 [3]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corvus frugilegus</td>
<td>wc</td>
<td>19</td>
<td>F</td>
<td>Neophobia -</td>
<td>Less neophobic individuals produced more (foraging context), but scrounged more than neophobic ones.</td>
<td></td>
<td>Jolles et al., 2013 [4]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>w</td>
<td>152</td>
<td>F</td>
<td>Sociability</td>
<td>Individuals with a higher centrality had more chance to discover new food patch, likely due to a greater access to social information</td>
<td></td>
<td>Aplin et al., 2012 [6]</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>36</td>
<td>S</td>
<td>Exploration -</td>
<td>Slow explorers were more socially attractive and choose feeding sites with conspecifics</td>
<td></td>
<td>Aplin et al., 2014 [7]</td>
<td></td>
<td>7</td>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Snijders et al., 2017 [8]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Taeniopygia guttata</td>
<td>c</td>
<td>24</td>
<td>F</td>
<td>Exploration NS</td>
<td>Neophobic individuals exhibit more exploration in response to a conspecific (on conspecific, no effect in control)</td>
<td></td>
<td>David et al., 2011 [9]</td>
<td></td>
<td>9</td>
</tr>
</tbody>
</table>

Additional notes:
- Aves
  - Conspecific attraction (mimicking social defeat or mate choice decisions)

References:
- [1] Kurvers et al. (2010b)
- [2] Kurvers et al. (2010a)
- [9] David et al. (2011)
Table 1.1. (Continued)

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

### Table 1.1

<table>
<thead>
<tr>
<th>Taxa &amp; Species</th>
<th>Pop.</th>
<th>N</th>
<th>Context</th>
<th>Social information</th>
<th>Perso. trait</th>
<th>Link</th>
<th>Details</th>
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<tbody>
<tr>
<td><strong>Pisces</strong></td>
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<td><em>Gasterosteus</em></td>
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<tr>
<td><em>aculeatus</em></td>
<td>wc</td>
<td>60</td>
<td>S</td>
<td>Schoaling tendency</td>
<td></td>
<td>Ward et al. (2004);[15]</td>
<td>Shy individuals tend to schoal more</td>
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<tr>
<td></td>
<td>F</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>wc</td>
<td>30</td>
<td>F</td>
<td>Sites with higher conspecific feeding rate</td>
<td></td>
<td>Webster et al. (2007);[16]</td>
<td>Exploration NS No effect of exploration on public information use</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>wc</td>
<td>43</td>
<td>F</td>
<td>Joining conspecifics feeding vs. non feeding conspecifics</td>
<td></td>
<td>Harcourt et al. (2010);[19]</td>
<td>Exploration NS Joining conspecifics feeding vs. non feeding conspecifics</td>
</tr>
<tr>
<td><strong>Poecilia reticulata</strong></td>
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<tr>
<td></td>
<td>wc</td>
<td>136</td>
<td>F</td>
<td>Scrounging for feeding site</td>
<td></td>
<td>Harcourt et al. (2010);[19]</td>
<td>Boldness NS Joining conspecifics feeding vs. non feeding conspecifics</td>
</tr>
<tr>
<td><strong>Pungitius</strong></td>
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<tr>
<td><em>wc</em></td>
<td>60</td>
<td></td>
<td>F</td>
<td>Public information</td>
<td></td>
<td>Webster et al. (2015);[21]</td>
<td>Sociability NS</td>
</tr>
<tr>
<td><strong>Symphodus tinca</strong></td>
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<td></td>
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</tr>
<tr>
<td><em>w</em></td>
<td>25</td>
<td></td>
<td>S</td>
<td>Schoaling tendency</td>
<td></td>
<td>Budaev et al. (1998);[22]</td>
<td>Activity + Active S. tinca schoal more</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
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<td></td>
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<tr>
<td><em>ocellatus</em></td>
<td>w</td>
<td>23</td>
<td>S</td>
<td>Schoaling tendency</td>
<td></td>
<td>Budaev et al. (1998);[22]</td>
<td>Activity NS No correlation in activity S. ocellatus</td>
</tr>
</tbody>
</table>

Personality traits did not affect the probability of behaving in a certain way. The table below further details these observations.

1.4 Personality differences: source of variability in social information use.

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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pop.</th>
<th>N</th>
<th>Social information</th>
<th>Perso. trait</th>
<th>Details</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Amphibia</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Tiliqua rugosa</td>
<td>w</td>
<td>23</td>
<td>Social network position for 81 days (mating, foraging)</td>
<td>Aggressiveness / Boldness</td>
<td>Less aggressive / shyer individuals interacted more with females within the network</td>
<td>[1]</td>
</tr>
<tr>
<td><strong>Aves</strong></td>
<td></td>
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<tr>
<td>Parus major</td>
<td>w</td>
<td>90</td>
<td>Social networking during foraging</td>
<td>Exploration</td>
<td>Fast Explorers had numerous but weaker and less persistent social bonds within social network</td>
<td>[2]</td>
</tr>
<tr>
<td>Parus major</td>
<td>w</td>
<td>13</td>
<td>Social networking during breeding season</td>
<td>Exploration</td>
<td>Slow explorers had a less central spatial position within the social network</td>
<td>[3]</td>
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<tr>
<td>Parus major</td>
<td>w</td>
<td>775</td>
<td>Social networking during foraging</td>
<td>Sociability</td>
<td>Individuals are repeatable in their social position within foraging social networks, implying constraints on the access and use of social information</td>
<td>[4]</td>
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<tr>
<td>Poecile atricapillus</td>
<td>w</td>
<td>68</td>
<td>Diffusion of social information through network (NDBA analysis) during foraging</td>
<td>Exploration</td>
<td>No effect of exploration on diffusion of social information</td>
<td>[5]</td>
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<td><strong>Pisces</strong></td>
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<tr>
<td>Gasterosteus aculeatus</td>
<td>wc</td>
<td>120</td>
<td>Social networking in shoal</td>
<td>Boldness</td>
<td>Shy individuals formed long-lasting bonds with few individuals.</td>
<td>[6]</td>
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<td>Neolamprologus pulcher</td>
<td>n/a</td>
<td>215</td>
<td>Social networking during group settlement in this cooperative breeder</td>
<td>Exploration Neophobia Aggressiveness</td>
<td>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.</td>
<td>[7]</td>
</tr>
<tr>
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<td>Social networking in shoal</td>
<td>Boldness Sociability</td>
<td>Shyer individuals, with a higher tendency to shoal (sociable), have more and stronger social bonds</td>
<td>[8]</td>
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</table>

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,
1.5 Aims of the thesis

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 constrains 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.
1.6 References


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1.6 References


Chapter 1 General introduction


Wilson, D. S. 1998. Adaptive individual differences within single populations. Philosoph-
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.](image-url)
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 sympathy 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
2.1 Study species & site

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 5-7 eggs. (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).
2.2 Social information use in collared and pied flycatchers

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).

![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).](image)
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)
2.3 Data recording

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. There 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).
2.3 Data recording

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.
2.4 References


Philosophical Transactions of the Royal Society B: Biological Sciences 365:1841–1852.
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 constrains. 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 agonstic 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
7.1 Summary of the results

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

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

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

Flycatcher 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 provisionning 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 ob-
serve 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),
7.2 What do we really measure with the ‘symbol experiments’?

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 mentionned 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 is no mustelids on Gotland, the nest boxes are well maintained, and their entrance is 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 SIIU hypotheses.

**Very selective territoriality of tits**

Tit aggressiveness and territoriality around secondary nest boxes is really occurring 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 that earlier on (Araya-Ajoy and Dingemanse 2014). Conspecific agonistic reaction may however originate from different motivation rules than heterospecific aggressiveness (avoiding paternity lost 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.**

<table>
<thead>
<tr>
<th>Copy/reject behaviour</th>
<th>SIIU</th>
<th>OAH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pairs with young males copy more than pairs with old ones (Ch 3 &amp; 5)</td>
<td>Young males copy more because inexperienced (&quot;copy if uninformed&quot;)</td>
<td>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.</td>
</tr>
<tr>
<td>Pairs with more aggressive old males reject more when tit clutch/brood size is small (Ch 5)</td>
<td>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”).</td>
<td>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.</td>
</tr>
<tr>
<td>Pairs with less aggressive old males are more likely to copy when tit density is high (Ch 5)</td>
<td>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.</td>
<td>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.</td>
</tr>
</tbody>
</table>
7.2 What do we really measure with the ‘symbol experiments’?

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

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 that 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.
7.3 What do we really measure with our personality assays?

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 operates, and not behaviours altered by stress (as it has been already described in collared flycatchers, Garamszegi 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 (herterospecific) 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 pasticity 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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Chapter 7 General Discussion


