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Liens entre la personnalité, la plasticité comportementale et la cognition : expériences chez le Diamant mandarin (*Taeniopygia guttata*) et le Molly voile (*Poecilia latipinna*)

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RÉSUMÉ

Les individus diffèrent largement entre eux dans leur tendance à modifier leur comportement en réponse aux changements environnementaux, *i.e., dans* leur niveau de plasticité comportementale. L'ajustement du comportement requiert la perception, le traitement et éventuellement la mise à jour du comportement en fonction des changements, ce qui suggère un rôle clef de la cognition et de la personnalité dans la mise en place d'un comportement plastique. En effet, les différences individuelles de comportement (*i.e.,* la personnalité) seraient un indicateur de la stratégie d'apprentissage des individus : les plus timides seraient lents à apprendre, sensibles aux variations subtiles dans les stimuli externes et capables de modifier rapidement leur comportement alors que les plus hardis seraient rapides à apprendre, superficiels dans leur exploration et routiniers dans l'expression de leurs comportements. Ainsi, certains individus seraient généralement plus sensibles aux conditions que les autres et devraient exprimer plus de plasticité comportementale quel que soit l'indice de la plasticité (*i.e.,* type de mesure) utilisé. Cependant, si initialement les études ont supporté cette hypothèse, les travaux récents démontrent rarement un lien entre personnalité et cognition. De plus, il n'existe pas de preuve au niveau individuel qu'il y aurait effectivement un lien entre apprentissage, un type de plasticité développementale (*i.e.,* changement de comportement en fonction des expériences passées) et un autre type de plasticité, la plasticité contextuelle (*i.e.,* changement de comportement en réponse immédiate aux stimuli externes), ni que cette dernière serait répétable entre les comportements et contextes.

Dans le but de mieux comprendre les mécanismes proximaux de la plasticité comportementale, j'ai déterminé dans le premier chapitre si la relation entre la personnalité et l'apprentissage pouvait expliquer la plasticité contextuelle en réponse à la présence ou l'absence d'une audience présentée sur une vidéo chez le Diamant mandarin (*Taeniopygia guttata*). Les résultats indiquent effectivement que les oiseaux moins néophobes étaient moins plastiques. En revanche, la néophobie n'était pas associée avec l'apprentissage suggérant que les individus plastiques ne sont pas nécessairement plus sensibles que les autres. Dans le second chapitre, j'ai tenté de mettre en évidence l'existence d'un facteur unique expliquant la plasticité contextuelle (*c.-à-d.* modification de la personnalité et des comportements de reproduction en fonction d'un gradient social) et l'apprentissage à renforcements inversés chez le Molly voile (*Poecilia latipinna*). Les individus plastiques n'étaient pas les mêmes dans tous les tests indiquant qu'exprimer de la sensibilité dans un contexte pourrait limiter l'expression de la sensibilité dans un autre contexte. Finalement, dans le troisième chapitre, j'ai démontré chez cette même espèce que l'anxiété, contrairement aux traits mesurés sur l'axe timidité-hardiesse (*c.-à-d.* néophobie et exploration), expliquait les scores d'apprentissage discriminant, spatial et à renforcements inversés lorsque les individus étaient familiarisés aux procédures. Dans ce cas, la timidité influence probablement l'approche des contingences environnementales alors que la réaction au stress (par exemple l'anxiété) influencerait la sensibilité permettant de répondre à ces contingences. Différentes étapes de l'apprentissage sont donc associées avec différents traits de personnalité. Ces résultats aident à comprendre les facteurs nécessaires à l'expression de la plasticité et mettent en évidence l'existence potentielle de pressions de sélection conflictuelles agissant sur les différentes étapes requises pour l'ajustement aux changements environnementaux.

Mots clefs : *Cognition, Apprentissage, Personnalité, Plasticité comportementale, Plasticité générale, Flexibilité, Sensibilité, Différences individuelles, Diamant mandarin, Molly voile*

ABSTRACT

Individuals differ widely among each other in their tendency to modify their behavior in response to environmental changes, (*i.e.,* in their behavioral plasticity). The adjustment of the behavior requires the perception, treatment and possibly updating of behavior as a function of change, which suggests a key role of cognition and personality in the expression of plasticity. Indeed, individual differences in behavior (*i.e.,* personality) would be an indicator of the learning strategy of individuals: shy individuals would be slow to learn, sensitive to subtle variations in external stimuli, and able to change their behavior quickly, while the bold ones would be quick to learn, superficial in their exploration and prone to routine. Thus, some individuals would generally be more responsive to the conditions than others and should express more behavioral plasticity regardless of the proxy used. However, while studies, initially, supported this hypothesis, recent work rarely demonstrates a link between personality and cognition. Moreover, there is no evidence at the individual level that learning, a type of developmental plasticity (*i.e.,* changes in behavior as a function of experiences that occurred in the past) and another type of plasticity, contextual plasticity (*i.e.,* changes in behavior that occurred as an immediate response to external stimuli) would be linked, nor that plasticity would be repeatable across behaviors and contexts.

In order to better understand the proximal mechanisms of behavioral plasticity, I investigated in the first chapter whether the relationship between personality and learning could explain contextual plasticity in response to the presence and absence of an audience displayed on video recordings in Zebra finches (*Taeniopygia guttata*). The results indicate that less neophobic birds were less plastic. In contrast, neophobia was not associated with learning suggesting that plastic individuals are not necessarily more sensitive than others. In the second chapter, I tried to highlight the existence of a single factor explaining contextual plasticity (in personality traits and mating behaviors measured across social gradients) and reversal learning in Sailfin mollies (*Poecilia latipinna*). Plastic individuals were not the same in all tests indicating that expressing sensitivity in one context might limit the expression of sensitivity in another context. Finally, in the third chapter, I demonstrated in this same species that anxiety, contrary to the personality traits from the shyness-boldness axis (*i.e.,* neophobia and exploration), explained individuals' performances in discriminant, spatial and reversal learning tasks when individuals were extensively familiarized with the procedures. Thus, shyness probably influences the time required to contact the environmental contingencies, whereas stress vulnerability (*i.e.,* anxiety) would affect individuals' sensitivity in response to them. Different steps of learning are therefore associated with different personality traits. These results help to understand the factors necessary for the expression of plasticity and highlight the potential existence of conflicting selection pressures acting on the different steps required for an individual to adjust its behavior to environmental conditions.

Keywords: *Cognition, Learning, Personality, Behavioral plasticity, General plasticity, Flexibility, Sensitivity, Individual differences, Zebra finch, Sailfin molly*

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&	Et
±	Plus ou moins
am	Avant midi (*Ante meridiem*)
°C	Degré Celsius
cm	Centimètres
et al.	Et les autres
e.g.,	Par exemple (*Exempli gratia*)
h	Heures
i.e.,	C'est-à-dire (*id est*)
L	Litres
mg	Milligrammes
mm	Millimètres
n	Effectif
pm	Après midi (*Post meridiem*)
SD	Écart-type (*Standard deviation*)
SEM	Erreur standard (*Standard Error of the Mean*)

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À la vie et à ceux que j'aime

Rien ne pourra ternir

L'éclat de ce qui reste à découvrir

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CHAPITRE I

Introduction générale

1) Mise en contexte

La plasticité comportementale (voir tableau I pour les différents types de plasticité), qui correspond à la capacité d'un génotype/d'un individu à produire différents phénotypes, dans ce cas des comportements, en réponse aux conditions (Hazlett 1995; DeWitt *et al*. 1998). C'est un aspect de plus en plus étudié et considéré comme crucial car il permettrait aux organismes de faire face aux changements environnementaux. Afin de s'ajuster, l'individu devra en premier lieu, être capable de percevoir les changements, de traiter l'information acquise et enfin d'éventuellement modifier son comportement (Hazlett 1995; DeWitt *et al*. 1998). Ce dernier point suggère un rôle clef de la personnalité et de la cognition dans la mise en place d'un comportement plastique tel que proposé par plusieurs revues de la littérature (Mathot *et al*. 2012; Dukas 2013; Snell-Rood 2013; Stamps 2016). En effet, la personnalité animale, qui s'exprime sous forme de variations interindividuelles dans les comportements qui sont constantes à travers le temps et les contextes, a été reliée à la cognition, notamment parce qu'elle pourrait expliquer des différences dans des processus importants pour la plasticité comportementale, incluant la sensibilité aux stimuli externes, le traitement et le stockage de l'information provenant de l'environnement ainsi que la prise de décision (Carere et Locurto 2011; Sih et Del Giudice 2012; Griffin *et al*. 2015). Notamment, les individus timides, c'est-à-dire néophobes, peu explorateurs, peu actifs et peu agressifs, démontrent souvent de meilleures performances en apprentissage à renforcements inversés (*i.e.,* la capacité à modifier son comportement en réponse à un changement dans les contingences déjà connues) ainsi que plus de plasticité dans leurs traits comportementaux en fonction du contexte ou 'norme de réaction comportementale' (Figure 1). Il est donc possible que certains individus soient généralement plus sensibles aux changements que les autres.

Au niveau interspécifique, les études suggèrent d'ailleurs une corrélation positive entre les indices de la plasticité. Notamment, il a été démontré que les espèces d'oiseaux, de primates et de carnivores ayant une taille relative du cerveau plus importante font plus d'innovations, c'est-à-dire qu'elles sont capables de trouver des solutions à des problèmes nouveaux (Reader et Laland 2002; Overington *et al*. 2009; Benson-Amram *et al*. 2016). Également, ces études suggèrent un lien positif entre la taille relative du cerveau, l'apprentissage et d'autres indices de la plasticité incluant l'apprentissage à renforcements inversés et la capacité d'envahir une plus grande diversité d'habitats (Timmermans *et al*. 2000; Sol et Lefebvre 2000; Sol *et al*. 2002, 2005a,b; Lefebvre *et al*. 2004).

Tableau I. Types de plasticité comportementale. Les définitions présentées ici sont tirées de Stamps *et al.* (2016), Stamps et Groothuis (2010) et Snell-Rood (2013).

Type de plasticité	Définition	Mesures
Plasticité contextuelle ou d'activation	**Changement de comportement immédiat en réponse aux stimuli extérieur**s déterminé par les mécanismes neuraux et hormonaux déjà présents chez un individu	• **Variations d'un trait comportemental entre deux ou plusieurs conditions*** Ex: norme de réaction.
Plasticité développementale	**Changement de comportement en fonction de l'expérience passée.** L'état neural et hormonal de l'individu a été modifié par l'expérience permettant la modification/production d'une nouvelle réponse comportementale	• **Effet de l'ontogénie** (période sensible, expériences lors du développement) • **Effet du stade/cycle de vie** (Expériences vécues avant une saison, stade de vie...etc.) • **Apprentissage.** Ex: apprentissage à renforcements inversés (flexibilité)**, habituation***…etc.
Plasticité endogène	**Changement de comportement dû aux variations spontanées de l'état interne de l'individu** (rythmes circadiens, circannuels…*etc.*)	• **Variations comportementales à court terme non expliquées par les conditions extérieures** Ex: variations intra-individuelles
Autres types de plasticité	Il existe d'autres termes et types de plasticité, notamment la plasticité temporelle (tous changements liés au temps et à l'âge) ou la plasticité exogène (tous changements liés aux stimuli extérieurs) qui sont plus générales et peuvent inclure deux ou trois des plasticités décrites ci-dessus.	

* Les variations comportementales peuvent être mesurées en tant que l'amplitude du changement (si on considère que chaque individu pourrait choisir de s'ajuster dans un sens comme dans l'autre, par exemple, dépendamment de son état) ou inclure aussi la direction du changement (si on s'intéresse aux conséquences liées à la direction du changement ou si on considère que les individus ont avantage à changer dans une seule direction seulement).

** Capacité à modifier son comportement en réponse à un changement dans les contingences déjà apprises, aussi appelée flexibilité (voir section 3b)

*** Diminution de la réponse à un ou des stimuli après une exposition répétée ou prolongée à ce ou ces-derniers

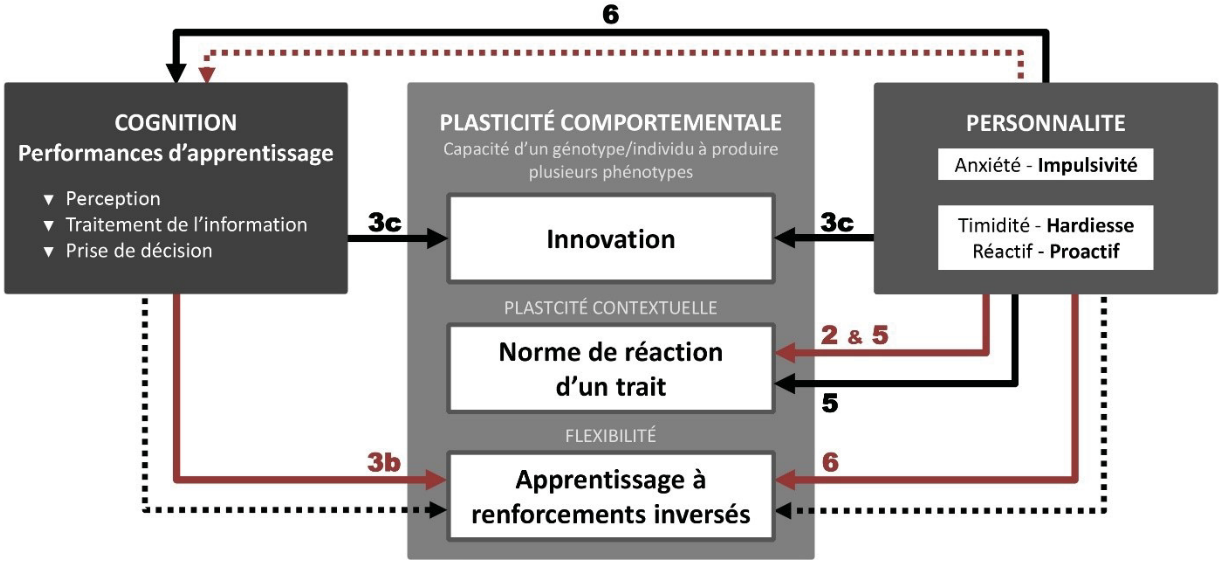

Figure 1. Liens entre la personnalité, la cognition et les indices de la plasticité comportementale au niveau interindividuel. Les flèches indiquent si les relations entre les mesures ont été trouvées dans le sens positif (noir), négatif (rouge) et si la majorité des études vont dans ce sens (flèche pleine) ou si une minorité d'études indique ce lien (flèche pointillée). Pour l'interprétation des liens, la boite représentant la personnalité est à considérer comme indiquant une personnalité hardie/proactive (en particulier, plus explorateur, actif, hardi et moins néophobe). Les numéros et lettres indiquent la section dans laquelle la relation est discutée.

Cependant, au niveau interindividuel, les résultats reportés dans la littérature indiquent que les indices de la plasticité comportementale ne sont pas toujours corrélés positivement entre eux (Figure 1). En effet, la timidité ne serait pas toujours liée à une plus grande plasticité, notamment les timides altèrent parfois moins leur comportement en fonction des contextes. De plus, les relations entre apprentissage, apprentissage à renforcements inversés et personnalité ne sont pas toujours mises en évidence dans le sens attendu et peuvent même être absentes dans certain cas. Finalement, une étude a démontré au niveau des génotypes chez la drosophile (individus descendants de lignées consanguines et d'une même lignée de type sauvage) l'existence d'une corrélation positive entre la norme de réaction dans le choix du site de nymphose et les performances d'apprentissage (Saltz *et al*. 2017). Cela indique potentiellement un lien entre ces deux traits dû à un déséquilibre de liaisons entre les allèles ou de la pléiotropie. Néanmoins, il n'est pas possible d'exclure la possibilité d'un compromis entre ces deux traits, par exemple si les besoins énergétiques en nature empêchent les individus d'investir autant dans l'apprentissage et la plasticité contextuelle (*i.e.,* norme de réaction). Dans ce cas, la corrélation positive pourrait aussi apparaître car seuls les individus (ou 'génotypes') de qualité seraient capables d'investir autant dans les deux traits (Saltz *et al.* 2017). L'existence d'un lien positif ou négatif entre l'apprentissage et la plasticité contextuelle reste donc à démontrer.

Malgré l'existence d'un certain consensus au sujet des mécanismes proximaux impliqués dans la plasticité comportementale, les résultats très contrastés requièrent donc une étude conjointe des différentes mesures de la plasticité (*e.g.,* plasticité contextuelle mesurée sur plusieurs traits) et des traits comportementaux lui étant associés. En effet, la question de la répétabilité de la plasticité et de ses liens avec la personnalité et la cognition au niveau de l'individu pourrait avoir des implications importantes au niveau évolutif, incluant la stabilité et la persistance des populations. Notamment, l'existence de plusieurs types d'individus pouvant réagir différemment permettrait aux populations de répondre de manière moins extrême aux changements environnementaux et augmenterait, par conséquent, les chances qu'un type d'individus soit capable de s'y adapter. Ainsi, étant donné l'intérêt porté aux conséquences évolutives des différences interindividuelles de comportement, j'espère mieux comprendre le rôle que pourrait jouer la personnalité et la cognition sur les différences de plasticité comportementale.

2) Différences interindividuelles de personnalité

Les animaux, en allant des arthropodes aux mammifères, présentent des traits de personnalité consistants à travers le temps et les contextes et pouvant être corrélés entre eux, formant alors « un syndrome comportemental » (Sih *et al*. 2004). Ainsi, lorsque confrontés à des environnements identiques, les individus exprimeront différemment certains traits tels que la néophobie, l'exploration, l'activité, la sociabilité ou encore l'agressivité (Sih *et al*. 2004; Sih et Bell 2008). Plus précisément, la personnalité animale s'inscrit dans un continuum timidité-hardiesse. Par exemple, les animaux plus hardis prendront plus de risques, seront plus actifs, auront moins peur de la nouveauté ou d'explorer leur environnement (Sih *et al*. 2004; Frost *et al*. 2007; Sih et Bell 2008). D'autres études classent les individus en fonction de leur variation dans la réactivité de l'axe hypothalamo-hypophyso-surrénalien qui contrôle la réaction au stress ainsi que les modifications physiologiques et comportementales lui étant associées (Koolhaas *et al*. 1999). Plusieurs études indiquent que les individus proactifs adoptent une stratégie active et manipulent leur environnement alors que les réactifs réagissent de manière passive mais sont davantage influencés par les stimuli extérieurs (Benus *et al*. 1991; Koolhaas *et al*. 1999; Groothuis et Carere 2005; Carere *et al*. 2005). En effet, les animaux proactifs ont tendance à être plus actifs dans les tâches comme la construction d'un nid (Sluyter *et al*. 1995) mais ils suivent plus facilement des routines contrairement aux réactifs qui s'ajustent aux changements, tel que démontré par plusieurs études (Benus *et al*. 1988; Benus 1999; David *et al*. 2004; Ellenberg *et al*. 2009; Natarajan *et al*. 2009). Par exemple, des études ont montré que les poissons peu explorateurs réagissent plus rapidement en cas d'attaque d'un prédateur (Jones et Godin 2010) ou que les souris mâles peu agressives sont capables d'ajuster leur niveau d'agressivité en fonction du sexe de l'intru rencontré sur leur territoire (Benus *et al*. 1990). D'ailleurs, les mâles agressifs (proactifs) sont plus compétitifs dans les colonies stables tandis que les mâles moins agressifs (réactifs) sont avantagés dans des conditions variables et moins prévisibles (Koolhaas *et al*. 1999). De même, plusieurs études sur les oiseaux montrent que le succès des deux styles de personnalité dépend de la stabilité de l'environnement social et de la disponibilité des ressources (Koolhaas *et al*. 1999). Les décisions comme le choix de l'habitat (Dubois et Giraldeau 2014) ou la manière d'acquérir de l'expérience (Frost *et al*. 2007) sont donc prises en fonction de la personnalité de l'individu. De plus, il a été démontré que ces variations de personnalité sont non seulement héritables (*e.g.,* Dingemanse *et al.* 2012a) ou transmissibles via l'épigénétique (Weaver *et al*. 2004;

Tobler et Sandell 2007), mais affectent aussi la valeur adaptative des individus en fonction des conditions environnementales (Dingemanse et Réale 2005; Réale *et al*. 2007; Carere et Locurto 2011). Notamment, une corrélation entre le niveau d'agressivité et de hardiesse a été générée dans une population d'épinoches à trois épines (*Gasterosteus aculeatus*) suite à l'exposition à la prédation (Bell et Sih 2007). Selon les auteurs de cette étude, le changement s'est opéré à cause de la prédation elle-même mais aussi grâce à la plasticité comportementale. En conséquence, la plasticité semble avantageuse si ceux qui l'expriment peuvent augmenter leurs chances de survie en ajustant leurs comportements aux variations telles que la prédation, l'environnement social ou les conditions abiotiques (*e.g.,* température…etc.). Étant donné que les traits de personnalité présentent un degré de plasticité variable selon les traits étudiés et les individus (Dingemanse *et al*. 2012b; Kluen et Brommer 2013), il reste à déterminer quels facteurs entrainent ces différences et peuvent la limiter.

3) Plasticité comportementale

a) Plasticité contextuelle et développementale

La plasticité contextuelle (Stamps 2016) aussi appelée 'plasticité d'activation' (Snell-Rood 2013) se définit comme la capacité d'un individu à faire varier son phénotype en réponse immédiate à un changement dans les stimuli externes. La plasticité contextuelle consisterait en une activation différentielle des réseaux neuronaux sous-jacents déjà présents ; notamment, la décision de se cacher ou de continuer à explorer s'il y a des indices de la présence d'un prédateur en serait un exemple (Snell-Rood 2013). La plasticité contextuelle est donc mesurée via la norme de réaction d'un trait comportemental, c'est-à-dire la variation d'un trait le long d'un gradient environnemental. La plasticité développementale est en revanche un indicateur de l'influence de l'expérience acquise dans les environnements passés sur l'individu, par exemple le développement en tant que timides ou hardis selon l'environnement dans lequel il a vécu. La plasticité développementale entrainerait la formation de nouveau réseaux de neurones permettant de mieux répondre aux défis auxquels l'individu a eu à faire face et pourrait donc être évalué via les performances d'apprentissage (Snell-Rood 2013). Je vais m'intéresser surtout à l'apprentissage discriminant (*e.g.,* Griffin *et al*. 2015) qui consiste en une relation prédictive entre un stimulus et, dans mon cas, une récompense alimentaire alors que les autres alternatives (*i.e.,* stimuli ou stimulus de même type/dimension) ne sont pas récompensées. Ce type d'apprentissage pourrait être aussi considéré comme de l'apprentissage associatif qui requiert l'association entre un stimulus et une récompense, sans nécessairement présenter d'autres stimuli. En effet, il est difficile de déterminer si l'animal est conditionné à répondre uniquement au stimulus récompensé indépendamment des autres ou s'il discrimine entre tous les stimuli.

b) Flexibilité : apprentissage à renforcements inversés

L'apprentissage à renforcements inversés, aussi appelé flexibilité, est très utilisé comme un indice de la plasticité comportementale dans les études en neurologie (Fellows et Farah 2003; Izquierdo *et al*. 2007; Haluk et Floresco 2009; Izquierdo et Jentsch 2012) et en écologie comportementale (*e.g.,* Guillette *et al*., 2010; Griffin *et al*., 2013; Lucon-Xiccato et Bisazza, 2014; Pintor *et al*., 2014). La flexibilité dans ce cas correspond à la capacité d'un individu à modifier une réponse précédemment apprise. Plus précisément, l'association stimulus-récompense est changée au profit d'un autre stimulus de même type/dimension initialement non récompensé, ce qui requiert donc l'inhibition de la réponse comportementale qui a été acquise initialement. De plus, la relation entre apprentissage et apprentissage inversé, bien qu'elle soit en de rares occasions positive (Raine et Chittka 2012) ou absente (Brust *et al*. 2013; Chow *et al*. 2015; Madden *et al*. 2018), est le plus souvent négative (Guillette *et al*. 2010; Griffin *et al*. 2013; Bebus *et al*. 2016), suggérant un compromis entre la capacité à acquérir rapidement et/ou retenir l'information plus longtemps et la capacité à remarquer les changements et/ou mettre à jour l'information (*e.g.,* Sih et Del Giudice 2012).

Au niveau du cerveau, l'apprentissage associatif et inversé serait traité au moins en partie par des aires similaires, *e.g.,* le *pallium* latéral du télencéphale, analogue à l'hippocampe, chez les poisson (Broglio *et al*. 2010) ou le *Wulst*, analogue au cortex visuel primaire, chez les oiseaux (Watanabe 2006). En revanche, il a été aussi montré chez les oiseaux et les mammifères que l’apprentissage inversé et l’apprentissage associatif étaient influencés par différentes aires cérébrales (Hartmann et Güntürkün 1998; Lissek *et al*. 2002; Bouton 2004; Dalley *et al*. 2004; Stollhoff 2005; Eisenhardt et Menzel 2007; Kehagia *et al*. 2010; Rygula *et al*. 2010). Notamment chez les oiseaux, des lésions au niveau du *nidopallium*, analogue au cortex préfrontal (Hartmann et Güntürkün 1998), empêcheraient l’inversion de contingences apprises précédemment, mais n’interfèreraient pas avec l’acquisition de nouvelles informations. Également, Bond *et al* (2007) ont mesuré l’apprentissage inversé chez trois espèces de corvidés aux capacités cognitives différentes et proposent l’idée selon laquelle l’apprentissage à renforcements inversés serait traité dans un *module* à part. En effet, les performances des oiseaux dans la tâche initiale d’apprentissage ne reflétaient pas les résultats obtenus lors de l’apprentissage à renforcements inversés. Une étude montre aussi chez deux espèces de lézards appartenant au genre *Acanthodactylus,* que l’espèce cherchant sa nourriture activement dans l’habitat réussissait mieux que l’espèce sédentaire (*i.e.,* embuscade des proies), une tâche d’apprentissage inversé non-spatiale; alors que les deux espèces ne différaient pas dans leur performance dans une tâche d’apprentissage spatial (Day *et al*. 1999). L’apprentissage inversé pourrait donc être une mesure de flexibilité qui refléterait la capacité des individus à occuper des niches écologiques plus instables (Shettleworth 2001; Day *et al*. 1999; Bond *et al*. 2007).

c) Innovations

L’innovation inclut des comportements allant de la découverte et la consommation d’une nouvelle source de nourriture à l'utilisation d'outils (Overington *et al.* 2009). Elle démontre donc l’aptitude d’un individu à produire de nouveaux comportements afin de résoudre des problèmes et serait donc indicatrice d’une grande richesse du répertoire comportemental. Pour cette raison, dans les études au niveau interspécifique, le nombre d’innovations par espèce démontrerait des capacités cognitives élevées et serait un indicateur indirect du potentiel d’une espèce à exprimer de la plasticité comportementale (Reader 2003, 2007; Reader et MacDonald 2003; Lefebvre 2011). Comme les espèces possédant des structures neurales plus développées peuvent traiter plus d’informations à propos de leur environnement social et physique (Sol *et al*. 2007), elles seraient capables d'innover et d'apprendre plus vite (Wyles *et al*. 1983; Wilson *et al*. 1985; Fitzpatrick 1988). En effet, le taux d'innovation est prédit par la taille relative du cerveau chez les primates, les oiseaux et les carnivores (Reader et Laland 2002; Overington *et al*. 2009; Benson-Amram *et al*. 2016). Par ailleurs, d'autres études montrent que les espèces ou individus plus innovants sont meilleurs dans des tâches cognitives, incluant l'apprentissage individuel (Timmermans *et al*. 2000; Boogert *et al*. 2008a; Overington *et al*. 2011; Griffin *et al*. 2013), l'apprentissage à renforcements inversés (Lefebvre *et al*. 2004) et l'apprentissage social (Reader et Laland 2002; Bouchard *et al*. 2007). Néanmoins, la néophobie, en particulier, limite la capacité à innover tel que montré au niveau interspécifique (Greenberg 1990; Seferta *et al*. 2001; Webster et Lefebvre 2001) et au niveau interindividuel (Webster et Lefebvre 2001; Bouchard *et al*. 2007; Boogert *et al*. 2008b; Biondi *et al*. 2010; Overington *et al*. 2011; Benson-Amram *et al*. 2013). Les plus néophobes (plus plastiques dans d'autres contextes) pourraient être plus lents à résoudre la tâche, probablement parce qu'ils expriment moins de diversité dans leur exploration et surtout mettent plus de temps à rentrer en contact avec les dispositifs de résolution de problème.

4) Coûts et bénéfices associés aux capacités cognitives

Les innovations permettent d'exploiter des ressources alternatives, améliorant ainsi les chances de survie des individus. Chez les oiseaux, de nombreuses innovations alimentaires ont pu être observées en différents lieux et contextes. L'une des premières innovations à avoir été documentée est celle des mésanges charbonnières (*Parus major*), qui ont appris à ouvrir les bouteilles de lait pour consommer la crème (Fisher et Hinde 1949). Plus récemment, des Sporophiles rougegorge (*Loxigilla noctis*) ont été observés alors qu'ils ouvraient des paquets de sucre (Reader *et al*. 2002). Les espèces innovantes sont favorisées et subissent une mortalité réduite lors d'un changement rapide des conditions environnementales comme lors d'une introduction dans un nouvel habitat (Sol et Lefebvre 2000; Sol *et al*. 2002; Sol *et al*. 2005). Similairement, une étude chez les poissons a montré que les individus ayant appris à éviter les stimuli indiquant la présence de prédateurs survivaient mieux à la réintroduction, ce qui suggère un lien possible entre apprentissage rapide et survie (Lonnstedt *et al*. 2012). Malgré les avantages que semblent procurer des capacités cognitives élevées, le développement et le maintien du tissu neural sont très couteux pour l'organisme (Laughlin *et al*. 1998). Notamment, plusieurs études ont démontré que les individus plus performants en apprentissage payaient des coûts importants comme une réduction de la compétitivité chez les larves de drosophile (*Drosophila melanogaster*) et la mésange charbonnière (Mery et Kawecki 2003; Cole et Quinn 2012), ou encore une réduction du succès reproducteur chez une espèce de papillon (*Pieris rapae*) (Snell-Rood *et al*. 2011). Similairement, chez les guppies (*Poecilia reticulata*), une sélection pour une taille de cerveau plus élevée entrainait aussi un compromis avec la reproduction (Kotrschal *et al*. 2013). De plus, du temps et de l'énergie sont requis pour l'échantillonnage de l'environnement, le traitement et le stockage de l'information qui sont des étapes nécessaires à l'apprentissage (Mery et Kawecki 2004; Mery 2005; Snell-Rood 2013).

5) Comment expliquer les différences de plasticité contextuelle ?

Les organismes démontrant une plus grande plasticité contextuelle (*e.g.,* une norme de réaction plus importante pour un trait comportemental) devraient modifier leur comportement d'une manière qui leur est avantageuse (Sih *et al*. 2004; Briffa *et al*. 2008; Snell-Rood 2013). Ainsi, certaines études montrent que la capacité à s'ajuster aux conditions permettrait aux individus d'une population de mieux survivre lorsque l'environnement est perturbé (Ghalambor 2002; Eggers *et al*. 2006; Fontaine et Martin 2006; Peluc *et al*. 2008; Charmantier *et al*. 2008). Par exemple, chez le Mésangeai imitateur (*Perisoreus infaustus*), les parents réduiront la taille des nichées et placeront les nids dans des lieux plus sûrs si la pression de prédation perçue est plus élevée (Eggers *et al*. 2006). Néanmoins, malgré les avantages de la plasticité, des différences interindividuelles dans la norme de réaction mesurée sur divers comportements sont fréquemment trouvés dans la plupart des populations (*e.g.,* Westneat *et al*. 2011; Morand-Ferron *et al*. 2011; Mathot *et al*. 2011;

Dingemanse *et al*. 2012b). Ces différences pourraient être dues aux coûts requis pour produire un comportement plastique (DeWitt *et al*. 1998). En lien avec cette idée, une étude théorique a proposé que, dans un contexte de fréquence dépendance négative (*i.e.,* les bénéfices d'une stratégie, fixe ou plastique, diminuent avec la fréquence des individus qui l'utilisent), les individus pourraient différer en termes de plasticité si ceux ayant été plastiques payent des coûts moins importants (ou obtiennent des bénéfices plus élevés) à être plastique à nouveau (Wolf *et al*. 2008). Dans ce cas, on s'attendrait à ce que l'expérience et l'apprentissage favorisent la plasticité comportementale (Morand-Ferron *et al*. 2011). En effet, l'apprentissage et la plasticité pourraient partager les mêmes mécanismes (*e.g.,* perception, mémoire…etc.) (Hazlett 1995). Lorsqu'un individu fait face à des situations différentes, la décision d'ajuster son comportement requiert d'ailleurs l'évaluation des gains associés avec chaque alternative (Harley 1981; Milinski 1984; Houston et Sumida 1987; Stephens et Clements 1998). Ainsi, les individus plastiques seraient capables d'identifier les situations récurrentes, peu dangereuses, de réduire leur stress (Shettleworth 2001; Martin et Réale 2008), de reconnaitre les prédateurs pour mieux les éviter (Griffin 2004) ou encore de maximiser les gains associés avec les différentes stratégies de recherche de nourriture (Dubois *et al*. 2010). Par ailleurs, si la capacité à s'ajuster est sujette aux mêmes coûts (*e.g.,* coûts cognitifs), cela implique que la plasticité devrait être générale. En effet, l'hypothèse a été émise selon laquelle les mesures de plasticité estimées à travers différents contextes et sur différents traits devraient être corrélées positivement (*e.g.,* Dingemanse et Wolf 2013).

Néanmoins, les études en laboratoires et sur le terrain ne permettent pas de démontrer que la plasticité est répétable ou que des traits cognitifs (ainsi que les traits de personnalité leur étant corrélés, voir section 6 pour plus de détails au sujet du lien entre personnalité et cognition) sont des prédicteurs de la plasticité contextuelle. Tout d'abord, les individus moins néophobes, plus hardis et explorateurs sont usuellement les plus innovants (*e.g.,* section 3c), les plus rapides à apprendre (*e.g.,* section 6) et parmi les premiers à s'habituer aux nouvelles conditions (Light *et al*. 2011; Rodríguez-Prieto *et al*. 2011; Dingemanse *et al*. 2012b). Par exemple, chez la truite arc-en-ciel et le Molly de l'Atlantique, les poissons avec une personnalité plus hardie/proactive sont plus responsifs au contexte social (Frost *et al*. 2007; Bierbach *et al*. 2015). Cependant, ce genre de personnalité correspond aussi au type 'proactif' qui est reconnu comme établissant plus facilement des routines et donc étant peu sensible aux changements dans les stimuli externes (*e.g.,* section 2). Ces résultats en ce qui concerne la relation entre la plasticité exprimée et les traits comportementaux pourraient être expliqués, entre autres, par des différences dans les bénéfices associés au changement de comportement (*e.g.,* Frost *et al*. 2007) et/ou l'état de l'individu (*i.e.,* réserves énergétiques, condition, sexe, âge…etc.) (*e.g.,* Betini et Norris 2012; Quinn *et al*. 2012 mais voir Mathot *et al.* 2012 pour une revue des études liant traits comportementaux et plasticité). Surtout, cela indique que la plasticité pourrait dépendre du contexte (et du trait), ce qui pose donc la question, à savoir, si la sensibilité aux stimuli devrait être corrélée entre les contextes, et si c'est le cas, positivement (*i.e.,* liée au type de personnalité) ou négativement (*i.e.,* l'attention disponible est limitée et dépendra du contexte) (Sih et Del Giudice 2012). Il est donc difficile de déterminer si les mêmes facteurs pourraient prédire les différences de plasticité. Je tenterai donc d'examiner le lien entre apprentissage et plasticité dans le chapitre II et la répétabilité de cette dernière dans le chapitre III.

6) Quel est le lien entre la personnalité et la cognition ?

Un grand nombre d'études ont démontré chez les arthropodes, les poissons, les oiseaux et les mammifères que les individus à la personnalité proactive ont de meilleures performances en apprentissage spatial, discriminant ou associatif (17 études, voir tableau I. Chapitre IV) tandis que ceux à la personnalité réactive/timide sont meilleurs en apprentissage à renforcements inversés (9 études, voir tableau I. Chapitre IV). Ces différences de performances pourraient être dues à un style cognitif où certains individus (proactifs/hardis) seraient des explorateurs rapides mais superficiels dans l'information qu'ils recueillent, tandis que d'autres (réactifs/timides) seraient des explorateurs plus lents, plus attentifs et plus précis. Ce compromis entre vitesse et précision pourrait expliquer les différences de performances suivant si l'individu décide ou pas d'investir du temps dans une tâche cognitive

(Chittka *et al*. 2009; *e.g.,* Ducatez *et al*. 2015) et pourrait découler d'un compromis entre gains potentiels et prise de risques (Sih et Del Giudice 2012). Les animaux hardis seraient prêts à payer les coûts liés à une exploration rapide, leur permettant d'apprendre rapidement et ainsi d'accumuler plus de gains (et donc augmenter leur valeur adaptative) dans un court lapse de temps (Biro et Stamps 2008; Réale *et al*. 2010). Au contraire, les individus réactifs accumuleraient moins de récompenses (du moins à court terme) mais seraient plus performants lorsqu'il s'agit de mettre à jour l'information et d'éviter des dangers, comme par exemple des chocs électriques (Budaev et Zhuikov 1998) ou des proies aposématiques qui sont non-comestibles (Exnerová *et al*. 2010).

Cependant, la personnalité n'explique pas toujours l'apprentissage (23 études) ou l'apprentissage à renforcements inversés (8 études), voire la relation peut être dans le sens opposé à ce qui est attendu (5 études pour l'apprentissage, 2 études l'apprentissage inversé voir tableau I. Chapitre IV). Ces contradictions pourraient être dues (i) à la complexité de la tâche, *i.e.,* les individus ne diffèrent pas suffisamment s'ils sont tous capables d'apprendre aussi vite dans les tâches simples (Amy *et al*. 2012; DePasquale *et al*. 2014; Mesquita *et al*. 2015; Mamuneas *et al*. 2015) et leurs performances pourraient être plus influencées par d'autres facteurs comme leur motivation ou encore (ii) à la procédure et/ou la mesure utilisée lors des tests cognitifs et de personnalité. En effet, les individus timides prennent du temps à entrer en contact avec les stimuli et pourraient être désavantagés lors des procédures impliquant peu de familiarisation au dispositif et aux stimuli (*e.g.,* Sommer-Trembo et Plath 2018). Également, la plupart des études en écologie comportementale utilisent les traits de personnalité variant sur l'axe proactivité-réactivité (majoritairement mesuré à l'aide de l'agressivité, la néophobie et l'exploration) ou hardiesse-timidité (incluant les mesures de néophobie, exploration et réaction face aux prédateurs) alors que l'impulsivité d'action et l'anxiété parfois démontrées comme étant sur le même axe (Steimer *et al*. 1997) sont susceptibles d'avoir un impact important sur la capacité à s'ajuster et l'apprentissage. Notamment, l'impulsivité d'action, c'est-à-dire un manque d'inhibition (Steimer *et al*. 1997) peut résulter en des performances moindres lors de l'apprentissage inversé (Izquierdo et Jentsch 2012). Au contraire, les individus anxieux sont capables d'inhiber leur comportement rapidement mais auraient plus de difficulté à former des associations probablement parce qu'ils concentreraient leur attention sur la recherche de stimuli indiquant des menaces. Ils seraient donc moins en mesure d'utiliser d'autres stimuli environnementaux (Eysenck *et al*. 2007; Grupe et Nitschke 2013). En effet, l'anxiété, mesurée en tant que la propension à éviter les espaces ouverts (*i.e.,* thigmotaxisme), a été reliée non seulement à des performances d'apprentissage réduites (Matzel *et al*. 2003, 2006; Herrero *et al*. 2006; Light *et al*. 2011) mais aussi à des différences dans les systèmes neuraux contrôlant la réaction au stress chez les rongeurs (Herrero *et al*. 2006; Rozeboom *et al*. 2007). Étant donné que les individus peuvent différer en termes d'anxiété sans nécessairement différer dans leur niveau d'exploration (Ohl *et al*. 2003) et que l'axe impulsivité-anxiété est associé à des différences fortes dans la sensibilité à certains stimuli, cela en fait un aspect de la personnalité intéressant à investiguer dans le cadre des styles cognitifs. L'influence respective de l'anxiété et de l'exploration/néophobie sur les performances et les stratégies d'apprentissage (*e.g.,* compromis entre vitesse et précision) contribuerait à expliquer les résultats contrastés dans la littérature (revus dans le tableau I du chapitre IV) et sera examinée dans le chapitre IV afin de mieux comprendre les facteurs associés à la plasticité comportementale.

7) Plasticité potentielle et réalisée

Lorsque l'on étudie la plasticité, il est important de distinguer entre la plasticité potentielle et réalisée (Stamps et Krishnan 2014; Stamps 2016). En effet, la plasticité potentielle correspond à la capacité d'un génotype d'exprimer de la plasticité comportementale alors que le changement de comportement qui est observé représente la plasticité réalisée. Cette différence peut expliquer les résultats contradictoires observés dans la littérature dans la mesure où les individus n'exprimeront pas toujours de la plasticité, en particulier si leur comportement initial continue à être suffisamment optimal dans les nouvelles conditions (Ydenberg et Prins 2012; Stamps et Krishnan 2014). Stamps et Krishnan (2014) montrent que les trajectoires développementales des individus mènent à des degrés de plasticité différents selon l'ordre d'exposition aux stimuli indiquant à quel point l'environnement est dangereux. Plus précisément, les individus plus hardis devraient exprimer moins de plasticité lorsque le danger diminue étant donné qu'ils ont des valeurs élevées de hardiesse et donc peu de marge pour augmenter. À l'inverse, les individus plus timides pourront donc apparaître comme étant moins plastiques lorsque le danger perçu augmente. Cet effet est susceptible d'influencer les mesures à court terme, ne serait-ce qu'en raison des limites imposées par les valeurs maximales pouvant prendre le trait (*e.g.,* Mathot *et al*. 2011). Notamment, cela pourrait créer des corrélations positives entre les mesures de plasticité mesurée sur le même gradient, d'où l'intérêt d'examiner l'amplitude et le sens des différences de comportement inter-contextes. J'investiguerai donc dans le chapitre II l'influence de l'apprentissage et de la personnalité sur la direction et l'amplitude de la plasticité.

8) Objectifs & hypothèses

Beaucoup de travaux tentent ainsi de déterminer quels traits comportementaux seraient de bons prédicteurs tant de la personnalité que de l'apprentissage. Néanmoins peu d'entre eux s'intéressent aux liens entre les différents indices de la plasticité eux-mêmes, comme l'apprentissage à renforcements inversés et la norme de réaction. Le premier objectif de ma thèse serait donc de déterminer si la plasticité comportementale, incluant des mesures de plasticité contextuelle sur plusieurs traits et développementale (*i.e.,* apprentissage à renforcements inversés), est répétable et donc si les différents indices de la plasticité utilisés sont corrélés positivement entre eux. Dans un second temps, je chercherai à savoir si la plasticité contextuelle mesurée sur des traits de personnalité est expliquée par des facteurs comme les performances d'apprentissage et la personnalité des individus. Finalement, je tenterai de déterminer si les individus diffèrent dans leurs performances et stratégies d'apprentissage (ou style cognitif, *i.e.,* la manière dont ils acquièrent, traitent, stockent et utilisent l'information), et si cela peut être expliquer par des différences dans leur sensibilité aux stimuli externes (*i.e.,* types de personnalité).

Plus précisément, l'objectif du premier chapitre (Chapitre II) est de vérifier le lien entre la plasticité contextuelle en fonction du contexte social (absence ou présence de congénères), l'apprentissage (incluant une tâche d'apprentissage discriminant avec deux niveaux de difficulté et une tâche d'apprentissage inversé) et la néophobie chez des Diamants mandarins (*Taeniopygia guttata*), un oiseau hautement grégaire. Je m'attends à ce qu'une plus grande plasticité contextuelle soit reliée à une personnalité plus néophobe, étant donné que les individus néophobes, réactifs, devraient être plus sensibles aux changements et/ou auraient avantage à approcher la nourriture près du nouvel objet plus rapidement lorsque l'environnement est perçu comme plus sûr. De plus, la plasticité contextuelle consistant en un ajustement quasi immédiat, devrait requérir des capacités cognitives (Snell-Rood 2013). On s'attendrait donc à ce que les variations interindividuelles de plasticité contextuelle puissent s'expliquer principalement par les vitesses d'apprentissage, en particulier lors de l'apprentissage à renforcements inversés.

L'objectif du deuxième chapitre (Chapitre III) est de vérifier la répétabilité de la plasticité contextuelle chez le Molly voile (*Poecilia latipinna*). Ce poisson se caractérise par l'utilisation des tactiques de reproduction alternatives ayant une base génétique (Travis et Woodward 1989; Fraser *et al*. 2014). Les mâles peuvent être *furtifs, i.e.,* favorisant les tentatives d'insémination directes plutôt que les autres comportements sexuels, ou *bourgeois, i.e.,* dominants face aux autres mâles, favorisant les parades et la garde des femelles. Notamment, ces tactiques peuvent être plastiques et leur utilisation modulée par le contexte social (*e.g.,* la taille des compétiteurs) (Travis et Woodward 1989; Fraser *et al*. 2014). Cela donne donc l'opportunité d'examiner si plusieurs mesures de la plasticité estimées sur différents traits de personnalité selon un gradient social seraient corrélées entre elles et avec la plasticité dans la tactique de reproduction. Si les mêmes mécanismes sont à la base des différences de sensibilité aux stimuli externes, quel que soit le contexte, on pourrait s'attendre à une corrélation positive entre toutes les mesures de plasticité comportementale. En revanche, il est possible que la capacité à répondre à un changement soit sujette à des compromis, en particulier si on considère les limites de l'attention que l'individu peut allouer à chaque aspect de l'environnement (Sih et Del Giudice 2012).

Le troisième chapitre (Chapitre IV) a donc pour but d'examiner si les différences d'exploration, néophobie et anxiété ainsi que les stratégies d'apprentissage (incluant le temps investi lorsqu'ils prennent une décision) permettent d'expliquer les performances dans une tâche d'apprentissage spatial, discriminant et à renforcements inversés chez le Molly voile. Notamment, on s'attend à ce que l'anxiété contribue fortement à expliquer les différences dans les performances, tandis que l'exploration et la néophobie devraient avoir un effet moindre lorsque les individus sont entrainés à la procédure, familiarisés au dispositif et aux stimuli. De plus, on s'attend à ce que le compromis entre vitesse et précision soit contextuel, c'est-à-dire qu'il varie selon la difficulté de la tâche (*e.g.,* Dyer et Chittka 2004) et/ou qu'il soit spécifique à une personnalité (*e.g.,* le compromis est susceptible d'être présent seulement chez les individus particulièrement désavantagés dans une situation, par exemple, les plus timides dans un environnement non familier). En effet, si les individus anxieux sont moins sensibles, investir du temps lors de l'apprentissage pourrait leur permettre de remarquer et d'associer le stimulus visuel à la récompense.

CHAPITRE II

Does personality affect the ability of individuals to track and respond to changing conditions?

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ABSTRACT

One possibility for why individual differences in behavioral plasticity are frequently associated with differences in personality might be that variation in personality is functionally related to variation in cognition. Evidence supporting a link between personality and cognition, however, is still limited and contradictory. In this study, we then conducted a laboratory experiment with zebra finches (*Taeniopygia guttata*) aimed at examining the role of cognition in shaping individual differences in contextual plasticity (*i.e.*, plasticity in behavior between contexts). Specifically, we measured neophobia by quantifying the latency of the birds to eat near a novel object in two different environments across a social gradient and assessed their learning performance on two discriminant tasks and a reversal task. In agreement with our expectation, we found that less neophobic individuals were less plastic in their responses compared to more neophobic ones. Less neophobic individuals were also faster to reach the learning criterion but only in the less difficult discriminant task they performed first. On the contrary, although we found evidence for individual consistency in learning performances, differences among individuals in the number of trials needed to pass the task in both the more difficult discriminant and reversal tasks were not associated with individual differences in neophobia. Thus, our findings indicate that individual differences in contextual plasticity do not necessarily result from some individuals being more sensitive to environmental changes. Instead, we suggest that differences among individuals in their level of plasticity might result from differences in the number of suitable habitats they may occupy.

Keywords: *animal personality, behavioral plasticity, neophobia, cognition, learning, zebra finch*

INTRODUCTION

Behavioral plasticity is the ability of individuals to change their behavior in response to variations in environmental (including social) conditions. Compared to individuals displaying relatively fixed behaviors, highly plastic individuals should be able to alter their behavior to maximize their success under any given circumstance. Yet, although natural selection should *a priori* erode variation in plasticity, individuals within the same population generally differ widely among each other in the way they cope with environmental changes (Sih and Bell 2008; Dingemanse *et al*. 2010; Kluen and Brommer 2013). A number of studies have reported that individual differences in behavioral plasticity are frequently associated with differences in personality (also referred to coping styles, behavioral syndromes or temperament). Specifically, experimental evidence indicates that proactive individuals, which are typically more active, explorative, aggressive and bold than reactive individuals seem to rely on routines, thereby exhibiting limited plasticity (Benus *et al*. 1987; Benus *et al*. 1990; Verbeek *et al*. 1994; Bolhuis *et al*. 2004; Guillette *et al*. 2011; Herborn *et al*. 2014). Yet, a few studies found the opposite trend (Frost *et al*. 2007; Bierbach *et al*. 2015). Hence, it remains unclear why personality and plasticity might be related. One possibility for why personality traits would affect the propensity of individuals to adjust their behavior to changing conditions is that variation in personality is functionally related to variation in cognition (Coppens *et al*. 2010; Carere and Locurto 2011; Sih and Del Giudice 2012; Griffin *et al*. 2015), which refers to the mechanisms by which animals acquire, process, store and act on information from the environment (Shettleworth 2001). More precisely, it has been suggested that differences in personality among individuals might reflect differences in how they trade off speed against accuracy (Sih and Del Giudice 2012): very active and bold individuals would explore their environment rapidly but inaccurately, and hence would be relatively insensitive to external stimuli, whereas less active and shy individuals would be slow and thorough explorers, and hence would pay more attention to external cues.

Although the study of animal personality has received considerable attention over the last decades, our understanding of the interplay among personality, behavioral plasticity and cognition remains limited and superficial. For instance, a number of studies have shown a correlation between learning speed and personality traits such as exploration (*e.g.*, Amy *et al*. 2012; Bousquet *et al*. 2015; Guillette *et al*. 2015) or neophobia (*e.g.*, Titulaer *et al*. 2012; Guenther *et al*. 2014; Trompf and Brown 2014). However, it remains unclear whether differences in learning performance among individuals are due to differences in their propensity to explore their environment and hence interact with the learning task rather than to differences *per se* in their ability to solve the task. Also, most authors that have investigated a possible link between personality and behavioral plasticity have focused on one particular type of plasticity measured from the rate of reversal learning (*e.g.*, Griffin *et al*. 2013; Lucon-Xiccato and Bisazza 2014; Pintor *et al*. 2014). Yet, the question of whether and how different types of behavioral plasticities might be related to one another remains unanswered (Stamps 2016). For instance, if an individual's performance on a reversal learning task assesses its ability to inhibit previously learned information (*i.e.*, its potential plasticity), it does not measure the extent to which it actually changes its behavior in response to changing conditions (*i.e.*, its realized plasticity) (Stamps 2016). Finally, most studies on the relationship between personality and cognition failed to demonstrate that individuals show consistent differences in both personality traits and cognitive performance (Griffin *et al*. 2015).

In this study, we then conducted a laboratory experiment with zebra finches (*Taeniopygia guttata*) aimed at: i) checking that consistent differences in personality among individuals are related to differences in their level of behavioral plasticity, and ii) examining the role of cognition in shaping individual differences in behavioral plasticity. More precisely, for each individual, we assessed its level of neophobia in two different environments across a social gradient and then we estimated the absolute value of the slope of the reaction norm as a measure of contextual plasticity (Stamps 2016; Dingemanse *et al*. 2010; Kluen and Brommer 2013). We assessed the level of contextual plasticity in neophobia because this personality trait is repeatable over consecutive trials in one particular context but varies greatly across different contexts (Kluen and Brommer 2013). Furthermore, individual differences in neophobia have been found to be associated with differences in activity, exploration and reaction to startle in zebra finches (David *et al*. 2011). We also measured the birds' performance on two discriminant tasks (in which the birds had to associate a color cue with a food reward) and on one reversal learning task (in which they had to learn a cue-reward association and then modify their response when the reward contingencies changed). We predict that individuals should show consistent differences in both their level of neophobia and learning speed, and that individual differences in neophobia should be negatively associated with differences in contextual plasticity. Furthermore, if there is a trade-off between speed and accuracy in learning (Sih and Del Giudice 2012), we expect that less neophobic individuals should be faster to reach the learning criterion in the two discriminant learning tasks while more plastic (more neophobic) individuals should need less trials to reverse a previously learned association. Finally, the presence of conspecifics has been shown to either encourage (Coleman and Mellgren 1994; Schuett and Dall 2009) or delay (van Oers *et al*. 2005; Mainwaring *et al*. 2011) object exploration, depending of the social relationships among the individuals involved. Because the presence of others may confer both benefits and costs, the way individuals should modify their behavior according to the social context could also depend on their learning speed if there is a trade-off between learning ability and competitive ability (Mery and Kawecki 2003). We then investigated whether the raw value of the slope of the reaction norm (used as a measure of behavioral adjustment) was correlated with individuals' learning speed in order to explore whether differences in learning ability, through impacting competitiveness could cause shifts in neophobic responses in opposite directions.

METHODS

a) Subjects

We used 22 adult zebra finches (10 males and 12 females) aged of 6-12 months. All the birds came from a local breeder (Exotic Wings & Pet Things, St Clements, Ontario, Canada) and were housed in same-sex cages (38 cm x 38 cm x 48 cm) with a maximum of 4 individuals per cage. Individuals were housed under a 10:14 h dark:light photoperiod and at a temperature of 23°C ±1°C. None of them had performed any learning task or personality test before. Outside the experimental sessions, they had unlimited access to fresh water, seeds, cuttlefish bone, oyster shell and egg food supplement. The experiments were conducted between June and September 2013 for males and between November 2013 and August 2014 for females. All individuals were exposed to the three experiments in the same order (*i.e.*, discriminant learning tests, personality test and reversal learning test) and were handled every day during all the duration of the experiments.

b) Discriminant learning tasks

Experimental apparatus

We estimated the birds' performance in two discriminant learning tasks: first (task 1), the birds were provided with 4 feeders of different colors (*i.e.*, green, blue, black and red) and we measured the number of trials needed to find 6 consecutive times the rewarded feeder (*i.e.*, the green one); second (task 2), they were provided with 4 white feeders that were placed behind 4 colored dots (*i.e.*, yellow, cyan, pink and black) and we measured the number of trials needed to find the rewarded feeder (*i.e.*, the feeder placed behind the yellow dot). The birds experienced task 2, 24 hours after they had reached the learning criterion in task 1. For both tasks, they were tested individually in the same experimental apparatus (Figure 1) made of white foam board and divided into one observation chamber (48 x 38 x 32 cm) and one choice chamber (48 x 22 x 32 cm) with 4 corridors (12 x 12 x 32 cm) that were separated from each other by a transparent removable partition. The feeders (4.5 x 4.5 x 2 cm), placed at the end of the corridors, could be refilled from the back of the apparatus through a removable partition without disturbing the birds. In addition, for task 2, a wheel, in the back of the apparatus, allowed the display of 4 different colored dots of 4 cm diameter behind the feeders. When in the observation chamber, the birds could simultaneously see the 4 colored dots and feeders.

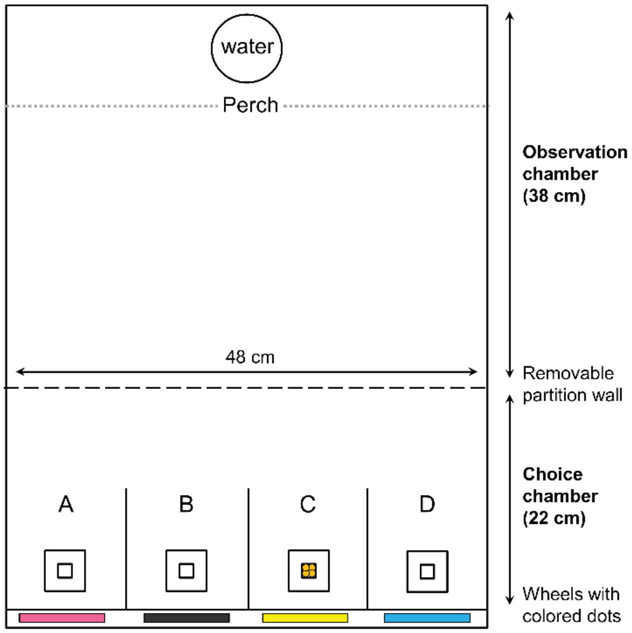

Figure 1. Top view of the experimental learning apparatus. In that particular case (*i.e.*, discriminant learning task 2), the 4 white feeders are placed in front of a colored dot and only the feeder placed in front of a yellow dot (*i.e.*, corridor C) contains 4 seeds.

Procedure

Prior to testing, we trained the birds to eat from the 5 different colored feeders (*i.e.*, white, green, blue, black and red) that were deposited within their home cages and we insured that no bird had an aversion for one particular color. Then, the birds were placed in the experimental apparatus to become familiarized with the environment. They spent at least 3 hours per day for 2 weeks in the apparatus, first with another companion from the same housing cage and then alone, until they could explore the 4 corridors and eat without fear from the feeders, whatever their position.

Before each testing day, the birds were food deprived for 3 hours (6:00AM to 9:00AM). They experienced a maximum of 25 trials per day during 4 consecutive days or until they had reached the learning criterion, whichever occurred first. In order to minimize handling stress during the experiment, we let the birds rest for 15 min after they had been introduced in the apparatus and then we did not catch them anymore until the end of the session. At the beginning of each trial, the bird was confined in the observation chamber for 2 min. Then, the observer gently lifted the removable partition, thereby allowing the bird to enter in the choice chamber and choose one of the 4 feeders. The rewarded feeder, whose position changed randomly from one trial to the next, always contained 4 millet seeds, while the other feeders were empty. Once the bird had chosen a corridor, we noted whether it had succeeded or failed. If the bird had succeeded, it could eat the 4 seeds before returning to the observation chamber. On the contrary, if the bird had failed, the observer either gently activated the removable partition to encourage the bird to return into the observation chamber if it had obtained food during the previous trial or let it explore the other corridors and find the rewarded feeder otherwise. Such a procedure was adopted to insure that all the birds ate approximately the same amount of food during each session and that differences among individuals in their learning score, therefore, were not due to differences in their level of satiety. Despite the fact that all the birds were familiarized with the experimental apparatus over a two-week period before being tested, one male stopped participating in task 1 after only a few trials, which prevented us to correctly measure its learning score on that task.

c) Reversal learning task

One to three months after the learning experiment was completed, we tested the birds on a reversal learning task and we measured the number of trials before they reversed their preference for a previously rewarded cue. This experiment was conducted on 2 consecutive days. On day 1, the birds performed the same discriminant learning task as described above where individuals needed to learn which colored feeder was rewarded (*i.e.,* task 1). We chose this task to be sure that all the birds rapidly reach the learning criterion and that learning is consolidated when they are tested in the reversal task. On day 2, we then first verified that all the birds were able to find the rewarded feeder 6 consecutive times, and next we measured the number of trials needed to reverse the previously learned association. The green colored feeder that used to contain seeds was then empty whereas the 3 other colored feeders were rewarded with 4 seeds. Each bird was tested until it was able to find consecutively two rewarded feeders. All but 4 injured birds (1 male and 3 females) were used for this experiment.

d) Neophobia

Following Herborn *et al.* (2010), we estimated neophobia as the mean baseline latency of the birds (*i.e*., their latency to feed in the absence of a novel object) minus their latency to feed in presence of a novel object, to control for individual differences in feeding motivation. For each individual, the measure was taken in 2 different contexts, and for each of them we used video recordings (see the "video recording" section for more details) depicted 8 or zero conspecifics. All the birds were food deprived 3 hours before the tests. They experienced 3 trials in a day: 2 without a novel object (*i.e.,* at 9:00 and 12:00) and one with a novel object (*i.e.,* at 15:00). This series of trials was replicated twice per context. Half of the individuals (N=10) were tested first with video recordings of 8 conspecifics and then with no companion while the order of the treatments was reversed for the other birds.

Experimental apparatus and procedure

The experimental apparatus was divided into 4 corridors (80 x 20 x 32 cm), thereby allowing 4 birds to be tested in a row. A transparent partition separated the observation chamber (30 x 20 x 32 cm) from the test chamber (50 x 20 x 32 cm) where we placed a feeder. Two screens, placed 10 cm behind the feeders, displayed videos of conspecifics at the end of the corridor. All individuals had been familiarized with the apparatus and trained to eat from the feeders before being tested. At the beginning of a trial, the observer first placed a bird during 3 min in the observation chamber, and then lifted the transparent partition. The bird could then access the test chamber and we measured the time before it started eating from the feeder. For the last trial, a novel object was placed at one cm apart from the feeder. Once a bird had reached the feeder, it could eat *ad libidum* for the duration of the test (*i.e.*, 10 min). A bird that never reached the feeder had a latency of 600 sec. Neophobia (each replicate and each context) was measured only once a week in order to avoid habituation to the novel objects that were all of similar size and color (*i.e.,* hairgrips and small plastic figurines).

Video recordings

The video of 8 familiar conspecifics was recorded for 2 hours with a Microsoft LifeCam Studio webcam recorder. There were an equal number of males and females that could interact freely in a home cage containing perches and water. Then, the recordings were edited using Windows Movie Maker so as to make video clips of 18 min which were continuously broadcasted during the neophobia tests. Male courtship songs were greatly limited in the final footage. Screens displayed a stationary picture of the empty cage in the context with no conspecific. Videos were displayed for the entire duration of the test at the end of each corridor on 2 flat AOC LCD monitors (35 x 20 cm) with screens split into 2 images. The audio was loud enough to imitate the real sound made by birds when housed in the aviary (around 55-65 dB). Previous studies have demonstrated that zebra finches are responsive to conspecifics on video recordings and emit direct songs toward them (Adret 1997; Ikebuchi and Okanoya 1999). Accordingly, we observed that all the birds responded to the recorded calls and interacted directly with the videos trying to reach their siblings. All the tests were recorded directly on a computer using a Microsoft LifeCam Studio webcam recorder.

e) Statistical analyses

We estimated the level of neophobia of each bird and in each of the 2 contexts as the relative latency approach (*i.e.*, mean latency to eat without a novel object estimated from the 2 repetitions minus latency to eat with a novel object). We excluded 2 individuals (one male and one female) because they never ate from the feeder in either of the 2 trials without a novel object, which prevented us from correcting their level of neophobia by subtracting their baseline latency.

For each bird, we also calculated 1) its level of contextual plasticity as the absolute value of the slope of the reaction norm and 2) its level of behavioral adjustment as the raw value of the slope.

First, to investigate whether the latency to approach a novel object was affected by the social context, we ran a linear mixed-effect model with Gaussian distribution using the package lme4 for R. The level of neophobia was entered as the dependent variable while the social context, the replicate number and the order of the treatment were considered as fixed factors. We ran the model while including or excluding i) a random intercept for the bird's identity, ii) a random slope for identity over social conditions to examine individual differences in behavioral adjustment across the two social conditions and iii) a random slope for identity over replicates to examine individual differences in behavioral adjustment over the replicates. Then, we compared the likelihood of the models with or without each random effect using the package anova for R (Schielzeth and Forstmeier 2009). We used again a Gaussian distribution for error terms.

Secondly, we tested whether the different learning scores (*i.e.*, the number of trials to reach the learning criterion in the discriminant leaning tasks 1 and 2 and in the reversal learning task) were related to each other using Pearson correlations.

Thirdly, we used backward stepwise regression analyses to determine which variables (*i.e.*, contextual plasticity, learning speeds on the discriminant and reversal tasks) best predicted neophobia. For each dependent variable, we retained the model that provided the best fit based on the Akaike's information criterion (AIC). As several individuals had a very low score of neophobia, we controlled for a floor effect by conducting the analyses while including and excluding individuals whose average latency approach without a novel object was less than 10 sec.

Fourth, because individuals reacted differently to the social context (*i.e.*, some individuals decreased their latency to approach a novel object when more companions were present, but others did the inverse), we tested whether the raw value of the slope of the reaction norm (*i.e.,* behavioral adjustment) was related to the birds' learning scores using a linear regression. We checked whether the reported effects were affected by the sex of the birds and, when required, we added the sex as a categorical variable (female=1; male=2) in the models.

Plasticity and personality measures were log transformed in order to satisfy the assumption of normality. All statistical analyses were performed using R 3.0.3 with thresholds set at 0.05.

RESULTS

Comparison of the models, that include and exclude the bird's identity as a random effect, revealed that individuals differed consistently among each other in their level of neophobia (χ^2_1 = 16.387, $P < 0.001$). Similarly, mixed-model analyses indicated that individuals significantly differed in the way they adjusted their level of neophobia across the social conditions (χ^2_3 = 16.527, $P = 0.001$) and the replicates (χ^2_3 = 16.425, $P = 0.001$). Yet, the replicate number (t_{58} = 0.384, $P = 0.703$) and the order of the treatment (t_{18} = -1.433, $P = 0.169$) had no significant effect on their average level of neophobia.

The mean number of trials required to reach the learning criterion was 21.43 (±7.58) on the learning task 1, 45.91 (±23.02) on the learning task 2 and 20.78 (±15.30) on the reversal learning task. On average, the birds needed more trials to reach the learning criterion in task 2 than in the two other tasks (t_{52} = 5.617, $P < 0.001$). Individual differences in learning scores were not explained by the sex of the birds (t_{52} = 0.683, $P = 0.498$) or their level of neophobia (t_{52} = 0.956, $P = 0.344$). We found a positive correlation between the performance scores on the two discriminant tasks (N = 21, R = 0.454, P = 0.039) and a negative correlation between the number of trials females required to pass task 2 and the speed at which they reversed a previously learned association w (N = 9, R = -0.771, P = 0.015; Figure 2). However, no such correlation was detected in males (N = 9, R = -0.451, P = 0.223; Figure 2) and we found no correlation either between individual scores on learning task 1 and reversal learning task (N = 17, R = -0.192, P = 0.461). Finally, we found no significant relationship between contextual plasticity and reversal learning speed (N = 18, R = -0.013, P = 0.960), neither in females (N = 9, R = 0.311, P = 0.416) nor in males (N = 9, R = 0.168, P = 0.666).

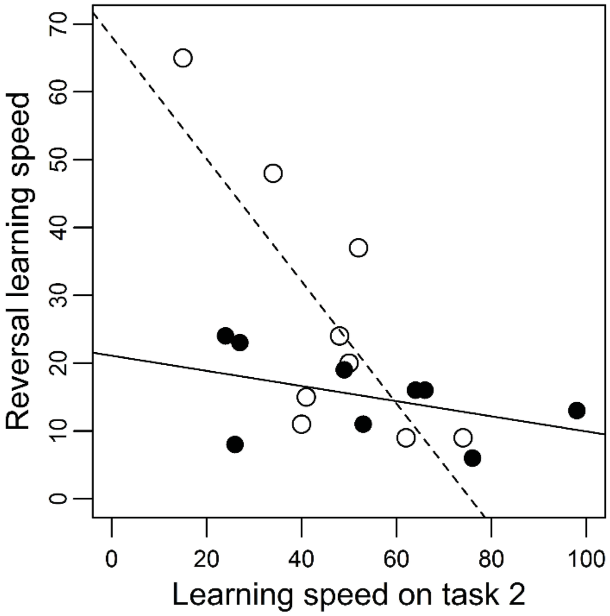

Figure 2. Relation between learning speeds in the reversal task and discriminant task 2 in males (filled circles, full line) and females (open circles, dotted line).

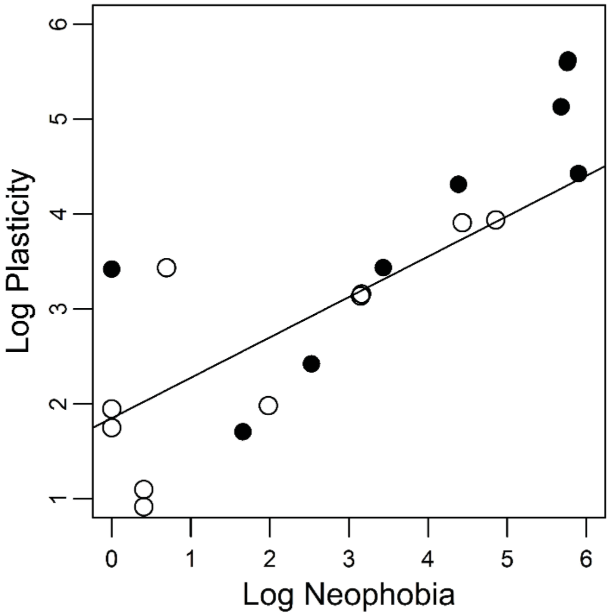

Figure 3. Relation between neophobia (measured with no conspecifics) and contextual plasticity (measured as the absolute value of the slope of the reaction norm). The 2 different symbols correspond to males (filled circles) and females (open circles).

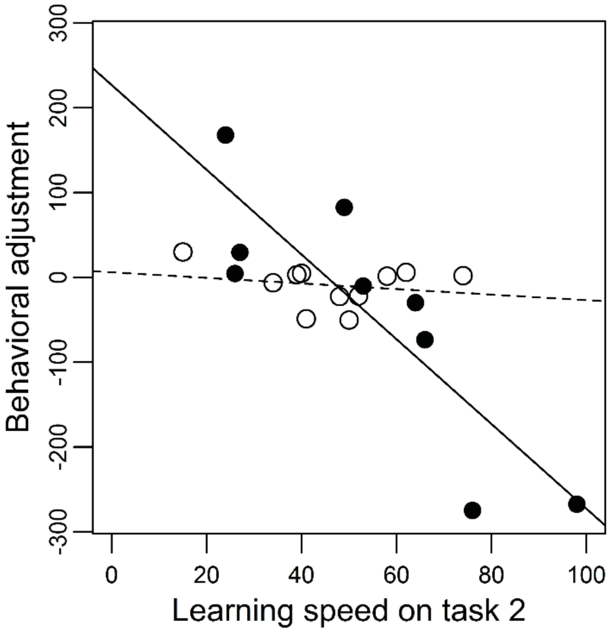

Figure 4. Behavioral adjustment in neophobic responses (measured as the raw value of the slope of the reaction norm) in relation to learning speed on the discriminant task 2 in males (filled circles, full line) and females (open circles, dotted line). Positive values of behavioral adjustment mean that the birds approached the novel faster when there were 8 conspecifics. On the contrary, negative slopes mean that individuals increased their level of neophobia in presence of conspecifics.

Neophobia was best explained by plasticity and learning speed on task 1 (Table I), with less neophobic individuals exhibiting less plasticity in their level of neophobia (Figure 3; t_{16} = 6.671, P < 0.001) and being faster learners compared to more neophobic individuals (t_{16} = 2.428, P = 0.032).

On the other hand, neophobia was not correlated with individuals' learning speed on the discriminant learning task 2 (t_{16} = -0.276, P = 0.787) and on the reversal learning task (t_{16} = -0.650, P = 0.528). These results were robust even when we excluded from the analyses individuals with very low values of neophobia; neophobia was still best explained by plasticity (t_{10} = 5.814, P = 0.001). Yet, learning scores on the three learning tasks had no significant effect and hence were excluded from the model (task 1: t_{10} = 0.262, P = 0.802; task 2: t_{10} = -

1.358, P = 0.223; reversal task: t_{10} = -0.343, P = 0.743). The reported effects were independent of the sex of the birds, which, therefore, was not included in the model.

Finally, the raw value of the slope of the reaction norm was negatively correlated with learning score on task 2 in males (t_8 = -4.644, P = 0.002; Figure 4) but not in females (t_{10} = -0.341, P = 0.741). Fast learning males, therefore, tended to increase their latency to approach a novel object as the number of companions increased, while those who took more time to reach the learning criterion on the discriminant task 2 tended to reduce the latency time to approach a novel object with 8 rather than no companions.

Table I. Results from the regression analysis exploring the link between neophobia (dependent variable) and contextual plasticity and learning speeds in the discriminant and reversal learning tasks (fixed factors)

Model	Df	Res Sum of Sq	AIC
Learning 1 + Learning 2 + Reversal learning	1	65.857	31.023
Learning 1 + Reversal learning	1	67.247	29.378
Null	1	78.731	28.058
Learning 1	1	68.757	27.755
Plasticity + Learning 2 + Reversal learning	1	20.860	11.478
Plasticity + Reversal learning	1	21.618	10.086
Plasticity	1	23.072	9.192
Plasticity + Learning 1 + Learning 2 + Reversal learning	1	13.899	6.685
Plasticity + Learning 1 + Learning 2	1	14.480	5.273
Plasticity + Learning 1 + Reversal learning	1	14.077	4.792
Plasticity + Learning 1	1	14.515	3.313

DISCUSSION

In agreement with our expectation, we found a significant relationship between neophobia and contextual plasticity, with less neophobic individuals exhibiting less plasticity in their responses compared to more neophobic individuals. Moreover, less neophobic individuals were also faster learners, but only in the less difficult task where the birds needed the fewest trials to reach the learning criterion. On the contrary, although the performance scores on the two discriminant learning tasks were positively correlated, which demonstrates that individual differences in cognitive abilities were consistent (Griffin *et al*. 2015), differences among individuals in the number of trials needed to pass the task in both the more difficult discriminant and reversal tasks were not associated with individual differences in neophobia.

Our results apparently contradict a number of earlier studies reporting significant correlations between personality traits and learning performance (Guillette *et al*. 2009, 2015; Titulaer *et al*. 2012; Brust *et al*. 2013; Carazo *et al*. 2014; Guenther *et al*. 2014; Trompf and Brown 2014; Bousquet *et al*. 2015). Yet, two reasons may explain why some individuals need less time than others to learn: either faster learners appear better to assess new situations and adjust their behavior accordingly simply because they explore their environment more quickly and hence encounter those new situations faster than do slow explorer individuals, or they actually differ in their sensitivity or ability to learn tasks. The effect of personality on learning reported by previous studies was probably due in most cases to differences in novelty responses among individuals that had not been sufficiently familiarized with the experimental apparatuses (but see Titualer *et al*. 2012), rather than to differences in cognitive ability. This statement is consistent with our finding that individual differences in neophobia was related to individual differences in learning speed only on the task that the birds experienced first and for which their performance, therefore, was more likely affected by how they reacted to novelty. A recent study by Ducatez *et al*. (2015) reported similar results in wild-caught Carib grackles (*Quiscalus lugubris*): the authors demonstrated that shyness was associated with problem-solving success but only for the first task the birds performed, while it has no significant effect on their success on any of the subsequent tasks. Furthermore, although we found a negative relationship between the number of trials females required to learn the most difficult discriminant task and their performance on the reversal learning task, as expected under the speed-accuracy trade-off hypothesis (Sih and Del Giudice 2012), neophobia was associated with none of these variables. Differences in contextual plasticity between personality types, therefore, seem unrelated to differences in cognitive types in zebra finches.

Thus, our findings indicate that individual differences in contextual plasticity do not necessarily result from some individuals being less sensitive than others to environmental changes. The most objective way to quantity the level of contextual plasticity of individuals, therefore, remains to directly measure the change in their behavior resulting from changes in their environment for each studied trait (*e.g.*, Morand-Ferron *et al*. 2011), instead of relying on reversal learning that is regularly used as a proxy for behavioral plasticity. Supporting this claim, we found that the speed at which adult zebra finches reversed a previously learned association was not correlated with their level of behavioral plasticity in neophobia estimated from the slope of the reaction norm. As highlighted by Stamps (2016), it is then crucial to make the distinction between potential and realized plasticity, to be able to compare the results of different studies. We suggest that differences in contextual plasticity that are not explained by differences in learning ability could result from differences in the number of suitable habitats that each behavioral type may occupy. More precisely, neophobic individuals could be as sensitive to environmental changes as less neophobic individuals but more willing to modify their behavior because they can forage only in particular conditions (*i.e.*, in familiar environments with low predation pressure) and hence have to adjust their behavior whenever the conditions are modified. This interpretation is consistent with the prediction from a recent simulation model demonstrated that more neophobic individuals, who are more constrained in their choice of habitat compared to less neophobic individuals, should be more responsive to changes in predation pressure (Dubois and Giraldeau 2014). An interesting avenue to explore would then consist in investigating to what extent contextual plasticity results from a decision versus cognitive limitations.

Finally, we found that the birds did not all reduce their latency to approach a novel object when more companions were present and that the way males (but not females) modified their behavior according to the social context was related to their performance on the most difficult discriminant task. More precisely, faster learning males tended to increase their latency as the number of companions increased while slow learners approached more quickly the novel object when more companions were present. This finding suggests that the costs of learning, though impacting an animal's competitive ability (Mery and Kawecki 2003), would affect how individuals respond to changes in their social environment. Indeed, although the presence of others can confer several anti-predatory advantages (Krause and Ruxton 2002), increasing group size also increases competition for limited resources. Yet, the balance between benefits and costs of living in large groups depends on individuals' competitive ability: more competitive males should have a higher tendency to aggregate compared to weaker competitors. Although we did not directly measure the males' competitive ability in our study, this explanation is very likely as males with the highest learning performance, and hence with the presumably weakest competitive abilities, took less time to reach the food when there was no bird behind the feeder. Hence our study suggests that shifts in neophobia in males would be mainly determined by their competitive ability.

In conclusion, although less neophobic individuals were less plastic in their responses compared to more neophobic ones, individual differences in neophobia were associated with differences in learning performance only on the less difficult task that the birds performed first. Our findings therefore suggest that individual differences in contextual plasticity would not necessarily result from some individuals being less sensitive than others to environmental changes. Instead, we suggest that differences among individuals in their level of plasticity might result from differences in the number of suitable habitats they may occupy, but this hypothesis remains to be experimentally tested.

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SUPPLEMENTARY MATERIAL I

Retest of the linear mixed model in the chapter II

I re-analysed the results presented in the Chapter II. A better approach for our small dataset would have been to compute a measure of repeatability using the rptGaussian function (package rptR) using permutations (n=1000) and a bootstrap (n=1000) to calculate the confidence interval and the P-value respectively. I ran this function while controlling for the treatment, the order of the treatment (categorical variable) and the replicate (standardized variable). The birds' level of neophobia was repeatable (R=0.443, SE=0.121, P=0.001, 95%CI [0.189, 0.656]).

The fixed effects were also retested (same model as above with a random slope for identity over the treatments) using a bootstrap procedure with 1000 iterations instead of the p-value from the lmerTest R package. The replicate [95%CI; -0.326, 0.466], the order of the treatment [95%CI; -1.388, 0.221] had no significant effect on their average level of neophobia.

Finally, given that the mean was used to compute the measure of plasticity (mean neophobia in presence of conspecifics minus mean neophobia in absence of conspecific, see figure 5 for individual variations in the degree of contextual plasticity), the repeatability estimate for neophobia would have been enough. However, I rechecked the effect of the random intercept for focal bird's identity and, the random slope for identity over the treatments using a similar method as in the paper (with and without the random effect). The model without any random effect was fit with the *gls* function in R (*Generalized least square*) which make it comparable with the linear mixed model fit with the function *lme* from the *nlme* package in R (Pinheiro and Bates 2000, Zuur *et al.* 2009). The fixed effect replicate was removed in order to make the model converge with *lme*. The results showed again that there were interindividual differences in neophobia ($\chi^2_1 = 17.464$, $P < 0.001$). In addition, the birds differed in the way they changed their level of neophobia ($\chi^2_1 = 17.598$, $P < 0.001$). Nevertheless, the best approach remains the one presented in the previous paragraphs.

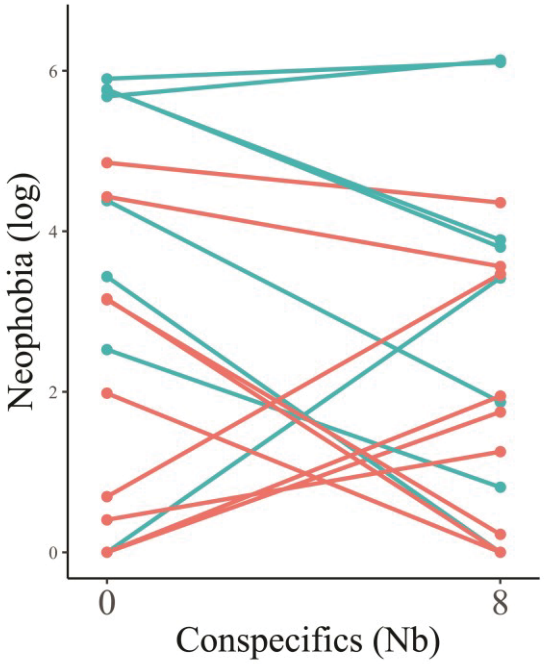

Figure S1. Latencies expressed by males (blue lines) and females (red lines) in absence (0) and in presence (8) of conspecifics.

CHAPITRE III

Are some individuals generally more behaviorally plastic than others? An experiment with sailfin mollies

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ABSTRACT

Individuals within the same population generally differ among each other not only in their behavioral traits but also in their level of behavioral plasticity (*i.e.,* in their propensity to modify their behavior in response to changing conditions). If the proximate factors underlying individual differences in behavioral plasticity were the same for any measure of plasticity (*i.e.,* whichever the context or trait measured), as commonly assumed, one would expect plasticity to be repeatable across behaviors and contexts. Yet, this assumption remains largely untested. Here we conducted an experiment with sailfin mollies (*Poecilia latipinna*) whose behavioral plasticity was estimated both as the change in their personality traits or mating behavior across a social gradient and using their performance on a reversal-learning task. We found that the correlations between pairwise measures of plasticity were weak and non-significant, thus indicating that the most plastic individuals were not the same in all the tests. This finding might arise because either individuals adjust the magnitude of their behavioral responses depending on the benefits of plasticity, and/or individuals expressing high behavioral plasticity in one context are limited by neural and/or physiological constraints in the amount of plasticity they can express in other contexts. Because the repeatability of behavioral plasticity may have important evolutionary consequences, additional studies are needed to assess the importance of trade-offs between conflicting selection pressures on the maintenance of intra-individual variation in behavioral plasticity.

Keywords: *Behavioral plasticity, Individual differences, General plasticity, Sailfin mollies*

INTRODUCTION

Over the past decades, considerable interest has been devoted to the study of animal personality, which is defined as a suite of individual differences in behavior that are consistent over time and contexts (Sih & Bell, 2008). Numerous studies on animal personality, notably, have demonstrated that individuals within the same population generally differ widely among each other not only in their behavioral traits such as their activity level, exploration tendency or aggressiveness, but also in their propensity to modify their behavior in response to changing conditions (that is in their level of behavioral plasticity, also referred to as contextual plasticity, activational plasticity, reversible plasticity or responsiveness; *e.g.,* Stamps, 2016). Behavioral plasticity is often considered advantageous (DeWitt, Sih & Wilson, 1998; Gabriel *et al*., 2005). Accordingly, comparative analyses have shown that bird species with relatively large brains and a high frequency of foraging innovations tend to be more successful invaders than less flexible species (Sol & Lefebvre, 2000; Sol, Timmermans & Lefebvre, 2002). Also, at the intraspecific level, two recent empirical studies found that individuals with greater behavioral plasticity had higher fitness, in terms of survival (Toscano, 2017) or mating success (Montiglio *et al*., 2017), compared to less plastic ones. If being plastic is advantageous, however, natural selection should erode variations in behavioral plasticity and several evolutionary explanations have thus been proposed to account for the maintenance of individual differences (Wolf, van Doorn & Weissing, 2008; Dubois, Morand-Ferron & Giraldeau, 2010; Wolf, Van Doorn & Weissing, 2011). Although those explanations rely on different processes (*e.g.,* state-dependent selection, frequency-dependent selection, positive feedback loops), they all implicitly assume that the proximate factors underlying individual differences in behavioral plasticity are the same for any measure of plasticity, and that an individual's plasticity, therefore, should be repeatable across behaviors and contexts (Dingemanse & Wolf, 2013).

In particular, in order to adjust its behavior to local conditions, an animal must detect and respond to environmental changes. Personality-related differences in behavioral plasticity could then result from individual differences in sampling behavior, sensitivity to external stimuli, risk-taking tendency or cognitive ability (Carere & Locurto, 2011; Sih & Giudice, 2012). Accordingly, several studies have shown that individual differences in behavioral plasticity or purported measures of plasticity such as reversal learning rate (*e.g.,* Guillette *et al*., 2010; Lucon-Xiccato & Bisazza, 2014; Pintor *et al*., 2014) are associated with differences in personality traits (*e.g.,* Gibelli & Dubois 2017; Guayasamin, Couzin & Miller, 2017; Guido *et al*. 2017; Mazza *et al*. 2018; see also reviews by Mathot *et al*., 2012 and Stamps, 2016), hence suggesting that certain behavioral traits or particular skills that are associated with them could prevent individuals from exhiting optimal behavioral plasticity. By contrast, however, several authors reported the opposite effect or no effect of personality type on how individuals respond to changing stimuli (*e.g.,* Logan 2016b; Bensky *et al*. 2017), whereas the few studies that have measured behavioral plasticity for the same individuals in several traits or contexts (Biro, Beckmann & Stamps, 2010; Morand-Ferron, Varennes & Giraldeau, 2011; Logan 2016a) or from different proxies (Brucks *et al*. 2017; Johnson-Ulrich *et al*. 2018) found weak or no support for a general plasticity. For instance, despite most individuals becoming more active and bold as temperature increased in damselfish (*Pomacentrus bankanensis*), Biro *et al*. (2010) found that the degree of plasticity in activity of a given individual was unrelated to its level of plasticity in boldness. In the same vein, Morand-Ferron *et al*. (2011) found that the most plastic individuals were not the same in two foraging games in nutmeg mannikins (*Lonchura punctulata*) while Mitchell & Biro (2017) reported that zebrafish (*Danio rerio*) that displayed high responsiveness to temperature were not more responsive to food deprivation. A lack of correlation in individual plasticity across contexts or behaviors could be explained by at least the two following causes.

First, behavioral plasticity would not be a general feature of an individual because its ability to perceive changes in environmental conditions and adjust its behavior accordingly, is affected by the magnitude of the changes. More precisely, the speed-accuracy trade-off hypothesis (Chittka, Skorupski & Raine, 2009) predicts that fast-exploring individuals should make faster but less accurate decisions compared to slow-exploring individuals that invest more time in decision process. Such a trade-off between speed and accuracy, however, would exist only when the variations in environmental conditions are subtle and hence require considerable sampling effort to be detected. Conversely, when changes in external stimuli are easy to detect, fast-exploring individuals might be capable of making fast and accurate decisions (Mamuneas *et al*., 2015). According to this idea, an individual that explores its environment superficially would then be unlikely to adjust its behavior to local conditions when the changes in environmental conditions are subtle but could exhibit greater plasticity when the magnitude of the change is large. Second, low individual consistency in plasticity across behaviors could result from physiological constraints that would reduce the capacity of individuals to adjust hormonally-mediated behaviors to changing environmental conditions (Hau & Goymann, 2015). For instance, experimentally elevated levels of testosterone have been shown to increase courtship behavior and aggression but to reduce parental care in several species (McGlothlin, Jawor & Ketterson, 2007), hence suggesting that its physiological state could, in some cases, prevent an individual to modify its behavior in response to changing environmental conditions. If the level of behavioral plasticity expressed by an individual is limited by similar constraints (*e.g.,* its ability to detect environmental changes or by its physiological state), we would then expect individual differences in behavioral plasticity to be repeatable and associated with individual differences in personality traits. However, the strength and direction of the correlations could vary depending on the measure of plasticity and/or on the magnitude of the change in environmental conditions.

In order to test whether some individuals are generally more behaviorally plastic than others, as commonly assumed, or if their ability to adjust their behavior in response to changing conditions is trait and/or context-dependent, we conducted an experiment with sailfin mollies (*Poecilia latipinna*). For each fish, we measured its behavioral plasticity both as the change in its personality traits (*i.e.,* exploration, neophobia and anxiety) or mating behavior (*i.e.,* number of nibbling bites) in response to changes in environmental stimuli and as its performance on a reversal-learning task. Then, we tested whether the different measures of behavioral plasticity were correlated between each other.

METHODS

Animals and housing conditions

We used 57 (41 males and 16 females) sexually mature sailfin mollies aged 4 months that had not participated in any previous experiment: 33 males were used as focal individuals whereas 8 other males and 16 females served as audience individuals. All individuals came from a commercial fish supplier (Mirdo Importations Canada Inc, Montreal, Quebec, Canada). The fish were kept in brackish water at 24±0.5°C with a 12:12 photoperiod and were fed with spirulina flakes (2% of their weight) and brine shrimps twice a day. Outside the experiments, focal males were housed either individually (15 individuals) in 3 L tanks (10×20×15 cm) or socially at a density of 3 ±1 fish (18 individuals) in 6 L tanks (20×20×15 cm), whereas the other fish that served as audience individuals were housed in 6 L tanks with a maximum of 4 ±1 same-sex congeners, for males and females, respectively. The experiments were conducted in June 2015 at the LARSEM (Laboratoire aquatique de recherche en sciences environnementales et médicales, Université Laval, Québec, Qc, Canada), were approved by the Animal Care Committee of the Université Laval (animal care permit #2015027-1) and conformed to all guidelines of the Canadian Council on Animal Care.

Male body length

The week before the beginning of the experiments, all male sailfin mollies were tranquilized with a low dose (5 mg L) of anaesthetic (TMS-222), tagged with an elastomer tag (Northwest Marine Technologies, Shaw Island, WA, USA) and photographed. Body length (distance from the tip of the snout to the base of the tail fin) was then measured (precision 0.1 mm) using Adobe Photoshop CC. The measurements were taken three times on each individual by the same examiner and then averaged. Based on the distribution of male body length, we then defined three categories of males: small (< 5.90 cm), medium (5.90-6.56 cm) and large (> 6.56 cm).

Measures of plasticity

All focal males were then tested in three experiments (*i.e.,* mating behavior, personality and reversal learning) in the same order. The experiments were performed between 8:30 am and 3:30 pm. All trials were conducted in a 54 L tank (60 l × 30 w × 30 h cm) whose sides were covered by black cloth in order to minimize disturbance and were recorded with a digital camera (JVC model GZ-MS120).

1. Mating behavior

As in Fraser *et al*. (2014), we quantified the mating behavior of each focal male first in a control condition (*i.e.,* with three females) and then in a competitive condition (*i.e.,* in presence of three male competitors and six females), with a one-week delay between the two conditions. For the competitive condition, we insured that the three males were of different sizes (*i.e.,* one small, one medium and one large fish) and that the size difference between two males was larger than 0.6 cm. Before being tested, the focal fish were isolated from their conspecifics for 24 h. For each test, we successively introduced into the tank the audience females, the audience males, when applicable, and finally the focal male. Then, during a 10-min observation period, we scored the male's sexual behavior as 1) the number of nibbles in the vicinity of a female's urogenital opening and 2) the number of gonoporal thrusts, as both traits have been shown to be plastic in response to changes in competitive conditions (Travis & Woodward, 1989; Fraser *et al*. 2014). After the tests were completed, we calculated the plasticity in mating behavior of each male as the difference in the number of nibbling bites or gonoporal thrusts between the control and competitive conditions both in absolute and relative values. For subsequent analysis, however, we used only plasticity in the number of nibbling bites as only this trait was significantly affected by the condition though both traits were correlated (supplementary material 1). Given that the males were housed with a number of conspecifics that varied between zero and four before being isolated for 24 h and then tested, we insured that the housing condition of the fish had no effect on their mating behaviors (supplementary material 1).

2. Personality

We conducted two behavioral tests that are commonly used to assess personality traits (Réale *et al*., 2007). Specifically, the open-field test was used to measure exploration and thigmotaxis, an indicator of anxiety (Maximino *et al*. 2010), while the novel object test was used to measure neophobia. All individuals performed the two tests in the same order (*i.e.,* open field test and novel object test) and each test was replicated twice without an audience (T1, T2) and twice with a randomly selected audience (T3, T4). For each test, the interval between the alone and audience treatments was 7 days, while the delay between two replicates for a given treatment varied between 6 and 24 h.

Open-field test: Exploration and anxiety

Prior to testing, the fish were familiarized with the tank for 30 min twice a day for 7 consecutive days. The tank was equipped with four transparent plastic containers ballasted with four to five sterilized black rocks, one in each corner, where we could confine the audience individuals (Fig. 1). Specifically, for the audience treatment, four individuals (*i.e.,* two males and two females) were placed in the containers (*i.e.,* one individual per container) before the focal fish was introduced, while the containers were kept empty for the alone treatment. The containers were closed at the top with a net, thereby preventing physical, but not chemical, interactions. At the beginning of a trial, we first introduced the focal fish in the center of the tank and then, once we had removed the landing net from the top of the tank, we monitored its movements for 5 min using a custom software. The images were divided into squares of 35 x 35 pixels (around 5 x 5 cm), so that we could estimate, for each focal fish, its exploration tendency, as the number of different squares visited during the 5-min observation period. The same recorded data were also used to measure thigmotaxis as the total number of squares visited by the fish that were located at the periphery of the walls and the containers (*i.e.,* grey area in Fig. 1) when tested alone.

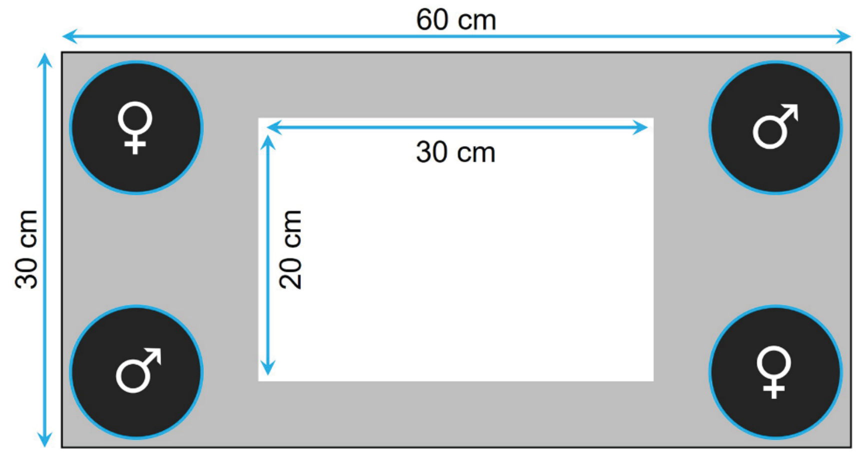

Figure 1. Top view of the tank used to measure exploration and anxiety. The four containers, placed in each corner of the tank, housed a single individual when the fish was tested with an audience or were kept empty otherwise. The grey area delimits the area considered to measure anxiety in the alone treatment.

Novel object test: Neophobia

We divided the test tank into three sections by two opaque removable partitions that could be moved with pulley system in order to avoid any disturbance (Fig. 2): the first section contained a transparent rectangular container (20 x 10 x 15 cm) where we could confine the audience individuals; the central section contained two plastic plants that could be used as a shelter; the end section contained a novel object that consisted of a small colored figurine (around 4 cm in diameter) placed 1 cm from the food box. The food box, which was made of a small net and contained brine shrimps, was used as an attractive olfactory signal to encourage the fish to approach the novel object. At the beginning of a trial, we introduced the focal fish into the first section of the tank, and then we gently removed the partitions A and B after 5 and 20 min, respectively (Fig. 2). We let the fish acclimatize for 20 min before removing partition B to ensure that no fish would swim erratically and enter in contact with the novel object by chance. Then, we estimated neophobia as the latency to come within 1 cm of the novel object. A trial ended when the focal fish had approached the food or after 20 min, whichever occurred first. For the audience treatment, two males were confined in the container before the focal fish was introduced, while the container was kept empty for the alone treatment. We placed the audience in the first section of the aquarium to maximize the chance of observing differences between the two treatments in the case where some fish would exhibit maximum latencies when tested alone.

After the two tests were completed, we estimated for each fish its levels of plasticity under three different social gradients as the difference in absolute and relative values between i) the two replicates of the alone treatment (*e.g.,* |T1-T2|) (gradient A), ii) the two replicates of the audience treatments (*e.g.,* |T3-T4|) (gradient B), and iii) the mean trait value in the alone treatment and the mean trait value in the audience treatment (*e.g.,* |(T1+T2-T3+T4)/2|) (gradient C). For each individual, therefore, we had a maximum of seven absolute or relative measures of plasticity in personality traits (*i.e.,* one for anxiety, three for exploration and three for neophobia). For statistical analysis, however, differences between two measures with the highest possible value (n=12) were replaced by missing data in order to avoid ceiling effects.

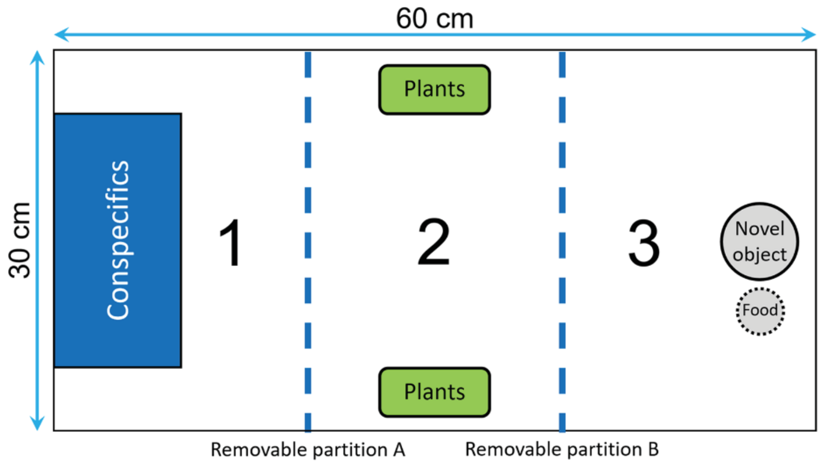

Figure 2. Top view of the tank used to measure neophobia. The tank was divided into three identical sections (30 x 20 cm) by two opaque removable partitions (blue dotted lines). Section 1 contained a transparent box used to confine the audience males, section 2 was equipped with two plastic plants that could be used as a shelter and section 3 contained a novel object and a food box.

3. Reversal learning

The fish were trained to perform an associative learning task and then were tested for reversal learning, often viewed as a measure of behavioral flexibility by psychologists and neuroscientists (Fellows & Farah, 2003; Izquierdo *et al*., 2007; Haluk & Floresco, 2009; Izquierdo & Jentsch, 2012). The tests were performed in a tank divided with a transparent removable partition into one observation compartment and one choice compartment that had two corridors, separated from each other by a porous partition (Fig. 3). Two visual cues of different shapes and colors (*i.e.,* a yellow cross and a blue square of around 4 x 4 cm) were placed at the end of each corridor. Two identical symbols were also placed in front of the corridors, to ensure that the fish could see them from the observation compartment. Prior to the start of the learning tests, following 2 days of food deprivation, the fish were habituated to the apparatus during three periods of 30 min each. We insured that they were all able to explore both corridors of the choice compartment to get food.

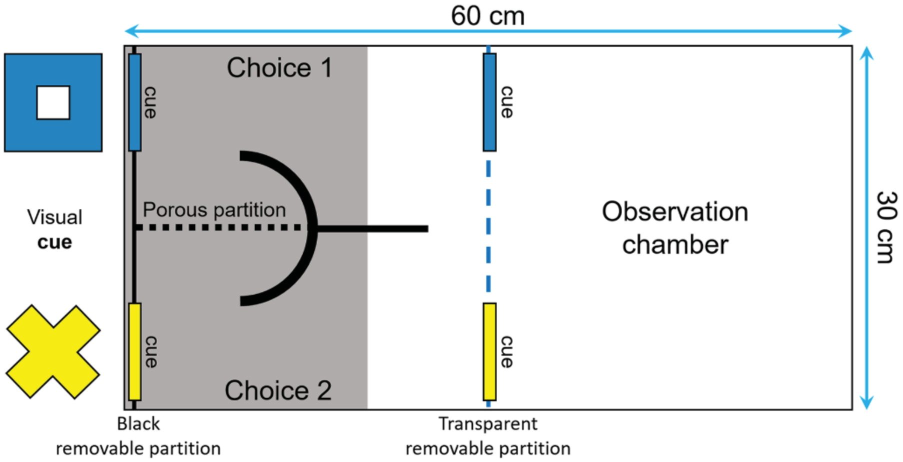

Figure 3. Top view of the tank used to measure reversal learning speed. The tank was divided in two sections (30 x 30 cm) by a transparent removable partition (blue dotted line): an observation compartment and a choice compartment divided into two corridors. Two visual cues (a blue square and a yellow cross of around 4 x 4 cm) were placed both in front and at the end of each corridor to ensure that the fish could see them from the observation compartment and learn which cue was rewarded.

The fish were tested after 24 h of food deprivation (unless they made no choice in the first 20 min in which case they were deprived of food for another 24-hour period) until they choose the correct corridor six consecutive times. During the test, the position of each cue remained constant from trial to trial, but the rewarded cue, as well as its position, were counterbalanced across subjects. At the beginning of each trial, the focal fish was placed in the observation compartment for 5 min or until it has ceased freezing or swimming erratically. We then placed three spirulina flakes on the side of the rewarded cue and gently lifted the removable partition to allow the fish to enter the choice compartment and make a decision. To prevent the food from scattering in the aquarium and from being visible from the observation compartment, it was placed behind a curved PVC partition. We considered that the fish had made a choice once half of its body had entered the choice compartment. If the fish succeeded, it could eat the three spirulina flakes before returning to the observation chamber. Otherwise, the observer gently activated the removable partition to encourage the fish to return into the observation compartment. One week later, the fish were tested for reversal learning after 2 days of food deprivation. To ensure that the fish remembered which cue was rewarded in the acquisition phase, we retested them using the same procedure as above until they choose the correct corridor six consecutive times. All individuals were then tested for reversal learning 2-2.5 h after they reached this criterion, except two fish that refused to participate in the reversal learning trials and hence were tested again after 24 h. The reversal learning trials were performed in the same manner as described above, except that the previously unrewarded cue was now rewarded, and the previously rewarded cue was unrewarded. Each fish was tested until it chose the correct corridor six consecutive times. The number of trials required by each fish to reach this criterion was then used as a proxy of its plasticity.

Statistical analyses

Our complete data set contained five missing values. In three occasions the missing values were due to technical problems. In the two other cases, we replaced the anxiety score of a fish by a missing value because it stayed immobile in the middle of the test arena for the entire duration of the test, while another individual was never able to explore the choice compartments of the learning apparatus during the familiarization period and hence had no value for the reversal learning test.

To explore how the nine measures of plasticity (*i.e.,* seven measures of plasticity in personality traits, one measure of plasticity in mating behavior and one measure of reversal learning speed) were related to each other, we used Spearman rank correlations to test for pairwise correlations and applied the improved Bonferroni correction to account for multiple comparisons (Hochberg, 1988). Correlations were calculated using both absolute and relative measures of plasticity. We also performed a Principal Component Analysis (PCA) on the nine measures of plasticity in absolute value to check whether a single factor (*i.e.,* general plasticity) explaining plasticity could be extracted and whether the level of plasticity in exploration and neophobia differed among the social gradients for a given individual with paired-t tests. Finally, we tested whether plasticity in exploration and neophobia in relative value was related to the level of expression of the trait during the first exposure to the stimuli (*i.e.,* T1 or T3). To do that, we divided the population in two groups of equal size according to either their scores in T1 or T3 and compared the relevant plasticity scores (*i.e.,* either gradient A or B) using t tests.

All statistical analyses were conducted on R 3.2.4 (R_Core_Team 2016). PCA was performed on the standardized data and using the dudi.pca function.

RESULTS

Although individual measures of plasticity in absolute value were positively correlated in the majority (31/36) of pairwise comparisons (Table I), none of these correlations were significant (Bonferroni corrected α =0.001). Explicitly, the correlations were at best moderate (*i.e.,* between 0.4 and 0.59) with an average correlation equal to 0.174. The correlations were even smaller when considering the differences in relative value (Table II) as always at least 43±6% (Mean±SE) of the focal fish adjusted their behavior to the changes in social conditions in the opposite direction to that of their congeners. For instance, 21 fish were more exploratory when tested with an audience than alone, but 12 other fish on the contrary had a higher exploration score in the alone treatment. Thus, our findings indicate that an individual's level of plasticity was weakly repeatable across contexts and behaviors. This conclusion is further supported by the fact that four principal components with eigenvalues greater than one were extracted from the PCA, with each of them explaining only a small portion of the total variance (Table III). Furthermore, the 4 first principal components had positive and negative loading values (Table III), which reflects the fact that the different measures of plasticity were not equivalent.

Table I. Pairwise Spearman rank correlations among the nine measures of behavioral plasticity estimated as the differences in absolute value.

		Neophobia A	Exploration A	Anxiety A	Neophobia B	Exploration B	Neophobia C	Exploration C	Mating behavior
Exploration A	r_s	0.369							
	P	0.053							
	N	28							
Anxiety A	r_s	0.530	0.281						
	P	0.004	0.148						
	N	27	28						
Neophobia B	r_s	0.259	0.309	-0.217					
	P	0.221	0.142	0.319					
	N	24	24	23					
Exploration B	r_s	0.171	0.277	-0.115	0.429				
	P	0.366	0.132	0.560	0.029				
	N	30	31	28	26				
Neophobia C	r_s	0.168	0.053	0.083	0.508	0.177			
	P	0.374	0.780	0.676	0.008	0.332			
	N	30	30	28	26	32			
Exploration C	r_s	0.348	0.231	0.294	0.417	-0.285	0.214		
	P	0.059	0.212	0.129	0.034	0.108	0.239		
	N	30	31	28	26	33	32		
Mating behavior	r_s	0.444	0.178	0.007	0.095	0.033	0.254	0.080	
	P	0.014	0.339	0.974	0.645	0.856	0.160	0.657	
	N	30	31	28	26	33	32	33	
Reversal learning	r_s	0.019	0.305	0.386	0.089	0.041	-0.047	0.154	-0.285
	P	0.922	0.101	0.043	0.667	0.824	0.798	0.401	0.113
	N	30	30	28	26	32	32	32	32

Note: Reversal learning scores (i.e. the number of trials to reach the learning criterion in the reversal task) were multiplied by -1 in such a way that the subjects that were faster to reverse had the highest scores.

Table II. Pairwise Spearman rank correlations among the nine measures of behavioral plasticity estimated as the differences in relative value.

		Neophobia A	Exploration A	Anxiety A	Neophobia B	Exploration B	Neophobia C	Exploration C	Mating behavior
Exploration A	r_s	-0.221							
	P	0.258							
	N	28							
Anxiety A	r_s	-0.005	-0.098						
	P	0.981	0.620						
	N	27	28						
Neophobia B	r_s	0.003	-0.391	0.188					
	P	0.987	0.059	0.391					
	N	24	24	23					
Exploration B	r_s	-0.165	0.174	-0.328	-0.189				
	P	0.384	0.350	0.089	0.355				
	N	30	31	28	26				
Neophobia C	r_s	0.000	0.260	-0.140	-0.018	0.312			
	P	0.999	0.166	0.479	0.930	0.082			
	N	30	30	28	26	32			
Exploration C	r_s	0.189	-0.106	-0.269	0.166	-0.160	-0.020		
	P	0.318	0.572	0.166	0.416	0.372	0.914		
	N	30	31	28	26	33	32		
Mating behavior	r_s	-0.275	-0.167	-0.035	0.115	0.114	0.312	-0.095	
	P	0.141	0.368	0.858	0.576	0.527	0.082	0.598	
	N	30	31	28	26	33	32	33	
Reversal learning	r_s	0.397	-0.103	-0.032	-0.275	-0.099	0.088	-0.325	0.328
	P	0.030	0.588	0.870	0.174	0.591	0.631	0.069	0.067
	N	30	30	28	26	32	32	32	32

Note: Reversal learning scores (i.e. the number of trials to reach the learning criterion in the reversal task) were multiplied by -1 in such a way that the subjects that were faster to reverse had the highest scores.

There were differences in the level of plasticity expressed by individuals depending on the social gradient they were exposed to. Most notably, the magnitude of the changes in behavioral responses was smaller when the fish were tested twice without an audience compared to when they were observed two times by different audience individuals or when we compared the average response with and without an audience (Fig. 4). Yet, only the difference between the gradient A and C was significant for measures of neophobia (t_{29}=-2.347, P=0.026). Finally, for the three personality traits measured, we found a significant association between the amount of plasticity exhibited (in relative value) and the value of the trait during the first trial (Neophobia, A: t_{16}=-2.244, P=0.040; B: t_{13}=-2.876, P=0.013; Exploration, A: t_{28}=-1.968, P=0.059; B: t_{29}=-2.012, P=0.054 & Anxiety, A: t_{21}=-2.646, P=0.015; see also supplementary material 2). Individuals that exhibited greater plasticity (in relative value), therefore, showed greater expression of the trait when they were exposed to the stimuli for the first time.

Table III. Loadings on the four extracted factors.

Plasticity measure	**PC1**	**PC2**	**PC3**	**PC4**
Neophobia A	0.705	0.502	-0.298	0.043
Exploration A	0.710	0.337	-0.035	-0.251
Anxiety A	0.235	0.689	0.313	-0.005
Neophobia B	0.477	-0.546	0.551	0.122
Exploration B	0.498	-0.021	-0.026	0.807
Neophobia C	0.514	-0.455	0.110	0.129
Exploration C	0.606	-0.241	0.452	-0.467
Mating behavior	0.568	-0.129	-0.704	-0.157
Reversal learning	-0.043	0.716	0.439	0.105
Eigenvalues	**2.487**	**1.934**	**1.397**	**1.002**
% of variance	**27.6%**	**21.5%**	**15.5%**	**11.1%**

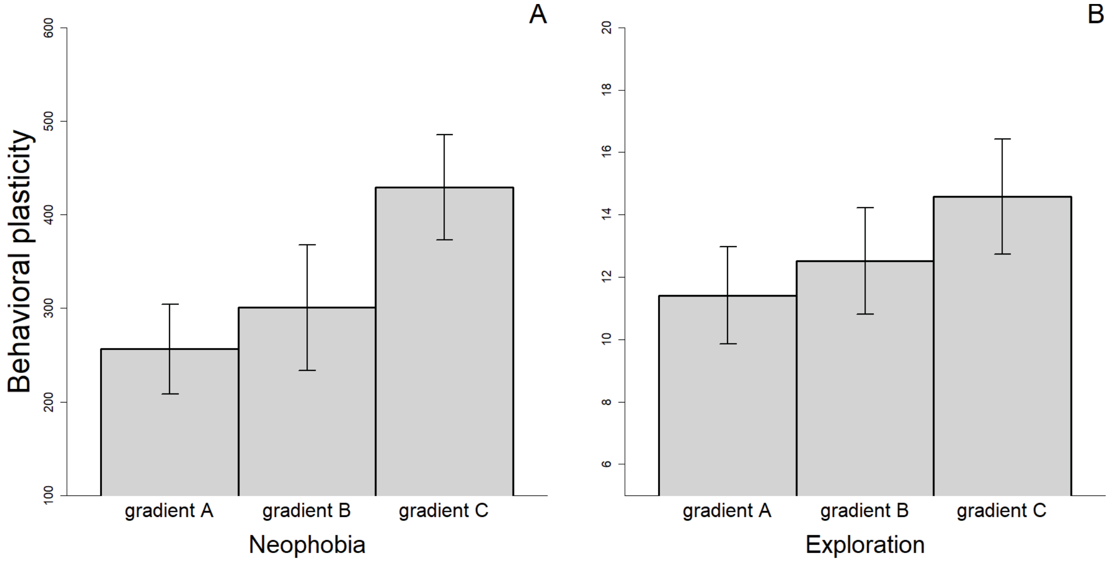

Figure 4. Mean (±SEM) behavioral plasticity in neophobia (panel A) and exploration (panel B) measured under three different social gradients. Behavioral plasticity was estimated as

the difference in absolute value between i) the two replicates of the alone treatment (gradient A), ii) the two replicates of the audience treatment (gradient B), and iii) the mean trait value in the alone treatment and the mean trait value in the audience treatment (gradient C).

DISCUSSION

Using sailfin mollies, we tested whether some individuals are generally more behaviorally plastic than others, or if an individual's ability to adjust its behavior in response to changing conditions is trait and/or context-dependent. We found that the correlations between pairwise measures of plasticity were non-significant, thus indicating that the most plastic individuals were not the same in all the tests. Although our sample size is small, and the power to detect significant associations is relatively low, this conclusion is supported by the fact that the correlations were only weak or moderate in strength. The correlations were particularly weak when considering not only the magnitude but also the direction of behavioral changes, as individuals differed widely from each other in how they were affected by the treatments. Two non-exclusive explanations could account for our finding.

First, the lack of correlation between the different measures of plasticity could result from differences among individuals in their internal state that would have affected their willingness to express behavioral plasticity in response to environmental conditions (Wolf & Weissing, 2010). Indeed, the extent to which an animal actually changes its behavior in response to changing stimuli is a measure of realized plasticity and hence does not necessarily reflect potential plasticity (Stamps & Krishnan, 2014; Stamps, 2016). Individuals with high potential plasticity, therefore, might have exhibited under certain conditions or for certain traits little plasticity, resulting in a weak association between the different measures of realized plasticity. Our results partly support this hypothesis, as they suggest that individuals would adjust the magnitude of their behavioral responses depending on the benefits of plasticity. Indeed, we found that the fish exhibiting the greatest plasticity in relative value in response to the social gradients A and B showed greater expression of the trait (*i.e.,* were the most neophobic, exploratory and anxious individuals) when they were exposed to the stimuli for the first time, probably because those individuals tend to overestimate the danger when confronted to a novel situation, thereby reacting inappropriately. In accordance to this idea, Mitchell and Biro (2017) also found that active individuals that deplete energy reserves at a faster rate than less active fish, were more responsive to food deprivation. Nonetheless, individuals that were the most plastic in their activity level in response to changes in food abundance were not the most plastic in response to changes in temperature (Mitchell & Biro, 2017). The importance of past behavior on the expression of behavioral plasticity, therefore, would depend on the environmental gradient used and/or on the trait being measured. Given the fact that all subjects in our study experienced the trials in the same order, however, this explanation alone cannot account for the absence of significant correlations among the different measures of plasticity.

Thus, another non-mutually exclusive interpretation of our findings is that behavioral plasticity is not a general characteristic of individuals, such that individuals expressing high behavioral plasticity in one context could be limited in the amount of plasticity they can express in other contexts. Particularly, different measures of behavioral plasticity taken under different conditions or using different traits, would not be equivalent because they are controlled by different neural, physiological or behavioral mechanisms, so that some behavioral traits might be more constrained than others. Supporting this idea, the PCA analysis revealed that the first component accounted for less than 28% of the total variance, which is low compared to results that are usually interpreted as support for a general factor (see Shaw & Schmelz, 2017 and references therein). Our interpretation is also supported by the fact that the rate of reversal learning, which is regularly used as a proxy for behavioral plasticity (*e.g.,* Guillette *et al*., 2010; Lucon-Xiccato & Bisazza, 2014; Pintor *et al*., 2014), was very weakly or not correlated with the other measures of individual plasticity. There is evidence that reversal learning tasks assess distinct neurological abilities from other tasks used to measure behavioral plasticity, such as set-shifting or self-control tasks (Audet &

Lefebvre, 2017). This might explain why different measures of plasticity are uncorrelated. Accordingly, we found that reversal learning performance loaded negatively on the first principal component contrary to the eight other measures of plasticity that had positive loadings. Individuals capable of inhibiting a previously rewarded behavior more quickly, therefore, would possess particular skills that would not be associated with greater plasticity in personality. In particular, our results are consistent with the hypothesis that plasticity in personality traits may be restrained by the inability of individuals to detect environmental changes. Indeed, as anticipated, fish exhibited on average greater plasticity between the alone and audience treatments than between the two trials of the audience treatment for both personality traits measured (*e.g.,* exploration and neophobia). Furthermore, the correlation between the levels of plasticity in exploration and neophobia was stronger when plasticity was measured as the difference between the two trials with a randomly selected audience than between the audience and alone treatments. This finding indicates that individuals were more consistent in their plasticity when the changes in environmental conditions were subtle, as only more neophobic (and less exploratory) individuals that explore their environment slowly and accurately could then detect and respond to such environmental changes (Sih & Giudice, 2012). Thus, our results suggest that trade-offs between conflicting selection pressures might maintain intra-individual variation in behavioral plasticity. However, in order to confirm this hypothesis, further studies will be required to demonstrate the adaptive nature of intra-individual differences in the expression of behavioral plasticity. Such studies will consist notably in i) testing the effect of spatial and/or temporal environmental heterogeneity on the repeatability of behavioral plasticity, and ii) measuring the fitness consequences of individual plasticity in various contexts.

Conclusions

In conclusion, although we cannot conclude from this study to what extent individuals are limited in their level of behavioral plasticity by neural and/or physiological constraints, our findings contradict the widespread (though largely untested) idea that some individuals would be generally more behaviorally plastic than others (Dingemanse & Wolf, 2013, but see

Audet & Lefebvre, 2017). Whether behavioral plasticity is a repeatable trait at the individual level may have important evolutionary consequences, for instance through affecting population stability or persistence (Wolf & Weissing, 2012; Sih *et al*., 2012). Additional studies, therefore, should be conducted to investigate the importance of trade-offs between conflicting selection pressures on the maintenance of intra-individual variation in behavioral plasticity and examine the fitness consequences of behavioral plasticity in different contexts.

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SUPPLEMENTARY MATERIAL 1

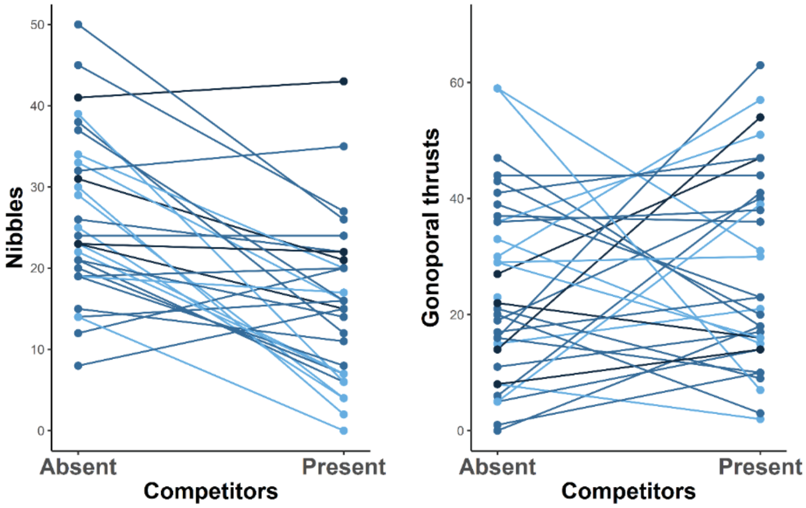

Figure S1. Number of nibbles and gonoporal thrusts by each male when it was tested either in the absence or in the presence of competitors. Colors indicate the male size category, with lighter colors representing smaller males.

None of the behaviors was influenced by the housing conditions prior to the 24h isolation period (LMM controlled for fish identity: nibbles: t_{31}=1.000, P=0.325, gonoporal thrusts: t_{31}=-0.590, P=0.559). The slopes for both mating behaviors (*i.e.,* differences in mating behavior between the conditions in which the competitors were absent and present) were correlated (N=33, r_s=0.58, P<0.001). Furthermore, the number of nibbling bites and gonoporal thusts were highly correlated in both conditions (LM: Competitors absent: t_{31}=6.816, P<0.001, Competitors present: t_{31}:2.329, P=0.027). However, the presence of competitors influenced the number of nibbles (LMM controlled for fish identity: t_{32}=-6.084, P<0.001) but not the number of gonoporal thrusts (LMM controlled for fish identity: t_{32}=-1.010, P=0.320).

SUPPLEMENTARY MATERIAL 2

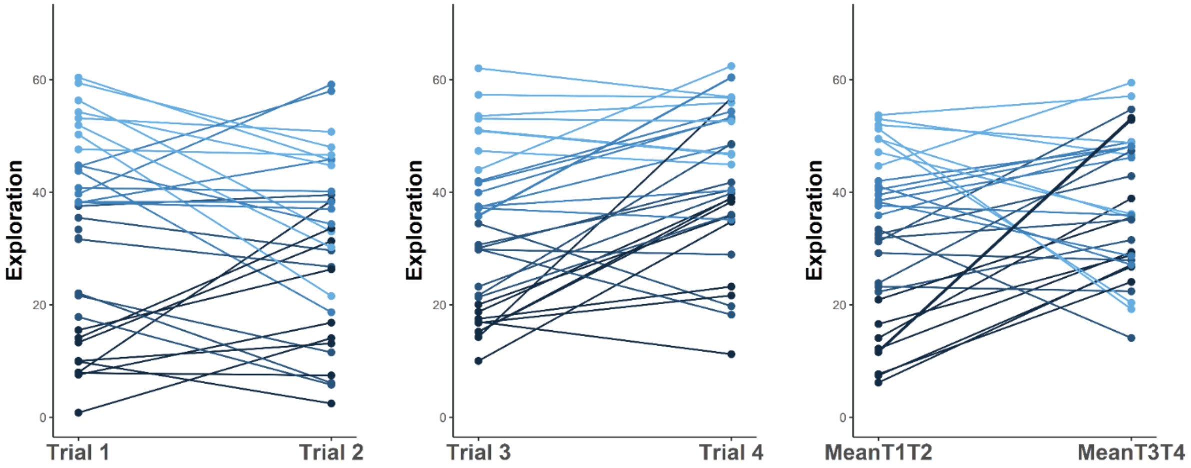

Figure S2A. Number of different squares visited by the fish during the 5-min observation period when they were either tested alone (i.e. Trials 1 and 2) or with a randomly selected audience (i.e. Trials 3 et 4). Colors indicate the quantile of personality scores measured during the first exposure to the stimuli, with lighter shades representing individuals with the highest exploratory scores. Individuals with maximal scores in both trials/conditions were not removed from the plots (but were removed from the analyses to avoid a ceiling effect).

Individuals significantly altered their exploration tendency across trials (LMM with a continuous variable for trials 1 through 4 and controlled for fish identity: t_{96}=3.136, P=0.003). Their behavior also differed on average between the alone and audience treatments (LMM with a fixed factor coding for the treatment and controlled for fish identity: t_{96}=2.665, P=0.009). In addition, the audience (n=7) had no effect on their personality (LMMs with and without a random intercept for the audience identity, on the data measured in presence of an audience with a random intercept for fish identity: χ^2_1=0.128, P=0.721). Similarly, the interval between T1-T2 and T3-T4 had no effect (LMMs with and without a random intercept for the scaled interval duration, on the data from the trial 2 and 4 controlled for the presence of an audience or not and with a random intercept for fish identity: χ^2_1=0.831, P=362).

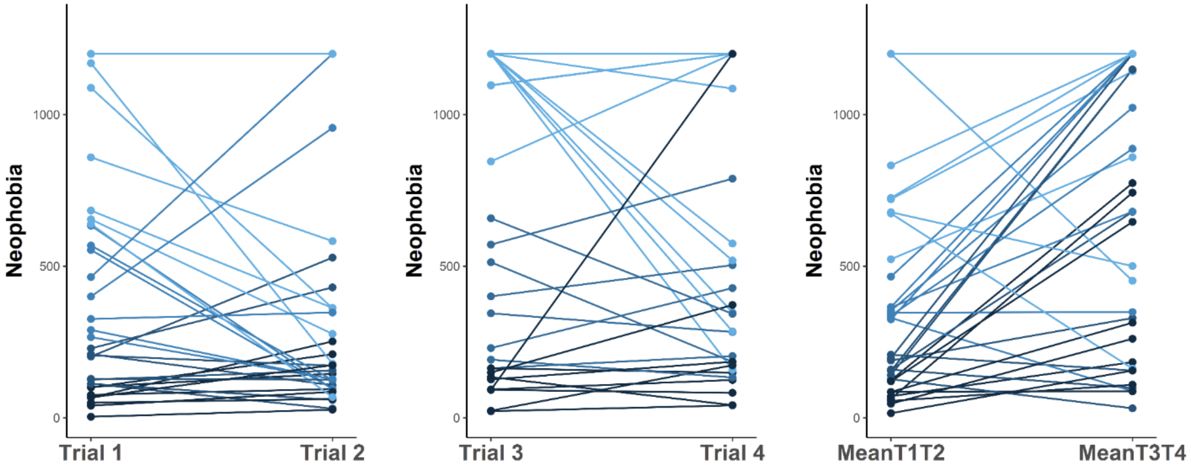

Figure S2B. Latency times taken by fish when they were tested either alone (i.e. Trials 1 and 2) or with a randomly selected audience (i.e. Trials 3 et 4). Colors indicate the quantile of the personality scores measured during the first exposure to the stimuli, with lighter shades representing individuals with the highest neophobia scores. Individuals with maximal scores in both trials/conditions were not removed from the plots (but were removed from the analyses to avoid a ceiling effect).

Individuals significantly altered their neophobia level across trials (LMM with a continuous variable for trials 1 through 4 and controlled for fish identity: t_{96}=3.880, P=0.003). Their behavior also differed on average between the alone and audience treatment (LMM with a fixed factor coding for the treatment and controlled for fish identity: t_{98}=5.195, P<0.001). In addition, the audience (n=9) had no effect on their personality (LMMs with and without a random intercept for the audience identity, on the data measured in presence of an audience with a random intercept for fish identity: $\chi^2_1 \approx 0$, P≈1). Similarly, the interval between T1-T2 and T3-T4 had no effect (LMMs with and without a random intercept for the scaled interval duration, on the data from the trial 2 and 4 controlled for the presence of an audience or not and with a random intercept for fish identity: $\chi^2_1 \approx 0$, P≈1).

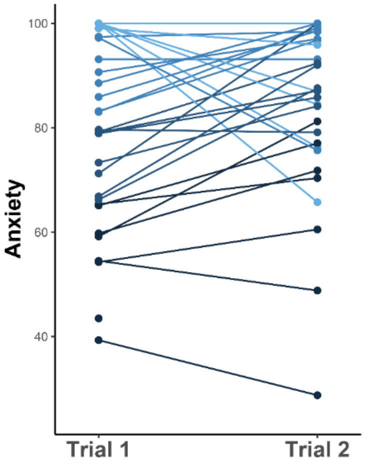

Figure S2C. Number of squares located at the periphery of the tank hat were visited by the fish without an audience (i.e. Trials 1 and 2). Colors indicate the quantile of the personality scores measured during the first exposure to the stimuli with lighter shades representing individuals with the highest anxiety scores. Individuals with maximal scores in both trials/conditions were not removed from the plots (but were removed from the analyses to avoid a ceiling effect).

CHAPITRE IV

Individual differences in anxiety are related to differences in cognitive performance and cognitive style

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ABSTRACT

Individuals of the same population generally differ in their cognitive abilities, that is in their capacity to acquire, process, store and act on information from the environment. The question of whether individuals with different personality types differ in their learning performances, despite being commonly addressed, has yielded mixed results. We propose that methodological differences among studies might have contributed to these contrasting results. Notably, the strength and direction of the association between personality and learning might be affected by which personality traits are considered and how they are measured. To test this hypothesis, we conducted an experiment with sailfin mollies (*Poecilia latipinna*). We assessed three personality traits that are likely to affect individuals' performance through influencing either their willingness to encounter the new situation (*i.e.,* exploration and neophobia) or their capacity to assess it (*i.e.,* anxiety). Then, we scored their performance in three learning tasks (*i.e.,* discriminant, spatial and reversal learning) after being extensively familiarized with the learning device (*i.e.,* all individuals were willing to encounter the task). As expected, only anxiety had a significant effect on learning performance, with less anxious fish performing better in the discriminant task but worse in the reversal task than highly anxious ones. Thus, our findings confirm a link between personality and cognition and are consistent with the idea that learning requires different steps that are each associated with different personality traits. Furthermore, despite the fact that highly anxious fish are less sensitive, some of them could perform well by increasing their response time.

Keywords: *Personality, Learning, Decision-making time, Cognitive style, Sailfin mollies*

INTRODUCTION

There is increasing empirical evidence that individuals differ in their cognitive abilities, that is in their capacity to acquire, process, store and act on information from the environment (Shettleworth 2001). At the intra-specific level, it has been suggested that differences in learning performances might be associated with differences in personality (i.e. a suite of individual behavioral differences that are consistent over time and contexts, Sih and Bell 2008), as personality characteristics could notably affect the way individuals sample their environment and hence their ability to rapidly detect environmental changes (Dall *et al*. 2005; Sih and Del Giudice 2012; Griffin *et al*. 2015). More precisely, because proactive individuals are risk-taking, bold, active and fast-exploring individuals, they should have more opportunities to learn new contingencies than reactive individuals that are risk-averse, shy, less active and slow-exploring (Koolhaas *et al*. 1999; Réale *et al*. 2007; Coppens *et al*. 2010; Carere and Locurto 2011; Sih and Del Giudice 2012; Griffin *et al*. 2015). In support of this expectation, a number of studies have found a positive association between boldness (or related traits) and learning performance (Dougherty and Guillette 2018; see also Table 1 and references therein). In contrast, several studies found no association between personality and cognition, while others reported an association in the opposite direction than expected.

We propose that the differences among studies in the reported results might be due to methodological differences, among other factors, the length of the familiarization period, or the personality traits that were measured and how they were measured. We focus on these factors since, in order to learn, an animal has first to encounter the new situation and then to assess it. These two distinct steps are likely to be affected by different personality traits that may differ in their level of consistency over time (Bell *et al*. 2009). This would cause variations in both the strength and direction of the correlations, depending on the frequency of encounter and the duration of familiarization with the environment, as well as on which traits and how they are measured. Specifically, the probability that an individual encounters a new situation should be higher in bold and exploratory individuals than in shy and less exploratory ones (Sih *et al*. 2004; Carere and Locurto 2011; Sih and Del Giudice 2012; Griffin *et al*. 2015). The effect of boldness and exploration on learning performances, however, should be stronger when individuals have been familiarized to the apparatus and experimental procedures over short periods of time before being tested. Supporting this idea, two experimental studies reported that less neophobic individuals had indeed greater cognitive performances than more neophobic ones, but only in the task they performed first. By contrast, neophobia had no significant effect on individuals' success on any of the subsequent tasks (Ducatez *et al*. 2015, Gibelli and Dubois 2017). Thus, because the familiarization period may vary considerably among studies, this factor could explain (at least partly) the apparent discrepancy in the effect of exploration and neophobia on learning performance.

Conversely, the ability of an animal to detect environmental changes is strongly influenced by its sensitivity to external stimuli, and hence may be mainly affected by stress-related personality traits. More precisely, as individuals with high levels of anxiety tend to focus their attention on threatening stimuli, they are less likely to use other environmental cues (Grupe and Nitschke 2013), and hence would be less capable of learning compared to less anxious individuals. Accordingly, differences in neurobiological processes involved in stress reactivity have been demonstrated to influence both anxiety behaviors and learning (*e.g.,* Moreira *et al*. 2004; Herrero *et al*. 2006; Johansen *et al*. 2011). Also, Bebus *et al*. (2016) reported that Florida Scrub-jays (*Aphelocoma coerulescens*) with low levels of corticosterone during development performed better on an associative learning task as adults than individuals that were exposed to high corticosterone levels. Finally, thigmotaxis (i.e. the tendency of animals to stay close to walls when exploring an open space), a risk-assessment behavior frequently used as an index of anxiety (Maximino *et al*. 2010), has been found to correlate negatively with learning performances, mostly in spatial tasks (Matzel *et al*. 2003, 2006; Herrero *et al*. 2006; Light *et al*. 2011). Measures of stress-related behaviors, however, may be considered as measures of exploration by certain authors (Matzel *et al*. 2003, 2006; Light *et al*. 2011; Etheredge *et al*. 2018). For instance, Depasquale *et al*. (2014) reported significant links between learning performance in a conditioning task, activity and exploration in Panamanian bishop fish (*Brachyrhaphis episcopi*). Yet, the strongest correlation was found between learning performance and freezing behavior, which is often used as a proxy of anxiety. Differences in the procedure used to assess the same personality trait, therefore, could also contribute in generating conflicting results (Carter *et al.* 2013).

In this study, we explored the relative influence of individual differences in exploration, neophobia and anxiety on both learning performance and cognitive style. Cognitive styles, defined as the specific strategies used by individuals to perform cognitive tasks (Bebus *et al*. 2016) may vary among individuals. Notably, because of the speed-accuracy trade-off, individuals might differ in how much time they take before making a decision or in their propensity to favor past over new information (Sih and Del Giudice 2012). We assessed the performance of Sailfin mollies (*Poecilia latipinna*) as well as the time they invested in decision-making in three cognitive tasks (*i.e.,* a discriminant, a spatial and a reversal learning task). Because the fish were extensively familiarized with the apparatus and experimental procedures prior to being tested, we expected learning performance to be mainly affected by anxiety. In addition, as high levels of anxiety are generally associated with lower learning performances, we predicted that the time required for a correct or an incorrect choice would differ only in highly anxious individuals, especially when confronted with a difficult task.

METHODS

Animals and housing conditions

We used 33 sexually mature male sailfin mollies aged 4 months that came from a commercial fish supplier (Mirdo Importations Canada Inc, Montreal, Quebec, Canada). The fish were kept in brackish water at 24±0.5°C with a 12:12 photoperiod and were fed with spirulina flakes (2% of their weight) and brine shrimps twice a day. Outside the experiments, focal males were housed either individually (15 individuals) in 3 L tanks (10×20×15 cm) or socially at a density of 3 ±1 fish (18 individuals) in 6 L tanks (20×20×15 cm). The experiments were conducted in June 2015 at the LARSEM (Laboratoire aquatique de recherche en sciences environnementales et médicales, Université Laval, Québec, Qc, Canada). The experimental procedures were approved by the Animal Care Committee of the Université Laval (animal care permit #2015027-1) and conformed to all guidelines of the Canadian Council on Animal Care (CCAC).

Personality traits

The trials were conducted between 8:30 am and 3:30 pm in a 54 L tank (60 l × 30 w × 30 h cm) whose sides were covered by black cloth to minimize disturbance and were recorded with a digital camera (JVC model GZ-MS120).

All individuals performed two tests (*i.e.,* open-field and novel object test) that are commonly used to assess personality traits (Réale *et al*., 2007). Specifically, the open-field test was used to measure exploration and thigmotaxis, an indicator of anxiety (Maximino *et al*. 2010), as the number of different squares (5 x 5 cm) visited during 5 min and the total number of visited squares that were located at the periphery of a wall, respectively. In contrast, the novel object test was used to measure neophobia as the latency to approach within 1 cm from a novel object within a 20-min period (for further details about the experimental procedures see Gibelli *et al*. 2018).

All individuals performed both tests in the same order (*i.e.,* open field test and novel object test) and each test was repeated twice with a 6 to 24 hr delay between the two replicates.

Learning performance

Experimental apparatus and general procedure

The tank was divided with a transparent removable partition into one observation compartment and one choice compartment that had two corridors, separated from each other by a porous partition (see Fig. 3 in Gibelli *et al*. 2018). Two visual cues of different shapes and colours (i.e. a yellow cross and a blue square of around 4 x 4 cm) were placed at the end of each corridor. Two identical cues were also placed in front of the corridors, to ensure that the fish could see them from the observation compartment. The rewarded cue was always counterbalanced across the subjects. The data in the learning trials were recorded at least 3 weeks after the end of the personality tests.

The trials were performed between 9:00 am and 2:00 pm and the fish received only one daily portion of food (instead of two) in the afternoon after the tests were completed. At the beginning of each trial, the focal fish was placed in the observation compartment for 5 min or until it has ceased freezing or swimming erratically. We then placed 3 spirulina flakes on the rewarded side (*i.e.,* spatial and reversal learning) or in front of the rewarded cue (*i.e.,* discriminant learning), and gently lifted the removable partition to allow the fish to enter the choice compartment and make a decision. To prevent the food from being visible from the observation compartment, it was placed behind a curved PVC partition. We considered that the fish had made a choice once half of its body had entered the choice compartment. If the fish succeeded, it could eat the 3 spirulina flakes before returning to the observation chamber. Otherwise, the observer gently activated the removable partition to encourage the fish to return into the observation chamber.

Discriminant learning task

As in Kotrschal and Taborsky (2010), we first trained the fish to associate a certain visual cue with a food reward and thereafter we determined the number of correct decisions made when presenting the cue. The training was conducted after 48h of food deprivation to ensure that all individuals were able to explore both corridors of the choice compartment before being tested. It consisted in 15 trials (*i.e.,* 5 trials per day every 2 days for 10 days) during which the fish could freely explore the experimental apparatus until they found the spirulina flakes that were dropped visibly in front of the rewarded cue. The position of the rewarded cue was pseudo-random (no more than 3 consecutive times on the same side) and the rewarded cues were presented in the same sequence for all fish. After the training was completed, the fish were again deprived of food for 24 h (or 48h if they made no choice in the first 20 min after 24-h of deprivation), and then they experienced 10 daily trials until they chose the rewarded cue six times consecutively. One individual was not able to explore both corridors and hence was not tested further.

Spatial and reversal learning tasks

One week later the fish were tested on a spatial learning task, in which they had to remember which of the two corridors of the tank contained food. Before being tested, they were deprived of food for 24 h (or 48 h if they made no choice in the first 20 min after 24h of food deprivation). The side of each visual cue (i.e. the yellow cross or the blue square) remained constant from one trial to the next and the fish were tested until they chose the correct corridor six consecutive times. Then after 2 to 2.5 h, they were tested on a reversal learning task in which the rewarded and unrewarded positions were switched, until they choose the rewarded cue six consecutive times. Two fish refused to participate in the reversal learning trials after the completion of the spatial task and hence were tested again after 24 h.

Statistical analysis

Our complete data set contained 5 missing values. On 3 occasions the missing values were due to technical problems. In the 2 other cases, we replaced the anxiety score of a fish by a missing value because the fish remained immobile in the middle of the test arena for the entire duration of the test, while another individual was never able to explore the choice compartments of the learning apparatus during the familiarization period and hence had no value for the reversal learning test.

First, we ensured that the three personality traits (i.e. exploration, anxiety and neophobia) were repeatable within individuals by fitting three linear mixed-effect models (*i.e.,* one model per trait) with a Gaussian distribution. The 2 replicates of a given trait were entered as the dependent variables, while the replicate number and the identity of the fish were entered as a fixed and a random factor, respectively. The repeatability of each trait was calculated using the rptGaussian function from the rptR package (Stoffel *et al*. 2017). Then we performed a principal component analysis (PCA) with the dudi.pca function (Chessel *et al*. 2004) to generate a composite variable for personality using the mean value of each personality trait. We removed all lines with missing values, standardized all the variables and extracted the loadings and the principal component scores (*i.e.,* composite variable(s)) of the principal component(s) with eigenvalues larger than 1. We also checked whether the principal components retained, if not related linearly, would be related quadratically (*e.g.,* Carazo *et al.* 2014).

Second, we checked whether the number of trials to reach the learning criterion differed between the tasks and if the fish differed between each other in their learning performance across the learning tasks. To do that, we created a linear mixed-effect model with a Gaussian distribution with the number of trials to reach the learning criterion as the dependent variable and the learning task (1= spatial learning, 2= reversal learning, 3=discrimination learning) as a fixed effect. To control for the identity of the fish and the rewarded cue, we added a random intercept for the cue and a random intercept for fish identity correlated with a random coefficient for the type of learning tasks (L= spatial and discrimination learning, R= reversal learning). Then, we used the 'anova' function to test for inter-individual differences by comparing the models with and without the intercept and slope for fish identity across the tasks.

Third, we tested whether the time before making a decision as well as the personality of the fish affected their probability of choosing the rewarded cue in a given trial using a generalized mixed-effects model with a binomial distribution from the lme4 R package (Bates *et al*., 2014). The success of the focal fish in each trial, estimated as a binary variable, was entered as the dependent variable, while the learning task, the time before making a decision and the extracted components scores of personality were entered as fixed factors. The time before making a decision was centered and scaled to prevent convergence errors. To control for the fish identity and the rewarded cue, we added a random intercept for the cue and a random intercept for fish identity correlated with a random coefficient for the type of learning tasks. The random coefficient for the type of task allowed the individuals to vary differently in their probability of success between the reversal and learning tasks. We used a model selection procedure based on the Akaike's Information Criterion for small sample (AIC_c) estimated with the MuMIn R package (Bartoń 2013) and selected the model with the smallest AIC_c.

Because there were significant interactions between the level of anxiety, the type of the task and the response time, we categorized each fish as less anxious (score < 84%, N=17) or highly anxious (score > 84%, N=16) and then we tested the effect of the response time on the probability of success for each type of fish and each task, separately. We also checked if the number of trials to reach the learning criterion in each task was related to an individual anxiety score using linear mixed models with a random intercept for the rewarded cue in the given learning task.

Fourth, we investigated whether the same individuals took consistently more time to decide when the decision-making time significantly influenced the chance of success. Specifically, for each individual (among those whose success was influenced by decision-making time), we counted the number of times its response time was above and below the median decision-time in the discriminant and reversal learning tasks. Then we tested whether the ratios of choices during which the fish had a response time above the median were correlated across the 2 tasks using a Spearman rank correlation test.

All statistical analyses were conducted on R 3.2.4 (R Core Team 2016).

RESULTS

The three personality traits were significantly repeatable between both trials (exploration: R=0.632, P=0.001; neophobia: R=0.433, P=0.018; anxiety: R=0.644, P=0.001). Furthermore, the principal component analysis extracted two components that collectively accounted for 88% of the variation (Table 2), revealing the existence of two independent dimensions. Specifically, exploration and neophobia loaded positively and negatively, respectively, on the

1st component, while anxiety loaded almost exclusively on the 2nd component. Furthermore, we found a significant quadratic relationship between the two first components (t_{29}=-3.119, P=0.004; Fig. 1) meaning that less neophobic and more exploratory fish had intermediate levels of anxiety.

Table II. Loadings from a PCA analysis exploring the relationships between the 3 personality traits (i.e., exploration, neophobia and anxiety).

	Principal component 1	**Principal component 2**
Exploration	0.902	0.028
Neophobia	-0.902	0.005
Anxiety	-0.020	0.999
Eigenvalue	**1.628**	**1.000**
% of variance	**54.3%**	**33.3%**

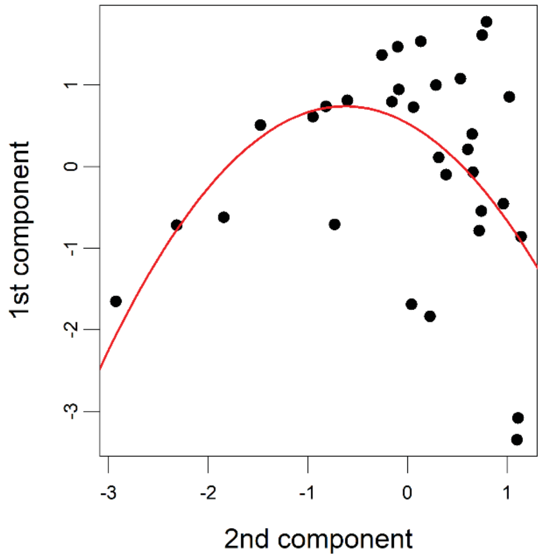

Figure 1. Relationship between the two principal components of personality extracted from the PCA. A high score on the 1st component represents a high level of exploration and a low level of neophobia and a high score on the 2nd component represents a high level of anxiety.

Individuals, on average, needed less trials to reach the learning criterion in the spatial learning task (mean ±SE: 10.875 ±0.948) than in the reversal (18.156 ±1.576; t_{43}=2.379, P=0.022) or discriminant (20.969 ±2.809; t_{62}=4.423, P<0.001) learning tasks. In addition, individuals significantly differed in their learning performance (χ^2_1=21.221, P<0.001) and individual differences in learning performances were explained by differences in anxiety (i.e. 2nd extracted component of the PCA). Specifically, highly anxious fish learned more slowly compared to less anxious ones (Table 3). Yet, there was a significant interaction between the level of anxiety and the task, indicating that the success of highly and less anxious fish depended on the task (Fig. 2). Accordingly, we found that less anxious individuals required less trials to reach the learning criterion than highly anxious individuals in the discriminant task (t_{29}=2.155, P=0.040). Inversely, highly anxious fish were faster to reach the learning criterion in the reversal task than less anxious fish (t_{28}=-2.901, P=0.007), while anxiety had no significant effect on individuals' performance in the spatial learning task (t_{29}=1.713, P=0.098).

Table III. Results from the model selection procedure exploring the link between individuals' learning success in all the tasks (dependent variable) and the type of task (either learning or reversal), personality (1st and 2nd components) and decision-making time during all the tasks (fixed factors). All models below delta=6 are shown.

Models	AICc	Delta
Task + time + 2nd component + task*2nd component + decision-making time*2nd component	1696.811	
Task + decision-making time + 2nd component + task*2nd component + time*2nd component + task*time	1698.647	1.835
Task + decision-making time + 2nd component + task*2nd component	1700.348	3.537
Task + decision-making time + 2nd component + time*2nd component	1700.527	3.716
Task + decision-making time + 2nd component + task*decision-making time + task*2nd component	1701.146	4.335
Task + decision-making time + 2nd component + task*decision-making time + time*2nd component	1702.207	5.396
Task*1st component + decision-making time*2nd component	1702.573	5.762

Table IV. Results from a generalized linear mixed model selected by AIC_c exploring the link between individuals' learning success and their learning strategy. The best model (AICc=1696.811) explaining individuals' learning success (binary variable), included the factor coding for the learning task, the decision-making time in each trial and the 2nd principal component scores extracted from the PCA (which represented the anxiety level of the fish) as fixed effects.

Variables	**Estimate**	**Std error**	**Z-value**	**P value**
Intercept	1.367	0.101	13.581	**<0.001**
Task (*i.e.,* learning or reversal)	-0.314	0.130	-2.413	**0.016**
2nd component (*i.e.,* anxiety)	-0.304	0.104	-2.929	**0.003**
Decision-making time	0.232	0.092	2.507	**0.012**
2nd component *Task	0.325	0.137	2.377	**0.018**
2nd component*decision-making time	0.206	0.084	2.445	**0.015**

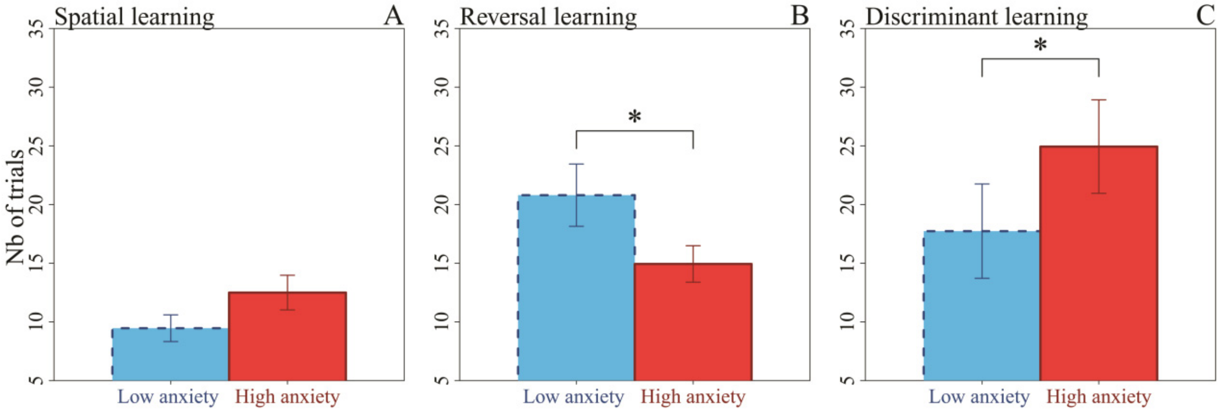

Figure 2. Number of trials to reach the learning criterion in individuals with a low level (dotted line, N=17) and a high level of anxiety (full line, N=16).

Finally, we detected a significant interaction between the level of anxiety of the fish and the time they spent before making a decision, indicating that the effect of the time before making a choice on the probability of success depended on the level of anxiety. Specifically, highly anxious fish had a higher probability of choosing the rewarded cue when they took more time before deciding in the reversal (z=2.241, P=0.025) and discriminant (z=2.202, P=0.028), tasks but not in the spatial learning task (z=0.510, P=0.610; Fig. 3). In contrast, the probability of success of less anxious individuals was not affected by the time they took before deciding in either task (spatial: z=1.114, P=0.265; reversal: z=-0.339, P=0.734; discriminant: z=1.016, P=0.310; Fig. 3). Finally, among anxious individuals, we found that the percentage of decisions for which the animal had a response time greater than the median time was correlated between the reversal and the discriminant learning tasks (N=16, r_s=0.865, P<0.001), which means that the longest individuals to make a decision were the same in both tasks.

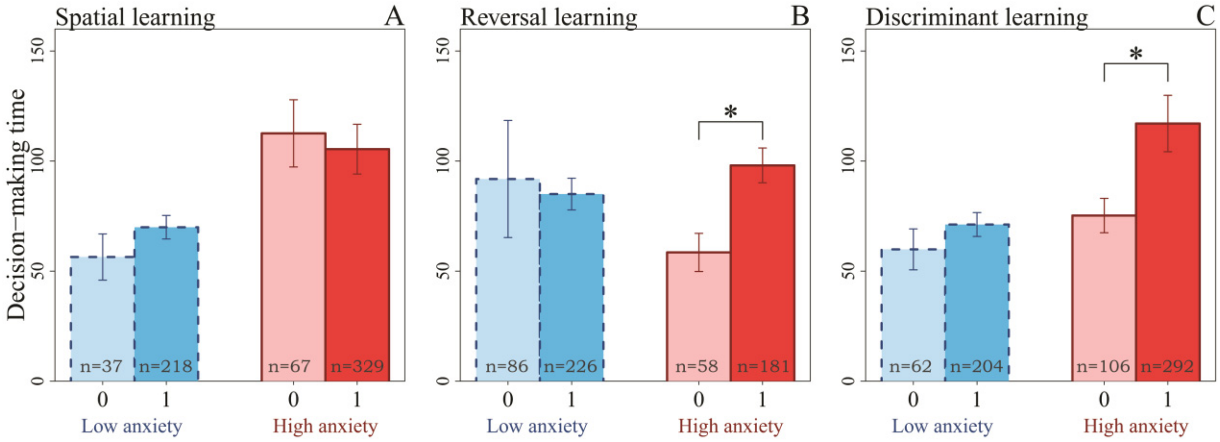

Figure 3. Mean time (±SE) before making a choice when the fish, with a low and a high level of anxiety, failed (0) or succeeded (1) in the spatial (A), reversal (B) and discriminant (C) learning tasks.

DISCUSSION

As anticipated, we found that the number of trials needed to reach the learning criterion did not differ between exploratory, less neophobic individuals and less-exploratory, more neophobic ones. By contrast, anxiety had a significant effect on individual learning performance in the two difficult tasks that required more trials to be solved. Specifically, less anxious fish performed better in the discriminant task but required more trials to reach the learning criterion in the reversal learning task than highly anxious individuals, while low and highly anxious fish did not differ in their learning performance in the spatial task. Anxiety is rarely studied in animal personality studies and the link between stress-related behavior (like anxiety) and learning performance, in particular, remains poorly examined. For instance, in a recent meta-analysis that was conducted to test the relationship between animal personality and cognition, Dougherty and Guillette (2018) only considered the big five personality traits (*i.e.,* exploration, boldness, activity, aggression and sociability), although other personality traits would be relevant for learning processes. Accordingly, we found that anxiety, which was not part of the behavioral syndrome between exploration and neophobia, was an important determinant of an individual's success in complex learning tasks. Highly anxious individuals would perform better in the reversal task but worse in the discriminant task than less anxious ones, probably because they constantly monitor their environment in search of potential threats. Consequently, they are very reactive to environmental changes and may inhibit a previously rewarded behavior very quickly but tend to make less accurate choices. This interpretation is supported by previous study findings that anxious rats were able to redirect their exploration effort toward the other alternatives in a holeboard test very quickly compared to less anxious individuals (Ohl *et al*. 2002). Thus, our findings are consistent with the hypothesis that the number of trials an individual takes to learn an association would depend (at least) on two distinct abilities that are associated with different personality traits. Specifically, high levels of exploration and boldness would increase the speed at which individuals solve a task by affecting their encounter rate with the task (or with the novel situation) (*e.g.,* Mesquita *et al*. 2015; Chung *et al*. 2017), while low levels of anxiety would increase the capacity of individuals to detect new stimuli and form new associations. In controlled laboratory experiments, we would then expect individual differences in exploration to be associated with differences in learning performances only when individuals are briefly familiarized with the apparatus (*e.g.,* Sommer-Trembo and Plath 2018).

Accordingly, Morand-Ferron *et al*. (2015) reported that the exploration score of great tits (*Parus major*) had no effect on their learning performance in the field when they were given a task that required their voluntary participation. Yet, further testing is required to examine how different personality traits would influence learning and cognition under natural conditions and under different degrees of familiarization, for example by controlling the duration (*i.e.,* number of days and/or number of training trials before testing), the testing arena (*i.e.,* integrated to the home cage or removed from it) or the social environment (*i.e.,* in presence of absence of an audience when testing a social species).

Individual success in learning tasks was also affected by the time an individual took before making a choice. Specifically, although highly anxious individuals, on average, performed worse than less anxious individuals in the discriminant task, their probability of making a correct choice increased with their response time. Thus, our findings confirm the idea that the strategy used by individuals to perform cognitive tasks may impact their success and are consistent with the trade-off hypothesis that less sensitive individuals may increase their chance of success by investing more time in examining the cues and making a response (Dyer and Chittka 2004). Furthermore, our results suggest that the learning strategy used by an individual would be (at least partly) constrained by its physiology. Indeed, we found that highly anxious individuals were consistent in their response time between the discriminant and reversal learning tasks, which suggest that some individuals would be less capable than others to increase their response time in order to increase their probability of success. In particular, spending a lot of time in examining the cues before making a choice may be energetically costly. Therefore, only anxious individuals with low energetic requirements could modulate their response time depending on the circumstances (Sih and Del Giudice 2012), while anxious individuals that are more affected by food deprivation would tend systematically to make a choice quickly and hence would have a higher probability of making an incorrect decision. This conclusion is supported by the fact that anxiety had no effect on individuals' learning performance in the spatial task. Yet individuals were tested in the spatial task after one week of resting and the spatial task required significantly less trials to be solved than the reversal and the discriminant tasks. For that reasons, it might have been less energetically demanding, thereby allowing all anxious individuals to wait before making a choice and to be as successful as less anxious individuals.

In conclusion, findings from the present study confirm the existence of a link between animal personality and cognition and support the idea that learning would require (at least) two distinct abilities that are associated with distinct personality traits. Specifically, the learning performance of an individual (i.e. the number of trials it takes to reach a learning criterion) would be affected first by its tendency to explore the environment (that determines its probability of encountering the new situations) and second by its reaction to stressful situations (that determines its ability to accurately assess the environmental stimuli). Furthermore, even if anxious individuals tend be less sensitive, some of them could nevertheless perform well on complex tasks by spending more time on examining the cues and making a decision. Because the same personality trait may be measured using a range of different behavioral assays and the subjects may be tested for learning after variable periods of familiarization, our finding can in part explain the differences reported in the literature concerning the link between personality and learning. However, additional studies would be required to explore the link between animal personality and cognition under natural conditions and look further whether other factors such as the learning measure or heterogeneity of the environmental conditions contribute to intra-and inter-specific differences.

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Table I. Studies investigating the relationship between personality and learning abilities. In the outcome column, **+** indicates a relationship in the expected direction (*e.g.,* fast/bold behavioral types exhibit greater learning performance or slow/reactive behavioral type exhibit greater reversal learning performances), 0 indicates no relationship and – indicates a relationship in the opposite direction. The learning abilities measured include conditioning tasks (C), discrimination learning (D), general learning ability (G), non-associative learning (N-a) and spatial learning (S). The sex of the subjects is denoted F for females, M for males and MF when both sexes were tested while NA indicates that the sex was not reported in the study.

Order	*Specie*	Details	N	Sex	Learning ability	Cue/task	Personality	Measure	Link	Authors
LEARNING										
Fish	*Gasterosteus aculeatus*	Wild-caught	10	M	**D**	Colors	Boldness	Exploration after a predator attack	**+**	Bensky *et al*. 2017
Fish	*Oncorhynchus mykiss*	Captive	95	NA	**C**	Predator odor	Boldness	Latency to emerge	**0**	Brown *et al*. 2013
Fish	*Brachyrhaphis episcopi*	Wild-caught	27	F	**C**	Light signal	Activity & exploration	Open-field (general activity)	**+**	DePasquale *et al*. 2014
							Activity & exploration	Open-field (time spent frozen)	**+**	
							Activity & exploration	Open-field (latency to reach the edge)	**+**	
Fish	*Poecilia reticulata*	Captive	32	M	**D**	Colors	Boldness	Predator inspection	**+**	Dugatkin and Alfieri. 2003
Fish	*Gambusia affinis*	Wild-caught	8	M	**D**	Objects' number	Activity	Locomotion during sociability trials	**0**	Etheredge *et al*. 2018
			8	M			Anxiety & Exploration	Scototaxis & thigmotaxis	**+**	
			11	F			Activity	Locomotion during sociability trials	**+**	
			11	F			Anxiety & Exploration	Scototaxis & thigmotaxis	**-**	
			19	MF			Sociability**	Preference for conspecifics	**-**	
Fish	*Gasterosteus aculeatus*	Wild-caught	47	MF	**S**	T-maze	Boldness	Time out of cover & catch order	**0**	Mamuneas *et al*. 2015
Fish	*Cyprinus carpio*	Captive	40	NA	**D**	Colors	Boldness	Latency to emerge	**-**	Mesquita *et al*. 2015

Fish	*Oncorhynchus mykiss*	Captive	42	NA	**C**	Light signal	Boldness	Time spent under cover	**+**	Sneddon. 2003
Fish	*Poecilia mexicana*	Captive	24	F	**C**	Sounds / light signal	Boldness	Latency to emerge & time spent frozen after a predator attack	**0**	Sommer-Trembo *et al*. 2018
Fish	*Poecilia reticulata*	Wild-caught	79	MF	**D**	Colors	Boldness	Novel object	**+**	Trompf and Brown. 2014
Bird	*Aphelocoma coerulescens*	Wild-caught	15	MF	**D**	Colors	Exploration	Open-field (latency to reach all the locations)	**0**	Bebus *et al*. 2016
			21	MF			Neophobia	Novel object	**0**	
Bird	*Anas platyrhynchos*	Captive	10	F	**S**	X-maze	Exploration	Novel environment without and with a novel object	**0**	Boursquet *et al*. 2015
Bird	*Taenopygia guttata*	Captive	14	MF	**D**	Colors	Activity	Locations visited	**0**	Brust *et al*. 2013
							Fearfulness	Tonic immobility	**0**	
Bird	*Gallus gallus domesticus*	Captive	20	F	**D**	Colored symbol	Exploration	Open-field (latency to walk)	**-**	de Haas *et al*. 2016
							Docility	Struggling rate & vocalization in manual restraint	**-**	
Bird	*Quiscalus lugubris*	Wild-caught	49	MF	**D**	Colors	Shyness	Latency to feed after a disturbance	**0**	Ducatez *et al*. 2015
							Neophobia	Novel object	**0**	
Bird	*Taenopygia guttata*	Captive	22	MF	**D**	Colors	Neophobia	Novel object	**0**	Gibelli and Dubois. 2017
Bird	*Milvago chimango*	Wild-caught	21	F	**D**	Colors	Neophobia	Latency to approach the apparatus	**0**	Guido *et al*. 2017
Bird	*Poecile atricapillus*	Wild-caught	22	MF	**D**	Sounds	Exploration	Novel environment	**+**	Guillette *et al*. 2009
Bird	*Poecile atricapillus*	Wild-caught	27	MF	**D**	Sounds	Exploration	Novel environment	**0**	Guillette *et al*. 2010
Bird	*Poecile atricapillus*	Wild-caught	24	MF	**D**	Sounds / Colors	Exploration	Novel environment	**0**	Guillette *et al*. 2015
Bird	*Phasianus colchicus*	Captive	80	MF	**D**	Distance	Exploration	Number of visited feeders	**+**	Madden *et al*. 2018
			173	MF	**D**	Colors	Exploration	Novel environment, object and approach of an unknown conspecific (PCA)	**0**	
Bird	*Melopsittacus undulatus*	Captive	30	M	**S**	Landmarks	Exploration	Novel & familiar environment	**0**	Medina-García *et al*. 2017

							Neophobia	Food & object neophobia	**0**	
Bird	*Parus major*	Wild	21	MF	**D**	Colors	Exploration	Novel environment	**0**	Morand-Ferron *et al*. 2015
Bird	*Corvus corax*	Captive & wild-caught	11	MF	**D**	Colors	Object exploration	Novel object (number of actions)	**+**	Range *et al*. 2006
					S	T-maze	Object exploration	Novel object (number of actions)	**+**	
Bird	*Parus major*	Wild-caught	52	MF	**D**	Colors	Exploration	Novel environment & Novel object	**0**	Titulaer *et al*. 2012
Mammal	*Sus scrofa domesticus*	Captive	60	MF	**S**	T-maze	Docility	Struggling rate	**0**	Bolhuis *et al*. 2004
Mammal	*Cavia porcellus*	Captive	20	MF	**D**	Object size	Boldness	Novel object	**0**	Brust and Guenther. 2017
							Aggressiveness	Aggressive behaviors	**0**	
							Sociability**	Positive contact with conspecifics	**-**	
Mammal	*Rattus norvegicus*	Sprague Dawley	162	M	**D**	Holeboard	Exploration	Open field (distance and speed)	**+**	Feyissa *et al*. 2017
							Anxiety	Elevated plus maze	**+**	
Mammal	*Mus musculus*	Outbred mice	40	MF	**G**	Spatial learning & problem solving	Anxiety	Open-field (movements, defecation, latency/time spent leaving the center)	**0**	Galsworthy *et al*. 2002
Mammal	*Cavia aperea*	Wild-caught	18	MF	**D**	3D shapes	Boldness	Novel object	**+**	Guenther *et al*. 2014
							Activity	Locomotion during learning trials	**+**	
							Aggressiveness	Dyad confrontations	**+**	
Mammal	*Rattus norvegicus*	Wistar rats	80	M	**S**	Spatial water maze	Anxiety	Open-field (time in the center) & Elevated plus maze	**+**	Herrero *et al*. 2006
Mammal	*Mus musculus*	CF1	30	M	**S**	Lashley III maze	Exploration	Open field with a novel object (time in the center)	**+**	Kazlauckas *et al*. 2005
Mammal	*Mus musculus*	CD-1 outbred	24	M	**G**	Diverse tasks*	Exploration	Novel object (% of time exploring)	**+**	Light *et al*. 2011
							Exploration	Open-field (% in the unwalled quadrant)	**+**	
Mammal	*Myodes glareolus*	Captive	86	MF	**D**	Odors	Boldness	Novel object	**+**	Mazza *et al*. 2018

							Activity & Exploration	Open-field (general activity & time in the center)	**+**	
Mammal	*Mus musculus*	CD-1 outbred	24	M	**G**	Diverse tasks*	Exploration	Open-field (% in the unwalled quadrant)	**+**	Matzel *et al*. 2006
Mammal	*Mus musculus*	CD-1 outbred	56	M	**G**	Diverse tasks*	Exploration	Open-field (% in unwalled quadrants)	**+**	Matzel *et al*. 2003
							Exploration	Open-field (general activity)	**+**	
Mammal	*Capra hircus*	Captive	16	MF	**D**	Color & shape	Exploration	Novel object & Novel environment	**0**	Nawroth *et al*. 2017
							Sociability**	Attraction to conspecifics and isolation test	**+**	
					N-a	Object switch	Exploration	Novel object & Novel environment	**-**	
							Sociability**	Attraction to conspecifics and isolation test	**0**	
Mammal	*Micromys minutus*	Captive	57	MF	**S**	6-arms-maze	Boldness	Latency to emerge & open-field (Time in the center)	**0**	Schuster *et al*. 2017
							Activity	Open-field (general activity)	**+**	
							Exploration	Novel object & Novel environment	**0**	
Reptile	*Eulamprus quoyii*	Wild-caught	64	MF	**S**	T-maze	Boldness	Latency to emerge after a simulated predator attack	**Quadratic**	Carazo *et al*. 2014
							Boldness	Neophilia	**0**	
							Exploration	Latency to visit a novel environment & locomotion	**0**	
Reptile	*Lampropholis delicata*	Wild-caught	50	M	**D** & **S**	Colors & Location	Activity, exploration & sociability	Open-field (general activity), latency to reach a goal compartment & preference for conspecifics (PCA)	**+**	Chung *et al*. 2017
			28	M	**D**	Colors			**+**	
Arthropod	*Portia labia*	Wild-caught	30	F	**D**	Prey size	Aggressiveness	Aggressive behaviors	**0**	Chang *et al*. 2016
Arthropod	*Camponotus aethiops*	Wild-caught	45	NA	**D**	Odors	Exploration	Open-field (general activity)	**-**	Udino *et al*. 2016
							Sociability**	Social behaviors	**0**	
							Aggressiveness	Agonistic behaviors	**0**	

REVERSAL LEARNING

Fish	*Salvelinus fontinalis*	Captive	14	NA	**S**	X-maze with landmarks	Boldness	Open-field (time in the center)	**+**	White *et al*. 2017
Fish	*Gasterosteus aculeatus*	Wild-caught	10	MF	**D**	Colors	Boldness	Exploration after predator attack	**0**	Bensky *et al*. 2017
Bird	*Aphelocoma coerulescens*	Wild-caught	15	MF	**D**	Colors	Exploration	Open-field (latencies to reach all the locations)	**0**	Bebus *et al*. 2016
			21	MF			Neophobia	Novel object	**+**	
Bird	*Taenopygia guttata*	Captive	11	MF	**D**	Colors	Activity	Locations visited	**0**	Brust *et al*. 2013
							Fearfulness	Tonic immobility	**+**	
Bird	*Milvago chimango*	Wild-caught	21	F	**D**	Colors	Neophobia	Latency to approach the apparatus	**-**	Guido *et al*. 2017
Bird	*Poecile atricapillus*	Wild-caugth	27	MF	**D**	Sounds	Exploration	Novel environment	**+**	Guillette *et al*. 2010
Bird	*Poecile atricapillus*	Wild-caught	24	MF	**D**	Sounds	Exploration	Novel environment	**0**	Guillette *et al*. 2015
Bird	*Quiscalus mexicanus*	Wild-caught	8	MF	**D**	Colors	Boldness	Time in the safer section	**0**	Logan 2016
							Exploration	Movements between sections of the aviary	**0**	
							Neophobia	Novel object	**0**	
Bird	*Phasianus colchicus*	Captive	173	MF	**D**	Colors	Exploration	Novel environment, object and approach of an unknown conspecific (PCA)	**+**	Madden *et al*. 2018
			80	MF	**D**	Distance	Exploration	Number of visited feeders	**0**	
Bird	*Corvus corax*	Captive & wild-caught	11	MF	**S**	T-maze	Object exploration	Novel object (number of actions)	**0**	Range *et al*. 2006
					D	Colors	Object exploration	Novel object (number of actions)	**0**	
Bird	*Cactospiza pallida*	Wild-caught	10	NA	**D**	Colors	Neophobia	Novel object/apparatus	**+**	Tebbich *et al*. 2012
Bird	*Camarhynchus parvulus*	Wild-caught	16	NA			Neophobia	Novel object/apparatus	**0**	
Bird	*Parus major*	Wild-caught	31	M	**D**	Colors	Exploration	Novel environment & Novel object	**-**	Titulaer *et al*. 2012
			21	F			Exploration	Novel environment & Novel object	**+**	

Bird	*Parus major*	Captive	67	M	**S**	Feeder position	Exploration	Novel environment	**+**	Verbeek *et al*. 1994
Mammal	*Sus scrofa domesticus*	Captive	60	MF	**S**	T-maze	Docility	Struggling rate	**+**	Bolhuis *et al*. 2004
Mammal	*Cavia aperea*	Wild-caught	9	MF	**D**	3D shapes	Boldness	Novel object	**0**	Guenther *et al*. 2014
							Activity	Locomotion during learning trials	**0**	
							Aggressiveness	Dyad confrontations	**+**	
Mammal	*Myodes glareolus*	Captive	86	MF	**D**	T-maze	Boldness	Novel object	**+**	Mazza *et al*. 2018
							Activity & Exploration	Open-field (general activity & time in the center)	**+**	

*Lashley III maze, passive avoidance, odor discrimination, associative fear conditioning and spatial mazes

**Sociability: we expect that asocial individuals to have higher learning performances

CHAPITRE V

Conclusions générales

1) Conclusions

En conclusion, les résultats de cette thèse montrent que la plasticité comportementale pourrait être difficile à estimer avec une mesure unique et générale (Chapitre III). Malgré une plasticité plus importante en réponse au gradient social (Chapitre II), les individus timides/réactifs ne différaient pas dans leurs performances d'apprentissage lorsqu'ils étaient familiarisés au dispositif et à la procédure (Chapitre II et IV). La timidité/réactivité serait donc un indicateur de la vitesse à laquelle les individus entrent en contact avec les contingences environnementales alors que l'anxiété reflèterait les différences de sensibilité aux stimuli externes (*i.e.,* performances d'apprentissage). De plus, il existe un effet du sexe sur les capacités d'apprentissage : le compromis négatif entre vitesse et précision au niveau de l'apprentissage était présent chez les femelles Diamants mandarins seulement (Chapitre II) et les mâles rapides dans une tâche d'apprentissage discriminant inhibait leur comportement en présence de congénères, indiquant qu'ils seraient probablement moins compétitifs (Chapitre II et résultats supplémentaires). L'expression de la plasticité pourrait donc être déterminée par les bénéfices qui lui sont associés et/ou être limitée par des contraintes neurales ou physiologiques dans d'autres contextes. De plus, l'association de différents traits de personnalité avec différentes étapes de l'apprentissage pourraient expliquer les corrélations faibles entre les mesures de plasticité comportementale et suggère que de pressions de sélection conflictuelles pourraient s'exercer sur les différents aspects requis pour l'expression de la plasticité comportementale.

a) Quels facteurs expliquent la plasticité comportementale ?

Nous n'avons pas trouvé de corrélations entre les indices de la plasticité comportementale incluant la norme de réaction et l'apprentissage à renforcements inversé ni chez les Diamants mandarins (N=18, R=-0.218, P=0.386, Chapitre II) ni chez les Mollies voiles (Chapitre III). Ce premier point indique donc que les différences de performances dans l'apprentissage à renforcements inversés ne reflètent pas des différences de plasticité contextuelle et ne peuvent donc pas être utilisées comme un indicateur général de la capacité à s'adapter aux variations environnementales. Similairement, nous n'avons pas été capables de mettre en évidence un facteur expliquant l'ensemble des mesures de plasticité relevées dans le chapitre III. Même en considérant uniquement la plasticité de la personnalité, la variance des différentes mesures n'était pas expliquée par une composante unique mais par trois différentes composantes. De plus, les mesures de personnalité dans le gradient social ont été prises dans le même ordre, ce qui aurait pu augmenter les corrélations entre les mesures de plasticité associées (voir section 7 de l'introduction : plasticité réalisée et plasticité potentielle). En conséquence, contrairement aux capacités cognitives (Shaw et Schmelz 2017; Cauchoix *et al*. 2018), les résultats suggèrent que la plasticité comportementale aurait une répétabilité très faible (*i.e.,* une corrélation moyenne de 0.17) et ne serait pas générale (Chapitre III). La plasticité de chaque trait est plutôt susceptible de varier en fonction des différentes caractéristiques de l'individu et/ou des coûts et bénéfices associés au trait lui-même (*e.g.,* Mathot *et al*. 2011; Mitchell et Biro 2017).

Cependant, nous avons quand même observé des corrélations plus fortes entre les mesures de plasticité prises sur différents traits de personnalité lorsque les changements étaient plus subtils (*e.g.,* entre les conditions différant par l'audience sélectionnée) que lorsqu'ils étaient plus évidents (*e.g.,* entre la condition seule et celle avec une audience) (Chapitre III). Cela suggère que lorsque les changements environnementaux sont potentiellement détectables par tous les individus, les différences interindividuelles de plasticité devraient être moins fortes. De plus, il est possible que les individus plus sensibles et plus timides aient été ceux capables de détecter les changements subtils dans les conditions sociales et de s'y ajuster (Koolhaas *et al*. 1999; Sih et Del Giudice 2012). En accord avec cette idée, les Diamants mandarins néophobes ont plus modifié leur comportement en fonction des conditions sociales que les moins néophobes (Chapitre II). En revanche, les individus plus plastiques dans leur personnalité ne réussissaient pas plus rapidement les tâches d'apprentissage (Chapitre II ; chapitre III : $P \geq 0.17$ pour l'apprentissage discriminant et $P \geq 0.05$ pour l'apprentissage spatial). Ce type de plasticité ne demanderait donc pas nécessairement de former des associations rapidement. Les différences de plasticité contextuelle pourraient plutôt être dues à la vitesse à laquelle les individus peu explorateurs et néophobes entrent en contact avec les contingences de leur environnement (Chapitre IV). En effet, les individus timides pourraient prendre plus de temps afin d'évaluer adéquatement les risques et acquérir de l'information dans le but de réduire leur incertitude (*e.g.,* Mathot *et al*. 2012). Ainsi, développer une plus grande sensibilité aux changements leur permettrait de choisir un habitat adapté et de limiter leur vulnérabilité à la prédation (*e.g.,* Dubois et Giraldeau 2014).

b) Comment la personnalité influence les performances d'apprentissage et le style cognitif ?

Les traits de personnalité mesurés sur l'axe hardiesse-timidité et proactivité-réactivité, incluant l'exploration et la néophobie, semblent donc refléter la vitesse à laquelle un individu entre en contact avec les contingences plutôt que sa capacité à détecter/traiter l'information. En effet, nous n'avons pas trouvé de lien entre cette dimension de la personnalité et les performances d'apprentissage discriminant, spatial ou à renforcements inversés lorsque les individus étaient bien familiarisés aux dispositifs (Chapitre II et IV). La néophobie expliquait seulement les performances dans la première tâche d'apprentissage testée dans le chapitre II, à l'instar de Ducatez *et al*. (2015) qui trouvaient aussi un effet de la timidité uniquement sur la première tâche chez le Quiscale merle (*Quiscalus lugubris*). Allant dans ce sens, une méta-analyse récente a aussi montré que les traits de personnalité (*i.e.,* cinq traits centraux de la personnalité incluant la hardiesse, l'exploration, l'activité, l'agressivité et la sociabilité) analogues aux *Big Five* chez les humains n'expliquaient pas les performances d'apprentissage, à l'exception d'un effet marginal de la hardiesse face à un prédateur (Dougherty et Guillette 2018).

L'axe impulsivité-anxiété semble en revanche avoir un impact important sur les performances d'apprentissage (Chapitre IV). En effet, les individus anxieux faisaient globalement plus d'erreurs suggérant que leur haut niveau de stress pourrait affecter négativement leur capacité à détecter les changements et/ou traiter l'information. Ils étaient néanmoins plus rapides lors de l'apprentissage à renforcements inversés, probablement parce qu'ils ont réussi à inhiber leur comportement rapidement contrairement aux moins anxieux, potentiellement plus impulsifs et persévérants (Steimer *et al*. 1997). De plus, nous avons observé que les plus anxieux avaient des chances de succès augmentées, s'ils investissaient plus de temps lors de leurs décisions dans l'apprentissage discriminant et à renforcements inversés. Parmi les anxieux, certains individus investissaient systématiquement plus de temps que les autres avant de faire un choix dans ces deux tâches d'apprentissage, ce qui suggère l'existence de contraintes limitant leur temps de décision. Notamment, ces deux tâches étaient les plus difficiles, requéraient plus d'essais et les coûts énergétiques nécessaires à l'échantillonnage de l'information étaient probablement plus élevés que pour la tâche spatiale qui était testée après une semaine de repos et dont les stimuli restaient au même endroit. Des différences dans les besoins énergétiques des individus pourraient donc être responsables du compromis entre vitesse et précision qui était observé chez les individus anxieux. Cette idée suggère que la sensibilité aux stimuli externes pourrait dépendre en partie d'un budget énergétique limité. Cela expliquerait aussi, malgré le fait que certains individus pourraient être généralement plus sensibles que les autres, les corrélations faibles observées entre les différentes mesures de plasticité (Chapitre III).

c) Différences entre les sexes dans l'apprentissage à renforcements inversés

Nous avons observé un compromis entre les vitesses d'apprentissage à renforcements inversés et d'apprentissage discriminant chez les femelles Diamants mandarins uniquement (Chapitre II). En tant qu'espèce monogame, les femelles Diamants mandarins sont très sélectives dans le choix de leur partenaire et investissent beaucoup de temps afin d'évaluer la qualité des mâles. Ce compromis entre apprentissage rapide (vitesse) et lent, mais flexible (rétention de l'information et précision) pourrait refléter l'existence de deux stratégies garantissant le maintien d'un bon succès reproducteur pour les femelles. Par ailleurs, d'autres études ont démontré chez les guppies (*Poecilia reticulata*) que les femelles étaient capables de contourner une barrière transparente et renversaient les associations plus rapidement que les mâles (Lucon-Xiccato et Bisazza 2014, 2017) et chez les mésanges charbonnières (*Parus major*) que la direction de l'association entre personnalité et apprentissage à renforcements inversés dépendait du sexe (Titulaer *et al*. 2012). Un effet du sexe sur la vitesse dans l'apprentissage à renforcements inversés suggère l'existence de styles cognitifs différents selon le sexe des individus et indique un rôle potentiel de la sélection sexuelle sur la cognition. En effet, les femelles et les mâles pourraient tirer des avantages différents des capacités cognitives. Par exemple, la persistance utile lors de la recherche de partenaire chez les mâles guppies, pourrait se traduire par des capacités moindres en apprentissage à renforcements inversés (*i.e.,* moins bonnes capacités à inhiber son comportement) en comparaison des femelles (Lucon-Xiccato et Bisazza 2014). Il serait donc important d'examiner les différences selon les sexes et les régimes de reproduction (*i.e.,* monogamie, polygynie...*etc*.). Notamment, on pourrait s'attendre à des différences plus marquées chez les espèces polygynes où l'investissement parental est plus inégal et/ou lorsque l'écologie des deux sexes est très différente (*i.e.,* différents microhabitats, distance de dispersion, intensité de la compétition…*etc.*).

d) Limitations

Dans le chapitre II, les tests des mâles et des femelles ont été réalisés à deux périodes différentes. Néanmoins les oiseaux étaient maintenus dans des conditions constantes d'humidité, température et photopériode tout au long de l'année. Les procédures associées aux soins des animaux étaient les mêmes pour les mâles et les femelles. Surtout, la personnalité, mesurée dans des conditions standards sans congénère, a été démontrée comme étant stable à moyen terme chez les diamants mandarins. En effet, la tendance à l'exploration (un trait généralement très corrélé avec la néophobie) restait stable sur une période de 7 mois chez cette espèce (David *et al.* 2012). Il est à noter qu'une autre étude a montré que la répétabilité de la néophobie chez les diamants mandarins était similaire entre les sexes mais faible. En revanche, cette même étude indique que cette faible répétabilité pourrait être due aux différences entre les objets nouveaux utilisés (Wuerz et Krüger 2015). Finalement, les corrélations sont fortes mais la taille de l'échantillon (n=18) doit être prise en considération et des études avec plus d'individus devraient être réalisées.

Dans le chapitre III, l'audience utilisée aurait pu avoir un effet important sur les mesures de personnalité chez les Mollies voiles. Par contre, les individus audience étaient contenus dans un espace restreint afin de limiter les interactions avec le mâle focal. L'audience s'est d'ailleurs révélée comme n'ayant pas d'effet significatif sur les mesures de personnalité.

Finalement, le fait que les tests de personnalité aient été réalisés sur de courtes périodes de temps (1 semaine entre les conditions) en général est une limitation importante. Les corrélations risquent donc d'être plus élevées en raison d'une confusion possible avec des effets environnementaux à court terme. Dans le chapitre III, ce problème a moins d'importance dans le mesure où nous ne trouvons pas de corrélations entre les mesures de plasticité et que nous argumentons pour l'absence d'une plasticité générale. En revanche, bien que la personnalité devrait être stable à travers le temps et les contextes, cela est à prendre en considération dans le chapitre II et IV.

2) Perspectives et résultats supplémentaires

a) Est-ce que l'apprentissage influence la plasticité chez les mollies voiles ? Effet possible de la capacité compétitive de l'individu.

Dans le chapitre III, l'apprentissage inversé n'était que très faiblement corrélé à la plasticité de la personnalité chez les mollies voiles. En revanche, des résultats additionnels indiquent que l'apprentissage pourrait être relié à la plasticité. Notamment, après sélection du meilleur modèle en fonction de critère d'information d'Akaike (AIC), la plasticité de l'un des comportements de reproduction (*i.e.,* les mordillements au niveau du pore urogénital) était expliquée par le taux de succès dans l'apprentissage discriminant (meilleur modèle : t_{30}=2.998, P=0.005). Notamment, l'apprentissage discriminant demandait à l'individu de suivre un stimulus visuel plutôt que de se fier à la position de la récompense, et similairement, l'expression des comportements de reproduction est fortement dépendante de ceux des compétiteurs et de leurs mouvements respectifs par rapport à la femelle. Allant dans ce sens, la précision dans l'apprentissage discriminant était aussi reliée à l'utilisation d'une tactique *furtive* en présence de compétiteurs, *i.e.,* plus de tentatives d'insémination directes que de mordillements près du pore urogénital (t_{30}=2.815, P=0.009). En effet, une plus grande précision lors de l'apprentissage bénéficierait aux mâles *furtifs* qui pourraient ainsi augmenter leur succès reproducteur, contrairement aux mâles *bourgeois* dont le succès n'en serait pas affecté d'après une étude chez un poisson *cyprinidé* (*Rhodeus ocellatus*) (Smith *et al*. 2015). Notamment des meilleures capacités cognitives pourraient permettre aux mâles de mieux distribuer leurs efforts de reproduction. En effet, les individus furtifs sont de moins bons compétiteurs qui ont de ce fait un accès réduit aux femelles lorsqu'ils sont en présence de mâles bourgeois dominants et souvent plus grands (Baird 1974; Travis et Woodward 1989). C'est probablement pour cette raison que les mâles ont modifié en particulier leurs comportements de mordillements (Chapitre III) qui demandent un accès relativement prolongé à la femelle en comparaison des tentatives d'insémination pouvant être très brèves. Cependant, cela implique aussi que la capacité compétitive des individus, en limitant la production de certains de leurs comportements, pourrait expliquer la plasticité contextuelle exprimée (*i.e.,* plasticité réalisée). Quelques exemples appuient cette idée. Entre autres, le statut de dominance des moineaux domestiques (*Passer domesticus*) déterminerait les comportements qu'ils peuvent adopter et leur degré de plasticité dans un contexte où les comportements sont sujets à la fréquence-dépendance négative (Lendvai *et al*. 2006). Plus précisément, les dominants augmentaient plus leur utilisation du chapardage au détriment de la production (*i.e.,* chercher la nourriture par eux-mêmes) en réponse à une perte d'énergie au cours de la nuit. Au contraire, les subordonnés étaient moins plastiques mais plus variables entre eux, probablement parce qu'ils n'étaient pas toujours capables de chaparder tous les individus du groupe, en particulier les dominants défendant parfois leur parcelle de nourriture chez cette espèce. Similairement, dans une autre étude, le lien entre une personnalité réactive et une plus grande plasticité, était significatif seulement chez les mésanges charbonnières (*Parus major*) dominantes qui étaient probablement moins limitées par les choix des autres (Quinn *et al*. 2012). Il est difficile de savoir si l'apprentissage favorisait directement la plasticité contextuelle des mâles ou bien si le lien est indirect, d'autant plus que des capacités cognitives élevées pourraient avoir un coût en termes de capacités compétitives (Mery et Kawecki 2003). Les résultats du chapitre II favorisent néanmoins la seconde hypothèse. En effet, l'apprentissage dans une tâche complexe était relié au sens dans lequel les Diamants mandarins se sont ajustés au contexte social. Ainsi, les oiseaux plus performants avaient tendance à augmenter leur néophobie lorsque des congénères étaient présents près du nouvel objet et du pot de nourriture, ce qui suggère également une possible influence des capacités compétitives. De futurs travaux devraient s'intéresser à différencier l'influence de l'apprentissage et des capacités compétitives sur la plasticité contextuelle. Notamment, est-ce que l'apprentissage serait relié à la plasticité contextuelle en réponse au contexte social seulement, *i.e.,* lorsque les individus peuvent prendre des décisions pour limiter la compétition et/ou peuvent interférer et limiter les comportements des autres ?

b) Quelle est l'importance de la familiarisation dans les tests cognitifs ?

Une des rares études ayant examiné les performances d'apprentissage directement en nature n'a pas trouvé de lien entre l'apprentissage et la tendance à l'exploration chez les mésanges charbonnières (*Parus major*) (Morand-Ferron *et al*. 2015). Malgré la nécessité de réaliser des études supplémentaires examinant la personnalité et l'apprentissage en nature, il est intéressant de constater une absence de lien lorsque les oiseaux pouvaient participer volontairement à résoudre la tâche et donc potentiellement réguler eux-mêmes leur temps avant d'approcher des stimuli nouveaux. La résolution des tests cognitifs en laboratoire doit être motivée, *e.g.,* via une privation de nourriture, et force les individus à rentrer en contact avec le dispositif. Cela peut donc créer de l'anxiété (*i.e.,* anxiété d'état) (Carter *et al*. 2013) chez les individus timides et réactifs en particulier, même si ces derniers n'ont pas forcément un niveau élevé d'anxiété de trait (Misslin et Cigrang 1986). Allant dans ce sens, lorsque les individus étaient familiarisés jusqu'à ce qu'ils ne démontrent plus aucun signe de stress et/ou entrainés répétitivement à suivre la procédure d'apprentissage (Annexe I), le lien entre apprentissage et personnalité était plus rarement mis en évidence dans le sens attendu (*i.e.,* les plus hardis sont les plus rapides à apprendre). En effet, quand le lien était absent ou trouvé dans le sens opposé, la familiarisation était importante dans 6/7 cas chez les poissons et 7/10 cas chez les mammifères tandis que parmi les résultats trouvés dans le sens attendu, une familiarisation aussi poussée était plus rare (3/9 chez les poissons et 4/16 chez les mammifères, annexe II). Chez les oiseaux, les individus étaient presque toujours hautement familiarisés à la procédure et d'ailleurs, le lien entre apprentissage et personnalité est absent la plupart du temps (Chapitre IV, table I). Ces observations indiquent que le degré de familiarisation dans les tests cognitifs devrait probablement être choisi avec attention suivant les objectifs de l'étude. Par exemple, si le dispositif mimique les contingences rencontrées en nature, peu de familiarisation pourrait être préférable si le but est d'évaluer les performances des individus dans un contexte naturel. Ces observations impliquent aussi que les individus timides pourraient être désavantagés, au moins à court terme, face aux changements d'origine anthropique, introduisant beaucoup de nouveauté dans l'habitat.

c) Les traits les plus plastiques prédisent moins l'apprentissage

Dans le chapitre II, le lien entre néophobie et apprentissage était faible. En effet, la néophobie n'expliquait que la première tâche d'apprentissage qui était aussi la plus simple. Similairement dans le chapitre III, la néophobie et l'exploration (variable composite) n'expliquaient pas l'apprentissage discriminant (t_{29}=-0.708, P=0.484) ou l'apprentissage à renforcements inversés (t_{28}=1.723, P=0.096). Il y avait seulement une légère tendance pour l'apprentissage spatial: les plus explorateurs et les moins néophobes étaient un peu plus rapides à apprendre (t_{29}=-1.882, P=0.070). Les poissons étaient familiarisés à la procédure et aux stimuli jusqu'à ce qu'ils soient tous capables d'explorer le dispositif sans crainte. L'habituation, *i.e.,* la diminution de leur réponse suite à l'exposition répétée aux stimuli, pourrait donc permettre aux individus timides d'arriver aux mêmes niveaux d'exploration que les individus hardis. Si l'habituation aux conditions est responsable de l'absence de différences dans les performances des individus, cela implique que les différences interindividuelles dans les traits de personnalité prédisant peu l'apprentissage devraient avoir tendance à se réduire au cours du temps. C'est effectivement ce qui apparait lorsque l'on teste les différences interindividuelles (estimées à l'aide de la comparaison de modèles linéaires mixtes avec et sans l'identité du poisson en facteur aléatoire, les données non-normales étaient transformées avec un log et le modèle contenait un facteur aléatoire pour le numéro de l'essai). Les Mollies voiles différaient entre eux dans leur tendance à explorer (X^2_1=11.640, P=0.001) et à exprimer de l'anxiété (X^2_1=19.890, P<0.001) lorsque les traits étaient relevés sur les 5 premières minutes (Chapitre III). En revanche, les différences interindividuelles se maintenaient uniquement pour l'anxiété pour l'intervalle de temps 5 à 10 minutes (X^2_1=8.421, P=0.004) et 10 à 15 minutes (X^2_1=12.316, P<0.001), tandis qu'elles ne se maintenaient pas au cours du temps pour l'exploration (5-10 min : X^2_1=0.171, P=0.679; 10-15 min : X^2_1=0.024, P=0.876). D'abord, l'absence de différences interindividuelles d'exploration se maintenant au cours du temps indique que l'aspect important dans cette mesure était la réaction à la nouveauté. En effet, l'exploration était corrélée à la néophobie (mesurée sur une période de 20 min) et l'aquarium a surement été considéré comme un environnement nouveau à cause de la présence de contenants vides utilisés par la suite pour les tests avec une audience. Ensuite, ces résultats ouvrent des possibilités intéressantes. Notamment, est-ce que les performances d'apprentissages pourraient être plutôt expliquées par les traits de personnalité ayant une plasticité réduite au cours du temps ? Par exemple, les mesures d'anxiété estimées via le thigmotaxisme chez les poissons ou via d'autres indices de l'émotivité chez les rongeurs (incluant la vigilance, l'urination et la défécation), sont généralement peu sujettes à l'habituation (Martin et Réale 2008; Maximino *et al*. 2010). En revanche, contrairement à notre étude, l'habituation des mesures d'exploration peut, à l'instar des mesures d'anxiété, être faible ou inexistante dans certaines populations (*e.g.,* Dingemanse *et al*. 2012). Il serait donc intéressant d'investiguer si le lien entre la personnalité et l'apprentissage pourrait dépendre de ce facteur. De plus, on peut se demander si les différences de performances entre les types de personnalité seraient plus facilement maintenues dans des environnements changeants. En effet, si les individus sont soumis à une plus grande hétérogénéité temporelle ou spatiale (s'ils sont forcés d'explorer) de leur environnement, ils n'auraient potentiellement pas le temps de s'habituer et les différences seraient maintenues à chaque pas de temps. Dans un environnement changeant, les individus timides seraient plus sensibles aux changements, ce qui leur permet probablement d'échapper aux prédateurs mais au détriment de la vitesse à laquelle ils rentrent en contact avec les contingences et apprennent ces dernières, alors que les individus proactifs seraient en mesure d'apprendre rapidement en s'exposant plus aux risques. Dans un environnement stable, au contraire, les différences devraient être peu marquées, tant parce que les individus peuvent s’habituer et aussi parce qu’ils pourraient probablement tous développer la capacité de détecter les stimuli pertinents.

3) Implications évolutives

Il a été proposé que les capacités cognitives pourraient être utilisées comme des indicateurs de la qualité génétique (*i.e.,* hypothèse des ‘bons gènes’) et donc être un critère potentiel lors du choix de partenaire chez les animaux et les humains (Jacobs 1996; Miller 2000; Boogert *et al*. 2011). Allant dans ce sens, les oiseaux jardiniers (*Ptilonorhynchus violaceus*) connus pour construire des nids élaborés, réussissant mieux des tâches de résolution de problème, étaient préférés par les femelles (Keagy *et al.* 2009). J’ai donc participé à des travaux ayant pour but de vérifier cette théorie chez les Diamants mandarins, une espèce monogame donnant des soins parentaux (Annexe I, Chantal *et al*. 2016). Les résultats suggèrent que la sélection sexuelle agirait sur les capacités cognitives si elles se traduisent par l’obtention d’une plus grande quantité de ressources par le mâle permettant ainsi d’augmenter les chances de survie de la progéniture du couple (*i.e.,* bénéfices directs). En effet, les femelles préféraient les mâles lorsqu’ils étaient plus efficaces pour résoudre un problème leur donnant accès à de la nourriture mais aussi, tout autant lorsqu’ils trouvaient plus de nourritures sans résoudre de tâche cognitive. De plus la préférence des femelles n’était pas basée sur la vitesse d’apprentissage des mâles suggérant qu’elles n’utilisaient pas de critères indirects basés sur la morphologie ou les parades pour les évaluer. En revanche, une étude chez les oiseaux jardiniers a montré que les mâles capables de moduler leur parade en réponse à la femelle avaient plus de chance d’être choisis (Patricelli *et al*. 2002). Dans le même ordre d’idée, chez les espèces pouvant adopter des tactiques de reproduction alternatives selon les conditions (*i.e.*, mâles *furtifs* ou *bourgeois*), les mâles altérant leur tactique en fonction des circonstances (*e.g.,* la densité des compétiteurs) pourraient avoir un succès reproducteur accru. Cependant, les individus ne pourraient pas être tous aussi efficaces quel que soit la tactique jouée. Par exemple, chez un poisson téléostéen (*Rhodeus ocellatus*), les mâles performants en apprentissage jouaient efficacement la tactique *furtive* mais de hautes performances dans l'apprentissage n'étaient pas nécessaires pour les mâles *bourgeois* (Smith *et al*. 2015). La plasticité comportementale étant le résultat de l'adaptation aux circonstances, elle est plus susceptible d'être la cible de la sélection sexuelle comme naturelle. En effet, les individus échouant à altérer leur comportement lorsque les conditions l'obligent ont peu de chance de survie. Les capacités cognitives pourraient donc être sélectionnées indirectement lorsqu'elles sont requises pour la production du comportement (*e.g.,* trouver une solution à un problème) et l'expression de celui-ci au bon moment (*e.g.,* se cacher des prédateurs au bon moment, moduler l'intensité des comportements de cour selon la réaction de la femelle…*etc.*). Le lien entre plasticité et apprentissage devrait donc être plus fort lorsque l'environnement est variable, les stimuli moins évidents mais fiables (Dunlap et Stephens 2016). Des études futures devraient porter attention aux conditions précises dans lesquelles la plasticité est exprimée, et examiner son association avec les capacités cognitives et la valeur adaptative de l'individu.

Mieux comprendre sous quelles conditions la plasticité évolue est un enjeu de conservation, sachant que certaines populations sont capables de survivre en exprimant de la plasticité en réaction aux changements environnementaux récents (*e.g.,* Charmantier *et al*. 2008). Cependant, l'instabilité croissante des environnements et la disparition sélective de certains types d'individus (*e.g.,* Louison *et al*. 2018) pourraient diminuer les chances que les populations se maintiennent. De plus, avec cette thèse, j'espère aussi apporter une meilleure compréhension de la personnalité et la cognition en général. En effet, certains traits de personnalité comme l'anxiété peuvent avoir des conséquences délétères chez de nombreuses espèces incluant l'humain. Notamment, une grande réactivité aux stimuli externes pourrait procurer un avantage en terme de flexibilité dans certaines conditions. En revanche, la sensibilité permettant de détecter et de former des associations avec les stimuli environnementaux demande un niveau modéré de stress et peut être augmentée via un investissement de temps dans la prise de décision.

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ANNEXE I. Male feeding efficiency, but not male problem-solving performance, influences female mating preferences in zebra finches

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Male foraging efficiency, but not male problem-solving performance, influences female mating preferences in zebra finches

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ABSTRACT

Experimental evidence suggests that females would prefer males with better cognitive abilities as mates. However, little is known about the traits reflecting enhanced cognitive skills on which females might base their mate-choice decisions. In particular, it has been suggested that male foraging performance could be used as an indicator of cognitive capacity, but convincing evidence for this hypothesis is still lacking. In the present study, we investigated whether female zebra finches (*Taeniopygia guttata*) modify their mating preferences after having observed the performance of males on a problem-solving task. Specifically, we measured the females' preferences between two males once before and once after an observation period, during which their initially preferred male was incapable of solving the task contrary to their initially less-preferred male. We also conducted a control treatment to test whether the shift in female preferences was attributable to differences between the two stimulus males in their foraging efficiency. Finally, we assessed each bird's performance in a color associative task to check whether females can discriminate among males based on their learning speed. We found that females significantly increased their preference toward the most efficient male in both treatments. Yet, there was no difference between the two treatments and we found no evidence that females assess male cognitive ability indirectly via morphological traits. Thus, our results suggest that females would not use the males' problem-solving performance as an indicator of general cognitive ability to gain indirect fitness benefits (*i.e.*, good genes) but rather to assess their foraging efficiency and gain direct benefits.

Subjects Animal Behavior, Zoology
Keywords Mate-choice, Foraging success, Problem-solving performance, Cognition, Sexual selection, Zebra finch

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INTRODUCTION

As the brain structures needed to acquire, process, store and use information from the environment are costly to develop and maintain, cognitive abilities in both humans and animals are often considered as an honest indicator of genetic quality that should be used as a mate-choice criterion (*Jacobs, 1996*; *Miller, 2000*; *Boogert, Fawcett & Lefebvre, 2011*). More precisely, improved cognitive abilities can help animals to respond quickly and adequately to environmental changes (*Kotrschal & Taborsky, 2010*). Females, therefore, might benefit from choosing a mate with higher cognitive ability because it

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would be better to cope with changing conditions, hence providing them and their offspring with better resources. Females could also gain indirect benefits when the cognitive traits are heritable (*Croston et al., 2015*). Supporting the idea that males with better cognitive skills are preferred as mates, two studies have demonstrated that males with better spatial learning abilities are more attractive to females in both meadow voles (*Microtus pennsylvanicus*) (*Spritzer, Meikle & Solomon, 2005*) and guppies (*Poecilia reticulata*) (*Shohet & Watt, 2009*). Also there is good evidence that birdsong, which is an indicator of brain development (*Farrell, Kriengwatana & MacDougall-Shackleton, 2015*), plays an important role in mate attraction (*Searcy & Andersson, 1986*; *Nowicki, Searcy & Peters, 2002*). Yet, relatively few studies except those concerning song learning in birds, have looked at how individuals assess the cognitive capacity of the opposite sex. Consequently, little is known about the traits reflecting enhanced cognitive skills on which females might base their mate-choice decisions in other taxa or even in bird species in which song complexity is not a meaningful indicator of cognitive capacity (*Boogert et al., 2011*; *Templeton, Laland & Boogert, 2014*).

Several authors have suggested that male foraging performance could be such a cue that females would use as an indicator of cognitive capacity (*Boogert, Fawcett & Lefebvre, 2011*). In particular, females could discriminate among males based on their ability to solve novel problems. Indeed, experimental evidence has shown that individuals of the same population may differ widely in their problem-solving success and that this trait correlates positively with performance on various learning tasks (*Bouchard, Goodyer & Lefebvre, 2007*; *Boogert, Giraldeau & Lefebvre, 2008*; *Cole, Cram & Quinn, 2011*; *Overington et al., 2011*; *Aplin, Sheldon & Morand-Ferron, 2013*; *Griffin et al., 2013*; *Templeton, Laland & Boogert, 2014*; *Shaw et al., 2015*). These findings suggest that males with better problem-solving ability would have higher general cognitive ability (*Shaw et al., 2015*). In addition, recent research has established a link between problem-solving ability and mating success, hence providing evidence that females would also obtain direct fitness benefits from choosing mates with better cognitive skills. Specifically, *Keagy, Savard & Borgia (2009)* and *Keagy, Savard & Borgia (2011)* have reported that male satin bowerbirds (*Ptilonorhynchus violaceus*) with better problem-solver ability in the field obtain more copulations, while two recent studies on great tits (*Parus major*) have demonstrated that more cognitively skilled mates that are faster problem solvers produce more offspring (*Cole et al., 2012*; *Cauchard et al., 2013*).

To date, however, evidence for the hypothesis that females use male foraging performance as an indicator of cognitive ability is indirect. Indeed, several studies in birds (*Hill, 1990*) and fish (*Pike et al., 2007*) have reported that females prefer brighter or more colored males, probably because they are more efficient in acquiring food and hence ingest more carotenoids responsible for brightly colored sexual ornaments. Yet, it is unclear whether carotenoid coloration reflects male foraging success and whether females use direct observation of male cognitive performance rather than traits that are correlated with cognition when choosing a mate. Only *Snowberg & Benkman (2009)* have demonstrated that female crossbills (*Loxi curvirostra*) rely on male foraging performance to choose a mate. More precisely, they found that females that had observed two males that differed in their feeding rate preferred the most efficient one. However, there is no evidence that male crossbills that are more efficient at extracting seeds from conifer cones have better cognitive skills. Therefore, no study has yet directly tested whether females discriminate among males through direct observation of their performance on a foraging task that indicates cognitively ability.

In the present study, we addressed this question by investigating whether female zebra finches (*Taeniopygia guttata*) modify their mating preferences after having observed the foraging performance of males on a problem-solving task. Although male song has been found to be important for female choice in this species (*Riebel, 2009*), recent findings indicate that song complexity would not be a good indicator of general cognitive ability (*Templeton, Laland & Boogert, 2014*), as previously thought (*Boogert, Giraldeau & Lefebvre, 2008*). Females, therefore, might benefit from using other cues that best reflect a male's overall cognitive ability, such as its ability to solve novel problems. Thus, to assess the influence of this cue on female mate-choice decisions, we trained males to solve a task, and then we measured the mating preferences of each female twice: before and after she had observed the performance of two stimulus males on the task (main treatment). We experimentally manipulated the performance of the two males during the observation period, so that each female could observe her initially preferred male that was incapable of solving the task (*i.e.*, the non solver) and her initially less-preferred male (*i.e.*, the solver) that, on the contrary, was highly efficient at solving the task. Furthermore, because only the solver could access food, we conducted a control treatment to test whether the change in females' preferences observed in the main treatment could be explained by differences among males in their foraging efficiency rather than in their ability to solve the task. Finally, we measured each bird's learning performance in a color associative task in order to check 1) whether females, prior to the observation period, could discriminate between the two males based on their learning performance and hence preferred the male that learned faster, and 2) whether the ability of females to assess male cognitive ability was related to their own learning performance.

METHODS

Subjects and housing

We used 40 (30 females and 10 males) commercially purchased unrelated adult zebra finches obtained from a local breeder (Exotic Wings & Pet Things, St Clements, Ontario, Canada). Twenty-two birds (18 females and 4 males) and 18 birds (12 females and 6 males) were used in the main and control treatments, respectively. Outside the testing periods, the birds were kept in groups of two or three in same-sex cages (10 × 40 × 30 cm) with a 14:10 h light: dark photoperiod at approximately 23 ± 1 °C. They had ad libitum access to seeds, water and cuttlefish bone. In addition, their diet was supplemented once a week with egg yolk mixture and vegetables. The experiments described in this study were approved by the Animal Care Committee of the University of Montreal (animal care permit #14-073) and conformed to all guidelines of the Canadian Council on Animal Care.

Main treatment

Problem-solving task

Before we measured the preferences of each female between one solver and one non solver, we trained the males to solve a task, which consisted of a transparent plastic tube filled with millet seeds and closed with a lid that the bird had to flip to get access to the food (Fig. 1). Training sessions occurred between 7 and 13h00 after overnight food deprivation and lasted for 20 consecutive days with two sessions per day separated by 3 h. Males were trained by pairs in their housing cage that was divided by an opaque partition in two sections. Thus, the birds could not scrounge food or observe each other's behavior. The day before the training began, we placed two apparati outside of the cage, to allow the birds to become familiar with them. Then the training procedure consisted of the following three steps: 1) we provided the birds with an open tube (*i.e.*, with no lid); 2) once the birds had eaten for 10 s in step 1, a lid was just deposited on the tube, so that the birds could easily get access to the food by pushing down the lid. An individual who succeeded in pushing down the lid had access to the food during 10 s before the lid was replaced; 3) once the birds had succeeded five times in step 2, the lid was pressed halfway so that the birds had now to flip the lid to get access to the food. The training was over when the birds could open the tube at least 10 times during a 60 min period.

Mate-choice apparatus and experimental procedure

We measured female mating preferences with a classical binary choice apparatus (Fig. 2) that comprised three compartments: A) the observation compartment where the focal female could see both males simultaneously, B) the choice compartment where she could see only one stimulus male at a time and C) the male compartment divided into two identical chambers, each housing a single male. Before the beginning of the experiment, males and females were placed individually in the apparatus during one hour for 10 days to become familiar with their environment. Then we measured each female's preference twice (*i.e.*, initial and final preferences): before and after an observation period, during which she could observe one of the two stimulus males solving the task while the other did not.

The initial preference of each focal female was measured following this procedure: after the two stimulus males had been placed in the male compartments, we introduced the test female in the observation compartment and after a 15 min period, we gently lifted the transparent partition between the observation and choice compartments. We then measured the time she spent on the perches in the neutral zone and in front of each male during two consecutive periods of 30 min each, switching the position of the males after 30 min. To control for differences in the stimulus males' songs, we masked their songs during the duration of the mate choice tests by playing a recorded chorus of calls and songs from male and female zebra finches. Furthermore, to ensure that the females were able to distinguish between the two males, we formed the pairs so that the two stimulus males differed in terms of size, plumage and beak color.

The five days following the initial preference test, each female was placed in the observation compartment for two periods per day during which she could observe the two

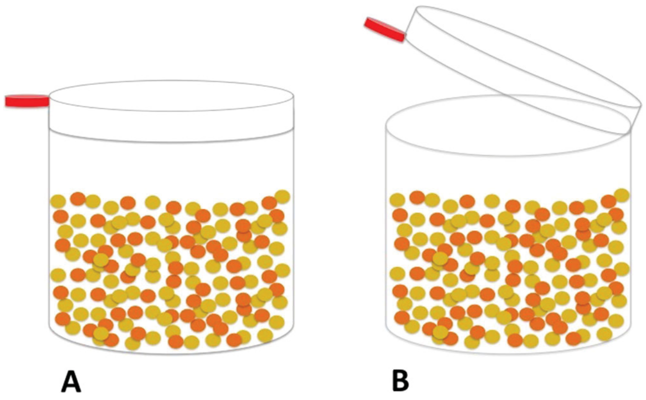

Figure 1 **Side view of the motor learning task.** The lid of the plastic tube was pressed either halfway to allow the bird to easily flip the lid or fully pressed to prevent the bird to get access to the food.

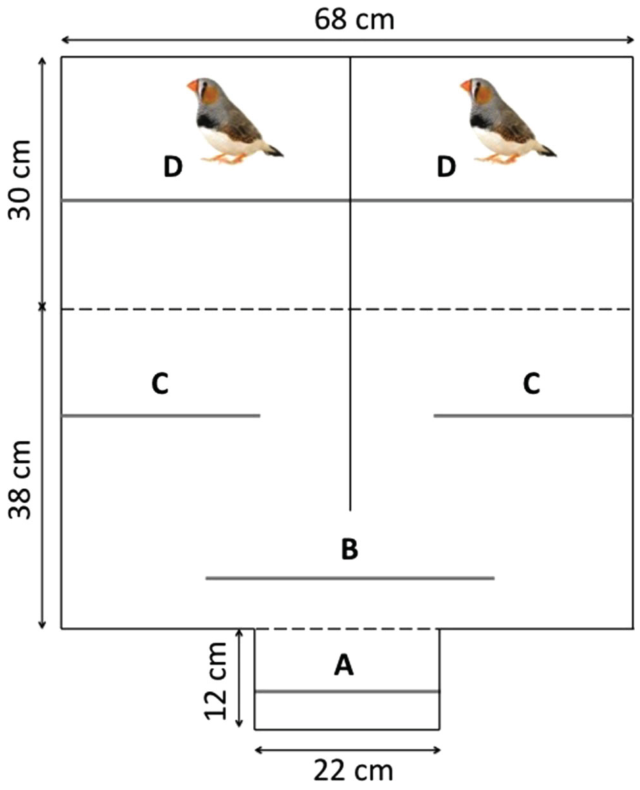

Figure 2 **Top view of the mate-choice apparatus with: the observation compartment (A), the male compartment (D) and the choice compartment divided into the neutral zone (B) and the choice zone (C).** The grey lines represent the perches while the black lines correspond to the partitions that were opaque (full lines) or clear (dashed lines).

stimulus males while they were interacting with the problem-solving task. Before each observation period, the two stimulus males were food deprived for 3 h. Then, in order to manipulate their success, one of them (*i.e.*, the solver) was provided with a tube the lid of which was pressed only halfway and hence that could be easily opened, while the other male (*i.e.*, the nonsolver) was provided with a tube the lid of which was fully pressed and hence that was impossible to open. For each female, the easy task was provided to her initially less-preferred male while the difficult task was provided to her initially preferred male. Each observation period ended after 60 min or once the most efficient male had solved the task 10 consecutive times, whichever occurred first. In addition, to prevent female-male interactions and other distractions during the observation periods, we placed three natural-spectrum, 60 W light bulbs directly in front of each male's compartment, making it harder for the males in their brightly lit environment to detect the female in her shaded compartment in front of them.

After 24 h, we measured the final preference of the focal female using the same procedure as for the initial tests. All females, except one female that was injured after the initial test, were tested for their final preferences. In addition, although females observed the performance of the males on the problem-solving task only during the observation sessions, males were provided with the task every day during habituation and testing periods, so that they do not forget how to flip the lid.

Control treatment

We used exactly the same procedure as described above, except for the observation period, during which the test female could observe twice a day the two stimulus males while they were searching for seeds within a dish (13 × 7 × 3.5 cm). The food dishes that were provided to the two stimulus males both contained a double layer of dried peas that acted as obstacles, thereby forcing the birds to move them around to detect and gain access to the millet seeds when they were present. In addition, in order to manipulate the feeding rate of the two stimulus males, the initially preferred male was provided a dish that contained no seeds while the other male was provided a dish with 30 millet seeds. Each observation period ended after 10 or 2 min after the most efficient male had stopped searching for food, whichever occurred first.

Associative learning task

We measured the performance of all individuals (*i.e.*, both males and females) in a color associative task as the number of trials needed to find six consecutive times the rewarded feeder. Specifically, the birds were tested individually in an experimental apparatus that comprised an observation chamber (20 × 50 × 30 cm) and a choice chamber (40 × 50 × 30 cm) that were separated from each other by a transparent removable partition. The choice chamber was divided into four symmetrical corridors, and at the end of each corridor we placed four white feeders that were positioned in front of four colored dots (*i.e.*, yellow, cyan, pink and black) whose position changed randomly from one trial to the next. The rewarded feeder (*i.e.*, the feeder placed in front of the yellow dot) always contained four millet seeds, while the other feeders were empty.

Prior to testing, we trained the birds to eat from the feeder that was deposited within their home cages. Then, the birds were placed in the experimental apparatus to become familiarized with the environment. They spent at least 3 h per day for two weeks in the apparatus until they could explore the four corridors and eat without fear from the feeders, whatever their position.

Before each testing day, the birds were food deprived for 3 h. They experienced a maximum of 25 trials per day during four consecutive days or until they had reached the learning criterion, whichever occurred first.

At the beginning of each trial, the bird was confined in the observation chamber for 2 min. Then, the observer gently lifted the removable partition, thereby allowing the bird to enter in the choice chamber and choose one of the four feeders. Once the bird had chosen a corridor, we noted whether it had succeeded or failed. If the bird had succeeded, it could eat the four seeds before returning to the observation chamber. On the contrary, if the bird had failed, the observer either gently activated the removable partition to encourage the bird to return into the observation chamber if it had obtained food during the previous trial or let it explore the other corridors and find the rewarded feeder otherwise. Such a procedure was adopted to insure that all the birds ate approximately the same amount of food during each session and that differences among individuals in their learning speed, therefore, were not due to differences in their level of satiety. All but three injured birds (two males and one female) were used for this experiment.

Statistical analyses

To determine whether the females were capable of discriminating between the two stimulus males based on their learning capacity, we tested whether the percentage of time spent in front of the male who resolved the color association task faster was significantly larger than 50% using a one-sample t-test. Because we used five different pairs of males for the preference tests, we also conducted a one-way ANOVA to assess whether female preferences differed among the pairs of stimulus males. Next, we compared the average learning performance of the females that expressed a marked preference (*i.e.*, spent 55% or more of their choosing time in front of one male) for either the fast or the slow learning male using a t-test, and we used a Pearson correlation coefficient to determine whether the relative time spent by females in front of their initially preferred male was correlated with the difference between the two stimulus males in their learning speed.

For both treatments, we assessed whether the change in the females' preferences (*i.e.*, the relative time spent in front of the most efficient male in the final preference test minus the relative time spent in front of the same male in the initial preference test) significantly differed from zero using a paired t-test, and then we performed a t-test to determine if the change in preferences differed between the two treatments. We also verified that the relative time spent in the choosing zone was not significantly different between the initial and final test preferences using a paired t-test, and for both variables (*i.e.*, change in the females' preferences and change in their relative time spent in the choice zone) we conducted a one-way ANOVA to test for an effect of pair identity. Finally, we used Pearson's correlation coefficient to test for an association between the change in females' preferences and their learning score. Data were excluded from the analyses when females spent less than 30% of their time in the choosing zone. Statistical analyses were done with SPSS 23.0 for Mac.

RESULTS

During the initial preference test, females on average (X ± SE) spent 47.83 ± 4.60% of their choosing time in front of the faster learner of the two stimulus males in the color association task, which is not significantly different from 50% ($t_{23} = -0.471$, $P = 0.642$). Furthermore, there was no significant effect of the identity of the stimulus males on the expression of female preferences ($F_{3,20} = 0.066$, $P = 0.977$). Female choice, therefore, was random with respect to male learning performance in the color association task. The relative time spent by females in front of their less-preferred male was not correlated either with the difference in learning speed between the two stimulus males ($r = -0.075$, $N = 30$, $P = 0.694$). This finding indicates that females that had to choose between two males that differed largely in their learning performance were not more likely to prefer the faster learner of the two stimulus males than those that had to choose between two potential mates with more similar learning speeds. Finally, the mean number of trials needed to solve the color associative learning task was not significantly different between females that preferred the faster learner and those that preferred the slower learner of the two males ($t_{10} = -0.622$, $P = 0.548$).

The time spent by females in the choice zone was not significantly different between the initial and final preference tests ($t_{27} = -0.335$, $P = 0.740$). On the contrary, we found that females significantly increased their preference toward the initial less-preferred male after having observed the performance of the two stimulus males in both treatments (main treatment: $t_{15} = 2.608$, $P = 0.020$; control treatment: $t_{11} = 2.472$, $P = 0.031$; Fig. 3). Yet, there was no significant effect of the treatment on the shift in female preferences ($t_{26} = 1.164$, $P = 0.255$) and neither variable was affected by the identity of the stimulus males (change in the relative time spent in the choice zone: $F_{4,24} = 0.072$, $P = 0.990$; change in the relative choosing time spent in front of the initially less-preferred male: $F_{4,23} = 0.832$, $P = 0.579$). Finally, we found no correlation between the females' learning speed in the color association task and the magnitude of the change in their mating preferences in the main treatment ($r = 0.178$, $N = 16$, $P = 0.509$) or in the control treatment ($r = 0.269$, $N = 11$, $P = 0.424$).

DISCUSSION

We found that zebra finch females significantly increased their mating preference toward the most efficient (initially less preferred) male, after having observed the performance of the two stimulus males in both treatments. Because in both treatments, the two stimulus males differed in their feeding rate, our results suggest that females use male foraging efficiency as a mate-choice criterion. This result is in agreement with the study of *Snowberg & Benkman (2009)* who reported that red crosbill females also preferred the male that was the more efficient forager. In zebra finches, variation among individuals in their feeding rate causes variation in their reproductive success (*Lemon & Barth, 1992*; *Lemon, 1993*). More precisely, because individuals with high rates of energy gain have more time and energy available for reproduction compared with less efficient foragers, they are able to produce more offspring that also survive better. Female zebra

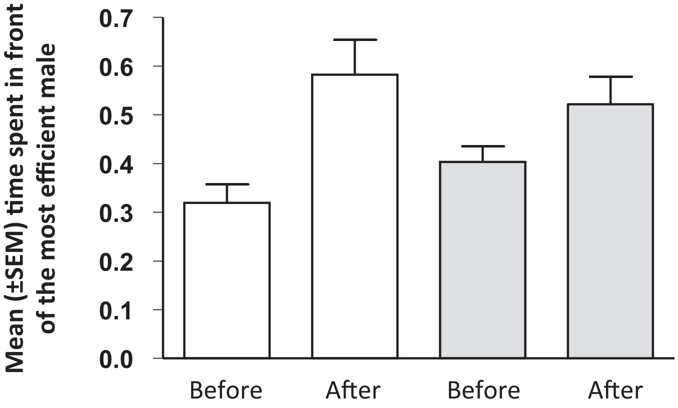

Figure 3 **Mean (± SEM) percent of choosing time spent in front of the male that was the most efficient forager, before and after females had observed the males' performance in the main (white bars) and control (grey bars) treatments.**

finches, therefore, can gain direct fitness benefits from choosing mates based on their foraging efficiency.

Yet, contrary to our expectations, we found no support for the hypothesis that zebra finch females discriminate among potential mates based on their problem-solving ability. Indeed, we detected no significant difference in the change of female preferences between the two treatments, which means that the capacity of the males to solve the task in the main treatment was unimportant for females compared to the males' feeding rate. Thus, our results indicate that female zebra finches do not use male problem-solving performance as an indicator of cognitive capacity. One reason that could explain this finding is that mate assessment based on male foraging performance likely requires considerable time, which would prevent most females from using this trait as a mate-choice criterion. Indeed, as zebra finches are opportunistic breeders, starting to breed immediately after rain (*Zann, 1996*), females have to make quick mating decisions. Under natural conditions, however, the probability of observing a cognitively demanding foraging behavior (*e.g.*, an innovation) is expected to be very low. In order to reduce the cost of mate assessment, females would then benefit from using morphological traits that are correlated with cognitive abilities, instead of assessing directly the males' cognitive performance. However, we found no evidence for this explanation.

Indeed, prior to the observation of the males' performance, females did not prefer the faster learner of the two stimulus males and we found no evidence, either, that they chose assortatively based on learning capacity. These findings indicate that female zebra finches do not assess male cognitive ability indirectly via morphological traits or courtship displays, irrespective of their own cognitive abilities. Although it is possible that we failed to detect a preference of females for the faster learner of the two stimulus males because there was not enough variation among them in their learning performance, this explanation is unlikely. Indeed, we found no correlation between the strength of female preferences and the difference in learning speeds between the two stimulus males, which means that the time spent by females in front of the fast-learning male was not influenced by the amount of variation between the two potential mates in their cognitive ability. So, our results suggest that females would not use the males' performance on different learning tasks as an indicator of general cognitive ability to gain indirect fitness benefits (*i.e.*, good genes) but rather to assess their foraging efficiency and hence gain direct fitness benefits. This conclusion is supported by the fact that several authors have reported non-significant correlations among individual performance on different cognitive tasks (*Boogert et al., 2011*; *Templeton, Laland & Boogert, 2014*; *Farrell, Kriengwatana & MacDougall-Shackleton, 2015*; *Kriengwatana et al., 2015*), which strongly suggests that different cognitive measures would each reflect a specific ability. As a consequence, though our results need to be further confirmed, we argue that cognitive traits could evolve through sexual selection only if enhanced cognitive skills enable males to acquire more resources and hence to produce more viable offspring.

In conclusion, our results showed that female zebra finches use direct observation of foraging efficiency to guide their mate-choice decisions, probably because females mated with highly efficient foragers are able to produce more offspring that survive better. Yet, we found no evidence that females assess males' cognitively ability either directly via observation of their performance on a problem-solving task or indirectly via morphological traits that are correlated with their learning ability. Thus, our results do not support the hypothesis that female zebra finches would use male learning ability as an indicator of general cognitive ability, but additional studies would be required to confirm our conclusions. In particular, given that male song is an important mate-choice criterion used by females, future studies should explore whether song advertises direct benefits, indirect benefits or both (*Farrell, Kriengwatana & MacDougall-Shackleton, 2015*).

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Véronique Chantal conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Julie Gibelli conceived and designed the experiments, performed the experiments, wrote the paper, reviewed drafts of the paper.
- Frédérique Dubois conceived and designed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

The experiments described in this study were approved by the Animal Care Committee of the University of Montreal (animal care permit #14-073) and conformed to all guidelines of the Canadian Council on Animal Care.

Data Deposition

The following information was supplied regarding data availability:

The raw data has been supplied as Supplemental Dataset Files.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.2409#supplemental-information.

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ANNEXE II. Degré de familiarisation aux tâches d'apprentissage dans les études testant le lien entre apprentissage et personnalité. Le 'LIEN' correspond à l'*outcome* dans la table I du chapitre IV, plus précisément si l'étude a trouvé un ou des lien(s) dans le sens attendu entre personnalité et apprentissage, *i.e.,* les proactifs sont plus performants (+) ou bien si le(s) lien(s) étaient dans le sens opposé à celui attendu (-) ou absent (0).

Auteurs	Ordre	*Espèce*	Apprentissage	LIEN		FAMILIARISATION				
				+	0/ -	Rang*	Dispositif ?	Procédure ?	Entraînement** ?	Commentaire
Dugatkin and Alfieri. 2003	Poisson	*Poecilia reticulata*	Discriminant	1	0	**1**	Oui	Non	Non	
Sneddon. 2003	Poisson	*Oncorhynchus mykiss*	Conditionnement	1	0	**1**	Oui	Non	Non	
DePasquale *et al*. 2014	Poisson	*Brachyrhaphis episcopi*	Conditionnement	3	0	**1**	Oui	**Oui**	Non	
Trompf and Brown. 2014	Poisson	*Poecilia reticulata*	Discriminant	1	0	**1**	Oui	Non	Non	Testés en groupe
Bensky *et al*. 2017	Poisson	*Gasterosteus aculeatus*	Discriminant	1	0	**2**	Oui	**Oui**	**Oui+**	
Etheredge *et al*. 2018	Poisson	*Gambusia affinis*	Discriminant	2	3	**2**	Oui	**Oui**	Oui	
Mamuneas *et al*. 2015	Poisson	*Gasterosteus aculeatus*	Spatial	0	1	**1**	Oui	Non	Non	
Brown *et al*. 2013	Poisson	*Oncorhynchus mykiss*	Conditionnement	0	1	**2**	Oui	Non	Non	Le stimulus utilisé (odeur) ne requiert pas ou peu de manipulations
Sommer-Trembo *et al*. 2018	Poisson	*Poecilia mexicana*	Conditionnement	0	1	**2**	Oui	**Oui**	**Oui+**	
Mesquita *et al*. 2015	Poisson	*Cyprinus carpio*	Discriminant	0	1	**2**	Oui	**Oui**	**Oui+**	
Range *et al*. 2006	Oiseau	*Corvus corax*	Discriminant	1	0	**1**	Oui	Non	Non	
	Oiseau	*Corvus corax*	Spatial	1	0	**2**	Oui	**Oui**	**Oui+**	Tâche similaire testée avant
Guillette *et al*. 2009	Oiseau	*Poecile atricapillus*	Discriminant	1	0	**2**	Oui	**Oui**	**Oui+**	Plusieurs tâches similaires testées avant
Madden *et al*. 2018	Oiseau	*Phasianus colchicus*	Discriminant	1	1	**2**	Oui	**Oui**	**Oui+**	Entraînement
Guillette *et al*. 2010	Oiseau	*Poecile atricapillus*	Discriminant	0	1	**2**	Oui	**Oui**	**Oui+**	Plusieurs tâches similaires testées avant
Titulaer *et al*. 2012	Oiseau	*Parus major*	Discriminant	0	1	**2**	Oui	**Oui**	**Oui+**	
Brust *et al*. 2013	Oiseau	*Taenopygia guttata*	Discriminant	0	2	**2**	Oui	**Oui**	**Oui+**	

Ducatez *et al*. 2015	Oiseau	*Quiscalus lugubris*	Discriminant	0	2	**2**	Oui	**Oui**	Oui	Tâche similaire testée avant
Boursquet *et al*. 2015	Oiseau	*Anas platyrhynchos*	Spatial	0	1	**2**	Oui	**Oui**	Oui	
Guillette *et al*. 2015	Oiseau	*Poecile atricapillus*	Discriminant	0	1	**2**	Oui	**Oui**	**Oui+**	
Morand-Ferron *et al*. 2015	Oiseau	*Parus major*	Discriminant	0	1	NA	NA	NA	NA	Animaux testés en nature
Bebus *et al*. 2016	Oiseau	*Aphelocoma coerulescens*	Discriminant	0	2	**2**	Oui	**Oui**	**Oui+**	
Medina-García *et al*. 2017	Oiseau	*Melopsittacus undulatus*	Spatial	0	2	**2**	Oui	**Oui**	**Oui+**	
Guido *et al*. 2017	Oiseau	*Milvago chimango*	Discriminant	0	1	**2**	Oui	**Oui**	**Oui+**	
Gibelli and Dubois. 2017	Oiseau	*Taenopygia guttata*	Discriminant	0	1	**2**	Oui	**Oui**	**Oui+**	
de Haas *et al*. 2016	Oiseau	*Gallus gallus domesticus*	Discriminant	0	2	**2**	Oui	**Oui**	**Oui+**	
Mazza *et al*. 2018	Mammifère	*Myodes glareolus*	Discriminant	2	0	**1**	Non	Non	Non	
Guenther *et al*. 2014	Mammifère	*Cavia aperea*	Discriminant	2	0	**2**	Oui	**Oui**	**Oui+**	
Feyissa *et al*. 2017	Mammifère	*Rattus norvegicus*	Discriminant	2	0	**1**	Oui	**Oui**	Non	
Light *et al*. 2011	Mammifère	*Mus musculus*	Général (PCA)	2	0	**1**	Oui	**Oui***	Non	
Matzel *et al*. 2006	Mammifère	*Mus musculus*	Général (PCA)	1	0	**1**	Oui	**Oui***	Non	
Matzel *et al*. 2003	Mammifère	*Mus musculus*	Général (PCA)	1	0	**1**	Oui	**Oui***	Non	
Herrero *et al*. 2006	Mammifère	*Rattus norvegicus*	Spatial	1	0	**1**	Non	Non	Non	
Kazlauckas *et al*. 2005	Mammifère	*Mus musculus*	Spatial	1	0	**1**	Oui	**Oui***	Non	
Schuster *et al*. 2017	Mammifère	*Micromys minutus*	Spatial	1	2	**1**	Non	Non	Non	
Nawroth *et al*. 2016	Mammifère	*Capra hircus*	Discriminant	1	1	**2**	Oui	**Oui**	**Oui+**	Animaux en contact avec les humains
			Non-associatif	0	2	**2**	Oui	**Oui**	**Oui+**	Animaux en contact avec les humains
Bolhuis *et al*. 2004	Mammifère	*Sus scrofa domesticus*	Spatial	0	1	**1**	Oui	**Oui**	Non	
Galsworthy *et al*. 2002	Mammifère	*Mus musculus*	Général (PCA)	0	1	**2(?)**	Oui	**Oui***	Oui(?)	Deux labyrinthes de pratique avant / (?) pas inclus dans les conclusions générales
Brust and Guenther. 2017	Mammifère	*Cavia porcellus*	Discriminant	1	3	**2**	Oui	**Oui**	**Oui+**	

*Rang Le rang 2 est donné lorsque les individus sont entraînés avant les tests d'apprentissage (Voir entraînement**)

**Entrainement Oui+: Jusqu'à absence de signe de stress et/ou suivi de la procédure par l'animal / Oui : 10 essais ou plus d'entraînements suivant la même procédure