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# Foraging plasticity variation in wild great tits along contrasted ecological habitats

Thomas Crouchet

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# THÈSE

En vue de l'obtention du  
**DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE**  
Délivré par l'Université Toulouse 3 - Paul Sabatier

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Présentée et soutenue par  
**Thomas CROUCHET**

Le 14 décembre 2023

**Variation de la plasticité de la recherche de nourriture des  
mésanges charbonnières sauvages dans des habitats  
écologiquement contrastés**

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Ecole doctorale : **SEVAB - Sciences Ecologiques, Vétérinaires, Agronomiques et  
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Thèse dirigée par  
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# FORAGING PLASTICITY VARIATION IN WILD GREAT TITS ALONG CONTRASTED ECOLOGICAL HABITATS

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Présentée par Thomas Crouchet

En vue de l'obtention du grade de Docteur de l'Université de Toulouse en  
Ecologie, Biodiversité et Evolution

1er octobre 2019 – 30 septembre 2023



*« Va prendre tes leçons dans la nature »*

*Léonard de Vinci*

## **AVANT-PROPOS**

J'ai commencé cette thèse à un moment où je me faisais à l'idée que la recherche était derrière moi. Plusieurs années après l'obtention de mon Master, malgré de nombreux stages aux quatre coins de l'Europe et plusieurs tentatives, la nouvelle que je n'attendais plus est tombée au début du mois de juillet 2019. J'étais en plein milieu d'une correction de copie du Brevet d'un niveau très modeste d'un élève de troisième de l'Oise quand mon téléphone sonna. Normalement, un correcteur ne doit pas trop s'éloigner de ses copies mais quand j'ai vu que mon correspondant était Philipp Heeb, je n'ai pas pu résister à l'envie de décrocher. Mes collègues correcteurs doivent encore se demander aujourd'hui ce qui, dans la copie de mon jeune élève anonyme de troisième, a bien pu me pousser à faire une danse de la joie au milieu du couloir. Après un modeste sms à mes proches, « je vais faire une thèse ! », je suis retourné à mes corrections de copie sans réaliser l'opportunité qui s'offrait à moi. Me voilà aujourd'hui, 4 ans plus tard, à la fin de cette thèse mais j'espère au début de mon aventure dans la recherche scientifique.

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Etre un doctorant, c'est d'après le Larousse, être un étudiant titulaire d'un master et préparant une thèse. A mon avis, il manque quelques éléments dans cette définition. Ce n'était pas seulement une préparation de thèse, c'était être menuisier (pour fabriquer des meubles sur lesquels poser des écrans et des mangeoires), électricien (pour réparer les câblages électriques sur des systèmes automatisés), informaticien (depuis la programmation jusqu'au dépannage de bug sur des mini-ordinateurs), technicien de surface (pour balayer inlassablement les volières à la recherche de la moindre petite graine au sol), enseignant (pour donner des TP à des étudiants de licence avides de savoir), chauffeur routier (pour transporter inlassablement du matériel entre Toulouse et Moulis), gestionnaire financier (pour s'occuper des commandes de matériels tout en respectant les marchés de l'Université sans exploser le budget), responsable des ressources humaines (pour recruter une équipe de stagiaires qui participe à la collecte des données), chef d'équipe (pour coordonner les stagiaires sur le terrain), archiviste (pour organiser la base de données après le terrain), soigneur animalier (parce que le bien-être animal des mésanges est essentiel), statisticien (pour faire parler les données collectées et

démêler les codes dans R), écrivain (pour réussir, je l'espère, à écrire une thèse intéressante), éditeur (parce qu'une fois qu'elle est écrite, il faut la relire et la corriger), conférencier (pour diffuser les nouveaux résultats à la communauté scientifique et au grand public)... Finalement, faire une thèse, c'est une expérience de vie, une aventure, c'est donc, comme le dit si justement Paul-Emil Victor : « *un état d'esprit. C'est être capable de refuser son destin, être prêt à partir à tout moment, concevoir encore et toujours de nouveaux projets, ne pas être assis, c'est en un mot vivre sa vie et la construire.* »

## **SUMMARY**

Phenotypic plasticity, and in particular its behavioral component, is considered to be a key trait that could help organisms facing the diversity of challenges from their environment and thus could precede and possibly facilitate adaptive evolution. Although evidence of inter-individual variation of behavioral plasticity has been found in a wide range of studies, little is known about the parameters at the origin of this variation. The overall aim of this PhD thesis is to investigate the factors that shape individual foraging decisions and plasticity. I conducted this research on wild populations of a passerine species living in contrasting habitats, the great tit (*Parus major*), and used newly developed automated feeders with a system of video playbacks that limit the impact of research on animal welfare. First, in line with theory, I provide evidence for the importance of environmental harshness on foraging plasticity whereby individuals originating from higher elevation were more risk-prone in their foraging decisions. These differences were strengthened by seasonal variation and modulated by age, body mass and sex. I then give experimental evidence that foraging decisions by individuals were modified by the size and species composition of the social group and were context-dependent as they were different in secured, stressful or disturbed situations. The degree of change in foraging varied among individuals based on their age and body mass. Finally, I show that the link between social foraging plasticity and cognitive abilities depended on the climatic season and the cognitive abilities measured. As such, the relation between plasticity and cognition appears to be more complex than initially expected. Furthermore, social plasticity is an intricate behavior resulting from an interaction of various cognitive abilities. My thesis thereby improves our understanding of the various factors shaping among and within individual variation in foraging and suggests that behavioral plasticity could be a key mechanism at disposition of individuals to face environmental challenges. The main next step is to investigate the consequences of plasticity variation on fitness in contrasted environments.

## **RÉSUMÉ**

La plasticité phénotypique, et en particulier sa composante comportementale, est considérée comme un trait clé qui pourrait aider les organismes à faire face à la diversité des défis de leur environnement et pourrait ainsi précéder et éventuellement faciliter l'évolution adaptative. Bien que des preuves d'une variation interindividuelle de la plasticité comportementale aient été trouvées dans un large éventail d'études, on sait peu de choses sur les paramètres à l'origine de cette variation. L'objectif général de cette thèse de doctorat est d'étudier les facteurs qui façonnent les décisions individuelles en matière de recherche de nourriture ainsi que leur plasticité. J'ai mené cette recherche sur des populations sauvages d'une espèce de passereau vivant dans des habitats contrastés, la mésange charbonnière (*Parus major*), et j'ai utilisé des mangeoires automatisées nouvellement développées avec un système de lecture vidéo qui limitent l'impact de la recherche sur le bien-être animal. Premièrement, conformément à la théorie, je fournis des preuves de l'importance de la rigueur de l'environnement sur la plasticité de la recherche de nourriture, en montrant que les individus originaires de plus hautes altitudes sont plus enclins à prendre des risques dans leurs décisions alimentaires. Ces différences sont renforcées par les variations saisonnières et modulées par l'âge, le poids et le sexe. Je donne ensuite des preuves expérimentales que les décisions de recherche de nourriture des individus sont modifiées par la taille et la composition spécifique du groupe social et dépendent du contexte car elles diffèrent entre des situations sécurisées, stressantes ou perturbées. Le degré de changement dans la recherche de nourriture varie selon les individus en fonction de leur âge et de leur poids. Enfin, je montre que le lien entre plasticité sociale de recherche de nourriture et capacités cognitives dépend de la saison climatique et des capacités cognitives mesurées. Ainsi, la relation entre plasticité et cognition apparaît plus complexe que prévu initialement. De plus, la plasticité sociale est un comportement complexe résultant de l'interaction de diverses capacités cognitives. Ma thèse améliore ainsi notre compréhension des différents facteurs qui déterminent la variation de la recherche de nourriture entre et au sein des individus et suggère que la plasticité comportementale pourrait être un mécanisme clé à la disposition des individus pour faire face aux défis environnementaux. La prochaine étape vise à étudier les conséquences de la variation de plasticité sur la valeur adaptative dans des environnements contrastés.



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De nombreuses personnes ont contribué à l'aboutissement de ces 4 années de travail et sans qui, cette thèse n'aurait jamais vu le jour. Merci à tous pour le soutien que j'ai reçu !

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# **CHAPTER I.**

## **GENERAL INTRODUCTION**





## I. 1. BEHAVIORAL PLASTICITY VARIATION

### I. 1. 1. Phenotypic plasticity

Organisms are constantly faced with shifts in their social and ecological environments and in many cases (especially species that live multiple years), organisms would benefit from some flexibility to better survive and reproduce (Wund 2012). A major problem is to react appropriately to stimuli, either internal or external, received from their environment. When signals from the environment are predictable and stable over time and space, a standardized response may allow an organism to respond to challenges efficiently. However, when signals are changing, animals need to adapt their response in order to maximize fitness. Phenotypic plasticity is the ability of a given genotype to express distinct phenotypes in different environmental circumstances (Bradshaw 1965). Adaptive phenotypic plasticity allows individuals to cope with a range of environments by adjusting various traits like gene expression, behavior or morphological development (Sultan 2021). For example, spadefoot toads (*Scaphiopus multiplicatus*) develop a carnivorous tadpole morph when fed with shrimp but an omnivorous morph when reared on detritus (Pfennig 1992). Facing seasonal variations, northern populations of common blackbirds (*Turdus merula*) migrate in order to avoid drastic changes in temperature and difficulty finding food or survive (Winger et al. 2019) but southern ones are annually sedentary (Partecke and Gwinner 2007) while mammals hibernate until the environmental conditions improve again and adapt the length of hibernation to the climatic conditions (Geiser 2013). When it perceives a strong predator cues, the zooplankton *Daphnia* can induce the production of a protective spine (Scheiner and Berrigan 1998).

Plasticity is especially important when the rate or amplitude of changes in the environment outpace genetic adaptation (Vinton et al. 2022). Facing such rapid changes, behavior is considered the most plastic phenotypic traits as it shows the quickest response to temporal changes (Gross et al. 2010). When exposed to higher urban noise, male buntings (*Emberiza schoeniclus*) adjusted their songs immediately, singing at a higher minimum frequency and a lower rate in order to still be heard by conspecifics and defend their territory efficiently (Gross et al. 2010). Urban coyotes (*Canis latrans*) diversified their diet more than rural counterparts and were less neophobic towards new situations (Murray et al. 2015). House wrens

(*Troglodytes aedon*) female were more vigilant when risk or predation was higher while males adapted their provisioning effort under similar circumstances (Dorset et al. 2017). Actually, the ability to adapt behavior in response to environmental variation, known as behavioral plasticity, can provide advantages to individuals in order to survive and reproduce (Mery and Burns 2010; Stamps 2016). But if information changes and becomes less accurate, it may lead to maladaptive plasticity. So understanding what drives behavioral plasticity and how those elements might change with space or time is key (Stevens et al. 2023).

### I. 1. 2. Cognitive abilities

To react efficiently to changing stimuli, an organism needs to perceive an environmental cue, to use past experiences in order to identify the relevant reaction, to choose among the memorized or learned behaviors and finally to act appropriately. All these characteristics imply abilities to gather and use information known as cognitive abilities (Shettleworth 2001). As cognitive abilities are needed for the expression of behavioral plasticity, we should expect coevolution of these two traits. Selection pressures usually do not act directly on underlying mechanisms like cognitive abilities but rather on the performance result, or plasticity in the present case (Varela et al. 2020). The potential correlation between plasticity and cognition is not trivial when considering the actual debate in evolutionary biology about the main driver of the origin of cognition. The social intelligence hypothesis proposes that the evolution of cognition is driven by the complexity of social interactions (Dunbar and Shultz 2007; Emery et al. 2007; Scheiber et al. 2008) whereas the predator-prey intelligence hypothesis posits an impact of the complexity of predator-prey interactions (Zuberbühler and Jenny 2002) and the ecological intelligence hypothesis suggests the challenges associated with the search and manipulation of food as an origin of cognition (Rosati 2017). These hypotheses, although partially competing, suggest a similar model where the complexity of environmental signals requires dynamic and relevant behaviors that must rely on cognition. Recent evidence in humans (Plomin 2001), birds (Shaw et al. 2015; Ashton et al. 2018; Ashton et al. 2022) and insects (Finke et al. 2023) suggested that cognitive abilities may be general, i.e. that an organism with high abilities in one domain also exhibit good performance in another one. But to date results are conflicting depending on the cognitive aspect considered (associative learning (Barou Dagues et al. 2020), inhibition (Garnham et al. 2022) or problem solving

(Liker and Bókonyi 2009)) and we still lack clear and univocal evidence of this relation between behavioral plasticity and cognitions. Actually, a large variety of abilities are hidden behind the word ‘cognition’ such as innovation, learning, memorization, inhibition of irrelevant behaviors (Shettleworth 2001) and it would be surprising, regarding the diversity of challenges organisms face, that all these cognitive traits have similar and simultaneous effects on behavioral plasticity. Thus, the link between plasticity and cognition could be more complex than expected and deserves more attention.

### I. 1. 3. Behavioral plasticity selection

The degree of adaptive plasticity varies both within and across species which brings the question of why some organisms are more plastic while others are relatively fixed in their phenotypic expression (Snell-Rood and Ehlman 2021a). A general explanation is linked to the benefit cost trade-offs an organism is dealing with while developing and maintaining behavioral plasticity. Limiting mechanisms could be related to morphological constraints, limits on sensory capabilities or cognitive abilities (Hazlett 1995; DeWitt et al. 1998). Organisms that rely on learning to adjust plastic behavior experience high costs of time in sampling the environment but also in development, energy and neural machinery in order to develop the neural networks necessary for their cognitively demanding behaviors (Mery and Kawecki 2005). By specializing on a particular fixed trait, non-plastic organisms may be able to achieve more extreme trait values, which can be advantageous facing predictable environments. In a predator free environment, specialist *Daphnia* that never produce a spine have a higher fitness than plastic individuals which are experiencing the cost of producing an unnecessary spine whereas in the presence of predators, specialist individuals that always develop a large spine would also be advantaged compared to plastic individuals that would produce a reduced spine (Snell-Rood and Ehlman 2021a). In addition, the development of efficient plastic phenotypes needs time which cannot be reached if the environment itself changes at a faster rate than the one an organism needs to develop its appropriate behavior (Snell-Rood and Ehlman 2021a). Under moderately varied environments, individuals could rely on consistent variation in their behavior, i.e. personality (Sih et al. 2004). Although appearing non-adaptive in a specific context, like the presence of a predator, fast explorer starlings (*Sturnus vulgaris*) found new foraging patches in a novel environment and so limit

starvation (Boogert et al. 2006). Therefore, phenotypic plasticity is predicted to be favored when costs of phenotype adjustments are low and predictive environmental cues are present (Schlichting and Pigliucci 1998).

Wild animals have remarkable variation in their behavioral plasticity, within and among populations (Stamps 2016). Selection can affect evolution even in the absence of mutation (West-Eberhard 2003). Following the plasticity-first hypothesis, environmentally initiated behavioral plasticity precedes, and even facilitates, evolutionary adaptation (Levis and Pfennig 2016). Thus, this variation is predicted to be refined by the process of natural selection, and if adaptive, transmitted to the future generations and spread in populations (Darwin 1859; Laland et al. 2015). In addition, exposure to a novel environment is likely to cause many individuals in a population to behave in new ways (West-Eberhard 2003). If plastic and non-plastic genotypes differ in their ability to persist under novel conditions, then plasticity may promote persistence and while many of these responses might be maladaptive, some might be beneficial under the new conditions (Wund 2012). After initial persistence via plasticity, genetic accommodation is expected to improve the form and expression of newly adaptive traits by reductions in costs or improvements of behaviors and integration with the rest of the phenotype (Levis and Pfennig 2016). In addition, an individual exhibiting considerable plasticity in one behavioral trait may also be plastic in another behavior, especially if they rely on related underlying mechanisms (Sheehy and Laskowski 2023). Tadpoles present both behavioral and morphological responses to perceived predation risk that are co-expressed suggesting that responding along one axis (moving behavior) does not limit their ability to respond along another distinct axis (tail morphology; Hossie et al., 2017). So we need to consider behavioral plasticity not as an isolated trait but within a plasticity syndrome, across behaviors or ecological contexts (Westneat et al. 2019). Given the obvious potential advantage of being able to adjust one's behavior to environmental conditions, understanding the causes of individual differences in plasticity is of major interest in behavioral ecology and evolutionary biology (Dingemanse and Wolf 2013)

## I. 2. CAUSES OF BEHAVIORAL PLASTICITY VARIATION

In a theoretical environment with unlimited resources and space, all organisms could survive and reproduce. But, if one factor is limiting, e.g. high risk of predation in an environment where all other resources (food, mates, shelters...) are unlimited, selection should be directional towards adaptation to this limiting factor (Darwin 1859). Organisms should tend to an optimal behavior in order to maximize fitness, but this optimal behavior depends on the closest adaptive peak available (Vinton et al. 2022): some individuals may avoid predators by moving in a new environment, others could hide to avoid being detected, others could look for conspecifics for protection, others could fight... (Caro 2005). But actually, more than one environmental factor at a time is impacting behaviors and phenotypes. We need to understand which selection pressures are acting on behavioral plasticity in order to predict future populations evolution. In order to reach this aim, an intraspecific approach, by comparing individuals between and within populations, will allow researchers to quantify the causes of variations in plasticity.

### I. 2. 1. Environmental variation

Variation of abiotic resources occurs in both time and space. Differences in variability of the environment can lead to corresponding plasticity of behavior between species as organisms inhabiting variable environments are more variable in their foraging behavior compared to other individuals from stable and less variable environments which express relatively fixed foraging behaviors (Niemelä et al. 2013). In moderately variable environments plastic organisms have an advantage since the cost of behavioral plasticity is covered by being able to use environmental cues to adapt behavior (Ghalambor et al. 2007). However, if an environment is not (or overly) variable, stereotypic organisms presenting fixed behaviors may dominate over plastic ones because in such environment the maintenance costs of underlying mechanisms allowing behavioral plasticity exceed the benefits (Niemelä et al. 2013). We can expect similar differences within species, at the inter-individual level.

Harsher environments are characterized by the correlated variation of several factors which reduces optimal environmental conditions imposing strong selection pressures and

competition for survival and reproduction as resources are less predictable (Botero et al. 2014). In winter for example, small birds face difficulty to meet their energetic needs as the days are shorter and food harder to find. Models predict that they should increase foraging effort in order to increase body mass and fat reserves to survive (McNamara et al. 1994). However, when the risk of predation also increases, foraging decisions are traded-off between the risk of starvation and the risk of predation (Lima 1986; McNamara and Houston 1990). Depending on the risk of predation, which can change dynamically over time, individuals need to adjust their foraging decisions, a stage in which plastic individuals should be at an advantage (Vinton et al. 2022). If favored by selection, we could expect that populations inhabiting harsher environments are more behaviorally plastic, including between various dynamic contexts, than conspecifics from milder locations. Promising evidence comes from birds populations living along altitudinal gradients, a spatial variation of harshness (Körner 2007). Birds from higher elevation are known to be more performant in learning and memorization than low elevation birds (Roth et al. 2010; Hermer et al. 2018), underlying abilities that are potentially necessary for behavioral plasticity. Therefore, altitudinal gradients as variable harsher environments constitute an interesting situation to investigate how environmental variation may impact behavioral plasticity. We have an urgent need to understand how behavioral plasticity may help deal with environmental variation considering the current expansion of urban environments. They constitute specific microclimates with different resource availability, different threats and disturbance that species all over the world have difficulties to cope with (Butchart et al. 2010). Facing an urban world and more general human-induced rapid environmental change (HIREC), behavioral plasticity is a good candidate to understand potential survival of individuals and populations (Snell-Rood 2013; Foster et al. 2015).

### I. 2. 2. Intrinsic characteristics

Intrinsic characteristics could also impact behavioral plasticity among individuals. The degree of such plasticity can vary during an organism's lifetime (Fischer et al. 2014; Bonamour et al. 2020). Changes in plasticity with age are expected if an organism does not have perfect information at birth but can improve its estimate of the environmental state by integrating information accumulated over a longer period of time (Dufty et al. 2002). In fact, in many species, younger animals need to acquire the skills to recognize and process food items in order

to meet their foraging needs. This acquisition can be socially influenced, by the observation or interaction with other individuals or their products (Galef and Giraldeau 2001), up to teaching (Thornton and McAuliffe 2006). In line with development of social learning, we can predict age differences in behavioral plasticity, with adult individuals being more plastic. Alternatively, after experiencing various behaviors in the face of environmental variation, adults may focus on the most efficient strategy they found to forage and only maintain the associated underlying mechanisms in order to limit costs (Wund 2012). If this was the case, we could predict that adults may not be the more plastic individuals. Integrating age differences in futures studies will help understand the age dependent variation of plasticity and associated costs (Fischer et al. 2014).

When environmental variation is predictable and weakly variable, plasticity may not be favored (Niemelä et al. 2013). In contrast, if the environment is stable or overly variable, individuals may gain from being consistent in their behavioral decisions (Mathot and Dingemans 2014). This consistency across situations or contexts, i.e. personality, has been identified in various traits such as aggressiveness, neophobia, risk-taking, exploration and sociality (Réale et al. 2007). Fast explorers, which are also bolder individuals (Bibi et al. 2023) are more attracted by novelty and more quickly gather information from their environment in order to reduce uncertainty compared to slower explorers. As a consequence, they are expected to more rapidly switch between behaviors, in order to match environmental variation (Rojas-Ferrer et al. 2020). Furthermore, consistent behavioral differences are sometimes partly context dependent, suggesting that personality may not always be a one dimensional continuum (Coleman and Wilson 1998). Under higher perceived risk of predation, fast explorers are known to be more flexible in their foraging decisions whereas slow explorers stick more to their routines (Quinn and Cresswell 2005; Coomes et al. 2022). Thus, we expect that depending on their personality, some animals may be more behaviorally plastic and personality and plasticity may co-vary if individuals differ in responsiveness to contextual changes in their environment (Stamps and Biro 2016; Hall et al. 2017; Montiglio et al. 2017). Including the different intrinsic characteristics detailed above can help us understand between individual variations in behavioral plasticity.

### I. 2. 3. Social environment

Among all the challenges individuals are daily facing, social ones are particularly demanding. Actually, most animals engage in interactions with conspecifics, and these interactions form a dynamic social environment (Pinter-Wollman et al. 2014). Facing social challenges, individuals able to their behavior adapt efficiently should be favored by social selection (McGlothlin et al., 2010; West-Eberhard, 1983; Wolf et al., 1999). This behavioral plasticity related to variation in the social environment, named social competence (Taborsky and Oliveira 2012), brings an interesting theoretical framework for the evolution of social plasticity (Taborsky 2021). Social plasticity may depend on past experiences as the social environment experienced during rearing influenced social behavior later in life in cooperatively breeding cichlids (*Neolamprologus pulcher*) (Taborsky et al. 2012). Individuals raised with older conspecifics, either with parents only or with parents and helpers, showed more appropriate behaviors in agonistic interactions than young raised in same-age sibling groups only, whereas the frequencies of other behaviors did not differ (Arnold and Taborsky 2010). In wolf spiders (*Schizocosa uetzi*), the mating decision of females is also dependent of past experience with males while immature as adult females preferred to mate with the type of male with which they were familiar (Hebets 2003). Social plasticity is also impacted by more recent interactions with conspecifics. Bird song is an extremely variable behavioral trait that plays an essential role in intra- and intersexual communication and song plasticity is known to change depending on the presence of potential competitors in the social audience (Jablonszky et al. 2022), which can impact the probability of breeding. In agonistic interactions, the result of previous social interactions influences current success in cichlids fishes as preassigned winners won more often than losers (Lerena et al. 2021). In addition, preassigned rank only influenced restrained aggression significantly, whereas contest outcome was not affected by rank.

In foraging situations, animals may tend to look for conspecifics in order to increase their probability to find food and limit predation risk (Hamilton 1971; Lima and Bednekoff 1999) although this can increase food competition (Ranta et al. 1993). Actually, deciding whether or not to join a group and choosing what size and composition of a group to join are complex decisions that can have lasting effects on an individual's survival. In group living cichlids, grouping decisions were indeed related to an individual's cognitive performance with faster



learners preferring to stay alone (Culbert et al. 2021). But foraging behavior also depends on social contexts as cichlids forage faster facing a competitor than against a spectator audience (Ólafsdóttir and Magellan 2016). Moreover, foraging strategies are dependent on the strategies performed by others, as illustrated by the producer scrounger paradigm (Giraldeau and Caraco 2000), where individuals can search for food or for opportunities to exploit the discoveries of others with each tactic more efficient when rare. In addition, neophobic zebra finches (*Taeniopygia guttata*) were more plastic in their foraging decisions (Gibelli and Dubois 2017), while faster learning individuals increased their latency to forage as the number of companions increased (Barou Dagues et al. 2020).

The social environment can also be generalized to individuals from different species in cooperative interactions (Bshary and Oliveira 2015), or mixed species group interactions (Sasvári 1992). Based on the complexity of social interactions, we can suppose that some underlying mechanisms may help individuals to perform efficiently facing social challenges (Wascher et al. 2018). There is reason to believe that an individual exhibiting strong behavioral plasticity in one social situation may also exhibit plasticity in another context (but see Morel-Journel et al., 2020). As such social plasticity can be investigated across contexts, as a plasticity syndrome (Sheehy and Laskowski 2023), which have consequences on potential sociality evolution (Varela et al. 2020).

Overall, the flexibility of a behavior is often affected by more than one environmental factor or across multiple axes (e.g. temperature, resource availability, past experiences or social landscapes) and these factors may interact to affect behavior expression non-additively (Stevens et al. 2023). Plasticity syndromes can help individuals more easily deal with such multifaceted changes. It is essential to consider these multifactorial environments in order to understand among and within populations and individual variation in plasticity (Foster 2013).

### **I. 3. THESIS AIM**

The overall aim of this PhD thesis was to investigate the causes of among-individual variation in foraging decisions and plasticity. Specifically, I examined the role of environmental harshness on foraging decisions under predation risk (Chapter 2). I also aimed at determining which ecological factors could induce variation in social foraging, overall context among others (Chapter 3). I finally tested the assumption that social behavior relies on cognitive using an experimental approach (Chapter 4). I conducted this research on ecologically contrasted wild populations of a passerine species, the great tit (*Parus major*) and focused on foraging decisions. My thesis thereby improves our understanding of the various causes of inter and intra individual variation in behavior and has potential implications for individual survival and population persistence in changing environments.

### **I. 4. STUDY SPECIES**

Greats tits are common small passerines (~ 18g) from the *Paridae* family which are abundant across Europe and Asia. They can be found from natural deciduous and mixed deciduous woodlands to highly urbanized cities, from sea level up to 3000 m asl. Their presence in a wide variety of environments made great tits a model study organism in behavioral ecology and evolutionary biology (e.g. Perrier et al., 2018). Great tits are socially monogamous and reproduce in tree cavities but also accept breeding in artificial nest boxes, which facilitates the study of their life-history traits (Perrins 1965; Krebs 1971). In Western Europe, reproduction occurs in spring but males start defending territories from January; females build the nest and lay 7-8 eggs on average in March-April (Lack 1964). After an incubation period, offspring hatch and the two social parents are involved in parental care and food provisioning at the nest for 19 to 21 days (Gosler 1993). Great tits are primarily insectivorous in the spring and summer but switch their diet throughout autumn and winter with an increased intake of seeds under such harsher conditions (Gosler 1993). While looking for food in winter, great tits usually form multispecies flocks with other species including blue tits (*Cyanistes caeruleus*) or marsh tit (*Poecile palustris*) in order to increase foraging success (Sasvári 1992). Foraging decisions in

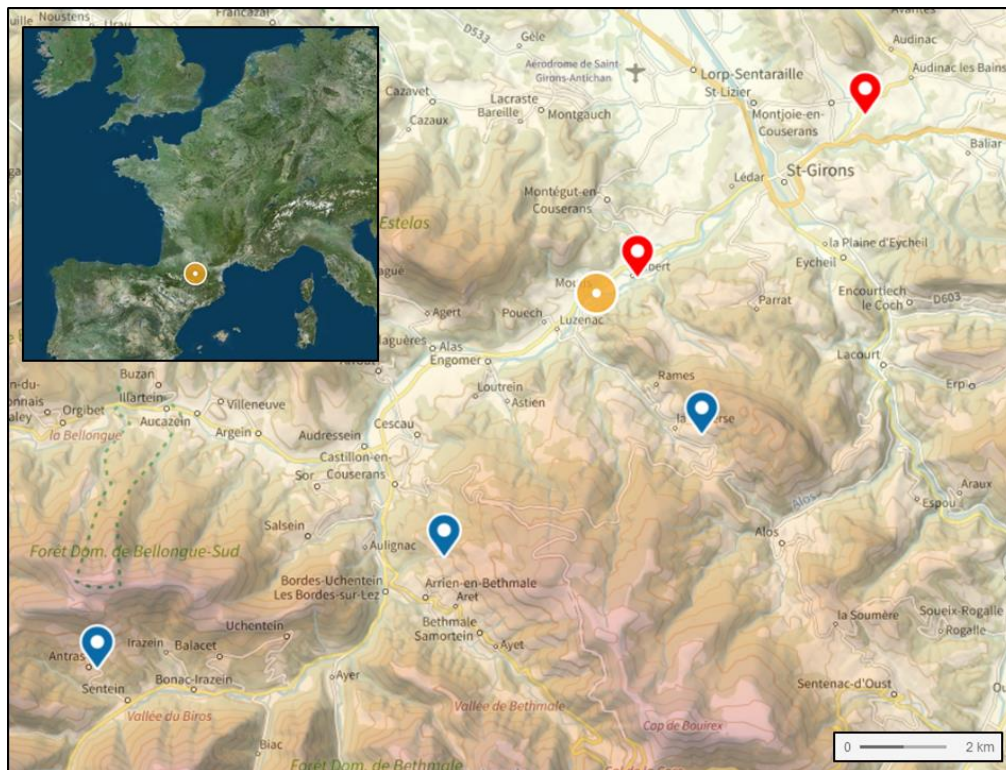
great tits are dependent on a starvation predation risk trade-off which has been well studied and modeled, notably in winter conditions (Lima 1986; Houston and McNamara 1993). Great tits are characterized by sexual dimorphism with males having a larger black breast stripe than females, but also related to size and mass which implicate dominance relations between individuals at foraging patches (Firth et al. 2015). Adults individuals usually have priority access to foraging patch compared to juveniles, and within adults, males outperformed females (Laet 1985; Hogstad 1989). Therefore, great tits are a model species to understand inter-individual variation of foraging decisions. Great tits are also well known for their cognitive abilities including problem solving (Cole et al. 2011), detour reaching (Isaksson et al. 2018; Coomes et al. 2022), reversal learning (Hermer et al. 2018) and also social learning (Landová et al. 2017), measured in the wild but also in captivity where the great tit acclimates well (Cole et al. 2011; Hämäläinen et al. 2019). A combination of these factors make the great tit an ideal species to study the causes of inter-individual variation of foraging plasticity, in relation with environmental variation.

## I. 5. STUDY SYSTEM

In order to understand the causes of among individual variation in foraging decisions, I utilized 5 ecologically contrasted populations of wild great tits spread along an altitudinal gradient in the French Pyrenees mountain (Aubert, 430 m asl., 42°57'51.4"N, 1°06'11.3"E; Montjoie, 445 m asl., 42°59'56.0"N, 1°10'09.3"E; Cap de Sour, 806 m asl., 42°55'51.4"N, 1°07'18.8"E; Antras, 891 m asl., 42°52'51.7"N, 1°05'44.4"E; Villargein, 898 m asl., 42°54'17.1"N, 1°02'48.0"E; Figure I.1). All these populations are at least 3 km apart and no movement between populations has been reported since the beginning of our group's population monitoring in 2012.

Along the altitudinal gradient, we recorded a decrease in mean temperature ( $\sim 5^{\circ}\text{C}/1000\text{ m}$ ; Bründl et al., 2019) and a variation in vegetation cover, with oaks (*Quercus robur*) more common at lower elevations while beeches (*Fagus sylvatica*) were dominant at higher elevations (Lejeune et al. 2019). These ecological changes impacted life-history traits (Bründl

et al. 2020) and were responsible of cognitive differences in great tits (Hermer et al. 2018; Cauchoix et al. 2020).

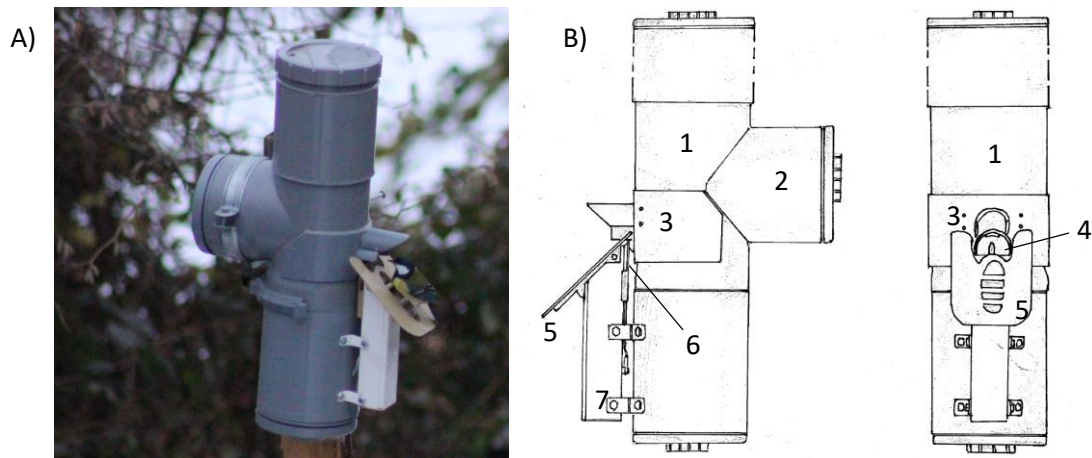


*Figure I.1: Localization of the different populations of great tits involved in experiments of the present study (high elevation=blue, low elevation=red, aviaries facilities=orange).*

In order to recreate various ecological contexts related to the social environment or risk of predation, I used video playbacks. In the past decades, video playbacks have been proven a powerful tool to create standardized and realistic stimuli (D’earth 1998; Oliveira, McGregor, et al. 2000) notably with recent progress in screen development (Bird and Emery 2008). Specifically, birds are known to perceive information provided by videos as realistic information of risk of predation (Zoratto et al. 2014), or social audience (Rieucan and Giraldeau 2009; Hämäläinen et al. 2019) and use them to make decisions and modify their behavior accordingly. The use of video playbacks allowed us to control environmental differences and specifically address questions related to the risk of predation or variation in the social environment. The use of such complex electronic devices required testing individuals outside of the natural environment. Although captivity can impact stress (Dickens et al. 2009),

our team was able to show that cognitive abilities are similar between wild birds tested in the wild or in temporary captivity (Cauchoix et al. 2017).

To reduce the stress associated with captivity, the majority of data was collected passively, using an electronic feeder, the OpenFeeder (Cauchoix et al., 2022; Figure I.2). It is based on an RFID (Radio Frequency Identification) recognition system which detects and records each visit of a bird equipped with a band containing a PIT-tag (Passive Integrated Transponders, IB Technology, UK), linked to the video stimuli visible on a nearby screen. Thus, I was able to collect foraging decisions from great tits without human intervention. Moreover, the OpenFeeder is equipped with four LEDs located around the feeding hole that can be used in association with a moving door to test associative learning abilities of great tits.



*Figure I.2: The OpenFeeder device, an automatic RFID based feeder. A) A great tit foraging on it and B) OpenFeeder container design: 1) food storage container, 2) electronic board compartment, 3) four LED displays, 4) feeding hole, 5) perch containing the RFID antenna, 6) door to control access to the feeding hole, 7) motor.*

## I. 6. THESIS STRUCTURE

Chapters 2, 3 and 4 of the thesis are empirical chapters presented in article based form for publication.

In Chapter 2, I tested whether foraging decisions under predation risk were different between individuals differing in their elevation of origin. I measured foraging preferences of great tits originated from low and high elevation facing control and predator video playbacks in temporary captivity. Foraging decisions are modeled to be a trade-off between the risk of starvation and the risk of predation (Lima 1986). Under harsher conditions, such as ones experienced during winter, small birds are expected to be more risk-prone regarding predators in order to reach their foraging needs and gain sufficient fat reserves to avoid starvation (Houston and McNamara 1993). As high elevation environment are even harsher conditions, I expected birds from high elevation to forage more in presence of a predator than their low elevation counterparts, especially in winter. As harsher conditions increase the risk of starvation and death, various intrinsic factors may interact with harshness in order to define foraging decisions. The body mass and fat reserves of individuals should modulate foraging decisions as birds with more energy stock may be more risk-averse regarding predators (McNamara and Houston 1990). I predicted that heavier birds or birds with more fat reserves should avoid more predators while foraging compared to lighter birds or ones with less fat reserves. This should be more visible in high elevation birds as they are facing higher metabolic needs to face lower temperatures. Moreover, foraging decisions depend on the access to good quality foraging patch, an ability dependent on dominance status (Ficken et al. 1990). I predicted that less dominant birds, i.e. females or yearlings, would therefore be more risk-prone than other birds. However, this effect may be less visible in low elevation populations as they face milder conditions and less difficulty to find foraging patches. Finally, fast explorers' birds are known to resume normal behavior faster following a predation threat (Quinn and Cresswell 2005). I expected such reactive individuals to be able to avoid more predators while foraging. Overall this chapter provides a global comprehension of how altitudinal differences influences changes in the starvation-predation trade-off and associated risk-taking behavior.

In Chapter 3, I investigated how foraging plasticity was impacted by the social environment under different ecological contexts. I manipulated social information through video playbacks by changing the group size and the species present in the social group and recorded foraging decisions of wild great tits in temporary captivity. The ability of an individual to adapt its behavior in response to variation in the social environment, i.e. social plasticity (or social competence) should be context-dependent (Taborsky and Oliveira 2012). In a secure situation, the foraging decisions trade-off should balance towards avoiding starvation (Bonter et al. 2013). A bird may gain an advantage facing a predictable food patch like a feeder to avoid conspecifics in order to reduce competition (Alatalo et al. 1987). I predicted that in control situations, great tits may prefer visit feeder alone in order to increase the efficiency of foraging. Great tits are known to forage in mixed species flocks in winter, with blue tits and marsh tits among others, against which they are known to be the dominant species (Sasvári 1992). I expected that facing blue tits, tested birds should reduce their preference to forage alone as blue tits are less competitive compared to great tits. However, social foraging decisions are not only based on the social environment and other factors, such as risk of predation, need to be integrated (Barta et al. 2004). I manipulated overall contexts and recorded repeated measures of foraging plasticity in either control, increased perceived predation risk or disturbance conditions. Group behavior should be advantageous when predation risk is higher (selfish herd, Hamilton, 1971) in order to increase the probability to detect a predator, despite competition for resources. I predicted that under a predation risk context, birds should prefer foraging in groups. More generally, in stressful conditions, social groups can act as a buffer or a facilitator (St. Lawrence et al. 2021) and I expected that under a disturbed context, great tit decisions should also shift towards a preference for foraging in groups. Finally, I examined how individual characteristics such as age or personality but also environmental conditions such as elevation of origin explained inter-individual differences in contextual social plasticity. When finding food is harder, for yearlings or in high elevation population as example, individuals should adapt their social behavior further, and I predicted more marked inter-individual differences in such cases.

In Chapter 4, I examined whether social foraging plasticity was related to cognitive abilities. I recorded various cognitive abilities, i.e. perception, attention, learning, memory and decision-

making processes (Shettleworth 2009) in foraging tasks. I used three distinct cognitive metrics as I wanted to test the great tits in ecologically relevant scenarios: associating a stimulus with a reward is very likely to occur in nature (associative learning, Morand-Ferron, 2017); avoiding maladaptive behavior facing social dominant or potential predator is common and useful (detour reaching, Hand, 1986); accessing food in an innovative way as been historically reported in the past in tits (problem-solving, Fisher & Hinde, 1949). Recent work has suggested that cognition is a general ability (Plomin 2001) leading to the expectation that birds would perform consistently across different cognitive abilities, from innovation to associative learning. Moreover, social foraging is a complex behavior that should rely on cognitive abilities. Selection pressures should act on behavioral performance and as a consequence enhanced cognitive abilities (Varela et al. 2020). I used the social foraging plasticity measures detailed in Chapter 3 as plasticity metrics collected on the same individuals. I predicted that great tits who were more plastic in their foraging decisions would more often solve cognitive tasks and do so faster. Finally, as social foraging plasticity is predicted to be context dependent (Taborsky and Oliveira 2012), I looked at how the environmental variation influenced this link between cognition and plasticity, an element rarely integrated in literature to date. Harsher conditions (e.g. higher elevation or in winter) challenge more individuals to find food and survive and are known to be associated with higher cognitive abilities in small bird populations (Kozlovsky et al. 2015a; Hermer et al. 2018). Therefore, I predicted that the link between social foraging plasticity and cognition would be more marked in these situations, but also in more stressful (e.g. predation risk or disturbance) conditions. Overall, this chapter provides experimental confirmation of the drivers of social foraging plasticity in birds.

To conclude, in Chapter 5, I bound all the results found during this PhD together in a general discussion. I aimed to highlight the interconnection and the novelty of these results for the field of behavioral plasticity. I point out directions in which future studies could orient in order to understand more deeply the interplay between behavioral plasticity and evolution. I also discuss the impact of foraging plasticity on potential species' evolutionary processes and consequences on individual and population survival under climate change or human-induced rapid environmental changes.





## **CHAPTER II.**

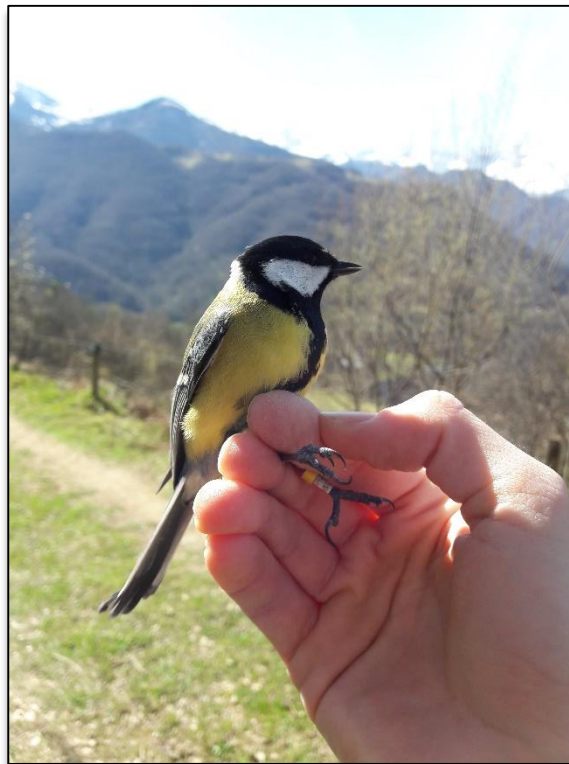
### **ALTITUDINAL DIFFERENCES IN FORAGING DECISIONS**

#### **UNDER PREDATION RISK IN GREAT TITS**

In press in Behavioral Ecology

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## II. 1. ABSTRACT

Foraging decisions under risk of predation are crucial for survival as predation risk can contribute to a reduction of food intake over time leading to a trade-off between starvation and predation. Environmental variation can provoke changes in food accessibility or predation risk that will in turn affect foraging decisions. Specifically, less predictable or harsher environments, such as those found at high elevation, should lead to more risk-prone foraging in order to prevent risk of starvation, but empirical confirmation of this hypothesis is lacking. In the current study, we used video playbacks combined with an automatic feeder to measure continuous foraging choices between control and predator videos by wild great tits originating from high and low elevations and tested under controlled conditions. Great tits discriminated between two conditions representing differences in predation risk and visited the feeder less frequently when a predator was shown. Moreover, we found that birds from low elevation populations were more risk-averse and visited the feeder significantly less when a predator video playback was broadcasted compared to high elevation individuals. This elevation related contrast was also dependent on the season, body mass and fat reserves of individuals, and was more marked in females. Furthermore, adults visited the feeder less in the presence of a predator compared to yearlings. These results are consistent with predictions from life history theory and starvation-predation trade-off hypotheses and could have implications for individual movements and population dynamics in changing environments.

### **Keywords:**

Behavioral plasticity, elevation, foraging, great tit, predation risk, risk-taking behavior, video playback

## II. 2. INTRODUCTION

Foraging decisions in the wild are in part driven by a starvation-predation risk trade-off (Houston et al. 1997). While it is vital to find food to survive, the associated risk-taking due to exposure to predators can lead to lethal consequences (Lima and Dill 1990). Animals are expected to evolve strategies to limit such risks and models have predicted the existence of behavioral variations in response to changes in predation pressure (Lima and Bednekoff 1999). For example, birds limit the time spent at foraging patches when the perceived risk of predation increased (Krams 2000; Verdolin 2006; Villén-Pérez et al. 2013). They can also rely on indirect cues of predator presence to stop their foraging activity such as mobbing calls (Desrochers et al. 2002), alarm calls (Lind et al. 2005) or odors (Amo et al. 2008). By choosing more exposed foraging patches when hungry, individuals may be more exposed to predators (Hilton et al. 1999). Likewise, through a dilution effect, foraging in groups can reduce the risk of being predated while foraging (Hamilton 1971; Morse 1978). As a consequence, birds in large flocks are more risk-prone (i.e. are willing to take more risks) than solitary conspecifics (Dolby and Grubb 2000). These foraging decisions can have effects on reproductive success and fitness as well as consequences on population dynamics (Cresswell 2008).

Theory on foraging strategies predicts that the starvation-predation risk trade-off should be impacted by environmental variation (Cresswell et al. 2009). Foraging decisions of passerines in winter should aim to optimize fat reserves in order to avoid starvation in harsher conditions (e.g. shorter days, less and more unpredictable food; Lima 1986; Houston and McNamara 1993). Therefore, individuals with higher metabolic rates (Mathot et al. 2015) or lower body mass (Rogers 1987) are more-risk prone, as their trade-offs tilt towards a higher risk of starvation (Pakanen et al. 2018). Similarly, individuals from different elevations face different foraging constraints as colder temperatures increase metabolic requirements and resource availability is more uncertain and scarce as elevation increases (Körner 2007). At high elevation, passerines have different daily routines, with foraging peaks in early morning and late afternoon, compared to low elevation birds which prefer to forage during the middle of the day (Pitera et al. 2018). These differences were more marked in harsher periods such as winter, where birds needed to make greater investments in foraging to reach their optimal level of

reserves to avoid starvation (Pitera et al. 2018). Foraging decisions are also predicted to depend on predation (McNamara et al. 1994). Predation risk might decrease with elevation in some cases (Sasvári and Hegyi 2011). For example, European sparrowhawk –a major songbird predator– abundance decreases with increased elevation (Newton et al. 1977; Newton et al. 1986). Reduced predator avoidance behaviors should arise at lower predation risk, a pattern confirmed in a meta-analysis pointing out that high elevation individuals show less intense predator avoidance behaviors on average (Stankowich and Blumstein 2005). However, not all studies show the same general pattern. In response to a threat, flight initiation distance in dark-eyed juncos (*Junco hyemalis*) from high elevation was greater than for low elevation individuals (Andrade and Blumstein 2020). Likewise, in a breeding context, latency of mountain chickadees (*Poecile gambeli*) to go back to their nest box after a predator presentation was longer in high elevation birds (Kozlovsky et al. 2015a). Results from these two studies do not match the prediction that birds from high elevation should show weaker anti-predator responses and suggest that the specific life-history contexts may influence risk-taking behavior. Indeed, parameters other than elevation may impact risk avoidance decisions, notably in a foraging context.

Apart from environmental variation, individuals may exhibit different risk-taking foraging behaviors depending on their individual attributes such as physiological state (McNamara and Houston 1990). Lighter individuals with fewer fat reserves may suffer faster from food deprivation and thus might forage under higher predation risk to avoid starvation (Rogers 1987). Moreover, females (Saitou 1979) and smaller or younger individuals (Hegner 1985; Sandell and Smith 1991) are usually subordinates and therefore are expected to have access to lower quality foraging habitats. As a consequence, these categories of individuals might have to forage in less optimal foraging patches with higher predation exposure thus taking more risks (Brown 1999; Brodin and Utku Urhan 2015). Furthermore, predator recognition and the ability to react properly to predators might require time to develop and not yet be fully operational in yearlings (Putman et al. 2015). Thus, anti-predator behavior could be age-dependent. Similarly, consistent behavioral variations among individuals, i.e. personality, could impact foraging decisions (Sih et al. 2004). The fast-slow exploration continuum (Dingemanse et al. 2002) is thought to be closely related to optimal foraging decisions

(Toscano et al. 2016). The link between exploration and foraging has been experimentally confirmed in different taxa under predation risk (Réale et al. 2007; Jones and Godin 2010; Dammhahn and Almeling 2012). In birds, the perception of predation risk is integrated differently by individuals based on their personality (Quinn and Cresswell 2005). Shy individuals appear to be more sensitive to the risk of predation while bolder individuals are more risk-prone in their foraging decisions (van Oers et al. 2004; Quinn et al. 2012; Coomes et al. 2022). However, the impact of personality on foraging decisions under predation risk has, to our knowledge, not yet been investigated across contrasting elevations.

In order to understand how elevation influences changes in the starvation-predation trade-off and associated risk-taking behavior, it is necessary to test individuals under controlled conditions (Kawecki and Ebert 2004). Bringing individuals into captivity allows standardization of recent exposure to predators, as well as controlling for food availability and energetic needs. In this study, we compared the foraging behavior of wild great tits (*Parus major*) brought into captivity from high and low elevation populations expected to be facing different ecological and predation pressures. We used video playbacks to test behavioral responses to predator encounters, as birds are known to perceive information provided by videos as realistic information of risk of predation (Zoratto et al. 2014), and use them to make decisions and modify their behavior accordingly. We expected that birds would forage less during predator presentations compared to control stimuli. Then, we examined whether there were differences in responses towards predators in relation to the elevation of origin of the birds and if age, personality, fat reserves or sex influenced these responses.

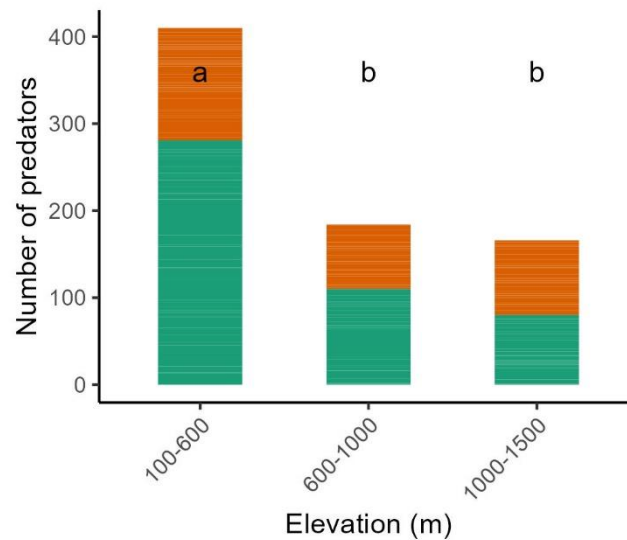
## II. 3. METHODS

### II. 3. 1. Study sites and species

We caught wild great tits (N=192) from 4 distinct populations in the French Pyrenees (Aubert, 430 m asl., 42°57'51.4"N, 1°06'11.3"E; Montjoie, 445 m asl., 42°59'56.0"N, 1°10'09.3"E; Antras, 891 m asl., 42°52'51.7"N, 0°56'44.4"E; Villargein, 898 m asl., 42°54'17.1"N,

1°02'48.0"E). These populations were at least 5 km apart and no movement between them has been detected since the beginning of our group's population monitoring in 2012. In previous work, we studied the variation of ecological factors along this elevational gradient including differences in winter mean temperature (from 8°C at 200 m asl. to -0.5°C at 2000 m asl. with a decrease of ~5°C/1000 m, Buisan et al. 2016), increased variance in temperature at higher elevation, and ensuing impacts on nesting density, the phenology of nesting behavior and fitness (see Bründl et al. 2019; Bründl et al. 2020). Likewise, there are significant differences in vegetation cover and parental behavior across the same gradient (Lejeune et al. 2019). Studies on birds from these populations have also shown contrasts in cognitive traits across this relatively modest elevational shift (Cauchoix et al. 2017; Hermer et al. 2018; Hermer et al. 2021). Based on this previous work, we grouped our capture sites by referring to "high" (Antras and Villargein; mean 894 m asl.) and "low" (Aubert and Montjoie; mean 437 m asl.) populations. At each elevation, we thus had several replicates where elevation was the key difference among experimental groups.

To verify that overall predation risk varied across elevations, we quantified relative predator abundance using camera traps (Busnell Trophy Cam HD Essential E2 ®) set in front of custom made resin great tit models placed 1.5m from the ground across our elevational range (See supplementary materials for images, Figure S. II.1). From February to August of 2016 and 2017, we conducted a total of 232 week-long monitoring sessions. We scored images for avian versus mammalian predators and found that overall predator abundance decreased from lower to higher elevations (Main effect: ANOVA,  $N=143$ ,  $F=6.53$ ,  $P=0.002$ ; 100-600m vs 600-1000m:  $T=2.32$ ,  $N=96$ ,  $Est.=1.92\pm 0.83$ ,  $P=0.058$ ; 100-600m vs 1000-1500m:  $T=3.47$ ,  $N=106$ ,  $Est.=2.72\pm 0.79$ ,  $P=0.002$ ; 600-1000m vs 1000-1500m:  $T=0.95$ ,  $N=104$ ,  $Est.=0.81\pm 0.86$ ,  $P=0.612$ ; Figure II.1). Mammal predators are known to attack small passerines on the ground, at feeders and in roosting boxes through fall and winter (Orell 1989), creating a world of fear experienced by great tits. Although sparrowhawks were absent from our images, previous studies on similar elevation gradients suggest that sparrowhawks show the same pattern as other predators (Newton et al. 1977; Newton et al. 1986).



*Figure II.1: Predator abundance distribution in great tit habitats. The predators, birds (dark orange) and mammals (green), were detected via camera traps along an elevation gradient in the Pyrenees split in three classes (100–600 m; 600–1000 m; 1000–1500 m). Letters above each bar denote significant differences in posthoc comparisons of altitudinal ranges.*

Captures using mist nets took place in 8 batches (24 individuals per batch) between mid-October 2020 and mid-March 2022 during fall (10 October – 20 December) and winter (21 December – 10 March). We marked each bird with a unique CRBPO (Centre de Recherche sur la Biologie des Populations d’Oiseaux, French bird ringing office) metal band and a colored band containing a PIT-tag (Passive Integrated Transponders, IB Technology, UK) for detection with an RFID (Radio Frequency Identification) reader. We used plumage dimorphism to sex (male or female) and age (adult or yearling) birds (Svensson 1992). We quantified fat reserves by scoring fat deposited in the furculum using a 4-point scale (0: no visible fat; 1: base of tracheal pit obscured by fat but less than half full; 2: fat filling the tracheal pit but not bulging; 3: fat filling tracheal pit, bulging and overlying pectoral muscle, modified from Gosler 1996). We also measured body mass at capture and at release using a digital scale (nearest 0.1g) and tarsus length (nearest 0.1mm) at capture as a proxy for body size.

### II. 3. 2. Housing and captivity schedule

Each aviary at the CNRS-SETE facilities (1 x 5 x 3 m, W x L x H) consisted of an indoor (1 x 1 m, W x L) and an outdoor (1 x 4 m, W x L) area (See supplementary materials for images, Figure



S. II.2). Birds were housed individually, we alternated cages by elevation so that neighbors came from different elevations, and one empty cage separated neighboring birds who nonetheless remained visually and acoustically connected to others in outdoor areas in order to minimize stress. Birds freely moved in their aviaries between the indoor and the outdoor areas. Cages were enriched with foliage for cover, an artificial tree, horizontal perches, a roosting box, and water. Birds were fed *ad libitum* with sunflower seeds and mealworms between video playback experiments. In each indoor area of the aviary, an automatic, RFID-based feeder, called the “OpenFeeder” (Cauchoix et al. 2022) provided sunflower seeds. Upon release in aviaries, an exploratory score was measured for each bird as the total number of movements (either flights or hops) completed during a 3 min period, following Dingemanse et al. 2002). This measure performed in a novel environment has been found repeatable in other populations of great tits (Dingemanse et al. 2012). Furthermore, the first measure of exploratory behavior in a novel environment is a good proxy for the personality of an individual (Niemelä and Dingemanse 2018). The predation risk experiment was performed on the last day of captivity (day 29) at which point birds were used to feeding from the OpenFeeder and had experience with images projected on video screens for other experiments. Previous exposure to screens entailed projection of different numbers of congeners presented on the screens, but our experimental birds had never seen predators on the screens. All birds had experienced the same tests prior to the present experiment. Sample sizes of some batches were lower than the maximum of 24 as a result of technical errors (N=6), a lack of interaction with the OpenFeeder (N=3), or death during a cold snap in January 2021 (N=1; final sample size: 182 birds rather than 192). After the predation risk experiment, we removed the RFID tag, inspected each bird to make sure it was in good condition, and released them at their respective capture sites.

### II. 3. 3. Video playback broadcasting

Perceived risk of predation was simulated with video playbacks (Oliveira, Rosenthal, et al. 2000; Rieucan and Giraldeau 2009; Zoratto et al. 2014; Snijders et al. 2017; Smit and van Oers 2019) which are an effective tool to test several individuals at the same time whilst controlling the predation risk stimuli. The stimuli were extracted from YouTube videos showing either a

blackbird (*Turdus merula*) for control stimuli or an Eurasian sparrowhawk (*Accipiter nisus*) for predation stimuli. Only sequences of birds perched and life size at full screen projection were kept. Sound was removed from videos to avoid potential influences of vocalizations. Each stimulus was created with OpenShot Video Editor software (OpenShot Studios, LLC.) and lasted 30s to mimic a realistic encounter with a wild bird (see supplementary materials).

The video presentations were performed during a morning session from 9 am to noon and an afternoon session from 1 pm to 4 pm. Outside of these periods, no video was projected on the screen and birds had *ad libitum* access to food. During the two experimental sessions, the OpenFeeder was the only source of food available. Every morning, aviaries were swept to remove potential food present on the ground. In each aviary a 22-inch computer monitor (Dell P2219H or P2217) placed next to an OpenFeeder in the indoor section was used to broadcast videos through a Raspberry Pi 3B+ (Raspberry Pi Foundation). Every 30s, the Raspberry Pi played a video randomly selected from 18 different recordings (9 sparrowhawk, 9 blackbird) such that each bird experienced an equal number of predator and control videos but in a different order. The large number of projections (720 total playbacks to each bird) ensured that each bird would see both control and predator stimuli when seeking food. Although video playbacks were broadcasted without interruption, birds freely decided when to forage and were only in close proximity with a video playback for a limited amount of time as birds come to the feeder, take a single seed, and eat it on a perch away from the feeder. All birds of a specific batch were tested simultaneously and could only see the computer screen of their own aviary. The RFID reader on the OpenFeeder recorded when the bird came to feed and during which video. If the bird arrived during the last 5s of a video, the current video stimulus was reread another time to avoid a shift in stimulus while the bird was feeding.

#### II. 3. 4. Data analysis

All analyses were performed using R software (R version 4.2.2, R Core Team 2022). Foraging behavior of each individual was quantified by pooling the number of visits to the OpenFeeder during the whole day of the experiment as feeding patterns did not shift throughout the day (i.e. we did not detect habituation to the setup; See supplementary materials). To examine

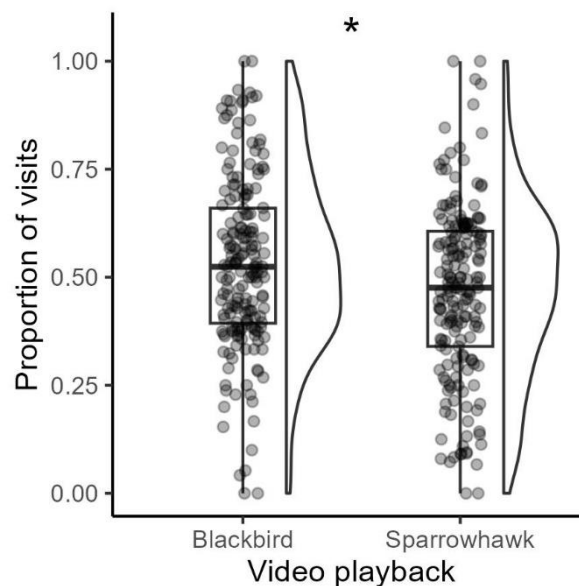
differences in feeder visitation rates between predation and control contexts, we compared the relative number of visits for these two conditions within individuals using a repeated measures ANOVA with season and site of capture as explanatory co-variables. In order to confirm the result of this analysis, we performed a permutation test (*permuco* package, Frossard and Renaud 2021) with 10 000 iterations following the same structure as the initial ANOVA (season and site of capture as fixed factors, bird identity nested in video playback as a random factor) and following the Kennedy method adjusted for exact permutation of repeated measures models (Kherad-Pajouh and Renaud 2015). To examine the effect of individual characteristics (age, sex, exploration, body mass, fat reserves and body size) on predator-context dependent foraging, we built generalized linear mixed models (GLMM, *lme4* package, Bates et al. 2014) with a binomial distribution and the relative number of visits to predation and control contexts as the response variable. We used the `cbind` function of the number of visits during sparrowhawk playback (“predator”) and number of visits during blackbird playbacks (“control”; 2 column matrix) to account for variation in total number of visits among individuals in the response variable. Individual characteristics (sex, age, elevation of origin, exploration score, body mass, fat reserves, tarsus length, season of experiment; see supplementary materials, Table S. II.1 for metric means and Table S. II.2 for sample sizes by category) were included as explanatory variables. Dominance may impact risk-prone foraging behavior more in harsher, high elevation populations so we added interaction effects between elevation and body mass, fat reserves, tarsus length, sex and age as these variables may impact dominance rank. We also included an interaction between elevation and season as we expected high elevation sites to increase in harshness more with season shifts relative to low elevation populations. Finally, we added an interaction between elevation and exploration score as previous work in a congener has shown elevational differences in exploration of a novel environment (Kozlovsky et al. 2015b). All numeric variables (exploration score, body mass, fat reserves, tarsus length) were centered on the mean and scaled by their standard deviation prior to integration in the model. Batch of capture was added as a random factor to control for variation due to series of capture and year effects. Results were similar when using body mass at capture or at release. Only the former is presented in the results (but see supplementary materials for model with body mass at release, Table S. II.3). Final models included all main effects, but only significant interactions (Faraway 2016). Post-hoc Tukey HSD tests (*emmeans*

package, Lenth et al. 2022) were run to assess the significance of differences between levels. Model performance was checked graphically using the *DARHMa* package (Hartig 2022). We also checked for multi-collinearity among fixed effects using the *performance* package to estimate the Variance Inflation Factor (VIF) which was below 5 for all variables (Lüdecke et al. 2021). While analyses were based on relative number of visits, figures represent the proportion of visits for graphical simplicity. The significance level for P-values was set at 0.05 (two-tailed tests).

## II. 4. RESULTS

### II. 4. 1. Impact of predation risk on foraging preferences

As expected, birds visited the feeder less when a predator (sparrowhawk) was presented on the screen compared to when a control bird (blackbird) was shown on the screen (rmANOVA,  $F=4.50$ ,  $df=181$ ,  $P=0.035$ ; Permutation test, 10 000 iterations,  $P=0.033$ ; Figure II.2).



*Figure II.2: Proportion of visits when a control (blackbird) or predator (sparrowhawk) was shown on the screen. Shown are the medians (black horizontal line), with the interquartile ranges (boxes) and distributions (violins) of the proportion of visits for each video playback category.*

#### II. 4. 2. Correlates of variation in risk-taking foraging strategies

The birds' decision to reduce foraging in predation contexts depended on elevation in interaction with four ecological or individual factors (Table II.1). First of all, the pattern was season-dependent (Elevation x Season:  $Z=2.51$ ,  $Est.=0.24\pm0.10$ ,  $P=0.012$ ; Table II.1). In fall, birds from high elevation visited the feeder significantly more during predator playbacks than their low elevation counterparts (post-hoc test:  $Z=5.42$ ,  $N=92$ ,  $Est.=1.46\pm0.10$ ,  $P<0.001$ ; Figure II.3A) whereas a tendency was detected in winter (post-hoc test:  $Z=2.17$ ,  $N=90$ ,  $Est.=1.15\pm0.07$ ,  $P=0.061$ ; Figure II.3A). Second, heavier birds visited the feeder less when a predator was present (Elevation x Body mass:  $Z=-2.00$ ,  $Est.=-0.12\pm0.06$ ,  $P=0.046$ ) but this pattern was only significant for birds from low elevation (post-hoc test:  $Z=-3.96$ ,  $N=90$ ,  $Est.=-0.16\pm0.04$ ,  $P<0.001$ ; Figure II.3B). Third, birds from high elevation visited the feeder more during predator playbacks when their fat reserves were higher (Elevation x Fat score:  $Z=-2.10$ ,  $Est.=-0.11\pm0.05$ ,  $P=0.036$ ; post-hoc test:  $Z=2.34$ ,  $N=92$ ,  $Est.=0.09\pm0.04$ ,  $P=0.019$ ; Figure II.3C) whereas feeder visits did not differ between contexts in relation to fat scores for birds from low elevation (post-hoc test:  $Z=-0.47$ ,  $N=90$ ,  $Est.=-0.02\pm0.04$ ,  $P=0.636$ ; Figure II.3C). Finally, female foraging preferences differed depending on their elevation of origin (Elevation x Sex:  $Z=2.91$ ,  $Est.=0.32\pm0.11$ ,  $P=0.004$ ) with females from high elevation visiting more often the feeder when a predator was present (post-hoc test:  $Z=4.92$ ,  $N=79$ ,  $Est.=1.46\pm0.11$ ,  $P<0.001$ ; Figure II.3D). Interestingly, males showed an opposite trend in their foraging decisions across elevations (post-hoc test:  $Z=1.97$ ,  $N=93$ ,  $Est.=1.15\pm0.08$ ,  $P=0.097$ ; Figure II.3D). Overall, when birds from high and low elevation differed in the proportion of visits during predator playbacks, high elevation birds were more risk-prone (Figure II.3).

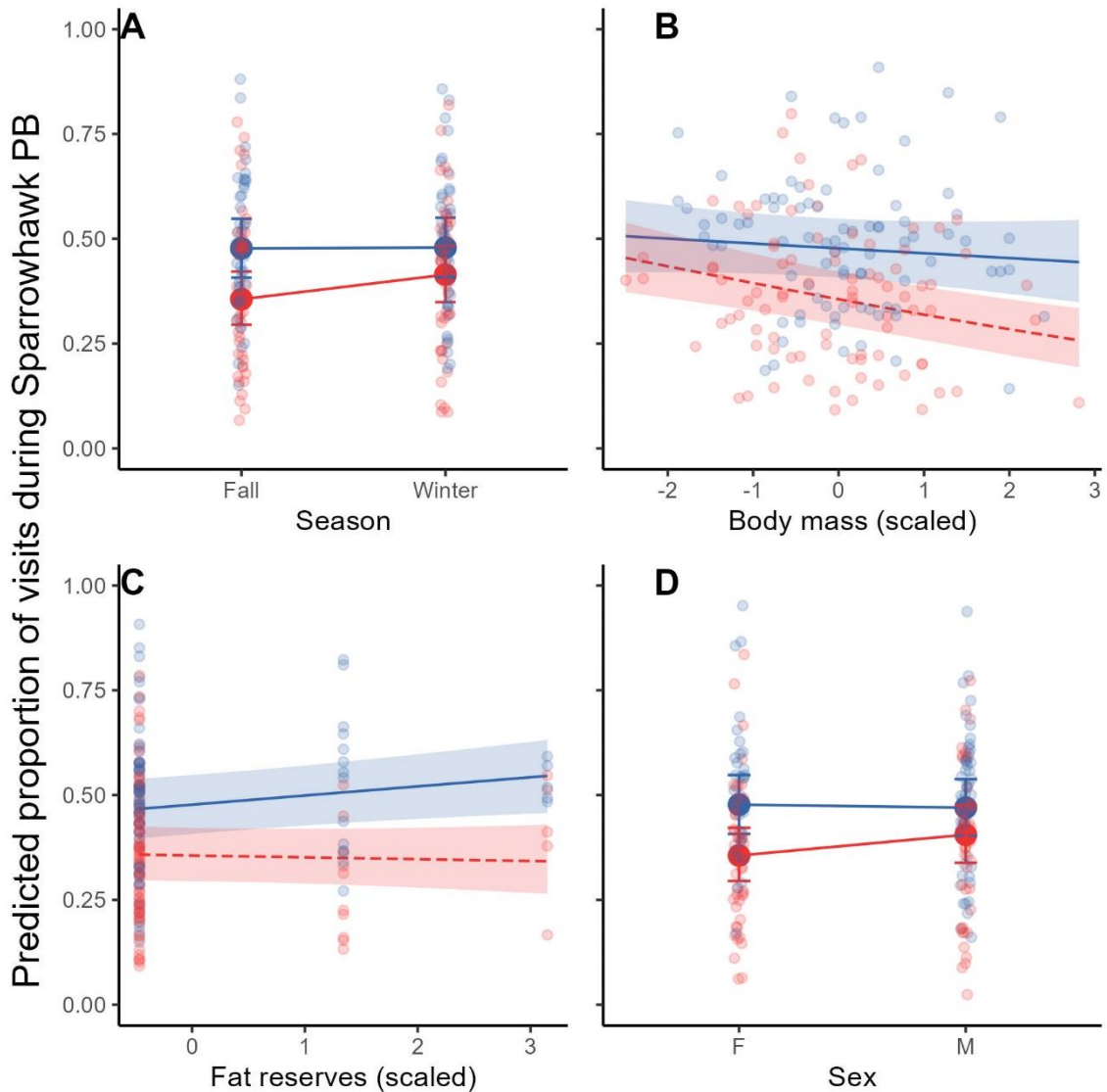
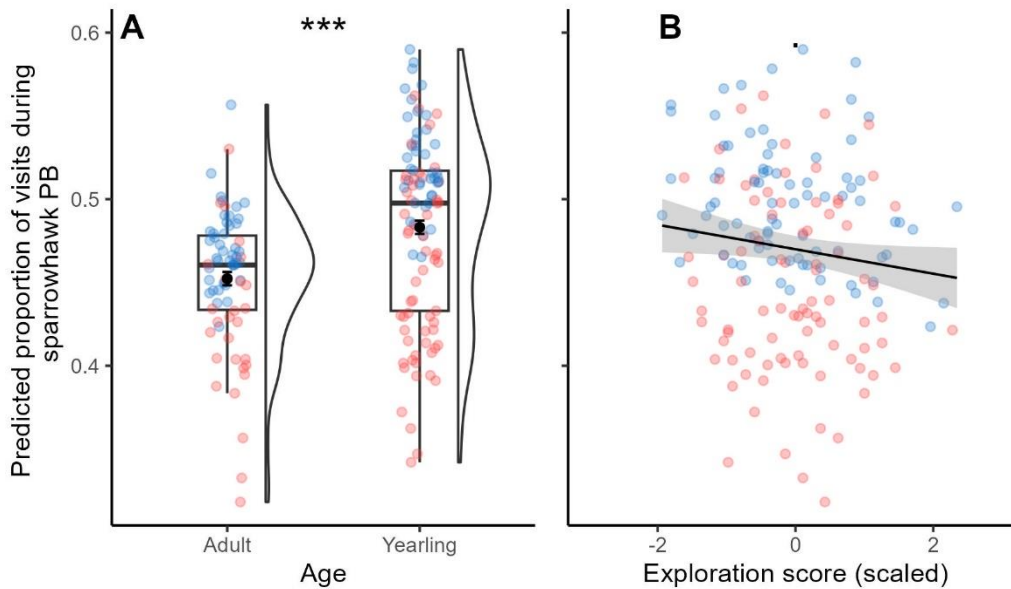


Figure II.3: Proportion of visits during predator playbacks according to elevation of origin of focal birds (blue=high elevation and red=low elevation) according A) season of the experiment, B) body mass, C) fat reserves and D) sex of focal individual. Shown in colored dots are the predicted values from the model using the number of visits under predation or control contexts (*cbind* function). Regression lines with 95% confidence intervals (panel B and C) and mean predicted proportion of visits  $\pm$  SE from the model (panels A and D) are shown.  $N=182$  individuals.

Yearlings made a greater number of visits to the feeder during predator stimuli relative to the control stimuli than did adults ( $Z=3.61$ , Est.= $0.18\pm 0.05$ ,  $P<0.001$ ; Figure II.4A). Great tits with high exploration scores tended to forage less during predator presentations than control

presentations compared to individuals with low exploration scores ( $Z=-1.80$ ,  $Est.=-0.04\pm 0.02$ ,  $P=0.071$ ; Figure II.4B). Tarsus length had no significant effect on the relative number of visits during predator presentations ( $Z=-0.16$ ,  $Est.=0.00\pm 0.03$ ,  $P=0.873$ ; Table II.1).



*Figure II.4: Proportion of visits during predator playbacks according to age and exploration scores. Black dots show the predicted mean proportion of visits  $\pm$  SE from the model with the predicted median and quartiles shown in the boxes (panel A) and the regression line with 95% confidence intervals (panel B). Predicted values from the model using the number of visits under predation or control contexts (cbind function) are in colored dots (blue=high elevation, red=low elevation), with their distribution (violins in Panel A).  $N=176$  individuals for Age and 182 individuals for exploration score.*

Table II.1: The relative number of visits to the OpenFeeder during predator (vs. control) video stimuli is influenced by a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird is more likely to visit the OpenFeeder during predator playbacks. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .

Model	Estimate	SE	95% conf int	Z value	P value
(Intercept)	-0.09	0.14	-0.37; 0.19	-0.64	0.524
<b>Elevation (Low)</b>	<b>-0.50</b>	<b>0.09</b>	<b>-0.68; -0.33</b>	<b>-5.59</b>	<b>&lt; 0.001</b>
Body mass	-0.05	0.05	-0.14; 0.05	-0.99	0.321
<b>Fat reserves</b>	<b>0.09</b>	<b>0.04</b>	<b>0.01; 0.16</b>	<b>2.34</b>	<b>0.019</b>
Sex (Male)	-0.03	0.08	-0.19; 0.13	-0.35	0.724
Season (Winter)	0.01	0.19	-0.36; 0.37	0.04	0.969
Tarsus length	0.00	0.03	-0.06; 0.05	-0.16	0.873
<b>Age (Yearling)</b>	<b>0.18</b>	<b>0.05</b>	<b>0.08; 0.28</b>	<b>3.61</b>	<b>&lt; 0.001</b>
Exploration Score	-0.04	0.02	-0.09; 0	-1.80	0.071
<b>Elevation x Body mass</b>	<b>-0.12</b>	<b>0.06</b>	<b>-0.23; 0</b>	<b>-2.00</b>	<b>0.046</b>
<b>Elevation x Fat reserves</b>	<b>-0.11</b>	<b>0.05</b>	<b>-0.21; -0.01</b>	<b>-2.10</b>	<b>0.036</b>
<b>Elevation x Sex</b>	<b>0.24</b>	<b>0.11</b>	<b>0.02; 0.46</b>	<b>2.10</b>	<b>0.036</b>
<b>Elevation x Season</b>	<b>0.24</b>	<b>0.10</b>	<b>0.05; 0.43</b>	<b>2.51</b>	<b>0.012</b>

## II. 5. DISCUSSION

The trade-off between starvation and predation in foraging decisions should change with environmental conditions (Bonter et al. 2013), for example, when facing less predictable or harsher environments like those encountered at higher elevations (Körner 2007; Pitera et al. 2018). To control for the short-term influence of various factors interacting with elevation on foraging decisions under the risk of predation (e.g. food availability or thermal conditions) birds in our experiment were tested under standardized, controlled conditions in temporary captivity. As expected, we found that birds from high elevation maintained higher foraging frequency at the feeder under increased perceived predation risk compared to birds originating from lower elevations (Figure II.3). This difference between high and low elevation birds was partly dependent on other factors, like the season (Table II.1) as it was only significant for birds tested in fall (Figure II.3A). In winter, individuals from low elevation became more risk-prone, approaching the risk levels during feeding of high elevation conspecifics. This could be linked



with an increase in the harshness of foraging conditions (food limitation) from fall to winter at low elevation, leading to a higher risk of starvation under wintering climatic conditions (Bejer and Rudemo 1985; Perdeck et al. 2000). In contrast, high elevation populations may experience more consistent harsher conditions from fall to winter. If conditions are already harsh in fall, birds may not shift their foraging decisions, which could explain the lack of seasonal difference of foraging decisions in high elevation birds. Food intake is critical to survival through winter and may therefore be the major driver of foraging decisions in our system where birds were kept in safe conditions (Houston and McNamara 1993). Likewise, predator abundance could also be one of the factors explaining elevation differences we detected as lower risks of predation at high elevation might lead to lower vigilance and a more risk-prone foraging strategy. In line with previous studies (Newton et al. 1977; Newton et al. 1986), we found that the number of predators detected decreased with elevation leading to a more intense “landscape of fear” at low elevation (Figure II.1). This could partly explain the more risk-prone foraging detected in high elevation birds.

Interestingly, birds were tested after 28 days spent under controlled conditions with the same food availability and predator risk conditions, yet differences in risk-prone foraging strategies persisted between high and low elevation. While captivity could influence behavior (Butler et al. 2006), if birds had mostly used recent information on predation risk to make foraging decisions, we should not have detected differences in behavior between high and low elevation birds. Indeed, this captive period with homogenized conditions could have attenuated differences in behavior between high and low elevation birds, implying that our results are conservative. Moreover, it seems likely that reactions to the video playback were weaker than would be during exposure to a real predator as video playbacks do not affect all sensory channels (e.g. no acoustic signals). Finally, birds came from a number of populations at each elevation suggesting that elevation or life history traits tightly linked to elevation per se rather than other peculiarities of the different populations are responsible for the differences we detected. Recent experimental studies have shown that presented with a disturbance or a threat, high elevation dark-eyed juncos flew away from a further distance (Andrade and Blumstein 2020) and high elevation mountain chickadees took longer to come back to their nest box (Kozlovsky et al. 2015a). While these studies show results going in the opposite

direction to ours, both were performed during the reproductive period when birds might be facing other life-history trade-offs (e.g. current vs future reproductive success). In contrast, individual survival is the key fitness criteria for birds in winter, thus reducing the number of likely trade-offs impacting foraging decisions. Differences between our results and recent studies highlights the importance of considering a variety of ecological factors and life-history trade-offs to understand risk sensitive foraging decisions.

Starvation risk is influenced by the reliability of access to food and being dominant generally provides such access (Ficken et al. 1990). In our study, we found that at low elevation, heavier birds were more risk-averse than lighter conspecifics (Figure II.3B). This result agrees with previous studies where body mass and risky decisions are negatively related (Rogers 1987; Macleod et al. 2005). Interestingly, lighter birds from both elevations appeared to be similarly risk-prone. These individuals may be facing similar high constraints to meet their nutritional needs since dominant individuals are usually heavier and have better access to food by competitively excluding lighter birds from food sources (Hegner 1985; Laet 1985; Ficken et al. 1990). Despite ample food availability during captivity, differences in foraging behavior related to mass at capture were apparent and similar to the relationship with mass at release (Table S. II.3: Relative number of visits to the OpenFeeder during sparrowhawk (vs. blackbird) video stimuli in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird is more likely to visit the OpenFeeder during sparrowhawk playbacks. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ . Table S. II.3). Birds can also modulate their metabolic effort to deal with starvation (Broggi and Nilsson 2023) which could reinforce the effects of weight we detected. In addition, fat reserves can influence foraging decisions as with more fat reserves available, an individual is less susceptible to face starvation risks (Houston and McNamara 1993). We found that for low elevation birds, the level of fat reserves did not impact risk-taking during foraging (Figure II.3C). In our controlled system, food access is relatively predictable and available *ad libitum* so birds may not need to rely strongly on fat reserves (Gosler 1996). However, we still found that high elevation birds presenting a higher level of fat reserves were more risk-prone in their foraging decisions (Figure II.3C). As starvation risk decreases with more fat reserves, we would expect birds with higher fat reserves

to be more risk-averse (McNamara and Houston 1990). We can speculate that with higher fat reserves, metabolic expenditure increased (Brodin 2001) and so birds from harsher conditions need to be more risk prone to meet increased foraging needs. Fat reserves and metabolic rates likely interact in complex ways and influence how risk taking during foraging shifts with environmental harshness.

We also showed that females – who are often subordinate to male great tits (Carrascal et al. 1998) – are sensitive to environmental contrasts (Figure II.3D). Since males have priority access to food, females need to develop alternative strategies to meet their foraging needs, such as better memorization (Brodin and Utku Urhan 2015). In harsher environments such as those found at high elevations where finding food is expected to be harder, adult males should be able to have priority access to food resources and thus should be more risk-averse than females (Lahti 1998). Finally, yearlings were more risk-prone regarding their foraging decisions, although we found no significant effect of elevation on their responses (Figure II.4A). Juveniles often have less access to food as they are subordinates to adults (Sandell and Smith 1991) and occupy less optimal habitats. Thus, adopting risk-prone foraging strategies could be the "best of a bad job" solution for non-dominant individuals allowing them to reach their minimal food intake and fat reserves (Krams et al. 2010). Alternatively, in some mammal and bird species, yearlings do not consistently discriminate between a predator and a non-predator (Kullberg and Lind 2002) and predator recognition improves with age (Putman et al. 2015). Learning allows individuals to adjust their behavior according to the local risks they face and thus limit the costs associated with excessive vigilance behaviors (Blanchard and Fritz 2007). Our experiment took place during the winter season where yearlings were about 6-9 months post hatch. Due to their younger age, these birds could have had fewer encounters with predators in their life to date than adults and thus might be less likely to consistently identify sparrowhawks as a potential threat. However, Kullberg and Lind (2002) showed that four months after fledging juvenile great tits were able to respond to a predator stimuli. It is possible that the reaction of yearlings towards sparrowhawks in our populations takes longer to develop than the one found by Kullberg and Lind (2002) and is thus driven by naivety towards predators. As an alternative, yearlings could be slower to react to a predator's appearance or disappearance on the screen. A fast response relies on a high level of behavioral

plasticity (Dingemanse and Wolf 2013), which has been shown to be lower for young individuals (Bonamour et al. 2020). Our study provides further evidence that age plays a critical role in driving behavioral foraging plasticity and suggests a mechanism to explain lower survival of first year birds compared to older ones (Martin, 1995). Nestlings face high rates of predation after fledging (Naef-Daenzer et al. 2001), and risk-prone yearlings might face higher rates of predation thus becoming proportionally less present in populations. Albeit difficult to quantify, future studies should examine the factors that underlie the ontogeny of risk-taking in juveniles and their effects on their first year survival.

Personality has been identified as a key component of individual decisions (Mathot et al. 2012; Rojas-Ferrer et al. 2020) and could have an important impact on foraging. However, we found no clear impact of exploration score in a novel environment on foraging decisions (Figure II.4B). Previous studies showed that fast explorers decreased their foraging activity more under predation risk (Abbey-Lee et al. 2016) and that they are more flexible in their reaction to predation risk by switching food preferences (Coomes et al. 2022) or returning to feed faster following a stressful disturbance (van Oers et al. 2004; Quinn and Cresswell 2005). Moreover, high elevation birds were identified as being slower explorers compared to low elevation birds (Kozlovsky et al. 2014). We therefore expected fast explorers to be more risk averse, especially for birds from low elevation, but this was not the case. In our experiment, we did not measure the rapidity to react to a change in the predation risk but overall preferences in foraging decisions. Such decisions are known to also depend on dominance status (Quinn et al. 2012). Future studies should directly examine whether exploration behavior is really associated with risk-prone strategies, in interaction with dominance status, and linked to other fitness traits.

Overall, we found that foraging decisions under predation risk vary among elevations in association with individual characteristics, in accordance with starvation-predation trade-off theory. The differences in risk-taking during foraging we detected were still persistent despite the fact that birds spent 28 days under standardized conditions where all individuals had the same levels of food, competition, ambient temperature, and risk of predation. The contrast between adults and juveniles raises the question of how and when individuals learn the proper responses to be adopted. It would also be important to determine how long individuals retain

information about predation risk in their habitat and use that information to modulate their foraging behavior. This question is not trivial as anthropogenic induced climate change is causing range shifts including movements towards higher elevations (Parmesan and Yohe 2003; Campos-Cerqueira et al. 2017), which brings individuals adapted to their population of origin into areas with different risks and constraints. If such areas include a higher risk of predation, these "immigrant" birds may take more risks and suffer higher mortality. On the other hand, if individuals avoid risk-taking when moving to areas with lower risk, they may miss out foraging opportunities and not get enough food. Further experiments should examine the mechanisms underlying risk-taking and whether there is a link between the ontogeny of risk-taking and the ability to move to new habitats. Such results would help us understand how individuals might cope with changing climates.

## II. 6. SUPPLEMENTARY MATERIALS

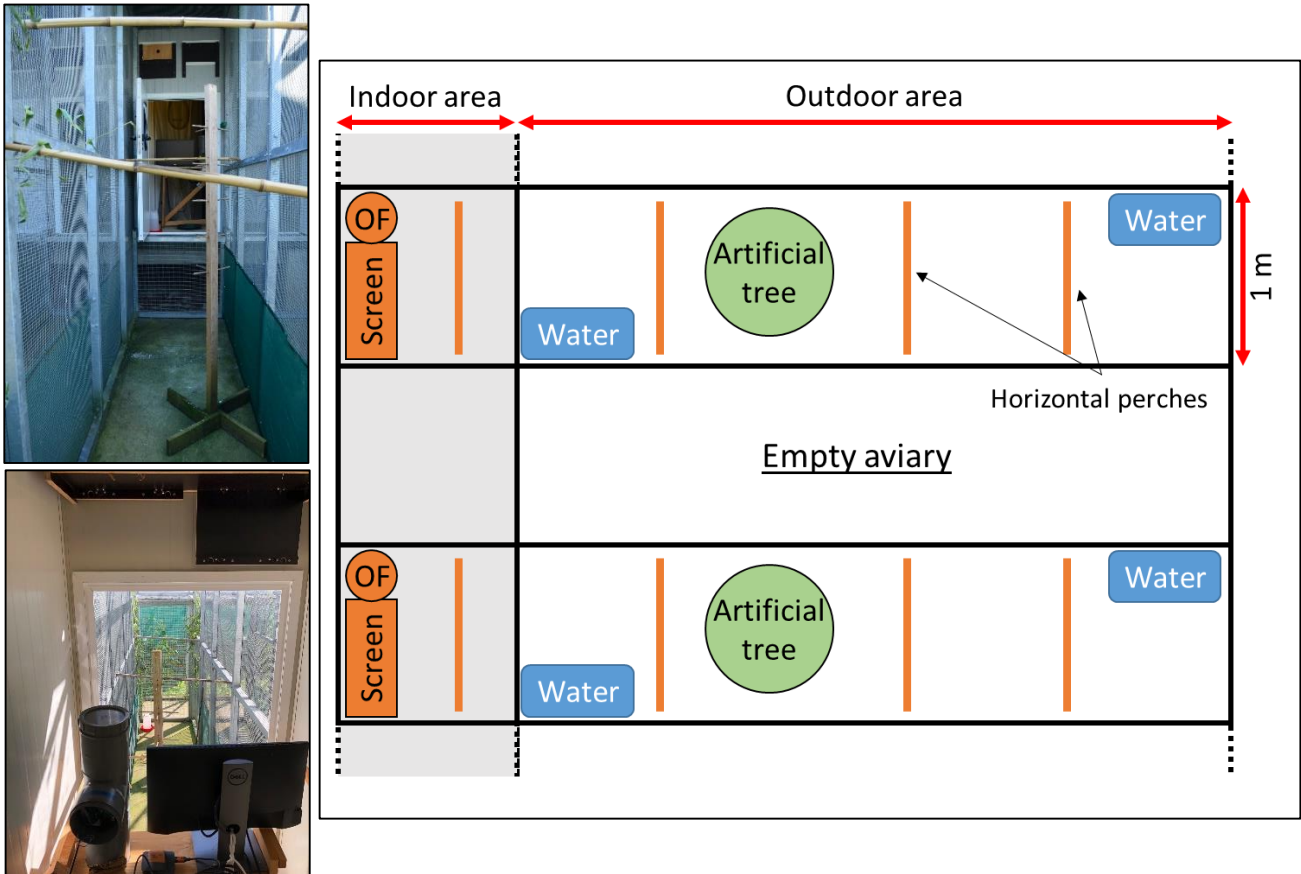
### II. 6. 1. Predator abundance quantification



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*Figure S. II.1: A) Camera traps (Bushnell Trophy Cam HD Essential E2 ®) set, B) Custom made resin great tit model and C) Experimental installation used to quantify predator abundance in our study populations.*

## II. 6. 2. Housing facilities



*Figure S. II.2: Pictures and schematic plan illustrating the aviaries at CNRS-SETE (1 x 5 x 3 m, W x L x H). Each aviary hosted one bird with one empty aviary between two birds to avoid physical contact between birds and to ensure that birds could not see their closest neighbor's screen (OF=OpenFeeder).*

### II. 6. 3. Video playback broadcasting

A single video file including the 18 video playbacks was broadcasted (9 Blackbirds (control) and 9 Sparrowhawk (predation) on the screen during the present experiment. While the file includes all 18 videos placed sequentially, videos were stored as separate clips for the experiment. Video playbacks were randomly chosen from the 18 video clips using a Python code written for Raspberry 3Pi by Jérôme Briot.

We examined habituation to video playbacks by comparing the relative number of visits during sparrowhawk stimuli during one hour periods throughout the day. We used a zero inflated GLMM with a binomial distribution with the relative number of visits during sparrowhawk displays (two-column matrix (cbind function) with the number of visits to the OpenFeeder during sparrowhawk playback and the number of visits to the OpenFeeder during blackbird playback) as the response variable, periods of the day as a fixed factor and bird identity as a random factor. The birds did not significantly change their foraging strategy throughout the day ( $X^2= 5.95$ ,  $N = 182$ ,  $P = 0.31$ ), suggesting that they did not habituate to the predation stimulus. We therefore used data from all the periods in our analyses in all subsequent analyses.



II. 6. 4. Table of morphological traits*Table S. II.1: Tarsus length and weight of the great tits from our study populations.*

Elevation	Tarsus (mm)		Weight (g)	
	Mean	SD	Mean	SD
High	22.34	0.64	17.34	0.95
Low	22.38	0.71	17.14	1.01

*Table S. II.2: Sample sizes of individuals tested in our experiment.*

Elevation	Sex		Age		Season	
	Female	Male	Yearling	Adult	Fall	Winter
High	36	56	44	48	46	46
Low	43	47	60	29	46	44

### II. 6. 5. Model construction with body mass at release

We performed the same analysis as described in the main text focusing on the factors predicting the relative number of visits to the OpenFeeder during each stimulus video but included the body mass at release instead of the body mass at capture. Results are overall similar regardless of which measure of body mass was used.

*Table S. II.3: Relative number of visits to the OpenFeeder during sparrowhawk (vs. blackbird) video stimuli in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird is more likely to visit the OpenFeeder during sparrowhawk playbacks. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .*

Model	Estimate	SE	95% conf int	Z value	P value
(Intercept)	-0.08	0.15	-0.38; 0.21	-0.55	0.580
<b>Elevation (Low)</b>	<b>-0.49</b>	<b>0.09</b>	<b>-0.67; -0.31</b>	<b>-5.39</b>	<b>&lt; 0.001</b>
Body mass	-0.03	0.04	-0.11; 0.04	-0.81	0.417
<b>Fat reserves</b>	<b>0.08</b>	<b>0.04</b>	<b>0.01; 0.15</b>	<b>2.34</b>	<b>0.019</b>
Sex (Male)	-0.04	0.08	-0.2; 0.12	-0.52	0.601
Season (Winter)	0.01	0.20	-0.37; 0.4	0.08	0.939
Tarsus length	0.00	0.03	-0.06; 0.06	-0.01	0.992
<b>Age (Yearling)</b>	<b>0.17</b>	<b>0.05</b>	<b>0.07; 0.27</b>	<b>3.47</b>	<b>0.001</b>
Exploration Score	-0.04	0.02	-0.08; 0.01	-1.57	0.117
<b>Elevation x Body mass</b>	<b>-0.12</b>	<b>0.05</b>	<b>-0.22; -0.02</b>	<b>-2.38</b>	<b>0.018</b>
<b>Elevation x Fat reserves</b>	<b>-0.13</b>	<b>0.05</b>	<b>-0.22; -0.03</b>	<b>-2.63</b>	<b>0.008</b>
Elevation x Sex	0.21	0.11	0; 0.43	1.95	0.051
<b>Elevation x Season</b>	<b>0.27</b>	<b>0.09</b>	<b>0.09; 0.46</b>	<b>2.92</b>	<b>0.003</b>



**CHAPTER III.**

**CONTEXT-DEPENDENT FORAGING PLASTICITY ALONG**

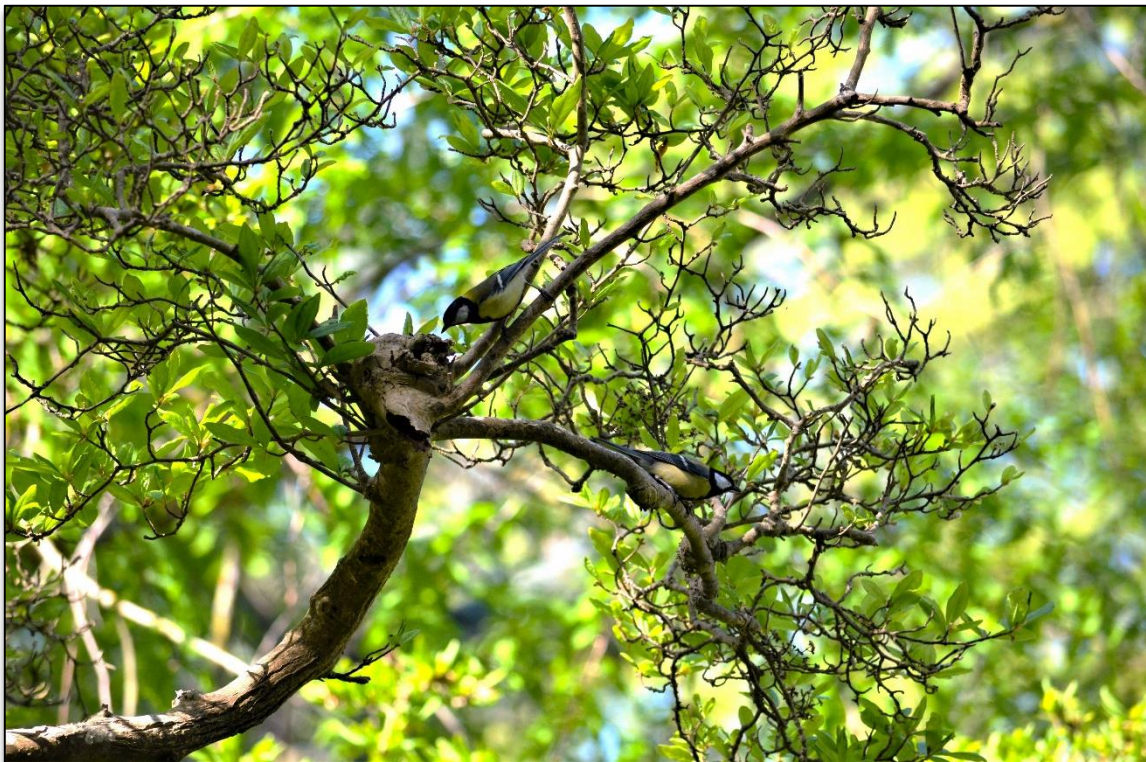
**SOCIAL AND ENVIRONMENTAL GRADIENTS IN GREAT**

**TITS**

In preparation

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### III. 1.ABSTRACT

Among the many factors that influence natural selection, the social environment which regroups other individuals, either con and hetero-specifics, can have a strong impact on fitness. Social selection should favor the evolution of "social competence", i.e. the ability of individuals to adapt their behaviors to variation in the social environment. Although there is evidence for temporal plasticity in social behaviors, the context dependency of this plasticity remains unexplored, especially during non-agonistic or non-reproductive interactions such as foraging. With video playbacks, we manipulated social audience perceived by wild great tits by changing its group size and species composition and measured social foraging plasticity. We also tested the effects of one secured and two stressful contexts on foraging decisions. We found that great tit foraging preference at a feeder were higher when foraging alone or when conspecifics were presented instead of blue tits. Moreover, in stressful contexts, birds were less socially plastic in their foraging decisions compared to more secured ones. Thus, social plasticity depends both on social information and environmental cues. Additionally, individual differences in context-dependent social foraging plasticity were affected by intrinsic factors such as age and weight. Facing nowadays fast changing environments, individuals' ability to plastically adapt their behaviors to new contexts may be an essential component for fitness.

**Keywords:**

Behavioral plasticity, elevation, foraging, great tit, predation risk, risk-taking behavior, video playback

## III. 2. INTRODUCTION

Organisms are constantly faced with shifts in their social and ecological environments and can improve their survival and reproductive success by having the flexibility to react appropriately to stimuli perceived from their environment (Wund 2012). Facing rapid changes, behavior is considered the most plastic phenotypic trait as it shows the quickest response to temporal changes (Gross et al. 2010). Individual variation in behavioral plasticity, the ability to adjust behaviors in response to changes in the environment (Mery and Burns 2010), has been found in a wide range of species (Mathot et al. 2012; Briffa et al. 2013; Bhat et al. 2015; Sassi et al. 2015). This plasticity should be especially favored when the rate of change of environmental variation overtakes evolutionary rate (Snell-Rood 2013). In order to predict the ability of populations to persist in new environments, we need to understand how behavioral plasticity allows to develop responses in different contexts (Stamps 2016).

Facing social challenges, individuals able to adapt their behaviors efficiently should be favored by social selection (McGlothlin et al., 2010; West-Eberhard, 1983; Wolf et al., 1999). The level of behavioral plasticity related to variations in social environments, named "social competence", has received specific attention for the study of ontogeny of social behaviors (Taborsky and Oliveira 2012). Fishes raised in isolation showed less appropriate behaviors in social interactions for resources access compared to young raised in social groups, confirming the importance of past social experiences on the development of social plasticity (Arnold and Taborsky 2010). But, most social environments are highly dynamic with the composition of interacting individuals also changing over short time scales (Richner and Heeb 1995). Social competence should help individuals to update their choices in real time in reaction to variation of characteristics of the social environment (Bshary and Oliveira 2015). Whilst foraging, zebra finches used available information about the social environment to adjust their foraging tactics and limit competition (Wolf & McNamara, 2013; Barou Dagues et al., 2020). However, recent work on sailfin mollies found weak correlations between plasticity in mating behavior and in social neophobia (Gibelli et al. 2018). This result suggests that individual social plasticity in a given situation may not be generalizable to another situation and behavior. Thus, social competence might be associated to changes in contexts. For example, when foraging in groups,

individuals improve the probability to detect predators while reducing the risk of being killed (Elgar 1989; Lima 1995). But at the same time, foraging in group increases the competition between individuals for resources (Ranta et al. 1993; Richner and Heeb 1995), leading to a trade-off where individuals are selected to maximize their net benefits. Thus, the best social decision is likely to depend on the perceived risk of predation but experimental confirmation are rare (but see Culbert et al., 2021). More work is needed to investigate how variation of the composition of the social group and of the environmental context may interact in foraging decisions and so social competence along both social and environmental variations.

Individuals vary in their ability to integrate social cues depending on their early social environment, (Taborsky et al., 2012) so we predict consistent differences in social competence abilities between individuals (Stamps 2016). Social environments are not limited to past experience or the number of individuals in a group but can also depend on species composition or the sex of other individuals (Sasvári 1992; Dolby and Grubb 2000). Individuals of different age, dominant rank or sex may integrate differently social factors in their decisions. Previous work found that nutmeg manikins had similar foraging decisions related to group size variation (Rieucau et al. 2010). In contrast, another study on cichlids showed that shy foragers were more reactive to social cues, thus highlighting the importance of individuals' personality on social competence variation (Ólafsdóttir and Magellan 2016). Therefore, further research is required to understand to which extent the rate of change in foraging behavior varies among individuals.

In this study, we investigated how the decision to forage at a patch was impacted by the social environment when facing different ecological contexts. We temporarily brought wild great tits (*Parus major*) in captivity and recreated different social groups with video playbacks of various number of great and blue tits near food as a stimulus. As these two species are known to forage in mix-species flocks and great tits are often dominant over blue tits (Sasvári 1992), we predict that great tits should choose to forage more often with blue tits than great tits so as to gain access to food. Moreover, we recorded foraging preferences in more or less stressful contexts to understand how social competence is context dependent whilst foraging. Group behavior should be advantageous whenever there is a predation risk, despite the increased competition

for resources (selfish herd effect, Hamilton, 1971). Additionally, facing a new disturbance, group behavior can be a strategy to diminish neophobia and favor access to foraging patches. Finally, we examined how individual characteristics such as age, personality or elevation of origin explained individual variations in contextual social competence. When finding food is harder, for yearlings or in high elevation habitats for example, individuals should adapt their social behavior, and we predict higher foraging plasticity for these individuals.

### III. 3.METHODS

#### III. 3. 1. Capture and housing

Between mid-October 2020 and mid-March 2022, we caught 192 wild great tits (*Parus major*) using mist nets at 2 high (Antras, 891 m asl., 42°52'51.7"N, 0°56'44.4"E; Villargein, 898 m asl., 42°54'17.1"N, 1°02'48.0"E), and 2 low elevation sites (Aubert, 430 m asl., 42°57'51.4"N, 1°06'11.3"E; Montjoie, 445 m asl., 42°59'56.0"N, 1°10'09.3"E) in the French Pyrenees. In previous studies, we have shown that birds differ in various traits between these elevations including laying date (Bründl et al. 2020), risk-taking foraging (Chapter 2), and reversal learning (Hermer et al. 2018). Likewise, habitat, temperature, and predation risk differ between high and low elevations sites (Bründl et al., 2020; Chapter 2). We trapped birds in 8 batches (24 individuals per batch). We identified each individual with a unique CRBPO (Centre de Recherche sur la Biologie des Populations d'Oiseaux) metal band and a colored RFID (Passive Integrated Transponders, IB Technology, UK) plastic band. We used plumage variation to sex (male or female) and age (adult or yearling) birds (Svensson 1992) and measured body mass at capture using a digital scale (nearest 0.1g).

We housed birds individually in aviaries at the CNRS-SETE in Moulis, with an empty cage between each individual which remained visually and acoustically connected to neighbors. Each aviary (1 x 5 x 3 m, W x L x H) contained foliage for cover, an artificial tree, horizontal perches, a roosting box, and water. An automatic RFID-based feeder (hereafter "OpenFeeder", Cauchoix et al. 2022) provided *ad libitum* sunflower seeds. In addition, birds had access to *ad*



*libitum* mealworms between video playback experiments. We collected an exploratory score for each bird as the total number of movements completed during a 3 min period, following Dingemanse et al. (2002), a measure known to be repeatable and a good proxy for personality (Dingemanse et al. 2012; Niemelä and Dingemanse 2018). We performed social foraging experiments after four days of acclimation to captivity and released birds at their respective capture sites after experiments were completed.

### III. 3. 2. Foraging plasticity

We used videos playbacks to simulate variation in the social environment. Video playbacks work well in a wide range of species, including great tits (Oliveira, McGregor, et al. 2000; Rieucau and Giraldeau 2009; Snijders et al. 2017; Hämäläinen et al. 2019; Smit and van Oers 2019) and have been used successfully in our facilities (Chapter 2). We extracted stimuli from videos of wild great or blue tits (*Cyanistes caeruleus*) foraging on fat balls at Moulis. Note that the nearest capture population is >2km away making it unlikely that focal great tits would recognize individuals in videos. We isolated 5 videos for each of 8 video categories based on species, number of birds present and sex of birds visible: background with no bird, 1 blue tit, 2 blue tits, 1 female great tit, 1 male great tit, 2 female greats tits, 2 male great tits, 2 mixed-sex great tits. We broadcasted videos continuously during two daily sessions (9 am to noon; 1 pm to 4 pm) for three days. Aviaries were swept at the start of each day to ensure that the only food available was from the OpenFeeder during playback sessions. Video playbacks were randomly selected, so each bird would see all categories stimuli equally when seeking food. Each stimulus lasted 30s to mimic natural encounter at a food patch and contained no sound to avoid influences of vocalizations (see Supplementary materials for videos). All birds of a specific batch were tested simultaneously. Each individual could only see the computer screen located next to the OpenFeeder of its own aviary as screens were placed at the interior portion of the cage and was blind of video playbacks seen by other birds around (see Supplementary materials for a plan, Figure S. III.1). The RFID reader on the OpenFeeder recorded when the bird came to feed and during which video. Sample sizes of some batches were lower than the maximum of 24 as a result of technical errors (N=6) or death during a cold snap in January 2021 (N=1; final sample size: 185 birds).

We created a different environmental context related to foraging for each day of the video presentation experiment. On the first day (“*Control*”), birds had access to the feeder with video projections. Tested individuals had not seen videos before this day. On the second day (“*Predation*”), we increased the perceived predation risk by presenting a taxidermized European Sparrowhawk (*Accipiter nisus*), a major predator of tits (Gosler 1993). During video presentation phases of this day, the taxidermized predator was exposed on a perch for 5 minutes every hour (i.e. 6 times during the day) at the outdoor extremity of aviaries (opposite to the OpenFeeder and computer screen, see Supplementary materials for images, Figure S. III.1). Simultaneously, we broadcasted audio playbacks of sparrowhawk vocalizations obtained from the Xeno Canto online database (<http://www.xeno-canto.org>) during predator presentations using a JBL Flip 4 loudspeaker. Due to technical constraints, we presented a taxidermized predator for each side of the aviaries building (half of each batch) at different hours of the day (e.g. 9:00 am on one side of the building and 9:30 am on the other side). Note that we did not present predators near the OpenFeeder as it was technically difficult and we did not broadcast predators on screens as we were concerned it would cause great tits to stop using OpenFeeder for subsequent experiments (Chapter 2). On the third day (“*Disturbance*”), a small door on the OpenFeeder hid 30% of the opening while food was still visible. Each time a bird came, the door fully opened, allowing complete access to food. This movement and the motorized door and associated sound initially caused a disturbance or stress at each visit. All birds experienced the three contexts in the same order (i.e. *Control*, *Predation*, *Disturbance*).

### III. 3. 3. Statistical analysis

We performed statistical analysis using R software (R version 4.2.2, R Core Team, 2022). To quantify the foraging behavior of each individual, we pooled the number of visits to the OpenFeeder per video playback category over the whole day of the experiment. We grouped male and female video playbacks together as there was no significant sex effect on foraging decisions (See Supplementary materials, Table S. III.1). Because playback categories had different numbers of video projections after the grouping, we calculated the mean number of visits per category (e.g. for 1 great tit situation, sum of visits with one male or one female great tit video playbacks divided by two as there were two video categories grouped).

To understand how social foraging preferences depended on the context, we built a linear mixed model (*lme4* package, Bates et al., 2014) with the mean number of visits to the feeder as the response variable. We log-transformed and scaled this variable prior to integration in the model to meet normality distribution. We added the size of the group on the playback video, the species on the playback and the general context (*Control*, *Predation*, *Disturbance*) as fixed factors, along with two and three way interactions. We did not find a significant three-way interaction (GroupSize x Species x Context,  $P=0.413$ , see Supplementary materials, Table S. III.2), and removed it from the initial model. In all models, we added bird identity as a random factor to account for repeated measures and the total number of visits performed during the day by each specific bird as a fixed factor to account for activity differences between birds.

To understand factors explaining among individual variation in social foraging plasticity, we extracted foraging plasticity as the mean number of visits with birds (mean of visits with 1 and 2 birds) since there was no difference in feeder visits with 1 vs 2 birds on the screen (see results) minus the number of visits with no birds on the screen. A positive value of plasticity corresponds to a preference for foraging with one or two birds while a negative value denotes a preference for visiting when alone. We built a linear mixed model with foraging plasticity as the response variable and species on the playback, the general context and individual characteristics (sex, age, elevation of origin, exploration score, body mass) as fixed factors. We mean centered and scaled by standard deviation the exploration score and body mass prior to integration in the model. We added three way interactions between Context, Species and each individual characteristic, as well as two-ways interactions between Context or Species and each individual characteristic variable. We removed all non-significant interactions from this model until the final model (see Supplementary materials, Table S. III.3 for initial full model). We added bird identity as a random factor to account for repeated measures (between Contexts). To assess the significance of differences between levels, we ran post-hoc Tukey HSD tests (*emmeans* package, Lenth et al., 2022). We checked model performance graphically using the *DARHMa* package (Hartig 2022). The significance level for p-values was set at 0.05 (two-tailed tests). Figures were built using the *interactions* package (Long 2019).

### III. 4.RESULTS

#### III. 4. 1. Impact of species information on social foraging preferences

Social foraging preference depended on the number of individuals present on the screen, in interaction with social audience's species (GroupSize x Species; Table III.1). Greats tits preferred to forage alone than when one bird was presented (species visible=great tit:  $Z=4.07$ ,  $N=185$ ,  $Est.=0.13\pm0.03$ ,  $P<0.001$ ; species visible=blue tit:  $Z=7.68$ ,  $N=185$ ,  $Est.=0.24\pm0.03$ ,  $P<0.001$ ) or two birds (great tit:  $Z=5.55$ ,  $N=185$ ,  $Est.=0.17\pm0.03$ ,  $P<0.001$ ; blue tit:  $Z=8.83$ ,  $N=185$ ,  $Est.=0.28\pm0.03$ ,  $P<0.001$ ). They did not show a preference for one compared to two individuals (great tit:  $P=0.303$ ; blue tit:  $P=0.484$ ; Figure III.1). Moreover, focal birds preferred foraging at the feeder when great tits were presented compared to blue tits (Overall species effect: see Table III.1; one bird:  $Z=-2.50$ ,  $N=185$ ,  $Est.=-0.08\pm0.03$ ,  $P=0.012$ ; two birds:  $Z=-2.17$ ,  $N=185$ ,  $Est.=-0.07\pm0.03$ ,  $P=0.03$ ; Figure III.1).

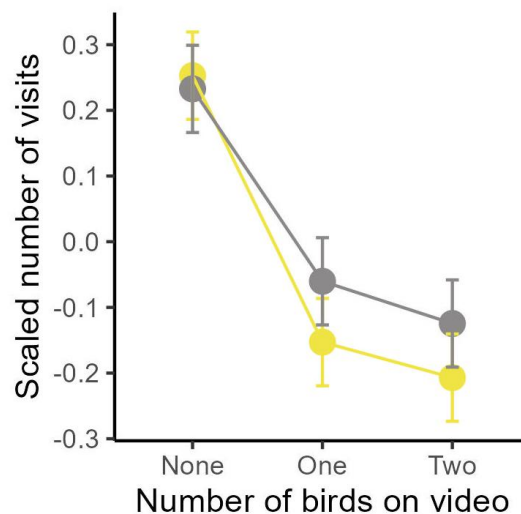


Figure III.1: Effect of number of birds and species (blue tits=yellow, great tits=grey) presented in video playbacks on scaled feeder visits by great tits. Colored dots are the predicted mean  $\pm$  SE from the model.  $N = 185$  individuals.

Additionally, the preference for foraging alone instead of with one or two birds changed with the context experienced by focal birds while foraging (GroupSize x Context; Table III.1) although not related to the species presented in the videos across contexts (Species x Context:  $P=0.851$ ; Table III.1). Preferences for foraging alone were higher in *Control* compared to *Predation* ( $Z=3.39$ ,  $N=185$ ,  $Est.=0.13\pm0.04$ ,  $P=0.002$ ) and *Disturbance* ( $Z=4.91$ ,  $N=185$ ,  $Est.=0.19\pm0.04$ ,  $P<0.001$ ) contexts, while no difference was visible between *Predation* and *Disturbance* contexts ( $P=0.260$ ; Figure III.2). Preferences for foraging in a social group were higher in *Disturbance* compared to *Control* (one bird:  $Z=3.70$ ,  $N=185$ ,  $Est.=-0.14\pm0.04$ ,  $P=0.001$ ; two birds:  $Z=4.84$ ,  $N=185$ ,  $Est.=-0.19\pm0.04$ ,  $P<0.001$ ) and *Predation* (one bird:  $Z=2.85$ ,  $N=185$ ,  $Est.=-0.11\pm0.04$ ,  $P=0.012$ ; two birds:  $Z=3.71$ ,  $N=185$ ,  $Est.=-0.14\pm0.04$ ,  $P=0.001$ ) contexts, with no significant difference between *Control* and *Predation* contexts (one bird:  $P=0.653$ ; two birds:  $P=0.475$ ; Figure III.2). Overall, during the *Disturbance* context, birds showed no significant changes in foraging preferences regardless of group size (all  $P>0.5$ ; Figure III.2), contrary to during *Control* and *Predation* contexts.

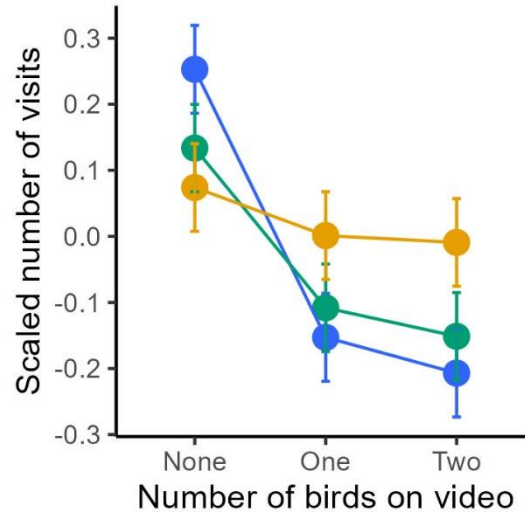


Figure III.2: Scaled number of visits to a feeder in relation to the number of birds present in video playbacks for three different contexts (Control=blue, Predation=green, Disturbance=orange). Colored dots are the predicted mean  $\pm$  SE from the model.  $N = 185$  individuals.

Table III.1: Factors impacting foraging preferences in great tits at a feeder. A linear model was fitted including *GroupSize*, *Context* (Control, Predation, Disturbance) and *Species* as fixed factors (Type III Anova). Values in bold are significant at  $P < 0.05$ .

Explanatory factors	Ch.sq	Df	P Value
(Intercept)	0.00	1	1.000
<b>GroupSize</b>	<b>117.25</b>	<b>2</b>	<b>&lt;0.001</b>
<b>Context</b>	<b>8.83</b>	<b>2</b>	<b>0.012</b>
<b>Species</b>	<b>4.23</b>	<b>1</b>	<b>0.040</b>
<b>Total Visits</b>	<b>8,174.58</b>	<b>1</b>	<b>&lt;0.001</b>
<b>GroupSize x Context</b>	<b>58.02</b>	<b>4</b>	<b>&lt;0.001</b>
<b>GroupSize x Species</b>	<b>7.97</b>	<b>2</b>	<b>0.019</b>
Species x Context	0.32	22	0.851

### III. 4. 2. Factors explaining among individual differences in social competence

Individual differences in foraging plasticity (i.e. difference between preference for foraging in groups vs alone) were context-dependent in interaction with two factors. First, the foraging plasticity variation was age-dependent (Context x Age; Table III.2) with yearlings being less plastic (i.e. plasticity closer to 0) in *Predation* ( $T=3.08$ ,  $Est.=-1.62\pm 0.53$ ,  $P=0.002$ ) and *Disturbance* ( $T=3.23$ ,  $Est.=-1.70\pm 0.53$ ,  $P=0.001$ ) contexts compared to adults. No significant difference was visible in the *Control* context ( $T=0.15$ ,  $Est.=-0.08\pm 0.53$ ,  $P=0.881$ ; Figure III.3A). Overall, there was no significant variation of plasticity in adults ( $P>0.4$ ) while yearlings changed their plasticity between contexts (*Control-Predation*:  $T=-4.34$ ,  $Est.=-1.62\pm 0.37$ ,  $P<0.001$ ; *Control-Disturbance*:  $T=-6.27$ ,  $Est.=-2.35\pm 0.37$ ,  $P<0.001$ ; *Predation-Disturbance*:  $T=-1.94$ ,  $Est.=-0.72\pm 0.37$ ,  $P=0.129$ ; Figure III.3A). Second, plasticity changed depending on bird's body mass (Context x Body mass; Table III.2). In the *Control* context, heavier birds were less plastic than lighter conspecifics as their plasticity was closer to 0 ( $Z=2.19$ ,  $Est.=0.61\pm 0.28$ ,  $P=0.029$ ; Figure III.3B). However, the weight of a bird no longer influenced foraging plasticity in *Predation* ( $Z=0.45$ ,  $Est.=0.12\pm 0.28$ ,  $P=0.655$ ; Figure III.3B) and *Disturbance* contexts ( $Z=-0.49$ ,  $Est.=-0.14\pm 0.28$ ,  $P=0.628$ ; Figure III.3B).

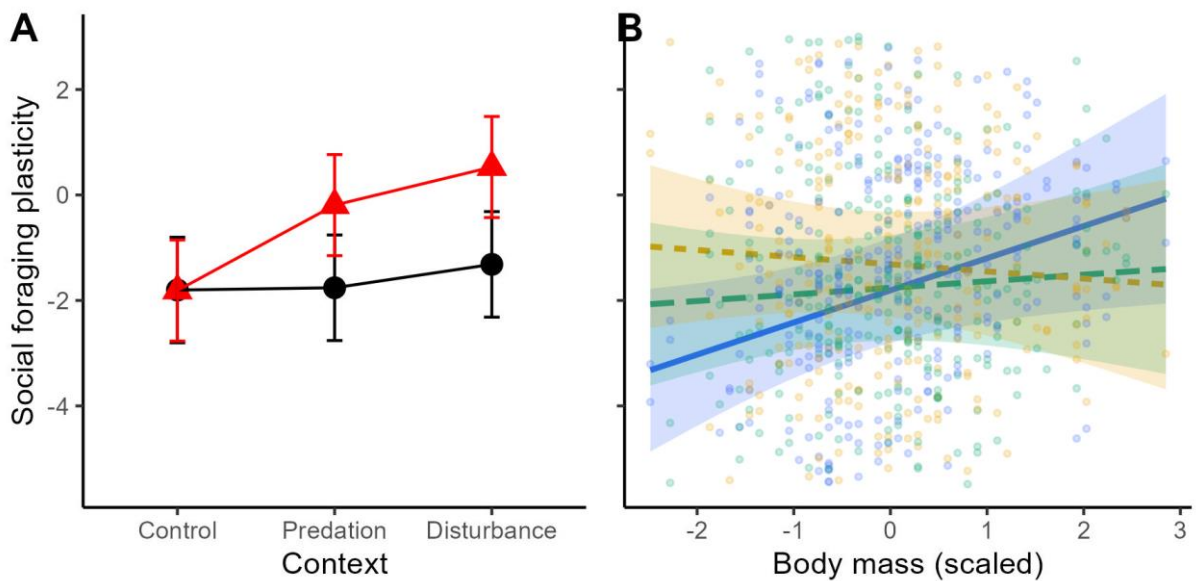


Figure III.3: Social foraging plasticity according to different contexts and A) age of individuals (adult=black, yearling=red) and B) body mass (Control=blue, Predation=green, Disturbance=orange). Shown in colored dots are the predicted mean  $\pm$  SE from the model (panel A) and the predicted values (panel B) from the model with the regression line with 95% confidence intervals (panel B).  $N = 185$  individuals.

Table III.2: Factors explaining individual differences in foraging plasticity in great tits. A linear mixed model was fitted with Context, Species, Elevation, Age, Exploration score, Body mass and Sex as fixed factors (Type III Anova). Non-significant interactions were removed from the model. Values in bold are significant at  $P < 0.05$ .

Explanatory factors	Ch.sq	Df	P Value
<b>(Intercept)</b>	<b>7.32</b>	<b>1</b>	<b>0.007</b>
<b>Context</b>	<b>24.89</b>	<b>2</b>	<b>&lt; 0.001</b>
Species	0.34	1	0.558
Elevation	0.09	1	0.760
<b>Age</b>	<b>7.96</b>	<b>1</b>	<b>0.005</b>
Exploration score	0.20	1	0.655
Body mass	0.79	1	0.375
Sex	1.27	1	0.260
<b>Context x Age</b>	<b>12.18</b>	<b>2</b>	<b>0.002</b>
<b>Context x Body mass</b>	<b>7.05</b>	<b>2</b>	<b>0.029</b>

### III. 5. DISCUSSION

In the present study, we examined which ecological factors could induce variation in social foraging. We found that birds used the number of individuals and the species projected on a screen as a social audience to make decisions. Interestingly, foraging decisions varied among different contexts as preference for foraging alone rather than in a group was less marked under predation and disappeared facing disturbance compared to control context. We also examined some of the factors explaining individual differences in social competence and pointed out the importance of age and body mass in the ability to change foraging plasticity. Facing nowadays fast changing environments, among individual variation in ability to plastically adapt their behaviors to new contexts may be an essential component for fitness.

Group foraging theory predicts that in many species, individuals should favor foraging alone rather than in a group to maximize foraging efficiency and limit competition (Clark and Mangel 1986; Ranta et al. 1993). As expected, in our experiment we found that great tits preferred foraging alone rather than with one or two conspecifics (Figure III.1). Tested birds may perceive birds on a screen as other individuals from the social environment that constitute potential competitors. Interestingly, this preference was visible as soon as one competitor was present and increasing the number of birds in the social environment did not have a significant impact. The costs of competition appear to be strong enough so birds preferred foraging alone (Ranta et al. 1993). But competition for food in great tits can also be interspecific such as found in mixed species flocks species (Morse 1970). It is expected that competition would be more intense among foraging great tits and as great tits are usually dominant over blue tits (Sasvári 1992), so we expected that great tits might prefer to join blue tits. We found that the preference of great tits for foraging with other individuals is less marked when the environment is composed of blue tits compared to great tits (Figure III.1). A possible explanation is that when looking for other individuals, a bird might try not to be the biggest target for predators and thus preferred be among similar size great tits rather than smaller blue tits in order to reduce the oddity effect (Rodgers et al. 2011). Futures studies should integrate the dominance rank of individuals in the social environment compared to the one of focal individual as these



specificities may also impact foraging decisions and plasticity of focal birds (Giraldeau and Caraco 2000).

Foraging decisions have been selected to optimize foraging intake and choices are expected to be context dependent (Houston et al. 1997). When predation risk increases, individuals are expected to forage more in groups in order to reduce the risk of predation and maximize the detection of potential threats (Lima 1995). However, birds did not change their foraging preferences under predation in our experiment (Figure III.2). We measured foraging plasticity of great tits in temporary captivity where each focal bird had *ad libitum* access to a feeder and could hide in foliage or a roosting box. Moreover, predation threat was not located near the foraging patch and the social audience but at the opposite side of the aviary. This relative safety at the foraging patch may limit the perception of the risk of predation in our system and the foraging decision may still be balanced towards avoiding starvation (Lima and Dill 1990). Nonetheless, the preference for foraging alone was less marked in *Predation* context compared to *Control* one. A similar study in nutmeg manikins found that birds preferred to avoid foraging alone to maximize feeding rate while decreasing the time devoted to scanning (Rieucou and Giraldeau 2009). Although not looking directly to forage with others, great tits in our experiment may reduce their foraging time alone and tolerate conspecifics in order to maximize their opportunity to forage while others are vigilant. Interestingly, when considering the *Disturbance* context, foraging plasticity regarding group size was not significant (Figure III.2). Since both the *Predation* and *Disturbance* correspond to a source of stress for great tits, we expected similar differences with the *Control* context. But facing a known source of foraging, starlings using social cues were as efficient as birds relying on personal information (Rafacz and Templeton 2003). Under the *Disturbance* context, great tits may have preferred personal information, explaining the apparent loss of plasticity (Kendal et al. 2005). Alternatively, foraging decision in the *Disturbance* context can be perceived as neophobia towards the door movement and noise on the feeder. Facing new objects, zebra finches habituated faster to neophobic stimuli if tested in social groups (St. Lawrence et al. 2021) while ravens spent more time close to a new object in groups compared to alone (Stöwe et al. 2006). Greats tits in our experiment may use the presence of conspecifics as a stress buffering to forage even in competitive situations, explaining the pattern observed. In future studies, it

would be interesting to manipulate the predictability of food access to understand how it influence context-dependent foraging plasticity (Seppänen et al. 2007), especially when considering increased difficulties to find food in fast changing environments (Vinton et al. 2022).

Selection pressures may favor more behaviorally plastic individuals facing environmental variation (Snell-Rood 2013) but environmental and intrinsic causes of among individual variation in plasticity are still poorly understood. We found that both age classes had similar social competence in *Control* context (Figure III.3A). But yearlings had lower plasticity under *Predation* or *Disturbance*. This age difference reflects the existence of temporal plasticity (Stamps 2016) in foraging decisions that could be linked to access to food. Yearlings are often subordinates to adults (Sandell and Smith 1991) and so need to be more risk-prone and less neophobic to find food (Crane & Ferrari, 2017; Chapter 2). Moreover, a recent study found that younger blue tits were less plastic in a breeding context (Bonamour et al. 2020). Our study provides another evidence of the age variation of plasticity that could explain the lower survival of first year birds compared to older individuals (Martin 1995). This is especially true in stressful conditions in our experiment and have strong implications for survival of future populations. We also found that in the *Control* context, heavier great tits were less plastic than lighter conspecifics, i.e. they did not have a preference between foraging alone or in groups (Figure III.3B). Heavier birds are usually dominant over lighter ones in small passerines (Hegner 1985; Sandell and Smith 1991) and so they do not have to choose or adapt their behavior to the social audience to guaranty food access. On the contrary, lighter birds should rely more on social cues to modify their foraging behavior and prefer foraging alone (Figure III.3B). As they are usually subordinates, by visiting the feeder alone in a secured context, they would be able to have an exclusive access to food for a longer period of time. However, in stressful or disturbed contexts, we no longer observed an effect of body mass on foraging plasticity (Figure III.3B). In less secured situations, all birds, irrespective of their body mass are at equality regarding the use of social information which suggest that in stressful or less predictable conditions, socially plastic individuals may not be advantaged.

Interestingly, all birds showed similar foraging plasticity to the presence of the two species in the social environment as we did not find any significant interactions between the species on playbacks and individual characteristics. If the stronger avoidance of blue tits compared to great tits while foraging is equivocal, we can assume that the presence of an individual, regardless of the species, is sufficient to induce the behavior of individuals (Morse 1970; Sasvári 1992). Moreover, we found no impact of the elevation of origin on great tits foraging plasticity. Distinct elevated populations are experiencing different levels of harshness (Körner 2007) which can impact their foraging behaviors (Chapter 2; Pitera et al., 2018). However, all birds in the present experiment were under controlled conditions with similar temperature and food access. Thus the potential elevation associated differences may be softening as the ecological context was too challenging for birds.

Overall, our results showed clear evidence that social competence is dependent on group composition and general context. In stressful contexts, birds were less plastic in their foraging decisions compared to more secure ones. Moreover, we found among individual differences in context-dependent social foraging plasticity. This could lead to selection with more plastic individuals having a higher fitness (Taborsky 2021). But as behavioral plasticity is context-dependent, its impact on evolution could be mitigated and more work is needed to understand its potential benefits for survival in novel environments (Snell-Rood 2013). Additionally, to be behaviorally plastic, an individual relies on cognitive abilities such as memorization, innovation or learning. Selection is predicted to act on performances like foraging decisions, not directly on underlying abilities such as learning (Dingemanse and Wolf 2013; Varela et al. 2020). Future studies will need to confirm the link between behavioral plasticity and cognitive abilities. Such result would help to understand the evolution of social plasticity and cognition (Wascher et al. 2018; Varela et al. 2020).

## III. 6.SUPPLEMENTARY INFORMATION

### III. 6. 1. Video playback broadcasting

Single video file including the 40 video playbacks broadcasted (5 in each of the following category: (no bird, 1 blue tit, 2 blue tits, 1 female great tit, 1 male great tit, 2 female great tits, 2 male great tits, 2 mixed-sex great tits) on the screen during the present experiment. While the file includes all 40 videos placed sequentially, videos were stored as separate clips for the experiment. Video playbacks were randomly chosen from the 40 video clips using a Python code written for Raspberry 3Pi by Jérôme Briot.

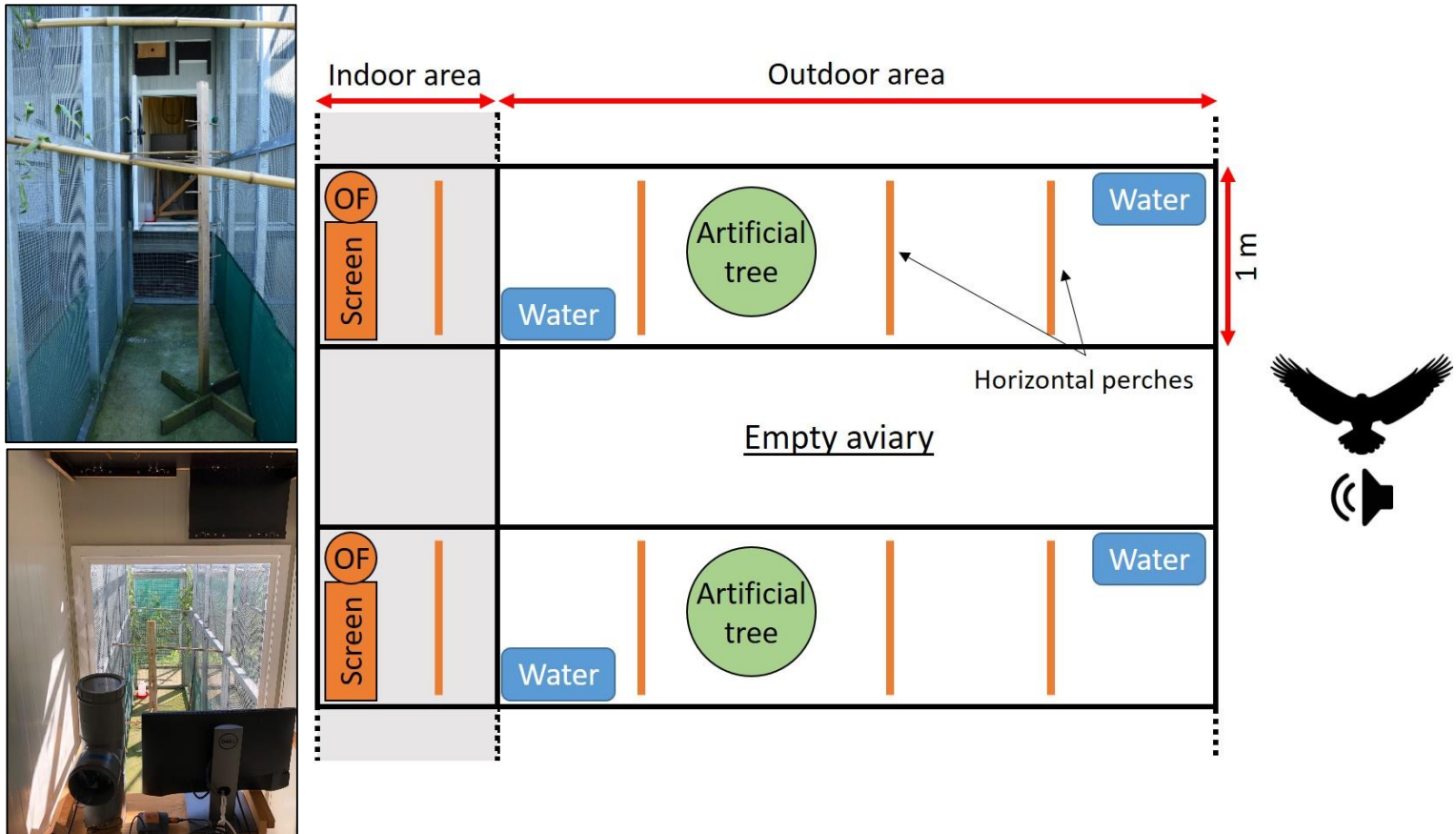
III. 6. 2. Housing facilities

Figure S. III.1: Pictures and schematic plan illustrating the aviaries at CNRS-SETE ( $1 \times 5 \times 3$  m,  $W \times L \times H$ ). Each aviary hosted one bird with one empty aviary between two birds to avoid physical contact between birds and to ensure that birds could not see their closest neighbor's screen (OF=OpenFeeder). The raptor symbol on the right of the schematic plan illustrate the location of the stuffed European Sparrowhawk presentation used for the Predation context (Day 2 of experiment).

### III. 6. 3. Impact of sex information on social foraging plasticity

To understand how social foraging plasticity was dependent on the sex of the social environment, we built a linear mixed model (*lme4* package, Bates et al., 2014) with the mean number of visits to the feeder as the response variable. Only visits where the sex of the stimulus playback was identifiable and non-mixed were kept (i.e. 1 female great tit, 1 male great tit, 2 female greats tits, 2 male great tits). This variable was log transformed and scaled prior to integration in the model to meet assumptions of normality. The size of the group on playback (1 or 2 birds), the sex on playback (female or male) and the general context (*Control*, *Predation*, *Disturbance*) were added as fixed factors, along with all two and three way interactions. The total mean number of visits performed during the day by each specific bird was also added as a fixed factor to account for activity differences between birds. Bird identity and sex of the focal bird were added as random factors to account for repeated measures and potential sex preferences. The best model was selected by removing all non-significant interactions and the final model did not include any interactions. Table S. III.1 presents the chi squared values and associated p values of the final model. The birds did not change their foraging strategy based on sex visible on video playback (Table S. III.1,  $X^2 = 0.80$ ,  $df = 1$ ,  $P = 0.372$ ). We therefore pooled data from different sexes together in all subsequent analyses.

*Table S. III.1: Type III ANOVA of the model of the impact of GroupSize, Context and Sex on scaled number of visits to the OpenFeeder. Values in bold are significant at  $P < 0.05$*

Explanatory factors	Chi.sq	df	P value
(Intercept)	0.00	1	1.000
Sex	0.80	1	0.372
<b>GroupSize</b>	<b>10.13</b>	<b>1</b>	<b>0.001</b>
<b>Context</b>	<b>16.54</b>	<b>2</b>	<b>&lt; 0.001</b>
<b>VisitsP.tot.LOG</b>	<b>2,569.74</b>	<b>1</b>	<b>&lt; 0.001</b>

III. 6. 4. Supplementary tables

*Table S. III.2: Factors impacting foraging preferences in great tits fitted with a linear mixed model with GroupSize, Context and Species as fixed factors and including three-way interaction, as well as all two-ways interactions (Type III Anova). Values in bold are significant at  $P < 0.05$ .*

Explanatory factors	Chi.sq	df	P value
(Intercept)	0.00	1	1.000
<b>GroupSize</b>	<b>117.25</b>	<b>2</b>	<b>&lt;0.001</b>
<b>Context</b>	<b>8.83</b>	<b>2</b>	<b>0.012</b>
<b>Species</b>	<b>4.23</b>	<b>1</b>	<b>0.040</b>
<b>Total Visits</b>	<b>8,174.58</b>	<b>1</b>	<b>&lt;0.001</b>
<b>GroupSize x Context</b>	<b>58.02</b>	<b>4</b>	<b>&lt;0.001</b>
<b>GroupSize x Species</b>	<b>7.97</b>	<b>2</b>	<b>0.019</b>
Context x Species	0.32	2	0.851
GroupSize x Context x Species	3.95	4	0.413

Table S. III.3: Factors explaining inter-individual differences in foraging plasticity in great tits fitted with a linear mixed model with Context, Season, Elevation, Age, Exploration score, Weight and Sex as fixed factors and including three-way interaction, as well as all two-ways interactions between Context or Species and all individual characteristics variables (Type III Anova). Values in bold are significant at  $P < 0.05$ .

Explanatory factors	Chi.sq	df	P value
<b>(Intercept)</b>	<b>36.16</b>	<b>1</b>	<b>0.000</b>
<b>Context</b>	<b>25.19</b>	<b>2</b>	<b>0.000</b>
Species	0.41	1	0.524
Elevation	0.09	1	0.760
Sex	1.27	1	0.260
<b>Age</b>	<b>7.96</b>	<b>1</b>	<b>0.005</b>
Exploration score	0.20	1	0.655
Weight at capture	0.79	1	0.375
Context x Species	0.85	2	0.655
Context x Elevation	4.24	2	0.120
Context x Sex	0.05	2	0.974
<b>Context x Age</b>	<b>9.54</b>	<b>2</b>	<b>0.008</b>
Context x Exploration score	1.37	2	0.504
Context x Weight at capture	4.14	2	0.126
Species x Elevation	0.08	1	0.783
Species x Sex	0.73	1	0.393
Species x Age	1.06	1	0.303
Species x Exploration score	0.23	1	0.632
Species x Weight at capture	0.35	1	0.555
Context x Species x Elevation	0.06	2	0.968
Context x Species x Sex	1.42	2	0.491
Context x Species x Age	0.29	2	0.865
Context x Species x Exploration score	0.43	2	0.807
Context x Species x Weight at capture	0.61	2	0.738





# **CHAPTER IV.**

## **IS FORAGING PLASTICITY RELATED TO COGNITIVE**

### **ABILITIES?**

In preparation

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## IV. 1. ABSTRACT

To navigate in the social environment which regroups other individuals, either con and hetero-specifics, individuals need to adapt their behavior to the available social information. In order to make the suitable responses, they must rely on their cognitive abilities. Although positive correlations are expected between plastic and cognitive traits these have not yet been confirmed. Moreover, as recent work pointed out the context-dependency of foraging plasticity, there is a need to understand how environmental variation may influence the correlation between cognition and plasticity. We measured social foraging plasticity of wild great tits in three different contexts using video playbacks to manipulate social group composition. On the same individuals, we measured cognitive performance in an inhibition, an innovation and a color associative learning tasks. We found that the relation between social foraging plasticity and cognitive abilities was dependent on environmental conditions such as the season. Moreover, the relation between cognition and plasticity depended on the cognitive ability measured, as associative learning success or learning speed were not related to foraging decisions. Our results provide evidence that the relations between behavioral plasticity in a social foraging situations and cognitive abilities is more complex than expected. Future studies need to consider more complex cognitive abilities in various ecological context in order to deepen the understanding of the link between cognition and plasticity and the potential coevolution between them.

### **Keywords:**

Behavioral plasticity, elevation, great tit, social foraging, ecological context, problem solving, associative learning

## IV. 2. INTRODUCTION

Facing environmental changes, behaviors can provide the first responses to animals and can be especially important when the rates of change outpace genetic adaptation (Vinton et al. 2022). The ability to adapt behaviors in response to environmental variations, defined as behavioral plasticity, can provide advantages to individuals in order to survive and reproduce (Stamps 2016). Evidence of inter-individual differences in behavioral plasticity has been found for foraging decisions (Chapter 2), mate choice (Chaine and Lyon 2008; Ah-King and Gowaty 2016), personality (Dingemanse et al. 2012) or social competence (Bshary and Oliveira 2015). As all individuals are not equal in their reaction to environmental variation, selection pressures should lead to the evolution of an optimal plasticity where the benefits are counterbalanced by the costs of development and maintenance (Snell-Rood and Ehlman 2021b). Natural selection should also favor the evolution of flexible behavior in response to variation in information provided by the social environment, i.e. social competence (Taborsky and Oliveira 2012). In order to be able to predict how plasticity may help persistence in fast changing environments, we need to understand the potential factors underlying these inter-individual differences in social plasticity (Niemelä et al. 2013; Snell-Rood 2013).

Behavioral plasticity should rely on underlying skills like cognitive abilities, e.g. perception, attention, learning, memory and decision-making processes (Shettleworth 2009). Living in groups implies the formation and maintenance of dynamic social relationships that are hypothesized to be one of the main drivers of the evolution of cognitive abilities (Dunbar and Shultz 2007; Emery et al. 2007; Wascher et al. 2018). Therefore, theory predicts that social plasticity and cognitive abilities are correlated and should co-evolve (Varela et al. 2020). Wild Australian magpies living in larger groups performed better in cognitive tasks (Ashton et al. 2018) while house sparrows in larger groups were more efficient in innovative tasks (Liker and Bókony 2009). Although these results are promising, studies of inter-individual variation of foraging plasticity have shown mixed evidence. More flexible great tits in foraging decisions performed better in an inhibitory control task (Coomes et al. 2022), but no relation was found between inhibitory control and foraging efficiency in red jungle-fowl (Garnham et al. 2022). This unclear relationship was also visible when considering different cognitive abilities, as

more plastic zebra finches were slow learners (Barou Dagues et al. 2020), while plastic house sparrows were fast learners (Katsnelson et al. 2011). These studies suggest that the link between plasticity and cognition is more complex than expected and deserves more attention.

Cognitive abilities regroup several distinct processes (Shettleworth 2009). The different cognitive processes are predicted to play important roles on fitness in both social and asocial contexts. A major question in evolution is whether cognition is a general ability, meaning that an individual performing well in one cognitive task will be efficient in others or that it is a domain specific competence and different types of knowledge have different mechanisms (Burkart et al. 2017). Recent evidence in humans (Plomin 2001), birds (Ashton et al. 2018; Ashton et al. 2022) and insects (Finke et al. 2023) show that cognitive abilities could be domain-general. But the complex link between plasticity and cognition might suggest that even if cognitive abilities could be related, not all of them are involved in social plasticity, or not to the same degree (Wascher et al. 2018). There is a need to test the link between plasticity and different cognitive abilities, such as innovation and learning, a step rarely found described in the literature.

The differences in plasticity expression also depend on various non-cognitive causes (Stamps 2016). For example, the higher perceived predation risk altered plasticity in social preferences in cichlids (Culbert et al. 2021). In a different study, fishes raised without a social environment showed less appropriate behaviors in social interactions for access to resources compared to young raised in social groups, confirming the importance of past social experiences on developmental plasticity (Arnold and Taborsky 2010). In birds, preference for foraging with conspecific great tits rather than blue tits was different in safe compared to stressful contexts, suggesting context-dependency of social plasticity (Chapter 3). As social plasticity depends on the environmental contexts, we need to integrate the influence of the environment on the relation between social plasticity and cognition. However, to date, this has been rarely explored in the literature. Nevertheless, under less constrained environmental conditions, plasticity may not be advantageous and the link between social plasticity and cognition may not be apparent (Niemelä et al. 2013; Vinton et al. 2022). Therefore, it is important to test for links between social plasticity and cognition in individuals originating from different environments. Elevation gradients can provide an interesting system as higher elevation is associated with

lower predation and unpredictable and harsher conditions due to climatic variations (Körner, 2007; Chapter 2).

In the present study, we investigated whether cognitive abilities predicted individual variation in social foraging plasticity. We measured foraging decisions along social and environmental gradients in populations of wild great tits (*Parus major*) temporarily brought into captivity. On the same individuals, we measured the cognitive abilities in one innovation (problem solving), one inhibition (detour reaching) and one associative learning tasks. Selection pressures should act on behavioral performance and as a consequence enhanced cognitive abilities (Varela et al. 2020). We predicted that individuals who were more plastic in their foraging decisions would solve faster innovation and inhibition tasks. Moreover, recent work has suggested that cognition is a general ability (Plomin 2001) leading to the expectation that more plastic individuals would perform consistently across different cognitive abilities, from innovation to associative learning. Finally, as foraging plasticity is known to be context dependent (Chapter 3), we looked at how the environment influenced the link between cognition and behavioral plasticity, a factor not yet integrated in literature. Under harsher conditions, individuals face greater challenges to find food and survive and are known to show higher cognitive abilities (Kozlovsky et al. 2015a; Hermer et al. 2018). We predicted that the link between social foraging plasticity and cognition would be more marked in stressful situations (e.g. predation risk or disturbance). Overall this study aims at understanding how ecological contexts and environmental harshness can influence the relation between cognition and plasticity in a foraging context.

## IV. 3. METHODS

### IV. 3. 1. Capture, housing and schedule

We brought into temporary captivity 192 wild great tits (*Parus major*) originating from high and low elevation populations (Antras, 891 m asl., 42°52'51.7"N, 0°56'44.4"E; Aubert, 430 m asl., 42°57'51.4"N, 1°06'11.3"E; Montjoie, 445 m asl., 42°59'56.0"N, 1°10'09.3"E; Villargein, 898 m asl., 42°54'17.1"N, 1°02'48.0"E) within 20 km around Moulis in the French Pyrenees. High elevation sites have longer snow cover period and lower temperature, resulting in behavioral differences of passerines compared to birds originated from low elevation sites (Chapter 2; Chapter 3; Bründl et al., 2019, 2020; Hermer et al., 2018; Lejeune et al., 2019). We caught birds in batches of 24 individuals between mid-October and mid-March in 2020, 2021 and 2022 and marked each individual with a unique CRBPO (Centre de Recherche sur la Biologie des Populations d'Oiseaux) metal band and a colored RFID (Passive Integrated Transponders, IB Technology, UK) plastic band. We scored sex (female or male) and age (yearling or adult) based on plumage variation (Svensson 1992) and measured body mass using a digital scale (nearest 0.1g) for each individual. We housed birds individually but within acoustic and visual contact with conspecifics to minimize stress in aviaries (1 x 5 x 3 m, W x L x H each) containing foliage for cover, perches and a shelter. Birds had ad libitum access to a RFID-feeder ("OpenFeeder", Cauchoix et al. 2022) filled with organic sunflower seeds. As a supplement, they had access to *ad libitum* mealworms and fat balls between experiments. Upon release in the cage, we measured exploratory behavior as the total number of movements made during 3 min in a new environment for each great tit following Dingemanse et al. (2002), a measure known to be repeatable and a good proxy for personality (Dingemanse et al. 2012; Niemelä and Dingemanse 2018).

As birds were captured by batches, all individuals within a batch followed the same experimental schedule. After four days of acclimation to captivity, we quantified social foraging plasticity in three different contexts. We then recorded cognitive abilities in an innovation and an inhibition tasks and later in an associative learning task before releasing birds at their respective capture sites.

### IV. 3. 2. Foraging plasticity

We measured behavioral plasticity as the preference for foraging in groups or alone following Chapter 3. We manipulated the social environment using video playbacks broadcasted continuously during two daily sessions (9 am to noon; 1 pm to 4 pm) for three days as in previous work (Chapter 2). Video stimuli of 30 s each represented 0, 1 or 2 wild great or blue tits (*Cyanistes caeruleus*) foraging on fat balls. The computer screen used for video presentation was located next to the OpenFeeder, the only food source available during experiments. OpenFeeders recorded each visit the bird made along with the context projected on the video screen. We pooled the number of visits to the OpenFeeder per video playback category over the whole day of the experiment. Based on previous analysis, the size of the group (1 or 2) and the sex of birds visible (female or male) did not significantly impact foraging decisions in great tits (Chapter 3), so we grouped these categories for the current analysis. We calculated foraging plasticity as the difference between the mean number of visits with birds (mean of visits with 1 and 2 birds) and the number of visits with no birds on the screen. A negative value of plasticity corresponds to a preference for foraging alone while a null value denotes the absence of plasticity. We extracted two foraging plasticity values, one for projections containing great tits and the other containing blue tits.

Moreover, we quantified the social foraging plasticity of each individual as described above for each of three different contexts (see Chapter 3 for details on each context). On the first day (“Control”), birds saw videos for the first time. On the second day (“Predation”), we increased perceived predation risk by presenting a taxidermized European Sparrowhawk (*Accipiter nisus*) with an audio playback for 5 minutes six times during the day. On the third day (“Disturbance”), each time a bird came to the feeder, a small door hiding part of the opening of the OpenFeeder fully moved allowing complete access to food but causing movements and noise potentially perceived as a disturbance by the birds. Among the 192 captured birds, 9 individuals were removed from analysis due to technical failures of the equipment.

### IV. 3. 3. Cognitive abilities

Great tits are known for their abilities to use social learning (Aplin et al. 2015) and to prevent this, all cognitive tasks described below were performed in the indoor area of each aviary,



where neighbors could not see what was happening in their aviaries. The day after the end of the social foraging experiment, we measured the great tit's ability to solve an inhibition task (detour reaching) and an innovation task (problem solving). The two tasks were presented separately with the order of presentation randomized across birds. The detour reaching task followed the setup described by Kabadayi et al. (Figure 1a, 2018) and consisted of a transparent cylinder (7.5 cm long with an outer diameter of 3 cm) containing a reward (one immobilized waxworm larvae, *Galleria mellonella*) and positioned perpendicularly to the focal individual's approach (see Supplementary materials, Figure S. IV.1). To succeed, the bird could access the reward through one of the side openings of the transparent cylinder. We did not include a training phase in this task as it can complicate behavioral interpretation: with training success can be due to inhibitory control or memory of a learned rule (Ashton et al. 2018; Isaksson et al. 2018). The problem solving task was inspired by the lever-pulling device in Cole et al. (Figure 1a and 1b, 2011) and consisted of a vertical transparent cylinder (7 cm with an outer diameter of 3 cm) containing a platform with a reward (one waxworm larvae) supported by a horizontal lever (see Supplementary materials, Figure S. IV.2). To succeed, the bird could access the reward by removing the lever, releasing the platform and the reward located on it. To maximize motivation, the experiment started at sunrise and was preceded by an overnight food deprivation. When the deprivation started, we also swept the floor to remove any seeds left on the floor. Moreover, during the two cognitive tasks, the reward of each task was the only source of food available. All tested birds saw these setups for the first time and were tested only once per task. Birds were monitored through a window and the device was removed and the second test started as soon as an individual succeeded in the task, or after 30 minutes. At the end of the two tasks (maximum after 1 hour), birds again had access to the OpenFeeders and *ad libitum* mealworms. We video recorded all tests and these were analyzed blind to bird identity using BORIS software (Friard and Gamba 2016). For each task, we recorded if a bird succeeded or not, and the latency to solve the task (for individuals who did not succeed, the latency was set to the maximum time possible, 1800s). Among the 183 tested birds, 50 never interacted with the detour reaching task and 83 did not interact with the problem solving task. These individuals were removed from analyses including innovation and inhibition variables.

We tested associative learning abilities with a go-no go paradigm implemented in the OpenFeeder (Cauchoix et al. 2022). The task was run over three days, in two daily sessions (9 am to noon; 1 pm to 4 pm) where the OpenFeeder was the only source of food available. Aviaries were swept at the start of each day to ensure that the only food available was from the OpenFeeder. During tests, a door completely blocked access to the seeds with four LEDs located around the feeding hole of the OpenFeeder that could be switched. If a bird landed on the OpenFeeder platform during the Go signal (LEDs on in white), the door opened and the bird had a 1s access to the seeds inside the OpenFeeder. However, if a bird landed on the OpenFeeder platform during the NoGo signal (LEDs off), the door stayed closed and the LEDs stayed off for an extra 10 seconds as a “punishment”. LEDs were turned on at random with a probability of 0.25 such that feeder could reward bird one quarter of the time. Before performing the task, birds were gradually habituated to OpenFeeder door’s movement and LED operation during a pretraining over five consecutive days in which the door masked an increasing proportion of the feeding hole each day and where LEDs gradually turned on in orange or purple. From the number and timing of visits to the OpenFeeder, we extracted the accuracy of visits (number of correct visits over the total number of visits) and the number of visits needed to reach a learning criterion of 8 correct visits out of 10 consecutive visits. Among the 183 tested birds, 4 did not interact sufficiently with the OpenFeeder to extract cognitive metrics and we removed them from analyses including the associative learning variables. All individuals performed innovation, inhibition and associative learning tasks on the same days.

#### IV. 3. 4. Statistical analysis

We performed statistical analysis using R software (R version 4.2.2, R Core Team, 2022). We first looked for a general cognitive ability in great tits (Plomin 2001). We performed Pearson pairwise correlations between the three tasks (*correlations* package, Makowski et al., 2020) for the ability and the latency to solve the cognitive task. As no correlation between cognitive tasks were identified, we kept each cognitive metric separate (see Supplementary materials for more details, Figure S. IV.3-4 and Table S. IV.1-2). Then, to understand how cognitive abilities could predict foraging plasticity we built linear mixed models (*lme4* package, Bates et al., 2014) with foraging plasticity as the response variable and cognitive abilities as explanatory variables. Due to considerable variation in sample sizes depending on the cognitive tasks (detour reaching:

133; problem solving: 100; associative learning: 177), we carried out separate analyses for each cognitive task (only 77 birds participated in all three tasks). Moreover, within a specific task, cognitive variables extracted were strongly correlated, a pattern expected as they measure various aspect of the same performance (see Supplementary materials, Figure S. IV.3-4). Therefore, we built a linear mixed model for each cognitive variable. First, we looked at the impact of solving ability (binary variables: ability to solve the detour reaching task, and the problem solving task and ability to learn the associative learning criterion) on foraging plasticity. Then, we analyzed the dependence of foraging plasticity on solving efficiency (latency to solve the detour reaching and the problem solving task in seconds, and the number of visits needed to reach the associative learning criterion). Finally, we looked at the influence of learning accuracy (two metrics: accuracy of the last half-day of the associative learning task, i.e. end accuracy; and difference between the accuracy of the 20 last visits and the 20 first visits in the associative learning task, i.e. accuracy improvement) on foraging plasticity. Each model included interactions between the cognitive variable and the overall context of foraging plasticity (*Control, Predation, Disturbance*) as previous work showed that foraging plasticity is context dependent (Chapter 3). Furthermore, we added the species of birds visible on playback videos (great or blue tit) as previous work showed species dependency of foraging plasticity (Chapter 3). Models also included elevation of origin (high or low) and season of experiment (fall or winter) to understand how environmental harshness could influence the link between plasticity and cognition. We found that individual characteristics did not significantly impact cognition in our experiment (see Supplementary materials, Table S. IV.3-10, linear mixed models with each cognitive measure as the response variable and sex, age, elevation of origin, exploration score, body mass, season of experiment as fixed factors), so we did not include them in the final statistical models. Bird identity was added as a random factor to account for repeated measures. For detour reaching and problem solving variables, we also added the order of the cognitive task as a random factor. We centered on the mean and scaled by standard deviation all numeric variables prior to integration in the models. Following a backward selection procedure, we kept all main effects but removed all non-significant interactions from each model until we obtained the final model (see Supplementary materials, Table S. IV.11-13 for full models). To assess the significance of differences between levels, we ran post-hoc Tukey HSD tests (*emmeans* package, Lenth et al., 2022). We checked model

performance graphically using the *DARHMa* package (Hartig 2022). The significance level for p-values was set at 0.05 (two-tailed tests). Figures were built using the *interactions* package (Long 2019).

## IV. 4. RESULTS

### IV. 4. 1. Impact of solving ability on foraging plasticity

The link between social foraging plasticity and the ability to solve the detour reaching task depended on the foraging context (Success x Context, Table IV.1). Successful birds were more plastic in the *Control* context, preferring to forage alone, compared to the *Predation* ( $T=-2.61$ ,  $Est.=-1.17\pm 0.45$ ,  $P=0.025$ ) or *Disturbance* context ( $T=-4.62$ ,  $Est.=-2.08\pm 0.45$ ,  $P<0.001$ ), while there was no significant difference between foraging plasticity in the *Predation* and *Disturbance* contexts ( $P=0.110$ ; Figure IV.1A). However, non-successful birds did not differ in social foraging plasticity and preferred to forage alone in all contexts (all  $P>0.2$ ; Figure IV.1A). In addition, the link between plasticity and ability to solve the problem solving task was season dependent (Success x Season, Table IV.1). Successful birds were less plastic (plasticity closer to 0) when tested in winter compared to birds tested in fall ( $T=-2.18$ ,  $Est.=-1.36\pm 0.62$ ,  $P=0.032$ ; Figure IV.1B). Moreover, we found a tendency for a difference in plasticity between successful and non-successful birds in winter ( $T=-1.76$ ,  $Est.=-1.44\pm 0.81$ ,  $P=0.084$ ) but not in fall ( $T=1.17$ ,  $Est.=0.73\pm 0.62$ ,  $P=0.243$ ; Figure IV.1B). Non-solver birds did not differ in their foraging plasticity in fall and winter ( $T=1.11$ ,  $Est.=0.81\pm 0.73$ ,  $P=0.268$ ; Figure IV.1B). Finally, there was no significant link between foraging plasticity and the ability to learn the associative learning criterion ( $P=0.471$ ; Table IV.1).

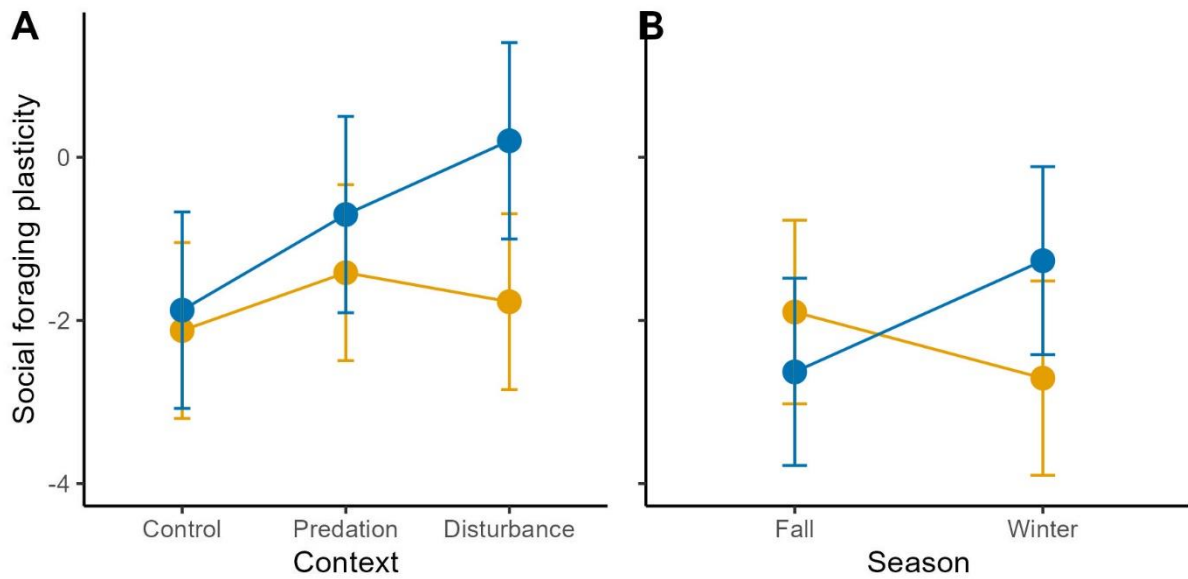


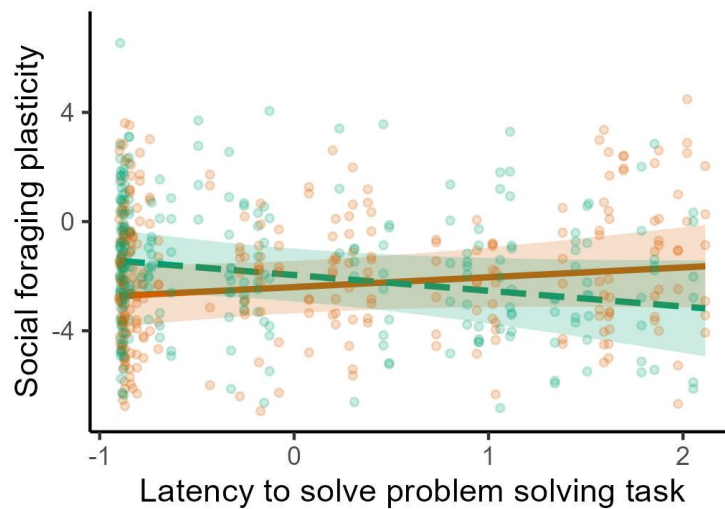
Figure IV.1: Social foraging plasticity in relation to solving ability in different contexts (A) and seasons (B). (Solving=blue, Non-solving=yellow). A) Detour Reaching task according to different contexts of plasticity (Control, Predation, Disturbance;  $N=133$  individuals) and B) Problem solving task according to seasons (fall, winter;  $N=100$  individuals). Shown in colored dots are the predicted mean  $\pm$  SE from the model.

Table IV.1: Factors explaining foraging plasticity in relation to solving ability of three cognitive tasks (Detour reaching task,  $N=133$  individuals; Problem solving task,  $N=100$  individuals; Associative learning criterion,  $N=179$  individuals). A linear mixed model was fitted with Success, Elevation, Season, Context and Species as fixed factors (Type III Anova). Non-significant interactions were removed from the final model. Values in bold are significant at  $P < 0.05$ .

Cognitive task Factors	Detour Reaching			Problem Solving			Associative learning		
	Ch.sq	Df	P value	Ch.sq	Df	P value	Ch.sq	Df	P value
(Intercept)	<b>9.51</b>	<b>1</b>	<b>0.002</b>	<b>23.10</b>	<b>1</b>	<b>&lt; 0.001</b>	<b>24.29</b>	<b>1</b>	<b>&lt; 0.001</b>
Success	0.05	1	0.825	0.58	1	0.448	0.52	1	0.471
Elevation	1.46	1	0.227	1.89	1	0.169	1.26	1	0.262
Season	0.29	1	0.589	1.39	1	0.239	1.00	1	0.317
Context	2.60	2	0.272	<b>9.36</b>	<b>2</b>	<b>0.009</b>	<b>28.39</b>	<b>2</b>	<b>&lt; 0.001</b>
Species	0.22	1	0.637	0.11	1	0.745	0.31	1	0.578
Success x Elevation	-	-	-	-	-	-	-	-	-
Success x Season	-	-	-	<b>5.73</b>	<b>1</b>	<b>0.017</b>	-	-	-
Success x Context	<b>8.04</b>	<b>2</b>	<b>0.018</b>	-	-	-	-	-	-

#### IV. 4. 2. Impact of solving efficiency on foraging plasticity

The relation between social foraging plasticity and the latency to solve the problem solving task depended on environmental variation (Efficiency x Season, Table IV.2). We found slopes going in the opposite direction between birds tested in fall and birds tested in winter. In winter, birds that needed more time to solve the problem solving task were more plastic than individuals quicker in solving efficiency, whereas in fall, birds showed an opposite pattern ( $T=2.05$ ,  $Est.=0.94\pm0.46$ ,  $P=0.043$ ; Figure IV.2). However, there was no link between plasticity and the latency to solve the detour reaching task ( $P=0.567$ ; Table IV.2) or the number of trials needed to reach the learning criterion in the associative learning task ( $P=0.894$ ; Table IV.2).



*Figure IV.2: Social foraging plasticity according to the latency to solve a problem solving task (birds tested in fall (orange) and winter (green)). Shown in colored dots are the predicted values from the model with the regression line with 95% confidence intervals.  $N=100$  individuals.*

Table IV.2: Factors explaining foraging plasticity in relation to solving efficiency of three cognitive tasks. (Detour reaching task, N=133 individuals; Problem solving task, N=100 individuals; Associative learning criterion, N=179 individuals). A linear mixed model was fitted with Efficiency, Elevation, Season, Context and Species as fixed factors (Type III Anova). Non-significant interactions were removed from the final model. Values in bold are significant at  $P < 0.05$ .

Cognitive task Factors	Detour Reaching			Problem Solving			Associative learning		
	Ch.sq	Df	P value	Ch.sq	Df	P value	Ch.sq	Df	P value
(Intercept)	<b>20.88</b>	<b>1</b>	<b>&lt;0.001</b>	<b>24.92</b>	<b>1</b>	<b>&lt;0.001</b>	<b>13.59</b>	<b>1</b>	<b>&lt;0.001</b>
Efficiency	0.33	1	0.567	0.23	1	0.635	0.02	1	0.894
Elevation	1.56	1	0.211	2.87	1	0.090	0.55	1	0.459
Season	0.25	1	0.614	0.95	1	0.331	0.01	1	0.937
Context	<b>15.84</b>	<b>2</b>	<b>&lt;0.001</b>	<b>9.36</b>	<b>2</b>	<b>0.009</b>	<b>6.53</b>	<b>2</b>	<b>0.038</b>
Species	0.22	1	0.639	0.11	1	0.745	0.42	1	0.517
Efficiency x Elevation	-	-	-	-	-	-	-	-	-
Efficiency x Season	-	-	-	<b>4.20</b>	<b>1</b>	<b>0.040</b>	-	-	-
Efficiency x Context	-	-	-	-	-	-	-	-	-

#### IV. 4. 3. Effect of accuracy in associative learning on foraging plasticity

The relationship between foraging plasticity and the accuracy at the end of the associative learning task depended on the elevation of origin of tested birds (Improvement x Elevation, Table IV.3). Birds presented an opposite plasticity-cognition relationship depending on their elevation of origin ( $T=-2.07$ ,  $Est.=-0.92\pm 0.45$ ,  $P=0.040$ ; Figure IV.3). Birds from high elevation with a higher accuracy at the end of the associative learning task preferred to do more foraging alone than individuals less accurate. Birds originating from low elevation and with more accuracy in associative learning task were not plastic in their foraging decisions while individuals with a lower accuracy preferred foraging alone, thus being more plastic. There was no significant relationship between foraging plasticity and the accuracy improvement (difference in accuracy between the end and the beginning of the associative learning task,  $P=0.362$ ; Table IV.3).

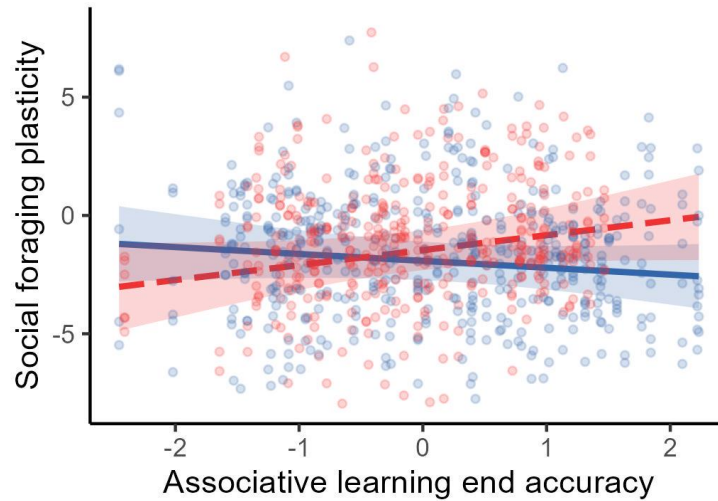


Figure IV.3: Social foraging plasticity according to the accuracy at the end of the associative learning task. Birds originated from high (blue) and low (red) elevations. Shown in colored dots are the predicted values from the model with the regression line with 95% confidence intervals.  $N=179$  individuals.

Table IV.3: Factors explaining foraging plasticity in relation to two measures of accuracy of three cognitive tasks. A linear mixed model was fitted with Accuracy, Elevation, Season, Context and Species as fixed factors (Type III Anova). Non-significant interactions were removed from the final model. Values in bold are significant at  $P < 0.05$ .  $N=179$  individuals.

Associative learning Factors	End accuracy			Accuracy improvement		
	Ch.sq	Df	P value	Ch.sq	Df	P value
(Intercept)	<b>21.46</b>	<b>1</b>	<b>&lt; 0.001</b>	<b>23.57</b>	<b>1</b>	<b>&lt; 0.001</b>
Accuracy	0.58	1	0.447	0.83	1	0.362
Elevation	1.12	1	0.290	1.52	1	0.217
Season	1.24	1	0.265	0.85	1	0.358
Context	<b>20.92</b>	<b>2</b>	<b>&lt; 0.001</b>	<b>21.86</b>	<b>2</b>	<b>&lt; 0.001</b>
Species	0.54	1	0.464	0.35	1	0.554
Accuracy x Elevation	<b>4.30</b>	<b>1</b>	<b>0.038</b>	-	-	-
Accuracy x Season	-	-	-	-	-	-
Accuracy x Context	-	-	-	-	-	-



## IV. 5. DISCUSSION

Behavioral plasticity should rely on cognitive abilities, so theory predicts the existence of positive relationships between plasticity and cognition (Varela et al. 2020). In the present study, we measured social foraging plasticity along an environmental gradient in great tits, as well as cognitive performances in three different cognitive tasks. We found that the relationship between plasticity and cognition is more complex than expected and instead depended on several elements. First, the relation between cognition and plasticity depended on the cognitive ability measured, as associative learning success or learning speed were not similarly related to foraging decisions depending on the cognitive task. Then, solving great tits were also more plastic in a secured situation compared when tested under predation or disturbance, while the context did not appear to impact non-solvers, proving the importance of the ecological context. Finally, plasticity cognition link also depended on the external environment as the negative relation between cognitive success and foraging plasticity was only visible in winter. These different elements may interact in the construction of a relationship between plasticity and cognition.

The relation between social foraging plasticity and cognitive abilities was more complex than theoretically expected as it depended on the cognitive ability measured. In humans, the g factor is a good indicator of overall intelligence, i.e. an individual with good performance in one cognitive task will also be efficient in another cognitive task (Deary 2001). Recent studies also pointed towards the existence of general cognition in non-human animals (Plomin 2001; Shaw et al. 2015; Ashton et al. 2018; Finke et al. 2023) so we expected related performances in various cognitive tasks in great tits. However, we did not find such relation between innovation, inhibition and associative learning in our populations (see Supplementary materials). Our results suggest that great tits do not rely on unique mechanism in order to solve different cognitive tasks and so an individual could be performant in one task (e.g. detour reaching) but not in another one (e.g. associative learning). Others also found that the g factor did not explain a significant part of among individual variance (Matzel et al. 2003; Barou Dagues et al. 2020; Poirier et al. 2020), providing evidence for a domain specific cognition. Under domain cognition, different types of knowledge often have different locations within the

global neural organization and thus different mechanisms (Hirschfeld and Gelman 1994). Although the origin of cognition is still debated, based on the absence of general cognitive ability in great tits we found here, it is not surprising to find that the relationship between social plasticity and cognition is dependent on the cognitive metric measured. Some cognitive abilities may be more related to social behavioral plasticity than others. We can expect that to maintain social relationships it is necessary to inhibit maladaptive behaviors such as confronting a dominant for access to food (Johnson-Ulrich and Holekamp 2020). Inhibition ability should be positively related to social plasticity, especially in subordinates, but we did not find a positive correlation between inhibition performance and ability to switch foraging choices. Social learning can allow the rapid transmission of behavior within a group, without necessarily relying on individual cognitive abilities and so socially plastic individuals may not need high innovative capacities (Laland 2004; Kendal et al. 2005). It would be interesting to investigate the link between social plasticity and other cognitive abilities such as reversal learning, social learning or spatial memorization as the underlying cognitive abilities necessary in such tasks are also needed to face the dynamic evolution of social environments. These future studies would help to confirm that social plasticity is a complex behavior resulting from an interaction of cognitive abilities.

Foraging choices are aimed at maximizing food intake to survive (Pyke 2019). More efficient great tits in detour reaching showed more flexibility in their foraging choices between a visible reward and a hidden one (Coomes et al. 2022). However, no relation between performance in inhibition task and foraging flexibility in decision to switch between foraging patches were identified in red jungle fowls (Garnham et al. 2022). These contrasted results suggest that the relation between plasticity in food item/patch choices and cognition is species specific rather than universal, as recently confirmed by a recent meta-analysis (Lambert and Guillette 2021). Foraging preferences as we measured them depended on the social environment characteristics but did not influence the social audience which was simulated with video playbacks. This type of social foraging plasticity is less dynamic than plasticity regarding producer-scrouter strategies where an individual has to adjust in real time its decision to other individuals' choices (Giraldeau and Caraco 2000). More plastic zebra finches in their foraging decisions in a producer-scrouter paradigm were slower learner in associative

learning (Barou Dagues et al. 2020). It would be interesting to dynamically modify social audience reaction to focal individual using interactive video playbacks with the possibility to adapt the video playback to the behavior of the focal birds (Ord & Evans, 2002; Rosenthal & Gil, 2019).

Foraging decisions are a trade-off between the risk of starvation and the risk of predation (McNamara and Houston 1990) as the perceived risk of predation impacts foraging choices (Chapter 2). Moreover, recent work highlighted the importance of context in differences among great tits in social behavioral plasticity (Chapter 3). So, we can expect that the context could also influence the relation between plasticity and cognition. Here, we found that less socially plastic birds tested in stressful contexts (*Predation* or *Disturbance* context) solved more innovation and inhibition tasks than more socially plastic individuals whereas no difference was visible in *Control* context. Our results are in accordance with previous work on great tits where exploratory behavior and detour reaching abilities predicted foraging flexibility, especially under higher predation risk (Coomes et al. 2022). Moreover, highly social cichlids faster to solve a reversal learning task were more plastic in their grouping preferences when predation risk increased (Culbert et al. 2021). Thus, contexts involving more challenges seem to reveal the relationships between plasticity and cognition. Future studies should investigate plasticity in non-foraging situations to refine our understanding of the relationship between behavioral plasticity and cognitive abilities. Understanding covariation patterns between plasticity in different contexts is critical to understand the potential coevolution of such traits (Morel-Journel et al. 2020).

The overall harshness of the environment is often related to increases in foraging demands and unpredictability of food availability, selection should thus favor individuals able to deal with such conditions. Chickadees have different foraging routines depending on their elevation (Pitera et al. 2018) while high elevation great tits are more risk-prone (Chapter 2). In addition, high elevation mountain chickadees solved a new problem faster than their low elevation counterparts (Kozlovsky et al. 2015a) and great tits from high elevation outperformed low elevation counterparts in associative and reversal learning (Hermer et al. 2018), confirming the higher cognitive abilities of birds living in more demanding conditions. But to date, no

evidence of the influence of environmental harshness on potential correlations between foraging plasticity and cognitive abilities is available. In this study, we found that great tits originating from high elevation with a higher accuracy in associative learning were more plastic in foraging decisions than individuals less accurate in this cognitive task. Moreover, in winter, birds needing more time to solve the innovation task were more plastic than quick solvers individuals. As such, our result provides proof of the influence of environmental harshness on the relationship between foraging plasticity and cognition. Future studies will need to consider environmental variation in order to disentangle the complex relation between social plasticity and cognition and estimate potential benefit of plasticity in wild animals' population dynamics (Vinton et al. 2022).

In conclusion, we found that the relation between social foraging plasticity and cognitive abilities in wild great tits originating from ecologically contrasted populations depended on the environmental context. Our results, confirm that the link between plasticity and cognition is more complex than expected. Social plasticity is a complex behavior that seems to emerge from the interaction of different domains of cognition. Although we considered different cognitive abilities, from innovation to learning, we did not find a general cognitive performance that could explain social plasticity variation. Future studies will need to confirm the benefit of higher social plasticity on reproductive success and survival. Such result would help to understand the evolution of social plasticity (Varela et al. 2020). Moreover, we found that environmental variation led to relations between social plasticity and cognition in certain contexts. These results, suggest that this association depends on contextual factors which could influence the persistence of individuals facing highly variable environments. Future work should measure the impact of these factors on cognitive abilities and on social plasticity. As such, urban areas and the various associated disturbances are a good factor to consider in the actual changing world (Caspi et al. 2022).

## IV. 6. SUPPLEMENTARY MATERIALS

### IV. 6. 1. Cognitive tasks apparatus



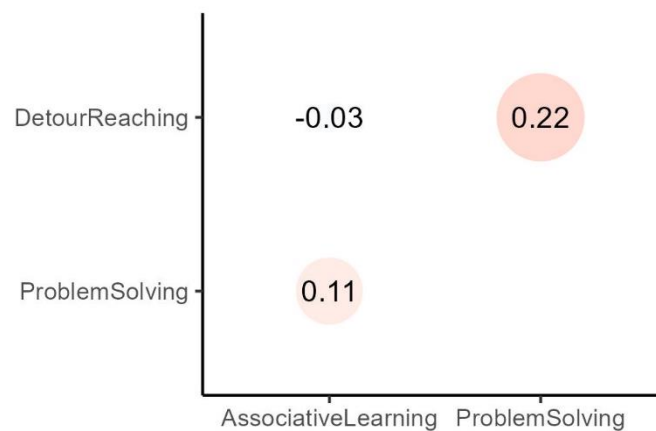
Figure S. IV.1: A) Experimental setup used for the inhibition task (detour reaching). The transparent tube is 7.5 cm long and has a diameter of 3 cm. B) Picture of a great tit (*Parus major*) next to the inhibition task. The reward is an immobilized waxworm larva (*Galleria mellonella*). The green bowl contained mealworms outside of the experiment and was placed here empty, to favor interactions with the inhibition task.



Figure S. IV.2: A) Experimental setup used for the innovation task (problem solving). The transparent tube is 7 cm long and has a diameter of 3 cm. A platform is located 3.5 cm above the gap. B) Picture of a great tit (*Parus major*) next to the innovation task. The reward is an immobilized waxworm larva (*Galleria mellonella*). The green bowl contained mealworms outside of the experiment and was placed here empty, to favor interactions with the inhibition task. The red cap is positioned on top of the problem solving test to prevent a bird from collecting the reward from above.

#### IV. 6. 2. Correlation among cognitive abilities from various tasks

Previous work in humans (Plomin 2001), insects (Finke et al. 2023) and birds (Shaw et al. 2015; Ashton et al. 2018; Ashton et al. 2022) highlighted the consistency of cognitive abilities across various tasks within individuals, arguing for a general intelligence factor. To examine relationships between cognitive performance across different tasks in great tits, we performed Pearson pairwise correlations between the three tasks (*correlations* package, Makowski et al., 2020). Variables were grouped into two major categories: solving ability (ability to learn the associative learning criterion, ability to solve the problem solving task and ability to solve the detour reaching task) and solving efficiency (number of visits needed to reach the associative learning criterion, accuracy of the last half-day of the associative learning task, length of the problem solving task in seconds, length of the detour reaching task in seconds). We also looked at two by two correlations between the different variables within each cognitive task following the same procedure.



*Figure S. IV.3: Matrix of pairwise correlation of solving ability in great tits. The number represents the Pearson coefficient of correlations (positive value in red, negative value in blue). The further the coefficient of correlation is from 0, the larger the circle surrounding it.  $N=77$  individuals.*



Figure S. IV.4: Matrix of pairwise correlation of solving efficiency in great tits. The number represents the Pearson coefficient of correlations (positive value in red, negative value in blue). The further the coefficient of correlation is from 0, the larger the circle surrounding it.  $N=77$  individuals.

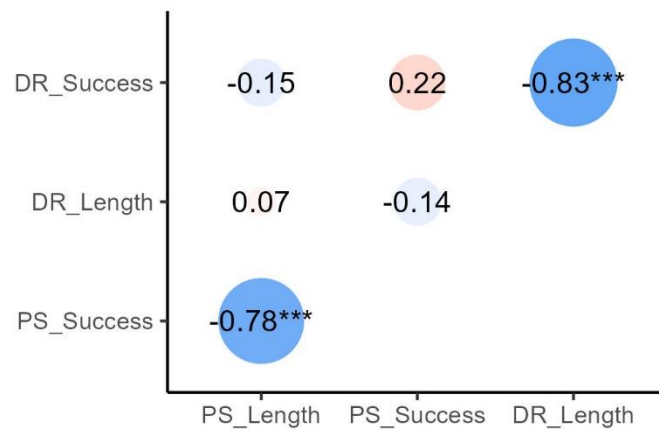


Figure S. IV.5: Matrix of pairwise correlation of innovation tasks in great tits. The number represents the Pearson coefficient of correlations (positive value in red, negative value in blue). The further the coefficient of correlation is from 0, the larger the circle surrounding it. The asterisks illustrate the significance of the test for equality at zero of each coefficient (\*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ ). (DR=Detour Reaching, PS=Problem Solving).  $N=83$  individuals.

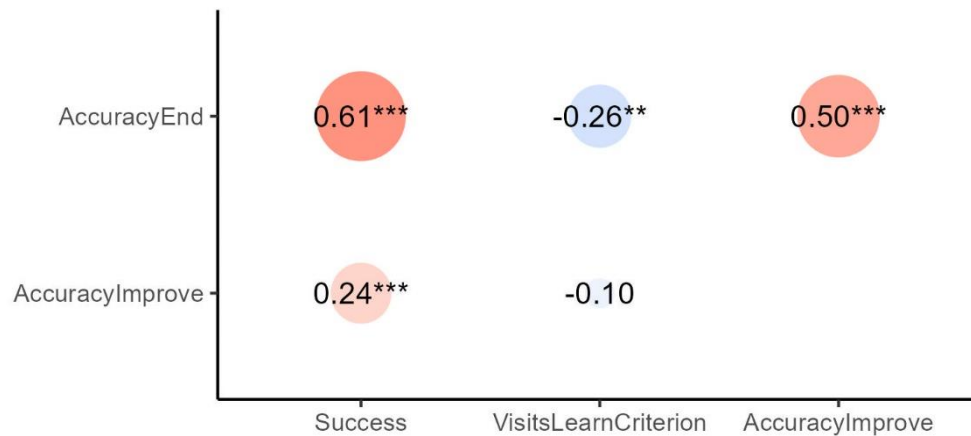


Figure S. IV.6: Matrix of pairwise correlation of associative learning task in great tits. The number represents the Pearson coefficient of correlations (positive value in red, negative value in blue). The further the coefficient of correlation is from 0, the larger the circle surrounding it. The asterisks illustrate the significance of the test for equality at zero of each coefficient (\*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ ).  $N=179$  individuals.

We did not find any consistency in solving ability or in solving efficiency between problem solving, detour reaching and associative learning (Figure S. IV.3-4). However, we found strong correlations between cognitive metrics within each test (Figure S. IV.5-6). In order to avoid potential confounding effects, we avoided including correlated cofactors in the same model in the main analysis.



In addition, to investigate the existence of a general cognitive parameter, we performed a principal component analysis (*FactoMineR* package, Lê et al., 2008). Only principal components with an eigenvalue  $> 1$  were extracted from the analysis.

*Table S. IV.1: Principal component analysis for the solving ability (ability to solve the problem solving task, ability to solve the detour reaching task and ability to learn the associative learning criterion) of great tits in the three tasks. Only principal components with an eigenvalue  $> 1$  are represented here.  $N=77$  individuals.*

Task	PC1	PC2
Detour reaching	0.779	-0.407
Problem solving	0.852	0.110
Associative learning	0.240	0.933
eigenvalue	1.390	1.048
percentage of variance	46.327	34.943

*Table S. IV.2: Principal component analysis for the solving efficiency (length of the detour reaching task in seconds, length of the problem solving task in seconds, number of visits needed to reach the associative learning criterion) of great tits in the three tasks. Only principal components with an eigenvalue  $> 1$  are represented here.  $N=77$  individuals.*

Task	PC1	PC2
Detour reaching	-0.636	0.659
Problem solving	0.401	0.840
Associative learning	0.887	0.092
eigenvalue	1.352	1.148
percentage of variance	45.053	38.280

A general intelligence factor could be highlighted if all tasks contributed to the first component in the same direction and explain  $> 30\%$  of overall variance (Galsworthy et al. 2005). This was the case in our analysis of both solving ability (46.327% of variance explained, Table S. IV.1) and solving efficiency (45.053% of variance explained, Table S. IV.2). However, all tasks did not contribute in the same way although and strongly to the first principal component, weakening the predicted existence of a general cognitive factor in our system.

### IV. 6. 3. Inter-individual differences in cognitive abilities

To understand inter-individual differences in cognitive abilities, we built linear mixed model with each cognitive measure as the response variable and various individual characteristics (sex, age, elevation of origin, exploration score, body mass, season of experiment) as fixed factors. We added batch of capture as a random factor to account for between year variation. For detour reaching and problem solving variable, we also added the order of the innovation task as a random factor. We centered on the mean and scaled by standard deviation exploration score and body mass prior to integration in the model. We checked model performance graphically using the *DARHMa* package (Hartig 2022). The significance level for p-values was set at 0.05 (two-tailed tests). We present here a summary of each model.

*Table S. IV.3: Ability to solve the detour reaching task in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird is more likely to solve the task. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=138$  individuals.*

Model	Estimate	SE	95% conf int	Z value	P value
(Intercept)	-0.31	<b>0.38</b>	-1.04; 0.43	-0.82	0.415
Elevation (Low)	0.61	0.31	-0.01; 1.22	1.94	<b>0.052</b>
Sex (Male)	-0.46	0.35	-1.15; 0.24	-1.30	0.195
Age (Yearling)	0.02	0.32	-0.61; 0.65	0.07	0.944
Season (Winter)	0.23	0.31	-0.38; 0.84	0.74	0.462
Exploration Score	-0.06	0.15	-0.36; 0.24	-0.39	0.697
Weight (g)	-0.09	0.18	-0.45; 0.26	-0.52	0.604

*Table S. IV.4: Ability to solve the problem solving task in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird is more likely to solve the task. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=104$  individuals.*

Model	Estimate	SE	95% conf int	Z value	P value
(Intercept)	-0.85	0.68	-2.18; 0.48	-1.25	0.212
<b>Elevation (Low)</b>	<b>1.17</b>	<b>0.42</b>	<b>0.34; 1.99</b>	<b>2.76</b>	<b>0.006</b>
Sex (Male)	-0.04	0.48	-0.98; 0.9	-0.08	0.934
Age (Yearling)	0.45	0.42	-0.36; 1.27	1.09	0.277
Season (Winter)	-0.05	0.50	-1.02; 0.93	-0.09	0.928
Exploration Score	0.00	0.20	-0.39; 0.39	0.01	0.994
Weight (g)	0.14	0.24	-0.33; 0.61	0.57	0.568

*Table S. IV.5: Ability to learn the associative learning criterion in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird is more likely to solve the task. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=184$  individuals.*

Model	Estimate	SE	95% conf int	Z value	P value
(Intercept)	0.20	0.55	-0.89; 1.28	0.36	0.722
Elevation (Low)	-0.28	0.29	-0.85; 0.29	-0.95	0.342
Sex (Male)	-0.29	0.34	-0.94; 0.37	-0.86	0.392
Age (Yearling)	-0.07	0.31	-0.68; 0.53	-0.24	0.814
Season (Winter)	-0.15	0.65	-1.42; 1.12	-0.23	0.819
Exploration Score	0.08	0.14	-0.21; 0.36	0.54	0.588
Weight (g)	0.25	0.17	-0.09; 0.59	1.43	0.154

Table S. IV.6: Length of the detour reaching task in seconds in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird is more likely to solve the task. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=138$  individuals.

Model	Estimate	SE	95% conf int	Z value	P value
<b>(Intercept)</b>	<b>705.33</b>	<b>128.56</b>	<b>451.59; 959.07</b>	<b>5.49</b>	<b>&lt; 0.001</b>
Elevation (Low)	-112.28	106.30	-322.09; 97.53	-1.06	0.292
Sex (Male)	192.17	121.69	-48; 432.34	1.58	0.116
Age (Yearling)	5.89	109.64	-210.49; 222.28	0.05	0.957
Season (Winter)	48.16	105.82	-160.69; 257.01	0.46	0.650
Exploration Score	66.53	52.54	-37.18; 170.24	1.27	0.207
Weight (g)	9.08	61.86	-113.02; 131.18	0.15	0.883

Table S. IV.7: Length of the problem solving task in seconds in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird was longer to solve the task. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=104$  individuals.

Model	Estimate	SE	95% conf int	Z value	P value
<b>(Intercept)</b>	<b>713.31</b>	<b>186.23</b>	<b>256.8; 1169.81</b>	<b>3.83</b>	<b>0.009</b>
Elevation (Low)	-130.45	106.95	-342.1; 81.19	-1.22	0.225
Sex (Male)	25.58	128.26	-228.31; 279.46	0.20	0.842
Age (Yearling)	-126.63	112.35	-348.96; 95.7	-1.13	0.262
Season (Winter)	64.08	139.15	-248.26; 376.42	0.46	0.656
Exploration Score	-0.94	52.55	-104.93; 103.05	-0.02	0.986
Weight (g)	-56.57	62.87	-180.97; 67.82	-0.90	0.370

Table S. IV.8: Number of visits needed to reach the associative learning criterion in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird needed more visits to reach the learning criterion. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=184$  individuals.

Model	Estimate	SE	95% conf int	Z value	P value
<b>(Intercept)</b>	<b>138.35</b>	<b>34.44</b>	<b>67.12; 209.58</b>	<b>4.02</b>	<b>0.001</b>
Elevation (Low)	-8.79	24.71	-57.79; 40.21	-0.36	0.723
Sex (Male)	21.98	29.40	-36.32; 80.27	0.75	0.456
Age (Yearling)	31.59	25.76	-19.48; 82.66	1.23	0.223
Season (Winter)	-10.93	36.12	-91.99; 70.12	-0.30	0.769
Exploration Score	-20.74	11.12	-42.78; 1.3	-1.87	0.065
Weight (g)	11.45	13.86	-16.02; 38.91	0.83	0.411

Table S. IV.9: Accuracy of the last half-day of the associative learning task in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird was more accurate. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=184$  individuals.

Model	Estimate	SE	95% conf int	Z value	P value
<b>(Intercept)</b>	<b>0.54</b>	<b>0.05</b>	<b>0.45; 0.63</b>	<b>11.87</b>	<b>&lt; 0.001</b>
Elevation (Low)	-0.05	0.03	-0.1; 0	-1.81	0.072
Sex (Male)	-0.02	0.03	-0.08; 0.04	-0.62	0.539
Age (Yearling)	0.00	0.03	-0.05; 0.06	0.03	0.975
Season (Winter)	-0.01	0.05	-0.12; 0.11	-0.15	0.882
Exploration Score	0.01	0.01	-0.02; 0.04	0.70	0.482
Weight (g)	0.01	0.02	-0.02; 0.04	0.44	0.660

*Table S. IV.10: Difference between the accuracy of the 20 last visits and the 20 first visits in the associative learning task in relation with a bird's elevation of origin and individual characteristics. A positive value for the estimate means that the bird improved more in accuracy. For each categorical variable, the reference level is presented in brackets. Values in bold are significant at  $P < 0.05$ .  $N=184$  individuals.*

Model	Estimate	SE	95% conf int	Z value	P value
(Intercept)	0.07	0.07	-0.08; 0.22	1.04	0.312
Elevation (Low)	-0.01	0.03	-0.07; 0.06	-0.19	0.853
Sex (Male)	0.03	0.04	-0.04; 0.11	0.89	0.377
Age (Yearling)	0.01	0.03	-0.06; 0.08	0.35	0.730
<b>Season (Winter)</b>	<b>0.20</b>	<b>0.09</b>	<b>0.01; 0.4</b>	<b>2.32</b>	<b>0.043</b>
Exploration Score	0.01	0.02	-0.02; 0.04	0.44	0.663
Weight (g)	-0.01	0.02	-0.05; 0.03	-0.44	0.659

Birds from low elevation solved more the problem solving task than their high elevation counterparts ( $Z=2.76$ ,  $Est.=1.17\pm 0.42$ ,  $P=0.006$ , Table S. IV.4). Moreover, birds tested in winter improved more in accuracy in the associative learning task ( $Z=2.32$ ,  $Est.=0.20\pm 0.09$ ,  $P=0.043$ , Table S. IV.10).

We also identified some trends with birds from low elevation tending to solve more the detour reaching task than their high elevation counterparts ( $Z=1.94$ ,  $Est.=0.61\pm 0.31$ ,  $P=0.052$ , Table S. IV.3), birds with higher exploration score tending to need less visits to learn the associative task criterion ( $Z=-1.87$ ,  $Est.=-20.74\pm 11.12$ ,  $P=0.065$ , Table S. IV.8) and low elevation birds tending to be less accurate at the end of the associative learning task compared to high elevation one ( $Z=-1.81$ ,  $Est.=-0.05\pm 0.03$ ,  $P=0.072$ , Table S. IV.9).

Overall, inter-individual differences in birds' cognitive abilities were not well explained by the individual characteristics tested. In the main analysis, we kept the two significant variables as cofactor of specific cognitive metric when looking for a link between foraging plasticity and cognitive ability.

IV. 6. 4. Supplementary tables

Table S. IV.11: Link between solving ability in various cognitive tasks (ability to solve the detour reaching task,  $N=133$ ; ability to solve the problem solving task,  $n=100$ ; ability to learn the associative learning criterion,  $N=179$ ) and foraging plasticity in great tits fitted with a linear mixed model (Type III Anova) including all interactions. Values in bold are significant at  $P < 0.05$ .

Cognitive task Factors	Detour Reaching			Problem Solving			Associative learning		
	Ch.sq	Df	P value	Ch.sq	Df	P value	Ch.sq	Df	P value
(Intercept)	<b>11.20</b>	<b>1</b>	<b>0.001</b>	<b>4.90</b>	<b>1</b>	<b>0.027</b>	<b>6.02</b>	<b>1</b>	<b>0.014</b>
Success	2.33	1	0.127	1.00	1	0.318	0	1	0.976
Elevation	0.68	1	0.409	3.59	1	0.058	0.69	1	0.407
Season	0.94	1	0.333	1.22	1	0.270	1.57	1	0.210
Context	2.60	2	0.272	3.44	2	0.179	<b>28.13</b>	<b>2</b>	<b>&lt; 0.001</b>
Species	0.22	1	0.637	0.11	1	0.745	0.31	1	0.578
Success x Elevation	0	1	0.967	1.71	1	0.191	0.01	1	0.939
Success x Season	3.77	1	0.052	<b>5.46</b>	<b>1</b>	<b>0.019</b>	0.60	1	0.437
Success x Context	<b>8.04</b>	<b>2</b>	<b>0.018</b>	1.07	2	0.587	4.38	2	0.112

Table S. IV.12: Link between solving efficiency in various cognitive tasks (length of the detour reaching task in seconds,  $N=133$ ; length of the problem solving task in seconds,  $N=100$ ; number of visits needed to reach the associative learning criterion,  $N=179$ ) and foraging plasticity in great tits fitted with a linear mixed model (Type III Anova) including all interactions. Values in bold are significant at  $P < 0.05$ .

Cognitive task Factors	Detour Reaching			Problem Solving			Associative learning		
	Ch.sq	Df	P value	Ch.sq	Df	P value	Ch.sq	Df	P value
(Intercept)	<b>10.35</b>	<b>1</b>	<b>0.001</b>	<b>20.39</b>	<b>1</b>	<b>&lt;0.001</b>	<b>7.02</b>	<b>1</b>	<b>0.008</b>
Efficiency	2.04	1	0.153	1.19	1	0.275	0.04	1	0.838
Elevation	1.65	1	0.199	2.81	1	0.094	0.53	1	0.465
Season	0.26	1	0.608	0.90	1	0.343	0.02	1	0.878
Context	<b>15.80</b>	<b>2</b>	<b>&lt;0.001</b>	<b>9.37</b>	<b>2</b>	<b>0.009</b>	<b>6.56</b>	<b>2</b>	<b>0.038</b>
Species	0.22	1	0.640	0.11	1	0.745	0.42	1	0.516
Efficiency x Elevation	0.18	1	0.675	0.13	1	0.723	1.34	1	0.246
Efficiency x Season	2.12	1	0.146	<b>3.91</b>	<b>1</b>	<b>0.048</b>	0.02	1	0.891
Efficiency x Context	0.05	2	0.974	2.57	2	0.277	3.81	2	0.149

Table S. IV.13: Link between A) final accuracy in associative learning task (accuracy of the last half-day of the associative learning task,  $N=179$ ) and B) accuracy improvement (difference between the accuracy of the 20 last visits and the 20 first visits in the associative learning task,  $N=179$ ) and foraging plasticity in great tits fitted with a linear mixed model (Type III Anova) including all interactions. Values in bold are significant at  $P < 0.05$ .

Associative learning Factors	Final accuracy			Accuracy improvement		
	Ch.sq	Df	P value	Ch.sq	Df	P value
(Intercept)	<b>7.82</b>	<b>1</b>	<b>0.005</b>	<b>10.58</b>	<b>1</b>	<b>0.001</b>
Accuracy	0.04	1	0.848	0.89	1	0.345
Elevation	1.15	1	0.285	1.63	1	0.201
Season	1.20	1	0.272	0.87	1	0.352
Context	<b>20.91</b>	<b>2</b>	<b>&lt; 0.001</b>	<b>21.86</b>	<b>2</b>	<b>&lt; 0.001</b>
Species	0.54	1	0.464	0.35	1	0.554
Accuracy x Elevation	<b>4.47</b>	<b>1</b>	<b>0.035</b>	0.28	1	0.594
Accuracy x Season	1.55	1	0.213	0.33	1	0.564
Accuracy x Context	1.61	2	0.448	1.74	2	0.418





## **CHAPTER V.**

### **GENERAL DISCUSSION**



## V. 1. MAIN FINDINGS

Phenotypic plasticity, and in particular its behavioral component, is considered to be a key trait that could help organisms facing the diversity of challenges from their environment (Snell-Rood 2013) and thus could precede and possibly facilitate adaptive evolution (i.e. plasticity-first hypothesis, Levis & Pfennig, 2016). Evidence of inter-individual variation of behavioral plasticity has been found in a wide range of studies (e.g. Abbey-Lee & Dingemanse, 2019; Briffa et al., 2008; McGhee et al., 2013; Sassi et al., 2015), and the potential causes of this variation are multiple and not fully understood. Yet identifying these factors is necessary to understand the selection pressures acting on wild populations and predict their response and evolution to future changing environments (Stevens et al. 2023). In this thesis, I adopted an intraspecific approach to investigate the causes of individual variation in foraging plasticity. To collect data, I used video playbacks and automatic feeders in controlled conditions. With the use of ecologically contrasted populations of wild great tits (*Parus major*), my findings identified different factors that could explain inter individual differences in foraging plasticity.

The results from Chapter 2 provide evidence for the importance of environmental harshness on foraging plasticity whereby individuals originating from higher elevation were more risk-prone in foraging decisions. This elevation difference depended on the season, as facing harsher winter conditions, birds became less risk averse in order to avoid starvation. Interestingly, intrinsic characteristics also impacted foraging decisions under predation risk as heavier birds tended to be more careful whereas females and yearlings took more risks to get access to food. Our results confirmed starvation-predation trade-off theory (McNamara and Houston 1990; Houston et al. 1997) complementing previous work on foraging routines (McNamara et al. 1994; Pitera et al. 2018). Inter-individual differences were detected despite the fact that birds spent 28 days under standardized conditions with similar levels of food, competition, ambient temperature, and risk of predation. It would be interesting to determine how long individuals retain information about predation risk in their habitat and use that information to modulate their foraging behavior, especially considering human-induced rapid environmental changes (Sih et al. 2011) and climate change (Cresswell et al. 2009).

In Chapter 3, I showed that foraging decisions changed with the composition of the social group. Birds preferred to forage alone rather than with conspecifics. In addition, the species present in the social audience impacted this preference as birds avoided blue tits more than great tits. I also provided experimental evidence of the context dependency of foraging decisions as an individual changed its foraging decisions regarding the overall ecological context experienced. Although in a secured situation, birds preferred to forage alone, whereas under enhanced predation risk or disturbance, they decided to forage more in groups. This result confirms the context-dependency of social plasticity (Taborsky and Oliveira 2012) and its importance in measuring social behaviors. Moreover, I found that the degree of change in foraging decisions depended on age as yearlings were less plastic under predation and disturbance situations compared to adults. This absence of preference in some contexts only present in younger individuals suggests that plasticity may need time to develop or that birds change plastically their foraging decisions depending on the ability to access food in line with dominance or experience. It would be interesting to investigate the ontogeny of plasticity to understand the reason for age-dependent differences in foraging decisions (Fischer et al. 2014).

In Chapter 4, I found that the link between plasticity and cognition was more complicated than expected. I showed that solvers in an innovation task were not necessarily more plastic in their foraging decisions. In addition, this relation depended on the external environment as the negative relationship between cognitive success and foraging plasticity was only visible in winter. Solvers were also more plastic in a secured situation compared to contexts under predation or disturbance, while the context did not impact non-solvers. The harshness and the stressful character of environmental conditions could thus impact foraging plasticity and the innovation ability. Moreover, the relation between cognition and plasticity depended on the cognitive ability measured, as associative learning success or learning speed were not related to foraging decisions. As behavioral plasticity should rely on cognitive abilities, theory predicts the existence of a positive link between plasticity and cognition (Varela et al. 2020). I provided experimental evidence for complexity in this relationship and that social plasticity is an intricate behavior resulting from an interaction of cognitive abilities. More studies looking at

several and complex cognitive abilities are needed in order to deepen our understanding of the link between cognition and plasticity and the potential coevolution between them.

Combined, the results of the present thesis have important consequences for our understanding of the evolution of plasticity in the past and also on potential consequences for survival and evolution of populations facing new environments in the future such as under climate change or human-induced rapid environmental changes (Caspi et al. 2022; Vinton et al. 2022).

In the present chapter, I will consider my main findings and their potential implications in four successive topics, as illustrated in Figure V.1:

- A) Environmental variation,
- B) Behavioral plasticity syndromes,
- C) Intrinsic characteristics and past experiences,
- D) Consequences of plasticity variation in a changing world.

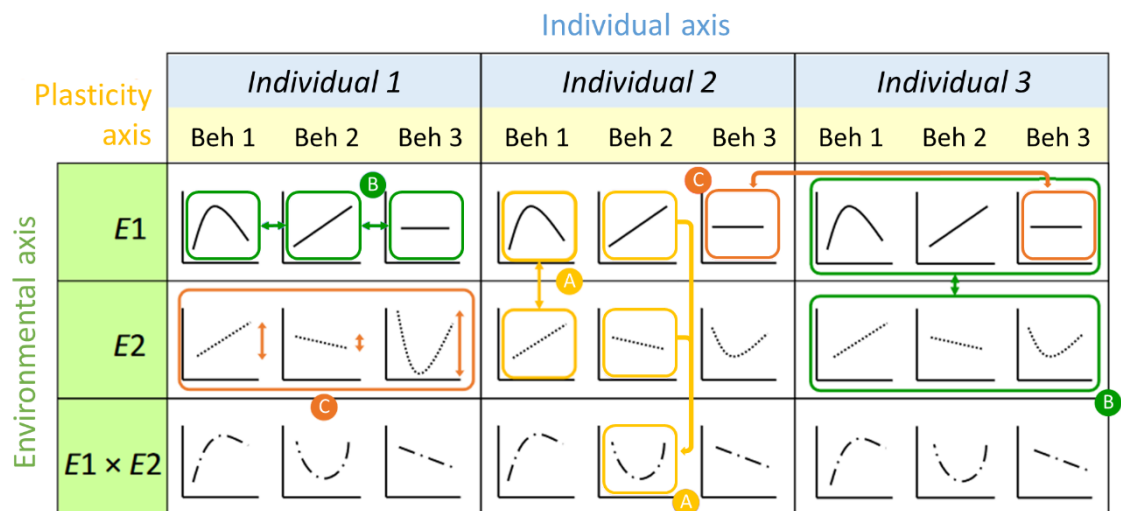


Figure V.1: Schematic representation of the topics discussed in the present chapter. It represents theoretical plasticity variation of three behaviors (Beh1, Beh2, Beh3) as a reaction norm for three individuals along two environmental gradients (E1 and E2). I will discuss A) how environmental variation impacted plasticity, B) the variation of plasticity between behaviors within and between environmental gradients (behavioral syndromes) and C) the impact of intrinsic characteristics on plasticity (individual variation). Figure extracted and modified from Morel-Journel et al., 2020.

## V. 2. ENVIRONMENTAL VARIATION

### V. 2. 1. Environmental harshness and chronic stress

Characteristics defining an environment, like temperature, naturally vary over time and space (Huntingford et al. 2013). When several environmental conditions are not optimal at the same moment or for a length of time relatively long, e.g. food supply is limited and unpredictable (Pravosudov and Clayton 2002) or extreme dry seasons (Schradin et al. 2023) such environments can be defined as harsher compared to environments with milder characteristics. Although extreme climatic conditions could be defined as harsh for all species (extreme high elevation for example), the perception of harshness may also depend on the species (Love and Wagner 2023). In southern Africa, facing severe dry events associated with a decline in food availability, bush Karoo rats (*Otomys unisulcatus*), an herbivorous species became scarce with the onset of the dry season while omnivorous striped mice (*Rhabdomys pumilio*) managed to endure droughts (Schradin 2005). In this example, the degree of harshness and its consequences appeared lower for striped mice than for bush Karoo rats. Consideration of the organism–environment relationship and its evolutionary history are important as an environment perceived as harsh for some species may be less demanding for another one. Under harsher conditions, the most efficient strategy is to save energy by reducing metabolism until more favorable conditions return, which is the strategy developed by some species facing particularly extreme temperature with hibernation or torpor (Geiser 2013). On the contrary, under stressful conditions, the optimal response is to increase available energy in order to face the origin of stress, like fleeing facing a predator (Lima 1998). Although opposite on the optimal response, harshness and stress are not incompatible and individuals can face stressful situations in harsh environments. In this condition, the organism’s decision is a trade-off between keeping and gaining as much energy as possible and using the energy to face the stressful event. This has been modeled in starvation-predation trade off theory (Houston and McNamara 1993) and confirmed by studies on small birds’ foraging decisions in winter (Lima and Dill 1990; Houston et al. 1997; Lima and Bednekoff 1999). In this thesis, I tested this starvation-predation balance across more or less harsh environments, a step rarely done in previous studies (but see Pitera et al., 2018). High elevation individuals were more risk-prone when visiting a feeder and this effect was even more visible in winter (Chapter 2).

Moreover, in harsher seasonal conditions like winter, birds succeeded more in an innovation task (Chapter 4). Thus, high elevation great tits seek to save energy and maximize food intake to limit starvation but while taking more risks. However, the limit of the present thesis is that I only compared populations well established at each elevation, where environments remained stable over years. The differences observed between high and low elevation birds may have a genetic origin and not be related to current changes, especially as birds were tested in standardized conditions regarding level of food, competition, ambient temperature and risk of predation. Alternatively, foraging decisions taken by great tits might be based on long lasting integration of information. It would be interesting to disentangle this two potential factors implying populations differences. Nevertheless, recent anthropogenic induced climate change is causing changes in the rate, variation, and autocorrelation of environmental variables (Vinton et al. 2022). As a consequence, some population range shifts, notably towards higher elevations. Other populations with limited dispersal but instead rely on phenotypic plasticity to avoid extinction. Evolutionary processes (e.g. selection, genetic variation) and ecological processes (e.g. life history, phenotypic plasticity) together influence how far a population can change and manage to reach a new theoretical phenotypic optimum and persist (Niemelä et al. 2013; Lawson et al. 2015; Vinton et al. 2022). It is therefore vital to integrate the impact of environmental components on population dynamics and life history to understand the impact of environmental change on the interplay between plasticity and adaptive evolution, especially as harsher events are predicted to become more frequent in the coming decades.

Another anthropogenic major impact, urbanization, also provokes rapid environmental changes exposing organisms to unprecedented challenges such as habitat change or widespread pollution, potentially ending in long term stress (Grimm et al. 2008). Although more predictable than natural habitats, urban areas offer dramatically different habitats for organisms (Vardi and Berger-Tal 2022). Because urban environments confront animals to extremely novel conditions, they can induce strong behavioral responses such that cities provide a unique opportunity to study the role of behavioral plasticity in urban evolution (Lowry et al. 2013; Caspi et al. 2022). Comparing urban and rural populations could help understanding how the long term stressors associated with urbanization might impact behavioral plasticity. Current methods of studying behavioral phenotypes typically involve

comparing the responses of individuals to a range of physical environments and/or within a single environmental gradient (Briffa et al. 2008). Based on results of the present thesis, I can expect strong differences in foraging decisions and overall behavioral plasticity between urban and rural populations. However, urban habitats are not homogenous and may differ greatly in the conditions they offer to wild animals as they represent a mosaic of microhabitats displaying heterogeneity in many factors (Pickett et al. 2017). To go further, we need to consider the impact of this urban heterogeneity on individuals by comparing populations within cities.

Finally, behavioral adjustments occur either when a city grows around a population or when an external, nonurban population colonizes a city. A population present during initial urbanization could split if individuals with certain behavioral phenotypes remain in their ancestral although altered habitat (Caspi et al. 2022). Studying behavioral plasticity of non-urban individuals in controlled conditions of urban stressors could provide predictions of the future capacities of urban naïve individuals to cope with urbanization. Previous studies have suggested that the ability to inhabit cities may be linked to advanced learning traits, a form of cognitive plasticity (Lee and Thornton 2021). Measuring behavioral plasticity under chronic exposure of specific sources of disturbances, such as light or sound pollution (Gaynor et al. 2018; Osbrink et al. 2021; McGlade et al. 2023) will provide insight about long term consequences of urbanization. These urban stressors must be studied separately to disentangle the effect of each component on animal decisions and analyze if behavioral plasticity under one environmental gradient (e.g. sound pollution) is linked to plasticity under another one (e.g. light pollution). There is also a need to study urban stressors combined (e.g. light and sound pollution together) to reflect more realistic environments and understand the potential additive or synergic effect on behavioral plasticity and potential consequences on population maintenance in urban areas (Dominoni et al. 2020; Stevens et al. 2023). During the course of my PhD, I ran such experiments on wild great tits experiencing sound, light or combined pollution but they are not included in the present thesis and will be the base of future publications.



### V. 2. 2. Social environment

Observing how individuals respond to changes in their physical environment is not sufficient to understand the ecological and evolutionary significance of a particular behavior. When the behavioral traits of other individuals influence how an organism perceives, processes, and responds to its environment, the specific composition of a group may have fitness consequences for all or some of its members. Therefore, social environment has the potential to substantially affect an individual's fitness by influencing the interaction between that individual and its physical environment (Guayasamin et al. 2017). As an example, shy sticklebacks (*Gasterosteus aculeatus*) became bolder when placed with a bolder partner, and their asocial behavior remains a significant predictor of their social behavior (Jolles et al. 2014). However, social environment is not limited to highly social groups but is also composed of others individuals from the same species (a partner, a competitor, a familiar or a related individual) or from different species (Sasvári 1992) so studies need to consider the social environment, even in non-strictly social species. This environment is highly dynamic as the behavior of one individual will impact decisions of others group members, and the composition of interacting individuals is changing on short time scales. In a foraging context for example, competition between different species of small passerines drives decisions and exploitation of foraging patches (Alatalo et al. 1987). Social foraging is a trade-off between the risk of competition and the benefits of increasing the probability to find food patches and avoid predators (Hamilton 1971; Lima 1995; Barta et al. 2004). In line with previous studies, I found that the composition of the social group (species and group size) influenced foraging decisions of wild great tits (Chapter 3) as great tits preferred foraging alone than with conspecifics and this preference was more marked facing blue tits than great tits. Moreover, I provided experimental evidence that this foraging plasticity depended on the overall context (Chapter 3) where preference to forage alone was no longer visible in a predation or a disturbance context. The ability of an individual to adapt its response to social information named social plasticity or social competence (Taborsky and Oliveira 2012; Wolf and McNamara 2013) can help it dealing with social challenges. Individuals with higher social plasticity should be favored by social selection (Wolf et al. 1999; McGlothlin et al. 2010). However, to fully understand which factors can influence social plasticity other aspects of social environment than group size and species need to be considered. Actually, agonistic interactions and dominance status

impact the accessibility of good quality foraging patches (Caraco et al. 1989; Liker and Barta 2002). It would be interesting to investigate if context-dependent social foraging is also impacted by hierarchy rank. Moreover, past experiences, such as a previous victory in a conflict, influenced the result of an agonistic interaction between two individuals (Lerena et al. 2021). Conflicts observed by a focal individual could also influence its own foraging choices, in network or cascade interactions (Sih et al. 2009). Although these questions could be explored with the video playbacks system used in this thesis, interactive video playbacks are a powerful tool to consider as it gives the possibility to adapt the video playback to the behavior of the focal birds (Ord and Evans 2002; Rosenthal, Gil G. 2019). With this more complex setup, it would be possible to more easily manipulate the role of the tested individual towards the social audience (e.g. as a dominant, a subordinate, as an owner of a resource or an intruder, Taborsky & Oliveira, 2012).

In addition, as previous interactions can impact social plasticity, studying individuals directly in their natural social network is necessary to integrate long lasting encounters, familiarity between individuals and potential interactions between social environment and abiotic characteristics. In a foraging context, great tits tempered their foraging decisions in order to stay with their partner, changing foraging strategy as a consequence (Firth et al. 2015). In a non-foraging context, the dear enemy phenomenon where birds defend their territory differently when facing neighbors or strangers (Temeles 1994) is an ideal framework to understand how individuals adapt their behaviors to social information and the identity of other individuals in the social group. Recent work pointed out that territory defense is dependent on temporal cues from the environment (Moser-Purdy et al. 2017; Jin et al. 2021; Jablonszky et al. 2022), and future studies would gain from the integration of environmental variation. As urban areas are characterized by altered areas for reproduction (James Reynolds et al. 2019), understanding how territory defense plasticity is impacted by urban stressors would help predict population persistence (and therefore conservation efforts) in urban areas. In fact, social relationships and potential associated social plasticity could shape population structure (Firth et al. 2015). Additionally, social plasticity is not predicted to be limited to agonistic interactions and may also be implicated in interspecific cooperation (Bshary and Oliveira 2015) and biological markets (Aureli et al. 2002; Kern and Radford 2018) where more

plastic individuals would be advantaged in delayed contingent cooperation. All these different cases need to be studied in parallel to identify the existence of a potential general ability of social plasticity (Taborsky and Oliveira 2012; Stamps 2016).

### **V. 3. BEHAVIORAL PLASTICITY SYNDROMES**

Responding to environmental variation requires coordinated change across several behaviors, a phenomenon defined as correlated behavioral plasticity or plasticity syndromes (Westneat et al. 2019). Understanding covariation patterns between different plastic behaviors in different contexts, their potential origins and how they are impacted by environmental conditions is critical to understand the potential coevolution of such traits (Morel-Journel et al. 2020). Behavioral syndromes are important when individuals repeatedly interact with each other and so may need to adjust their behavior during or between social interactions in various contexts (Sheehy and Laskowski 2023). In Chapter 3, I pointed out that social foraging plasticity of great tits was dependent on the context as birds preferred to forage alone in a secured situation while they did not present a clear preference under predation or disturbance. Here, the members of social audience were either present or absent and did not change their behavior based on what focal individual did. Yet, if an individual's ability to behave in a plastic way is limited in a stressful or disturbing situation, plasticity may not allow individuals to maintain themselves in the face of an external source of disturbance. So the outlined impact of the context on plasticity can have consequences on the maintenance of populations in specific environments. Indeed Less predictable environments are a potential source of stress where plasticity is expected, at a certain level, to have a major role in favoring individual survival (Vinton et al. 2022). Faced with changes caused by humans such as urbanization, where pollution represents chronic stress, the decline in plasticity could prove even more harmful, especially if individuals depend on plastic behaviors for their choices but cannot use it. To go further, it would be interesting to measure plasticity across different situations directly in natural and altered environments, such as along an urbanization gradient. Such measures should not be restricted

to foraging plasticity but also be considered in different situations like the response to acoustic cues of the presence of predators. Great tits are known to use a rich acoustic repertory to inform other individuals for the presence of predators (Suzuki 2011; Dutour et al. 2016). An alarm call is usually produced to alert other individuals to escape and hide, while mobbing calls encourage individuals to join in order to chase the predator (Lind et al. 2005). So in response to acoustic cues provided by the social environment, an individual should adapt plastically its reaction. We could then link this plasticity to the plasticity of other behaviors occurring at the same period of the year such as territory defense against predators or food provisioning to chicks (Temeles 1994; Sanz et al. 2000; Suzuki 2011). There is reason to believe that an individual that exhibits considerable plasticity in one behavioral trait may also exhibit plasticity in another behavioral trait (Sheehy and Laskowski 2023). In a different sets of experiments to the one presented here, I investigated this question on wild great tits during reproductive period. As they are still at the analysis stage, I did not include them in the present thesis and will use them in future publications instead. Mixed models and reaction norms approaches are powerful tools to go further in this direction as they characterize many aspects of individual behavioral variation simultaneously (Dingemanse et al. 2010). The core idea is that the slope of an individual's reaction norm in one behavior may predict the slope of its reaction norm in another behavior. Positive correlations could be caused by shared mechanisms in the maintenance of plasticity. Alternatively, a negative correlation in the magnitude of plasticity could reflect trade-offs due to associated costs, while the absence of a correlation suggests the traits are decoupled (O'Dea et al. 2022). Predicting whether and how these correlations change is especially important in the face of climate change and anthropogenically induced environmental change as correlated behavioral plasticity may facilitate or constrain adaptive change in populations. Reaction to acoustic signals is an interesting playground as vocalizations are known to be impacted by urban sound pollution (Templeton et al. 2016).

As individuals are interacting across many social contexts with the same partners, plastically adjusting several behaviors can help individuals navigate the complex social landscape, thus favoring social plasticity (Taborsky 2021). The requirements of living with other individuals, either in a permanent social system or in seasonal large groups, and forming and maintaining

social relationships are hypothesized to be one of the major drivers behind the evolution of cognitive abilities (Emery et al. 2007; Wascher et al. 2018). Actually, the different hypothesis for the origin of cognition have the same base logic that the complexity of interactions with the environment (social or not) have led to the development and diversification of cognition (Shettleworth 2009). I found that good solvers in problem solving were not plastic, suggesting a negative correlation between plasticity and innovation and a potential trade-off in the development of these two abilities (Chapter 4). I also found no clear relation between detour reaching and plasticity, pointing out that inhibition and foraging plasticity may be decoupled (Chapter 4; O’Dea et al., 2022). Thus, the relation between social foraging plasticity and cognitive abilities was more complex than theoretically expected as it depended on the cognitive abilities measured. In humans (*Homo sapiens*), the g factor has been found to be a good indicator of overall intelligence, i.e. an individual with good performance in one cognitive task will also be efficient in another cognitive task (Deary 2001). However, in non-human animals, although recent studies pointed towards the existence of general cognition in some species (Plomin 2001; Ashton et al. 2018; Finke et al. 2023), others found that the g factor did not explain a consequent part of inter-individual variance (Matzel et al. 2003; Barou Dagues et al. 2020; Poirier et al. 2020), thus the existence of general cognition is still debated. The alternative hypothesis, domain specific cognition, states that different types of knowledge often have different locations within the global neural organization and thus different mechanisms (Hirschfeld and Gelman 1994). Results of the present thesis provide further evidence for this hypothesis as there was no relation between cognitive performance in innovation, inhibition and associative learning tasks (Chapter 4). It would be interesting to investigate the link between social plasticity and other cognitive abilities such as reversal learning, social learning or spatial memorization as the underlying cognitive abilities necessary in such tasks are also needed to face dynamic evolution of social environment. These future studies would help to confirm that social plasticity is a complex behavior resulting from an interaction of cognitive abilities. I also found that the relation between plasticity and cognition depended on the season and context (Chapter 4). If environments vary across multiple axes (e.g. temperature, resource availability, pollution or social landscapes), then correlated behavioral plasticity can help individuals more easily navigate such multifaceted changes (Sih et al. 2011). As the plasticity-cognition link depended on the overall context, this could have important ecological and

evolutionary consequences facing rapid environmental changes (Martin 2021). It is necessary to measure the potential link between plasticity and cognition in anthropogenic modified environments such as urban areas to investigating how (or whether) correlated plasticity change across contexts. This may help reveal insights into the mechanisms linking behaviors and the selection pressures generating those correlations or their absence (Sheehy and Laskowski 2023). Moreover, studying the plasticity-cognition link in natural environment will allow us to understand how differential life-history trade-offs (e.g. current vs future reproductive success during the reproductive period) are also impacting such behavioral plasticity syndromes (Reed et al. 2011).

#### **V. 4. INTRINSIC CHARACTERISTICS AND PAST EXPERIENCES**

Among individuals, the ones who present the most adaptive trait should be favored by natural selection (Darwin 1859). While it is vital to find food to survive, the associated risk-taking due to exposure to predators can lead to death so animals are expected to evolve strategies to limit such risks (Lima and Dill 1990; Lima and Bednekoff 1999). Thus, foraging decisions are driven by a starvation-predation risk trade-off (Houston et al. 1997). Moreover, facing harsher conditions like food unpredictability and short supply, individual decisions to forage should tilt even more toward avoiding starvation and be more risk prone (Houston and McNamara 1993). Under such circumstances, an individual should be as heavy as possible in order to minimize the risk of starvation as fatter individuals can survive longer without food than lighter counterparts, although, from the predation risk point of view, an individual should limit the time spent foraging and stay lighter to minimize the risk of being predated (Lima 1986). I found that under predation risk, heavier birds were more risk averse in their foraging decisions than lighter ones and that this effect was especially visible in winter (Chapter 2). So, individual variation in body mass can impact foraging decisions, following the starvation-predation trade-off theory. Moreover, I showed that the body mass of great tits impacted their foraging plasticity in interaction with the overall contexts (Chapter 3). Heavier birds were less plastic in

their social foraging plasticity under secured conditions compared to lighter birds but I found no such relation facing a disturbance (Chapter 3). The impact of body mass on foraging plasticity deserves more investigation to understand how it can influence decisions in altered environments. But to face starvation, birds also rely on their fat reserves and predictions are similar regarding foraging decisions between fat reserves and body mass (Houston and McNamara 1993). I also found an influence of fat reserves on foraging decisions (Chapter 2). However, a main difference of fat reserves compared to body mass is its temporal variation within a day as they are adjusted as insurance against some period of stress or overnight deprivation (Gosler 1996; Gentle and Gosler 2001). To go further, it would be interesting to examine the temporal variation of foraging plasticity in accordance with fat levels, and foraging routines (i.e. daily decisions variation of when to forage or not) are an interesting trait to study (McNamara et al. 1994). I could predict that a plastic individual would be more able to adapt its foraging routines to daily variation of food availability and potential stressors in fast changing environments, which could help it to survive and so be favored by selection (Levis and Pfennig 2016; Pitera et al. 2018).

Consistent individual differences in behavior (i.e. animal personality) are widespread and do not necessarily imply that individuals are not behaviorally plastic as under changing conditions, individuals can adjust their behavior while remaining consistently different from each other (Mathot and Dingemanse 2014). The exploration behavior in a novel environment has been well studied in small passerines as a good proxy for personality (Dingemanse et al. 2002; Dingemanse et al. 2012; Niemelä and Dingemanse 2018). Shy individuals appear to be more sensitive to the risk of predation while bolder individuals are more risk-prone in their foraging decisions (van Oers et al. 2004; Quinn et al. 2012; Coomes et al. 2022). However, I did not find a clear relation between personality and foraging plasticity under predation risk (Chapter 2 and 3). Although differences of explorative behavior have been identified between elevations (Kozlovsky et al. 2014), the harshness of the environment may not impact foraging differences among differently explorative individuals (Chapter 2). But, as foraging plasticity itself is context-dependent (Chapter 2), the relation between exploration, and more broadly personality, and behavioral plasticity needs to be tested in different contexts, notably in differently variable environments (Niemelä et al. 2013). Organisms can adopt either proactive

or reactive strategies for coping with environmental fast changes, and the coping style that an individual adopts is associated with a specific level of plasticity (Koolhaas et al. 1999). Proactive individuals use less environmental information, being less plastic in their responses than reactive individuals whose behavior is more dependent on environmental cues (Koolhaas et al. 1999). Personality-related differences in plasticity can have important ecological and evolutionary consequences, mainly because it may constrain the ability of individuals to express optimal behavior facing environmental changes, notably for proactive individuals (Mathot and Dingemanse 2014). Studying the impact of personality on plasticity differences in natural environments will also help to link it to reproductive effort, a promising concern as previous studies pointed out that depending on the context, personality types may explain plasticity variation and impact reproductive success in changing environments (Westneat et al. 2011; Nicolaus et al. 2015; Hall et al. 2017).

Young individuals do not always know how to access food (Thornton and McAuliffe 2006; Franks and Thorogood 2018) or to identify predators (Putman et al. 2015) ending in variation of behavioral expression during an organism's lifetime. This age difference between younger individuals and adults may be due to limited prior information about the state of the environment, whereas older individuals are influenced by the information they have accumulated earlier. After a phase of learning and ontogeny of antipredator recognition, younger great tits performed like adults facing predator cues (Kullberg and Lind 2002). Alternatively, age difference may be due to intrinsic characteristics variation caused by age such as dominance status as younger individuals are usually subordinates over adults in small passerines (Sandell and Smith 1991). In agreement of these previous studies, I found an age difference in foraging decisions under predation risk in wild great tits, with younger individuals being more risk-prone in their choices (Chapter 2). To identify the cause of such age differences in risk-taking behavior, future studies should examine the factors that underlie the ontogeny of foraging decisions in juveniles. However, I found that risk-taking decisions were still dependent on the population of origin after almost one month in controlled conditions. To disentangle the genetic impact from a potential influence of environment on ontogenesis, it is necessary to measure the development of risk-taking foraging within a common garden approach where all individuals experience the same conditions since birth. I also found that



foraging plasticity was different between age classes (Chapter 3) with yearlings being less plastic in stressful and disturbed context than adults. An increase of plasticity with age is expected if an organism does not have perfect information at birth but can improve its estimate of the environmental state by integrating information accumulated over a longer period of time (Fischer et al. 2014). In support with this prediction, early life experiences and environment affect social plasticity once adults through developmental plasticity (Arnold and Taborsky 2010). In addition, plasticity may vary with age in a nonlinear pattern: if early in life, it is optimal to delay behavioral adjustments until sufficient information has been collected, toward the end of life, behavioral adjustments may also be disfavored because their beneficial effects can no longer be fully exploited before death (Fischer et al. 2014). Albeit difficult to realize in natural environment as it needs to have access to the same individual through a relatively long period, futures studies should examine the evolution of individual's plasticity over the course of life and measure the intra-individual variation of plasticity. To go further, comparing patterns of correlated plasticity at different ages will help in gaining a broader understanding of correlational selection pressures at the origin of plasticity syndromes (Sheehy and Laskowski 2023). Moreover, observed patterns of age-dependent plasticity have been suggested to result from changes in the availability, reliability, and usefulness of environmental information over the course of an individual's life (Dufty et al. 2002). Organisms living in a fluctuating environment with a limited ability to read environmental cues need to integrate current and past information in order to optimally adjust their phenotype to the state of the environment (Fischer et al. 2014). Measuring the evolution of plasticity in highly variable environments will help understand the impact of environmental cues reliability on the development of plastic behaviors and understand the potential role of plasticity in individual persistence facing fast changing environments.

## **V. 5. CONSEQUENCES OF PLASTICITY VARIATION IN A CHANGING WORLD**

I discussed the different causes of behavioral plasticity variation in the previous sections of this chapter. Environmental variation and intrinsic characteristics can impact plasticity differences among individuals. However, the plasticity may also play a role in individual survival facing environmental variation (Sih et al. 2011). There is a rich ecological literature showing that increased plasticity and cognition helped individuals to respond to challenges in their environment (Vardi and Berger-Tal 2022). In particular, plastic genotypes are superior in variable environments when sufficiently reliable environmental cues are available and costs of plasticity are low (Vinton et al. 2022). However, the benefits of plasticity might be limited when the environment changes too quickly as the information collected is rapidly unreliable in this case (DeWitt et al. 1998). By impacting individual survival, behavioral plasticity might influence evolutionary processes (Ghalambor et al. 2007; Wund 2012). Urban environments expansion exposes animals to extremely novel conditions and provide a unique opportunity to study the role of behavioral plasticity in evolution. According to the plasticity-led evolution hypothesis, adaptive evolution is initiated and directed by phenotypic plasticity (Levis and Pfennig 2016) and this process starts when a genetically diverse population experiences a new environment, like urbanization expansion. Among all individuals moving into cities from nonurban areas or undergoing cities expansion, more behaviorally plastic ones should settle more easily in urban environments. This founder effect implies that only highly plastic individuals arrive and survive in cities (Sol et al. 2002). To do so, they need to find food and shelter, avoid unfamiliar risks and new threats, communicate with conspecifics using potentially altered channels in order to ensure successful establishment through reproduction (Sol et al. 2013). Future studies should compare the reproductive success in urban areas of more or less behaviorally plastic individuals to confirm this first theoretical step. As various behaviors are impacted by urban stressors and nevertheless necessary for individuals to persist, this link needs to be explored in different contexts but also in correlated behavioral plasticity. It might help identify some plasticity syndromes more likely to help face urban areas. Then, for evolution to initiate, the founder population's behavioral changes must persist across generations. To date, we still lack experimental evidence of transmission from parents to

offspring of plasticity abilities and future studies should try to investigate this by comparing behavioral plasticity of adults with the one of their descendants. The adoption of novel behavioral traits and subsequent specialization to urban niches may lead to the development of a behaviorally distinct urban ecotype (Sol et al. 2013; Caspi et al. 2022). Nonrandom mating can spread an emerging ecotype such that plastic changes induced by urbanization become prolific, for example, through the release of cryptic genetic variation (West-Eberhard 2003). Concurrently, assortative mating by behavioral phenotype can further prevent genetic mixing between urban and source populations. As a result, such individuals may become reproductively isolated from ancestral nonurban populations or less plastic urban populations, leading to population divergence and in the end speciation (Snell-Rood and Ehlman 2021a).

## V. 6. GENERAL CONCLUSION

The main aim of this thesis was to explore the causes of individual variation in foraging decisions and social foraging plasticity. By comparing ecologically contrasted wild populations of great tits, I could identify the importance of environmental harshness (Chapter 2), ecological context (Chapter 3), social audience composition (Chapter 3) and different intrinsic characteristics (Chapter 2 and 3) on foraging decisions in passerines. I was also interested in behavioral syndromes by investigating the potential relationship between cognitive abilities and social foraging plasticity and pointed out the complexity of this link (Chapter 4). In all these chapters, I relied on new tools such as automated feeders and complex video playbacks system that proved to be promising for future studies, especially as they limited the impact of research on animal welfare. Overall, my findings suggest that behavioral plasticity is highly variable among individuals and could be a key mechanism at disposition of individuals to face environmental challenges. The main next step is to investigate the consequences of plasticity variation on fitness in contrasted environments.

On a more personal point of view, I learned that a question, even a seemingly simple one, often does not have a single answer, and that each answer in turn calls for further investigation. I thus find myself, at the end of my thesis, with more questions about behavioral plasticity than 4 years ago, each more interesting than the other, and I realize that I have only scratched the surface, at my modest level, of the fascinating world of behavioral ecology. My experiences also taught me that great and blue tits can be particularly aggressive when caught at natural capture sites (my fingers still remember this) and that great tits can always positively surprise you with their behavior, their way of resolving a task or reaction to a stimulus. These unexpected behaviors are always constructive steps in the thinking process. This thesis confirmed my passion for behavioral ecology research and my wish to study in more detail animal behavior ecology and evolution in other contexts, situations and species in future research projects.

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*« Qu'est-ce qu'un scientifique après tout ? C'est un homme curieux qui regarde à travers un trou de serrure, le trou de serrure de la nature, essayant de savoir ce qui se passe. »*

*Jacques-Yves Cousteau*

*« Lorsque les sciences dévoilent les secrets de la nature,  
ce que celle-ci perd de mystérieux, elle le gagne en merveilleux. »*

*Paul Carvel*

