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Rôle de la sélection intersexuelle dans l'évolution de la cognition mâle et femelle : approche observationnelle et théorique

Par

Marie Barou Dagues

Département des Sciences Biologiques

Faculté des Arts et des sciences

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A été évaluée par un jury composé des personnes suivantes

Sandra Binning
Président-rapporteur

Frédérique Dubois
Directrice de recherche

Tadeusz Kawecki
Examinateur externe

François-Xavier Dechaume-Moncharmont
Membre du jury

Résumé

Choisir un partenaire sexuel est une décision importante pour un animal. Parce que cette décision va considérablement affecter son succès reproducteur, l'individu doit se baser sur un ensemble de traits qui reflètent la qualité du partenaire. Depuis peu, une attention particulière est portée sur l'importance de la cognition dans le contexte de choix de partenaire. En effet, la capacité à percevoir, intégrer, mémoriser et utiliser l'information disponible dans l'environnement permet aux individus de répondre de manière appropriée aux problèmes qu'ils rencontrent et d'ajuster leur comportement en conséquent. Si les femelles retirent un bénéfice à s'apparier avec des mâles capables de répondre aux changements de leur environnement, ces derniers pourraient avoir un accès privilégié à l'appariement lors du choix de partenaire des femelles. Certaines évidences appuient cette idée en démontrant notamment des relations positives entre les capacités cognitives des mâles et leur succès d'appariement et reproducteur et en révélant des préférences sexuelles femelles pour des traits cognitifs mâles. Cependant, ces résultats restent très contrastés, particulièrement chez les animaux non humains où l'importance du choix de partenaire dans l'évolution de la cognition n'est pas encore clairement définie.

L'objectif de ma thèse était donc d'explorer le rôle du choix de partenaire dans l'évolution de la cognition mâle et femelle en combinant l'approche observationnelle sur une espèce d'oiseaux monogame et l'approche théorique en utilisant un modèle à base d'agents. Plus précisément, en réalisant des expériences en laboratoire sur le Diamant mandarin (*Taeniopygia guttata*), j'ai notamment testé si les femelles démontrent une préférence pour des mâles capables d'ajuster leur comportement d'approvisionnement en réponse à un changement environnemental. J'ai ensuite examiné, dépendamment de leurs propres capacités cognitives, si les femelles expriment des préférences pour des mâles performants dans quatre tests psychométriques différents. J'ai finalement exploré les rôles respectifs de la sélection naturelle et intersexuelle en simulant l'évolution de la cognition sous différents scénarios environnementaux.

Les résultats de cette thèse ont révélé que les femelles diamants mandarin exprimaient une préférence pour les mâles capables d'ajuster leur comportement d'approvisionnement ainsi que les mâles performants dans certaines tâches cognitives. Cependant, ces préférences n'étaient pas unanimes et dépendaient des propres capacités cognitives des femelles à performer dans ces différentes situations. À l'échelle évolutive, la sélection intersexuelle à travers le choix de partenaire modifiait les patrons d'évolution de la cognition prédits lorsque la sélection naturelle opérait seule. En effet, elle favorisait l'évolution de bonnes capacités cognitives lorsque les contraintes environnementales étaient faibles, mais maintenait de la diversité cognitive lorsque ces contraintes étaient élevées. Dans l'ensemble, ces résultats suggèrent que le choix de partenaire jouerait un rôle important dans l'évolution et le maintien de diversité cognitive au sein des populations. Néanmoins, les conséquences évolutives du choix de partenaire sur les capacités cognitives des individus dépendraient de l'avantage adaptatif à s'apparier avec un mâle plus performant, c'est-à-dire de la capacité cognitive mâle considérée, des caractéristiques des femelles et de l'environnement dans lequel ce choix est fait.

Mots-clés: sélection intersexuelle, capacités cognitives, préférence sexuelle, diversité cognitive, Diamant mandarin, modèle à base d'agents.

Abstract

Choosing a mate is an important decision for an animal. Because this decision significantly affects an individual's reproductive success, it must base its choice according to different traits that reflect the quality of potential mates. Recently, a particular attention has been given to cognitive traits in mate choice context. Indeed, the ability to perceive, integrate, memorize and use the information available in the environment allows individuals to act properly when facing a problem and to adjust their behaviours accordingly. Given that females could benefit from choosing males capable of responding to environmental changes, those with good cognitive abilities should have privileged access to females in mate choice contexts. Some evidence supports this idea by revealing positive relationships between males' cognitive abilities and their mating and reproductive success as well as female mating preference for male cognitive abilities. However, these results stay contrasted, particularly in non-human animals for which the importance of mate choice in the evolution of cognition is still not clearly defined.

The objective of my PhD was to explore the role of mate choice in the evolution of male and female cognition by combining an observational approach using a monogamous bird species and a theoretical approach using an agent-based model. Specifically, by running laboratory experiments on zebra finches (*Taeniopygia guttata*), I tested whether females demonstrated a mate preference for males able to adjust their foraging behaviour following an environmental change. Then, I investigated whether females, depending on their own cognitive abilities, demonstrated a mate preference for better performers in four different psychometric tests. I finally explored the relative role of natural and sexual selection by simulating the evolution of cognition under different environmental scenarios.

The results of this PhD project revealed that zebra finch females preferred males exhibiting greater behavioural plasticity in their foraging tactic use as well as males performing better in several cognitive tasks. However, females' preference for cognitive abilities was not unanimous but depended on females' own abilities to perform in these tasks. At the evolutionary scale, intersexual selection through mate choice changed the evolutive patterns observed under natural selection alone. In fact, intersexual selection promoted good cognitive abilities under most favourable environments but maintained cognitive diversity under the harsher ones. Taken together, these results suggest that mate choice plays an important role in the evolution and maintenance of cognitive diversity within populations. Nevertheless, the evolutive consequences of mate choice on individual cognitive abilities should depend on i) the adaptive value of mating with a male with better performance, and thus, on the cognitive ability considered, ii) the female characteristics and iii) the local environment during mate choice.

Key words: intersexual selection, cognitive abilities, sexual preference, cognitive diversity, Zebra finch, agent-based model.

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Liste des sigles et des abréviations

ACP	Analyse en composante principale (PCA en anglais)
AICc	Akaike's information criterion corrected for small sample sizes
A_j	Female accuracy
AL	Associative Learning
α	Cognitive factor
&	Et
±	Plus ou moins
am	Avant midi (Ante meridiem)
C	Clumped
C_i	Cognitive cost
CI	Confident Interval
°C	Degré Celsius
cm	Centimètres
D	Nuit (Dark)
ε	amount of error
E_i	Estimated value
et al.	Et les autres
e.g.	Par exemple (Exempli gratia)
FE	Foraging experiment
GLMM	Generalized Linear Mixed Model
h	Heures
I_i	Male cognitive trait value
IC	Inhibitory Control
i.e.	C'est-à-dire (id est)
L	Jour (Light)
LMM	Linear Mixed Model

MCE	Mate choice experiment
MS	Motor Shaping learning
mm	Millimètres
n	Effectif
Np	Number of patches
pm	Après-midi (Post meridiem)
%	pourcentage
P	P value
PS	Producer-scrounger
R	Number of items per patch
S	Scattered
S_j	Female selectivity
SD	Écart-type (Standard deviation)
SL	Spatial Learning
Tm	Mating phase
Tr	Reproductive phase
W_i	Foraging success

À mes grands-mères,

Viviane et Marcelle,

Deux forces de la nature

Et continuelles sources d'inspiration

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Chapitre I - Introduction générale

La sélection sexuelle est responsable de l'évolution d'une grande diversité de traits dans le règne animal. Mais depuis les deux dernières décennies, une attention particulière est portée sur l'importance de la cognition dans le contexte de choix de partenaire. Dans cette introduction, je présenterai les principaux concepts ainsi que les évidences qui m'ont amené à construire ce projet de recherche. La première section présentera les bases fondamentales de la sélection sexuelle et du choix de partenaire, dans la seconde section, j'aborderai la notion de cognition chez les animaux ainsi que son implication lors du choix de partenaires et la troisième section présentera les objectifs et prédictions de cette thèse.

Sélection sexuelle

La sélection sexuelle, proposée par Darwin (1859, 1871), a émergé du dimorphisme qu'il a observé entre mâles et femelles de la même espèce.

> *"I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection; that is, individual males have had, in successive generations, some slight advantage over other males, in their weapons, means of defence, or charms; and have transmitted these advantages to their male offspring."*
>
> Charles Darwin, *On the Origin of Species,* 1859.

Si, *a priori*, les deux sexes vivent dans le même milieu, ils sont soumis aux mêmes contraintes environnementales et donc, selon sa théorie de la sélection naturelle (Darwin, 1859), devraient exprimer des phénotypes similaires. Pourtant, chez de nombreuses espèces, les mâles arborent des couleurs vives ou des attributs encombrants dont ils ne semblent retirer aucun bénéfice en termes de survie. En revanche ces caractères sexuels secondaires leur confèrent un avantage pour accéder à un partenaire sexuel et auraient donc évolué à travers l'avantage qu'ils confèrent aux mâles en compétition pour féconder les femelles. Il distingue donc le processus de sélection naturelle au sens strict, qui élimine les phénotypes limitant les chances de survie et/ou la fécondité des individus, du processus de sélection sexuelle qui élimine les phénotypes ayant un accès limité aux partenaires sexuels. Même si le processus de sélection sexuelle a longtemps été considéré comme mineur (Wallace, 1891), de nombreuses études démontrent dorénavant qu'il est fondamental chez de nombreux taxa, les mâles possédant ces attributs particuliers ayant en effet un avantage pour féconder les gamètes femelles (Andersson, 1994; Bateman, 1948).

Pourquoi les mâles compétitionnent pour féconder les femelles? Chez les espèces à reproduction sexuée, il existe une asymétrie entre les deux sexes à investir dans la production de descendants qui peut être à l'origine de la compétition pour l'accès au sexe opposé (Danchin et al., 2005). Dans le cas où cet investissement se limite à la production des gamètes (anisogamie sans soins parentaux), la femelle investit davantage que le mâle dans la production de jeunes, car elle produit peu de gamètes riches en substances énergétiques alors que le mâle produit de nombreux petits gamètes mobiles. Une grande quantité de gamètes mâles est donc disponible pour une faible quantité de gamètes femelles. Dans ce contexte, si l'aptitude des femelles est en grande partie déterminée par l'accès aux ressources énergétiques pour pouvoir fabriquer les œufs, celle des mâles dépend majoritairement de l'accès aux femelles fertilisables. De ce fait, il existe une compétition entre les mâles pour accéder aux femelles (Davies et al., 2012). Dans le cas où l'investissement pour la production de jeunes inclut les soins parentaux, l'asymétrie créée par l'anisogamie peut être renforcée, équilibrée ou renversée quand on considère l'investissement dans les soins parentaux. Chez les mammifères, l'asymétrie peut être renforcée, car la femelle porte les petits et s'occupe d'eux pendant la période de lactation alors que le mâle contribue beaucoup moins au soin des jeunes. Chez les poissons, l'asymétrie peut être renversée, car ce sont souvent les mâles qui s'occupent des œufs. Si les deux sexes investissent à parts égales dans les soins parentaux, comme c'est souvent le cas chez les oiseaux monogames, les deux sexes peuvent se montrer sélectifs dans leur choix de partenaire (Darwin, 1871). Cela dit, l'investissement dans la production et le soin des jeunes n'est pas le seul facteur expliquant le degré de compétition pour l'accès au partenaire sexuel. En effet, de plus en plus d'évidences montrent que les mâles peuvent se montrer sélectifs dans leur choix de partenaire, même chez des espèces polygynes ou qui ne prodiguent aucun soin parental, et ce, lorsque l'on tient compte de certains facteurs écologiques et sociaux (Chevalier et al., 2020; Edward & Chapman, 2011; Hare & Simmons, 2019). Bien que Darwin attribuait aux femelles le rôle du sexe sélectif et aux mâles celui du sexe en compétition, ce prérequis n'est plus valide dans la définition moderne de la sélection sexuelle (Shuker, 2010). Dorénavant, la sélection sexuelle inclut l'ensemble des appariements ou fertilisations non aléatoires (Andersson, 1994), issus de la compétition entre partenaires sexuels (Shuker, 2010). Dans le cadre de cette thèse, nous nous sommes concentrés sur le choix de partenaire des femelles. Ainsi, elles seront considérées ci-après comme le sexe sélectif alors que les mâles seront considérés comme le sexe en compétition.

La compétition entre les mâles pour l'accès à la fécondation des œufs femelles se fait à plusieurs niveaux. En nature, la première difficulté rencontrée consiste à détecter la présence d'un partenaire sexuel potentiel dans l'environnement. Les mâles et les femelles se déplacent généralement ou émettent des signaux dans le milieu pour augmenter les chances de rencontrer un membre du sexe opposé, et en fonction de la durée de la période de reproduction et de la densité des mâles et des femelles dans l'environnement, cette étape peut limiter leurs chances de se reproduire (Danchin et al., 2005). Dans ce cas, les traits qui vont faciliter la rencontre entre mâles et femelles (e.g. organes sensoriels et/ou locomoteurs mâles plus efficaces, couleurs vives augmentant les chances de détection par les femelles) vont être favorisés par sélection sexuelle (Andersson & Iwasa, 1996). Une fois que les femelles sont détectées, la deuxième difficulté pour les mâles est d'accéder à la copulation. Dans ce cas, on distingue la compétition par interférence, reposant sur les interactions directes des mâles (i.e. sélection intrasexuelle), de la compétition par exploitation, reposant sur les interactions entre mâles et femelles (i.e. sélection intersexuelle). La compétition par interférence se manifeste souvent par des affrontements physiques entre mâles pour accéder directement aux femelles ou une ressource qu'elles convoitent (Danchin et al., 2005). Les traits qui vont évoluer par sélection intrasexuelle sont donc des traits facilitant la victoire de ces affrontements (i.e. traits « d'armements » comme des structures offensives, défensives ou des signaux de menace; Herron & Freeman, 2014) ou des traits permettant aux moins bons compétiteurs d'éviter ces affrontements (i.e. des stratégies alternatives; Andersson & Iwasa, 1996). D'autre part, la compétition par exploitation s'exerce à travers le choix de partenaire des femelles. Ce type de sélection a lieu lorsque ni le sexe sélectif ni des ressources particulièrement convoitées ne sont défendables. Dans ce cas, ce sont des traits qui vont attirer les femelles et permettre à certains compétiteurs d'en avoir un accès privilégié qui vont évoluer. Ces traits « d'ornements » sont très diversifiés et peuvent prendre la forme de couleurs vives, d'appendices particuliers, de comportements extravagants comme le chant, les parades nuptiales et danses stéréotypées ou encore d'offrandes de nourriture ou de territoire (Rosenthal, 2017). En utilisant ces traits, les femelles peuvent se montrer exigeantes en estimant et choisissant un partenaire qu'elles considèrent de bonne qualité. Plus rarement, la compétition par exploitation peut prendre la forme de coercition et les traits facilitant la reproduction forcée (e.g. attribut de préhension, forme du pénis et du tractus génital, comportement agressif; Andersson & Iwasa, 1996) vont être également favorisés chez certaines espèces. Cependant, la copulation n'est pas nécessairement synonyme de fécondation. En effet, la troisième difficulté à laquelle les mâles font face a lieu lors de la compétition spermatique (Davies et al., 2012). Si la fertilisation est interne et que les femelles ont copulé avec au moins deux mâles sur une courte période, les spermatozoïdes des mâles vont entrer en compétition à l'intérieur du tractus génital de la femelle pour fertiliser ses œufs. Généralement, la compétition spermatique concerne un ensemble d'attributs morphologiques, comportementaux et physiologiques comprenant la taille, le nombre et la structure des spermatozoïdes, la morphologie de l'appareil reproducteur mâle et femelle, les processus et structures de stockage du sperme (Herron & Freeman, 2014). Ce type de compétition favorise aussi le développement de stratégies visant à réduire les chances de copulation de la femelle avec des rivaux (e.g. gardiennage, bouchon de copulation, séquestration, allongement du temps de copulation; Andersson & Iwasa, 1996). Finalement, chez certaines espèces de mammifères, rongeur et cétacés, la compétition peut se prolonger après la copulation avec l'avortement forcé et l'infanticide (Herron & Freeman, 2014).

Parmi ces niveaux de compétition, le choix de partenaire sexuel est, encore à l'heure actuelle, un des processus les plus étudiés par les biologistes du comportement. Pour cause, plusieurs mécanismes expliquent l'évolution du choix de partenaire. Tout d'abord, il peut être basé sur l'exploitation d'un biais sensoriel préexistant lorsque la présence de certains stimuli diminue le temps de réaction des femelles et augmente la probabilité et le seuil de détectabilité des mâles qui en sont porteurs (hypothèse du biais sensoriel, Andersson & Simmons, 2006; Ryan, 1990). Dans d'autres cas, la préférence femelle pour certains traits peut évoluer grâce à la transmission de bénéfices génétiques non additifs à la descendance (i.e. compatibilité génétique) comme c'est le cas pour le complexe majeur d'histocompatibilité (Andersson & Simmons, 2006; Tregenza & Wedell, 2000). Mais communément, la préférence pour un trait évolue parce que les femelles retirent de leur choix des bénéfices directs leur permettant d'augmenter leur succès reproducteur (Mays & Hill, 2004) ou indirect leur permettant de produire une descendance de bonne qualité génétique. Pour obtenir des bénéfices directs, le trait en question doit refléter l'habilité du mâle à fournir des avantages matériels comme un territoire, des ressources alimentaires, un nid/terrier de bonnes qualités ou des soins parentaux et une protection plus importante contre les prédateurs ou les rivaux (Møller & Jennions, 2001). Dans le cas de bénéfices indirects, la préférence femelle est corrélée génétiquement avec un trait mâle directement sélectionné par les femelles parce qu'il reflète l'attractivité (i.e. processus d'emballement Fisherien, Fisher, 1930) ou la qualité génétique du partenaire (principe du handicap, Zahavi, 1975; handicap d'immunocompétence, Folstad & Karter, 1992; Hamilton & Zuk, 1982). Cela dit, ces processus évolutifs ne sont pas mutuellement exclusifs et dénotent de la complexité associée à l'évolution des traits sexuels secondaires.

Choix de partenaire sexuel

Le choix de partenaire est un processus qui intervient lorsque l'effet d'un ou plusieurs traits chez un sexe entraine un appariement non aléatoire avec les membres du sexe opposé (Halliday, 1983; Kokko et al., 2003). Plusieurs étapes sont fondamentales lors du choix de partenaire en particulier pour les espèces prodiguant des soins parentaux où le choix peut se poursuivre tout au long de la vie. Le choix de pré-appariement (« premating choice ») implique la détection et l'évaluation des signaux mâles et précède le choix péri-appariement (« perimating choice ») qui inclut toutes activités avant, pendant et juste après copulation, lorsque les partenaires sont en contact physique rapproché. Finalement, le choix post-appariement (« postmating choice ») concerne les décisions que la femelle va prendre lors de la compétition spermatique ou lors de l'investissement parental des petits issus de l'appariement (Rosenthal, 2017). D'un point de vue terminologique, le choix de partenaire peut désigner la décision de s'apparier avec un individu particulier, mais fait plus souvent référence à la préférence sexuelle d'une femelle, c'est-à-dire aux propriétés sensorielles et comportementales qui vont influencer les chances qu'elle s'apparie avec un phénotype donné (Edward, 2015; Jennions & Petrie, 1997). La préférence sexuelle est elle-même subdivisée en deux caractéristiques : la *fonction de préférence* (« preference function »), et la *sélectivité* de la femelle (i.e. « choosiness »). Généralement, la fonction de préférence est définie par l'ordre dans lequel la femelle va ranger les partenaires potentiels (Edward, 2015). Certains auteurs distinguent les fonctions de préférence de type « ouvertes » lorsque les valeurs extrêmes du trait sont préférées ou de type « fermées » lorsqu'une valeur intermédiaire est préférée par les femelles (Neelon et al., 2019; Reinhold & Schielzeth, 2015). Ils la caractérisent ensuite par un pic (la valeur du trait préférée), une tolérance (le degré d'acceptation des valeurs du trait déviant du pic), une force (à quel point l'attractivité diminue au fur et à mesure que la valeur du trait dévie du pic) et une réceptivité (niveau de réponse de la femelle sur toutes les valeurs du trait; Neelon et al., 2019; Reinhold & Schielzeth, 2015). Pour d'autres, la fonction de préférence peut avoir une certaine forme et une force (Cotton et al., 2006; Edward, 2015; Jennions & Petrie, 1997). La forme de la fonction de préférence peut correspondre à 1) un seuil, lorsque les phénotypes mâles inférieurs ou supérieurs à cette valeur sont respectivement rejetés et acceptés, 2) une catégorie lorsque l'estimation des phénotypes mâles est qualitative (e.g. présence ou absence d'une caractéristique), 3) une forme directionnelle, lorsqu'il existe une relation linéaire entre la préférence et la valeur du trait, 4) une forme stabilisante lorsque les valeurs intermédiaires du trait mâle sont préférées et 5) une forme disruptive lorsque les valeurs extrêmes du trait mâle sont préférées (Edward, 2015; Rosenthal, 2017). De plus, la force de la préférence correspond à la différence que la femelle va exprimer entre différents phénotypes mâles. Par exemple, pour une fonction de préférence directionnelle, la force est représentée par la pente de la relation entre la préférence de la femelle et la valeur du trait mâle. Généralement, la sélectivité d'une femelle, définie par la quantité d'énergie qu'elle investit pour chercher des partenaires de qualité (Edward, 2015), va dépendre de sa condition. Il est souvent présumé que plus une femelle est en bonne condition, plus elle se montre exigeante, car elle dispose de plus de ressources pour faire face aux contraintes lors du choix de partenaire (Cotton et al., 2006). La distinction entre la fonction de préférence et la sélectivité de la femelle est importante, car elle permet de dissocier la préférence interne (i.e. innée ou acquise) d'une femelle pour un trait donné, de l'effort qu'elle est prête à investir dans la reproduction dans le contexte donné au moment du choix (Cotton et al., 2006). En pratique, la fonction de préférence et la sélectivité peuvent être difficiles à distinguer l'un de l'autre, mais aussi à distinguer du choix réalisé de la femelle. En effet, les femelles doivent souvent faire face à de nombreuses contraintes qui les obligent à faire des compromis pendant leur choix de partenaire (Jennions & Petrie, 1997). Les coûts associés à la recherche et l'estimation des différents partenaires potentiels vont interagir avec leur sélectivité et donc influencer la finalité de leurs choix. Cela dit, certaines stratégies vont permettre à la femelle de juger la qualité des mâles tout en limitant les coûts d'échantillonnage.

Pour maximiser ses bénéfices, la femelle doit estimer avec précision la qualité des différents partenaires qui se présentent à elle. Pour cela, elle peut adopter différentes stratégies dépendamment du temps qu'elle dispose pour s'apparier et produire une descendance, de sa mobilité et de sa capacité à retenir les informations provenant des mâles qu'elle échantillonne (Janetos, 1980). En fonction de ces contraintes, on distingue souvent les stratégies dites « absolues » des stratégies dites « comparatives » et celles dites « séquentielles » de celles dites » simultanées » (Zandberg et al., 2020). En utilisant une stratégie absolue, la femelle compare les estimés des mâles à sa fonction de préférence interne (e.g. « fixed-threshold decision », « one-step decision process »; Janetos, 1980; Real, 1990) et prend le risque de ne pas trouver de partenaire si sa préférence est plus élevée que la qualité des mâles présents dans la population. En revanche, avec une stratégie comparative, la qualité d'un mâle dépend de la qualité des autres mâles dans la population (e.g. « comparaison séquentielle »; « best-of-n-males »; Bateson & Healy, 2005; Janetos, 1980; Real, 1990; Zandberg et al., 2020) et la femelle peut ajuster sa préférence en fonction de la qualité des mâles disponibles. Lorsque les mâles sont dispersés, la femelle estime un mâle après l'autre et doit mémoriser la valeur attribuée à chacun avant de prendre une décision (i.e. stratégie séquentielle; Bateson & Healy, 2005; Rosenthal, 2017). Cependant, les femelles peuvent faire des erreurs d'estimations, particulièrement lorsque les conditions rendent l'estimation et la mémorisation de la qualité des mâles difficile (Bateson & Healy, 2005; Candolin et al., 2003; Fawcett & Johnstone, 2003; Jennions & Petrie, 1997; Ronald et al., 2012; Rowe, 1999). À l'inverse, lorsque les mâles sont regroupés au même endroit, les femelles peuvent facilement comparer les mâles simultanément et limiter le temps et le coût associés au processus d'apprentissage et de mémorisation (Zandberg et al., 2020). Cela dit, même si la femelle utilise cette stratégie d'échantillonnage, son choix réalisé peut fortement dévier de sa préférence s'il existe un conflit entre ses intérêts et ceux des mâles. Par exemple, chez les espèces qui forment des leks, il peut exister chez les mâles un compromis entre l'expression de traits favorisant la victoire de combats et de traits qui augmentent leur attractivité auprès des femelles. Dans ce cas, les mâles victorieux peuvent être différents des mâles préférés et l'issu des combats peut obliger les femelles à s'apparier avec un mâle non préféré. Chez les espèces soumises à des contraintes de temps, de mobilité ou de capacité de mémorisation, la femelle n'a pas nécessairement de préférence sexuelle pour un trait donné et elle s'apparie avec le premier mâle rencontré (Janetos, 1980). Pour d'autres, c'est la compétition entre femelles pour l'accès au partenaire qui peut limiter l'évolution de la préférence femelle (Dechaume-Moncharmont et al., 2016). Par exemple, chez les espèces monogames où le nombre et la qualité des mâles disponibles diminuent au fur et à mesure de la saison de reproduction, la compétition perçue par les femelles peut diminuer leur sélectivité et donc les conduire à s'apparier avec des mâles (choix réalisé) dont les valeurs de traits dévient fortement de la valeur préférée du trait.

Mesurer la préférence sexuelle

Qu'est-ce qui est mesurée pour estimer la préférence? Souvent, les études en nature sont basées sur le résultat de l'appariement (i.e. succès reproducteur). L'objectif de ces études est d'identifier comment la femelle alloue ses ressources (temps, énergie, gamètes) entre les mâles et comment ce différentiel affecte l'aptitude des mâles et de la femelle (Rosenthal, 2017; Wagner, 1998). Cela implique entre autres de relever le nombre de descendants produits par observation directe ou par analyse génétique. Néanmoins, trois problèmes sont à noter avec cette façon d'estimer la préférence sexuelle des femelles. D'une part, le succès reproducteur ne permet pas i) d'identifier si la variance dans le succès reproducteur des mâles est directement reliée à la variance dans la préférence et/ou à la décision de la femelle lors du choix de partenaire (choix réalisé), ii) de distinguer l'effet de la sélection naturelle de celui de la sélection sexuelle sur la survie des rejetons et iii) de mesurer le choix de la femelle plusieurs fois étant donné que chaque évènement d'appariement affecte l'expérience et la motivation de la femelle lors des évènements d'appariements subséquents (Rosenthal, 2017). De façon complémentaire, les études en laboratoire quant à elles sont basées sur les comportements précurseurs de la copulation mesurés dans des conditions contrôlées, standardisées et répétées. Ces mesures ont souvent l'avantage de refléter avec précision le comportement de la femelle face à différents mâles qui varient sur la base d'un ou plusieurs traits. Même si ces conditions expérimentales sont parfois critiquées, car jugées trop simplifiées par rapport au contexte naturel, ce type de mesure reste à l'heure actuelle la façon la plus fiable pour mesurer la préférence des femelles pour un trait mâle.

Comment la mesure de préférence est relevée? La préférence de la femelle peut être mesurée dans un test de non-choix (« no-choice test) qui consiste à noter la réponse sexuelle de la femelle lorsqu'elle se retrouve face à des partenaires potentiels présentés un à la fois de façon séquentielle (Rutstein et al., 2007). Chez les oiseaux, la réponse sexuelle des femelles peut être très stéréotypée, auquel cas les femelles peuvent facilement être catégorisée comme réceptives ou non (i.e. diamant mandarin, Forstmeier, 2004). Chez les rongeurs et les mammifères, des comportements pré-copulatoires comme la lordose sont souvent révélateurs de la préférence de la femelle pour certains mâles (e.g. Rutstein et al., 2007; Rosenthal, 2017). Le test de non-choix donne la possibilité à la femelle d'intéragir physiquement avec le mâle et permet directement de relever l'intérêt de la femelle pour ce mâle. Cependant, la préférence peut être sous-estimée dans ce type de dispositif, car la femelle n'a aucune garantie de rencontrer un autre mâle si elle décide de rejeter celui qu'on lui présente (Dougherty & Shuker, 2015). De plus, l'ordre dans lequel les partenaires potentiels sont présentés de façon séquentielle peut influencer l'issu des interactions et donc la mesure de préférence. Alternativement, il est possible de mesurer la préférence en plaçant un groupe de mâles et de femelles ensemble et en les laissant interagir librement jusqu'à l'appariement (Rutstein et al., 2007). C'est la méthode utilisée par Grillet et al. (2006) chez la drosophile (*Drosophila melanogaster*), où la latence de chaque femelle avant la copulation avec les différents mâles du groupe est utilisée comme mesure de préférence. L'efficacité de ce dispositif expérimental dépend fortement de l'espèce, car le résultat de l'appariement est influencé par la composition du groupe et si certains mâles ne sont plus disponibles après l'appariement, la mesure de préférence est moins fiable pour les femelles qui s'apparient en dernières. Finalement, la méthode la plus utilisée et souvent jugée plus fiable consiste à laisser la femelle choisir entre plusieurs partenaires potentiels présentés simultanément ("choice paradigm" ou "choice design », Dougherty & Shuker, 2015). Dans ce cas, il est possible de présenter aux femelles des mâles exprimant des phénotypes extrêmes ou des stimuli artificiels pour cibler des traits particuliers tout en standardisant le reste du phénotype des partenaires présentés (e.g. signaux visuels : Gierszewski et al., 2017; Romano & Stefanini, 2021; signaux sonores: Neelon et al., 2019). Dans les deux cas, la préférence de la femelle est souvent estimée par le temps total passé devant chaque mâle/stimulus qui lui est présenté (e.g. Pilakouta & Alonzo, 2014; Witte, 2006). Pour cela, la femelle est placée au centre d'un dispositif face à plusieurs partenaires potentiels variant sur la base du trait donné. Parce que la comparaison simultanée est plus efficace, ce type de dispositif expérimental permet à la femelle d'identifier des différences plus subtiles entre les mâles et d'exprimer une préférence plus forte pour certains traits (Dougherty & Shuker, 2015). Cependant, l'utilisation de ce dispositif est parfois critiquée, car ne permettent pas toujours de distinguer entre la préférence sexuelle et la préférence sociale, et le temps passé par la femelle devant chaque mâle peut être confondu avec sa personnalité (David & Cezilly, 2011). Chez plusieurs espèces, il a été malgré tout démontré que la femelle s'apparie effectivement avec le mâle devant lequel elle passe le plus de temps (i.e. diamant mandarin; Cummings & Mollaghan 2006; Witte, 2006).

À quelle échelle la préférence est relevée? La préférence des femelles est mesurée à l'échelle interspécifique dans les études qui s'intéressent à la reconnaissance spécifique, à l'échelle intraspécifique pour celles qui explorent l'évolution des traits sexuels secondaires et à l'échelle intra populationnelle pour celles qui tentent de démontrer l'existence d'une préférence pour un trait particulier. Par exemple, dans le cas des études intra populationnelles, la préférence des femelles peut être notée de manière discrète (i.e. oui ou non pour chaque stimulus présenté) ou continue (temps passé devant chaque stimulus). Si les femelles montrent un biais significatif vers un stimulus mâle plutôt qu'un autre, il est possible de conclure qu'en moyenne ce stimulus est préféré par les femelles de la population. Malgré qu'elle soit très répandue, cette méthode peut masquer les différences individuelles de préférence entre les femelles. Elle peut amener à conclure que le trait en question n'est pas important parce que la majorité des femelles n'a pas exprimé le même biais pour un stimulus donné, et peut seulement mettre en évidence des préférences directionnelles (Wagner, 1998). De plus en plus d'études ne se limitent plus à tester l'existence de préférence femelle à l'échelle de la population, mais s'intéressent également aux différences de préférences observables entre les femelles (revue dans Cotton et al., 2006; Jennions & Petrie, 1997; Ryan et al., 2009). Entre autres, ces études ont pour objectif de comprendre pourquoi les femelles varient dans leur préférence sexuelle et qu'elles en sont les conséquences d'un point de vue évolutif sur les traits mâles et femelles.

Différences individuelles de préférence, consistance et répétabilité

Lorsqu'un groupe de femelles est présenté avec le même choix de partenaires, toutes les femelles n'expriment pas la même préférence pour le même mâle ou pour la même valeur de trait (e.g. Rowland et al., 1995). Certaines femelles font des erreurs d'estimation (e.g Ryan et al., 2007), ont de moins bonnes capacités à discriminer les mâles conspécifiques (e.g. Howell et al., 2019), sont moins réceptives sur le plan hormonal au moment du choix (e.g. Ryan et al., 2007), sont moins sélectives ou ont une fonction de préférence différente (Cotton et al., 2006; Jennions & Petrie, 1997). Par exemple, la condition des femelles interagit souvent avec l'investissement qu'elles sont prêtes à allouer au choix de partenaire (Ryan et al., 1992). Les sources de ces variations sont nombreuses en allant des différences génétiques, de trajectoires développementales jusqu'au contexte environnemental et social dans lequel se fait le choix (Cotton et al., 2006). Pour cette raison, le choix de partenaire est souvent mesuré plusieurs fois pour une même femelle face au même échantillon de mâles pour augmenter la fiabilité de la mesure de préférence et réduire les effets stochastiques au moment du test (Wagner, 1998).

Généralement, ces différences individuelles sont caractérisées par une mesure de répétabilité et/ou de consistance pour chaque femelle. La mesure de consistance d'une femelle représente souvent la variance de préférence d'un essai à l'autre et la répétabilité consiste à diviser la variance interindividuelle par la variance intra individuelle (Cummings & Mollaghan, 2006). Ainsi, plus la variance interindividuelle est grande comparée à la variance intra-individuelle, plus le comportement de la femelle est considéré répétable est donc plus la mesure de préférence reflète *a priori* la fonction de préférence de la femelle. Il est généralement considéré que la répétabilité d'un trait fournit un index du niveau de variance phénotypique entre les individus et constitue théoriquement la valeur maximale d'héritabilité du trait (Jennions & Petrie, 1997). Par exemple, si les femelles ne montrent pas de répétabilité dans leur préférence, il est souvent considéré qu'aucune variance héritable dans la préférence de ce trait n'est présente dans la population (e.g. Forstmeier & Birkhead, 2004). Cependant, cet argumentaire est critiqué dans le cas de la préférence sexuelle, car la mesure de répétabilité peut être plus faible que l'héritabilité réelle de la préférence (Dohm, 2002; Jennions & Petrie, 1997; Rosenthal, 2017). En effet, il est difficile de déterminer si une femelle exprime une préférence de façon consistante grâce à l'estimé de répétabilité, car un faible estimé peut refléter à la fois une préférence unanime (variance intra et interindividuelle faible) et une préférence aléatoire (variation intra et interindividuelle élevée; Cumming & Mollaghan, 2006). Un faible estimé de répétabilité peut émerger lorsque la mesure de préférence ne se fait pas exactement sur le même trait à chaque essai. Par exemple, lorsque l'on présente plusieurs mâles à des femelles, leurs comportements et leurs traits morphologiques ne sont pas toujours manipulables donc même si ces derniers sont présentés et classés sur la base d'un trait, ils varient sur un tout autre ensemble de caractéristiques qui peuvent affecter la préférence de la femelle d'un essai à l'autre (Candolin et al., 2003). De plus, la présentation d'un stimulus peut affecter la réponse aux stimuli subséquents (Rosenthal, 2017), et une mesure de répétabilité peut être compromise si les essais sont réalisés sur une courte période de temps. Si les femelles varient dans leur fonction de préférence, il est également possible que certaines femelles, démontrant une forte préférence pour une valeur de trait, soient plus consistantes entre les essais que des femelles ne montrant aucune préférence pour le trait considéré (Jennions & Petrie, 1997).

Même si les préférences sexuelles ont souvent une base génétique (Bakker & Pomiankowski, 1995), l'expérience de la femelle au cours de sa vie peut affecter sa préférence sexuelle et son choix de partenaire (Candolin, 2019; Cotton et al., 2006). Cette capacité d'apprendre de son expérience passée offre à la femelle une certaine flexibilité dans son choix, ce qui est crucial dans un environnement changeant (Chaine & Lyon, 2008; Qvarnström et al., 2000). Pour des femelles naïves d'expérience sexuelle, la préférence sexuelle peut être particulièrement labile et affectée par son expérience personnelle (e.g empreinte; Slagsvold et al., 2002 ; information privée ou personnelle; Hebets & Sullivan-Beckers, 2010; Ryan et al., 2009) et sociale via l'observation du choix de partenaire de ses conspécifiques (i.e. information publique; Hebets & Sullivan-Beckers, 2010). Particulièrement, quand une femelle se retrouve face à plusieurs partenaires potentiels, elle détecte un ensemble d'informations (e.g. visuelles, olfactives, auditives) et d'indices sexuels grâce à son système sensoriel. Ces informations sont envoyées à des mécanismes centraux pour être intégrées et traitées. À cette étape, la femelle estime la valeur des indices sexuels de chaque mâle, retient ces informations et en déduit la qualité générale de chaque partenaire potentiel. En fonction de son expérience passée et de sa condition présente, elle va ensuite décider de s'apparier avec un des mâles échantillonnés ou de les rejeter (Cauchoix & Chaine, 2016). Ainsi, le choix de partenaire peut faire intervenir des capacités cognitives particulières chez les femelles (Rystrom et al., 2019) que l'on rassemble souvent sous le terme de *cognition*.

Cognition

La cognition fait référence aux capacités cognitives permettant aux animaux de prélever de l'information par les sens, de l'acquérir, l'intégrer, la retenir et l'utiliser pour prendre des décisions (Shettleworth, 2001). Même si cette définition est critiquée par les plus conservateurs, qui définissent la cognition comme l'habilité de comprendre, de penser et de traiter la connaissance par le raisonnement (Papineau & Heyes, 2006), elle est utilisée par la grande majorité des auteurs de ce domaine. Ces processus incluent (1) la perception : la détection d'un signal environnemental, son identification et son estimation pour être traduite en représentation neuronale, (2) l'apprentissage : l'acquisition des représentations neuronales qui peut être responsable de la modification de l'état ou du comportement d'un individu suite à une expérience, (3) la mémoire : la rétention des représentations neuronales à court et long terme et (4) la prise de décision : processus non aléatoire conduisant à sélectionner l'une des alternatives disponibles lors d'une situation de choix (Cauchoix & Chaine, 2016). Évidemment, l'utilisation de processus cognitifs est fondamentale non seulement lors du choix de partenaire, mais aussi pour s'approvisionner, communiquer, se déplacer dans l'espace, interagir avec ses congénères, s'occuper de sa progéniture et faire face à des prédateurs. De manière générale, ces mécanismes permettent aux animaux de traquer les changements dans leur milieu de vie et de résoudre une partie des problèmes qu'ils rencontrent.

Ces habilités sont mises en évidence chez de nombreux taxa que ce soit chez les mammifères (e.g. Holekamp & Benson-Amram, 2017; Matzel & Sauce, 2017), les oiseaux (e.g. Cussen, 2017; Healy et al., 2010; Searcy & Nowicki, 2019), les poissons (e.g. Lucon-Xiccato & Bisazza, 2017; Kimber et al., 2014), les reptiles (e.g. Kis et al., 2015), les amphibiens (e.g. Liu et al., 2016), les insectes (e.g. Chittka et al., 2019) et les mollusques (Darmaillacq et al., 2014). Par exemple, pour survivre aux hivers rigoureux, certaines espèces d'oiseaux cachent leur nourriture pour faire des réserves avant cette période et sont capables de les retrouver et d'en consommer en grande majorité. Ces espèces ont souvent une meilleure mémoire spatiale et un hippocampe (zone du cerveau associée à la cognition spatiale) plus large que les espèces qui ne cachent pas leur nourriture (Pravosudov & Roth, 2013). Chez les nectarivores, les individus mémorisent la localisation des fleurs qu'ils ont exploitées et vidées pour pouvoir ajuster leur approvisionnement à d'autres fleurs non exploitées (Jelbert et al., 2014). Pour de nombreux oiseaux et mammifères, l'innovation ou l'acquisition de nouvelles sources de nourriture ou de nouvelles façons d'y accéder (i.e. utilisation d'outil) est commune, que ce soit par apprentissage social ou individuel (Emery & Clayton, 2009; Lefebvre et al., 2004). Les mésanges par exemple, sont connues pour avoir consommé la crème du lait en perçant l'opercule des bouteilles (Fisher & Hinde, 1949) et les macaques japonais pour laver les pommes de terre avant de les consommer (Kawai, 1965). En fonction de l'espèce étudiée, on retrouve différentes façons de mesurer la cognition animale.

Mesurer les capacités cognitives

Les capacités cognitives sont souvent difficiles à quantifier parce qu'elles sont inférées du comportement des individus ou de certains traits indirectement associés à ces capacités. Par exemple, dans les études comparatives, choisir une tâche qui permet de mesurer la performance d'espèces éloignées phylogénétiquement peut s'avérer compliqué, voire impossible. Pour cette raison, la taille relative du cerveau, souvent corrélée à la fréquence d'apparition de certains comportements comme l'utilisation d'outil, d'innovation (Reader & Laland, 2002) ou la performance dans des tests d'apprentissage (Kotrschal et al., 2013b), est une mesure qui est régulièrement utilisée pour étudier l'évolution de la cognition à l'échelle interspécifique (Lefebvre & Sol, 2008). Dans d'autres cas, lorsque l'objectif est d'estimer les différences individuelles de capacité cognitives au sein de la même espèce, le comportement de chaque individu est noté de façon similaire et répétée dans des tests psychométriques (ou batterie de tests; Shaw & Schmelz, 2017; Völter et al., 2018). Chaque tâche cible une capacité cognitive particulière et chaque individu est placé seul face à plusieurs alternatives dont l'une d'entre elles permet d'accéder à une récompense. On note à chaque essai si l'individu fait le bon choix ou pas pour pouvoir lui attribuer un score à la fin du test. En fonction de la tâche et/ou du design expérimental, ce score peut être continu (e.g. la vitesse d'apprentissage : le temps/le nombre d'essais nécessaire pour atteindre un critère de bonnes réponses) ou discret (e.g. tâche résolue ou non).

Chez les animaux non humains, on retrouve généralement les tests d'apprentissage associatif, où on mesure la capacité des individus à associer le choix d'un signal à une récompense (i.e. discrimination de couleurs, d'odeurs, de sons; Guenther & Brust, 2017) puis à renverser cet apprentissage en modifiant l'alternative qui était récompensée dans la tâche précédente (i.e. apprentissage renversé; Ashton et al., 2018). On peut mesurer la capacité de l'individu à apprendre la localisation de nourriture (i.e. apprentissage spatial) dans un labyrinthe ou face à des parcelles de nourriture cachées (Galsworthy et al., 2005; Shaw et al., 2015). On retrouve également des tests de mémoire (i.e. mémoire associative, spatiale) pour mesurer la capacité de rétention d'un apprentissage après un certain délai (Ashton et al., 2018; Galsworthy et al., 2005). La résolution de problème / l'innovation est un autre test psychométrique qui vise à mesurer la capacité de l'individu à résoudre à un nouveau problème (e.g. retirer un obstacle, tirer ou appuyer sur un dispositif pour obtenir la récompense; Galsworthy et al., 2005; Guenther & Brust, 2017; Johnson-Ulrich et al., 2020). Cette capacité est d'ailleurs souvent confondue avec l'apprentissage moteur qui correspond plutôt à la capacité d'améliorer l'exécution d'un acte moteur avec l'expérience (Shaw et al., 2015). L'apprentissage social, souvent inclus dans les tests psychométriques chez les primates, consiste à mesurer la capacité d'un individu résoudre une nouvelle tâche après avoir observé un démonstrateur la résoudre au préalable (Guenther & Brust, 2017). Finalement, il est possible de mesurer la capacité d'un individu à inhiber un comportement préféré qui n'est plus approprié pour accéder à la nourriture (i.e. contrôle inhibiteur; Ashton et al., 2018; Shaw et al., 2015). Évidemment, en fonction de l'espèce et de son écologie, certaines capacités et tâches cognitives sont plus pertinentes que d'autres à considérer.

Chez l'humain, les tests psychométriques sont effectués pour estimer l'intelligence générale des individus. Ce concept suggère que la performance d'un individu dans une tâche cognitive donnée permet de prédire sa performance dans d'autres tâches cognitives (Deary et al., 2010; Mackintosh, 1998). En utilisant des analyses en composantes principales, il est possible d'extraire un facteur 'g' qui explique en moyenne 50% de la variance interindividuelle chez l'humain. Même si son existence est encore débattue, ce concept est un des plus répliqués en science cognitive (Burkart et al., 2017; Deary, 2001). Chez les animaux non humains, quelques études ont mis en évidence des corrélations positives entre l'apprentissage associatif et l'apprentissage renversé (e.g. bourdon, *Bombus terrestris*; Raine & Chittka, 2012), entre le contrôle inhibiteur et l'apprentissage renversé (e.g. abeille, *Apis mellifera*; Chandra et al., 2000), entre l'apprentissage social et l'innovation (pigeons, *Columba livia*; Bouchard et al., 2007) et entre la résolution de problème et la complexité du chant qui peut être utilisé comme une mesure de capacité d'apprentissage chez les oiseaux (diamant mandarin, *Taeniopygia gutatta;* Boogert et al., 2008). Cependant, les évidences en faveur du facteur 'g' dans les études sur les animaux non humains sont contrastées et dépendent de l'espèce considérée (Burkart et al., 2017; Matzel et al., 2003; Poirier et al., 2020). En effet, l'approche modulaire, qui met l'emphase sur l'évolution de capacités cognitives adaptées aux problèmes rencontrés par l'espèce dans son milieu, est aussi souvent utilisée. Selon cette approche, la sélection naturelle devrait promouvoir des modules cognitifs spécialisés en fonction des contraintes environnementales de l'espèce (Thornton & Boogert, 2019; Shettleworth, 2012; Boogert et al., 2018).

La capacité d'apprendre de son expérience passée offre à l'individu la possibilité d'ajuster son comportement lorsque les conditions environnementales sont altérées (i.e. plasticité comportementale; (voir aussi « flexibilité comportementale » : Audet & Lefebvre, 2017; « flexibilité cognitive » : Fuss & Witte, 2019; « flexibilité comportementale » : Leal & Powell, 2012; « plasticité phénotypique réversible » : Morand-Ferron et al., 2010; « plasticité contextuelle » : Stamps, 2016 ; « variabilité comportementale » : Tervo et al., 2014; « réactivité » : Wolf et al., 2008). Bien que la plasticité comportementale puisse s'exprimer sous la forme de réponses conditionnelles à court terme (e.g. réponse physiologique ou réflexe comportemental; « rule of thumb » Stephens et al., 2007), ces ajustements peuvent aussi faire intervenir des mécanismes d'apprentissage, de mémorisation et de prise de décision (Beauchamp, 2000; Hamblin & Giraldeau, 2009; Fawcett et al., 2012). En effet, l'individu doit remplacer un comportement qui est sous-optimal par un autre comportement qui lui permet d'obtenir de l'information sur les nouvelles conditions. Ainsi, estimer la plasticité comportementale d'un individu permet d'évaluer indirectement ses capacités cognitives (Fuss & Witte, 2019). Pour mesurer la plasticité comportementale, certains psychologues utilisent des tests d'apprentissage inversé (e.g. Bond et al., 2007; Raine & Chittka, 2012), des tests de transfert d'attention (« set-shifting ») où l'individu doit apprendre à se focaliser sur la bonne dimension (i.e. olfactive, visuelle, tactile, spatiale) ou encore des tests de contrôle inhibiteur (Audet & Lefebvre, 2017). En écologie comportementale, la plasticité comportementale peut aussi être mesurée grâce à des tests d'innovation (Sol et al., 2002), correspondre à la mesure d'un comportement sur un gradient environnemental (norme de réaction, Dingemanse et al., 2010) ou encore à l'ajustement de deux alternatives comportementales sur un gradient environnemental (Morand-Ferron et al., 2010). Cette dernière est notamment intéressante pour mesurer la plasticité comportementale des individus dans un contexte d'approvisionnement social.

Au sein d'un groupe, le comportement des uns requiert souvent l'ajustement du comportement des autres. C'est le cas du jeu producteur-chapardeur (PC), issu de la théorie évolutive des jeux et développé par Barnard et Sibly (1981). Les individus ont le choix entre chercher leur propre nourriture (i.e. produire) ou la soustraire à leurs congénères (i.e. chaparder). Ils alternent entre les deux tactiques pour optimiser la quantité de nourriture qu'ils consomment dans leur groupe. Le gain reçu par un individu est influencé par ses propres choix, mais aussi par ceux de ses congénères (i.e. fréquence-dépendance; Giraldeau & Caraco, 2000) de sorte que plus les chapardeurs sont répandus dans la population, moins c'est rentable d'utiliser cette stratégie (i.e. fréquence-dépendance négative; Barnard & Sibly, 1981; Mottley & Giraldeau, 2000). Les stratégies des individus dans ce jeu peuvent également être affectées par des paramètres environnementaux comme la probabilité de rencontrer une parcelle de nourriture (Beauchamp et al., 1997) et le nombre d'individus dans le groupe (Vickery et al., 1991). Aussi, si les conditions se stabilisent, le groupe peut atteindre un équilibre (i.e. stratégie comportementale stable; Fawcett et al., 2012) où chaque individu va stabiliser son utilisation de tactiques d'approvisionnement et obtenir les mêmes gains que ses congénères. Ainsi, il est possible de relever l'utilisation des tactiques d'approvisionnement dans différentes conditions de distribution de nourriture et de mesurer si les individus modifient leur tactique d'approvisionnement en fonction des conditions (Barou Dagues, Hall & Giraldeau, 2020 ; Morand-Ferron et al., 2010). Pour exprimer de la plasticité comportementale dans ce contexte, les individus doivent percevoir la perte d'efficacité de leur stratégie, renverser leur apprentissage pour modifier leur stratégie et optimiser leur approvisionnement en fonction des nouvelles conditions; Barou Dagues, Hall & Giraldeau, 2020).

Quelle que soit la mesure de cognition utilisée, il faut s'assurer que les différences interindividuelles ne soient pas le reflet de facteurs non cognitifs internes (reliés au sujet; biais de perceptions, moteur, de motivation, de personnalité; Griffin et al., 2015; Rowe & Healy, 2014; Schubiger et al., 2020) ou externes (reliés au dispositif expérimental ou à l'environnement dans lequel le sujet est testé; Schubiger et al., 2020). Par exemple, la performance d'un individu en apprentissage associatif ou spatial peut être influencée par des biais de côtés (Guo et al., 2009), des préférences ou aversions pour certaines couleurs ou odeurs (Teichmann et al., 2020) et certains traits de personnalité comme l'exploration ou l'anxiété (Gibelli et al., 2019). La performance dans des tâches de résolutions de problèmes est souvent confondue avec la motivation, la persistance, la néophobie, l'exploration ou encore le rang de dominance de l'individu (Boogert et al., 2008; Gibelli et al., 2019; Griffin & Guez, 2014; van Horik et al., 2016) alors que le sexe, l'âge, et le rang de dominance de l'individu focal et du démonstrateur sont des facteurs importants lorsqu'on mesure la performance en apprentissage social (Aplin et al., 2013). La personnalité, qui fait référence aux différences individuelles stables et consistantes dans le temps et entre les contextes (Dall et al., 2004), fait l'objet d'un intérêt particulier lorsque la performance cognitive d'un individu est mesurée. En effet, elle peut générer des différences interindividuelles dans la manière de collecter l'information et de prendre des décisions (i.e. styles cognitifs; Griffin et al., 2015; Sih & Del Guidice, 2012). Cependant, l'effet de ces différents styles sur les performances cognitives semble varier d'une espèce à l'autre (Dougherty & Guillette, 2018) et même d'une population à une autre (Dalesman, 2018). Pour limiter l'effet de ces facteurs confondant, il est possible de sélectionner des individus qui ont grandi dans les mêmes conditions, de les habituer pendant de longues périodes de temps aux procédures et aux dispositifs expérimentaux et de les tester au même âge dans des conditions similaires. La motivation est généralement homogénéisée par des périodes de jeûne avant les tests et certaines mesures sont prises pendant les expériences pour être contrôlées à postériori dans les analyses statistiques. Sinon, comme pour la préférence sexuelle, il est possible de mesurer la performance des individus plusieurs fois pour estimer le degré de répétabilité des individus. Cependant, la mesure de répétabilité des performances cognitives est à interpréter avec précaution, car elle est généralement faible à modérée chez les animaux non humains (Cauchoix et al., 2018). Par exemple, au fur et à mesure des répétitions, la majorité des individus améliorent leur performance dans la tâche cognitive, la variance interindividuelle diminue et fait ainsi diminuer la mesure de répétabilité.

Valeur adaptative des capacités cognitives

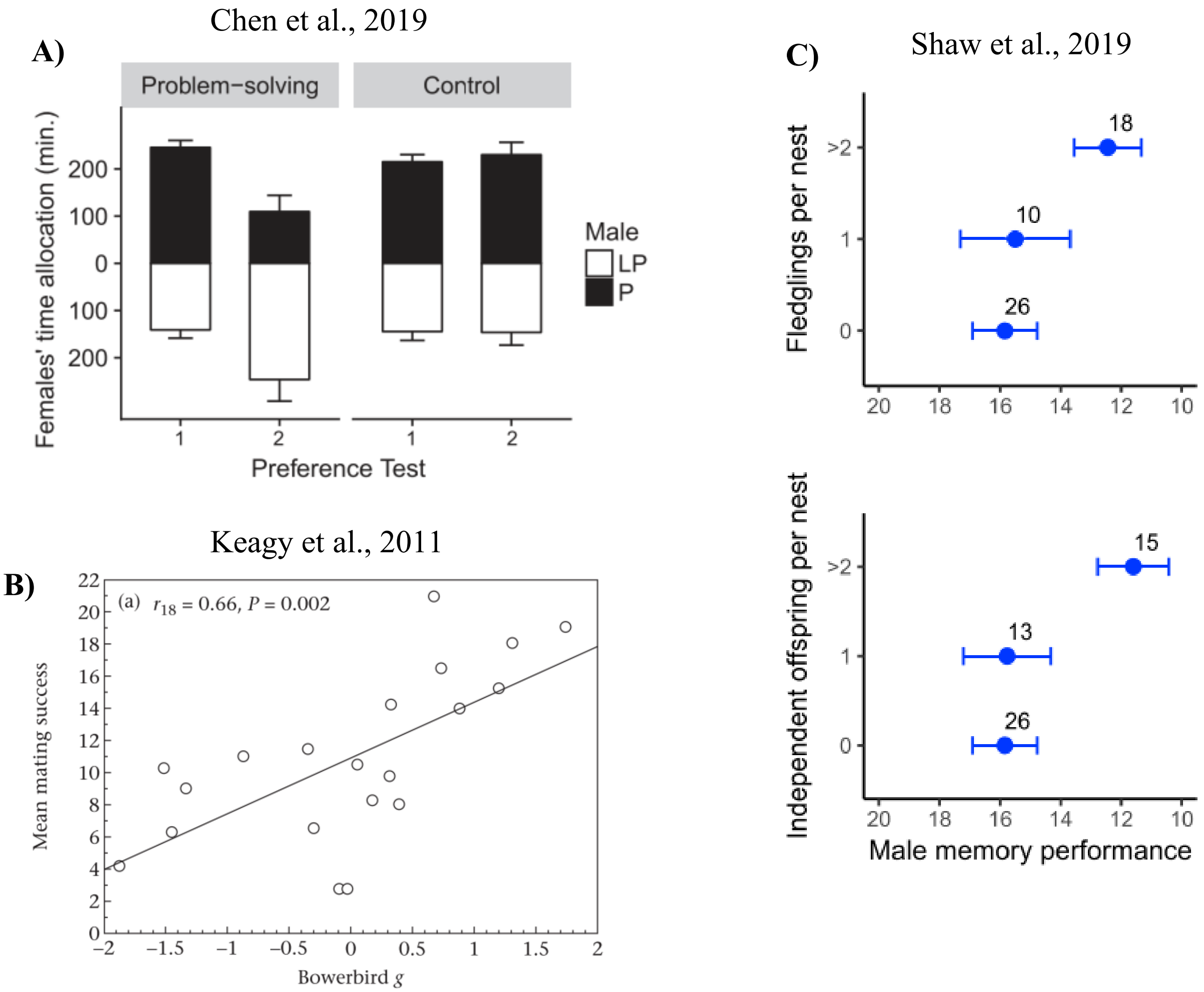
Obtenir une mesure fiable des performances cognitives est une étape nécessaire pour pouvoir déterminer si ces traits évoluent, c'est-à-dire s'ils sont (1) variables d'un individu à l'autre, (2) héritables et (3) si ces variances héritables sont associées à meilleure survie et/ou succès reproducteur (Darwin, 1871). Actuellement, de nombreuses études montrent, en effet, que les individus de différentes espèces varient de manière consistante dans leurs capacités cognitives (Boogert et al., 2018; Broaddus, 2013; Cole et al., 2010; Guenther & Brust, 2017; Guillette et al., 2015; Lucon-Xiccato & Bisazza, 2017; Matzel et al., 2003; Thornton & Lukas, 2012). Cette diversité cognitive est en partie expliquée par des différences interindividuelles génétiques (i.e. héritabilité des capacités cognitives; Croston et al., 2015; Navas González et al., 2019; Langley et al., 2020), des différences environnementales (e.g. effet maternel: Basatemur et al., 2012; Munch et al., 2018; stress environnementaux: Buchanan et al., 2013; transmission culturelle et sociale : Langley et al., 2018, 2020) vécues pendant le développement et l'interaction des deux (Buchanan et al., 2013). Par exemple, le facteur g (i.e. capacité cognitive générale) est fortement héritable chez l'humain et semble l'être modérément chez certaines espèces de souris et de primates (revue dans Croston et al., 2015). Chez les oiseaux, les performances cognitives sont souvent faiblement corrélées, remettant en cause l'existence du facteur g chez ces espèces (Poirier et al., 2020). Cependant, plusieurs études récentes démontrent que la performance dans différentes tâches cognitives est modérément à faiblement héritables (Langley et al., 2020; Quinn et al., 2016; Sorato et al., 2018) suggérant plutôt la transmission de spécialisations cognitives. De plus, certaines caractéristiques du chant, souvent utilisées comme mesure indirecte des capacités d'apprentissage, semblent être fortement à modérément héritables (Croston et al., 2015). Concernant le lien entre la variance héritable de la cognition et l'aptitude des individus, peu d'évidences directes existent pour le moment (Mery et Kawecki, 2002; Morand-Ferron et al., 2016). Cela dit, de nombreuses études ont examiné la relation entre les différences individuelles de performances cognitives et des proxis d'aptitude incluant le succès reproducteur (Cauchard et al., 2017; Preiszner et al., 2017; Shaw et al., 2019; Smith et al., 2015), la survie (Huebner et al., 2018; Langley et al., 2020; Madden et al., 2018; Maille & Schrade, 2016; Shaw et al., 2015; Sol et al., 2005), la condition corporelle (Buchanan et al., 2013; Huebner et al., 2018) et le succès d'approvisionnement (Pasquier & Grüter, 2016). Par exemple, la performance dans une tâche d'apprentissage associatif détermine la stratégie d'approvisionnement des adultes chez les moineaux domestiques (*Passer domesticus* ; Katsnelson et al., 2010) et la vitesse d'apprentissage augmente le succès d'approvisionnement et reproducteur des individus chez les sauterelles (*Schistocerca americana*; Dukas & Bernays, 2000). Les individus rapides à résoudre de nouveaux problèmes prennent plus de poids que les autres pendant la saison sèche chez les microcèbes mignons (*Microcebus murinus*; Huebner et al., 2018), fournissent plus de nourriture à leurs petits et obtiennent un meilleur succès d'envol de leurs jeunes chez la mésange charbonnière (*Parus major*; Cauchard et al., 2017). Chez le Cassican fluteur (*Cracticus tibicen dorsalis*), les individus plus performants dans une batterie de 4 tâches cognitives ont un meilleur succès reproducteur que les autres (Ashton et al., 2018). De plus, la capacité d'ajuster son comportement en fonction de son environnement permet d'avoir une meilleure habilitée à identifier les changements sociaux au sein de groupes chez les primates (Amici et al., 2018), d'améliorer le succès d'invasion (Sol & Lefebvre, 2000) et d'obtenir un meilleur succès reproducteur (Betini & Norris, 2012) chez les oiseaux.

D'un point de vue adaptatif, ces évidences supportent les trois conditions pour que la cognition puisse évoluer par sélection naturelle et l'idée d'une sélection directionnelle pour des individus plus performants sur le plan cognitif. Cependant, la variance génétique au sein d'une population peut persister grâce à la présence d'une sélection fréquence dépendante, de mutations, d'une faible pression de sélection (i.e. lien faible entre la variance du trait et la survie et/ou le succès reproducteur) ou de comportements optimaux qui varient dans l'espace et dans le temps (revue dans Dall, 2004). Certaines études soulèvent notamment l'idée que le lien entre les performances cognitives et l'aptitude des individus dépend des conditions environnementales (Huebner et al., 2018; Madden et al., 2018; Preizner et al., 2017). Par exemple, la performance des microcèbes mignons (*Microcebus murinus*) dans un labyrinthe n'est pas associée à une meilleure condition corporelle ou un meilleur taux de survie suggérant que les capacités d'apprentissage spatial se sont pas déterminantes pendant la saison sèche chez cette espèce (Huebner et al., 2018). Madden et al. (2018) ont également démontré que performer dans certaines tâches cognitives pouvait être mal adaptatif. Parmi des faisans (*Phasianus colchicus*) nourris en continu pendant leur développement, les plus performants en apprentissage renversé avaient moins de chances de survivre une fois relâchées en nature. Ces résultats sont en adéquation avec les modèles d'évolution de l'apprentissage qui prédisent que ces compétences sont adaptatives lorsque l'environnement change de manière prévisible, mais seraient mal adaptatives lorsque l'environnement reste stable ou change de manière imprévisible (Dunlap & Stephens, 2016). En effet, selon ces modèles, l'apprentissage implique un compromis entre les coûts et les bénéfices à développer de bonnes capacités qui dépendent de l'environnement. Par exemple, la performance d'apprentissage, associé à la production de tissus nerveux (Chittka & Niven, 2009; Kotrschal et al., 2013a), pourrait être en compromis avec la production de tissus intestinaux (Kotrschal et al., 2013a; Kotrschal et al., 2013b) et reproducteurs (Snell-Rood et al., 2011), mais aussi avec les traits d'histoires de vie comme des retards dans le développement (Snell-Rood et al., 2011), une durée de vie plus courte (Burger et al., 2008) ou de moins bonnes capacités compétitives (Mery & Kawecki, 2003). D'un point de vue énergétique, apprendre de son environnement implique des coûts d'échantillonnage (Dubois et al., 2010) et métaboliques, ne serait-ce que pour créer et maintenir les connexions synaptiques qui sous-tendent l'intégration, la mémorisation et l'utilisation de l'information (Dukas, 1999). Par exemple, chez les abeilles, investir dans de bonnes capacités d'apprentissage est en compromis avec le fait d'investir dans un bon système immunitaire (Alghamdi et al., 2008; Gegear et al., 2006). Cela dit, en étant coûteuses à maintenir et généralement associées à un meilleur succès reproducteur, ces capacités cognitives pourraient permettre aux mâles d'avoir un accès privilégié aux femelles et de bénéficier ainsi d'un meilleur succès d'appariement.

Choix de partenaire et cognition

Si un certain nombre d'études suggèrent que les capacités cognitives évoluent par sélection naturelle, d'autres suggèrent également que la sélection sexuelle jouerait un rôle important. L'idée que la sélection sexuelle puisse favoriser l'évolution des capacités cognitives est une idée au départ introduite par Darwin (1871) qui n'a intéressée les psychologues évolutionnaires qu'un siècle plus tard (Miller & Todd, 1998; Miller, 2001, 2007). Par exemple, Miller (2001) argumente dans son hypothèse du ''mating mind'' que « *l'intelligence* » chez l'humain est un indicateur fiable de la qualité génétique des individus, car coûteux à produire et à maintenir. Elle augmenterait le succès d'appariement et reproducteur des individus dits plus intelligents (Kolk & Barclay, 2019) et donc contribuerait à l'augmentation de la taille du cerveau chez l'humain. Néanmoins, l'importance de la sélection sexuelle dans l'évolution de la cognition chez les animaux incluant l'humain est encore discutée à l'heure actuelle. En principe, si certains processus cognitifs permettent à des mâles de détecter des femelles réceptives, de remporter des combats, de fertiliser les gamètes femelles ou d'empêcher l'accès d'une femelle à d'autres mâles après la copulation, ces compétences devraient leur permettre d'augmenter leur succès d'appariement et reproducteur. Cependant, les résultats des études actuelles sont contrastés. En effet, la sélection intrasexuelle pré et post copulatoire semble dans certains cas favoriser l'évolution de bonnes capacités cognitives (oiseaux : Araya-Salar et al., 2018; Garamszegi et al., 2005; Matthews et al., 2007; humain : Arden et al., 2009; amphibien : Mai et al., 2020; insectes : Mery et Kawechi, 2002; Rouse et al., 2020 ; poisson : Smith et al., 2015). Dans d'autres cas, cependant, elle défavorise (primate : Schillaci, 2006) ou n'affecte pas (primate non humain : Schillaci, 2006) l'évolution de la cognition.

Dans le cas de la sélection intersexuelle, si certains processus cognitifs permettent à des mâles d'acquérir davantage de ressources, de territoires ou de se rendre plus attractifs, les femelles pourraient sélectionner leur partenaire sur la base de ces compétences afin d'obtenir des avantages en termes de succès reproducteur (figure 1C; Andersson & Simmons, 2006; Araya-Salar et al., 2018; Boogert, Fawcett & Lefebvre, 2011; Fuss & Witte, 2019; Geher & Kaufman, 2011; Miller & Todd, 1998; Miller, 2001; Shaw et al., 2019; Verzijden et al., 2012). En effet, elles pourraient obtenir des bénéfices directs (i.e. cadeaux nuptiaux, allopatrie, un territoire de qualité, un nid de qualité; soins parentaux; défense contre les prédateurs; Boogert, Fawcett & Lefebvre, 2011), et indirectes, si ces capacités cognitives mâles sont héritables (Croston et al., 2015; Langley et al., 2020; Smith et al., 2015 mais voir Sauce et al., 2018; Sorato et al., 2018; Quinn et al., 2016), qui leur permettraient de produire des rejetons possédant ces capacités cognitives (Boogert, Fawcett & Lefebvre, 2011). Certaines études montrent qu'effectivement l'apprentissage spatial, la mémorisation, la résolution de problème ou la plasticité comportementale augmentent le succès d'appariement des mâles (figure 1B; mammifère : Jones et al., 2003; oiseau : Keagy et al., 2009, 2011, 2012; Patricelli et al., 2002; insecte : Montiglio et al., 2017). D'autres études montrent également que les femelles expriment une préférence pour les mâles plus performants dans des tâches de résolutions de problèmes (figure 1A; *Melopsittacus undulatus*; Chen et al., 2019; Striedter & Burley, 2019), de contrôle inhibiteur (*Gasterosteus aculetaus*; Álvarez-Quintero et al., 2021; Minter et al., 2017), d'apprentissage spatial (*Poecilia reticulata*; Shohet & Watt, 2009; *Microtus pennsylvanicus*; Spritzer et al., 2005) ou des batteries de tests (*Homo sapiens sapiens*: Prokosch et al., 2009). Cependant, l'importance de la sélection intersexuelle dans l'évolution de la cognition est remise en question dans certains cas lorsqu'aucune relation n'est trouvée entre les capacités cognitives et le succès d'appariement des mâles (oiseau : Isden et al., 2013) ou lorsque les femelles ne démontrent pas de préférence pour les capacités cognitives mâles (*Taeniopygia guttata* : Chantal et al., 2016; *Melopsittacus undulatus :* Medina-García & Wright, 2021).



Chen et al., 2019

Keagy et al., 2011

Shaw et al., 2019

Figure 1. A) Préférence pour les mâles capables de résoudre un problème chez la perruche ondulée (*Melopsittacus undulatus*). Les mâles initialement préférés sont présentés par les barres noires (P) et les mâles initialement non préférés par les barres blanches (LP). L'observation de mâles, initialement non préférés, capables de résoudre un problème a induit un changement de préférence des femelles envers ces mâles (Chen et al., 2019), B) Relation positive entre le succès d'appariement et le facteur général de cognition des mâles chez le Jardinier satiné (*Ptilonorhynchus violaceus*; Keagy et al., 2011), C) Relation positive entre le succès reproducteur et la capacité de rétention des mâles chez le rouge-gorge de Nouvelle-Zélande (*Petroica longipes*; Shaw et al., 2019).

Pour cause, il est encore difficile de savoir quels traits les femelles utilisent pour sélectionner leur partenaire sexuel dans ce contexte. Dans la plupart des études, les femelles n'observent pas directement les mâles performer dans des tâches cognitives. Ainsi, il est possible que les capacités cognitives mâles soient sélectionnées de façon indirecte si ces compétences sont positivement corrélées à des traits sexuels secondaires (Boogert, Fawcett & Lefebvre, 2011; Catchpole & Slater, 2008; Madden et al., 2011). Chez certaines espèces, les capacités cognitives participent au développement de comportements de cour complexes. C'est le cas chez les oiseaux où la performance dans différentes tâches a été associée au chant (Boogert et al., 2008; Boogert, Anderson, et al., 2011; Farrel et al., 2011 mais voir Anderson et al., 2017; Sewall et al., 2013; Templeton et al., 2014) à la production de danses élaborées et à la construction de nids complexes (Isden et al., 2013; Keagy et al., 2009, 2011; Madden, 2001; mais voir Day et al., 2005). Chez les Diamants Mandarins, les jeunes mâles apprennent à chanter et danser de façon stéréotypée pendant une phase de sensibilisation (Zann, 1996). Ils varient grandement dans leur comportement de cour à l'âge adulte (Williams, 2001) parce que la qualité des comportements dépend de l'identité du tuteur, des conditions pendant le développement (Holveck et al., 2008) et des capacités d'apprentissage de l'individu (Boogert, Fawcett & Lefebvre, 2011). De plus, certains ornements colorés chez les animaux sont basés sur la consommation de caroténoïdes (Griffith et al., 2006), qui est fortement influencée par l'efficacité de l'individu de trouver de la nourriture riche en caroténoïdes dans son environnement. Si certains traits ornementaux reflètent des capacités cognitives associées aux succès d'approvisionnement (oiseau : Mateos-Gonzalez et al., 2011; poisson : Pinto et al., 2021), les mâles pourraient démontrer leurs capacités cognitives via leurs traits sexuels secondaires. Néanmoins, observer des mâles en réponse à un changement environnemental pourrait permettre à la femelle d'évaluer rapidement leurs capacités cognitives et les bénéfices directs qu'elle pourrait retirer de l'appariement. Le Diamant Mandarin par exemple est une espèce sociale monogame vivant en Australie dans un milieu très aride où la disponibilité et la distribution de la nourriture sont directement affectées par les averses (Zann, 1996). Mâles et femelles s'approvisionnent en groupes de centaines d'individus pendant l'année, mise à part au cours de la saison de reproduction où les groupes se réduisent à une dizaine d'individus. À cette période, les individus sont soumis à des changements drastiques dans la répartition de la nourriture et sont souvent amenés à ajuster leurs tactiques d'approvisionnement en fonction des conditions locales et des congénères de leur groupe (Zann, 1996). Dans ce contexte, les femelles peuvent observer à de multiples occasions les mâles se comporter face à ces changements et potentiellement orienter leur choix en fonction de leur capacité à s'y ajuster. Bien que les femelles aient une préférence pour des chants de qualité, des ornements orange et des danses rythmées, ces traits sont moins labiles que le comportement des mâles et pourraient être moins fiables pour la femelle dans un environnement naturel changeant. Pourtant, aucune étude ne s'est intéressée à l'importance de la plasticité comportementale dans le contexte de choix de partenaire.

De plus, même si la plupart des évidences actuelles supportent l'idée que le choix de partenaire, via l'obtention de bénéfices directs et indirects des femelles, peut favoriser l'évolution de bonnes capacités cognitive, il est aussi possible que le choix de partenaire maintienne de la diversité cognitive. Par exemple le choix de partenaire peut maintenir de la variance génétique par sélection fréquence dépendante négative (e.g. préférence pour le phénotype rare; Graber et al., 2014), via l'appariement assortatif (Jiang et al., 2013), si la préférence est condition dépendante (e.g. Cotton et al., 2006) ou varie avec l'âge (e.g. Munro et al., 2014), si le contexte environnemental conduit à un choix réalisé qui s'éloigne de la préférence des femelles (Baur et al., 2019, Rosenthal, 2017) ou même si les femelles n'ont pas les mêmes capacités à estimer les traits des mâles (Rystrom et al., 2019; Howell et al., 2019). En effet, l'étude de l'évolution de la cognition par sélection intersexuelle tient rarement compte des caractéristiques femelles chez les animaux non humains (chez les humains : Escorial & Martín-Buro, 2012; Plomin & Deary, 2015; Śmieja & Stolarski, 2018). Par exemple, les femelles varient dans leur préférence sexuelle en partie parce que l'estimation des traits mâles implique des processus cognitifs (e.g. Rystrom et al., 2019; Howell et al., 2019) et sont énergivores (voir *Différences individuelles de préférence, consistance et répétabilité).* Actuellement, seule l'étude d'Álvarez-Quintero et al. (2021) tient compte des capacités cognitives femelles lors du choix de partenaire pour les capacités cognitives mâles chez les animaux non humains. Ils ont démontré chez l'épinoche à trois épines (*Gasterosteus aculetaus*) que la préférence femelle pour des mâles plus performants en contrôle inhibiteur était affectée par la performance femelle dans cette même tâche.

Objectifs et hypothèses

L'objectif de ma thèse est donc d'explorer l'importance de la sélection intersexuelle à travers le choix de partenaire dans l'évolution de la cognition mâle et femelle. Dans un premier temps, je chercherai à démontrer la présence de préférence sexuelle femelle pour la plasticité comportementale mâle. J'essaierai en particulier de comprendre si les femelles expriment une préférence unanime pour des mâles capables d'ajuster leur comportement d'approvisionnement lorsque la distribution de nourriture est modifiée au cours du temps. Ensuite, je chercherai à déterminer si les femelles expriment une préférence sexuelle pour la performance des mâles dans quatre tests psychométriques (i.e. apprentissage associatif, apprentissage spatial, apprentissage moteur progressif et contrôle inhibiteur) et si elles varient dans leur préférence pour ces traits en fonction de leurs propres capacités cognitives et/ou leur condition corporelle. Dans un troisième temps, l'objectif sera d'explorer l'interaction de la sélection naturelle et intersexuelle sur l'évolution de la cognition. À l'aide d'un modèle à base d'agent, j'essaierai de prédire quand et comment ces forces respectives agissent sur l'évolution de la capacité d'agents mâles à résoudre un problème pour accéder à de la nourriture et sur la capacité d'agents femelles à estimer ce trait cognitif mâle dans différents scénarios environnementaux.

Dans le premier chapitre (Chapitre II), les objectifs seront (1) de vérifier que les mâles Diamant mandarin (*Taeniopygia guttata*) expriment et diffèrent dans leur plasticité comportementale lorsque la distribution de nourriture change dans leur environnement, (2) de tester si ce proxy de capacités cognitives est associé à des traits sexuels secondaires appris pendant le développement et utilisés par les femelles chez cette espèce, et (3) de déterminer si les femelles expriment une préférence pour les mâles les plus plastiques dans leur comportement (figure 2). Dans un contexte où la capacité d'ajuster son comportement d'approvisionnement est *a priori* adaptative, les femelles devraient retirer des bénéfices à s'apparier avec les mâles capables d'ajuster leur comportement d'approvisionnement. Ainsi, en réponse au changement de distribution de nourriture, on s'attend à ce que les mâles expriment et diffèrent dans leur degré de plasticité comportementale indépendamment d'autres traits sexuels secondaires et que les femelles préfèrent en moyenne les mâles plus plastiques dans leur comportement d'approvisionnement.

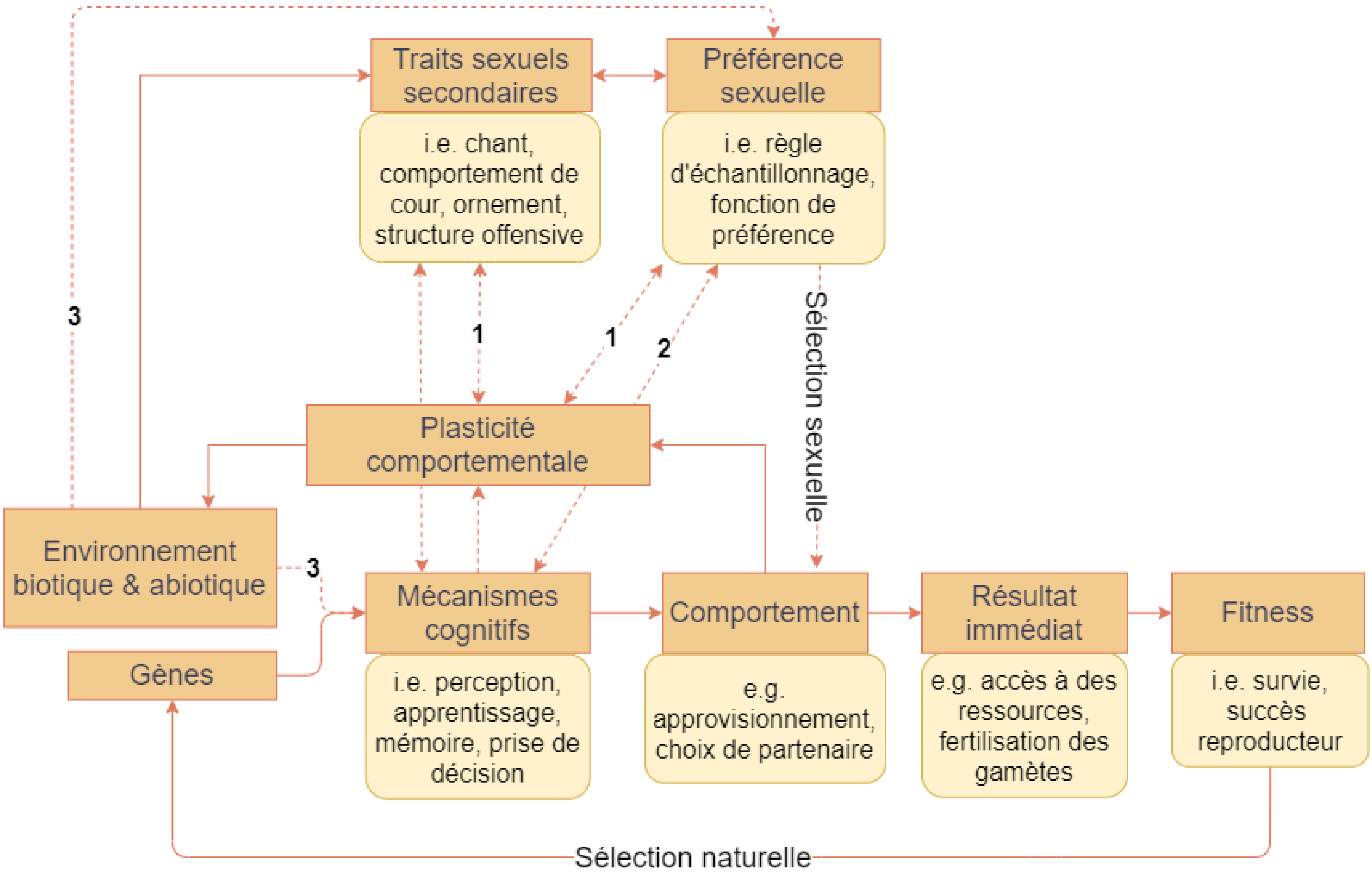


Figure 2. Schéma général de l'effet de la sélection naturelle et sexuelle sur l'évolution de la cognition (inspiré de Shettleworth, 2010). Les flèches pleines indiquent les relations pour lesquelles les tendances sont connues et les flèches pointillées celles pour lesquelles les tendances sont moins claires. Les chiffres représentent les relations étudiées dans chacun des chapitres de cette thèse.

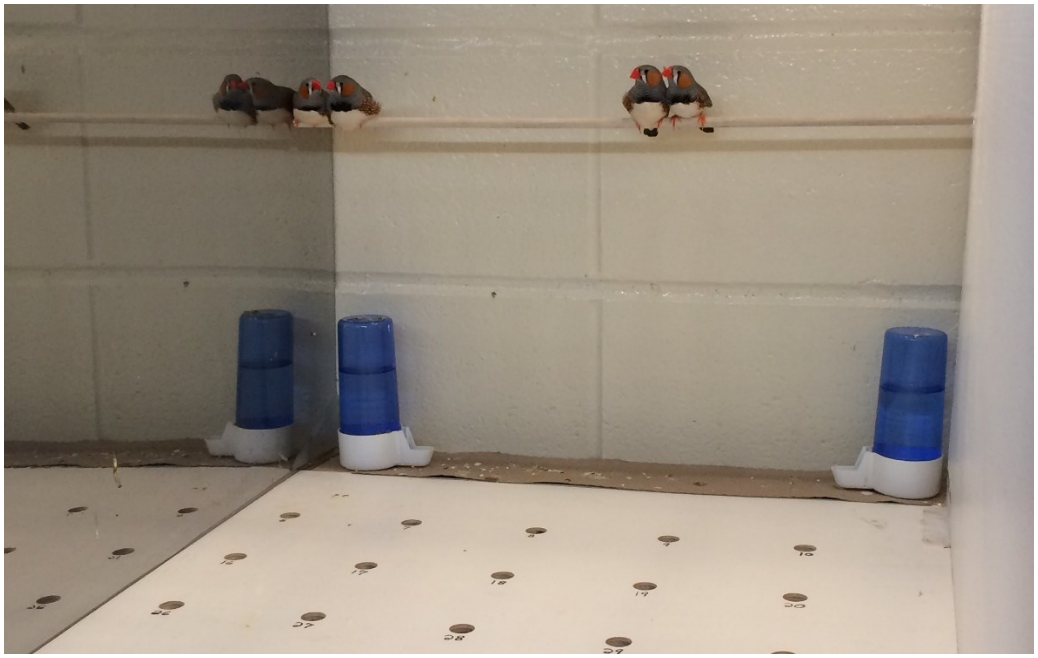
Si les femelles expriment une préférence pour la plasticité comportementale des mâles, il est probable que les mécanismes cognitifs impliqués dans l'expression de plasticité comportementale soient sélectionnés par les femelles lors du choix de partenaire (figure 2). Cela dit, la préférence des femelles pourrait varier en fonction des leurs propres capacités cognitives et de leur propre condition corporelle. Dans ce contexte, le second chapitre (Chapitre III) aura pour objectifs (1) de mesurer la performance des mâles et des femelles en apprentissage associatif, apprentissage spatial, apprentissage moteur progressif et en contrôle inhibiteur et de vérifier leurs indépendances, (2) de tester si les femelles expriment une préférence sexuelle pour ces différentes performances cognitives mâles, et (3) de déterminer si elles varient dans leur préférence en fonction de leur propre performance cognitive et/ou à leur condition corporelle. Sachant que chez les oiseaux, les performances cognitives sont peu corrélées les unes aux autres, on s'attend à ce que les performances mâles dans une tâche ne reflètent pas leurs performances dans les autres tâches. On s'attend également à ce que les femelles démontrent une préférence pour les performances cognitives mâles. De plus, sachant que le choix de partenaire implique l'utilisation de processus cognitifs et peut s'avérer coûteux pour les femelles, on s'attend à ce que les femelles plus performantes dans les différentes tâches cognitives et en meilleure condition corporelle expriment des préférences plus fortes que les autres femelles pour les différentes performances cognitives mâles.

Si effectivement les femelles sélectionnent des mâles exprimant certaines capacités cognitives et diffèrent dans leur préférence en fonction de leur propre capacité cognitive et/ou de leur condition, le rôle du choix de partenaire dans l'évolution de la cognition devrait fortement déprendre des conditions environnementales (figure 2). Dans le troisième chapitre (Chapitre IV), les objectifs seront donc de prédire (1) quand et comment les capacités cognitives mâles et femelles évoluent lorsque le choix de partenaire est aléatoire (i.e. effet de la sélection naturelle seule) et (2) quand et comment les capacités cognitives mâles et femelles évoluent lorsque les femelles ont une préférence pour les mâles plus performants (i.e. effets de la sélection naturelle et intersexuelle). En partant du principe que la cognition mâle devrait évoluer particulièrement lorsque les femelles retirent un bénéfice direct en termes de succès reproducteur, on s'attend à ce que la sélection intersexuelle joue un rôle important sur l'évolution de la cognition dans la plupart des environnements, en renforçant ou en agissant contre la sélection naturelle.

Chapitre II - Do female zebra finches prefer males exhibiting greater plasticity in foraging tactic use?

Marie Barou Dagues[1*], Étienne Richard-Dionne[1], Frédérique Dubois[1]

[1]Département des Sciences Biologiques, Université de Montréal, Montréal, QC H2V 2S9 Canada



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Abstract

There is ample evidence that phenotypic traits are important mate-choice criteria. Yet, we still know little about the importance of behavioural plasticity in attracting mates, although females could gain direct and/or indirect fitness benefits by choosing males that can adjust their behaviour to environmental fluctuations. Plasticity in foraging tactic use, particularly, might be a key determinant of fitness that could guide mate choice. In this study, we thus asked whether female zebra finches (*Taeniopygia guttata*) prefer males exhibiting greater plasticity in their foraging tactic use. We measured individual plasticity in a producer-scrounger game where males and females, playing in turn, were exposed to two seed distribution treatments, and females could monitor the males' behaviour, unbeknownst to them. Subsequently, we measured the time each female spent in front of the males they had previously observed in the expectation that females would exhibit a general preference for males with greater plasticity in tactic use. Contrary to our expectation, we found that females did not unanimously prefer the males exhibiting greater plasticity but differed widely in their preference with more plastic females showing a stronger preference for male plasticity compared to the other females. Thus, our findings suggest that differences among females in their mating preference would contribute to maintaining differences in plasticity in tactic use.

Keywords: plasticity in tactic use, mate preference, sexual selection, zebra finch

Significant statement

Mate choice is a crucial decision in an individual's life that directly impacts its fitness. Given that females could benefit from choosing males capable of responding to changes in environmental conditions, we asked in this study whether female zebra finches (*Taeniopygia guttata*) prefer males exhibiting greater plasticity in their foraging tactic use. We let females observe males expressing plasticity in a social foraging context and scored their mate preference for male plasticity. We found that females differed in their preference for male plasticity in tactic use, with more plastic females exhibiting a stronger preference for male plasticity compared to the others. Our results indicate that behavioural plasticity may be used as a mate choice criterion and hence suggest that mate choice might contribute to maintaining differences in male behavioural plasticity.

Introduction

Mate choice is a crucial decision in an individual's life that directly impacts its fitness (Bateson, 1983; Andersson, 1994). Consequently, a large number of studies have been conducted over the last three decades to identify which traits are used by choosing individuals (usually females) as mate-choice criteria. Many of them have focused on male phenotypic traits that are costly to produce or maintain (i.e. the handicap principle; Zahavi, 1975) and hence indicate the quality of potential mates (e.g. Andersson and Simmons 2006). There is ample evidence that females in captive zebra finch (*Taeniopygia guttata*) populations use phenotypic traits (e.g. symmetry in secondary sexual characters, Swaddle & Cuthill, 1994; song quality, Tomaszycki & Adkins-Regan, 2005; foraging efficiency, Chantal et al., 2016; beak colour and cheek patch size, Burley et al., 2018) that reflect the fitness of potential mates (Price & Burley, 1994; Naguib & Nemitz, 2007; Ritschard & Brumm, 2012). For instance, female zebra finches demonstrate mating preference for males performing long-lasting courtship dances (Zann, 1996) as well as for males with similar personality traits as their own (Schuett et al., 2011). Surprisingly, however, we know very little about the importance of male plasticity in behavioural traits (also called "behavioural plasticity": Komers, 1997 and "behavioural reaction norm": Dingemanse et al., 2010) in a mate-choice context, although direct and indirect evidence strongly suggests that females could benefit from choosing males capable of responding to changes in environmental conditions.

First, empirical evidence indicates that individuals widely differ in the amount of plasticity they exhibit in response to changing environmental conditions (e.g. Barou Dagues, Hall & Giraldeau, 2020; Dingemanse et al., 2010; Dingemanse & Wolf, 2013; Morand-Ferron et al., 2010) and that differences in plasticity can be associated with fitness differences in terms of survival (e.g. plasticity in activity level; Toscano, 2017) or reproductive success (e.g. plasticity in nest defence; Betini & Norris, 2012). Behavioural plasticity, a special case of phenotypic plasticity that involves fast and often reversible responses to environmental changes (Komers, 1997), is considered to be highly advantageous in predictable changing environments, as it would allow individuals to behave optimally in any situation (Komers, 1997). It is worth mentioning, however, that an individual able to express plasticity for a given behavioural trait in a given context might not be able to express plasticity for other behavioural traits or in other contexts (Morand-Ferron et al., 2010; Gibelli et al., 2018). Second, several studies found that individual variation in response to changing conditions is repeatable through time (e.g. plasticity in foraging tactic use, Morand-Ferron et al., 2010; plasticity in activity rate, Mitchell & Biro, 2017). This finding suggests that the expression of plasticity could be related to intrinsic traits, and hence could be heritable (Dingemanse & Wolf, 2013). For these reasons, females could gain direct and/or indirect fitness benefits by mating with males exhibiting response to environmental changes. Third, indirect evidence that females would use male plasticity as a mate-choice criterion comes from studies that have reported a positive effect of male plasticity on mating success (i.e. modulation of display intensity on the proportion of courted females, Patricelli et al., 2002; plasticity in exploration activity on the time of mount, Han & Brooks, 2014; plasticity in digging behaviour on mating frequency, Carballo et al., 2017; plasticity in activity on the proportion of mating, Montiglio et al., 2017). Such studies, however, were unable to establish whether females actually choose a mate based on this trait, or simply prefer males that are more efficient at attracting or maintaining their attention. For instance, although female satin bowerbirds (*Ptilonorhynchus violaceus)* prefer the most intensely displaying males, the most successful males are the ones who modulate the intensity of their display in response to female signals, in order to remain attractive without threatening the females (Patricelli et al., 2002). Thus, there is no direct evidence that females would observe the responses of males to environmental changes and then use this trait to select a mate.

In this study, we investigated the importance of plasticity in foraging tactic use in zebra finches in a mate choice context. We let females forage and observe males foraging on a board where the food distribution was changed in the environment and asked whether they prefer males exhibiting a greater response in foraging tactic use. Specifically, we measured individual plasticity in a frequency-dependent context where the birds could either search for food by themselves (thereby using the producer tactic) or search for joining opportunities (thereby using the scrounger tactic). We manipulated the distribution of the food that was either clumped into a small number of large patches or dispersed into a large number of small patches. Although the treatments are expected to promote respectively scrounging and producing at the flock level (e.g. Beauchamp & Giraldeau, 1996; Vickery et al., 1991), individuals can also adjust their tactic use in response to the behavioural change of their conspecifics making difficult to predict the adaptive direction of the change for a given individual. Then, during each trial, we noted the foraging tactic use of the focal bird in order to estimate its degree of change in tactic use between both treatments, and its feeding success that has been found to guide female mate choice as well (Chantal et al., 2016; Snowberg & Benkman, 2009). Subsequently, in a mate choice experiment, we measured the time spent by females in front of the males they had previously observed (Witte, 2006) and calculated a preference score for plasticity based on preference for each of the four males. Although no mate preference for male foraging behaviour has been reported by a previous study in zebra finches (Boogert et al., 2010), we measured this trait, in addition to body size, body condition and courtship activity, to test their correlations with individual plasticity and estimate their potential effects on male mating success. We used zebra finch, an Australian species which lives in very arid habitats, because males and females forage in stable flocks across the year and are often confronted with drastic changes in food availability and food distribution in response to rainfall (Zann, 1996). In this context, females likely observe repeatedly males that must respond to those drastic changes and then should benefit from mating with males that can adjust their foraging behaviour to local and current conditions. We expected (i) individuals to differ in their plasticity in foraging tactic use independently of the other traits measured and (ii) females to demonstrate a general mate preference for male plasticity in tactic use.

Methods

Subjects and housing conditions

We used 16 male and 25 female domesticated zebra finches aged of six months at the beginning of the experiment. All the birds came from a local breeder (Oisellerie de l'Estrie, Thetford Mines, Canada) ensuring that all individuals were unrelated to each other. The birds were arranged into 11 unisex foraging flocks (i.e. four male and seven female flocks, appendix 1, Table S1) of four birds each. Male and female flocks were kept in separated rooms at sexual maturity until the beginning of the experiments to prevent olfactory, visual and auditory contacts. All individuals were identified by two coloured numbered leg rings (i.e. one blue and one white for each male) and were kept, outside of testing, with their flock mates in cages (50x39.5x39.5cm) at 23°C (±1°C) and 34% relatively humidity on a 12L:12D photoperiod cycle for the foraging experiment and 14L:10D for the mate-choice experiment. They had ad libitum access to water, mixture of seeds, spray millet, vitamin mixture and oyster scales. The data were not collected blindly as we observed and noted the behaviour of each focal, colour-banded individual during all the experiments.

We first measured individual plasticity in producer-scrounger tactic use allowing flocks of four males or four females to forage in turn under two different seed distributions. Females could thus observe the males' foraging behaviour and experienced the same environmental change. Subsequently, we measured the time spent by females in front of the males they had previously observed using a four-choice test. Each female went through a 10-day foraging experiment and a two-day mate-choice experiment while the males repeated the same procedure two or three times with different female flocks. Note that in order to collect data on each male at least twice, we had to reuse 11 females in the foraging experiment, but we did not consider the results on females' behaviour for statistical analyses (see appendix 1, Table S1 for more details). The experiments lasted 12 weeks over the course of 2017-06-05 and 2019-01-22.

Foraging experiment

We conducted the experiment in an indoor aviary (225x155x244 cm). The birds were observed through a one-way mirror (from outside the aviary) while searching for food on a 114.5 x 114.5 cm wooden board placed within an experimental device and that contained 100 wells (1.3 cm diameter and 1.0 cm depth, spaced 10 cm apart in a 10 x 10 grid pattern) serving as food patches. The experimental device was divided in two equal non-acoustically isolated compartments (122x110x60cm) that were occupied each by one male and one female flock. Both compartments were separated by a one-way mirror and the male compartment was enlightened by two neon lights to be clearly visible from the female compartment. The females could hence see and hear the males regardless their locations on the board, but the males could only hear the females (appendix 2, Fig. S1).

Before the experiments, the birds had been gradually familiarized to the experimental device and procedure with their flock mates for 10 days. During the first five days, we filled all the wells, and once all the birds from the flock were used to feeding in the wells, we progressively reduced the number of rewarded wells as well as the quantity of food per well. Then the birds experienced for five days the same procedure as for the testing period, except that 10 randomly chosen wells were filled with 10 seeds before each trial and we recorded no data. Also, we ensured that all birds were used to go on the board once we turned on the light and that birds within flocks all foraged together. During the 10-day testing period, one male and one female flock had access to the board for four trials per day between 8h00 and 12h00 after 14h of food deprivation. For each of the eight daily trials, we provided food alternately to the female or to the male flock, so that females and males played in turn (with females always foraging first and observed the male after). All flocks went through two seed distribution treatments for five consecutive days per treatment: scattered (S) with five millet seeds in 10 wells (i.e. low scrounging food condition) and clumped (C) with 10 millet seeds in five wells (i.e. high scrounging food condition). We balanced the order of the treatments so that four female flocks were tested first in the S treatment and then in the C treatment while the other three female flocks experienced the treatments in the inverse order. Obviously, the males that foraged in the adjacent compartment of a flock of females followed the same order of treatments as they did. Before a trial, we dispersed white millet seeds in randomly selected wells (i.e. matching with the treatment S or C) and covered the wooden board with a piece of tissue. After the light turned off, we removed the tissue and went out from the aviary. The trial began when the light turned on and ended after three min. Because the data in each trial are highly interdependent (e.g. Giraldeau et al., 1990; Koops & Giraldeau, 1996), we noted the behaviour of only one focal bird per trial, and randomly observed all individuals once a day, in a different order and at different times, day after day. If the focal bird did not participate during its trial, we recorded it as a missing value and performed an additional trial at the end of the day session (five times over the 608 observations). The behaviour recording was performed with the JWatcher software. Specifically, we recorded 1) the number of producer and scrounger events defined as pecking either in a full unoccupied well (i.e. producer) or in a well where at least one other flock member was present (i.e. scrounger), and 2) the number of seeds eaten per event (i.e. head up with a seed in the beak).

Mate-choice experiment

We used a four-chamber mate-choice apparatus placed in the same aviary as for the foraging experiment. The apparatus was composed by a central observation chamber (30x30x38cm), four choice chambers (30x10.5x38cm) and four male chambers (30.5x30x38cm; figure 1) that were separated from each other by transparent plexiglass partitions. Prior to testing, males and females had been gradually and separately familiarized with the apparatus and experimental procedures for five days (i.e. during the afternoons of the last five days of the foraging experiment). The males of a given flock were first placed individually in a male chamber for six trials of 30 min. Then, they were familiarized with the procedure (lights on and off) and manipulations (removal of the partitions) for four trials of 30 min. Females were trained in the same way but individually placed in the central zone. We ensured that females were active during the experiment and for that reason we had to exclude four females from the analyses (see supplementary material appendix 1 Table S1 for details about excluded individuals and flock composition).

We then measured the mate preferences of each female two days after the end of the foraging experiment. All females went over one trial per day for two days and we interchanged the position of the males in opposite chambers. Before a trial, the experimenter introduced in the dark the four males and the focal female in the mate-choice apparatus. Then, we turned on the light as the beginning of the trial and the female went through 10 min of observation in the central chamber and 15 min with access to the four choice chambers to express a choice. We videotaped all trials and used Jwatcher software to record the time the focal female spent in front of each male (i.e. in each choice chamber). We also recorded the time each male spent dancing in front of the female during the observation phase as a measure of courtship activity.

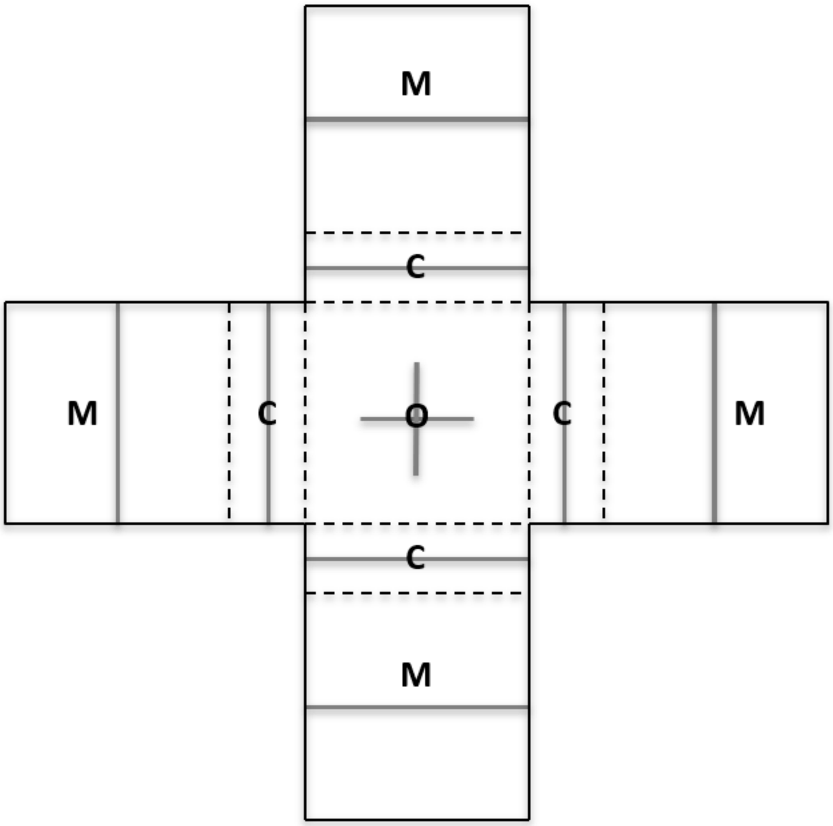

Figure 1. Top view of the four-chamber mate-choice apparatus with: a central observation chamber (O), four choice chambers (C) and four male chambers (M). Solid and doted black lines represent the opaque and transparent partitions, whereas the male and female perches are represented with grey lines. The transparent partitions were removed during the mate choice phase allowing females to perch in front of each male.

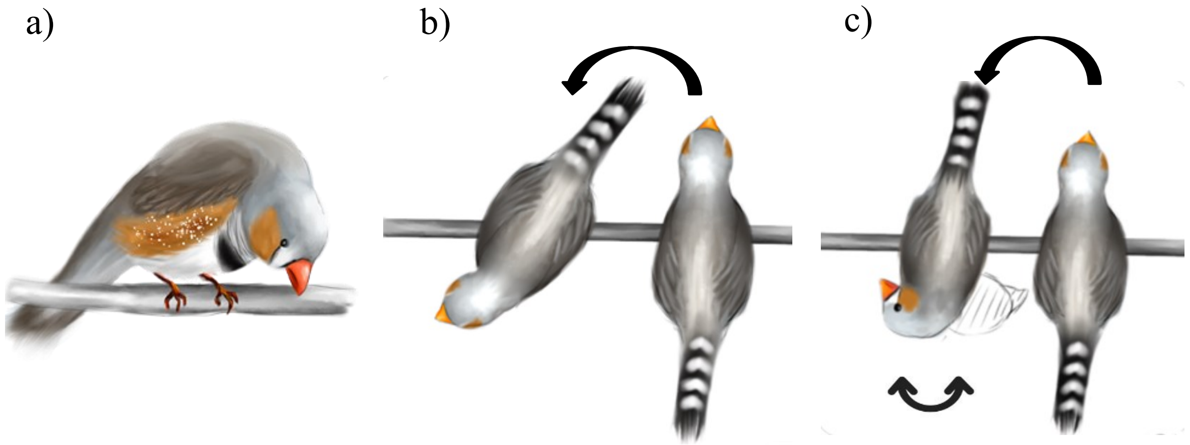

Figure 2. Male zebra finch dancing behaviours: a) Bill wiping, b) Head-tail twist, c) Turn-around (drawings by Sandrine Bélanger)

In order to estimate the time each male spent dancing, we first categorized the courtship activity into five dancing behaviours: Bill wiping, Head-tail twist, Turn-around, Hop, and Others (Ullrich et al., 2016; Zann, 1996). Bill wiping was defined as male facing the female, a body twist, lower and rotate head, beak scraping, raise head, and a body twist (figure 2a); Head-tail twist as male facing the female, rotating twisting the head and the tail (figure 2b); Turn-around as the male facing the female, rotating 180° back to the female and then looking at her (figure 2c); Hop as a lateral skip with both feet in the air; and Others as wing and leg stretching and body plumage fluffing. Then, we defined a dancing sequence as a series of behaviours expressed without an interruption of more than three sec and calculated for each male the sum of all dancing sequences to assess the total time it spent dancing.

Measures of phenotypic traits

We weighted all individuals before and after the experimental phase and used the mean weight as a measure of body mass. We also measured three times for each bird its tarsus and wing lengths on the right side and used the average measures for the estimation of body size and body condition.

Statistical analyses

Foraging tactic use and individual differences in plasticity in tactic use

To test whether birds adjusted their foraging tactic use according to the food distribution treatment, we performed generalized linear mixed models (GLMMs) with a binomial distribution. We defined the response variable as a two-column matrix with the number of wells produced and the number of wells scrounged by the focal individual at each trial. The fixed effects were the z-transformed number of seeds per well to test for a treatment effect, the z-transformed number of seeds eaten per trial, the trial number in each treatment, the order of treatments, the sex of individuals (i.e. as a confounding variable) and all the two-way interactions. As random effects, we included the foraging flock (individuals of the same sex foraging flock together) and individual identity nested in flock allowing both intercepts and slopes to vary between individuals across the treatment seeds. We used the Akaike's information criterion (AICc) for small sample sizes (Akaike, 1973) to determine the best fixed effect structures overall the set of models in the foraging experiment. To determine if the birds differed in their foraging tactic use and in their level of plasticity in tactic use, we tested the significance of the random effects structure (i.e. the intercepts for individual differences in tactic use, the slopes for individual differences in the change in tactic use and their correlation) using likelihood ratio tests (Pinheiro & Bates, 2000) with the best model (i.e. with the lowest AICc).

Plasticity in foraging tactic use

We first calculated individual producer-scrounger tactic use as the proportion of wells produced over the sum of all wells produced and scrounged in the last two days for each treatment. We selected data from the last two days of each treatment (e.g. Morand-Ferron & Giraldeau, 2010) to ensure that individual tactic use reflected the current seed distribution when the flock was near the equilibrium (i.e. the average rates of producing and scrounging reach stable values; Mottley & Giraldeau, 2000) and tested the repeatability of individual tactic use over the last two days. We used the rpt() function from the package RptR (Stoffel et al., 2017) including the producer-scrounger tactic use as response variable, the day of the experiment and the sex as fixed effects and the individual identity as random effect. Then, we quantified individual degree of plasticity in tactic use between the two treatments as the absolute value of the difference in producer-scrounger tactic use between the Scattered and Clumped treatments. As the birds foraged in a frequency-dependent context, we used this measure to estimate whether an individual was able to adjust its foraging tactic use according to the change in food distribution we imposed but also according to its conspecifics' behaviour. Thus, the more an individual changed its producer-scrounger tactic use between the treatments (irrespective to the direction of the change), the highest score it obtained. We used the function rpt() to test whether males' plasticity was consistent across the two or three repetitions of the foraging experiment with different female flocks. We included the males' degree of plasticity as a response variable and their identity as a random effect. We also explored whether male plasticity was associated with other male phenotypic traits. We estimated the body size by performing a PCA analysis with unrotated factor solution with the mean body mass, the mean tarsus length and the mean wing length. All variables loaded positively on the first component that accounted for 71.88% of the variance and so we used it as a measure of body size. We performed a linear regression including the body size as the response variable and the weight as a fixed effect and used the residuals as a measure of body condition. Subsequently, we tested the correlation between the males' level of plasticity in tactic use and their intake rate in the foraging experiment, their total amount of spent dancing (courtship activity), their body condition and their body size using Spearman multiple correlations. Finally, given that individuals could visit different numbers of wells during each trial, and that few visits could have made the estimated degree of plasticity in tactic use less reliable, we checked whether the number of wells visited by each individual was associated with its degree of plasticity in tactic use using a linear mixed model (LMM). We included the mean number of wells visited per trial by the focal bird as the response variable and the degree of plasticity in tactic use, the seed distribution treatment (i.e. scattered or clumped) and the sex as fixed effects. The individual identity nested in the foraging flock was also included as a random effect allowing the intercepts to vary between individuals.

Female mate preference for male plasticity

Performing a one-sample t-test (two-sided alternative hypothesis), we first checked whether the time spent in front of the preferred male (i.e. the male in front of which the female spent the most of her choosing time; Witte, 2006) was higher than 25% (i.e. random choice). Then, as the assumption of normality was not met, we used a two-sided Wilcoxon test to test whether the degree of plasticity of the preferred males was significantly higher than the average degree of plasticity of all males. Subsequently, we performed a LMM to test whether the female degree of plasticity in tactic use (entered as the response variable) was related to the degree of plasticity of the male they preferred. We included the male plasticity in tactic use, the trial number and their interaction as fixed effects and both male and female identity as random effects allowing the intercepts to vary between individuals. Also, to ensure that the females did not choose males according to their propensity to produce or scrounge, we performed the same analysis using a two-sided Wilcoxon test to determine whether, on average, the proportion of foraging tactic use over the experiment (10 days) of the preferred males were significantly different from the average proportion of foraging tactic use of all males. Then, we performed a LMM to test whether the females' foraging tactic use (entered as the response variable) was related to the tactic use of their preferred male (included as a fixed effect). We control for the trial number and the interaction between the male tactic use and the trial number as fixed effects and both male and female identity as random effects.

Because these analyses only consider the preferred male, they do not take into account the fact that more than one male can exhibit high degree of plasticity (which could cause the females to divide their choosing time) and so do not allow to directly test our prediction that females would express a preference for male plasticity in tactic use. Subsequently, we then calculated for each female *i* a preference score for male plasticity (*Pfi)*, that considers the time spent in front of the four males, using the following equation:

$$Pf_i = \frac{1}{D_{max}} \sum_{j=0}^{n-1} T_j(D_j) \ ,$$

where *n* is the number of males the female could choose among (i.e. always N = 4), T_j is the percentage of choosing time she spent in front of the male *j*, *Dj* the degree of plasticity of the male *j* in its foraging flock and $D_{\max}$ the maximum degree of plasticity in the males' flock. Thus, according to this equation, a female spending all her time in front of the male with the highest plasticity score will get a preference score of 100 while a female spending all her time in front of a male expressing no plasticity will get a preference score of 0 (for more details about the measure, see supplementary materials; appendix 3, Table S2). To test whether females demonstrated a consistent preference score for male plasticity between the two trials, we used the rpt() function including the preference score as the response variable and the individual identity as a random effect. To determine whether the females' preference score for male plasticity Pf_i (entered as the response variable) depended on their own degree of plasticity in tactic use (included as a fixed effect), we performed a LMM. We controlled for the trial number in the mate choice experiment, the interaction between trial number and female plasticity and the variance of plasticity within male flocks by including them as fixed effects. The female identity and the male flock observed in the PS game were entered as random effects allowing intercepts to vary between individuals.

Data availability

The datasets generated and/or analyzed during the current study are gathered in the Annexes (table A1 and table A2).

Results

Foraging tactic use and individual differences in plasticity in tactic use

Birds visited on average 6.48 ± 2.53 (mean ± SD) and 4.73 ± 1.99 wells and consumed on average 11.47 ± 4.06 and 11.52 ± 4.11 seeds in the scattered and the clumped treatment, respectively. Based on 608 observations, the trial number, the sex and all interactions were excluded during the GLMM model selection (see supplementary material, appendix 4, Table S3, for the result of both selected and full models). However, the best model revealed that the birds relied more on the producer tactic when the food was scattered rather than clumped in a few patches (mean ± SD, frequency of producer events: S treatment: 0.656 ± 0.274, C treatment: 0.530 ± 0.314; treatment fixed effect, Table 1) and when the birds experienced first the scattered rather than the clumped treatment (order of treatment fixed effect, Table 1). Also, individuals from the same flock differed between each other in their producer-scrounger tactic use (intercept (individual: flock) random effect, Table 1) and individual differences in tactic use were associated with differences in intake rate. Specifically, birds that invested more in the producer tactic experienced greater foraging success, irrespective of the treatment (Table 1). We also found that the birds in the same flock differed in their degree of plasticity in tactic use (GLMM: treatment (individual: flock) random effect, Table 1, Fig. 3) and these differences were not correlated with individual differences in tactic use (GLMM: intercept(individual:flock) * treatment(individual:flock) random effect, Table 1).

Table 1. Results from the model of producer–scrounger (PS) foraging experiment (GLMM with a binomial distribution, see Statistical Analysis section for details; 608 observations on 25 females and 16 males)

Fixed effects	Estimates	SE	*z*	*P*
Intercept	0.268	0.168	1.596	0.110
Treatment	-0.243	0.072	-3.352	**<0.001**
Intake rate	0.323	0.046	7.042	**<0.001**
Order of treatment	0.351	0.120	2.922	**0.003**
Random effects	Variance	LRT	df	*P*
Intercept (individual: flock)	0.891	375.67	1	**<0.001**
Treatment (individual: flock)	0.026	4.796	1	**0.028**
Intercept (individual: flock) * treatment (individual: flock)	-	0.907	1	0.763
Intercept (flock)	0.003	0	1	1
Treatment (flock)	0.022	0.79	1	0.374

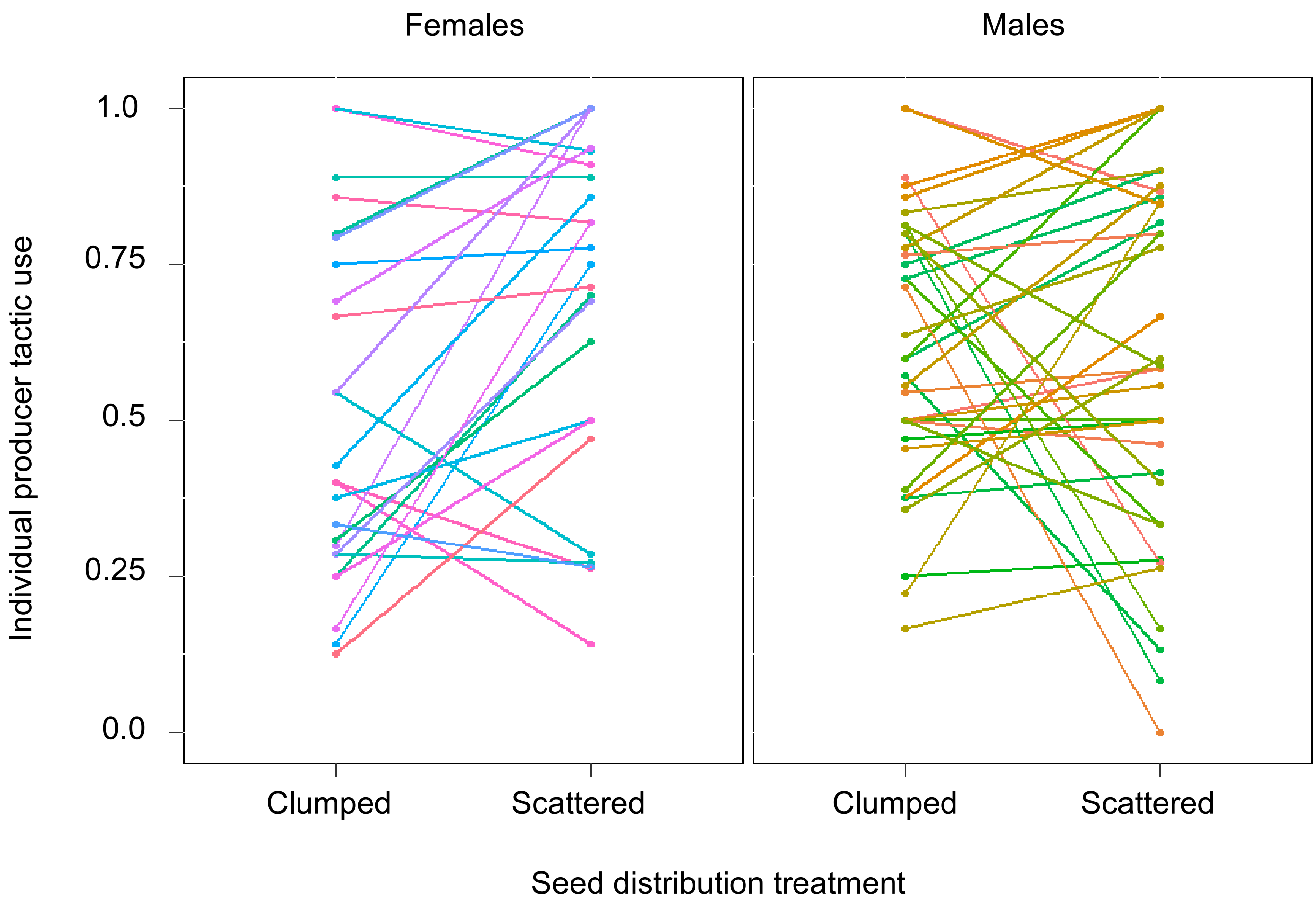

Figure 3. Change in tactic use by females (left panel, N=25 females) and males (right panel, N= 16 males) in response to change in food distribution. Each point represents the proportion of tactic use in the last two days for each food distribution treatment and the line of each individual represents the plasticity in tactic use between both treatments. Each individual is represented by a colour and note that the number of points indicated on the male Fig. is larger than 16, as four males were tested three times and 12 males twice.

Plasticity in foraging tactic use

Over the last two days of each treatment, the birds were repeatable in their producer-scrounger tactic use (R=0.37, SE=0.082, 95% confidence intervals [CI], [0.197, 0.494]), $P<0.001$, N=243 observations on 41 individuals) suggesting that individual tactic use reflected the current seed distribution in each treatment. Males varied in their degree of plasticity tactic use (0.238 ± 0.214; mean ± SD) but showed no repeatability in their degree of plasticity across repetitions when they were observed by different female foraging flocks (R=0, SE=0.098, 95% confidence intervals [CI], [0, 0.308], $P=0.5$, N=36 observations on 16 males; figure 4).We also found that males' plasticity in tactic use was not associated with their food intake rate, time spent dancing in front of females (courtship activity), body condition or body size (Table 2) and that the estimate of plasticity was equally reliable from one individual to another. Indeed, the mean number of wells visited by the birds was not related to their degree of plasticity in tactic use or sex (both variables were excluded during model selection) but was higher in the scattered compared to the clumped treatment (LMM: $t=6.865$, $P<0.001$, see supplementary materials, appendix 4, Table S3 for the results of both selected and full models).

Female mate preference for male plasticity

Females spent, on average, 75.06 ± 24.31% of their choosing time in front of the preferred male, which is significantly higher than expected if they had made a random choice (*t* test: two-tailed, $t_{33}=12.663$, $P<0.001$, N=21). However, females did not generally demonstrate a preference for more plastic males as revealed by the fact that the level of plasticity of the preferred males was not higher than the average level of male plasticity (Wilcoxon-test: two-tailed, w=655, $P=0.425$, N=42). In fact, females' degree of plasticity was positively related to the degree of plasticity of their preferred male (LMM, $t_{17}=2.241$, $P=0.039$, N=42 observations; Table 3a), irrespective of the trial number (not kept during model selection, see supplementary materials, appendix 4, Table S3, for results of both selected and full models), hence indicating that more plastic females had a stronger preference for male plasticity. Also, the proportion of tactic use of the preferred males did not differ from the average male tactic use (Wilcoxon-test: two-tailed, w=485.5, $P=0.221$, N=42) and we found no relationship between the females' proportion of tactic use and the proportion of tactic use of their preferred male (LMM, $t_{13}=-0.915$, $P=0.376$, N=42 observations, see

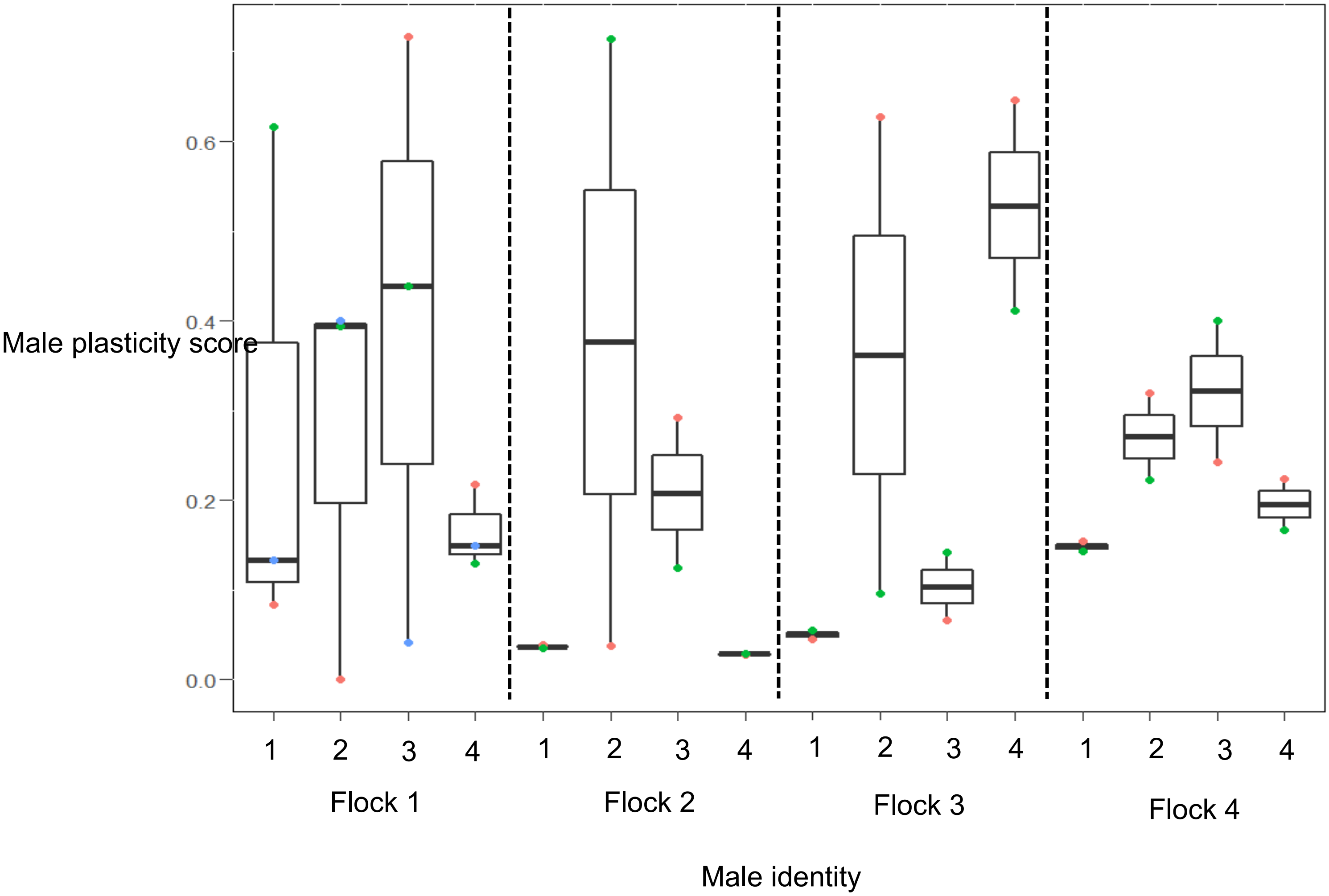

Figure 4. The degree of plasticity in tactic use expressed by the 16 males that were divided into four flocks. For each male, the foraging experiment was repeated two (flock 2, 3 and 4) or three (flock 1) times with different female flocks, with each corresponding to a measure of plasticity for each repetition. The medians of plasticity in tactic use for each male with the 25th and the 75th quartiles are shown, and red, green and blue points represented respectively the first, second and third repetitions.

Table 2. Spearman correlation matrix of males' plasticity in foraging tactic use with their intake rate in the foraging task, courtship activity in the mate choice experiment, body condition and body size

Plasticity in tactic use			
Intake rate	**Activity**	**Body condition**	**Body size**
Rs=-0.07	Rs=-0.30	Rs=0.33	Rs=-0.04
P=0.779	P=0.254	P=0.217	P=0.871
N=16	N=16	N=16	N=16

Table 3. Results from the LMM models of mate preference for male plasticity in tactic use with a) the preference for the preferred male and b) the preference score based on the time spent in front of each of the four males (42 observations on 21 females)

a) Fixed effects	Estimates	SE	*t*	*P*
Intercept	0.195	0.071	2.756	**0.012**
Female plasticity in tactic use	0.433	0.193	2.241	**0.039**
Random effects	Variance	LRT	df	*P*
Intercept (male identity)	0.016	3.576	1	0.059
Intercept (female identity)	0.018	1.370	1	0.242

b) Fixed effects	Estimates	SE	*t*	*P*
Intercept	31.12	12.26	2.538	**0.017**
Female plasticity in tactic use	81.11	30.02	2.702	**0.011**
Trial number	21.32	10.77	1.979	0.063
Variance of plasticity in male flock	16.55	116.72	0.142	0.888
Female plasticity * Trial number	-45.78	33.76	-1.356	0.191
Random effects	Variance	LRT	df	*P*
Intercept (individual identity)	286.9	2.	1	0.118
Intercept (male flock)	0	0	1	1

supplementary materials, appendix 4, Table S3, for results of both selected and full models). Similar results were obtained when considering the preference score. Indeed, we found significant repeatability in female mate preference for male plasticity between the two trials (R=0.388, se=0.183, 95% confidence intervals [CI], [0, 0.675], *P*=0.041, N=42 observations on 21 females) though the strength of repeatability apparently differed among females (Fig. 5, dotted lines). Females differed between each other in their preference score, and we found that females with greater plasticity showed a stronger preference for male plasticity than the other females (LMM: t_{32}=2.702, *P*=0.011, N=42 observations; Fig. 5; Table 3). Yet, the preference score tended to be higher in the second than in the first trial as revealed by a marginal effect of the mate-choice trial number (LMM: t_{198}=1.979, *P*=0.063; Fig. 5, Table 3b). Finally, there was no significant interaction between the trial number and the plasticity expressed by females (LMM: t_{19}=-1.356, *P*=0.191, Table 3b) and no effect of the variance of plasticity in male flock (LMM: t_{18}=0.142, *P*=0.888; Table 3b).

Discussion

In this study, we asked whether female zebra finches prefer males exhibiting greater plasticity in their foraging tactic use. In accordance with previous studies, we found that zebra finches differed significantly in their producer-scrounger tactic use and adjusted their tactic use in response to changes in seed distribution (e.g. Morand-Ferron & Giraldeau, 2010; Morand-Ferron et al., 2010). Furthermore, males within flocks varied in their plasticity in producer-scrounger tactic use, suggesting that females could all benefit from discriminating among potential mates based on their propensity to modify their foraging behaviour in response to changing conditions. Contrary to our expectation, however, females did not unanimously prefer the most plastic males and varied widely in their preference with females exhibiting greater plasticity consistently showing a stronger preference for male plasticity compared to the other females. Then, our results suggest that plasticity in tactic use might be an important trait used by females as a mate choice criterion.

The preference for male plasticity might seem *a priori* non-adaptive as male plasticity was not repeatable in our study, thus suggesting that females would not necessarily obtain a fitness advantage by choosing a male who displays plasticity in foraging tactic use. The lack of consistency

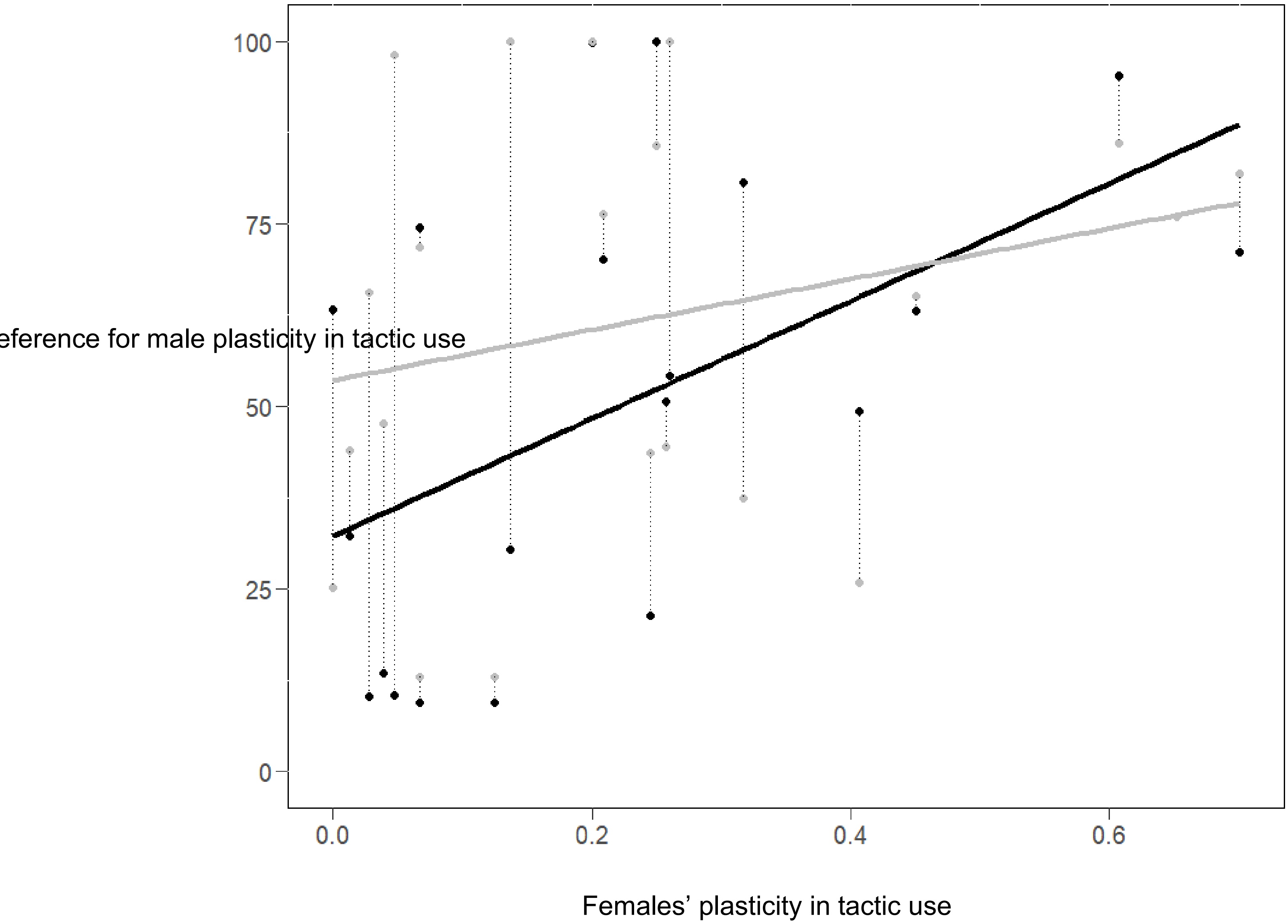

Figure 5. Females' mate preference for male plasticity in foraging tactic use (150 min of observation in the foraging task, N=21 females) in the first (black circle) and the second (grey circle) trials. The grey dotted line represents the difference of preference between both trials for a given female and the black and grey lines represent linear regression respectively for the first and the second trial.

in male plasticity, however, could be attributable to the fact that four birds per flock were searching for food over a relatively small area, making the payoff received by each individual strongly affected by the behaviour of others. The strength of frequency-dependent selection, indeed, has been found to be stronger in areas with high population density (Kilgour et al., 2018; Minter et al., 2015). The degree of plasticity expressed by each bird in our experiment (i.e. its realized plasticity), therefore, may not accurately reflect its potential plasticity (Stamps, 2016; Stamps & Krishnan, 2014). This interpretation is consistent with the fact that previous studies that measured plasticity in tactic use in conditions where the frequency dependence was much weaker, reported consistent individual differences (i.e. *Lonchura striata domestica*; Barou Dagues, Hall & Giraldeau, 2020) across time (i.e. *Lonchura unctulate*; Morand-Ferron et al., 2010). In any case, the absence of repeatability we found in male plasticity means that females could not choose overall more plastic males based on phenotypic or morphological traits that would be reflective of their ability to adjust their foraging behaviour, but rather strongly suggests that they would assess male plasticity through direct observation of their behaviour. In support to this idea, we found that male plasticity in tactic use was not related to foraging activity (i.e. mean number of wells visited in each trial, intake rate), courtship activity, body condition or body size. Zebra finches, in nature, form during the non-reproductive season stable flocks with high population density (Zann, 1996) and can identify individuals using vocal signatures (Elie & Theunissen, 2018). Even when the strength of frequency-dependent selection is high, females could then observe the same males multiple times responding to frequent environmental changes in nature, and actually use this trait as a mate choice criterion.

We found that females were repeatable in their mate preference score for male plasticity in tactic use, which strongly suggests that this trait is an important mate-choice criterion. However, we noted that some females were less repeatable than others in their preference for male plasticity in tactic use. This result is consistent with previous studies that reported a low degree of repeatability in mate choice preference (e.g. Forstmeier & Birkhead, 2004). For some females, a lack of repeatability may be due, for instance, to a lack of motivation or receptivity (Rowland et al., 1995) or a lack of attractivity for the considered trait (Jennions & Petrie, 1997). Nevertheless, we found that females differed among each other in their preference for male plasticity, regardless of the measure of preference we used. Specifically, females exhibiting greater plasticity in tactic use demonstrated a stronger preference for male plasticity, which would contribute to the maintenance of individual differences in male plasticity in tactic use. At least two alternative hypotheses may explain the differences among females in the expression of their preference for male plasticity in tactic use. First, if individuals achieve higher breeding success by pairing assortatively with respect to their plasticity in tactic use, females with greater and lower degree of plasticity should respectively express a stronger preference for greater and lower plastic males. In support to this idea, many studies found evidence for associative mating for size (e.g. Fazhan et al., 2017; Matos & McGregor, 2002), age (e.g. Hofler, 2007), colour patterns (e.g. Bowers et al., 2017; MacDougall & Montgomerie, 2003; or personality (e.g. Ariyomo & Watt, 2013; Fargevieille et al., 2017; Montiglio et al., 2016). Second, the differences in the expression of females' preference for male plasticity would reflect differences in their ability to assess male plasticity, which may be cognitively demanding (Jennion & Petrie, 1997). Indeed, in order to assess a male's plasticity in producer-scrounger tactic use, females would need to be able to 1) gather information about environmental conditions and detect relevant changes in external stimuli, 2) estimate the frequency at which the male uses both foraging tactics under every environmental condition and assess the magnitude of the change in its tactic use, and finally 3) recall a great deal of information on many potential mates. Mate-assessment based on plasticity in tactic use would then be particularly demanding. Our findings suggest indeed that females exhibiting greater plasticity in tactic use (and hence that were *a priori* more sensitive and responsive to this environmental change), would have been more accurate to assess plasticity in tactic use of the four potential mates before making a choice. Even if all females would benefit from mating with the most plastic males, the cost of developing the cognitive machinery necessary to accurately assess male plasticity in tactic use might then contribute in maintaining individual differences in plasticity.

In conclusion, our study provides interesting insights about the importance of plasticity in tactic use in a mate choice context and suggests that individual differences among females in their mate choice preference would contribute to maintaining differences in plasticity in tactic use within populations. Yet, additional studies would be required to convincingly determine if and how females use this male ability as a mate choice criterion, explore whether the use of this trait is constant or context-dependent and estimate the benefits females would obtain by mating with more plastic males. Thereafter, it might be useful to discriminate between the assortative mating and cognitive skills hypotheses by investigating whether female zebra finches exhibiting greater plasticity would have specific cognitive abilities that would allow them to assess this trait more accurately.

Ethical approval

All captures were done in the dark and the birds were gradually familiarized with all experiment devices and procedures. The experiments were conducted from 2017-06-05 to 2019-01-22 within the UdeM animal care facility. All procedures were in compliance with the guidelines of the Canadian Council for Animal Care and were approved by the committee of ethics on animal use of the University of Montreal (animal care permit #17-047).

Acknowledgments

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Supplemantary materials

Table S1. Starting and ending dates of experimental testing for each female foraging flock and participation or not of each female in the foraging experiment (FE) and mate choice experiment (MCE). Females which did participate in the FE and the MCE are highlighted in grey, whereas the four females which did not participate in the MCE are not highlighted. Among the 25 tested females, 11 females were used twice in the FE either to complete another female foraging flock (N=3) or to be able to measure the repeatability of male plasticity in tactic use (n=8). For females that were used twice, we only included in the analysis the data for the first test.

ID	Begining of experiment	End of experiment	Foraging Flock	Foraging treatment	Participation in FE	Participation in MCE	Males Flock observed
O14	05/06/2017	22/06/2017	GA	C-S	Yes	Yes	G2
O15	05/06/2017	22/06/2017	GA	C-S	Yes	Yes	G2
O16	05/06/2017	22/06/2017	GA	C-S	Yes	Yes	G2
O17	05/06/2017	22/06/2017	GA	C-S	Yes	Yes	G2
O7	05/06/2017	22/06/2017	GB	S-C	Yes	Yes	G1
O5	05/06/2017	22/06/2017	GB	S-C	Yes	Yes	G1
O6	05/06/2017	22/06/2017	GB	S-C	Yes	Yes	G1
O13	05/06/2017	22/06/2017	GB	S-C	Yes	Yes	G1
O2	03-07-2017	20/07/2017	GC	C-S	Yes	Yes	G1
O3	03/07/2017	20/07/2017	GC	C-S	Yes	Yes	G1
O11	03/07/2017	20/07/2017	GC	C-S	Yes	Yes	G1
O4	03/07/2017	\	GC	C-S	Yes	No	G1
O12	03-07-2017	20/07/2017	GD	S-C	Yes	Yes	G2
O9	03/07/2017	\	GD	S-C	Yes	No	G2
O8	03/07/2017	\	GD	S-C	2nd time	\	G2
O10	03/07/2017	\	GD	S-C	2nd time	\	G2
O8	26/09/2017	03/07/2017	GE	S-C	Yes	Yes	G1
O10	26/09/2017	03/07/2017	GE	S-C	Yes	Yes	G1
O18	26/09/2017	\	GE	S-C	Yes	No	G1
O16	26/09/2017	\	GE	S-C	2nd time	\	G1
O34	19/12/2018	05/01/2019	GG	S-C	Yes	Yes	G3
O28	19/12/2018	05/01/2019	GG	S-C	Yes	Yes	G3
O30	19/12/2018	05/01/2019	GG	S-C	Yes	Yes	G3
O25	19/12/2918	05/01/2019	GG	S-C	Yes	Yes	G3
O26	19/12/2918	05/01/2019	GH	C-S	Yes	Yes	G4
O33	19/12/2018	05/01/2019	GH	C-S	Yes	Yes	G4

O29	19/12/2018	05/01/2019	GH	C-S	Yes	No	G4
O27	19/12/2918	05/01/2019	GH	C-S	Yes	Yes	G4
O34	11/01/2019	\	GG	C-S	2nd time	\	G4
O28	11/01/2019	\	GG	C-S	2nd time	\	G4
O30	11/01/2019	\	GG	C-S	2nd time	\	G4
O25	11/01/2019	\	GG	C-S	2nd time	\	G4
O26	11/01/2019	\	GH	S-C	2nd time	\	G3
O33	11/01/2019	\	GH	S-C	2nd time	\	G3
O29	11/01/2019	\	GH	S-C	2nd time	\	G3
O27	11/01/2019	\	GH	S-C	2nd time	\	G3

Figure S1. The foraging apparatus seen from the outside of the aviary with the females' compartment on the left (darker) and the males' compartment on the right (lighter) divided by a one-way mirror film. The plastic grid on the front is removable allowing the experimenter to access inside each compartment. A perch was fixed at the bottom of each compartment and the wooden board contained 50 wells per compartment.

Table S2. Two examples of time spent by females in front of four males exhibiting different degrees of plasticity in foraging tactic use and their respective mate preference score Pf for male plasticity.

Female ID	Male 1: Plasticity =1	Male 2: Plasticity = 0.5	Male 3: Plasticity = 0.5	Male 4: Plasticity = 0	Female score of preference for plasticity
1	100%	0%	0%	0%	100
2	0%	0%	0%	100%	0
3	0%	100%	0%	0%	50
4	0%	50%	50%	0%	50
5	50%	0%	0%	50%	50
6	25%	25%	25%	25%	50
Female ID	Male 5: Plasticity =0.8	Male 6: Plasticity = 0.5	Male 7: Plasticity = 0.3	Male 8: Plasticity = 0.2	Female score of preference for plasticity
7	100%	0%	0%	0%	100
8	0%	0%	0%	100%	25
9	0%	100%	0%	0%	62.25
10	0%	50%	50%	0%	50
11	50%	0%	0%	50%	62.25
12	25%	25%	25%	25%	56.25

As male plasticity was not repeatable, it was nearly impossible to compose *a priori* male flocks according to this trait, and so, to control for variance in male plasticity between flocks. The preference score we calculated for each female depends on both the time she spent in front of each of the four males observed and their respective degree of plasticity. According to the equation, a random choice is equal to 50% when the variance in male plasticity is maximal (females 1 to 6) but can deviate from 50% if the variance of plasticity between males is lower (e.g. females 9 and 11). For this reason, we statistically controlled for the male flock each female observed and the variance of plasticity in the LMM analysis using data on female preferences. Measuring female preference using this score is more relevant in our study than using other measures, such as the ranks for instance, because it allows us to conserve the variance of plasticity among males within flocks (and hence to estimate its effect) and to compare the females' preference based on the male trait at the population level. Furthermore, it represents a more realistic measure as females, in nature, are unlikely to encounter the same males with exactly the same trait value.

Table S3. Estimates, AICc values, ΔAICc and weight of the selected model compared to full model without interaction for (a and b) the GLMM and LMM analysis of data from the foraging experiment, (c and d) the LMMs analysis of data from the mate choice experiment

(a) Models	Intercept	Sex	Order of treatment	Treatment	Trial	NbSeed	AICc	ΔAICc	weight
Selected model	0.268	/	0.351	-0.243	/	0.323	1900.4	0	0.825
Full model	0.413	-0.145	0.353	-0.242	0.006	0.324	1903.5	3.1	0.175

(b) Models	Intercept	Sex	Individual Plasticity	Treatment	-	-	AICc	ΔAICc	weight
Selected model	24.215	/	/	8.687	/	/	666.2	0	0.555
Full model	24.937	-0.505	-1.892	8.688	/	/	670.5	4.27	0.065

(c) Models	Intercept	-	Male Plasticity	-	Trial	-	AICc	ΔAICc	weight
Selected model	0.185	/	0.530	/	/	/	16.1	0	0.568
Full model	0.163	/	0.540	/	0.044	/	22.2	6.11	0.027

(d) Models	Intercept	-	Male Tactic use	-	Trial	-	AICc	ΔAICc	weight
Selected model	0.597	/	-0.108	/	/	/	-19.1	0	0.786
Full model	0.590	/	-0.105	/	0.013	/	-11.7	7.46	0.019

Chapitre III - Females' mate preferences for male cognitive abilities are associated with their own cognitive abilities

Marie Barou Dagues[1*], Frédérique Dubois[1]

[1]Département des Sciences Biologiques, Université de Montréal, Case postale 6128, Succursale Centre-ville, Montréal QC, Canada

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Abstract

Over the last decade, there has been a growing interest in evaluating the role of intersexual selection in the evolution of male cognitive abilities. Yet, because most studies have assumed that all females should prefer males with better cognitive abilities, and as such have ignored differences in female preferences, evidence supporting female mate preference for male cognitive traits remains weak. Here, we asked whether females preferred males that generally performed better in four different cognitive tasks and whether their mate preference depended on their own characteristics. Specifically, we tested whether females in better body condition and with better cognitive performances demonstrated stronger preferences for better cognitive performers. We conducted a mate-choice experiment on 21 zebra finch (*Taeniopygia guttata*) females that could choose among four males they had previously observed while they were foraging in groups and displaying courtship behaviour. Thereafter, we measured females' body condition as well as the performances of males and females in an associative learning, a motor shaping, a spatial learning and an inhibitory control tasks. We found that male cognitive abilities could not be reduced to a general cognitive factor and that male inhibitory control and associative learning performances were more important during mate choice compared to male motor shaping and spatial learning performances. Furthermore, as anticipated, females differed in their mate preferences, and these differences were associated with their own cognitive performances and, to a lesser extent, to their own body condition. Although the nature and the causality of these relationships need further investigation, our findings suggest that differences among females in their needs and/or ability to assess male traits would affect the relative importance attached to different cognitive abilities. As the adaptive value of male cognitive abilities depends on the ecology of the species, our results also suggest that the importance of mate choice on cognitive traits would vary among populations and over time depending on local conditions.

Keywords: intersexual selection, cognitive abilities, body condition, individual differences, inhibitory control, associative learning

Introduction

Understanding how cognitive abilities evolve within populations is a major issue in evolutionary and behavioural ecology (Thornton & Lukas, 2012). Although most of the research on this topic has been focusing on the role of natural selection (Shettleworth, 2010), there has been a growing interest over the last decade in evaluating the importance of intersexual selection in the evolution of male cognitive abilities. Explicitly, it is assumed that males with better cognitive abilities pay energetic and developmental costs for producing and maintaining neuronal processes (Laughlin et al., 1998) but are in return more efficient foragers (Raine & Chittka, 2008), better parents (e.g.Wetzel, 2017) and survive better (Cole et al., 2012). As such, they might provide females with direct (Branch et al., 2019; Cauchard et al., 2013; Preiszner et al., 2016; Shaw et al., 2019) and/or indirect (Iwasa & Pomiankowski, 1999) fitness benefits, if cognitive abilities are heritable (Croston et al., 2015; Langley et al., 2020; Smith et al., 2015; but see Sauce et al., 2018; Sorato et al., 2018). Thus, the idea that female mate choice might contribute to the evolution of cognitive abilities (Darwin, 1871) has been the subject of research in both human and nonhuman animals (Boogert, Fawcett & Lefebvre, 2011; Hollis & Kawecki, 2014; Miller & Todd, 1998). Yet, experimental and empirical evidence regarding female mate preference for male cognitive performances remains contrasted. Indeed, a number of studies found that males with better cognitive performances are preferred by females (e.g. Álvarez-Quintero et al., 2021; Chen et al., 2019; Prokosch et al., 2009; Shohet & Watt, 2009; Striedter & Burley, 2019) or have a higher mating success (Araya-salas et al., 2018; Boogert, Anderson et al., 2011; Keagy et al., 2009, 2011, 2012; Minter et al., 2017) compared to males with poor performance. However, other studies found no relationship between the overall performance of males and their mating success (Isden et al., 2013; Keagy et al., 2011) or demonstrated that other traits than male cognitive performance *per se*, are used as a mate-choice-criteria (e.g. Boogert et al., 2008; Boogert et al., 2011; Chantal et al., 2016; Howell et al., 2020; Keagy et al., 2012).

Several confounding factors can account for this discrepancy. They could include non-cognitive differences among individuals in their motivation to resolve a task or in their personality traits (Camacho-Alpízar et al., 2020; van Horik et al., 2016; van Horik & Madden, 2016). Methodological differences in the experimental procedures (Shaw & Schmelz, 2017; Thornton et al., 2014) or measures used to estimate female mate preference (Forstmeier & Birkhead, 2004;

Rosenthal, 2017) are also likely to provide contrasting results. In fact, laboratory studies generally consider that female preference for overall better performers would be adaptive and, as such, assess female preference for a general cognitive factor (review in Boogert et al., 2011). However, male cognitive abilities are not always highly correlated with each other and, for that reason, cannot systematically be reduced to a general cognitive factor (Poirier et al., 2020). In birds for instance, the adaptive value of male cognitive abilities can vary according to the ecological environment as well as the species considered (Morand-Ferron & Quinn, 2015). Specifically, male performance on problem-solving and memory tasks are important determinants of nestling provisioning and parental care (Wetzel, 2017; Cauchard et al., 2017; Shaw et al., 2019), whereas inhibitory control is enhanced under unpredictable environments (Van Horik et al., 2019). By contrast, spatial learning ability is an important determinant of success in food-storing (Pravosudov & Clayton, 2002) and migratory (Pettit et al., 2013) species, while associative learning ability correlates with foraging efficiency (Raine & Chittka, 2008) and anti-predator response (Dutour et al., 2019; Mitchell et al., 2011; Morand-Ferron, 2017). If females obtain fitness benefits by choosing better performing males, the importance they give to cognitive abilities might then vary both among species according to their ecology, and among females within species according to their needs and/or ability to accurately assess male skills.

Studies in behavioural ecology generally assume that females should unanimously prefer better performers, but evidence exists that they often differ consistently in their mate preference for different traits (Forstmeier & Birkhead, 2004; Jennions & Petrie, 1997). Specifically, mate preference is known to be state and context-dependent (Cotton et al., 2006; Howell et al., 2019) and to vary among females according to their ability to accurately assess male sexual phenotypic traits (Álvarez-Quintero et al., 2021; Corral-López et al., 2017; Rystrom et al., 2019). For instance, Howell et al. (2019) found that the performance on a novel foraging task and body mass of female zebra finches were positively associated with their preference for conspecific over heterospecific males and for high over low-quality male songs, respectively. Hence, differences among females in their mating preferences for male cognitive traits could be related to differences in their own cognitive abilities and/or own body condition, that are both likely to influence the costs of sampling during mate assessment (Miller & Todd, 1998; Swaddle & Page, 2007). Explicitly, we would expect females in poor condition and/or with poor assessment abilities to be less selective with regards to traits that are highly demanding to accurately assess (Riebel, 2011; Rosenthal, 2017; Ryan et al., 2009).

Rather than exploring the mechanism of *how* females assess male cognitive abilities (i.e. which traits are used as mate-choice criteria), our experiment was designed to test whether females preferred males that generally performed better in four different cognitive tasks and whether their mate preference depended on their own characteristics. Specifically, we tested whether females in better body condition and with better cognitive performances demonstrated stronger preferences for better cognitive performers. As male cognitive abilities can be assessed by females using multiple traits (e.g. song: Howell et al., 2020; foraging performance: Chantal et al., 2016; plasticity in foraging tactic use: Barou Dagues et al., 2020; personality: Schuett et al., 2011), we let 21 females observe four potential partners that naturally varied in their phenotypic and behavioural traits, for 10 days, while they were foraging in groups. Before expressing their preference, females could also observe the males while they were displaying courtship behaviour. During the mate choice trials, we measured the time each female spent in front of each male in a four-chamber choice apparatus. Then, we measured the performance of all males and females, while alone, in an associative learning, a motor shaping, a spatial learning and an inhibitory control tasks as well as a proxi of health using their body condition. Because we could not reduce the four male cognitive abilities to a general cognitive factor, we estimated, for each female, a preference score for each of the four male cognitive abilities and tested whether the preference for each ability varied among females depending on females' own characteristics.

Methods

Subjects and housing conditions

We used a total of 22 female and 16 male zebra finches aged six months at the beginning of the experiments. All the birds came from a local breeder (Oisellerie de l'Estrie, Thetford Mines, Canada) and were identified by two coloured leg rings. Outside the experimental trials, they were kept with their same-sex flock mates in cages (50 x 39.5 x 39.5 cm) at 23°C (±1°C) and 34% relatively humidity on a 12L:12D photoperiod cycle (7am-7pm) and were supplied with water, vitamins and food ad libitum. All experimental trials took place in an indoor aviary (225 x 155 x

244 cm) between 8am and 5pm at the University of Montreal between May 2017 and September 2019 after the birds had been food deprived overnight for 15h (between 5pm and 8am).

Ethical note

All procedures were in compliance with the guidelines of the Canadian Council for Animal Care and were approved by the Animal Care committee of the University of Montreal (animal care permit #17-047). All captures were done in the dark and the birds always had auditory contact with their flock mates to reduce the stress. Six females died because of eggs stuck in their cloaca and two males died due to unknown causes. Because several birds were not always active during testing periods, the sample size decreased progressively with the experimental progress (supplementary material, Figure S2A).

Social foraging observations

The birds were arranged into 11 unisex foraging flocks (i.e. four male and seven female flocks) of four birds each. Before the mate preference trials, each female flock was allowed to repeatedly observe a flock of four males that naturally varied in their phenotypic and behavioural traits in a social foraging context. Specifically, a female flock was introduced with a male flock in two separate compartments where they could search for food on a wooden board that contained 50 wells, among which only five or 10 were filled with 10 or five millet seeds, respectively. Both compartments were separated by a one-way mirror, so that the females could see and hear the males foraging on the board as well as all their behaviour, interactions, song and phenotype, while the males could only hear but not see the females. The flock composition stayed the same during all the observation phase and outside the observation phase, females and males could not see and hear each other (see Barou-Dagues, Richard-Dionne & Dubois, 2020 for the apparatus representation and more details about the methods). The social foraging observations were part of a study where individual foraging tactic use and intake rates were measured (see Barou Dagues et al., 2020 for more details about the methods and group composition).

Mate choice observations and preference trials

The birds were gradually familiarized with the mate-choice device and experimental procedures (14L:10D photoperiod cycle). Female preferences were measured in a four-chamber mate-choice device that was composed of a central observation chamber (30 x 30 x 38 cm), four choice chambers (30 x 10.5 x 38 cm) and four male chambers (30.5 x 30 x 38 cm) that were separated from each other by transparent plexiglass partitions (for the apparatus figure, see Barou-Dagues, Richard-Dionne & Dubois, 2020). For each female, we conducted two mate preference trials with a one-day interval, where she could choose among the four males she had previously observed in the social foraging context. Specifically, the focal female was first placed in the central observation chamber of the mate-choice device where she could observe the males' courtship behaviours during 10 min. Then the experimenter removed the transparent partition, thereby allowing the female to perch in front of any male in the choice chambers during 15 min. For a given female, the males' position in the device was exchanged between trials to control for a potential location bias. For each trial, we recorded the time spent in front of each male (i.e. in each choice chamber) of 17 females using Jwatcher.

Cognitive trials

We carried out a series of four cognitive tasks, *a priori* ecologically relevant for zebra finches for communication (Boogert et al., 2008), anti-predator behaviours (Morand-Ferron, 2017), nest building (Guillette & Healy, 2019) and resource exploitation under changing environmental conditions (Healy et al., 2010; Zann, 1996). We measured the performance of each individual in: (i) an associative learning, (ii) a motor shaping, (iii) a spatial learning and (iv) an inhibitory control tasks. Specifically, the birds needed to: (i) associate a colour with a variable reward, (ii) learn progressively to flip the lids off foraging wells, (iii) learn the location of a rewarded well and (iv) inhibit ineffective prepotent responses by flipping a transparent lid off a foraging well (figure 1).

Associative learning task

The birds were tested in an individual cage (52 x 29 x 37 cm) containing a central perch with water and two upper perches in the corner allowing them to access the coloured feeders (figure 1a). The cage was covered by opaque panels on the top, on each side and on the back and contained a LED

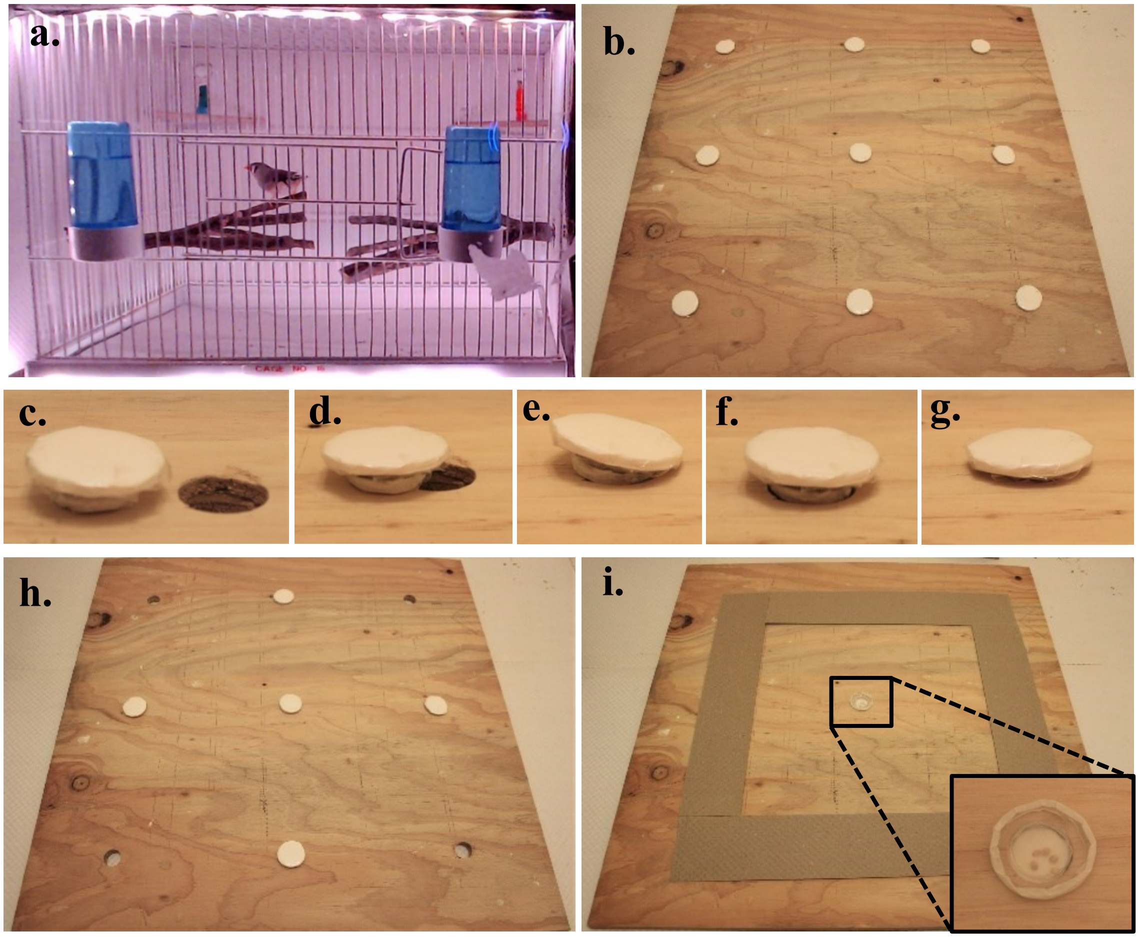


Figure 1. Experimental devices for cognitive test batteries with (a) the associative learning task, (b) the motor shaping lid flipping board, with (c)-(g) the levels of difficulty, assessed by the degree to which the bird had to manipulate the lid to access the food, (h) the spatial learning board, and (i) the inhibitory control board with the transparent lid.

band to light the inside. Thus, without being seen by the birds, the experimenter could insert and observed the birds via a mirror. At the beginning of a given trial, the focal individual was placed on the central perch in front of the two-coloured feeders which contained both feeders and different amounts of food: one coloured feeder (i.e. pink or green) always contained five ± one millet seeds and the other always contained two ± one millet seeds. Before the beginning of the tests, we individually familiarized the birds to forage in both filled feeders and progressively trained them to the experimental procedure (feeder handling) for four days. Both coloured feeders initially contained the same amount of food that we progressively decreased over the days. If a bird had a side or colour bias (considered as four consecutive choices of the same alternative) we removed its favoured alternative until it ate in the other one. The experimental phase took place the fifth day between 8am and 12pm and was composed of six blocks of 10 consecutive trials each, spaced by a 15min-resting period to keep the birds motivated. A trial began right after the experimenter inserted both coloured feeders at the corners of the cage. If the bird chose a feeder (i.e. perched in front of it), the experimenter removed the non-chosen one and let the bird eat for 30s before removing the chosen feeder. If the bird did not make a choice after 1 min, the experimenter removed the feeders, and this trial was restarted after 1 min. We changed the position of the coloured feeders following a semi-random chosen colour side sequence (i.e. each colour was placed 30 times on each side but not more than twice consecutively on the same side) and all birds were tested with the same colour side sequence. Half of the birds had to learn to prefer the green and the other half had to learn to prefer the pink feeder. We noted a trial as successful when the birds chose the most rewarded coloured feeder and as failed when they chose the less rewarded one. At the end of the task, we estimated a score for each bird as the number of trials required to succeed in eight over 10 consecutive trials. The birds that were fast to learn the association had a low score while those that never reached this criterion had a maximum score of 60 trials. We obtained an associated learning score for 14 males and 20 females (figure S2).

Motor shaping task

The birds were individually presented with a wooden board (70 x 70 cm) that contained nine wells (2 cm diameter and 1cm depth, spaced 20.5 cm apart in a three x three grid pattern) placed within the aviary (figure 1b). Each well contained three millet seeds and was covered by a lid. The lids consisted of a large cardboard circle (3 cm diameter and 3mm depth) stuck to a smaller cardboard circle (2 cm diameter and 3 mm depth) and a 5-cent coin. Before the experiment, we trained the birds to forage on the wooden board with free access to filled wells during 2h in a flock of four birds. Then, to ensure the birds were individually able to forage on all the wells in the board, we performed four individual 15 min-training trials where we progressively reduced the amount of food in the wells. To solve the task progressively and get the food reward, the birds went through a shaping procedure comprising five levels of difficulty (figure 1c-g). At level 1, we placed the lids next to the wells; at level 2, we half-covered each well with the lids; at level 3, we fully covered the wells with the lids; at level 4, we half-sank the lids into the wells and at level 5, we totally sank the lids into the wells. Each trial began when the light turned on and ended when the bird completed the level. To successfully complete a level and pass to the next one, the bird needed to flip the lid off and forage in three out of the nine available wells. If the bird foraged in less than three wells, the trial ended after 15 min and the bird returned to the previous level of difficulty. After each trial, we removed the lids that the focal bird did not flip allowing it to reach the 20 seeds per hour required for its energetic needs (Zann, 1996). The birds went through a maximum of nine trials per day for a maximum of 20 trials. At the first trial (i.e. level 1), we noted the latency to touch the first lid as a measure of neophobia and for each level of difficulty, we noted if the bird solved or not the level. The performance of each bird was estimated as the total number of trials required to solve the 5 levels of difficulty. The birds that were fast to solve the task had then a low score while those that did not learn and never reached the 5th level of difficulty had a maximum score of 20. We obtained a motor shaping score for 14 males and 17 females (figure S2).

Spatial learning task

We used the same wooden board as for the motor shaping task (figure 1h). As in Ashton et al. (2018) all wells, but the four in the corners, were covered by a white lid. Amongst the five other wells, only one well, whose position was randomly chosen for each bird, contained five millet seeds. The day before the birds started the task, we performed at least three familiarization trials of 10 min each to ensure that they were able to flip the five lids and feed in the five wells. During a three-day experiment, the birds performed first a baseline trial and then three test trials with a delay of five min, 24h and 48h, respectively. All trials consisted of letting each individual flip the 5 lids on the board and find the location of the rewarded well. As in the motor shaping task, all trials began when the light was turned on and ended when the bird had removed all the lids on the board.

If the bird did not remove all the lids in all trials, it was recorded as a missing value (i.e. N= 1 bird). We noted the number of wells the birds flipped the lid off before finding the rewarded well and used, as an estimate of their score, the total number of unrewarded wells they flipped the lid off before finding the rewarded well during the 3 test trials. The birds that found the rewarded well without any error had a score of zero, while the birds that found the rewarded well with the maximum of errors had a score of 12. We obtained a spatial learning score for 13 males and 14 females (figure S2).

Inhibitory control task

We used the same board as for the motor shaping task (figure 1b) but prevented the access to all the wells except the one in the center of the board. As in standard detour paradigm, we replaced the opaque lid by a transparent one to create a situation where a direct access to the visible food reward is blocked and a detour behaviour must be executed to reach it (Kabadayi et al., 2018). The transparent lid was composed by a disk (3 cm diameter and 2 mm depth) of acetate sheet surrounded by white tape and glued to a cylinder (0.4 cm large) of acetate sheet (figure 1i). The birds could thus see the seeds through the transparent lid and had, therefore, to inhibit an ineffective response (i.e. pecking on the transparent part of the lid) and instead gain access to the reward by flipping the lid (i.e. by pecking on or grabbing the white part of the lid). The experiment began with a training phase that consisted in placing five millet seeds around the well and the transparent lid next to it to decrease neophobia for this novel object. The birds needed to forage next to the lid in three trials of five min to move to the test phase. At the beginning of each test trial, we placed five millet seeds within the well, covered by the transparent lid and placed the bird on the perch in front of the board. We began a trial by turning on the light and ended it by turning off the light either when the bird pecked on the transparent part of the lid or after it flipped the lid and ate the seeds. If the bird did not go on the board or did not interact with the lid after 10 min, we ended the trial and noted it as a missing value. Each trial was performed at one-min intervals and all trials for a given individual were carried out on the same day. A trial was considered successful if the individual inhibited the prepotent response of pecking on the transparent part of the lid and rather flipped it to gain access to the food reward. Conversely, the trial was considered unsuccessful if the bird first pecked on the transparent part of the lid. The score of inhibitory control, estimated for 12 males and 12 females (figure S2), corresponded to the number of trials before successfully flipping the transparent lid for the first time, with a maximum score of 20 if the bird did not learn the task. Thus, a high score is indicative of a low performance in the task. Note that the measures of the inhibitory control performance using one, two or three consecutive flips of the transparent lid were highly correlated (Spearman rank correlations: one vs two lids flipped: ρ= 0.835, S=378.97, P<0.001; one vs three lids flipped: ρ= 0.758, S=556.61, P<0.001) and that no bird successfully flipped the transparent lid in their first attempt. Thus, we can ensure that flipping the transparent lip was not executed by chance and that pecking on the transparent part of the lid was a strong prepotent response at the beginning of the test.

Measures of body condition

On the same day for all birds and with few minutes interval, we measured tarsus and wing length three times on the right side. We used the average measures and extracted individuals' body size from a principal component analysis (PCA) with unrotated factor solution (using the *princomp* function) in order to extract the principal component accounting for most of variance (i.e. the first component explained 82.66 % of the variance; permutation tests: p<0.001; Vieira, 2012). Item-components coefficients greater than 0.5 (absolute value) were considered salient items (Budaev, 2010). We also weighed all individuals before and after the experimental phase and used the mean weight as a measure of body mass. As a measure of body condition, we used the residuals from a linear regression between body size and body mass. This index is often used to estimate health and vigour in zebra finch (Ewenson et al., 2001; but see, Labocha & Hayes, 2012). High positive or negative residual values are indicative of individuals in good or poor body condition, respectively (figure S1B).

Statistical analysis

Relationships among individual performances on the four cognitive tasks and body condition

To ensure that the motor shaping score was not related to the level of neophobia, we performed a Pearson correlation test. Then, to test whether individual cognitive performances and body condition were related to each other, we performed Spearman's rank pairwise correlations as the assumption of normality was not met and we used a Bonferroni correction to control for multiple comparisons ($\alpha = 0.005$). Since the results from Spearman correlations revealed similar results from datasets separated by sex (supplementary materials, figure S4), we chose to pool the male and female datasets together to increase the sample size and statistical power. Also, to test whether the four cognitive performances could be reduced to one or two principal components, we ran a permutation test on a principal component analysis (PCA) using the *sign.pc()* function.

Female preference for male cognitive abilities

As in Barou-Dagues, Richard-Dionne & Dubois (2020), we calculated for each female i, her preference *Pfi* for each of the four male cognitive traits using the following equation:

$Pf_i = \frac{1}{C_{max}+3} \sum_{j=0}^{n-1} T_j (C_j + 3)$ (Eq. 1),

where n is the number of males the female could choose among (i.e. always $n = 4$), T_j is the percentage of choosing time she spent in front of the male j, *Cj* the z-scored performance of the male j in one of the four tasks (i.e. associative learning, motor shaping, spatial learning or inhibitory control) and C_{max} the maximum performance in the given task in the male's flock. Since the lower z-scored performance was -2.338, we added 3 to all performances in order to obtain positive measures of cognitive abilities for all males in all tasks. Thus, according to Eq. (1), a female spending all her time in front of either the poorer or the better performing male has a preference score of 100 or 0 respectively, while a female with no preference spending the same time in front of the poorer and better performing males gets a score of 50. In total, we then calculated eight preference scores for each female (i.e. one per cognitive trait and one per mate choice trial). It is worth mentioning that the preference score is calculated at the male group level, and as such, depends on the male flock composition. We statistically controlled for this effect *a posteriori* as we could not *a priori* compose male flocks according to the four cognitive traits, and so, could not account for the variance in cognitive abilities among males within flocks before measuring female preference (see statistical analysis below).

To test whether females' preference for a male cognitive ability was associated with their preference for other male cognitive abilities, we performed Spearman's rank pairwise correlations with the females' preference scores averaged for the two trials (Bonferroni correction with $\alpha = 0.008$). Then, using t-tests, we investigated for each cognitive trait whether females, on average, expressed a preference significantly different from a random preference (i.e. the mean of 1000 preference scores for a given randomly permutated trait). To test whether females demonstrated a consistent mate choice preference for each cognitive trait between the 2 trials, we also used the *rpt* function from the package *RptR* (Stoffel et al., 2017) including the preference for each cognitive trait as a response variable and the female identity as a random effect. Then, the repeatability estimates and p-values were calculated over 1000 permutations.

Individual differences in female cognitive abilities, body condition and mate preferences

As the females did not all participate in the four cognitive tasks (inactive or dead females; supplementary materials, figure S2), we employed the multiple imputation (MI) method, one of the more efficient and less error-prone techniques, to replace missing values (i.e. 38 over 136 scores, 27.9 % of missing data; Nakagawa & Freckleton, 2011; Newman, 2014). With this procedure, the available data is first used to impute multiple data sets by performing an unbiased single imputation routine (like stochastic regression imputation) over *m* number of imputations. Then, after analyzing statistically each imputed data set, the parameter estimates and their SEs are extracted and pooled together over all data sets in order to account for the variance between imputations (Nakagawa & Freckleton, 2011; Newman, 2014). By choosing 100 imputations, we achieved 99% efficiency of the estimates regardless of the number of missing values within each cognitive task (see Graham et al., 2007 for more details). To perform this procedure, we used the function *amelia* in the package *Amelia* (Honaker et al., 2012). Then, we explored whether females' preference scores for male cognitive traits were related to their own body condition or cognitive abilities using a model selection approach. Because this study did not aim at identifying the phenotypic traits used by females to assess male cognitive traits, we did not estimate the female preference for male body condition. By contrast, there is evidence that females' mate preferences are affected by their body condition (Cotton et al., 2006). Consequently, we included it as an explanatory variable. Thus, we performed four different LMM selections using as the response variable, respectively, the female preference scores for the male performances in the associative learning, motor shaping, spatial learning and inhibitory control tasks (*lmer* function from the package *lme4*, Bates et al., 2020). The four most complicated models included the females' performance in the four cognitive tasks, their body condition, the trial number and the interaction between the trial and each trait as fixed effects. In order to control for differences in male flock composition, we included the male flock as a random effect as well as the female identity, allowing intercepts to vary between females and between male flocks. We investigated all possible models (including the intercept-only model) and retained as candidates the best fitting models (i.e. ΔAICc < 2; Akaike, 1973) for each imputed dataset. Then, across all imputed datasets, we selected the five more frequent candidate models for each male cognitive trait (see Table S1 in supplementary materials for the final models selected). In order to estimate the effect of each fixed parameter, we first performed the model-averaging procedure for each imputed dataset using the function *model.avg* in the package *MuMIn* (Barton, 2016) and then pooled together all estimates, adjusted standard errors, Z scores and Pvalues from model-averaging across all imputed datasets. All analyses were conducted in R (v.4.0.2; R Development Core Team 2017).

Data availability

The datasets generated and/or analysed during the current study are gathered in the Annexes (table A3 and table A4).

Results

Cognitive task performances and body condition

Most of the birds reached the criterion in the associative learning, the motor shaping and the inhibitory control tasks (supplementary materials, figure S3a, b, d) and obtained a better learning score than expected by chance in the spatial learning task (figure S3c). Yet, individuals differed greatly in their performance on the four cognitive tasks: the number of trials needed to resolve the colour discrimination task varied between 10 and 60 trials (mean ± SE: 29.41 ± 16.09, N=34), the total number of trials across the five levels of difficulty to resolve the lid flip task ranged from 5 to 20 (11.13 ± 5.53, N=31), the total number of trials in the three trials of spatial memory task ranged from 1 to 9 (5.22 ± 2.14, N=27) and the number of trials to flip the transparent lid in the inhibitory control task ranged from 2 to 17 (5 ± 3.73, N=24). No correlation was found between the motor shaping score and the neophobic level of individuals (Pearson correlation test: *r*=0.265, *P*=0.165, N=29) neither between the performance of individuals on the four tasks and their body condition after a Bonferroni correction for multiple comparisons was applied (figure 2A). Also, the permutation test revealed that none of the component extracted from the four cognitive task

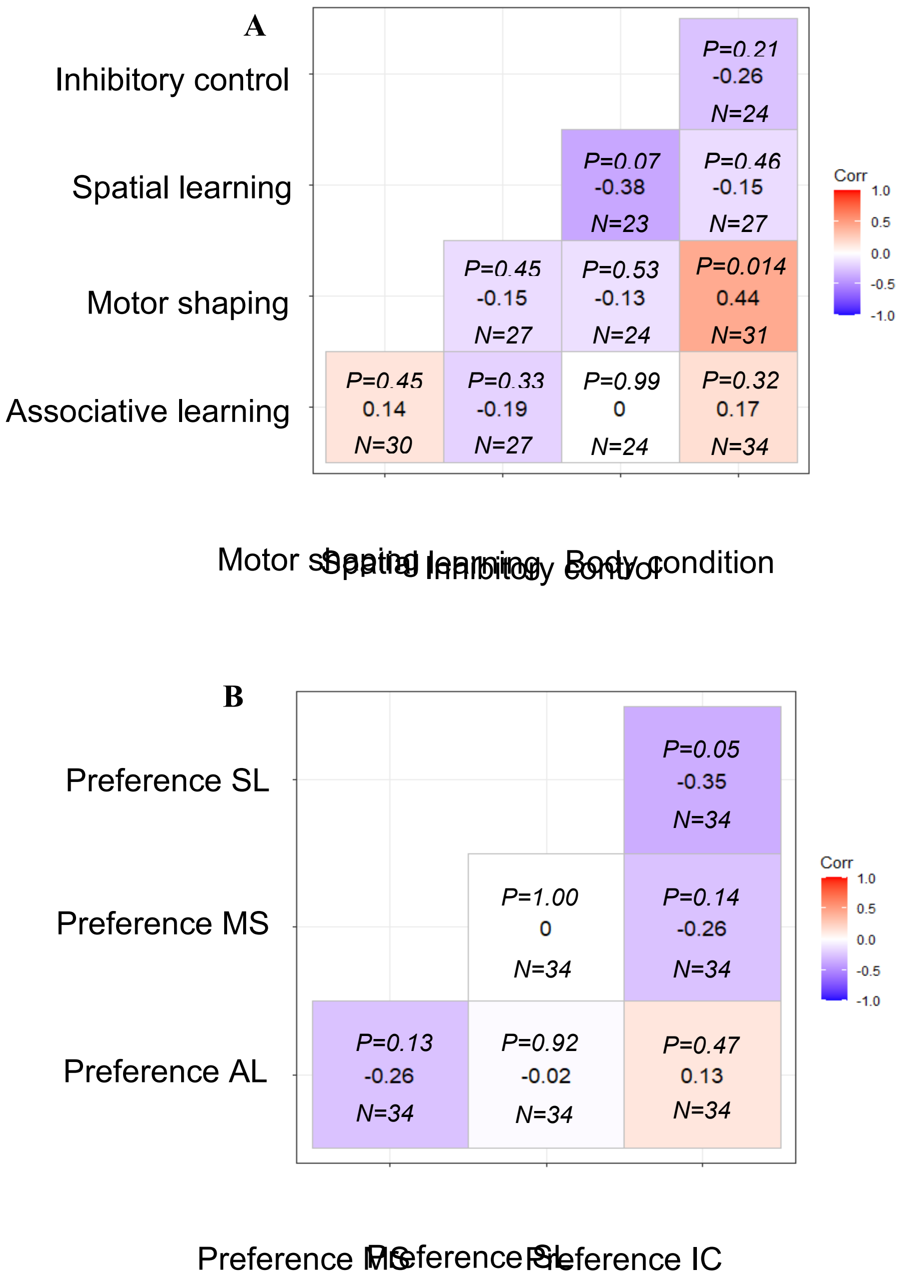


Figure 2. Pair-wise correlations between (A) individuals' performances on the four cognitive tasks and their body condition (Bonferroni correction, α=0.005) and (B) females' preference scores at each trial for the male cognitive performances (AL: associative learning, MS: motor shaping, SL: spatial learning and IC: inhibitory control, Bonferroni correction, α=0.008). The colours represent the magnitude and direction of the relationships with orange and purple colours indicating, respectively, positive and negative relationships. For each pair-wise correlation, the numbers indicated in the cells of the tables correspond respectively, to the p-value, Spearman correlation coefficient and sample size.

performances significantly differed from the components extracted from a random matrix (permutation test, PC1: *P*=0.796, PC2: *P*=0.275; PC3: *P*=0.437, PC4: *P*=0.222).

Female mate preference for male cognitive traits and individual differences

We found that females' preference for a given male cognitive trait was not associated with their preference for the other male cognitive traits, after applying a Bonferroni correction for multiple comparisons (figure 2B). Furthermore, female preference for each cognitive trait did not significantly deviate from random (t-tests: associative learning: *t*=0.131, *P*=0.792; motor shaping: *t*=-0.669, *P*=0.518; spatial learning: *t*=-0.444, *P*=0.656; inhibitory control: *t*=0.576, *P*=0.580), indicating that females did not unanimously prefer the males with better cognitive performance on the four cognitive tasks. Accordingly, we found that females with better performances on the associative learning task showed a stronger preference for better inhibitory control performers (figure 3B, table 1). To a lesser extent, females in better body condition tended to prefer better spatial learners (figure S5b, table 1).

Females were repeatable in their mate preference between the first and second mate choice trials for the male inhibitory control performance (R= 0.816, CIs [0.564, 0.926], se=0.094, *P*<0.001) but not for the three other cognitive task performances (associative learning: R=0, CIs [0, 0.444], se= 0.134, *P*=1; motor shaping: R=0.070, CIs [0, 0.507], se= 0.158, *P*=0.435; spatial learning: R=0.043, CIs [0, 0.478], se= 0.148, *P*=0.479). The lack of repeatability in female mate preferences is partly explained by the fact that only some females increased their preference from the first to the second mate choice trial for two male cognitive abilities, as revealed by significant interactions between the female characteristics and the trial number (table 1). Specifically, females with better associative learning performance and in better body condition increased their preference for poor associative learners (figure 3A; figure S5a) while females with better inhibitory control performances increased their preference for better spatial learners (table 1). Except this last relationship, all relationships remained significant after using a Bonferroni correction for the 4 LMMs ($\alpha = 0.0125$).

Table 1. Pooled estimates, adjusted standard error, *Z* values and *P* values from model-averaging procedures of the five best-fitted candidate models retained after model selection with females' mate choice preference for (A) the associative learning (AL), (B) the motor-shaping (MS) (C) the spatial leaning (SL) and (D) the inhibitory control (IC) performance as a response variable. Significant values are highlighted in bold. Of the 44 effects initially included in the four more complex LMMs, 23 effects were kept during model selections, among them five significantly differed from α = 0.05 and five were marginal.

(A) Mate preference for the associative learning task performance

Fixed effects	Estimates	Adjusted SE	*Z value*	*P value*
Intercept	77.143	3.310	24.301	**<0.001**
Trial number	7.420	3.761	1.982	**0.055**
Female AL performance	12.905	3.205	4.150	**0.005**
Female SL performance	5.213	4.014	1.482	0.275
Female IC performance	-7.904	3.107	2.770	0.096
Female Body Condition	0.974	3.933	0.781	0.493
Female AL performance * Trial	-15.873	4.480	3.595	**0.004**
Female SL performance * Trial	-2.804	5.366	0.659	0.559
Female IC performance * Trial	7.882	4.277	1.932	0.129
Female Body Condition * Trial	10.661	5.355	1.988	0.068

(B) Mate preference for the motor-shaping task performance

Fixed effects	Estimates	Adjusted SE	*Z value*	*P value*
Intercept	67.420	3.412	20.320	**<0.001**
Female AL performance	-1.707	2.999	0.816	0.472
Female MS performance	1.635	3.219	3.043	0.072
Female SL performance	1.582	3.441	0.948	0.447
Female IC performance	9.281	3.181	1.014	0.431

(C) Mate preference for the spatial learning task performance

Fixed effects	Estimates	Adjusted SE	*Z value*	*P value*
Intercept	65.375	8.086	8.168	**<0.001**
Trial number	4.236	7.482	0.569	0.572
Female MS performance	8.494	5.673	1.537	0.208
Female IC performance	-4.811	6.763	1.055	0.407
Female Body condition	-12.340	6.344	1.950	0.067
Female IC performance * Trial	19.418	7.789	2.559	**0.049**

(D) Mate preference for the inhibitory control task performance

Fixed effects	Estimates	Adjusted SE	*Z value*	*P value*
Intercept	79.131	6.792	16.689	**<0.001**
Female AL performance	7.363	1.945	3.857	**0.001**
Female MS performance	2.881	3.083	1.503	0.369
Female SL performance	-8.190	2.698	3.459	0.104
Female IC performance	-8.786	2.619	3.491	0.068
Female Body condition	5.579	3.031	1.976	0.187

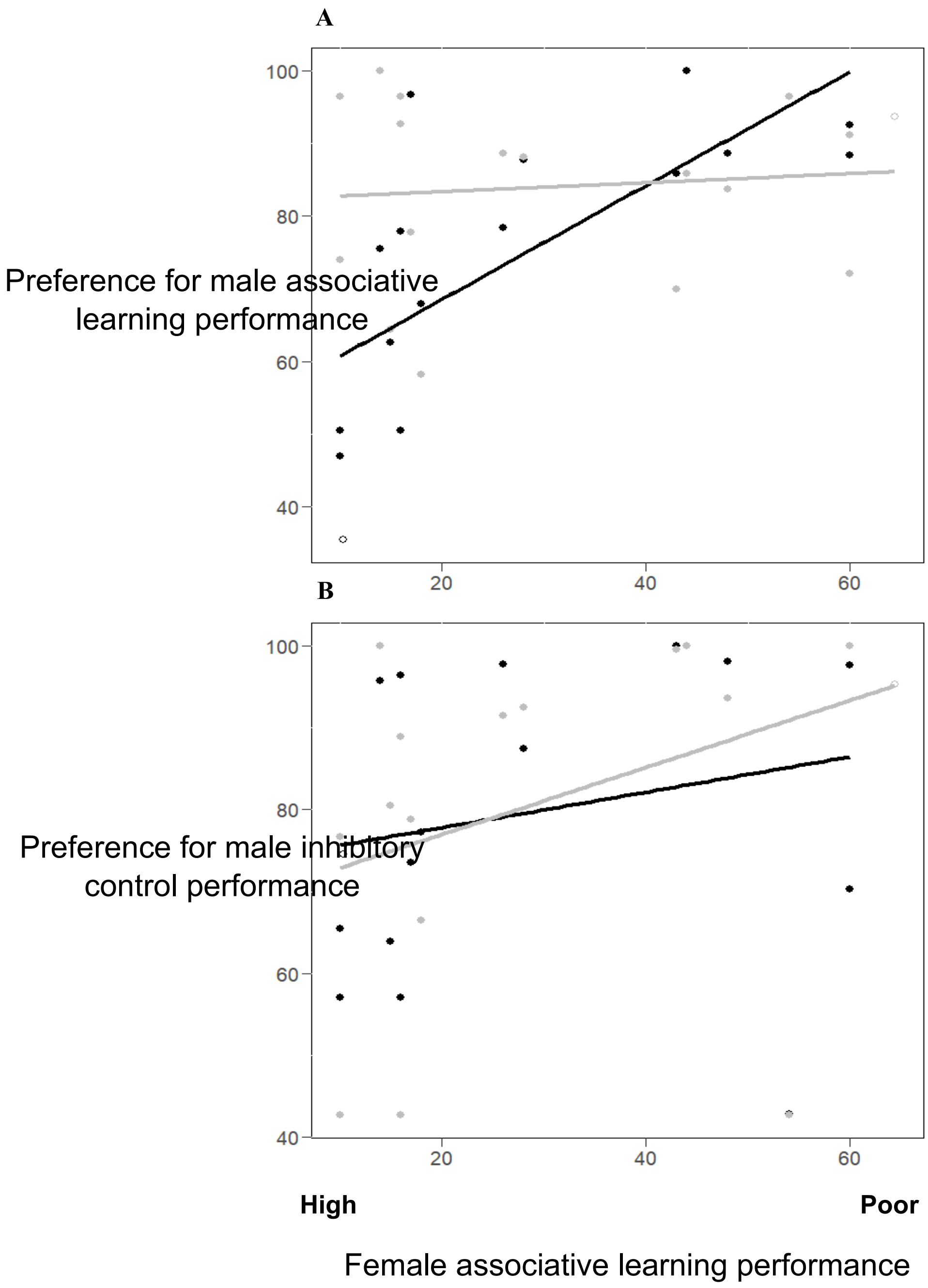


Figure 3. Relationship between females' performance in either the associative learning task and their preference for male performance in the associative learning task (A) and inhibitory control task performance (B), from an imputed data set randomly chosen (nb. 34). Black and grey solid circles represent female preference in the first and the second mate choice trials, respectively, and empty circles represent the imputed data from one randomly selected simulation. A score of 100 represents a preference for males performing poorly whereas a score of 0 represents a preference for males performing great in the cognitive task. Both dark and grey lines represent the predicted values from the LMMs.

Discussion

Our results demonstrated that individuals' performances on the four cognitive tasks were not associated with each other, thus refuting the idea of a general intelligence in zebra finches. Furthermore, we found that male inhibitory control and associative learning performances were more important during mate choice than male motor shaping and spatial learning performances. In addition, females differed in their preference for male cognitive abilities, depending on their own performance on the tasks and body condition. Taken together, our findings suggest that some male cognitive abilities would be less relevant than others depending on the ecology of the considered species, and that females' mate preference for male cognitive abilities may be constrained by their own characteristics.

Conducting animal psychometric tests can be challenging as both cognitive and non-cognitive factors generally contribute to individual task performance (van Horik & Madden, 2016; Völter et al., 2018). To minimize the effect of such confounding factors in our study, all birds were tested at the same age and food deprived at the same time. In addition, they received long training sessions before each cognitive task, which enables us to reduce the confounding effects of neophobia and body condition on individual performance. We found weak or no correlations between individuals' cognitive performances on the four tasks. Given that we did not measure the repeatability of the cognitive performances and had a relatively small sample size, our results must be interpreted cautiously regarding the strength and direction of the correlations (Shaw & Schmelz, 2017). However, our findings are in agreement with several previous studies (e.g. Shaw et al., 2015; Völter et al., 2018) including a meta-analysis that found weak support for general intelligence in non-human animals (Poirier et al., 2020). As male performances vary markedly across the four cognitive tasks, females could select mates with specific cognitive skills rather than a general ability to perform in all tasks. Indeed, our findings demonstrated that male inhibitory control and associative learning performances were more important during mate choice than male motor shaping and spatial learning performances. For now, no studies have yet investigated the adaptive value of male cognitive abilities in wild zebra finches (Healy et al., 2010). If associative learning and inhibitory control abilities are heritable (Langley et al., 2020) in this species, females might obtain more benefits by mating with males with these skills compared to males with motor shaping and spatial learning skills. However, further investigations are needed to understand why, in our study, captive females showed stronger preference for poor associative learners at the second trial. For instance, the ability to learn an association could prevent them from coping with a changing environment (Barou-Dagues et al., 2020) and females could instead benefit from mating with males able to adjust their behaviour (Barou Dagues et al., 2020).

Moreover, females differed widely in their preference for each male ability, depending on their own characteristics. Indeed, we found that females performing better on the associative learning task demonstrated a stronger preference for better inhibitory control performers and increased their preference for poor associative learners. To a lesser extent, females in better body condition demonstrated a stronger preference for spatial learners and increased their preference for poor associative learners as well. Our findings are consistent with previous research showing that females' preference for better performers or more attractive males may be affected by their own cognitive ability (e.g. Álvarez-Quintero et al., 2021; Howell et al., 2019; Rystrom et al., 2019). In fact, females can adjust their mate preferences and achieve high reproductive success (Qvarnström et al., 2000) in response to changes in experience (Tinghitella et al., 2013) or body condition (Cotton et al., 2006). In our study, the effect of female body condition on mate preference for male cognitive abilities was marginal. However, it might have been underestimated as our birds were all fed and treated for parasite infection, which has likely reduced the variance in body condition compared to what is found within wild populations. In addition, we found that females' preferences were only repeatable for male performance on inhibitory control. As such, we cannot exclude the possibility that only this ability would be selected through female mate choice in zebra finches (Forstmeier & Birkhead, 2004). Thus, our results generally suggest that females' cognitive abilities and condition affect their mate preference for male cognition, but the causation of the relationships between females' characteristics and their preference for particular cognitive abilities needs further investigation.

Importantly, because females' cognitive abilities and/or condition may be influenced by the local environment (e.g. food availability, predator pressures or population size), our findings suggest that the importance of mate choice on male cognitive abilities should vary among populations and over time (Qvarnström et al., 2000; Riebel, 2011). Further studies would be required to 1) evaluate the role of repeatable female cognitive abilities on mate preference for male cognition in natural conditions, 2) estimate the heritability of male and female cognitive traits and 3) quantify the female fitness benefits from mating with better performers in various ecological circumstances (Madden et al., 2011). Also, because female zebra finches, in our study, expressed their mating preference without having observed the males performing in the cognitive tasks, our results confirm that intersexual selection on male cognitive abilities may occur through mate choice decisions based on morphological or behavioural traits that co-vary with male cognitive abilities. For example, females in nature might use phenotypic traits reflecting good condition, such as carotenoid-based sexual traits whose expression is influenced by male foraging efficiency (Boogert, Fawcett & Lefebvre, 2011; Collins et al., 1994). Alternatively, females may use more complex behavioural traits (e.g. song quality, courtship behaviours, innovativeness or behavioural plasticity; Boogert et al., 2008; Boogert, Fawcett & Lefebvre, 2011; Boogert, Anderson et al., 2011; Barou-Dagues et al., 2020; Chen et al., 2018; Riebel, 2009) that are potentially costly in terms of time, energy and/or experience to accurately assess (Madden et al., 2011). If indirect assessment of certain male cognitive abilities is error-prone, and hence requires better cognitive abilities (Riebel, 2011), intersexual selection, therefore, might act on female cognitive traits as well (Ryan et al., 2009). Thus, more research is needed to determine whether females use several phenotypic traits that are strongly related to different aspects of male cognition or mostly a single trait that is related to multiple cognitive abilities in order to evaluate the explanatory role of each cognitive ability in the mate choice context.

In conclusion, our study provides evidence that female zebra finches vary in their mate preference for independent male cognitive abilities, according to their own cognitive abilities and body condition. The strength of intersexual selection should thus vary among populations and over time depending on local ecological conditions as well as among male cognitive abilities. In addition, our results strongly suggest that intersexual selection on male cognitive abilities would occur through mate choice decisions based on phenotypic traits that co-vary with male cognition. Empirical and theoretical studies are required now to identify which traits are correlated with male cognitive abilities to better understand the role of intersexual selection in maintaining variation in male and female cognition.

Supplementary materials

A

Body size	Component 1
Tarsus length	-0.707*
Wing length	-0.707*
Eigenvalue	1.29
%Total variance explained	**82.66**

B

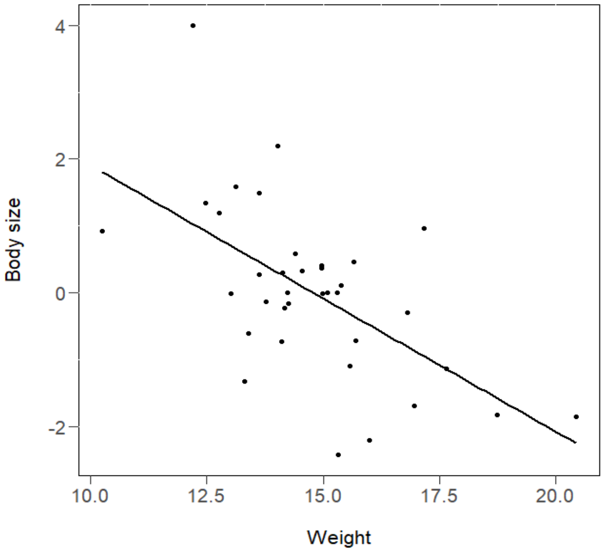


Figure S1. (A) Eigenvector coefficients and variance in body size measures explained by the first principal component extracted from PCA analysis (N=36). A low score on the first component represents taller birds. (B) Relationship between body size and weight. Each point represents an individual and the black line represents the linear regression. We used the residuals between the linear regression and each point to estimate individual body condition. Thus, high positive residuals correspond to individuals in good body condition after correcting for their size.

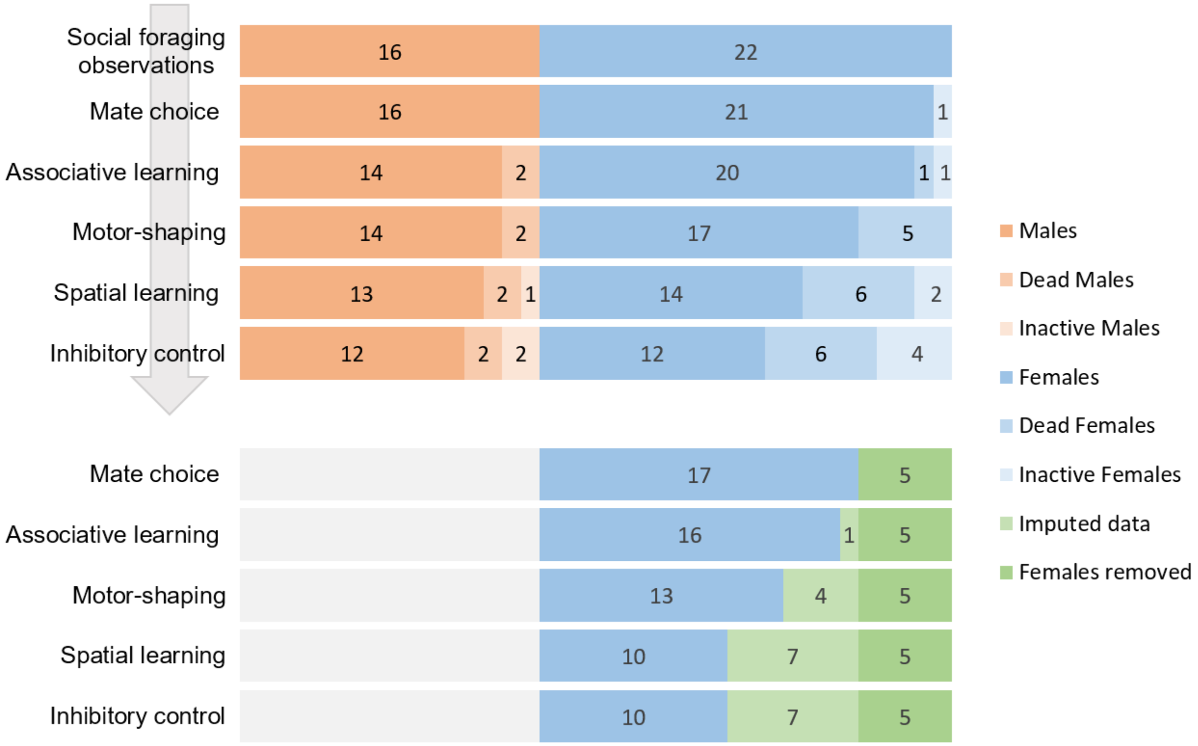


Figure S2. Sample size used in (A) each experiment in timeline order and (B) mate choice statistical analysis. The number of males and females are respectively represented in red and blue colours. The active, dead and inactive individuals are respectively represented from the darker to the lighter colours. The females removed from the mate choice statistical analysis are represented in darker green and the missing values replaced by imputed data are represented in lighter green.

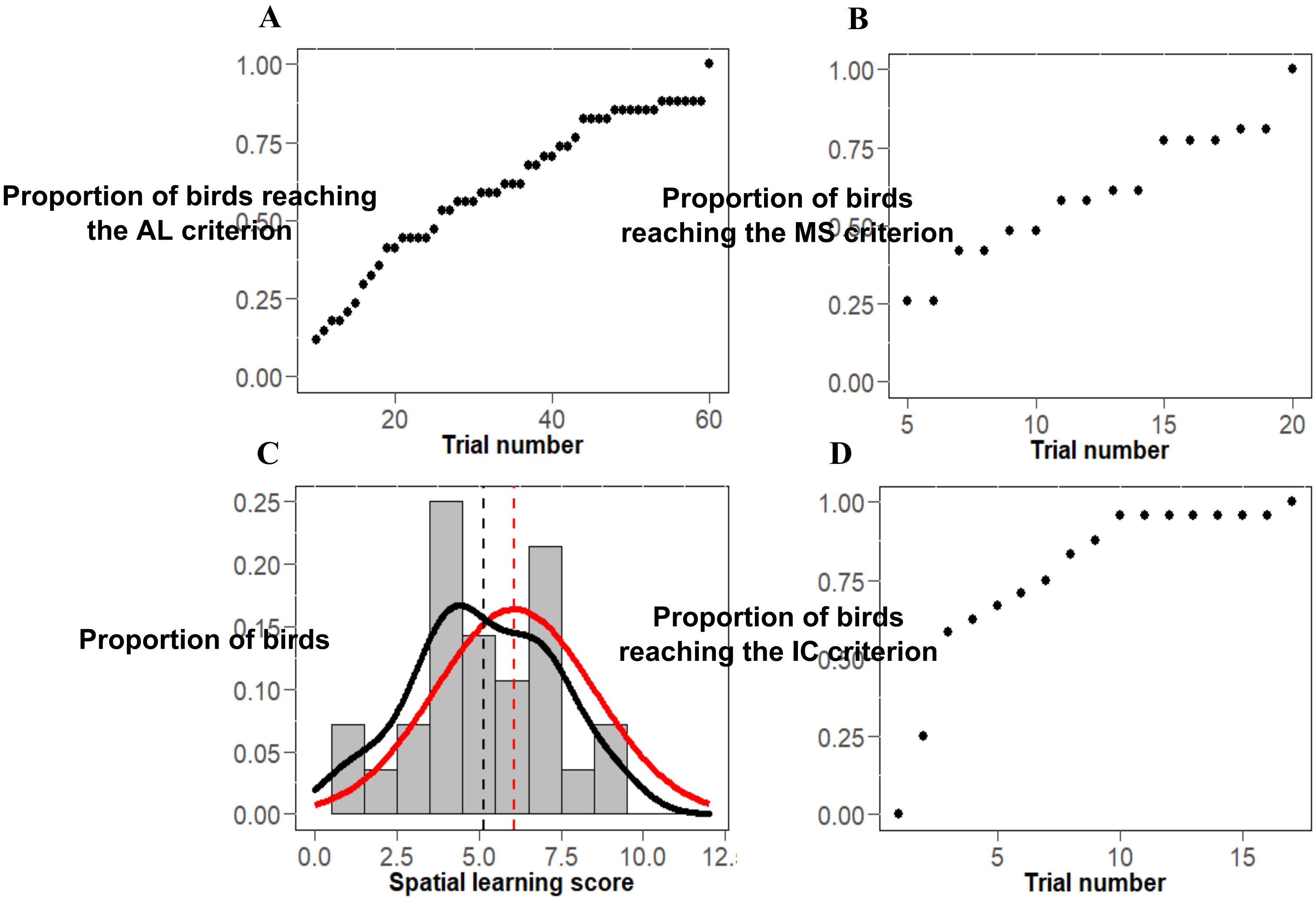


Figure S3. (A) The proportion of birds reaching the associative learning (AL), (B) the motor shaping (MS) and (D) the inhibitory control (IC) criterion over the 60, 20 and 20 trials respectively. (B) The proportion of birds that obtained a spatial learning score. The histogram in grey represents the observed subjects' spatial learning scores, the solid black line the distribution of the data and the black dashed line the observed mean in the spatial learning task. The solid red line represents the expected distribution of the spatial learning scores if the birds had chosen randomly wells at each trial (i.e. based on a simulation repeated 100 times) and the red dashed line the expected mean of the scores.

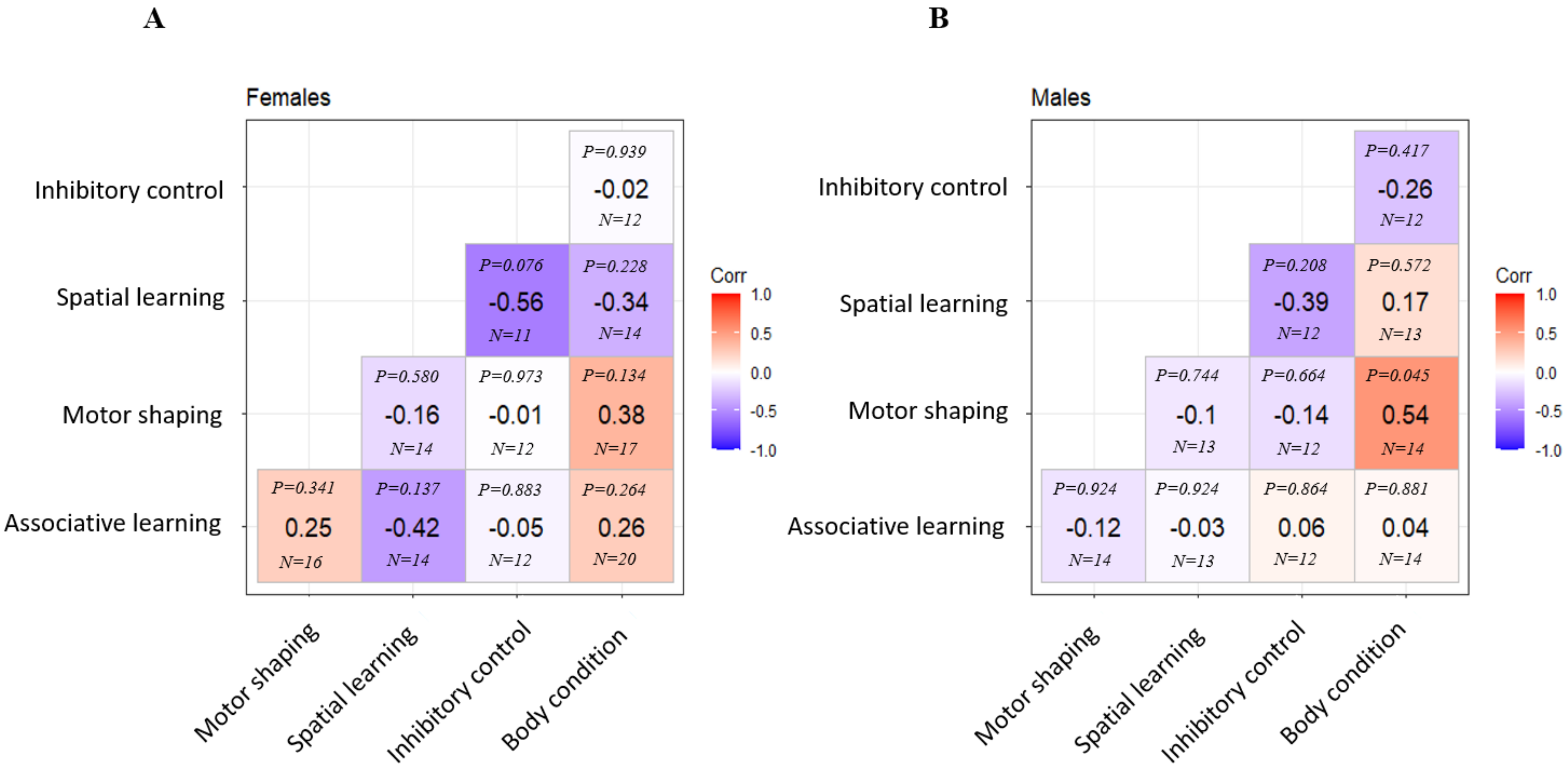


Figure S4. Pair-wise correlations (Bonferroni correction, α=0.005) between individuals' performances on the four cognitive tasks and body condition in females (A) and males (B) The colours represent the magnitude and direction of the relationships with orange and purple colours indicating, respectively, positive and negative relationships. For each pair-wise correlation, the numbers indicated in the cells of the tables correspond respectively, to the p-value, Spearman correlation coefficient and sample size.

Table S1. Fixed effects included from the five best-fitting candidate LMMs with females' mate preference for (A) associative learning (AL), (B) motor-shaping (MS), (C) spatial learning (SL) and (D) inhibitory control (IC) performances. Intercept-only models are represented by in grey.

(A) Mate choice preference for associative learning performance

Candidate models	AL	MS	SL	IC	Body condition	Trial	AL*Trial	MS*Trial	SL*Trial	IC*Trial	Body condition*Trial	MeanAICc	MeanWeight
Model 1	X			X	X	X	X			X	X	280.926	0.413
Model 2	X				X	X	X				X	284.664	0.366
Model 3	X		X		X	X	X		X		X	284.509	0.258
Model 4	X			X		X	X			X		286.370	0.177
Model 5	X						X					292.572	0.053

(B) Mate choice preference for motor-shaping performance

Candidate models	AL	MS	SL	IC	Body condition	Trial	AL*Trial	MS*Trial	SL*Trial	IC*Trial	Body condition*Trial	MeanAICc	MeanWeight
Model 1				X								293.927	0.206
Model 2	X			X								294.907	0.126
Model 3			X	X								295.791	0.140
Model 4		X		X								295.120	0.118
Model 5												301.000	0.127

(C) Mate choice preference for spatial learning performance

Candidate models	AL	MS	SL	IC	Body condition	Trial	AL*Trial	MS*Trial	SL*Trial	IC*Trial	Body condition*Trial	MeanAICc	MeanWeight
Model 1				X		X				X		322.815	0.199
Model 2		X			X							323.681	0.122
Model 3				X	X							323.503	0.123
Model 4		X		X	X							323.478	0.086
Model 5												325.000	0.092

(D) Mate choice preference for inhibitory control performance

Candidate models	AL	MS	SL	IC	Body condition	Trial	AL*Trial	MS*Trial	SL*Trial	IC*Trial	Body condition*Trial	MeanAICc	MeanWeight
Model 1		X	X	X	X							265.374	0.397
Model 2			X	X								271.985	0.201
Model 3	X			X	X							273.069	0.227
Model 4	X			X								275.203	0.168
Model 5	X											277.818	0.137

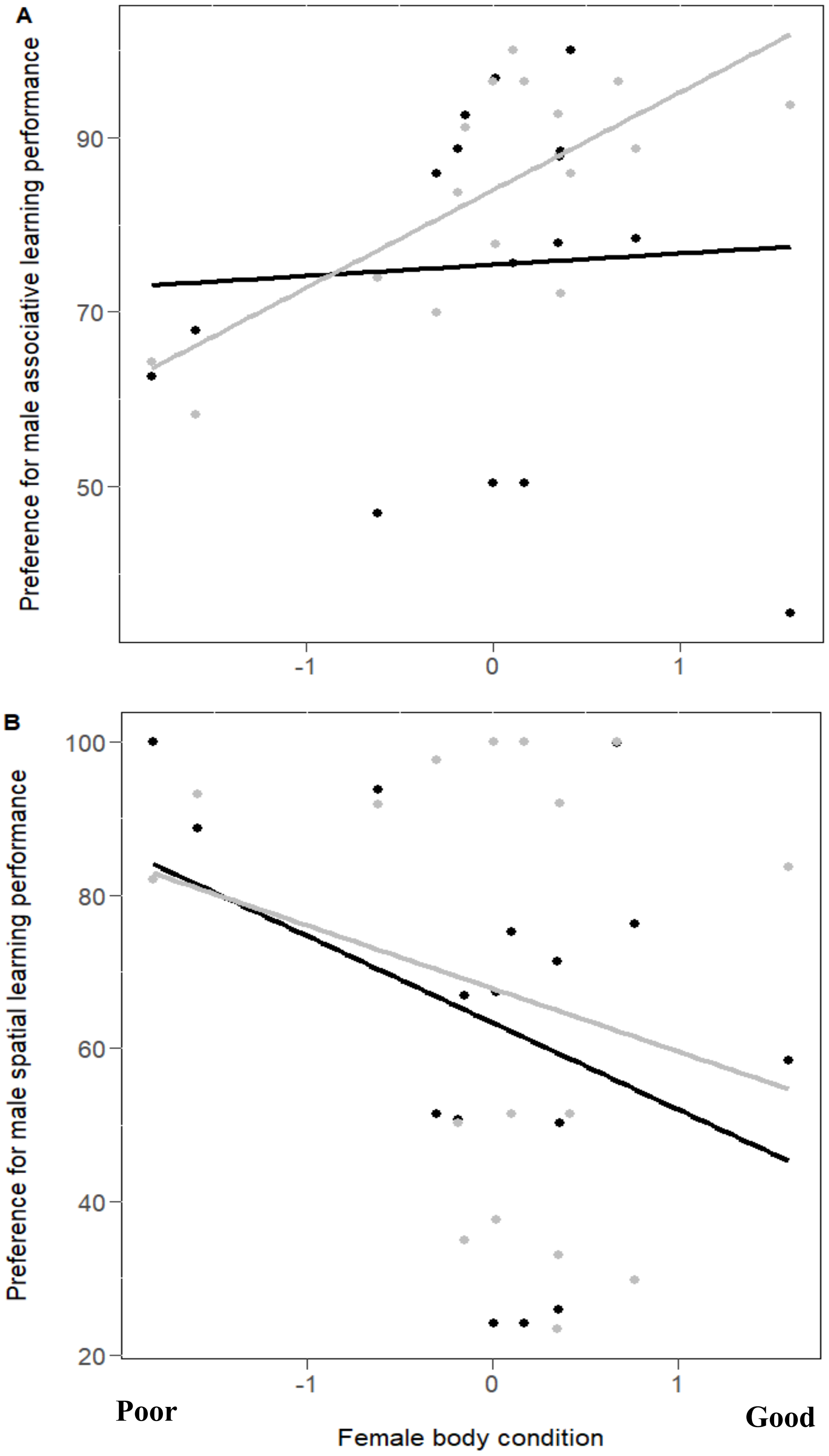
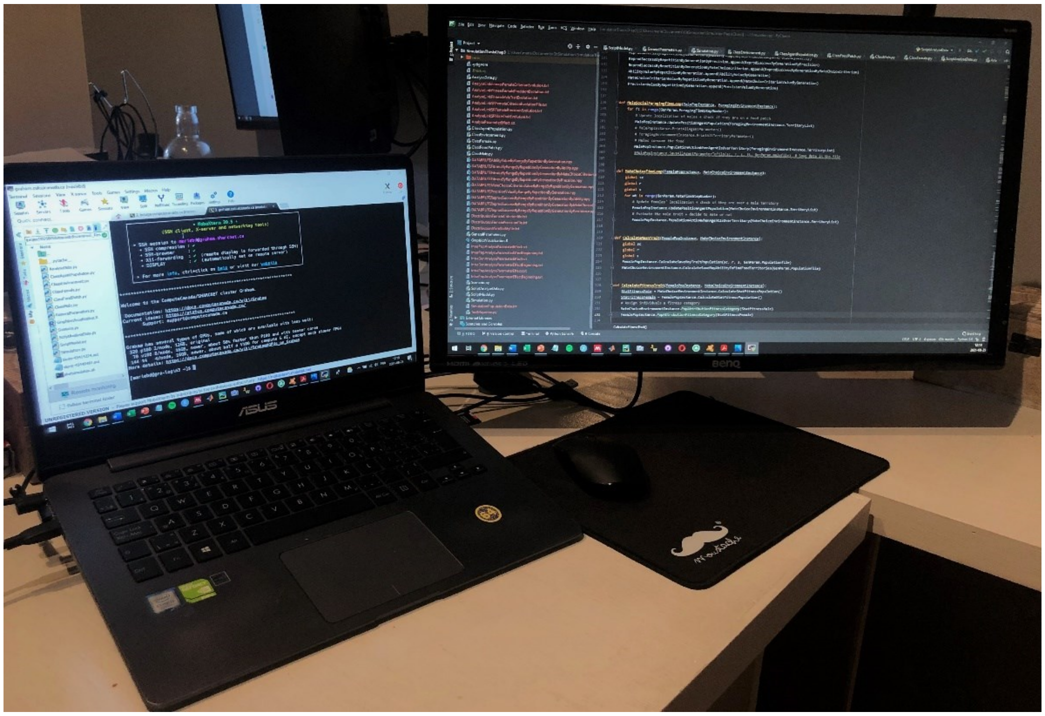


Figure S5. Relationships between females' body condition and their preference for male (A) associative learning task performance and (B) spatial learning task performance. Black and grey solid circles represent female preference in the first and the second mate choice trials, respectively.

Chapitre IV - Exploring the interplay between natural and intersexual selection on the evolution of cognitive traits

Marie Barou Dagues[1*], Frédérique Dubois[1]

[1]Département des Sciences Biologiques, Université de Montréal, Case postale 6128, Succursale Centre-ville, Montréal QC, Canada



In preparation

Abstract

There has been an increased focus on the role of natural selection in shaping cognitive abilities, but the importance of sexual selection and the interaction between both forces remain largely unknown. The intersexual selection through female mate choice might be an important driver of the evolution on cognitive traits, especially in monogamous species, where females may obtain direct fitness benefits by choosing mates with better cognitive abilities. To disentangle the effects of natural and sexual selection, here we use an agent-based simulation model and compare the model's predictions when females randomly mate with the first encountered male (i.e. under natural selection) versus when they choose among males based on their cognitive trait values (i.e. under natural and intersexual selection). Males and females are characterized, respectively, by their problem-solving ability and assessment ability. Each generation is divided into (1) a choosing phase during which females assess the cognitive abilities of potential mates until eventually finding an acceptable one, and (2) a reproductive phase during which all males compete for limited resources, that are exploited at a rate, which depends on their cognitive abilities. Because males provide paternal care, the foraging success of mated males determines the breeding success of the pair through its effect on nestling provisioning efficiency. The model predicts that intersexual selection plays a major role in most ecological conditions, by either reinforcing or acting against the effect of natural selection. The latter case occurs under harsh environmental conditions, where intersexual selection contributes to maintaining cognitive diversity. Our findings thus demonstrate the importance of considering the interaction between both selective forces and highlight the need to build a conceptual framework to target relevant cognitive traits.

Key words: intersexual selection, cognitive performance, mate choice, problem-solving ability, provisioning ability

Introduction

Cognition is defined as the neural processes by which animals sense, process, retain and act on the available information (Shettleworth, 2001). At such, it plays an important role in mediating how animals behave and interact with their environment and may have important fitness consequences (Morand-Ferron & Quinn, 2015). The most direct evidence for a link between cognitive abilities and fitness benefits comes from studies on wild populations where individuals that performed better on cognitive tasks were more successful foragers (e.g. Raine & Chittka, 2008), survived better (Cole et al., 2012), had more mating partners (Keagy et al., 2009), produced more offspring (Cole et al., 2012; Cauchard et al., 2013; Ashton et al., 2018) and had higher provisioning and fledging rate (Cauchard et al., 2017; Preiszner et al., 2017; Wetzel, 2017). Given that cognitive abilities are, to some extent, heritable (Croston et al., 2015; Hopkins et al., 2014; Langley et al., 2020; Navas Gonzalez et al., 2019; but see Quinn et al., 2016), these findings indicate that cognitive traits might evolve by natural and sexual selection. Recently, there has been an increased focus on the role of natural selection in shaping cognitive abilities (e.g. Rowe & Healy, 2014; Morand-Ferron & Quinn, 2015). By contrast, the importance of sexual selection and the interplay between natural and sexual selection on the evolution of cognitive traits remain largely unexplored (Boogert et al., 2011).

Yet it is acknowledged that natural and sexual selection may interact to shape the evolution of phenotypic (Jiménez-Arcos et al., 2017; Castillo & Núñez-Farfán, 2008; Ryder et al., 2012) and signalling (Ríos-Chelén, 2009) traits, hence the importance of considering both selective forces. Intra and intersexual selection could actually improve male cognitive abilities (e.g. Arden et al., 2009; Boogert et al., 2011; Garamszegi et al., 2005; Schillaci, 2006). For instance, intra-sexual selection might enhance male cognition if males with greater cognitive abilities are better able to locate and discriminate among mates. Accordingly, studies based on experimental evolution revealed that males of polygamous lines facing high levels of sexual competition had better performance on certain cognitive tasks compared to males of monogamous lines facing no competition (Hollis & Kawecki, 2014; Baur et al., 2019). Specifically, intra-sexual selection improved cognitive abilities that affected the capacity of males to discriminate between receptive and unreceptive females but not their learning speed. Alternatively, intersexual selection might be a driver of cognitive abilities if females gain direct fitness benefits by choosing males with cognitive abilities that are correlated with their foraging success, predator avoidance or parental care capacity (Rosenthal, 2017; Snowberg & Benkman, 2009; Wetzel, 2017). There are lines of evidence that intersexual selection may shape the evolution of male cognition (Boogert et al., 2011; Branch et al., 2019; Cauchard et al., 2013; Cole et al., 2012; Keagy et al., 2009, 2011; Minter et al., 2017; Preiszner et al., 2017; Shaw et al., 2019; Shohet & Watt, 2009; Wetzel, 2017). For instance, several studies found indirect support that females would prefer males with greater cognitive abilities, by demonstrating that they base their mate choice decision on secondary sexual characters (e.g. male song, plumage coloration) that correlate with better cognitive skills (Cauchard et al., 2017; Howell et al., 2020). A more direct support for this hypothesis comes from an experiment in which females increased their preference towards initially non-preferred males, after they had observed that these males (but not their rivals) could solve a specific problem (Chen et al., 2019). Yet, other studies found no relationship between male cognitive performance measures and mating success (Keagy et al., 2011; Isden et al., 2013; Chantal et al., 2016; Preiszner et al., 2017).

The discrepancy among studies strongly suggests that the importance given by females to different male cognitive traits would vary among species/populations according to their ecology as well as among females according to their own characteristics. For instance, as problem-solving skills are potentially important determinants of parental care (Wetzel, 2017), they might be the principal targets of mate choice in monogamous species with bi-parental care. The importance given by females to male cognitive skills that correlate with provisioning effort, however, should depend, among other factors, on the quality, quantity or distribution of available resources, as well as on the ability of females to accurately assess male cognitive traits. Supporting this idea, recent studies have demonstrated that female preferences for male cognitive skills vary depending on their own performances on cognitively demanding tasks (Álvarez-Quintero et al., 2021; Barou Dagues & Dubois, under review). Finally, the effect of natural and sexual selection should interact as the ecological conditions experienced by individuals act on the variance in male performance on cognitive tasks and, as such, determine the potential for intersexual selection.

Here, we developed an agent-based model to explore the relative importance of natural and intersexual selection on male cognitive traits that provide direct fitness benefits to females and on female cognitive traits allowing to accurately assess male cognitive traits. Males and females were thus characterized, respectively, by their problem-solving ability and capacity to reliably assess males' cognitive trait, and we simulated the evolution of male and female cognitive traits over time under different ecological scenarios. A simulation is divided into two phases (1) a choosing phase during which females assess the cognitive abilities of potential mates until eventually finding an acceptable one, and (2) a reproductive phase during which all males compete for limited resources that are exploited at a rate, which depends on their cognitive abilities. Because males provide paternal care, the foraging success of mated males determines the breeding success of the pair through its effect on nestling provisioning efficiency. Each scenario (i.e. set of parameter values) was run when females randomly mated with the first encountered male (i.e. under natural selection alone) and when they could choose among males based on their cognitive trait values (i.e. under natural and intersexual selection) to be able to disentangle their respective effects. We found that intersexual selection though female mate choice played a major role in most conditions, by either reinforcing or acting against the effect of natural selection under favourable or harsh environments, respectively. As such, we predict that female mate choice may contribute to maintaining cognitive diversity.

An agent-based simulation model

A population contains a constant number of 100 males and 100 females that can move over a two-dimensional grid containing 196 (14x14) territories. Each male i is characterized by a cognitive trait value (I_i) ranging from 0 to 10, that represents the number of time steps required to solve a novel problem and access to food. This ability is especially relevant for species that need to remove obstacles, use tools or innovate, as the faster they resolve the problem the faster they gain access to the food resource (e.g. Huebner et al., 2018; Cole et al., 2011). Thus, a low cognitive trait value represents males with good cognitive abilities while a high cognitive trait value represents males with poor cognitive abilities. Each female j is characterized by two state-dependent variables that represent, respectively, their capacity to accurately assess male cognitive trait value (A_j) ranging from 0 to 5 and their selectivity (S_j) ranging from 0 to 10. A simulation consists of 1000 consecutive generations, each of them divided into two phases: 1) a choosing phase during which females search for a breeding partner, and 2) a reproductive phase during which all males compete for limited resources. The foraging success of males directly depends on their cognitive trait value and on the cost of cognition. Furthermore, we assume that mated males provide parental care. As such, their forging success determines the breeding success of the pair, through its effect on nestling provisioning efficiency (figure 1, for more details about the code, see figure S1, S7).

Choosing phase

At the beginning of the choosing phase, males and females in turn are randomly assigned to a unique location on the grid. Males stay in their assigned territory, while females can move among male territories during Tm time steps or until finding an acceptable mate using a random walk (i.e. only one random move per time step to any male territory). When a female moves on a male's territory that is not paired yet, she assesses the value of the male cognitive trait during the A_j time steps. Specifically, the variable A_j represents the number of time steps devoted to assessment of the male cognitive trait value. We assume that females with a value of 5 (i.e. that spent 5 time units per male for mate assessment) perfectly assess male cognitive trait values while females with smaller values, obtain wrong estimates, the amount of error (ε) being inversely proportional to A_j, such as: $\varepsilon = 5 - A_j$. Thus, the estimated value (E_i) corresponds to the exact trait value, to which we randomly add or subtract ε. Based on her estimate of the male's trait value and her minimum acceptance value (i.e. selectivity S_j), the female then either accepts to mate with the male (if $E_i \leq S_j$) or moves to another male territory. Specifically, the variable S_j ranges from 0 to 10 and females with a value of zero, therefore, only accept to mate with males with the higher cognitive trait value. For the first generation, the female accuracy and selectivity trait values are randomly drawn from discrete uniform distributions. Subsequently, the female offspring inherit their mother's.

Reproductive phase

During T_r time steps (the duration of the reproductive phase) all males (i.e. mated and unmated ones) search for food patchily distributed. More precisely, the environment contains as above 196 territories among them N_F contains R food items. At the beginning of a reproductive period, each male is randomly assigned to a territory and then can move from one territory to another using a random walk (i.e. only one random move per time step to one of the territories located in the 4 cardinal directions). When a male moves on a territory that contains food, it must wait for I_i time steps before it can start exploiting it. For the first generation, the cognitive trait value is randomly drawn from a discrete uniform distribution with all values having the same probability of being picked. Subsequently, the male offspring inherit their father's trait. Males suffer a cognitive cost that is inversely proportional to their cognitive trait value.

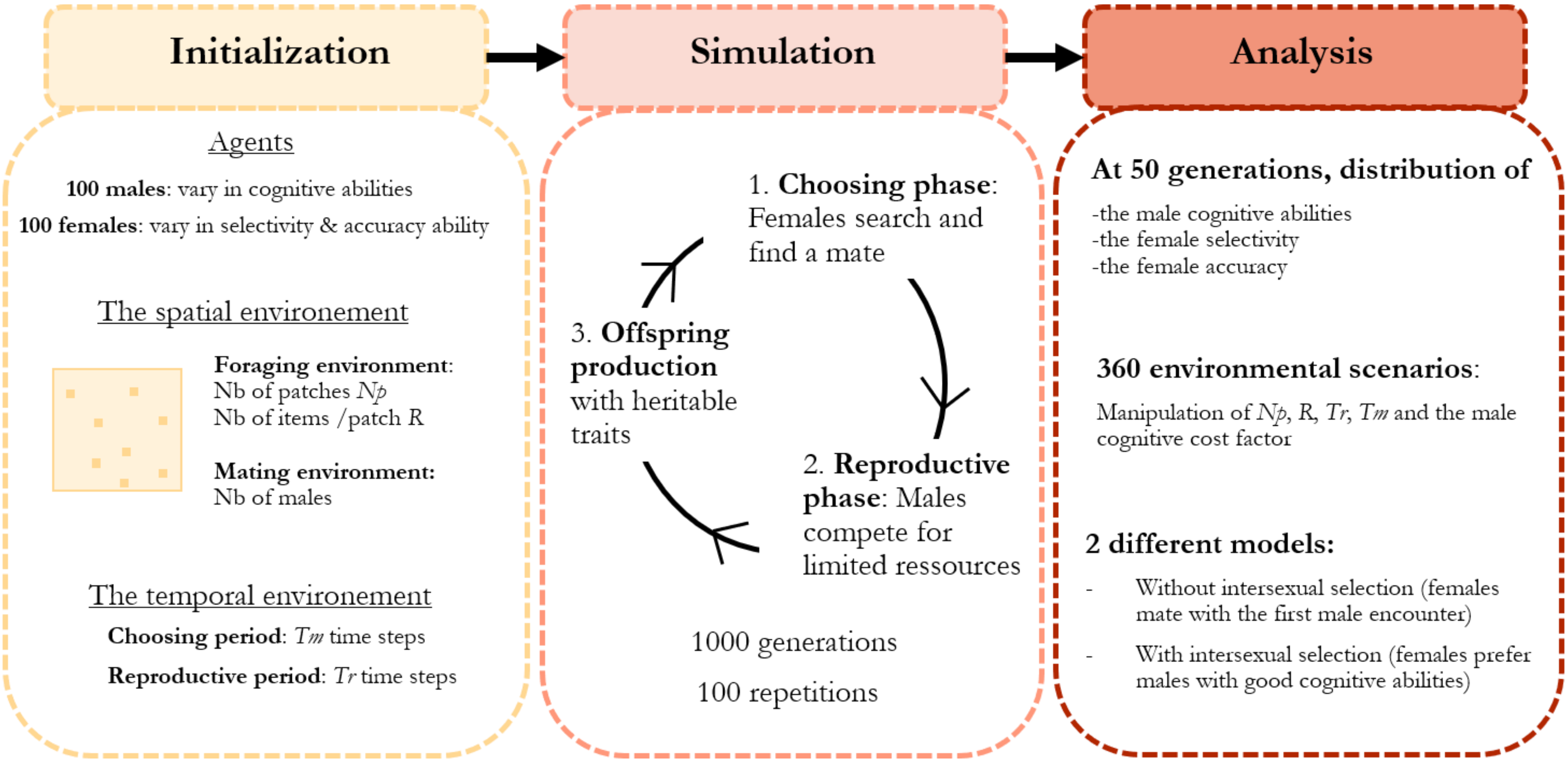


Figure 1. Overview of the model initialization, simulation processes and analysis.

Thus, each male i is characterized by its foraging success W_i that is initialized to zero at the beginning of the reproductive phase and then is incremented by one each time it gets a food item. At the end of the reproductive phase, the cognitive cost $C_i = -\propto [10 - I_i]$ is deduced from W_i. The cognitive factor $\propto$ used in this equation allows us to manipulate the cost of cognition on males' foraging success (Table 1). We assume that each male can consume only one food item at each time step and that a food patch can be simultaneously exploited by several males. In that case, each male that joins the patch must wait the number of time steps associated with its cognitive trait value before it can get food. The number of food patches is kept constant throughout the reproductive phase. Therefore, once a food patch is depleted, it is immediately replaced by another one, whose location is randomly chosen among all unoccupied and empty territories.

At the end of the reproductive phase, we attribute females a reproductive score ranging from 0 to 11. Specifically, unmated females are attributed a score of zero while the score attributed to mated females is proportional to the foraging success of their mating partner. To homogenize variance in reproductive success across all environmental conditions and among simulations, we attributed a reproductive score of zero to females whose partner had a foraging success equal or less than zero. For the other females whose partner had a foraging success greater than 1, their score was incremented by 1 for every 10 units of foraging success with a maximum reproductive score of 11. We assume that breeding pairs produce male and female offspring in equal proportion. In addition, population size is kept constant from one generation to the next and the population is completely renewed at each generation. Among all the offspring produced, therefore, 100 males and 100 females are randomly selected at the end of each mating period to constitute the next generation. To account for stochastic effects, the same simulation was run 100 times.

Analyses

In order to predict the relative importance of natural and sexual selection on the evolution of male and female cognition under different scenarios, we manipulated (i) the food distribution (i.e. N_p and R), (ii) the duration of the reproductive phase (i.e. Tr), (iii) the duration of the mating period (i.e. Tm) and iv) the cognitive cost C_i via the cognitive factor (i.e. $\propto$; table 1), for a total of 360 sets of parameter values. By completely renewing the population at each generation and setting a perfect trait heritability, we imposed a very strong selective pressure. Then, we only studied the

Table 1. Definition of the manipulated environmental and agent parameters. For each parameter, the symbol and the tested values are specified.

Environmental parameters	Symbol	Tested values
Number of food patches	*Np*	5, 25, 45, …,185
Number of food items	*R*	10,100,200
Length of the reproductive phase (in time steps)	*Tr*	50, 200
Length of the choosing phase (in time steps)	*Tm*	5, 200
Agent parameters		
Cognition factor	$\propto$	1, 6, 10

evolution of cognitive traits within populations after 50 generations. After 1000 generations, all populations reach fixation, and the predicted patterns remain unchanged if we look at the variance among populations (supplementary materials, figure S2, S3, S4, S5). Each set of parameter values was run when 1) females randomly mated with the first encountered male (i.e. under natural selection alone) and 2) when they could choose among males based on their cognitive trait value (i.e. under natural and sexual selection) to be able to disentangle the effects of natural and sexual selection.

Predictions

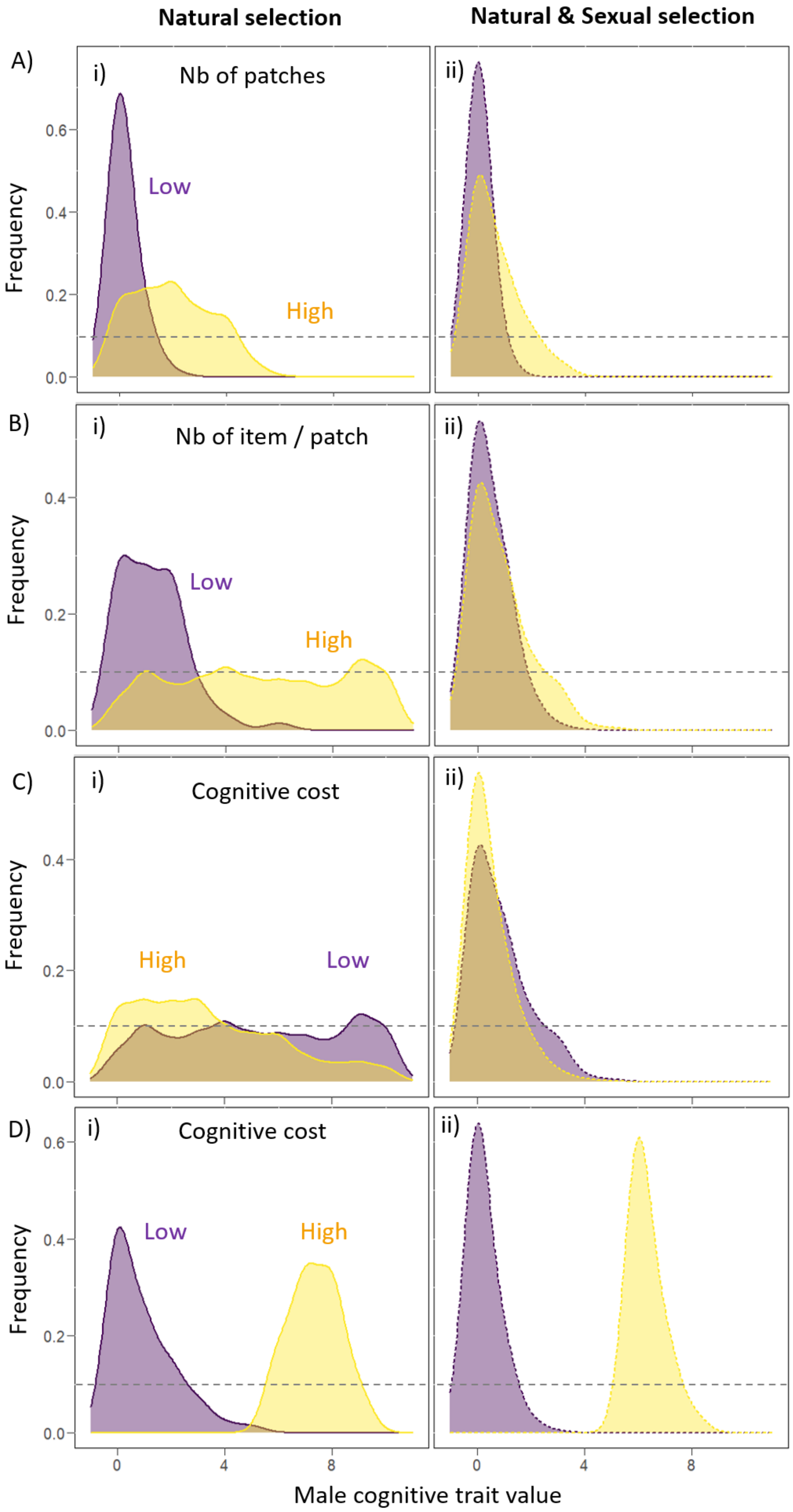
Evolution of cognition under natural selection

The model predicts that natural selection should enhance the male cognitive ability and reduce male cognitive diversity when the number of food patches, their value and the length of the reproductive phase are small. By contrast, the strength of natural selection should be weak and, as such, male cognitive diversity should not be eroded, when the food is abundant and the reproductive phase is long (figure 2Ai, 2Bi 2Ci; supplementary materials, figure S3). Under such conditions males can indeed easily find food, and all have a high foraging success, irrespective of their cognitive abilities. The cost of cognition, therefore, has almost no effect on males' foraging success under such conditions, and hence has a low impact on female reproductive score (figure 2Ci). By contrast, when the reproductive phase is short, the cost of cognition has a stronger impact on the reproductive success of the pair as males have a lower foraging success: increasing the cost of cognition then progressively eliminates the males with the greatest cognitive abilities, thereby leading to a reduction in male cognitive diversity (figure 2Di).

Evolution of cognition under natural and sexual selection

Depending on environmental conditions, the model predicts that intersexual selection may have little or no effect, reinforce the effect of natural selection or act against it (figure 4; supplementary materials, figure S4). Logically, the strength of intersexual selection depends on average female traits (i.e. accuracy and selectivity), whose expression is affected by ecological conditions (figure 3, S2). Specifically, we found that less accurate females, that rapidly visit potential mates and, as such, have higher chances to find an acceptable one compared to more accurate ones, are often favoured (figure S2, S6). This happens especially when natural selection alone favours male with good abilities (i.e. long reproductive phase), while diversity in female accuracy is maintained in the harshest environmental conditions (i.e. short reproductive period, high cognitive cost). By contrast, the evolution of female selectivity over time is affected by the benefits of choosing a male with greater cognitive abilities, which depend on the ecological conditions (i.e. duration of the reproductive phase, number of quality of food patches, figure 3A, 3B), the cost of cognition, and the likelihood of finding an acceptable mate (i.e. duration of the choosing phase, figures 3C, S5). Logically, less selective females are favoured when the length of the mating period is short, while increasing the time for finding a mate increases diversity in female selectivity and, as such, enhances the effect of intersexual selection.

In all environmental conditions, sexual selection favours males with greater cognitive abilities (figure 2Aii, Bii, Cii), except when the duration of the reproductive phase is short and the cost of cognition is so large that males achieving the greatest reproductive success are the ones with the lowest cognitive abilities (figure 2Dii). For that reason, intersexual selection should reinforce the effect of natural selection when natural selection alone favours males with better cognitive skills (figure 2Aii, 2Bii, 4B), while maintaining enough cognitive diversity for intersexual selection to act on. Yet, when natural selection eliminates almost all the cognitive diversity by favouring males with better cognitive abilities, intersexual selection has inevitably a weak effect (figure 4A). This



Natural selection
Natural & Sexual selection
A)
i)
Nb of patches
ii)
Low
High
B)
i)
Nb of item / patch
ii)
Low
High
C)
i)
Cognitive cost
ii)
High
Low
D)
i)
Cognitive cost
ii)
Low
High
Frequency
0.0
0.2
0.4
0.6
0
4
8
Male cognitive trait value

Figure 2. Effect of environmental parameters on the pooled distribution of male cognitive trait values at the 50th generation from 100 repetitions, under natural selection alone (left panels) or under natural and sexual selection (right panel). Low and high male cognitive trait values respectively mean that the males have good and low cognitive abilities. A) $Tr = 200$, $Tm = 200$, $R = 10$, $\alpha = 1$ and Np is manipulated B) $Tr = 200$, $Tm = 200$, $Np = 85$, $\alpha = 1$ and R is manipulated, C) $Tr = 200$, $Tm = 200$, $R = 100$, $Np = 85$ and α is manipulated, D) $Tr = 50$, $Tm = 200$, $R = 100$, $nP = 85$ and α is manipulated. The purple and yellow colors respectively represent low and high values of the manipulated factor and the grey dashed line represent the initial distribution of the trait.

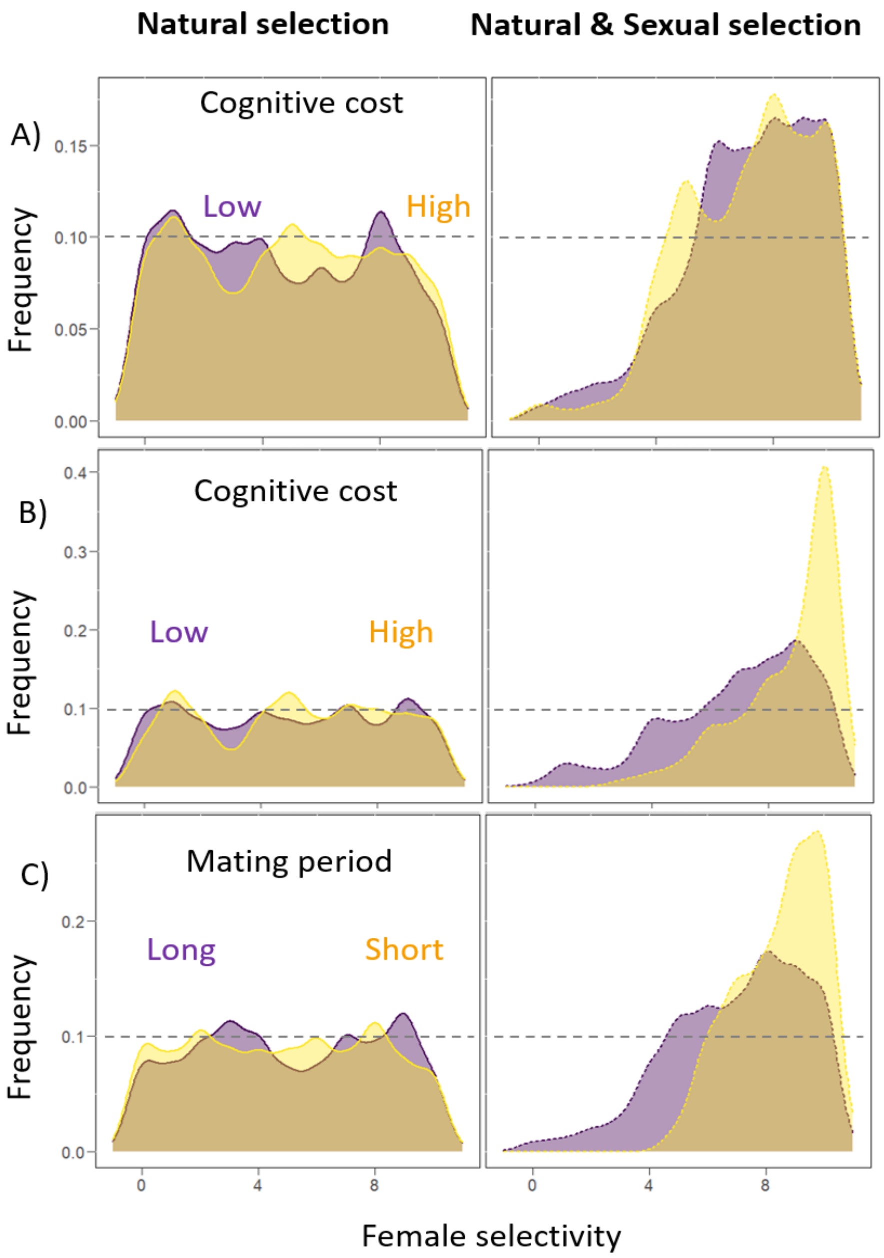


Figure 3. Effect of environmental parameters on the pooled distribution of female selectivity values at the 50th generation from 100 repetitions, under natural selection alone (left panels) or under natural and sexual selection (right panel). Low and high female selectivity values respectively mean that the females have high and low preference for good male cognitive abilities. A) *Tr* = 200, *Tm* = 200, *R = 100, Np* = 85 and *α* is manipulated, B) *Tr* = 50, *Tm* = 200, *R = 100, Np* = 85 and *α* is manipulated, C) *Tr* = 200, *R* = 10, *Np* = 85, *α* = 1 and *Tm* is manipulated. The purple and yellow colors respectively represent low and high values of the manipulated factor. The patterns found in A) are similar when the number of patches and the number of items per patch are manipulated and the grey dashed line represents the initial distribution of the trait.

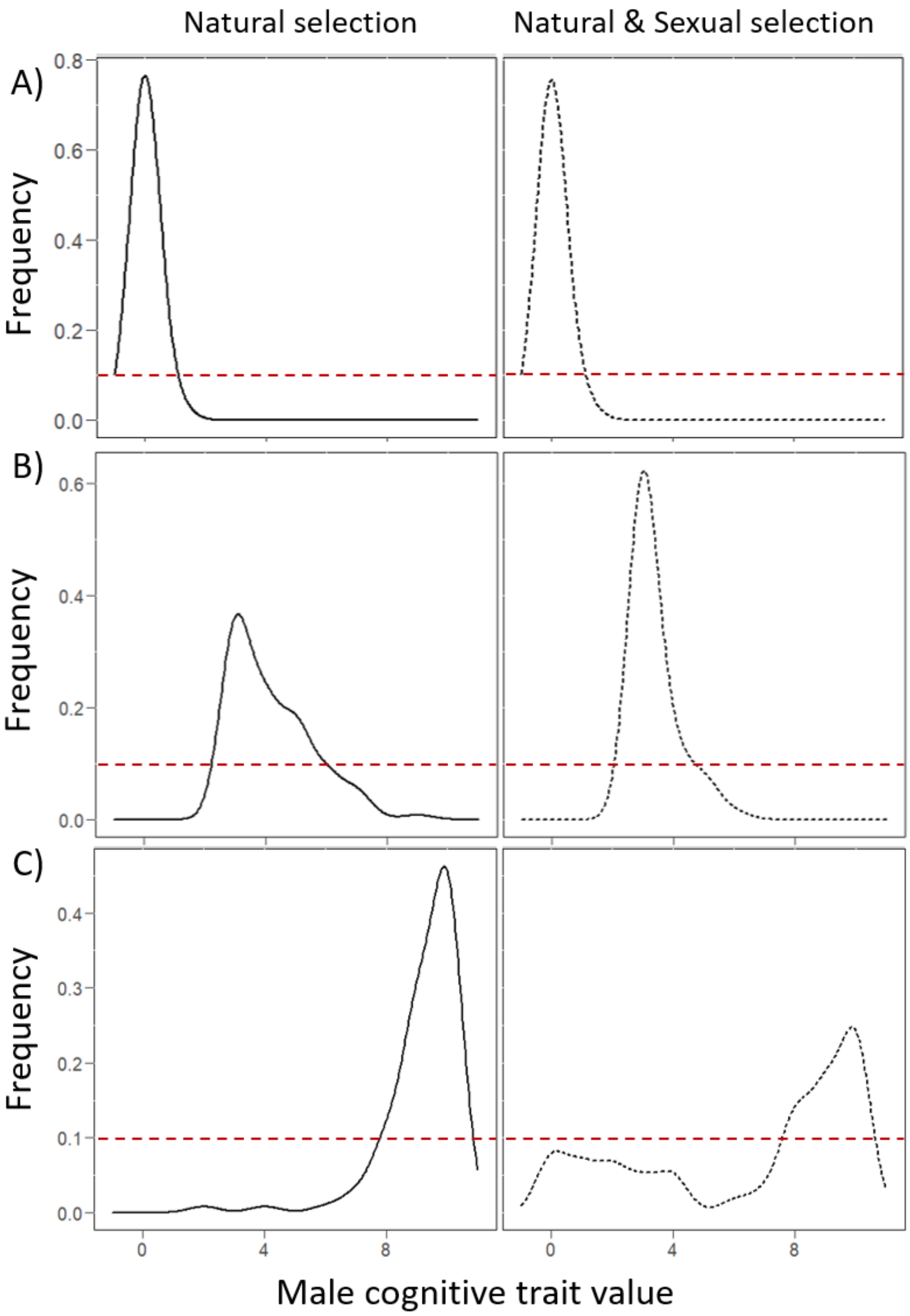


Figure 4. Pooled distribution of male cognitive trait values at the 50th generation from 100 repetitions, under natural selection alone (solid lines) or under natural and sexual selection (dashed lines). Plot A: *Tr* = 50, *Tm* = 200, *Np* = 185, *R* = 100 and *α* = 1, Plot B: *Tr* = 50, *Tm* = 5, *Np* = 105, *R* = 100 and *α* = 6, Plot C: *Tr* = 50, *Tm* = 5, *Np* = 5, *R* = 10 and *α* = 10. Low and high male cognitive trait values respectively mean that the males have good and low cognitive abilities, and the red dashed line represents the initial distribution of the trait.

is the case for instance when the food patches are poor and limited, the length of the reproductive phase is short, and the cost of cognition is weak (figure S4).

On the contrary, when natural selection alone favours males with poor cognitive abilities, intersexual selection tends to eliminate, at least partially, these males who are progressively replaced by individuals with superior abilities (figure 4C). In fact, more accurate and selective females should select males with good abilities while less accurate and less selective females should select males with poor abilities. Such a scenario, in which intersexual selection should act against natural selection and maintain cognitive diversity, occurs in the harshest environments (i.e. poor patches, short mate choice and reproductive phases) when the cost of male cognition is large (figure S4, S5, S6).

Discussion

Our results demonstrate that the relative importance of natural and sexual selection on male and female cognition depends on environmental conditions. Thus, our study highlights the importance of considering the interaction between both selective forces, as ecological conditions experienced by individuals acts on the variance in male cognitive traits and hence on the potential for sexual selection. Specifically, under natural selection, we found that the evolution of male cognition was mainly driven by the intensity of resource competition and the cost of male cognition. When food resources were limited (i.e. under strong competition), natural selection tended to favour males with good cognitive abilities that have privileged access to them. By contrast, when resources were abundant (i.e. under weak competition), natural selection had a weak effect and maintained most of the initial cognitive diversity. These predictions agree with several theoretical and experimental studies demonstrating that social competition is an important driver of the evolution of cognition (e.g. Morand-Ferron et al., 2015; Pravosudov & Roth, 2013; Szabo et al., 2020). For instance, Pravosudov and Roth (2013) reported that food-caching black-capped chickadees (*Poecile atricapillus*) facing severe winter conditions are more accurate in a spatial memory task and faster in habituation and problem-solving tasks, compared to individuals facing milder winter conditions. However, as cognition is costly, in terms of production and maintenance of neuronal and physiological processes involved in cognitive mechanisms (Dukas, 1999; Jaumann et al., 2013; Laughlin et al., 1998), good cognitive abilities should be favoured only when the benefits, notably in terms of foraging success, exceed the costs (Niemelä et al., 2013). In support, we found that natural selection decreased male cognitive diversity within populations when the reproductive phase was short, by respectively promoting good, intermediate and low cognitive abilities under low, intermediate and high male cognitive costs. As confirmed by numerous studies, cognition can trade off with other fitness related traits, such as development time (Christiansen et al., 2016; Snell-Rood et al., 2011), lifespan (Burger et al., 2008), competitive abilities (Mery & Kawecki, 2003) or immune response (Alghamdi et al., 2008; Gegear et al., 2006; Iqbal & Mueller, 2007). For instance, honeybees suffer from significant cognitive impairment under energetic stress (Jaumann et al., 2013) suggesting that trade offs with energy use can prevent good cognitive abilities from evolving in populations (Dunlap & Stephens, 2016).

The expected patterns of evolution under natural selection changed under most conditions when including the effect of intersexual selection. Indeed, we found that intersexual selection had no or very little effect only when natural selection eroded most of the variance in male cognitive abilities, that is under strong resource competition and with a low cognitive cost. In all other conditions, intersexual selection through female mate choice either reinforced or acted against the effect of natural selection. Specifically, intersexual selection reinforced the effect of natural selection when male cognitive ability was a reliable indicator of the reproductive success of the pair (Boogert et al, 2011). This happened when the reproductive phase was long because the variance in male foraging success was then very large, resulting in a strong positive correlation between male cognitive trait value and breeding success. Obviously, the effect of intersexual selection was even stronger when the most selective females were maintained within the population, and so when their likelihood of finding an acceptable mate was high (i.e. long choosing phase). This, however, occurred very rarely as we did not allow unmated females to decrease their acceptance threshold at the end of the mate choice phase or to have a last mating chance (e.g. Janetos, 1980). Also, because we have assumed that males can have only one mating partner and the sex-ratio is balanced, we have imposed a very strong competition among females. For these reasons, we found that the least accurate but most rapid females were favoured in most conditions and that intersexual selection had a weak effect on female cognition. The strength of intersexual selection, however, is likely stronger under natural populations, than that we predict. Further studies would then be required to better understand the effect of sexual selection on female assessment accuracy in relation to social mating system conditions.

Interestingly, when natural selection alone favoured males with poor cognitive abilities, intersexual selection acted against natural selection by favouring the extreme male trait values and promoting the maintenance of diversity in female traits (selectivity and accuracy). Under such conditions, population was made up of males with good cognitive abilities that were very efficient at finding food but suffered a large cost of cognition, and of males with low cognitive abilities that obtained food at a lower rate but suffered no cost. Thus, selective and accurate females that preferred males with superior cognitive traits, achieved similar reproductive success than less selective and less accurate ones. As such, our results support the idea that cognitive diversity can be maintained by intersexual selection through female mate choice (fish: Álvarez-Quintero et al., 2021; birds: Barou-Dagues, Richard-Dionne & Dubois, 2020; Barou Dagues & Dubois, in preparation; humans: Escorial & Martín-Buro, 2012; Plomin & Deary, 2015; Śmieja & Stolarski, 2018). Although more evidence is needed to determine which ecological conditions contribute to maintaining differences in female preference for male abilities, our predictions are nevertheless consistent with the fact that no study so far has demonstrated an unanimous female preference for male cognitive abilities.

More generally, our study supports the idea that intersexual selection is an important driver of the evolution of cognition and highlights the need of building a conceptual framework to target relevant cognitive traits. Indeed, since correlations between individual performances on different cognitive tasks may vary among species (Burkart et al., 2017; Poitier et al., 2020), sexual selection should favour different cognitive abilities depending on the female needs and thereby on the ecological and social mating system conditions. For instance, as problem-solving skills are potentially important determinants of parental care (Cauchard et al., 2017; Preiszner et al., 2016; Wetzel, 2017), they might be the principal targets of intersexual selection in monogamous species with bi-parental care. Inversely, as spatial memory allows individuals to survive during winter by recovering food items in thousand caches, it should be targeted by natural and sexual selection in species experiencing harsh conditions during winter (Boogert et al., 2011). Further experimental and meta-analytic studies are then required to better understand how natural selection interplays with sexual selection under different ecological environments and across mating systems when females may obtain both direct and indirect fitness benefits. Experiments designed to assess the heritability of cognitive trait measures (e.g. Smith et al. 2015) will also be useful to make more realistic predictions concerning the relative importance of both selective forces. In our simulation model, indeed, we have assumed that cognitive traits and female preferences are 100% heritable, thereby increasing the rate at which natural and sexual selections operate. Thus, investigating how genetic (Croston et al., 2015) and non-genetic (i.e. maternal effect: Basatemur et al., 2012; Munch et al., 2018; cultural transmission: Langley et al., 2018, 2020) factors affect the heritability of cognitive traits and hence their rate of evolution would allow to better understand to what extent differences in cognition reflect adaptations to ecological conditions.

Supplementary materials

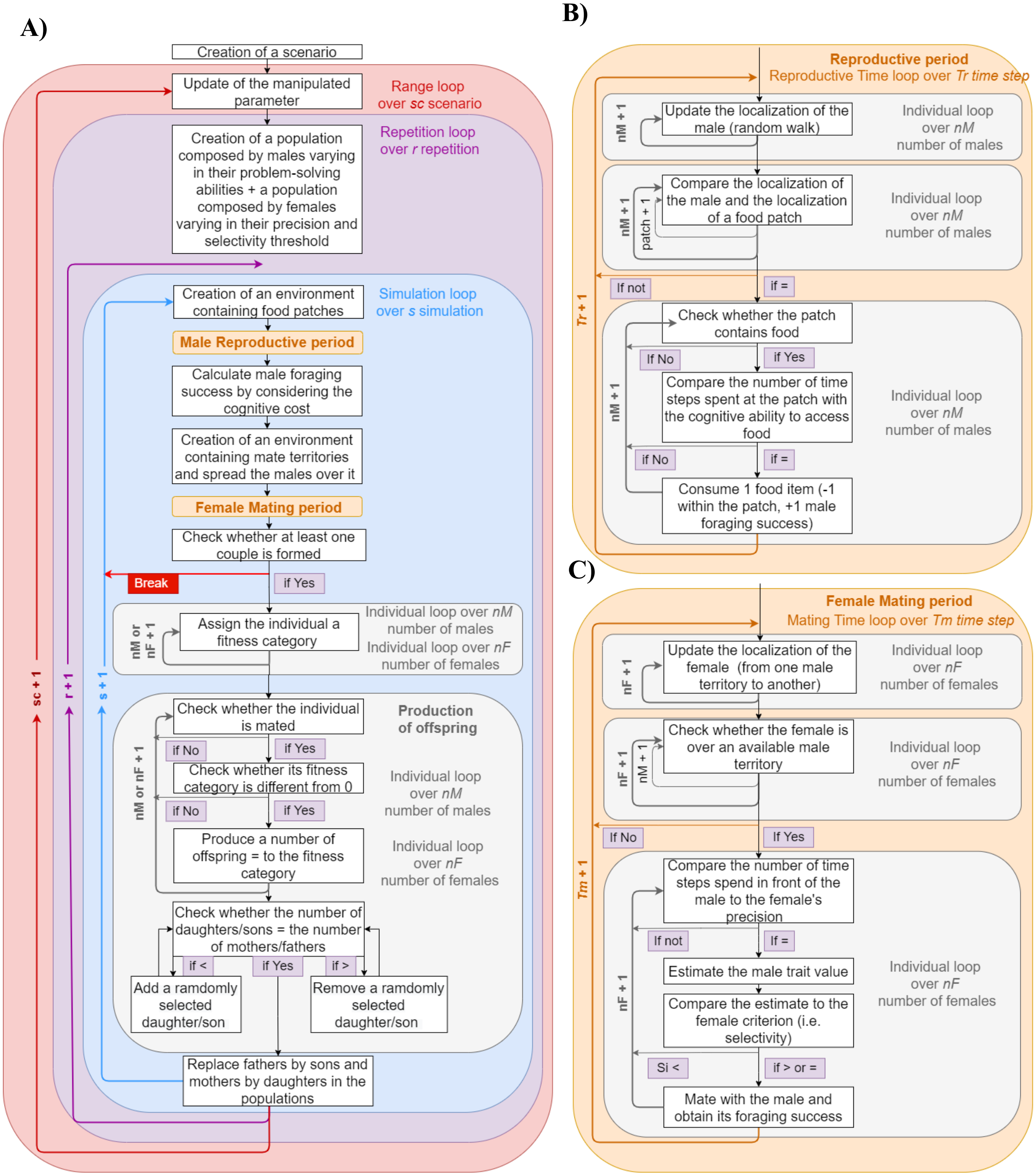


Figure S1. Diagram of the agent-based model with A) the main simulation, B) the reproductive period and C) the mating period simulation. Male reproductive and female mating periods are independent *per se* but are coded in this order for simplicity.

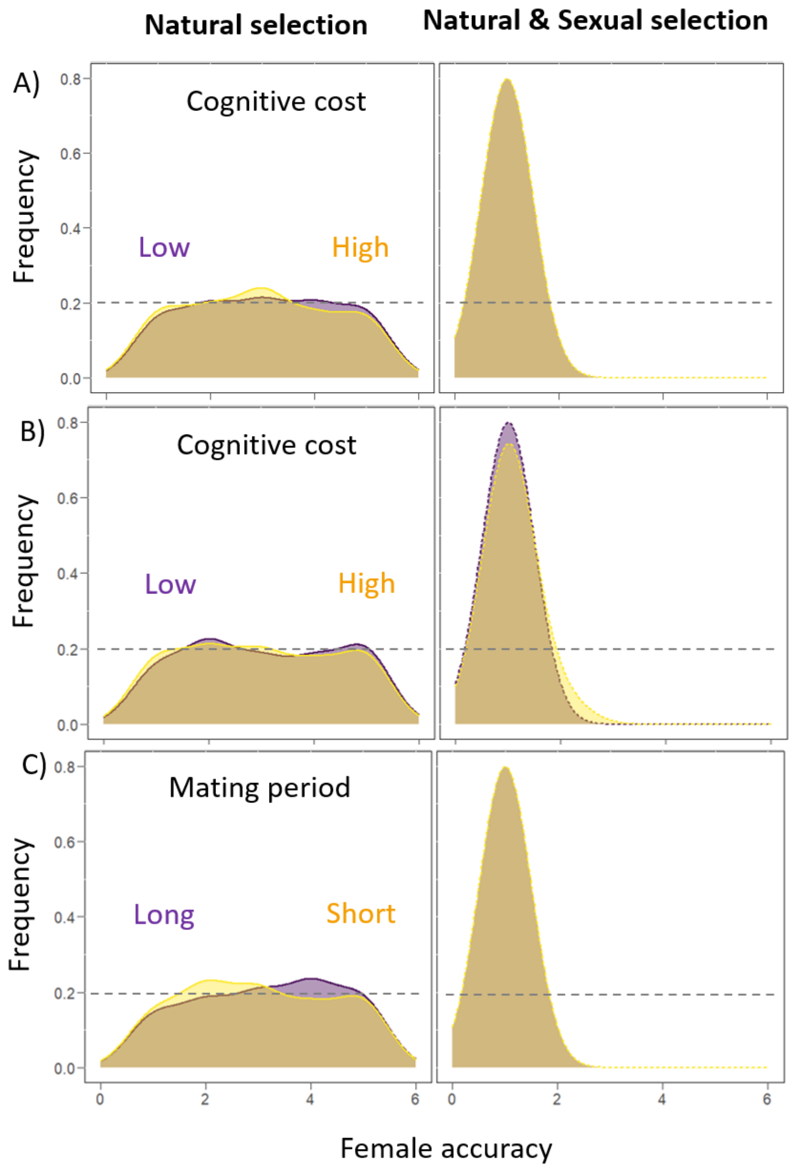


Figure S2. Effect of environmental parameters on the distribution of female accuracy values at the 50th generation under natural selection alone (left panels) or under natural and sexual selection (right panels). Low and high female accuracy values respectively mean that females make no and large assessment errors. A) *Tr* = 200, *Tm* = 200, *R = 100, Np* = 85 and *α* is manipulated, B) *Tr* = 50, *Tm* = 200, *R = 100, Np* = 85 and *α* is manipulated, C) *Tr* = 200, *R* = 10, *Np* = 85, *α* = 1 and *Tm* is manipulated. The purple and yellow colors respectively represent low and high values of the manipulated factor. The patterns found in A) are similar when the number of patches and the number of items per patch are manipulated and the grey dashed lines represent the initial distribution of the trait.

Sélection naturelle

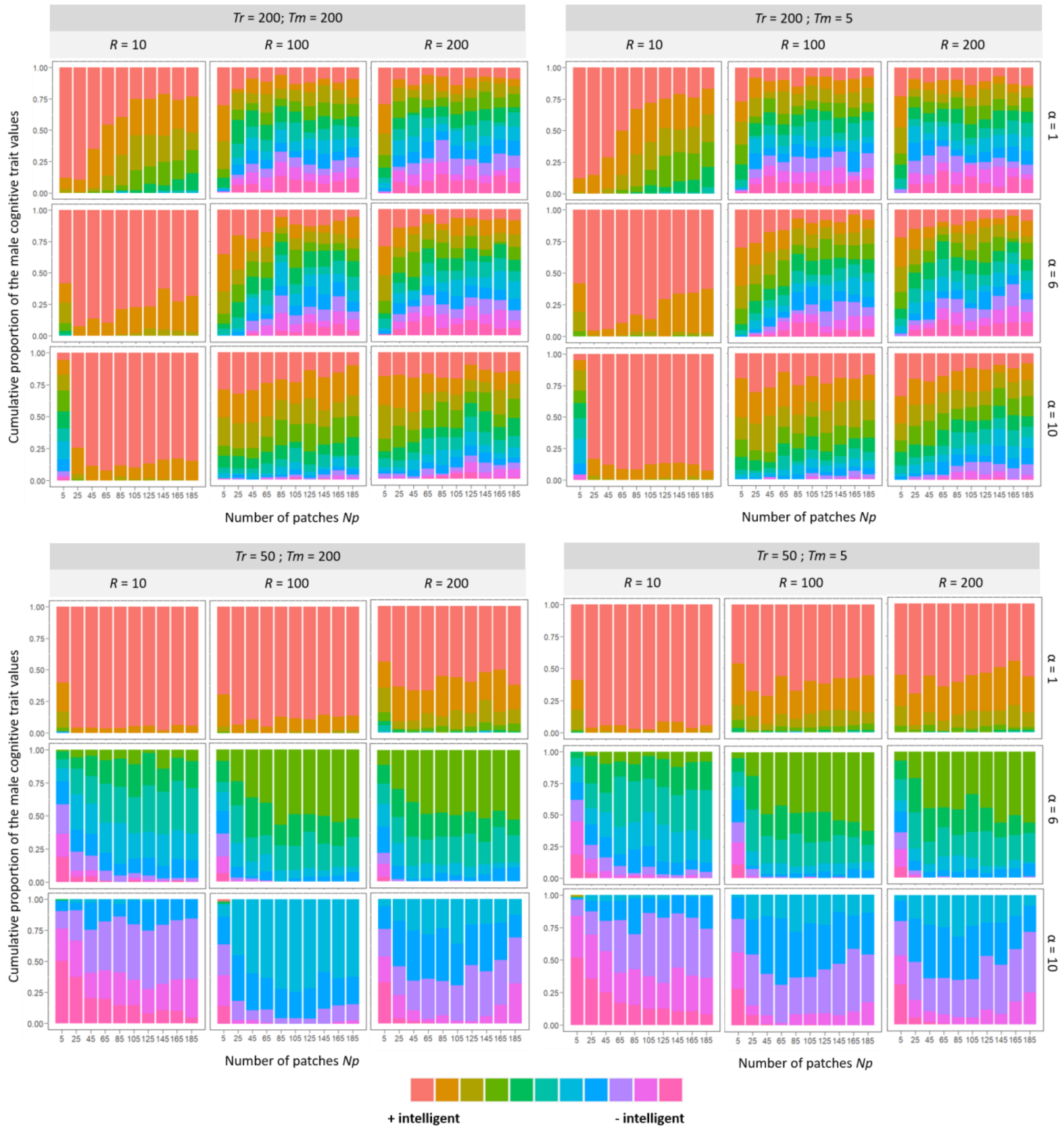


Figure S3. Mean frequency of male cognitive trait values in the 360 environmental conditions in which we made vary the quantity and quality of food patches, the lengths of the reproductive and choosing phases and the cost of male cognition under natural selection from the last 50 generations over 100 repetitions. Each color represents a male trait value from red (i.e. males with a better cognitive ability) to purple (i.e. males with a poorer cognitive ability).

Sélection naturelle et sexuelle

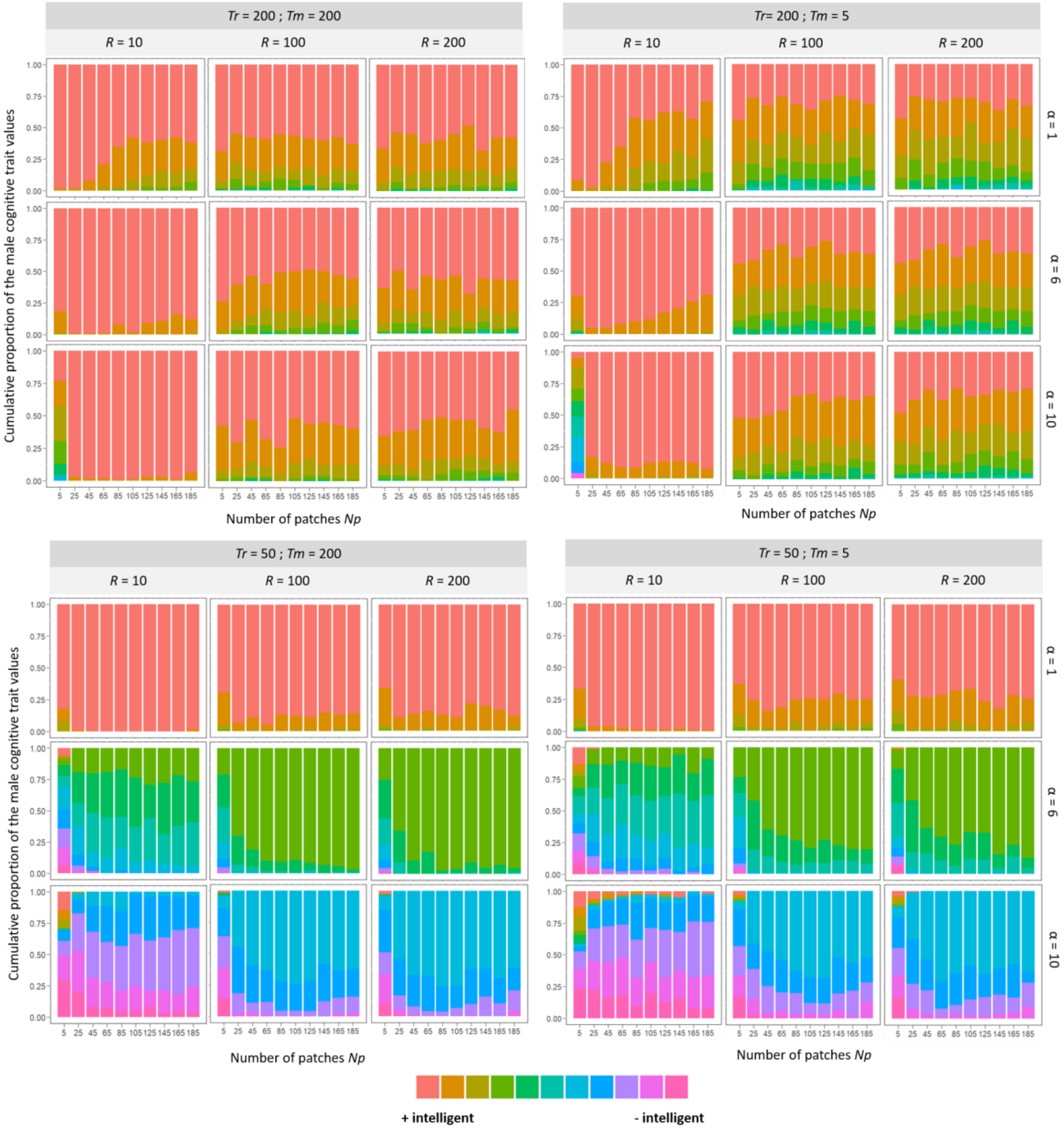


Figure S4. Mean frequency of male cognitive trait values in the 360 environmental conditions in which we made vary the quantity and quality of food patches, the lengths of the reproductive and choosing phases and the cost of male cognition under natural and sexual selection from the last 50 generations over 100 repetitions. Each color represents a male trait value from red (i.e. males with a better cognitive ability) to purple (i.e. males with a poorer cognitive ability).

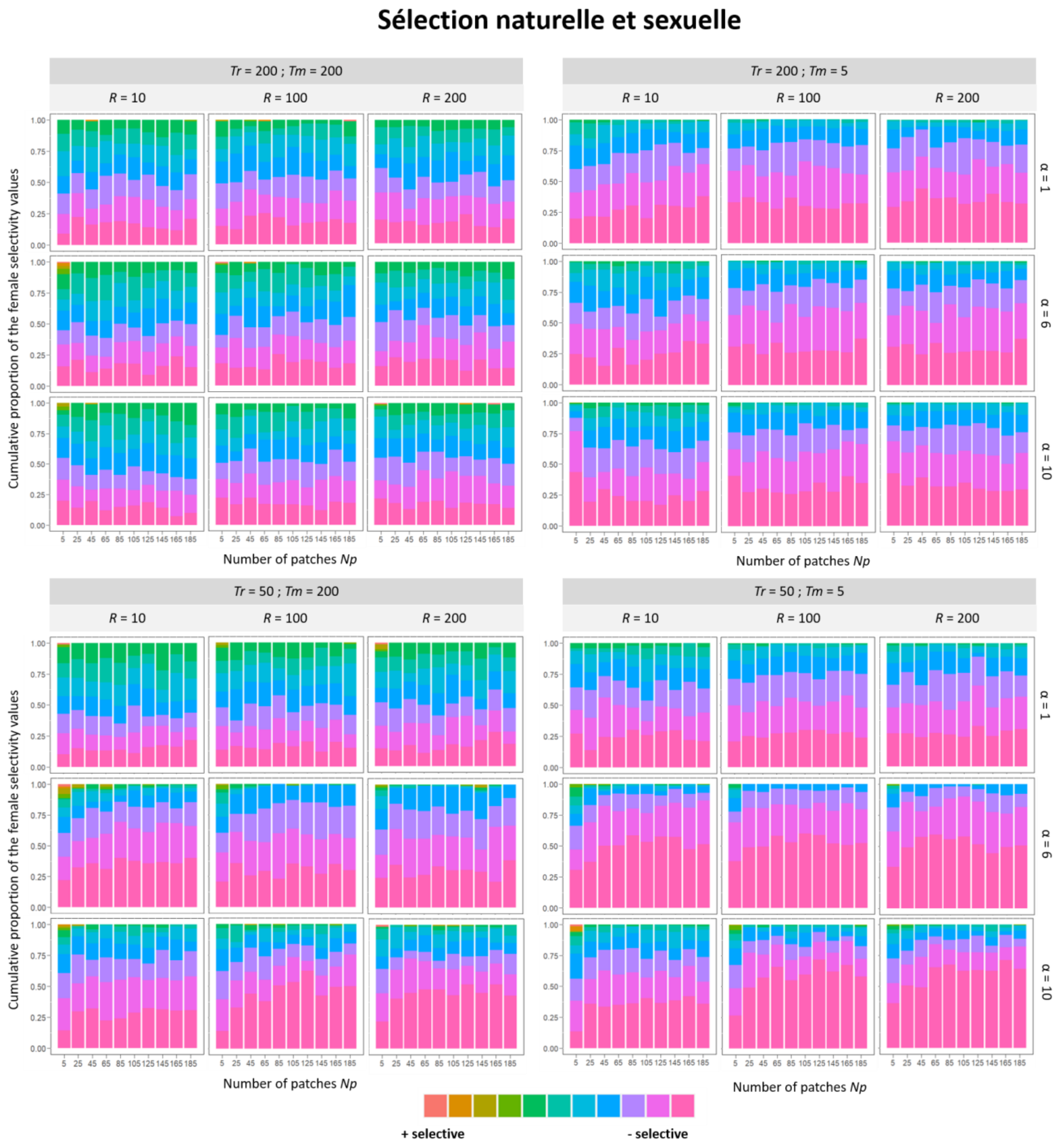


Figure S5. Mean frequency of female selectivity values in the 360 environmental conditions in which we made vary the quantity and quality of food patches, the lengths of the reproductive and choosing phases and the cost of male cognition under natural and sexual selection from the last 50 generations over 100 repetitions. Each color represents a female trait value from red (i.e. females with high selectivity threshold) to purple (i.e. females with low selectivity threshold).

Figure S6. Mean frequency of female accuracy values in the 360 environmental conditions in which we made vary the quantity and quality of food patches, the lengths of the reproductive and choosing phases and the cost of male cognition under natural and sexual selection from the last 50 generations over 100 repetitions. Each color represents a female trait value from red (i.e. females with low accuracy ability) to purple (i.e. females with high accuracy ability).

Figure S7: Code of the model. The code includes two parts. The first one contains the script for the simulation (*Main simulation script*, *General Parameters, Simulation, Class environment, Class Agent, ClassFoodPatch, ClassMale, ClassFemale)* and the second one the script for the analyse of data (*Main Data Analysis, Data Analysis)*. This code was written for Python 3.6.

Main simulation script

```
import numpy
import time
import ScriptAnalyseData
import GeneralParameters as GenParam
import Simulation
import multiprocessing as mp
import os

def main(manager, pool):
    Time1 = time.time()

    # Creation of a data file
    GenParam.Populationfile = open('SimulationPopulationData.txt', 'w')

GenParam.Populationfile.write("Range\tRepetition\tGeneration\tMoyPrecision\tMoyMateInitialCriterion\t"
                                 "SdPrecisionPopulation\tSdMateInitialCriterion\tMoyAbilityTerritories\t"
                                 "SdAbilityTerritories\n")

    # Run the simulation
    Simulation.RangeLoop(manager, pool)

    pool.close()
    pool.join()
    Time2 = time.time()

    # Close the file
    GenParam.Populationfile.close()

    # Check how many times no one mated in a given simulation
    if Simulation.CountNbOfBreakMale == 0 and Simulation.CountNbOfBreakFemale == 0:
        ScriptAnalyseData.AnalyseDataReady = "Yes"
        print("CountNbOfBreakMale", Simulation.CountNbOfBreakMale,
              "CountNbOfBreakFemale", Simulation.CountNbOfBreakFemale)

        # Save the datafiles
        with open('DATABRUTEAbilityValueByRangeByRepetitionByGeneration.npy', 'wb') as f:
            numpy.save(f, GenParam.AbilityValueByRangeByRepetitionByGeneration)
        with open('DATABRUTEMateChoiceCriterionValueByRangeByRepetitionByGeneration.npy', 'wb') as f:
            numpy.save(f, GenParam.MateChoiceCriterionValueByRangeByRepetitionByGeneration)
        with open('DATABRUTEPrecisionValueByRangeByRepetitionByGeneration.npy', 'wb') as f:
```

```
            numpy.save(f, GenParam.PrecisionValueByRangeByRepetitionByGeneration)
        with open('DATABRUTEFitnessByRangeByRepetitionByGenerationByAbility.npy', 'wb') as f:
            numpy.save(f, GenParam.FitnessByRangeByRepetitionByGenerationByAbility)
        with open('DATABRUTEFitnessByRangeByRepetitionByGenerationByMateChoiceCriterion.npy', 'wb') as
f:
            numpy.save(f, GenParam.FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion)
        with open('DATABRUTEFitnessByRangeByRepetitionByGenerationByPrecision.npy', 'wb') as f:
            numpy.save(f, GenParam.FitnessByRangeByRepetitionByGenerationByPrecision)
        with open('DATABRUTEReprodSuccessByRangeByRepetitionByGenerationByAbility.npy', 'wb') as f:
            numpy.save(f, GenParam.ReprodSuccessByRangeByRepetitionByGenerationByAbility)
        with open('DATABRUTEReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion.npy',
'wb') as f:
            numpy.save(f, GenParam.ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion)
        with open('DATABRUTEReprodSuccessByRangeByRepetitionByGenerationByPrecision.npy', 'wb') as f:
            numpy.save(f, GenParam.ReprodSuccessByRangeByRepetitionByGenerationByPrecision)

    else:
        print("CountNbOfBreakMale", Simulation.CountNbOfBreakMale,
              "CountNbOfBreakFemale", Simulation.CountNbOfBreakFemale)
    Time3 = time.time()
    print("Total Time =", Time3-Time1, "Time Simulation", Time2-Time1, "Time Analyse", Time3-Time2)

if __name__=='__main__':
    manager = mp.Manager()
    pool = mp.Pool(1)  # Number of repetitions that need to be run simultaneously
    print("cpu count:", os.cpu_count())
    main(manager, pool)
```

General Parameters

```
import multiprocessing as mp

Range = mp.Value('i', 10)
FoodPatchNumber = mp.Value('i', 5)
IncreaseVariable = mp.Value('i', 20)

# Data files
malefile = None
femalefile = None
maleterritoryfile = None
Populationfile = None
DistributionAbilityMalefile = None

# Fixed variables
TotalNumberOfSimulation = 1000  # Number of generations
TotalNumberOfScenarioRepetition = 100  # Number of repetitions
MatrixSize = 14  # Size of the matrix long = large
```

```
CostCognitionFactor = 1  # Cost of male cognitive abilities
FertilityFactor = 1  # Female fertility
FemaleNumber = 100  # Number of females nF
MaleNumber = 100  # Number of females nM

# Manipulated variables
ForagingTimeStepNumber = 200  # Number of time steps in the foraging period
MateTimeStepNumber = 200  # Number of time Steps in the mating period
FoodPatchQuality = 100  # Number of food items contained in each patch
MaleAbilityToFindFood = 10  # Maximum number of time steps before a male find food
TimeStepNbCompleteInformation = 5  # Number of time steps needed for females to perfectly assess the
male trait

# Lists including all data needed to run AnalyseData
AbilityValueByRangeByRepetitionByGeneration = []
MateChoiceCriterionValueByRangeByRepetitionByGeneration = []
PrecisionValueByRangeByRepetitionByGeneration = []
FitnessByRangeByRepetitionByGenerationByAbility = []
FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion = []
FitnessByRangeByRepetitionByGenerationByPrecision = []
ReprodSuccessByRangeByRepetitionByGenerationByAbility = []
ReprodSuccessByRangeByRepetitionByGenerationByPrecision = []
ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion = []
```

Simulation

```
import GeneralParameters as GenParam
from functools import partial
import ClassFemale
import ClassMale
import ClassFoodPatch
import ClassEnvironment
import ClassAgentPopulation

sc = 0
r = 0
s = 0
CountNbOfBreakMale = 0
CountNbOfBreakFemale = 0

# Iterations over different environmental conditions
def RangeLoop(manager,pool):
    global sc
    for sc in range(GenParam.Range.value):
        print("RangeNb", sc)
        RepetitionLoop(manager,pool)
```

```
# Run several simulation simultaneously
def Parallelized_function(AbilityValueByRepetitionByGeneration,
                          MateChoiceCriterionValueByRepetitionByGeneration,
                          PrecisionValueByRepetitionByGeneration,
                          FitnessByRepetitionByGenerationByAbility,
                          FitnessByRepetitionByGenerationByMateChoiceCriterion,
                          FitnessByRepetitionByGenerationByPrecision,
                          ReprodSuccessByRepetitionByGenerationByAbility,
                          ReprodSuccessByRepetitionByGenerationByPrecision,
                          ReprodSuccessByRepetitionByGenerationByMateChoiceCriterion, iterable_item):
    # Creation of a population containing a list of males
    MalePopInstance = ClassAgentPopulation.AgentPopulation(ClassMale.Male, GenParam.MaleNumber)
    #print(id(MalePopInstance), " ID male pop intance")
    # Creation of a population containing a list of females
    FemalePopInstance = ClassAgentPopulation.AgentPopulation(ClassFemale.Female,
GenParam.FemaleNumber)
    GenerationLoop(MalePopInstance,
                   FemalePopInstance,
                   AbilityValueByRepetitionByGeneration,
                   MateChoiceCriterionValueByRepetitionByGeneration,
                   PrecisionValueByRepetitionByGeneration,
                   FitnessByRepetitionByGenerationByAbility,
                   FitnessByRepetitionByGenerationByMateChoiceCriterion,
                   FitnessByRepetitionByGenerationByPrecision,
                   ReprodSuccessByRepetitionByGenerationByAbility,
                   ReprodSuccessByRepetitionByGenerationByPrecision,
                   ReprodSuccessByRepetitionByGenerationByMateChoiceCriterion)


def RepetitionLoop(manager,pool):
    global r
    AbilityValueByRepetitionByGeneration = manager.list()
    MateChoiceCriterionValueByRepetitionByGeneration = manager.list()
    PrecisionValueByRepetitionByGeneration = manager.list()
    FitnessByRepetitionByGenerationByAbility = manager.list()
    FitnessByRepetitionByGenerationByMateChoiceCriterion = manager.list()
    FitnessByRepetitionByGenerationByPrecision = manager.list()
    ReprodSuccessByRepetitionByGenerationByAbility = manager.list()
    ReprodSuccessByRepetitionByGenerationByPrecision = manager.list()
    ReprodSuccessByRepetitionByGenerationByMateChoiceCriterion = manager.list()

    func = partial(Parallelized_function,
                   AbilityValueByRepetitionByGeneration,
                   MateChoiceCriterionValueByRepetitionByGeneration,
                   PrecisionValueByRepetitionByGeneration,
                   FitnessByRepetitionByGenerationByAbility,
                   FitnessByRepetitionByGenerationByMateChoiceCriterion,
```

```
                FitnessByRepetitionByGenerationByPrecision,
                ReprodSuccessByRepetitionByGenerationByAbility,
                ReprodSuccessByRepetitionByGenerationByPrecision,
                ReprodSuccessByRepetitionByGenerationByMateChoiceCriterion)
    results = pool.map(func, range(GenParam.TotalNumberOfScenarioRepetition))

    GenParam.FoodPatchNumber.value = GenParam.FoodPatchNumber.value +
GenParam.IncreaseVariable.value


GenParam.AbilityValueByRangeByRepetitionByGeneration.append(AbilityValueByRepetitionByGeneration)

GenParam.MateChoiceCriterionValueByRangeByRepetitionByGeneration.append(MateChoiceCriterionValu
eByRepetitionByGeneration)

GenParam.PrecisionValueByRangeByRepetitionByGeneration.append(PrecisionValueByRepetitionByGenerat
ion)


GenParam.FitnessByRangeByRepetitionByGenerationByAbility.append(FitnessByRepetitionByGenerationBy
Ability)

GenParam.FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion.append(FitnessByRepetitionBy
GenerationByMateChoiceCriterion)

GenParam.FitnessByRangeByRepetitionByGenerationByPrecision.append(FitnessByRepetitionByGeneration
ByPrecision)

    GenParam.ReprodSuccessByRangeByRepetitionByGenerationByAbility.
append(ReprodSuccessByRepetitionByGenerationByAbility)

GenParam.ReprodSuccessByRangeByRepetitionByGenerationByPrecision.append(ReprodSuccessByRepetiti
onByGenerationByPrecision)

GenParam.ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion.append(ReprodSucces
sByRepetitionByGenerationByMateChoiceCriterion)


def GenerationLoop(MalePopInstance,
                FemalePopInstance,
                AbilityValueByRepetitionByGeneration,
                MateChoiceCriterionValueByRepetitionByGeneration,
                PrecisionValueByRepetitionByGeneration,
                FitnessByRepetitionByGenerationByAbility,
                FitnessByRepetitionByGenerationByMateChoiceCriterion,
                FitnessByRepetitionByGenerationByPrecision,
                ReprodSuccessByRepetitionByGenerationByAbility,
                ReprodSuccessByRepetitionByGenerationByPrecision,
```

```
            ReprodSuccessByRepetitionByGenerationByMateChoiceCriterion):
    global s
    global CountNbOfBreakMale
    global CountNbOfBreakFemale

    FitnessByGenerationByAbility = [[] for x in range(GenParam.TotalNumberOfSimulation)]
    FitnessByGenerationByMateChoiceCriterion = [[] for x in range(GenParam.TotalNumberOfSimulation)]
    FitnessByGenerationByPrecision = [[] for x in range(GenParam.TotalNumberOfSimulation)]

    ReprodSuccessByGenerationByAbility = [[] for x in range(GenParam.TotalNumberOfSimulation)]
    ReprodSuccessByGenerationByPrecision = [[] for x in range(GenParam.TotalNumberOfSimulation)]
    ReprodSuccessByGenerationByMateChoiceCriterion = [[] for x in
range(GenParam.TotalNumberOfSimulation)]

    AbilityValueByGeneration = [[] for x in range(GenParam.TotalNumberOfSimulation)]
    MateChoiceCriterionValueByGeneration = [[] for x in range(GenParam.TotalNumberOfSimulation)]
    PrecisionValueByGeneration = [[] for x in range(GenParam.TotalNumberOfSimulation)]

    for s in range(GenParam.TotalNumberOfSimulation):
        # Create the foraging environment
        #print("Generation nb:", s)
        ForagingEnvironmentInstance = ClassEnvironment.Environment() # Creation of an environment
with of patches
        ForagingEnvironmentInstance.CharacterizeTerritory(ClassFoodPatch.FoodPatch,
GenParam.FoodPatchNumber.value)
        ForagingEnvironmentInstance.setInitialPositionTerritoryList()  # Set the localization of each patch

        # Male Foraging period
        MaleSocialForagingTimeLoop(MalePopInstance, ForagingEnvironmentInstance)

        # Create the mating environment
        MateChoiceEnvironmentInstance = ClassEnvironment.Environment()  # Creation of an environment
containing mate
        MateChoiceEnvironmentInstance.CharacterizeTerritoryWithList(MalePopInstance.AgentList)  #
Populate by males
        MateChoiceEnvironmentInstance.AppliedCostCognitionToFitness() # Calculate the foraging success
of each male
        MateChoiceEnvironmentInstance.setInitialPositionTerritoryList()  # Set the localization of each male

        # Female Mating period
        MateChoiceTimeLoop(FemalePopInstance, MateChoiceEnvironmentInstance)

        # List of males' and females' foraging success
        # Males
        FitnessByAbilityList = [[] for x in range(GenParam.MaleAbilityToFindFood+1)]
        #print(id(FitnessByAbilityList), "ID fitness by abilitylist")
        MateChoiceEnvironmentInstance.FitnessByAbility(FitnessByAbilityList)
        #print(FitnessByAbilityList, "FitnessByAbilityList")
```

```
        FitnessByGenerationByAbility[s].append(FitnessByAbilityList)

        # Females
        FitnessByMateChoiceCriterionList = [[] for x in range(GenParam.MaleAbilityToFindFood+1)]
        FemalePopInstance.FitnessByMateChoiceCriterion(FitnessByMateChoiceCriterionList)
        FitnessByGenerationByMateChoiceCriterion[s].append(FitnessByMateChoiceCriterionList)
        FitnessByPrecisionList = [[] for x in range(GenParam.TimeStepNbCompleteInformation+1)]
        FemalePopInstance.FitnessByPrecision(FitnessByPrecisionList)
        FitnessByGenerationByPrecision[s].append(FitnessByPrecisionList)

        # Is Anyone Mated?
        MateChoiceEnvironmentInstance.IsAnyoneMated()  # break if no one is mated
        if MateChoiceEnvironmentInstance.AnyoneMated == False:
           print("Aucun mâle apparié")
           CountNbOfBreakMale = CountNbOfBreakMale + 1
           break
        FemalePopInstance.IsAnyoneMated()
        if FemalePopInstance.AnyoneMated == False:
           print("Aucune femelle appariée")
           CountNbOfBreakFemale = CountNbOfBreakFemale + 1
           break

        CalculateMeanTrait(FemalePopInstance, MateChoiceEnvironmentInstance)
        CalculateFitnessTrait(FemalePopInstance, MateChoiceEnvironmentInstance)

        # List of males' and females' reproductive success
        ReprodSuccessByAbilityList = [[] for x in range(GenParam.MaleAbilityToFindFood + 1)]
        ReprodSuccessByPrecisionList = [[] for x in range(GenParam.TimeStepNbCompleteInformation +
1)]
        ReprodSuccessByMateChoiceCriterionList = [[] for x in range(GenParam.MaleAbilityToFindFood +
1)]
        # Production of offspring
        CreationOfNextGenerationWithHeritableTrait(FemalePopInstance,
                                                   MateChoiceEnvironmentInstance,
                                                   MalePopInstance,
                                                   ReprodSuccessByAbilityList,
                                                   ReprodSuccessByPrecisionList,
                                                   ReprodSuccessByMateChoiceCriterionList)

        ReprodSuccessByGenerationByAbility[s].append(ReprodSuccessByAbilityList)
        ReprodSuccessByGenerationByPrecision[s].append(ReprodSuccessByPrecisionList)

ReprodSuccessByGenerationByMateChoiceCriterion[s].append(ReprodSuccessByMateChoiceCriterionList)
        AbilityValueByGeneration[s].append(MalePopInstance.AbilityValueByRange())

MateChoiceCriterionValueByGeneration[s].append(FemalePopInstance.MateChoiceCriterionValueByRange(
))
        PrecisionValueByGeneration[s].append(FemalePopInstance.PrecisionValueByRange())
```

```
            #print('Current Process:', mp.current_process().name)

    FitnessByRepetitionByGenerationByAbility.append(FitnessByGenerationByAbility)

FitnessByRepetitionByGenerationByMateChoiceCriterion.append(FitnessByGenerationByMateChoiceCriteri
on)
    FitnessByRepetitionByGenerationByPrecision.append(FitnessByGenerationByPrecision)
    ReprodSuccessByRepetitionByGenerationByAbility.append(ReprodSuccessByGenerationByAbility)
    ReprodSuccessByRepetitionByGenerationByPrecision.append(ReprodSuccessByGenerationByPrecision)

ReprodSuccessByRepetitionByGenerationByMateChoiceCriterion.append(ReprodSuccessByGenerationByM
ateChoiceCriterion)
    AbilityValueByRepetitionByGeneration.append(AbilityValueByGeneration)
    MateChoiceCriterionValueByRepetitionByGeneration.append(MateChoiceCriterionValueByGeneration)
    PrecisionValueByRepetitionByGeneration.append(PrecisionValueByGeneration)


def MaleSocialForagingTimeLoop(MalePopInstance, ForagingEnvironmentInstance):
    for ft in range(GenParam.ForagingTimeStepNumber):
        # Update localization of males + check if they are on a food patch
        MalePopInstance.UpdatePositionAgentPopulation(ForagingEnvironmentInstance.TerritoryList)
        # MalePopInstance.PrintAllAgentParameter()
        # ForagingEnvironmentInstance.PrintAllTerritoryParameter()
        # Males consume the food

MalePopInstance.PopulationActionWhenAgentIsOverTerritory(ForagingEnvironmentInstance.TerritoryList)
        #MalePopInstance.SaveAllAgentParameterToFile(sc, r, s, ft, GenParam.malefile)  # Save data in the file


def MateChoiceTimeLoop(FemalePopInstance, MateChoiceEnvironmentInstance):
    global sc
    global r
    global s
    for mt in range(GenParam.MateTimeStepNumber):
        # Update females' localization + check if they are over a male territory
        FemalePopInstance.UpdatePositionAgentPopulation(MateChoiceEnvironmentInstance.TerritoryList)
        # Estimate the male trait + decide to mate or not

FemalePopInstance.PopulationActionWhenAgentIsOverTerritory(MateChoiceEnvironmentInstance.Territory
List)


def CalculateMeanTrait(FemalePopInstance, MateChoiceEnvironmentInstance):
    global sc
    global r
    global s
    FemalePopInstance.CalculateSaveMoyTraitPopulation(sc, r, s, GenParam.Populationfile)
```

```
MateChoiceEnvironmentInstance.CalculateSaveMoyAbilityToFindFoodTerritories(GenParam.Populationfile)


def CalculateFitnessTrait(FemalePopInstance, MateChoiceEnvironmentInstance):
    StatFitnessMale = MateChoiceEnvironmentInstance.CalculateStatFitnessPopulation()
    StatFitnessFemale = FemalePopInstance.CalculateStatFitnessPopulation()
    # Assign individuals a fitness category
    MateChoiceEnvironmentInstance.PopAttributionFitnessCategory(StatFitnessMale)
    FemalePopInstance.PopAttributionFitnessCategory(StatFitnessFemale)


def CreationOfNextGenerationWithHeritableTrait(FemalePopInstance,
                                               MateChoiceEnvironmentInstance,
                                               MalePopInstance,ReprodSuccessByAbilityList,
                                               ReprodSuccessByPrecisionList,
                                               ReprodSuccessByMateChoiceCriterionList):
    # Production of sons and daughters
    PossibleValueOfAbilityToFindFood = MateChoiceEnvironmentInstance.CreationListHeritableTrait()
    MatedFemalePrecisionMatedCriterion = FemalePopInstance.CreationListHeritableTrait()
    # print("List of abilities", PossibleValueOfAbilityToFindFood,
    # "List of Precision and Criterion", MatedFemalePrecisionMatedCriterion
    FemalePopInstance.ReprodSuccessByPrecision(ReprodSuccessByPrecisionList)
    FemalePopInstance.ReprodSuccessByMateChoiceCriterion(ReprodSuccessByMateChoiceCriterionList)
    MateChoiceEnvironmentInstance.ReprodSuccessByAbility(ReprodSuccessByAbilityList)

    # Replace fathers by sons and mothers by daughters for the next generation
    MalePopInstance.ReinitializeAgentPopulation(PossibleValueOfAbilityToFindFood)
    #print("male ability new generation", MalePopInstance.AgentList[0].AbilityToFindFood,
    # "Time to access food", MalePopInstance.AgentList[0].TimeBeforeAccessFood,
    # "quality:", MalePopInstance.AgentList[0].Quality)
    FemalePopInstance.ReinitializeAgentPopulation(MatedFemalePrecisionMatedCriterion)
    # print("Precision new generation", FemalePopInstance.AgentList[0].Precision,
    # "Criterion new generation", FemalePopInstance.AgentList[0].MateInitialCriterion
    list.clear(PossibleValueOfAbilityToFindFood)
    list.clear(MatedFemalePrecisionMatedCriterion[0])
    list.clear(MatedFemalePrecisionMatedCriterion[1])
```

Class Environment

```
import random
import GeneralParameters as GenParam
import numpy as np
from itertools import repeat

class Environment:
    def __init__(self):
        self.TerritoryList = []
        self.AnyoneMated = False
```

```
    def CharacterizeTerritory(self, EnvironmentType, EnvironmentNumber):
        for EnvironmentIndex in range(EnvironmentNumber):
            self.TerritoryList.append(EnvironmentType(EnvironmentIndex + 1))


    def CharacterizeTerritoryWithList(self, TerritoryList):
        self.TerritoryList = TerritoryList


    def AppliedCostCognitionToFitness(self):
        for TerritoryInstance in self.TerritoryList:
            #print("AbilityToFindFood", TerritoryInstance.AbilityToFindFood,
            # "Quality", TerritoryInstance.Quality, "CostCogn", TerritoryInstance.CostCognition)
            if TerritoryInstance.Quality <= (GenParam.CostCognitionFactor*TerritoryInstance.CostCognition):
                TerritoryInstance.Quality = 0
                #print("Quality", TerritoryInstance.Quality)
            else:
                TerritoryInstance.Quality = TerritoryInstance.Quality - \
                                  (GenParam.CostCognitionFactor*TerritoryInstance.CostCognition)
                #print("CostCognitionFactor", GenParam.CostCognitionFactor,
                # "CostCognition", TerritoryInstance.CostCognition, "Quality after CostCogn",
TerritoryInstance.Quality)


    def setInitialPositionTerritoryList(self): # Unique and random position
        Coordinate = [(random.randint(0, GenParam.MatrixSize-1),
                      (random.randint(0, GenParam.MatrixSize-1))) for _ in range(len(self.TerritoryList))]
        UniqueCoordinate = list(set(Coordinate))

        while (len(UniqueCoordinate) < len(self.TerritoryList)):
            UniqueCoordinate.append((random.randint(0, GenParam.MatrixSize-1),
                          (random.randint(0, GenParam.MatrixSize-1))))
            UniqueCoordinate = list(set(UniqueCoordinate))

        for TerritoryInstance in self.TerritoryList:
            TerritoryInstance.Position = list(UniqueCoordinate[TerritoryInstance.ID - 1])


    def getAllTerritoryPosition(self):
        AllTerritoryPosition = []
        for TerritoryInstance in self.TerritoryList:
            AllTerritoryPosition.append(TerritoryInstance.Position)
        return AllTerritoryPosition


    def IsAnyoneMated(self):
        NumberTerritoryMated = 0
```

```
    for TerritoryInstance in self.TerritoryList:
        #print("Male ID", TerritoryInstance.ID, "is available", TerritoryInstance.Availability)

        if TerritoryInstance.Availability == False:
            NumberTerritoryMated = NumberTerritoryMated + 1
            #print("NumberTerritoryMated", NumberTerritoryMated)
            self.AnyoneMated = True
            #print("AnyoneMated", self.AnyoneMated)

    if NumberTerritoryMated == 0:
        self.AnyoneMated = False


def CalculateSaveMoyAbilityToFindFoodTerritories(self, Populationfile):
    AbilityTerritories = []
    #print("AbilityTerritoriesBefore", AbilityTerritories)

    for TerritoryInstance in self.TerritoryList:
        AbilityTerritories.append(TerritoryInstance.AbilityToFindFood)
    MoyAbilityTerritories = sum(AbilityTerritories) / len(AbilityTerritories)
    #print("MoyAbilityTerritories", MoyAbilityTerritories)
    SdAbilityTerritories = sum([((x - MoyAbilityTerritories) ** 2)
                                for x in AbilityTerritories]) / len(AbilityTerritories)
    #print("SdAbilityTerritories", SdAbilityTerritories)
    #Populationfile.write(" "+str(MoyAbilityTerritories)+" "+str(SdAbilityTerritories)+"\n")


def CalculateStatFitnessPopulation(self):
    FitnessPop = []
    FitnessPopPositiveQuality = []
    for TerritoryInstance in self.TerritoryList:
        FitnessPop.append(TerritoryInstance.Quality)
    for IndexQuality in FitnessPop:
        if IndexQuality > 0:
            FitnessPopPositiveQuality.append(IndexQuality)
    #print("FitnessPopListMale", FitnessPopPositiveQuality)
    if len(FitnessPopPositiveQuality) > 0:
        Q1FitnessMale = np.percentile(FitnessPopPositiveQuality, 25, interpolation='midpoint')
        MoyFitnessMale = sum(FitnessPopPositiveQuality) / len(FitnessPopPositiveQuality)
        Q2FitnessMale = np.percentile(FitnessPopPositiveQuality, 75, interpolation='midpoint')
        MaxFitnessMale = max(FitnessPopPositiveQuality)
    else :
        Q1FitnessMale = 0
        MoyFitnessMale = 0
        Q2FitnessMale = 0
        MaxFitnessMale =0
    return Q1FitnessMale, MoyFitnessMale, Q2FitnessMale, MaxFitnessMale
```

```
def PopAttributionFitnessCategory(self, StatFitnessMale):
    for TerritoryInstance in self.TerritoryList:
        TerritoryInstance.AttributionFitnessCategory(StatFitnessMale)


def CreationListHeritableTrait(self):
    SonAbility = []
    for TerritoryInstance in self.TerritoryList:
        if TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory != 0:

            if TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 1:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 1 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                                        (1 * GenParam.FertilityFactor)
            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 2:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 2 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                                        (2 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 3:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 3 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                                        (3 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 4:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 4 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                                        (4 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 5:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 5 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                                        (5 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 6:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 6 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                                        (6 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 7:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 7 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                                        (7 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 8:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 8 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
```

```
                                        (8 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 9:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 9 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                        (9 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 10:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 10 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess +\
                                        (10 * GenParam.FertilityFactor)

            elif TerritoryInstance.Availability == False and TerritoryInstance.FitnessCategory == 11:
                SonAbility.extend(repeat(TerritoryInstance.AbilityToFindFood, 11 * GenParam.FertilityFactor))
                TerritoryInstance.ReproductiveSuccess = TerritoryInstance.ReproductiveSuccess + \
                                        (11 * GenParam.FertilityFactor)
            else:
                raise RuntimeError("error in Reproductive success attribution Male")

    if len(SonAbility) == 0:
        while len(SonAbility) < GenParam.MaleNumber:
            RandomTerritoryInstance = random.choice(self.TerritoryList)
            SonAbility.append(RandomTerritoryInstance.AbilityToFindFood)
    while len(SonAbility) < GenParam.MaleNumber:
        RandomItemFromListCrit = random.choice(SonAbility)
        SonAbility.append(RandomItemFromListCrit)
    while len(SonAbility) > GenParam.MaleNumber:
        RandomItemFromListCrit = random.choice(SonAbility)
        SonAbility.remove(RandomItemFromListCrit)
    return SonAbility


def getAllTerritoryQuality(self):
    AllTerritoryQuality = []
    for TerritoryInstance in self.TerritoryList:
        AllTerritoryQuality.append(TerritoryInstance.Quality)
    return AllTerritoryQuality


def PrintAllTerritoryParameter(self):
    for TerritoryInstance in self.TerritoryList:
        print(TerritoryInstance)


def SaveAllTerritoryParameterToFile(self, Range, Repetition, SimulationNb, TimeStep, Territoryfile):
    for TerritoryInstance in self.TerritoryList:
        Territoryfile.write(str(Range)+"\t\t"+
                  str(Repetition)+"\t\t"+
```

```
                                str(SimulationNb) + "\t\t" +
                                str(TimeStep) + "\t\t" +
                                str(TerritoryInstance))


    def FitnessByAbility(self, FitnessByAbilityList):
        for TerritoryInstance in self.TerritoryList:
            FitnessByAbilityList[TerritoryInstance.AbilityToFindFood].append(TerritoryInstance.Quality)
            #print("male num", TerritoryInstance.ID,
            # " with ability",TerritoryInstance.AbilityToFindFood, "and quality", TerritoryInstance.Quality)


    def ReprodSuccessByAbility(self, ReprodSuccessByAbilityList):
        for TerritoryInstance in self.TerritoryList:

ReprodSuccessByAbilityList[TerritoryInstance.AbilityToFindFood].append(TerritoryInstance.ReproductiveSu
ccess)
```

Class Agent

```
import random
import GeneralParameters as GenParam
import numpy as np
from itertools import repeat
import math

class AgentPopulation:
    def __init__(self, AgentType, AgentNumber):
        self.AgentList = []
        self.CharacterizeAgentPopulation(AgentType, AgentNumber)
        self.AnyoneMated = False


    def CharacterizeAgentPopulation(self, AgentType, AgentNumber):
        for AgentIndex in range(AgentNumber):
            self.AgentList.append(AgentType(AgentIndex + 1))


    def UpdatePositionAgentPopulation(self, TerritoryList):
        for AgentInstance in self.AgentList:
            AgentInstance.UpdatePosition(TerritoryList)
            AgentInstance.IsAgentOverTerritory(TerritoryList)


    def getAllAgentPosition(self):
        AllAgentPosition = []
        for AgentInstance in self.AgentList:
```

```
            AllAgentPosition.append(AgentInstance.Position)
        return AllAgentPosition


    def PopulationActionWhenAgentIsOverTerritory(self, TerritoryList):
        for AgentInstance in self.AgentList:
            if AgentInstance.AgentOverTerritory == True:
                #print("True")
                AgentInstance.ActionWhenAgentIsOverTerritory(TerritoryList)


    def AttributeAgentPopulationWithMalePosition(self,TerritoryList):
        for AgentInstance in self.AgentList:
            AgentInstance.AttributeMalePosition(TerritoryList)


    def IsAnyoneMated(self):
        NumberAgentMated = 0
        for AgentInstance in self.AgentList:
            #print("Female ID", AgentInstance.ID, "is mated", AgentInstance.FoundMate)

            if AgentInstance.FoundMate == True:
                NumberAgentMated = NumberAgentMated + 1
                #print("NumberAgentMated", NumberAgentMated)
                self.AnyoneMated = True
                #print("AnyoneMated", self.AnyoneMated)

        if NumberAgentMated == 0:
            self.AnyoneMated = False


    def CalculateSaveMoyTraitPopulation(self, Scenario, Repetition, SimulationNb, Populationfile):
        PrecisionPopulation = []
        MateInitialCriterionPopulation = []
        MoyPrecisionPopulation = 0
        MoyMateInitialCriterionPopulation = 0
        SdPrecisionPopulation = 0
        SdMateInitialCriterionPopulation = 0
        #print("PrecisionPopulationBefore", PrecisionPopulation)
        for AgentInstance in self.AgentList:
            PrecisionPopulation.append(AgentInstance.Precision)
            MateInitialCriterionPopulation.append(AgentInstance.MateInitialCriterion)
        MoyPrecisionPopulation = sum(PrecisionPopulation)/ len(PrecisionPopulation)
        #print("MoyPrecisionPopulation", MoyPrecisionPopulation)
        MoyMateInitialCriterionPopulation =
sum(MateInitialCriterionPopulation)/len(MateInitialCriterionPopulation)
        #print("MoyMateInitialCriterionPopulation", MoyMateInitialCriterionPopulation)
        SdPrecisionPopulation = math.sqrt(sum([((x - MoyPrecisionPopulation) ** 2) for x in
```

```
PrecisionPopulation]) / len(PrecisionPopulation))
        #print("SdPrecisionPopulation", SdPrecisionPopulation)
        SdMateInitialCriterionPopulation = math.sqrt(sum([((x - MoyMateInitialCriterionPopulation) ** 2) for x in MateInitialCriterionPopulation])\
                                          / len(MateInitialCriterionPopulation))
        #print("SdMateInitialCriterionPopulation", SdMateInitialCriterionPopulation)
        #Populationfile.write(str(Scenario)+" "+str(Repetition)+" "+str(SimulationNb)+" "+str(MoyPrecisionPopulation)+
        #                      " "+str(MoyMateInitialCriterionPopulation)+" "+str(SdPrecisionPopulation)+" "
        #                      +str(SdMateInitialCriterionPopulation))

    #def CalculateSaveDataFitnessPrecisionPopulation(self):
    #    FitnessPop = []
    #    for AgentInstance in self.AgentList:
    #        FitnessPop.append(AgentInstance.Quality)


    def CalculateStatFitnessPopulation(self):
        FitnessPop = []
        FitnessPopPositiveQuality = []
        for AgentInstance in self.AgentList:
            FitnessPop.append(AgentInstance.Quality)
        for IndexQuality in FitnessPop:
            if IndexQuality > 0:
                FitnessPopPositiveQuality.append(IndexQuality)
        # print("FitnessPopListfemale", FitnessPopPositiveQuality)
        if len(FitnessPopPositiveQuality) > 0:
            Q1FitnessFemale = np.percentile(FitnessPopPositiveQuality, 25, interpolation='midpoint')
            MoyFitnessFemale = sum(FitnessPopPositiveQuality) / len(FitnessPopPositiveQuality)
            Q2FitnessFemale = np.percentile(FitnessPopPositiveQuality, 75, interpolation='midpoint')
            MaxFitnessFemale = max(FitnessPopPositiveQuality)
        else :
            Q1FitnessFemale = 0
            MoyFitnessFemale = 0
            Q2FitnessFemale = 0
            MaxFitnessFemale = 0
        return Q1FitnessFemale, MoyFitnessFemale, Q2FitnessFemale, MaxFitnessFemale


    def PopAttributionFitnessCategory(self, StatFitnessFemale):
        for AgentInstance in self.AgentList:
            AgentInstance.AttributionFitnessCategory(StatFitnessFemale)


    def CreationListHeritableTrait(self):
        DaughterPrecision = []
        DaughterCriterion = []
        for AgentInstance in self.AgentList:
```

```
            if AgentInstance.FoundMate == True and AgentInstance.FitnessCategory != 0:

                if AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 1:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 1 * GenParam.FertilityFactor))
                    #print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 1 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (1 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 2:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 2 * GenParam.FertilityFactor))
                    #print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 2 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (2 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 3:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 3 * GenParam.FertilityFactor))
                    #print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 3 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (3 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 4:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 4 * GenParam.FertilityFactor))
                    #print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 4 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (4 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 5:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 5 * GenParam.FertilityFactor))
                    # print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 5 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (5 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 6:
```

```
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 6 * GenParam.FertilityFactor))
                    # print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 6 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (6 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 7:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 7 * GenParam.FertilityFactor))
                    # print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 7 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (7 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 8:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 8 * GenParam.FertilityFactor))
                    # print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 8 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (8 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 9:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 9 * GenParam.FertilityFactor))
                    # print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 9 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (9 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 10:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 10 * GenParam.FertilityFactor))
                    # print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 10 *
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess + \
                                                        (10 * GenParam.FertilityFactor)

                elif AgentInstance.FoundMate == True and AgentInstance.FitnessCategory == 11:
                    DaughterPrecision.extend(repeat(AgentInstance.Precision, 11 * GenParam.FertilityFactor))
                    # print("List of daughters precision", DaughterPrecision)
                    DaughterCriterion.extend(repeat(AgentInstance.MateInitialCriterion, 11 *
```

```
GenParam.FertilityFactor))
                    # print("List of daughters selectivity", DaughterCriterion)
                    AgentInstance.ReproductiveSuccess = AgentInstance.ReproductiveSuccess +\
                                                        (11 * GenParam.FertilityFactor)
                else:
                    raise RuntimeError("error in Reproductive success attribution Female")

        if len(DaughterPrecision) == 0 and len(DaughterCriterion) == 0:
            while len(DaughterPrecision) < GenParam.FemaleNumber and len(DaughterCriterion) <
GenParam.FemaleNumber:
                RandomAgentInstance = random.choice(self.AgentList)
                DaughterPrecision.append(RandomAgentInstance.Precision)
                DaughterCriterion.append(RandomAgentInstance.MateInitialCriterion)

        while len(DaughterPrecision) < GenParam.FemaleNumber and len(DaughterCriterion) <
GenParam.FemaleNumber:
            #print("length list of daughters precision", len(DaughterPrecision),
            # "and length list of daughters selectivity", len(DaughterCriterion))
            RandomItemFromListCrit = random.choice(DaughterCriterion)
            DaughterCriterion.append(RandomItemFromListCrit)
            RandomItemFromListPrec = random.choice(DaughterPrecision)
            DaughterPrecision.append(RandomItemFromListPrec)
            #print("RandomItemFromListPrec", RandomItemFromListPrec)
            #print("list of daughters precision", DaughterPrecision)
            #print("length", len(DaughterPrecision))

        while len(DaughterPrecision) > GenParam.FemaleNumber and len(DaughterCriterion) >
GenParam.FemaleNumber:
            #print("length list daughter precision", len(DaughterPrecision),
            # "and length list daughterCriterion",len(DaughterCriterion))
            RandomItemFromListCrit = random.choice(DaughterCriterion)
            DaughterCriterion.remove(RandomItemFromListCrit)
            RandomItemFromListPrec = random.choice(DaughterPrecision)
            DaughterPrecision.remove(RandomItemFromListPrec)
            #print("RandomItemFromListPrec", RandomItemFromListPrec)
            #print("list of daughters precision", DaughterPrecision)
            #print("length", len(DaughterPrecision))
        return DaughterPrecision, DaughterCriterion


    def ReinitializeAgentPopulation(self, ListHeritableTrait):
        for AgentInstance in self.AgentList:
            AgentInstance.EvolutionaryUpdateCharacteristic(ListHeritableTrait)


    def PrintAllAgentParameter (self):
        for AgentInstance in self.AgentList:
            print(AgentInstance)
```

```
    def SaveAllAgentParameterToFile(self, Range, Repetition, SimulationNb, TimeStep, Agentfile):
        for AgentInstance in self.AgentList:
            Agentfile.write(str(Range)+"\t\t"+
                            str(Repetition)+"\t\t"+
                            str(SimulationNb)+"\t\t"+
                            str(TimeStep)+"\t\t"+
                            str(AgentInstance))


    def MateChoiceCriterionValueByRange(self):
        MateChoiceCriterionValueList = []
        for AgentInstance in self.AgentList:
            MateChoiceCriterionValueList.append(AgentInstance.MateInitialCriterion)
        return MateChoiceCriterionValueList


    def AbilityValueByRange(self):
        AbilityValueByRangeList = []
        for AgentInstance in self.AgentList:
            AbilityValueByRangeList.append(AgentInstance.AbilityToFindFood)
        return AbilityValueByRangeList


    def PrecisionValueByRange(self, ):
        PrecisionValueList = []
        for AgentInstance in self.AgentList:
            PrecisionValueList.append(AgentInstance.Precision)
        return PrecisionValueList


    def FitnessByMateChoiceCriterion(self, FitnessByMateChoiceCriterionList):
        for AgentInstance in self.AgentList:

FitnessByMateChoiceCriterionList[AgentInstance.MateInitialCriterion].append(AgentInstance.Quality)


    def FitnessByPrecision(self, FitnessByPrecisionList):
        for AgentInstance in self.AgentList:
            FitnessByPrecisionList[AgentInstance.Precision].append(AgentInstance.Quality)


    def ReprodSuccessByMateChoiceCriterion(self, ReprodSuccessByMateChoiceCriterionList):
        for AgentInstance in self.AgentList:

ReprodSuccessByMateChoiceCriterionList[AgentInstance.MateInitialCriterion].append(AgentInstance.Repro
ductiveSuccess)
```

```


    def ReprodSuccessByPrecision(self, ReprodSuccessByPrecisionList):
        for AgentInstance in self.AgentList:

ReprodSuccessByPrecisionList[AgentInstance.Precision].append(AgentInstance.ReproductiveSuccess)
```

Class Food Patch

```
import GeneralParameters as GenParam

class FoodPatch:
    def __init__(self, ID):
        self.ID = ID
        self.Position = []
        self.Quality = GenParam.FoodPatchQuality
        self.Availability = True


    def __str__(self):
           return 'FoodPatch(ID='+str(self.ID)+', Position='+str(self.Position)+\
                  ', nombre item de nourriture disponible = '+str(self.Quality)+ ')'
```

Class Male

```
import random
import GeneralParameters as GenParam

class Male:
    def __init__(self, ID):
        self.ID = ID
        self.Position = []
        self.setInitialPosition()
        self.Quality = 0
        #self.setCognition()  # Attribution of a cognitive ability score for the male instance
        self.AgentOverTerritory = False
        self.TerritoryVisited = ()
        self.AgentOverWhichIndexTerritory = 0
        self.Availability = True
        self.AbilityToFindFood = self.setInitialAbilityToFindFood()
        self.TimeBeforeAccessFood = 0
        self.FitnessCategory = 0
        self.ReproductiveSuccess = 0
        self.CostCognition = self.setInitialCostCognition()


```

```
    def __str__(self):
        return str(self.ID)+"\t\t"+str(self.Quality)+"\t\t"+str(self.AbilityToFindFood)+"\t\t"\
              +str(self.Availability)+"\t\t"+str(self.ReproductiveSuccess)+'\n'


    def setInitialPosition(self):
        self.Position = [random.randint(0, GenParam.MatrixSize - 1), random.randint(0, GenParam.MatrixSize -
1)]


    #Characterization of males when they are an AgentPop (during foraging period)
    # and an Environment component (during mating period) ###
    def setPosition(self, x, y):
        self.Position.clear()
        self.Position = [x, y]


    def setInitialAbilityToFindFood(self):
        return random.randint(0, GenParam.MaleAbilityToFindFood)


    def setInitialCostCognition(self):
        return (GenParam.MaleAbilityToFindFood - self.AbilityToFindFood)


    def AttributionFitnessCategory(self, StatFitnessMale):
        if self.Quality <= 0:
            self.FitnessCategory = 0
        elif 1 <= self.Quality <= 10:
            self.FitnessCategory = 1
        elif 11 <= self.Quality <= 20:
            self.FitnessCategory = 2
        elif 21 <= self.Quality <= 30:
            self.FitnessCategory = 3
        elif 31 <= self.Quality <= 40:
            self.FitnessCategory = 4
        elif 41 <= self.Quality <= 50:
            self.FitnessCategory = 5
        elif 51 <= self.Quality <= 60:
            self.FitnessCategory = 6
        elif 61 <= self.Quality <= 70:
            self.FitnessCategory = 7
        elif 71 <= self.Quality <= 80:
            self.FitnessCategory = 8
        elif 81 <= self.Quality <= 90:
            self.FitnessCategory = 9
        elif 91 <= self.Quality <= 100:
            self.FitnessCategory = 10
```

```
    elif 101 <= self.Quality:
        self.FitnessCategory = 11
    else:
        raise RuntimeError("error fitness Category male")
    #print("maleID", self.ID, "male fitness category", self.FitnessCategory)
    return self.FitnessCategory


def EvolutionaryUpdateCharacteristic(self, ListHeritableTrait):
    IndexAbilityToFindFood = random.randint(0, len(ListHeritableTrait)-1)
    #print("IndexAbilityToFindFood", IndexAbilityToFindFood, "ListHeritableTrait", len(ListHeritableTrait))
    self.AbilityToFindFood = ListHeritableTrait.pop(IndexAbilityToFindFood)
    #print("ability to find food of the new generation", self.AbilityToFindFood,
    # "list of hertiable trait", ListHeritableTrait)
    self.setInitialPosition()
    self.Quality = 0
    self.AgentOverTerritory = False
    self.AgentOverWhichIndexTerritory = 0
    self.Availability = True
    self.TerritoryVisited = ()
    self.TimeBeforeAccessFood = 0
    self.FitnessCategory = 0
    self.ReproductiveSuccess = 0


### Characterization of males when they are an AgentPop component (During foraging period) ###
def UpdatePosition(self, TerritoryList):
    if self.AgentOverTerritory == False:
        # Random Walk for males
        DirectionPosition = random.randint(1, 4)  # create an object with 25% of chance to be chosen
        if DirectionPosition == 1:  # if this object is equivalent to 1
            self.Position[0] += -1  # Move the given female to the left to one unit
            if self.Position[0] < 0:  # if the updated Position[0] is outboard the matrix
                self.Position[0] = (GenParam.MatrixSize - 1)  # Move the female to the other side of the matrix
        elif DirectionPosition == 2:  # if this object is equivalent to 2
            self.Position[0] += 1  # Move the given female to the right to one unit
            if self.Position[0] > (GenParam.MatrixSize - 1):  # if the updated Position[0] is outboard the matrix
                self.Position[0] = 0  # Move the female to the other side of the matrix
        elif DirectionPosition == 3:  # if this object is equivalent to 3
            self.Position[1] += -1  # Move down the given female  to one unit
            if self.Position[1] < 0:  # if the updated Position[1] is outboard the matrix
                self.Position[1] = (GenParam.MatrixSize - 1)  # Move the female along the top of the matrix
        elif DirectionPosition == 4:  # if this object is equivalent to 4
            self.Position[1] += 1  # Move up the given female to one unit
            if self.Position[1] > (GenParam.MatrixSize - 1):  # if the updated Position[0] is outboard the matrix
                self.Position[1] = 0  # Move the female to the other side of the matrix
        else:
            raise RuntimeError("error Direction position male")
```

```
    def IsAgentOverTerritory(self, TerritoryList):
        for TerritoryInstance in TerritoryList:
            if self.Position == TerritoryInstance.Position and TerritoryInstance.Availability == True:
                self.AgentOverTerritory = True
                self.AgentOverWhichIndexTerritory = TerritoryInstance.ID - 1
                #print("I am over a territory", self.IsAgentOverTerritory, " Patch nb",
                #self.AgentOverWhichIndexTerritory, "containing", TerritoryInstance.Quality, "food items",
                #"at", TerritoryInstance.Position)


    def ActionWhenAgentIsOverTerritory(self, TerritoryList):
        if TerritoryList[self.AgentOverWhichIndexTerritory].Quality > 0:
            if self.TimeBeforeAccessFood < self.AbilityToFindFood:
                self.TimeBeforeAccessFood += 1
                #print("i am the agent", self.ID, " i am wating :", self.TimeBeforeAccessFood, "before eat")
            else:
                TerritoryList[self.AgentOverWhichIndexTerritory].Quality -= 1
                #print(" patch nb :", TerritoryList[self.AgentOverWhichIndexTerritory].ID,
                # ", i have :", TerritoryList[self.AgentOverWhichIndexTerritory].Quality, "food item left")
                self.Quality += 1
                #print(" because the agent", self.ID, " ate", self.Quality, "food item")
        else:
            self.AgentOverTerritory = False
            #print("i am the agent", self.ID, "i am not eating anymore")
            #print("now i am here", self.Position, " i ate ", self.Quality, "food items")
            self.TimeBeforeAccessFood = 0
            Coordinate = 0
            CoordinateIsUnique = False
            while not (CoordinateIsUnique):
                CoordinateIsUnique = False
                Coordinate = [random.randint(0, GenParam.MatrixSize - 1),
                              (random.randint(0, GenParam.MatrixSize - 1))]
                for TerritoryInstance in TerritoryList:
                    if Coordinate == TerritoryInstance.Position:
                        break
                    else:
                        CoordinateIsUnique = True
            TerritoryList[self.AgentOverWhichIndexTerritory].Position = Coordinate
            TerritoryList[self.AgentOverWhichIndexTerritory].Quality = GenParam.FoodPatchQuality
            # print("TerritoryID=", TerritoryInstance.ID, "containing", TerritoryInstance.Quality,
            # "food item, its localization is ", TerritoryInstance.Position,
            # "is it available?", TerritoryInstance.Availability)
```

Class Female

```
import random
import GeneralParameters as GenParam

class Female:
    def __init__(self, ID):
        self.ID = ID
        self.Position = []
        self.setInitialPosition()
        self.Precision = self.DefinePrecision()
        self.FoundMate = False
        self.AgentOverTerritory = False
        self.TerritoryVisited = []
        self.AgentOverWhichIndexTerritory = 0
        self.AgentOverWhichTerritoryID = 0
        self.TimeInFrontOfMate = 0
        self.EstimateMate = ()
        self.MateInitialCriterion = self.setMateInitialCriterion()
        self.Quality = 0
        self.FitnessCategory = 0
        self.ReproductiveSuccess = 0


    def __str__(self):
        return str(self.ID)+"\t\t"+\
               str(self.Precision)+"\t\t"+\
               str(self.MateInitialCriterion)+"\t\t"+\
               str(self.EstimateMate)+"\t\t"+\
               str(self.FoundMate)+"\t\t"+\
               str(self.Quality)+"\t\t"+\
               str(self.ReproductiveSuccess)+'\n'


    def setInitialPosition(self):
        self.Position = [random.randint(0, GenParam.MatrixSize - 1), random.randint(0, GenParam.MatrixSize -
1)]


    def AttributeMalePosition(self, TerritoryList):
        MaleIndex = random.randint(0, len(TerritoryList) - 1)
        self.Position = TerritoryList[MaleIndex].Position


    def DefinePrecision(self):
        Precision = random.randint(1, GenParam.TimeStepNbCompleteInformation)
        return Precision


    def setMateInitialCriterion(self):
```

```
        setMateInitialCriterion = random.randint(0, GenParam.MaleAbilityToFindFood)
        return setMateInitialCriterion


    def AttributionFitnessCategory(self, StatFitnessFemale):
        if self.Quality <=0:
            self.FitnessCategory = 0
        elif 1 <= self.Quality <= 10:
            self.FitnessCategory = 1
        elif 11 <= self.Quality <= 20:
            self.FitnessCategory = 2
        elif 21 <= self.Quality <= 30:
            self.FitnessCategory = 3
        elif 31 <= self.Quality <= 40:
            self.FitnessCategory = 4
        elif 41 <= self.Quality <= 50:
            self.FitnessCategory = 5
        elif 51 <= self.Quality <= 60:
            self.FitnessCategory = 6
        elif 61 <= self.Quality <= 70:
            self.FitnessCategory = 7
        elif 71 <= self.Quality <= 80:
            self.FitnessCategory = 8
        elif 81 <= self.Quality <= 90:
            self.FitnessCategory = 9
        elif 91 <= self.Quality <= 100:
            self.FitnessCategory = 10
        elif 101 <= self.Quality:
            self.FitnessCategory = 11
        else:
            raise RuntimeError("error fitness Category female")
        #print("femaleID", self.ID, "female fitness category", self.FitnessCategory)
        return self.FitnessCategory


    def EvolutionaryUpdateCharacteristic(self, ListHeritableTrait):
        IndexPrecision = random.randint(0, len(ListHeritableTrait[0])-1)
        #print("index precision", IndexPrecision)
        self.Precision = ListHeritableTrait[0].pop(IndexPrecision)
        #print("precision ListHeritableTrait", ListHeritableTrait[0], "Precision selected", self.Precision)
        IndexCriterion = random.randint(0, len(ListHeritableTrait[1])-1)
        #print("Index criterion", IndexCriterion)
        self.MateInitialCriterion = ListHeritableTrait[1].pop(IndexCriterion)
        #print("criterion ListHeritableTrait", ListHeritableTrait[1], "Criterion selected", self.MateInitialCriterion)
        self.setInitialPosition()
        self.FoundMate = False
        self.AgentOverTerritory = False
        self.TerritoryVisited = []
```

```
        self.AgentOverWhichIndexTerritory = 0
        self.AgentOverWhichTerritoryID = []
        self.TimeInFrontOfMate = 0
        self.EstimateMate = ()
        self.Quality = 0
        self.FitnessCategory = 0
        self.ReproductiveSuccess = 0


    def UpdatePosition(self, TerritoryList):
        MaleIndex = []
        #print("TerritoryVisited", self.TerritoryVisited)
        if self.TerritoryVisited != None:
            for TerritoryInstance in TerritoryList:
                if self.Position == TerritoryInstance.Position and TerritoryInstance.Availability == True:
                    self.AgentOverWhichTerritoryID = TerritoryInstance.ID
                    #print("AgentOverWhichTerritoryID", self.AgentOverWhichTerritoryID,
                    # "TerritoryInstance.ID", TerritoryInstance.ID)
            for MateVisitID in self.TerritoryVisited:
                #print("TerritoryVisited list", self.TerritoryVisited, "MateVisitIndex", MateVisitID)
                if MateVisitID == self.AgentOverWhichTerritoryID and self.FoundMate == False:
                    #print("MateVisitIndex",MateVisitID, "AgentOverWhichTerritoryID",
self.AgentOverWhichTerritoryID)
                    MaleIndex = random.randint(0, len(TerritoryList)-1)
                    #print("MaleIndex", MaleIndex)
                    self.Position = TerritoryList[MaleIndex].Position
                    #print("localization of the female", self.Position,
                    # "localization of the male", TerritoryList[MaleIndex].Position)


    def IsAgentOverTerritory(self, TerritoryList):
        for TerritoryInstance in TerritoryList:
            if self.Position == TerritoryInstance.Position and TerritoryInstance.Availability == True:
                self.AgentOverTerritory = True
                self.AgentOverWhichIndexTerritory = TerritoryInstance.ID - 1
                #print("I am over a territory", self.AgentOverTerritory, " Patch nb",
                #self.AgentOverWhichIndexTerritory, "containing", TerritoryInstance.Quality, "seeds",
                # "at", TerritoryInstance.Position)


### For simulation WITHOUT Sexual selection, use this function : females mate with the first male
encounter
    #def ActionWhenAgentIsOverTerritory(self, TerritoryList): #
    #   if self.AgentOverTerritory == True:
    #       self.FoundMate = True
    #       TerritoryList[self.AgentOverWhichIndexTerritory].Availability = False
    #       #print("i found a mate :",  self.FoundMate, " the male is not available anymore rigth?",
    #       TerritoryList[self.AgentOverWhichIndexTerritory].Availability)
```

```
    #       self.Quality = TerritoryList[self.AgentOverWhichIndexTerritory].Quality


### For simulation WITH Sexual selection, use this function : females prefer males with good cognitive abilities
    def ActionWhenAgentIsOverTerritory(self, TerritoryList): #
        if self.TimeInFrontOfMate < self.Precision and self.FoundMate == False:
            #print("i am the female nb", self.ID, "my precision = ", self.Precision,
            # "i am in front of a male since", self.TimeInFrontOfMate, "time step ")
            self.TimeInFrontOfMate += 1
        else:
            HeadsOrTails = random.randint(0, 1)

            if HeadsOrTails == 0:
                self.EstimateMate = TerritoryList[self.AgentOverWhichIndexTerritory].AbilityToFindFood -\
                                    (GenParam.TimeStepNbCompleteInformation - self.Precision)
            else:
                self.EstimateMate = TerritoryList[self.AgentOverWhichIndexTerritory].AbilityToFindFood +\
                                    (GenParam.TimeStepNbCompleteInformation - self.Precision)
            #print("i estimate him as = ", self.EstimateMate," 0 =- et 1 = + ", HeadsOrTails,
            # "with an error of:",ErrorEstimation,
            # "in reality his quality is ", TerritoryList[self.AgentOverWhichIndexTerritory].AbilityToFindFood)

            if self.EstimateMate <= self.MateInitialCriterion:
                self.FoundMate = True
                TerritoryList[self.AgentOverWhichIndexTerritory].Availability = False
                #print("i found a mate :",  self.FoundMate,
                # "is the male still available?", TerritoryList[self.AgentOverWhichIndexTerritory].Availability)
                self.Quality = TerritoryList[self.AgentOverWhichIndexTerritory].Quality
            else:
                self.AgentOverTerritory = False
                self.TimeInFrontOfMate = 0
                self.TerritoryVisited.append(self.AgentOverWhichTerritoryID)
                self.EstimateMate = ()
                #print("TerritoryVisited", self.TerritoryVisited,
                # "AgentOverWhichTerritoryID", self.AgentOverWhichTerritoryID)
```

Main Data Analysis

```
import AnalyseData
import numpy


def main():
    #Scenario.SetScenarioNumber(GenParam.SelectedScenario)

    #Ouverture des fichiers outputs
```

```
DisctributionMaleAbilityfile = open('DisctributionMaleAbilityfile.txt', 'w')
DisctributionMaleAbilityfile.write("Range\t"
                                   "Population\t"
                                   "Generation\t"
                                   "Male\t"
                                   "AbilityToFindFood\n")

DisctributionFemaleCriterionfile = open('DisctributionFemaleCriterionfile.txt', 'w')
DisctributionFemaleCriterionfile.write("Range\t"
                                       "Population\t"
                                       "Generation\t"
                                       "Female\t"
                                       "Criterion\n")

DisctributionFemalePrecisionfile = open('DisctributionFemalePrecisionfile.txt', 'w')
DisctributionFemalePrecisionfile.write("Range\t"
                                       "Population\t"
                                       "Generation\t"
                                       "Female\t"
                                       "Precision\n")

InterPopAnalyseParameterEffectfile = open('InterPopAnalyseParameterEffect.txt', 'w')
InterPopAnalyseParameterEffectfile.write("Range\t"
                                         "InterPopulation50GenerationMeanAbility\t"
                                         "InterPopulation50GenerationSdAbility\t"
                                         "IntraPopulation50GenerationMeanSdAbility\t"
                                         "InterPopulation50GenerationMeanCriterion\t"
                                         "InterPopulation50GenerationSdCriterion\t"
                                         "IntraPopulation50GenerationMeanSdCriterion\t"
                                         "InterPopulation50GenerationMeanPrecision\t"
                                         "InterPopulation50GenerationSdPrecision\t"
                                         "IntraPopulation50GenerationMeanSdPrecision\n")

IntraPopAnalyseParameterEffectfile = open('IntraPopAnalyseParameterEffect.txt', 'w')
IntraPopAnalyseParameterEffectfile.write("Range\t"
                                         "Population\t"
                                         "IntraPopulation50GenerationMeanAbility\t"
                                         "IntraPopulation50GenerationSdAbility\t"
                                         "IntraPopulation50GenerationMeanCriterion\t"
                                         "IntraPopulation50GenerationSdCriterion\t"
                                         "IntraPopulation50GenerationMeanPrecision\t"
                                         "IntraPopulation50GenerationSdPrecision\n")

IntraGenAnalyseParameterEffectfile = open('IntraGenAnalyseParameterEffect.txt', 'w')
IntraGenAnalyseParameterEffectfile.write("Range\t"
                                         "Population\t"
                                         "Generation\t"
                                         "IntraGenerationMeanAbility\t"
```

```
                                        "IntraGenerationSdAbility\t"
                                        "IntraGenerationMeanCriterion\t"
                                        "IntraGenerationSdCriterion\t"
                                        "IntraGenerationMeanPrecision\t"
                                        "IntraGenerationSdPrecision\n")

    InterPopAnalyseParameterEffectBeginningfile = open('InterPopAnalyseParameterEffectBeginning.txt',
'w')
    InterPopAnalyseParameterEffectBeginningfile.write("Range\t"
                                                "InterPopulation50GenerationMeanAbility\t"
                                                "InterPopulation50GenerationSdAbility\t"
                                                "IntraPopulation50GenerationMeanSdAbility\t"
                                                "InterPopulation50GenerationMeanCriterion\t"
                                                "InterPopulation50GenerationSdCriterion\t"
                                                "IntraPopulation50GenerationMeanSdCriterion\t"
                                                "InterPopulation50GenerationMeanPrecision\t"
                                                "InterPopulation50GenerationSdPrecision\t"
                                                "IntraPopulation50GenerationMeanSdPrecision\n")

    IntraPopAnalyseParameterEffectBeginningfile = open('IntraPopAnalyseParameterEffectBeginning.txt',
'w')
    IntraPopAnalyseParameterEffectBeginningfile.write("Range\t"
                                                "Population\t"
                                                "IntraPopulation50GenerationMeanAbility\t"
                                                "IntraPopulation50GenerationSdAbility\t"
                                                "IntraPopulation50GenerationMeanCriterion\t"
                                                "IntraPopulation50GenerationSdCriterion\t"
                                                "IntraPopulation50GenerationMeanPrecision\t"
                                                "IntraPopulation50GenerationSdPrecision\n")

    IntraGenAnalyseParameterEffectBeginningfile = open('IntraGenAnalyseParameterEffectBeginning.txt',
'w')
    IntraGenAnalyseParameterEffectBeginningfile.write("Range\t"
                                                "Population\t"
                                                "Generation\t"
                                                "IntraGenerationMeanAbility\t"
                                                "IntraGenerationSdAbility\t"
                                                "IntraGenerationMeanCriterion\t"
                                                "IntraGenerationSdCriterion\t"
                                                "IntraGenerationMeanPrecision\t"
                                                "IntraGenerationSdPrecision\n")

    AnalyseParameterEffectfile = open('AnalyseParameterEffect.txt', 'w')
    AnalyseParameterEffectfile.write("Range\t"
                                  "MeanAbility\t"
                                  "SdAbility\t"
                                  "MeanCriterion\t"
                                  "SdCriterion\t"
```

```
                        "MeanPrecision\t"
                        "SdPrecision\n")

    AnalyseLinkFitnessMaleTraitEvolutionFile = open('AnalyseLinkFitnessMaleTraitEvolution.txt', 'w')
    AnalyseLinkFitnessMaleTraitEvolutionFile.write("Range\t"
                                 "Generation\t"
                                 "AbilityToFindFoodCategory\t"
                                 "MeanQuality\t"
                                 "SdQuality\n")

    AnalyseLinkFitnessFemaleCriterionEvolutionFile = open('AnalyseLinkFitnessFemaleCriterionEvolution.txt',
'w')
    AnalyseLinkFitnessFemaleCriterionEvolutionFile.write("Range\t"
                                     "Generation\t"
                                     "MateInitialCriterionCategory\t"
                                     "MeanQualitybyMateInitialCriterion\t"
                                     "SdQualitybyMateInitialCriterion\n")

    AnalyseLinkFitnessFemalePrecisionEvolutionFile =
open('AnalyseLinkFitnessFemalePrecisionEvolution.txt', 'w')
    AnalyseLinkFitnessFemalePrecisionEvolutionFile.write("Range\t"
                                     "Generation\t"
                                     "PrecisionCategory\t"
                                     "MeanQualitybyPrecision\t"
                                     "SdQualitybyPrecision\n")

    AnalyseLinkSRMaleTraitEvolutionFile = open('AnalyseLinkSRMaleTraitEvolution.txt', 'w')
    AnalyseLinkSRMaleTraitEvolutionFile.write("Range\t"
                             "Generation\t"
                             "AbilityToFindFoodCategory\t"
                             "MeanReprodSuccess\t"
                             "SdReprodSuccess\n")

    AnalyseLinkSRFemaleCriterionEvolutionFile = open('AnalyseLinkSRFemaleCriterionEvolutionFile.txt', 'w')
    AnalyseLinkSRFemaleCriterionEvolutionFile.write("Range\t"
                                 "Generation\t"
                                 "MateInitialCriterionCategory\t"
                                 "MeanReprodSuccess\t"
                                 "SdReprodSuccess\n")

    AnalyseLinkSRFemalePrecisionEvolutionFile = open('AnalyseLinkSRFemalePrecisionEvolution.txt', 'w')
    AnalyseLinkSRFemalePrecisionEvolutionFile.write("Range\t"
                                 "Generation\t"
                                 "PrecisionCategory\t"
                                 "MeanReprodSuccess\t"
                                 "SdReprodSuccess\n")
```

```
     #Calculate and save mean trait values across all ranges of the parameters
    with open('DATABRUTEAbilityValueByRangeByRepetitionByGeneration.npy', 'rb') as f:
        AbilityValueByRangeByRepetitionByGeneration = numpy.load(f, allow_pickle=True)
    with open('DATABRUTEMateChoiceCriterionValueByRangeByRepetitionByGeneration.npy', 'rb') as f:
        MateChoiceCriterionValueByRangeByRepetitionByGeneration = numpy.load(f, allow_pickle=True)
    with open('DATABRUTEPrecisionValueByRangeByRepetitionByGeneration.npy', 'rb') as f:
        PrecisionValueByRangeByRepetitionByGeneration = numpy.load(f, allow_pickle=True)
    with open('DATABRUTEFitnessByRangeByRepetitionByGenerationByAbility.npy', 'rb') as f:
        FitnessByRangeByRepetitionByGenerationByAbility = numpy.load(f, allow_pickle=True)
    with open('DATABRUTEFitnessByRangeByRepetitionByGenerationByMateChoiceCriterion.npy', 'rb') as f:
        FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion = numpy.load(f, allow_pickle=True)
    with open('DATABRUTEFitnessByRangeByRepetitionByGenerationByPrecision.npy', 'rb') as f:
        FitnessByRangeByRepetitionByGenerationByPrecision = numpy.load(f, allow_pickle=True)
    with open('DATABRUTEReprodSuccessByRangeByRepetitionByGenerationByAbility.npy', 'rb') as f:
        ReprodSuccessByRangeByRepetitionByGenerationByAbility = numpy.load(f, allow_pickle=True)
    with open('DATABRUTEReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion.npy',
'rb') as f:
        ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion = numpy.load(f,
allow_pickle=True)
    with open('DATABRUTEReprodSuccessByRangeByRepetitionByGenerationByPrecision.npy', 'rb') as f:
        ReprodSuccessByRangeByRepetitionByGenerationByPrecision = numpy.load(f, allow_pickle=True)

    # Calculate and save the final data
    AnalyseData.AnalyseParameterEffect(AbilityValueByRangeByRepetitionByGeneration.tolist(),
                                       MateChoiceCriterionValueByRangeByRepetitionByGeneration.tolist(),
                                       PrecisionValueByRangeByRepetitionByGeneration.tolist(),
                                       IntraGenAnalyseParameterEffectfile,
                                       IntraPopAnalyseParameterEffectfile,
                                       InterPopAnalyseParameterEffectfile)
    print("bla1")

    AnalyseData.AnalyseParameterEffectBeginning(AbilityValueByRangeByRepetitionByGeneration.tolist(),
                                                MateChoiceCriterionValueByRangeByRepetitionByGeneration.tolist(),
                                                PrecisionValueByRangeByRepetitionByGeneration.tolist(),
                                                IntraGenAnalyseParameterEffectBeginningfile,
                                                IntraPopAnalyseParameterEffectBeginningfile,
                                                InterPopAnalyseParameterEffectBeginningfile)
    print("bla2")

    AnalyseData.MeanFitnessMaleByAbility(FitnessByRangeByRepetitionByGenerationByAbility.tolist(),
                                         AnalyseLinkFitnessMaleTraitEvolutionFile)
    print("bla3")


AnalyseData.AnalyseLinkFitnessFemaleCriterion(FitnessByRangeByRepetitionByGenerationByMateChoiceCr
iterion.tolist(),
                                                  AnalyseLinkFitnessFemaleCriterionEvolutionFile)
```

```
AnalyseData.AnalyseLinkFitnessFemalePrecision(FitnessByRangeByRepetitionByGenerationByPrecision.tolis
t(),
                                                  AnalyseLinkFitnessFemalePrecisionEvolutionFile)

AnalyseData.AnalyseLinkReprodSuccessMaleTrait(ReprodSuccessByRangeByRepetitionByGenerationByAbili
ty.tolist(),
                                                  AnalyseLinkSRMaleTraitEvolutionFile)

AnalyseData.AnalyseLinkReprodSuccessFemaleCriterion(ReprodSuccessByRangeByRepetitionByGeneration
ByMateChoiceCriterion.tolist(),
                                                        AnalyseLinkSRFemaleCriterionEvolutionFile)
    print("bla4")


AnalyseData.AnalyseLinkReprodSuccessFemalePrecision(ReprodSuccessByRangeByRepetitionByGeneration
ByPrecision.tolist(),
                                                        AnalyseLinkSRFemalePrecisionEvolutionFile)
    AnalyseData.DistributionMaleAbility(AbilityValueByRangeByRepetitionByGeneration.tolist(),
                                        DisctributionMaleAbilityfile)
    print("bla5")


AnalyseData.DistributionFemaleCriterion(MateChoiceCriterionValueByRangeByRepetitionByGeneration.toli
st(),
                                            DisctributionFemaleCriterionfile)
    print("bla6")

    AnalyseData.DistributionFemalePrecision(PrecisionValueByRangeByRepetitionByGeneration.tolist(),
                                            DisctributionFemalePrecisionfile)


if __name__ == '__main__':
    main()
```

Data Analysis

```
import GeneralParameters as GenParam
import math

def DistributionMaleAbility(
        AbilityValueByRangeByRepetitionByGeneration,
        DisctributionMaleAbilityfile):
    for sc in range(GenParam.Range.value):
        for r in range(GenParam.TotalNumberOfScenarioRepetition):
            for s in range(GenParam.TotalNumberOfSimulation):
                for MaleIndex in range(GenParam.MaleNumber):
                    Ability = AbilityValueByRangeByRepetitionByGeneration[sc][r][s][0][MaleIndex]
                    DisctributionMaleAbilityfile.write(str(sc) + "\t" +
```

```
                            str(r) + "\t" +
                            str(s) + "\t" +
                            str(MaleIndex) + "\t" +
                            str(Ability) +"\n")


def DistributionFemaleCriterion(
    MateChoiceCriterionValueByRangeByRepetitionByGeneration,
    DisctributionFemaleCriterionfile):
  for sc in range(GenParam.Range.value):
    for r in range(GenParam.TotalNumberOfScenarioRepetition):
      for s in range(GenParam.TotalNumberOfSimulation):
        for FemaleIndex in range(GenParam.FemaleNumber):
          Criterion = MateChoiceCriterionValueByRangeByRepetitionByGeneration[sc][r][s][0][FemaleIndex]
          DisctributionFemaleCriterionfile.write(str(sc) + "\t" +
                              str(r) + "\t" +
                              str(s) + "\t" +
                              str(FemaleIndex) + "\t" +
                              str(Criterion) +"\n")



def DistributionFemalePrecision(
    PrecisionValueByRangeByRepetitionByGeneration,
    DisctributionFemalePrecisionfile):
  for sc in range(GenParam.Range.value):
    for r in range(GenParam.TotalNumberOfScenarioRepetition):
      for s in range(GenParam.TotalNumberOfSimulation):
        for FemaleIndex in range(GenParam.FemaleNumber):
          Precision = PrecisionValueByRangeByRepetitionByGeneration[sc][r][s][0][FemaleIndex]
          DisctributionFemalePrecisionfile.write(str(sc) + "\t" +
                              str(r) + "\t" +
                              str(s) + "\t" +
                              str(FemaleIndex) + "\t" +
                              str(Precision) +"\n")



def AnalyseParameterEffect(
    AbilityValueByRangeByRepetitionByGeneration,
    MateChoiceCriterionValueByRangeByRepetitionByGeneration,
    PrecisionValueByRangeByRepetitionByGeneration,
    IntraGenAnalyseParameterEffectfile,
    IntraPopAnalyseParameterEffectfile,
    InterPopAnalyseParameterEffectfile):
  for sc in range(GenParam.Range.value):
    IntraPopulation50GenerationMeanAbilityList = []
    IntraPopulation50GenerationSdAbilityList = []
```

```
IntraPopulation50GenerationMeanCriterionList = []
IntraPopulation50GenerationSdCriterionList = []
IntraPopulation50GenerationPrecisionList = []
IntraPopulation50GenerationSdPrecisionList = []
for r in range(GenParam.TotalNumberOfScenarioRepetition):
    IntraGenerationMeanAbilityList = []
    IntraGenerationSdAbilityList = []
    IntraGenerationMeanCriterionList = []
    IntraGenerationSdCriterionList = []
    IntraGenerationMeanPrecisionList = []
    IntraGenerationSdPrecisionList = []
    for s in range((GenParam.TotalNumberOfSimulation-50), GenParam.TotalNumberOfSimulation):
        AbilityList = AbilityValueByRangeByRepetitionByGeneration[sc][r][s][0]
        #print(AbilityList)
        IntraGenerationSumAbility = sum(AbilityList)
        # print(len(AbilityValueByRangeByRepetitionByGeneration[sc][r][s]))
        IntraGenerationMeanAbility = IntraGenerationSumAbility / len(AbilityList)
        IntraGenerationMeanAbilityList.append(IntraGenerationMeanAbility)
        IntraGenerationSdAbility = math.sqrt(sum([((x - IntraGenerationMeanAbility) ** 2)
                                  for x in AbilityList]) / len(AbilityList))
        IntraGenerationSdAbilityList.append(IntraGenerationSdAbility)

        CriterionList = MateChoiceCriterionValueByRangeByRepetitionByGeneration[sc][r][s][0]
        IntraGenerationSumCriterion = sum(CriterionList)
        # print(len(MateChoiceCriterionValueByRangeByRepetitionByGeneration[sc][r][s]))
        IntraGenerationMeanCriterion = IntraGenerationSumCriterion / len(CriterionList)
        IntraGenerationMeanCriterionList.append(IntraGenerationMeanCriterion)
        IntraGenerationSdCriterion = math.sqrt(sum([((x - IntraGenerationMeanCriterion) ** 2)
                                    for x in CriterionList]) / len(CriterionList))
        IntraGenerationSdCriterionList.append(IntraGenerationSdCriterion)

        PrecisionList = PrecisionValueByRangeByRepetitionByGeneration[sc][r][s][0]
        IntraGenerationSumPrecision = sum(PrecisionList)
        # print(len(PrecisionValueByRangeByRepetitionByGeneration[sc][r][s]))
        IntraGenerationMeanPrecision = IntraGenerationSumPrecision / len(PrecisionList)
        IntraGenerationMeanPrecisionList.append(IntraGenerationMeanPrecision)
        IntraGenerationSdPrecision = math.sqrt(sum([((x - IntraGenerationMeanPrecision) ** 2)
                                    for x in PrecisionList]) / len(PrecisionList))
        IntraGenerationSdPrecisionList.append(IntraGenerationSdPrecision)
        IntraGenAnalyseParameterEffectfile.write(str(sc) + "\t" +
                                  str(r) + "\t" +
                                  str(s) + "\t" +
                                  str(IntraGenerationMeanAbility) + "\t" +
                                  str(IntraGenerationSdAbility) + "\t" +
                                  str(IntraGenerationMeanCriterion) + "\t" +
                                  str(IntraGenerationSdCriterion) + "\t" +
                                  str(IntraGenerationMeanPrecision) + "\t" +
                                  str(IntraGenerationSdPrecision) + "\n")
```

```
       IntraPopulation50GenerationMeanAbility = sum(IntraGenerationMeanAbilityList) / \
                               len(IntraGenerationMeanAbilityList)
       IntraPopulation50GenerationMeanAbilityList.append(IntraPopulation50GenerationMeanAbility)
       IntraPopulation50GenerationSdAbility = sum(IntraGenerationSdAbilityList) / \
                              len(IntraGenerationSdAbilityList)
       IntraPopulation50GenerationSdAbilityList.append(IntraPopulation50GenerationSdAbility)

       IntraPopulation50GenerationMeanCriterion = sum(IntraGenerationMeanCriterionList) / \
                                len(IntraGenerationMeanCriterionList)

IntraPopulation50GenerationMeanCriterionList.append(IntraPopulation50GenerationMeanCriterion)
       IntraPopulation50GenerationSdCriterion = sum(IntraGenerationSdCriterionList) / \
                               len(IntraGenerationSdCriterionList)
       IntraPopulation50GenerationSdCriterionList.append(IntraPopulation50GenerationSdCriterion)

       IntraPopulation50GenerationPrecision = sum(IntraGenerationMeanPrecisionList) / \
                              len(IntraGenerationMeanPrecisionList)
       IntraPopulation50GenerationPrecisionList.append(IntraPopulation50GenerationPrecision)
       IntraPopulation50GenerationSdPrecision = sum(IntraGenerationSdPrecisionList) / \
                               len(IntraGenerationSdPrecisionList)
       IntraPopulation50GenerationSdPrecisionList.append(IntraPopulation50GenerationSdPrecision)

       IntraPopAnalyseParameterEffectfile.write(str(sc) + "\t" +
                               str(r) + "\t" +
                               str(IntraPopulation50GenerationMeanAbility) + "\t" +
                               str(IntraPopulation50GenerationSdAbility) + "\t" +
                               str(IntraPopulation50GenerationMeanCriterion) + "\t" +
                               str(IntraPopulation50GenerationSdCriterion) + "\t" +
                               str(IntraPopulation50GenerationPrecision) + "\t" +
                               str(IntraPopulation50GenerationSdPrecision) + "\n")

     InterPopulation50GenerationMeanAbility = sum(IntraPopulation50GenerationMeanAbilityList) / \
                             len(IntraPopulation50GenerationMeanAbilityList)
     InterPopulation50GenerationSdAbility = math.sqrt(sum([((x -
InterPopulation50GenerationMeanAbility) ** 2)
                                    for x in IntraPopulation50GenerationMeanAbilityList]) /
                                 len(IntraPopulation50GenerationMeanAbilityList))
     IntraPopulation50GenerationMeanSdAbility = sum(IntraPopulation50GenerationSdAbilityList) / \
                              len(IntraPopulation50GenerationSdAbilityList)

     InterPopulation50GenerationMeanCriterion = sum(IntraPopulation50GenerationMeanCriterionList) / \
                              len(IntraPopulation50GenerationMeanCriterionList)
     InterPopulation50GenerationSdCriterion = math.sqrt(sum([((x -
InterPopulation50GenerationMeanCriterion) ** 2)
                                     for x in IntraPopulation50GenerationMeanCriterionList])/
                                  len(IntraPopulation50GenerationMeanCriterionList))
     IntraPopulation50GenerationMeanSdCriterion = sum(IntraPopulation50GenerationSdCriterionList) / \
```

```
                                  len(IntraPopulation50GenerationSdCriterionList)

        InterPopulation50GenerationMeanPrecision = sum(IntraPopulation50GenerationPrecisionList) / \
                                 len(IntraPopulation50GenerationPrecisionList)
        InterPopulation50GenerationSdPrecision = math.sqrt(sum([((x -
InterPopulation50GenerationMeanPrecision) ** 2)
                                         for x in IntraPopulation50GenerationPrecisionList]) /
                                      len(IntraPopulation50GenerationPrecisionList))
        IntraPopulation50GenerationMeanSdPrecision = sum(IntraPopulation50GenerationSdPrecisionList) / \
                                  len(IntraPopulation50GenerationSdPrecisionList)

        InterPopAnalyseParameterEffectfile.write(str(sc) + "\t" +
                                str(InterPopulation50GenerationMeanAbility) + "\t" +
                                str(InterPopulation50GenerationSdAbility) + "\t" +
                                str(IntraPopulation50GenerationMeanSdAbility) + "\t" +
                                str(InterPopulation50GenerationMeanCriterion) + "\t" +
                                str(InterPopulation50GenerationSdCriterion) + "\t" +
                                str(IntraPopulation50GenerationMeanSdCriterion) + "\t" +
                                str(InterPopulation50GenerationMeanPrecision) + "\t" +
                                str(InterPopulation50GenerationSdPrecision) + "\t" +
                                str(IntraPopulation50GenerationMeanSdPrecision) + "\n")

    IntraGenAnalyseParameterEffectfile.close()
    IntraPopAnalyseParameterEffectfile.close()
    InterPopAnalyseParameterEffectfile.close()



def AnalyseParameterEffectBeginning(
        AbilityValueByRangeByRepetitionByGeneration,
        MateChoiceCriterionValueByRangeByRepetitionByGeneration,
        PrecisionValueByRangeByRepetitionByGeneration,
        IntraGenAnalyseParameterEffectBeginningfile,
        IntraPopAnalyseParameterEffectBeginningfile,
        InterPopAnalyseParameterEffectBeginningfile):
    for sc in range(GenParam.Range.value):
        IntraPopulation50GenerationMeanAbilityList = []
        IntraPopulation50GenerationSdAbilityList = []
        IntraPopulation50GenerationMeanCriterionList = []
        IntraPopulation50GenerationSdCriterionList = []
        IntraPopulation50GenerationPrecisionList = []
        IntraPopulation50GenerationSdPrecisionList = []
        for r in range(GenParam.TotalNumberOfScenarioRepetition):
            IntraGenerationMeanAbilityList = []
            IntraGenerationSdAbilityList = []
            IntraGenerationMeanCriterionList = []
            IntraGenerationSdCriterionList = []
            IntraGenerationMeanPrecisionList = []
```

```
IntraGenerationSdPrecisionList = []
for s in range(50):
    AbilityList = AbilityValueByRangeByRepetitionByGeneration[sc][r][s][0]
    # print(AbilityList)
    IntraGenerationSumAbility = sum(AbilityList)
    # print(len(AbilityValueByRangeByRepetitionByGeneration[sc][r][s]))
    IntraGenerationMeanAbility = IntraGenerationSumAbility / len(AbilityList)
    IntraGenerationMeanAbilityList.append(IntraGenerationMeanAbility)
    IntraGenerationSdAbility = math.sqrt(sum([((x - IntraGenerationMeanAbility) ** 2)
                             for x in AbilityList]) / len(AbilityList))
    IntraGenerationSdAbilityList.append(IntraGenerationSdAbility)

    CriterionList = MateChoiceCriterionValueByRangeByRepetitionByGeneration[sc][r][s][0]
    IntraGenerationSumCriterion = sum(CriterionList)
    # print(len(MateChoiceCriterionValueByRangeByRepetitionByGeneration[sc][r][s]))
    IntraGenerationMeanCriterion = IntraGenerationSumCriterion / len(CriterionList)
    IntraGenerationMeanCriterionList.append(IntraGenerationMeanCriterion)
    IntraGenerationSdCriterion = math.sqrt(sum([((x - IntraGenerationMeanCriterion) ** 2)
                              for x in CriterionList]) / len(CriterionList))
    IntraGenerationSdCriterionList.append(IntraGenerationSdCriterion)

    PrecisionList = PrecisionValueByRangeByRepetitionByGeneration[sc][r][s][0]
    IntraGenerationSumPrecision = sum(PrecisionList)
    # print(len(PrecisionValueByRangeByRepetitionByGeneration[sc][r][s]))
    IntraGenerationMeanPrecision = IntraGenerationSumPrecision / len(PrecisionList)
    IntraGenerationMeanPrecisionList.append(IntraGenerationMeanPrecision)
    IntraGenerationSdPrecision = math.sqrt(sum([((x - IntraGenerationMeanPrecision) ** 2)
                              for x in PrecisionList]) / len(PrecisionList))
    IntraGenerationSdPrecisionList.append(IntraGenerationSdPrecision)

    IntraGenAnalyseParameterEffectBeginningfile.write(str(sc) + "\t" +
                                  str(r) + "\t" +
                                  str(s) + "\t" +
                                  str(IntraGenerationMeanAbility) + "\t" +
                                  str(IntraGenerationSdAbility) + "\t" +
                                  str(IntraGenerationMeanCriterion) + "\t" +
                                  str(IntraGenerationSdCriterion) + "\t" +
                                  str(IntraGenerationMeanPrecision) + "\t" +
                                  str(IntraGenerationSdPrecision) + "\n")

IntraPopulation50GenerationMeanAbility = sum(IntraGenerationMeanAbilityList) / \
                          len(IntraGenerationMeanAbilityList)
IntraPopulation50GenerationMeanAbilityList.append(IntraPopulation50GenerationMeanAbility)
IntraPopulation50GenerationSdAbility = sum(IntraGenerationSdAbilityList) / \
                        len(IntraGenerationSdAbilityList)
IntraPopulation50GenerationSdAbilityList.append(IntraPopulation50GenerationSdAbility)
IntraPopulation50GenerationMeanCriterion = sum(IntraGenerationMeanCriterionList) / \
                           len(IntraGenerationMeanCriterionList)
```

```
IntraPopulation50GenerationMeanCriterionList.append(IntraPopulation50GenerationMeanCriterion)
      IntraPopulation50GenerationSdCriterion = sum(IntraGenerationSdCriterionList) / \
                           len(IntraGenerationSdCriterionList)
      IntraPopulation50GenerationSdCriterionList.append(IntraPopulation50GenerationSdCriterion)
      IntraPopulation50GenerationPrecision = sum(IntraGenerationMeanPrecisionList) /\
                          len(IntraGenerationMeanPrecisionList)
      IntraPopulation50GenerationPrecisionList.append(IntraPopulation50GenerationPrecision)
      IntraPopulation50GenerationSdPrecision = sum(IntraGenerationSdPrecisionList) / \
                           len(IntraGenerationSdPrecisionList)
      IntraPopulation50GenerationSdPrecisionList.append(IntraPopulation50GenerationSdPrecision)

      IntraPopAnalyseParameterEffectBeginningfile.write(str(sc) + "\t" +
                               str(r) + "\t" +
                               str(IntraPopulation50GenerationMeanAbility) + "\t" +
                               str(IntraPopulation50GenerationSdAbility) + "\t" +
                               str(IntraPopulation50GenerationMeanCriterion) + "\t" +
                               str(IntraPopulation50GenerationSdCriterion) + "\t" +
                               str(IntraPopulation50GenerationPrecision) + "\t" +
                               str(IntraPopulation50GenerationSdPrecision) + "\n")

    InterPopulation50GenerationMeanAbility = sum(IntraPopulation50GenerationMeanAbilityList) / \
                         len(IntraPopulation50GenerationMeanAbilityList)
    InterPopulation50GenerationSdAbility = math.sqrt(sum([((x -
InterPopulation50GenerationMeanAbility) ** 2)
                               for x in IntraPopulation50GenerationMeanAbilityList]) /
                             len(IntraPopulation50GenerationMeanAbilityList))
    IntraPopulation50GenerationMeanSdAbility = sum(IntraPopulation50GenerationSdAbilityList) / \
                          len(IntraPopulation50GenerationSdAbilityList)
    InterPopulation50GenerationMeanCriterion = sum(IntraPopulation50GenerationMeanCriterionList) / \
                          len(IntraPopulation50GenerationMeanCriterionList)
    InterPopulation50GenerationSdCriterion = math.sqrt(sum([((x -
InterPopulation50GenerationMeanCriterion) ** 2)
                                for x in IntraPopulation50GenerationMeanCriterionList])
                              / len(IntraPopulation50GenerationMeanCriterionList))
    IntraPopulation50GenerationMeanSdCriterion = sum(IntraPopulation50GenerationSdCriterionList) / \
                           len(IntraPopulation50GenerationSdCriterionList)
    InterPopulation50GenerationMeanPrecision = sum(IntraPopulation50GenerationPrecisionList) / \
                          len(IntraPopulation50GenerationPrecisionList)
    InterPopulation50GenerationSdPrecision = math.sqrt(sum([((x -
InterPopulation50GenerationMeanPrecision) ** 2)
                                for x in IntraPopulation50GenerationPrecisionList]) /
                              len(IntraPopulation50GenerationPrecisionList))
    IntraPopulation50GenerationMeanSdPrecision = sum(IntraPopulation50GenerationSdPrecisionList) / \
                           len(IntraPopulation50GenerationSdPrecisionList)

    InterPopAnalyseParameterEffectBeginningfile.write(str(sc) + "\t" +
                             str(InterPopulation50GenerationMeanAbility) + "\t" +
```

```
                                                          str(InterPopulation50GenerationSdAbility) + "\t" +
                                                          str(IntraPopulation50GenerationMeanSdAbility) + "\t" +
                                                          str(InterPopulation50GenerationMeanCriterion) + "\t" +
                                                          str(InterPopulation50GenerationSdCriterion) + "\t" +
                                                          str(IntraPopulation50GenerationMeanSdCriterion) + "\t" +
                                                          str(InterPopulation50GenerationMeanPrecision) + "\t" +
                                                          str(InterPopulation50GenerationSdPrecision) + "\t" +
                                                          str(IntraPopulation50GenerationMeanSdPrecision) + "\n")

    IntraGenAnalyseParameterEffectBeginningfile.close()
    IntraPopAnalyseParameterEffectBeginningfile.close()
    InterPopAnalyseParameterEffectBeginningfile.close()



def MeanFitnessMaleByAbility(
        FitnessByRangeByRepetitionByGenerationByAbility,
        AnalyseLinkFitnessMaleTraitEvolutionFile):
    MeanSDQualityOverRepetition = []
    for sc in range(GenParam.Range.value):
        MeanSDQualityOverRepetition.append([])
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanSDQualityOverRepetition[sc].append([])
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanSDQualityOverRepetition[sc][s].append([])
                for AbilityIndex in range(GenParam.MaleAbilityToFindFood+1):
                    MeanSDQualityOverRepetition[sc][s][r].append([])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanList = []
                SdList = []
                for AbilityIndex in range(GenParam.MaleAbilityToFindFood+1):
                    if len(FitnessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]) != 0:
                        SumQuality =
sum(FitnessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex])
                        #print(len(FitnessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]))
                        MeanQuality = SumQuality/\
                                      len(FitnessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex])
                        MeanList.append(MeanQuality)
                        SdQuality = math.sqrt(sum([((x - MeanQuality) ** 2) for x in
FitnessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]]) /
len(FitnessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]))
                        SdList.append(SdQuality)
                        MeanSDQualityOverRepetition[sc][s][r][AbilityIndex].append(MeanQuality)
                        MeanSDQualityOverRepetition[sc][s][r][AbilityIndex].append(SdQuality)
                        #print(MeanSDQualityOverRepetition[sc][s][r][AbilityIndex])
                    else:
```

```
                        MeanSDQualityOverRepetition[sc][s][r][AbilityIndex].append(0)
                        MeanSDQualityOverRepetition[sc][s][r][AbilityIndex].append(0)
                        #print(MeanSDQualityOverRepetition[sc][s][r][AbilityIndex])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanList = []
            SdList = []
            for AbilityIndex in range(GenParam.MaleAbilityToFindFood+1):
                SumMeanQuality = 0
                SumSDQuality = 0
                for r in range(GenParam.TotalNumberOfScenarioRepetition):
                    SumMeanQuality = SumMeanQuality +
MeanSDQualityOverRepetition[sc][s][r][AbilityIndex][0]
                    SumSDQuality = SumSDQuality + MeanSDQualityOverRepetition[sc][s][r][AbilityIndex][1]
                    #print(SumMeanQuality)
                    #print(SumSDQuality)
                MeanMeanQuality = SumMeanQuality / (GenParam.TotalNumberOfScenarioRepetition)
                MeanList.append(MeanMeanQuality)
                MeanSdQuality = SumSDQuality / (GenParam.TotalNumberOfScenarioRepetition)
                SdList.append(MeanSdQuality)
                AnalyseLinkFitnessMaleTraitEvolutionFile.write(str(sc) + "\t" +
                                                               str(s) + "\t" +
                                                               str(AbilityIndex) + "\t" +
                                                               str(MeanMeanQuality) + "\t" +
                                                               str(MeanSdQuality) + "\n")

    AnalyseLinkFitnessMaleTraitEvolutionFile.close()



def AnalyseLinkFitnessFemaleCriterion(
        FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion,
        AnalyseLinkFitnessFemaleCriterionEvolutionFile):
    MeanSDCriterionOverRepetition = []
    for sc in range(GenParam.Range.value):
        MeanSDCriterionOverRepetition.append([])
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanSDCriterionOverRepetition[sc].append([])
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanSDCriterionOverRepetition[sc][s].append([])
                for CriterionIndex in range(GenParam.MaleAbilityToFindFood+1):
                    MeanSDCriterionOverRepetition[sc][s][r].append([])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanList = []
                SdList = []
                for CriterionIndex in range(GenParam.MaleAbilityToFindFood+1):
```

```
                    if
len(FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex]) != 0:
                        SumQuality =
sum(FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex])

#print(len(FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][AbilityIndex]))
                        MeanQuality =
SumQuality/len(FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex
])
                        #MeanList.append(MeanQuality)
                        SdQuality = math.sqrt(sum([((x - MeanQuality) ** 2) for x in
FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex]]) /
len(FitnessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex]))
                        #SdList.append(SdQuality)
                        MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex].append(MeanQuality)
                        MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex].append(SdQuality)
                        #print(MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex])

                    else:
                        MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex].append(0)
                        MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex].append(0)
                        #print(MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanList = []
            SdList = []
            for CriterionIndex in range(GenParam.MaleAbilityToFindFood+1):
                SumMeanQuality = 0
                SumSDQuality = 0
                for r in range(GenParam.TotalNumberOfScenarioRepetition):
                    SumMeanQuality = SumMeanQuality +
MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex][0]
                    SumSDQuality = SumSDQuality + MeanSDCriterionOverRepetition[sc][s][r][CriterionIndex][1]
                    #print(SumMeanQuality)
                    #print(SumSDQuality)
                MeanMeanQuality = SumMeanQuality / (GenParam.TotalNumberOfScenarioRepetition)
                MeanList.append(MeanMeanQuality)
                MeanSdQuality = SumSDQuality / (GenParam.TotalNumberOfScenarioRepetition)
                SdList.append(MeanSdQuality)
                AnalyseLinkFitnessFemaleCriterionEvolutionFile.write(str(sc) + "\t" +
                                                                     str(s) + "\t" +
                                                                     str(CriterionIndex) + "\t" +
                                                                     str(MeanMeanQuality) + "\t" +
                                                                     str(MeanSdQuality) + "\n")
    AnalyseLinkFitnessFemaleCriterionEvolutionFile.close()
```

```
def AnalyseLinkFitnessFemalePrecision(
        FitnessByRangeByRepetitionByGenerationByPrecision,
        AnalyseLinkFitnessFemalePrecisionEvolutionFile):
    MeanSDPrecisionOverRepetition = []
    for sc in range(GenParam.Range.value):
        MeanSDPrecisionOverRepetition.append([])
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanSDPrecisionOverRepetition[sc].append([])
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanSDPrecisionOverRepetition[sc][s].append([])
                for PrecisionIndex in range(GenParam.TimeStepNbCompleteInformation+1):
                    MeanSDPrecisionOverRepetition[sc][s][r].append([])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanList = []
                SdList = []
                for PrecisionIndex in range(GenParam.TimeStepNbCompleteInformation+1):
                    if len(FitnessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex]) != 0:
                        SumQuality =
sum(FitnessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex])
                        #print(len(FitnessByRangeByRepetitionByGenerationByPrecision[sc][0][s][0][PrecisionIndex]))
                        MeanQuality =
SumQuality/len(FitnessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex])
                        #MeanList.append(MeanQuality)
                        SdQuality = math.sqrt(sum([((x - MeanQuality) ** 2) for x in
FitnessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex]]) /
len(FitnessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex]))
                        #SdList.append(SdQuality)
                        MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(MeanQuality)
                        MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(SdQuality)
                        #print(MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex])
                    else:
                        MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(0)
                        MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(0)
                        #print(MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanList = []
            SdList = []
            for PrecisionIndex in range(1, GenParam.TimeStepNbCompleteInformation +1):
                SumMeanQuality = 0
                SumSDQuality = 0
                for r in range(GenParam.TotalNumberOfScenarioRepetition):
                    SumMeanQuality = SumMeanQuality +
MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex][0]
                    SumSDQuality = SumSDQuality + MeanSDPrecisionOverRepetition[sc][s][r][PrecisionIndex][1]
```

```
                    #print(SumMeanQuality)
                    #print(SumSDQuality)
                MeanMeanQuality = SumMeanQuality / (GenParam.TotalNumberOfScenarioRepetition)
                MeanList.append(MeanMeanQuality)
                MeanSdQuality = SumSDQuality / (GenParam.TotalNumberOfScenarioRepetition)
                SdList.append(MeanSdQuality)
                AnalyseLinkFitnessFemalePrecisionEvolutionFile.write(str(sc) + "\t" +
                                                                    str(s) + "\t" +
                                                                    str(PrecisionIndex) + "\t" +
                                                                    str(MeanMeanQuality) + "\t" +
                                                                    str(MeanSdQuality) + "\n")
    AnalyseLinkFitnessFemalePrecisionEvolutionFile.close()



def AnalyseLinkReprodSuccessMaleTrait(
        ReprodSuccessByRangeByRepetitionByGenerationByAbility,
        AnalyseLinkSRMaleTraitEvolutionFile):
    MeanSDReprodMaleOverRepetition = []
    for sc in range(GenParam.Range.value):
        MeanSDReprodMaleOverRepetition.append([])
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanSDReprodMaleOverRepetition[sc].append([])
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanSDReprodMaleOverRepetition[sc][s].append([])
                for PrecisionIndex in range(GenParam.MaleAbilityToFindFood+1):
                    MeanSDReprodMaleOverRepetition[sc][s][r].append([])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanList = []
                SdList = []
                for AbilityIndex in range(GenParam.MaleAbilityToFindFood+1):
                    if len(ReprodSuccessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]) != 0:
                        SumReprodSuccess =
sum(ReprodSuccessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex])

#print(len(ReprodSuccessByRangeByRepetitionByGenerationByAbility[sc][0][s][0][AbilityIndex]))
                        MeanReprodSuccess =
SumReprodSuccess/len(ReprodSuccessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]
)
                        #MeanList.append(MeanReprodSuccess)
                        SdReprodSuccess = math.sqrt(sum([((x - MeanReprodSuccess) ** 2) for x in
ReprodSuccessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]]) /
len(ReprodSuccessByRangeByRepetitionByGenerationByAbility[sc][r][s][0][AbilityIndex]))
                        #SdList.append(SdQuality)
                        MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex].append(MeanReprodSuccess)
                        MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex].append(SdReprodSuccess)
```

```
                        #print(MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex])
                    else:
                        MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex].append(0)
                        MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex].append(0)
                        #print(MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanList = []
            SdList = []
            for AbilityIndex in range(GenParam.MaleAbilityToFindFood+1):
                SumMeanReprodSuccess = 0
                SumSdReprodSuccess = 0
                for r in range(GenParam.TotalNumberOfScenarioRepetition):
                    SumMeanReprodSuccess = SumMeanReprodSuccess + \
                                           MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex][0]
                    SumSdReprodSuccess = SumSdReprodSuccess + \
                                         MeanSDReprodMaleOverRepetition[sc][s][r][AbilityIndex][1]
                    #print(SumMeanReprodSuccess)
                    #print(SumSdReprodSuccess)
                MeanMeanReprodSuccess = SumMeanReprodSuccess /
(GenParam.TotalNumberOfScenarioRepetition)
                MeanList.append(MeanMeanReprodSuccess)
                MeanSdReprodSuccess = SumSdReprodSuccess /
(GenParam.TotalNumberOfScenarioRepetition)
                SdList.append(MeanSdReprodSuccess)
                AnalyseLinkSRMaleTraitEvolutionFile.write(str(sc) + "\t" +
                                                          str(s) + "\t" +
                                                          str(AbilityIndex) + "\t" +
                                                          str(MeanMeanReprodSuccess) + "\t" +
                                                          str(MeanSdReprodSuccess) + "\n")
    AnalyseLinkSRMaleTraitEvolutionFile.close()



def AnalyseLinkReprodSuccessFemaleCriterion(
        ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion,
        AnalyseLinkSRFemaleCriterionEvolutionFile):
    MeanSDReproCriterionOverRepetition = []
    for sc in range(GenParam.Range.value):
        MeanSDReproCriterionOverRepetition.append([])
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanSDReproCriterionOverRepetition[sc].append([])
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanSDReproCriterionOverRepetition[sc][s].append([])
                for CriterionIndex in range(GenParam.MaleAbilityToFindFood+1):
                    MeanSDReproCriterionOverRepetition[sc][s][r].append([])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
```

```
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanList = []
                SdList = []
                for CriterionIndex in range(GenParam.MaleAbilityToFindFood+1):
                    if
len(ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex]) !=
0:
                        SumReprodSuccess =
sum(ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex])

#print(len(ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][0][s][0][AbilityInde
x]))
                        MeanReprodSuccess =
SumReprodSuccess/len(ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][
0][CriterionIndex])
                        #MeanList.append(MeanQuality)
                        SdReprodSuccess = math.sqrt(sum([((x - MeanReprodSuccess) ** 2) for x in
ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex]]) /
len(ReprodSuccessByRangeByRepetitionByGenerationByMateChoiceCriterion[sc][r][s][0][CriterionIndex]))
                        #SdList.append(SdReprodSuccess)
                        MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex].append(MeanReprodSuccess)
                        MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex].append(SdReprodSuccess)
                        #print(MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex])
                    else:
                        MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex].append(0)
                        MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex].append(0)
                        #print(MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanList = []
            SdList = []
            for CriterionIndex in range(GenParam.MaleAbilityToFindFood+1):
                SumMeanReprodSuccess = 0
                SumSdReprodSuccess = 0
                for r in range(GenParam.TotalNumberOfScenarioRepetition):
                    SumMeanReprodSuccess = SumMeanReprodSuccess +
MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex][0]
                    SumSdReprodSuccess = SumSdReprodSuccess +
MeanSDReproCriterionOverRepetition[sc][s][r][CriterionIndex][1]
                    #print(SumMeanReprodSuccess)
                    #print(SumSdReprodSuccess)
                MeanMeanReprodSuccess = SumMeanReprodSuccess /
(GenParam.TotalNumberOfScenarioRepetition)
                MeanList.append(MeanMeanReprodSuccess)
                MeanSdReprodSuccess = SumSdReprodSuccess /
(GenParam.TotalNumberOfScenarioRepetition)
                SdList.append(MeanSdReprodSuccess)
                AnalyseLinkSRFemaleCriterionEvolutionFile.write(str(sc) + "\t" +
```

```
                                                                str(s) + "\t" +
                                                                str(CriterionIndex) + "\t" +
                                                                str(MeanMeanReprodSuccess) + "\t" +
                                                                str(MeanSdReprodSuccess) + "\n")

    AnalyseLinkSRFemaleCriterionEvolutionFile.close()


def AnalyseLinkReprodSuccessFemalePrecision(
        ReprodSuccessByRangeByRepetitionByGenerationByPrecision,
        AnalyseLinkSRFemalePrecisionEvolutionFile):

    MeanSDReproPrecisionOverRepetition = []
    for sc in range(GenParam.Range.value):
        MeanSDReproPrecisionOverRepetition.append([])
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanSDReproPrecisionOverRepetition[sc].append([])
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanSDReproPrecisionOverRepetition[sc][s].append([])
                for PrecisionIndex in range(GenParam.TimeStepNbCompleteInformation+1):
                    MeanSDReproPrecisionOverRepetition[sc][s][r].append([])
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            for r in range(GenParam.TotalNumberOfScenarioRepetition):
                MeanList = []
                SdList = []
                for PrecisionIndex in range(GenParam.TimeStepNbCompleteInformation+1):
                    if len(ReprodSuccessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex])
!= 0:
                        SumReprodSuccess =
sum(ReprodSuccessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex])

#print(len(ReprodSuccessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex]))
                        MeanReprodSuccess =
SumReprodSuccess/len(ReprodSuccessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionI
ndex])
                        #MeanList.append(MeanReprodSuccess)
                        SdReprodSuccess = math.sqrt(sum([((x - MeanReprodSuccess) ** 2) for x in
ReprodSuccessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex]]) /
len(ReprodSuccessByRangeByRepetitionByGenerationByPrecision[sc][r][s][0][PrecisionIndex]))
                        #SdList.append(SdReprodSuccess)

MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(MeanReprodSuccess)
                        MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(SdReprodSuccess)
                        #print(MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex])
                    else:
                        MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(0)
                        MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex].append(0)
                        #print(MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex])
```

```
    for sc in range(GenParam.Range.value):
        for s in range(GenParam.TotalNumberOfSimulation):
            MeanList = []
            SdList = []
            for PrecisionIndex in range(1, GenParam.TimeStepNbCompleteInformation+1):
                SumMeanReprodSuccess = 0
                SumSdReprodSuccess = 0
                for r in range(GenParam.TotalNumberOfScenarioRepetition):
                    SumMeanReprodSuccess = SumMeanReprodSuccess +
MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex][0]
                    SumSdReprodSuccess = SumSdReprodSuccess +
MeanSDReproPrecisionOverRepetition[sc][s][r][PrecisionIndex][1]
                    #print(SumMeanReprodSuccess)
                    #print(SumSdReprodSuccess)
                MeanMeanReprodSuccess = SumMeanReprodSuccess /
(GenParam.TotalNumberOfScenarioRepetition)
                MeanList.append(MeanMeanReprodSuccess)
                MeanSdReprodSuccess = SumSdReprodSuccess /
(GenParam.TotalNumberOfScenarioRepetition)
                SdList.append(MeanSdReprodSuccess)
                AnalyseLinkSRFemalePrecisionEvolutionFile.write(str(sc) + "\t" +
                                                                str(s) + "\t" +
                                                                str(PrecisionIndex) + "\t" +
                                                                str(MeanMeanReprodSuccess) + "\t" +
                                                                str(MeanSdReprodSuccess) + "\n")

    AnalyseLinkSRFemalePrecisionEvolutionFile.close()
```

Chapitre V - Conclusions générales

Principales contributions de la thèse

L'idée que la sélection sexuelle puisse favoriser l'évolution des capacités cognitives (Darwin, 1871) n'est considérée à sa juste valeur que depuis les deux dernières décennies. Dans ce contexte, l'étude de l'évolution de la cognition par sélection intersexuelle chez les animaux en est encore à ses balbutiements et les résultats des recherches actuelles sont inconsistants. De nombreuses questions subsistent : (i) est-ce que les capacités cognitives des mâles leur permettent d'accéder plus facilement à des femelles ? (ii) est-ce que les femelles expriment une forte préférence unanime pour des mâles plus performants ou est-ce que cette préférence dépend de leurs propres caractéristiques? (iii) comment les femelles estiment les capacités cognitives mâles, via l'observation directe des performances mâles ou via des traits phénotypiques associés aux capacités cognitives mâles? (iv) est-ce que les capacités cognitives mâles sont sélectionnées ensemble sous un facteur général d'intelligence ou est-ce que certaines capacités cognitives sont plus pertinentes que d'autres lors du choix de partenaire? (v) dans quelle mesure les conditions environnementales affectent l'importance et la direction de la sélection intersexuelle sur l'évolution de la cognition? (vi) est-ce que les capacités cognitives mâles sont adaptatives et apportent des bénéfices directs à leur partenaire sexuelle ou est-ce qu'il s'agit simplement d'un signal honnête de la qualité des mâles (bénéfice indirect pour les femelles)? Dans cette thèse, j'ai exploré certaines de ces questions en combinant des expériences en laboratoire sur une espèce d'oiseau monogame sociale et un modèle à base d'agent simulant l'évolution de la cognition par sélection intersexuelle dans différents scénarios environnementaux (figure 3). De façon générale, nos résultats démontrent que le choix de partenaire peut jouer un rôle important dans l'évolution de la cognition mâle et femelle. Dans les sections suivantes, j'explique en quoi cette thèse nous permet de répondre à certaines de ces questions et apporte des pistes de réflexion quant à l'inconsistance des résultats des études actuelles dans le domaine.

Les capacités cognitives des mâles leur permettent d'avoir un accès privilégié aux femelles. Lorsque les capacités cognitives permettent à des mâles d'acquérir davantage de ressources, les femelles devraient sélectionner leur partenaire sur la base de ces compétences afin d'obtenir des avantages directs en termes de succès reproducteur (Chapitre IV). C'est sur ce présupposé que se basent plusieurs études récentes démontrant des relations positives entre les capacités cognitives mâles et le succès reproducteur de leurs couples (Branch et al., 2019; Cauchard et al., 2013; Preiszner et al., 2016; Shaw et al., 2019). Chez le Diamant mandarin, la capacité des mâles à ajuster leur comportement d'approvisionnement en réponse à un changement de distribution (Barou-Dagues, Richard-Dionne & Dubois, 2020; Chapitre II) et à performer dans différentes tâches cognitives (Chapitre III) influence la préférence sexuelle des femelles. Cependant, les femelles n'expriment pas une préférence unanime pour les mâles plus performants (Chapitre II et III). En effet, que ce soit pour un trait *a priori* adaptatif ou pour des performances cognitives relevées dans des tests psychométriques, les femelles varient dans leur préférence dépendamment de leur propre degré de plasticité comportementale (Chapitre II), de leurs propres performances cognitives et de leur condition corporelle (Chapitre III). De façon consistante, certaines études démontrent l'existence de variances dans les préférences femelles pour les traits sexuels secondaires (e.g. Jennions & Petrie, 1997; Rosenthal, 2017; Ryan et al., 2009; mais voir Wang et al., 2017). Un élément important que l'on met en donc évidence dans cette thèse, c'est qu'il est crucial de prendre en considération les différences individuelles chez les femelles lorsqu'on étudie le choix de partenaire pour la cognition mâle. Par définition, le choix de partenaire fait référence aux interactions entre une femelle et des partenaires potentiels qui mènent à l'appariement (Ryan et al., 2009). Partir du principe que toutes les femelles expérimentent les mêmes interactions et prennent les mêmes décisions est une simplification qui peut avoir des conséquences importantes sur le design des recherches. Nos résultats, et ceux d'une récente étude d'Álvarez-Quintero et al. (2021), sont les seuls qui font actuellement état d'un lien entre les capacités cognitives des femelles et les différences de préférences femelles pour des capacités cognitives mâles. Ils ont démontré chez l'épinoche à trois épines (*Gasterosteus aculetaus*) que la préférence femelle pour des mâles plus performants en contrôle inhibiteur était affectée par la performance femelle dans cette même tâche. Ainsi, cette thèse valide partiellement notre hypothèse initiale en démontrant que les capacités cognitives des mâles leur permettent d'avoir un accès privilégié *à certaines femelles* chez le Diamant mandarin.

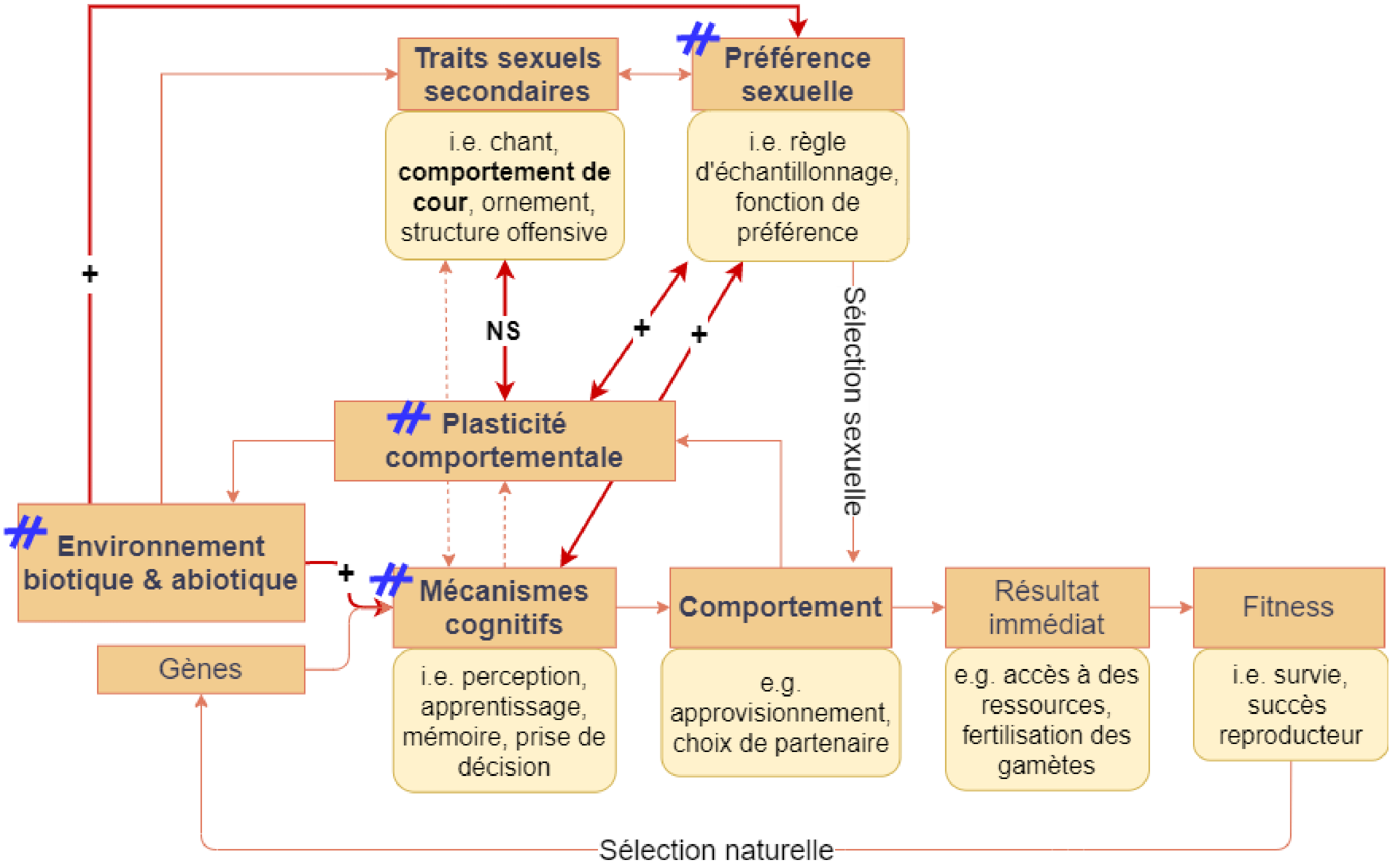


Figure 3. Schéma général de l'effet de la sélection naturelle et sexuelle sur l'évolution de la cognition (inspiré de Shettleworth 2010). Les flèches pleines orange indiquent les relations pour lesquelles les tendances sont connues et les flèches pointillées celles pour lesquelles les tendances sont moins claires. Les flèches pleines rouges indiquent les contributions de cette thèse et les signes bleus indiquent la présence de variance dans les traits mesurés.

Différences de préférences pour la cognition mâle: support d'hypothèses alternatives

Dans cette thèse, trois hypothèses pourraient expliquer pourquoi les femelles diffèrent dans leurs préférences. Tout d'abord, l'appariement assortatif, une hypothèse particulièrement supportée chez l'humain, stipule que les individus s'apparient à un partenaire qui leur ressemble (Escorial & Martín-Buro, 2012; Plomin & Deary, 2015; Śmieja & Stolarski, 2018). Parce que l'appariement assortatif augmente *a priori* la qualité des relations chez l'humain (Śmieja & Stolarski, 2018), les hommes et les femmes ont tendance, entre autres, à s'apparier avec un partenaire qui possède les mêmes capacités cognitives (Mascie-Taylor & Vandenberg, 1988). Chez les animaux non humains, plusieurs études supportent également l'hypothèse de l'appariement assortatif pour d'autres traits comme la taille corporelle (e.g. Fazhan et al., 2017; Montiglio et al., 2016), l'âge (Jiang et al., 2013), les patrons de couleurs (e.g. MacDougall & Montgomerie, 2003) ou la personnalité (e.g. Ariyomo & Watt, 2013). Dans cette thèse, cette hypothèse pourrait expliquer pourquoi les femelles capables d'ajuster leur comportement d'approvisionnement ont démontré une plus forte préférence pour la plasticité comportementale des mâles (Chapitre II). Cependant, aucune évidence d'appariement assortatif n'a été mise en évidence pour les capacités cognitives mesurées dans les tests psychométriques (Chapitre III).

Alternativement, les femelles peuvent varier dans leur préférence, car elles ne possèdent pas toutes les mêmes capacités à estimer les traits mâles qui reflètent leurs capacités cognitives. En effet, le choix de partenaire implique des processus cognitifs, allant de la réception des signaux sexuels par le système sensoriel de la femelle jusqu'à l'évaluation de ces informations en utilisant un ensemble de règles de décision pour agir en conséquence (Ryan et al., 2009). Chaque étape qui mène au choix de partenaire est donc gouvernée par les capacités et les contraintes cognitives de la femelle. Dans cette thèse, toutes les femelles ont chacune pu observer librement 4 mâles simultanément en train de s'alimenter (i.e. 10 jours dans le jeu producteur-chapardeur; Chapitre II) et parader (i.e. 10 min dans l'expérience de choix de partenaire, Chapitre II) dans les mêmes conditions. Dans le contexte d'approvisionnement social, en plus de devoir s'approvisionner dans un environnement changeant, les femelles ont dû observer le comportement et le phénotype de chaque mâle, traiter ces informations, les retenir pour pouvoir les utiliser lors du choix de partenaire. Dans le contexte de choix de partenaire, les mâles pouvaient, cette fois-ci, voir les femelles et exprimaient un ensemble de comportements de cour pour attirer leur attention. Dans ce cas, il est probable que l'ensemble de ces informations n'aient pas été perçues et traitées de la même manière par toutes les femelles (Cauchoix & Chaine, 2016). Conformément à l'hypothèse des capacités cognitives, nous avons trouvé que seules les femelles capables d'ajuster leur comportement d'approvisionnement (Chapitre II), les femelles performantes en apprentissage associatif (Chapitre III) exprimaient une forte préférence pour les capacités cognitives mâles. De plus, certaines études montrent que les femelles, avec l'expérience, ajustent leurs préférences sexuelles avec le temps (e.g. Collins, 1995; Wagner et al., 2001). Dans cette thèse, étant donné que les femelles étaient sexuellement naïves au premier essai, les interactions avec les 4 mâles à l'issue du premier essai ont pu influencer les interactions à l'essai suivant. Ainsi, cette hypothèse des capacités cognitives pourrait également expliquer pourquoi les femelles plus performantes en apprentissage associatif et en contrôle inhibiteur ont augmenté leur préférence pour certaines capacités mâles entre les essais un et deux du test de choix de partenaire.

Cela dit, il est également possible que la condition des femelles ait influencé leur choix de partenaire sexuel (Cotton et al., 2006). Le choix de partenaire étant un processus coûteux en temps et en énergie, les femelles doivent faire des compromis entre l'énergie qu'elles ont en réserve et celle qu'elles sont prêtes à investir pour trouver un partenaire de qualité. Dans ce contexte, l'hypothèse de la condition corporelle stipule que les femelles en bonne condition corporelle auraient davantage de ressources pour échantillonner et estimer la qualité des différents mâles et pour s'apparier avec les mâles jugés de meilleure qualité (Cotton et al., 2006; Hebets et al., 2008; Hingle et al., 2001). Par exemple, Howell et al. (2019) ont démontré que chez les diamants mandarins, la masse des femelles était positivement corrélée à la préférence pour des mâles ayant un chant de bonne qualité. Dans cette thèse, la variance de condition corporelle entre les femelles était non négligeable : la femelle en meilleure condition avait un score de condition 135% supérieur à la condition moyenne des femelles dans la colonie alors que la femelle en moins bonne condition avait un score de condition 30 % inférieur à la condition moyenne. Cette hypothèse pourrait expliquer les relations marginales trouvées entre la condition corporelle des femelles et leur préférence pour certaines capacités cognitives mâles (Chapitre III). Néanmoins, des études complémentaires sur des individus sauvages (i.e. non nourris ni traités contre les parasites) sont nécessaires pour confirmer le rôle de la condition des femelles dans leur choix de partenaire pour la cognition mâle.

Évidence pour une estimation indirecte des capacités cognitives mâles

Pour comprendre pourquoi les femelles varient dans leur préférence pour la cognition mâle et déterminer les contraintes auxquelles elles font face, il faut identifier les traits qu'elles utilisent pour estimer les capacités cognitives des mâles (Boogert, Fawcett & Lefebvre, 2011). Deux hypothèses s'opposent actuellement : la première stipule que les femelles estiment les capacités cognitives mâles directement par l'observation de leur performance cognitive et la seconde stipule qu'elles utilisent plutôt des traits phénotypiques indirectement corrélés aux capacités cognitives mâles pour faire leur choix (revue dans Boogert et al., 2011). Les résultats de cette thèse supportent la seconde hypothèse. En effet, les femelles ont exprimé des préférences pour la performance des mâles dans les 4 tests psychométriques sans les avoir observés interagir dans ces différentes tâches (Chapitre III). Cela dit, nos résultats suggèrent fortement que les femelles auraient utilisé la plasticité comportementale des mâles lors de la phase d'approvisionnement sociale (Chapitre II) plutôt que d'autres traits phénotypiques. En effet, la plasticité comportementale des mâles n'était pas associée au temps passé à danser devant les femelles, à leur condition et taille corporelle, ou à la quantité de graines consommées pendant cette période (Chapitre II). De plus, la plasticité dans les tactiques d'approvisionnement des mâles, bien que peu répétable (Chapitre II), était préférée de façon consistante par les femelles (Chapitre II). Autrement dit, même si un mâle n'exprimait pas le même degré de plasticité comportementale d'un groupe de femelles à un autre (probablement à cause de la forte fréquence dépendance agissant sur le comportement des mâles), il était préféré par les femelles qui l'observaient être plastique dans son comportement. D'autres traits sexuels secondaires peu labiles, comme le chant ou les couleurs vivent des mâles, pourraient être à l'origine de cette préférence pour la plasticité. Par exemple, la complexité du chant chez le Diamant mandarin refléterait la capacité des mâles à résoudre des problèmes (Boogert et al., 2008). Cependant, cette hypothèse reste à vérifier étant donné la labilité de la plasticité comportementale dans nos expériences. Ainsi, cette thèse ouvre une nouvelle avenue sur l'étude du choix de partenaire pour la cognition mâle en considérant la plasticité comportementale comme une capacité attractive pour les femelles.

Support de l'hypothèse des capacités cognitives modulaires/spécialisées

Pour étudier la préférence des femelles pour des capacités cognitives mâles, il est possible d'utiliser la performance générale des mâles dans des tests psychométriques (i.e. facteur 'g') ou de considérer chaque capacité mâle comme indépendante (i.e. capacité modulaire). Chez l'humain, le facteur de cognition générale est souvent utilisé pour estimer la préférence des femmes pour les hommes plus intelligents, car il explique en moyenne 50% de la variance interindividuelle (Deary, 2001) et est fortement héritable (Plomin & Deary, 2015; Plomin & Spinath, 2002). Cependant, chez les animaux non humains, le facteur 'g' explique une part de variance interindividuelle bien inférieure et l'hypothèse de cognition générale n'est souvent pas supportée (Langley et al., 2020; Matzel et al., 2003; Poirier et al., 2020). De façon similaire, nos résultats réfutent l'hypothèse de cognition générale chez le Diamant mandarin. En effet, que l'on considère les mâles et les femelles ensemble ou séparément, les mesures de performances cognitives dans les 4 tests psychométriques étaient faiblement ou non corrélées les uns avec les autres (Chapitre III). Un test de permutation d'une analyse en composante principale (ACP) sur les 4 performances cognitives a également révélé que la variance expliquée par chacun des axes n'était pas différente de la variance expliquée par ces axes sur une matrice aléatoire (Test de permutation, CP1 : P=0.796, CP2 : P=0.275; CP3 : P=0.437, CP4 : P=0.222).

Dans ce contexte, en testant la préférence des femelles pour chaque capacité cognitive mâle, il est également possible d'explorer si certaines capacités sont plus pertinentes que d'autres dans le contexte du choix de partenaire. Pour qu'une capacité cognitive mâle soit favorisée par sélection sexuelle, la préférence femelle pour cette capacité mâle doit être répétable (Forstemeier & Birkhead, 2004) et adaptative (i.e. il doit exister une forte corrélation entre les traits utilisés par les femelles et le succès reproducteur du couple; Boogert, Fawcett & Lefebvre, 2011; Chapitre IV). Bien qu'aucune mesure de succès reproducteur n'ai été relevée dans cette thèse, les différences de préférence entre femelles diamants mandarins étaient répétables pour la plasticité comportementale (Chapitre II) et la performance des mâles dans la tâche de contrôle inhibiteur (Chapitre III). Selon certains, ces résultats pourraient indiquer que ces deux performances mâles sont plus importantes que l'apprentissage spatial, l'apprentissage moteur progressif, et l'apprentissage associatif dans le contexte de choix de partenaire chez les diamants mandarins (Jennions & Petrie, 1997). Néanmoins, nous avons également noté que certaines femelles, de par leurs différences de capacités cognitives et de condition corporelle, étaient moins consistantes que d'autres dans leur préférence pour certaines performances mâles (i.e. plasticité comportementale, apprentissage associatif et contrôle inhibiteur, Chapitre II et III). Dans ce contexte, nos résultats indiquent que l'apprentissage spatial et moteur progressif semblent moins pertinent chez cette espèce. Cela dit, des mesures d'aptitudes sont maintenant requises pour démontrer l'avantage adaptatif de la plasticité comportementale, du contrôle inhibiteur et de l'apprentissage associatif dans le contexte du choix de partenaire chez le Diamant mandarin.

Par ailleurs, certains résultats remettent en cause l'idée que les mâles plus performants devraient toujours être considérés plus attractifs par les femelles. Nous avons démontré que les femelles, indépendamment de leurs capacités cognitives et de leur condition corporelle, exprimaient au second essai une forte préférence pour les mâles moins performants dans la tâche d'apprentissage associatif (Chapitre III). Si performer dans cette tâche est en réalité mal adaptatif chez cette espèce (comme peuvent l'être d'autres capacités chez d'autres espèces, Madden et al., 2018), il est possible que les femelles développent une préférence pour les mâles moins performants pour cette capacité cognitive. En effet, lorsque les conditions environnementales limitent l'acquisition de nourriture et que le coût à produire, maintenir et exprimer de bonnes capacités cognitives est élevé, les femelles retirent un avantage direct à s'apparier avec des mâles qui ne payent pas de tels coûts (Chapitre IV). Dans ce contexte, la sélection intersexuelle éliminerait les mâles plus performants ainsi que les femelles qui s'apparieraient préférentiellement avec ces mâles (Chapitre IV).

Importance des facteurs environnementaux sur la force et la direction de la sélection sexuelle

Pour comprendre comment la cognition évolue par sélection naturelle et sexuelle, il faut identifier les conditions environnementales dans lesquelles les capacités cognitives mâles et les préférences femelles pour ces traits sont adaptatives. En manipulant la distribution de la nourriture, le temps alloué à l'approvisionnement et au choix de partenaire ainsi que le coût associé à l'expression de bonnes capacités cognitives, nos résultats indiquent que les conditions environnementales affectent la force et la direction de la sélection intersexuelle sur l'évolution de la cognition (Chapitre IV). Actuellement, peu d'études mettent en évidence les conséquences adaptatives des différences individuelles de capacités cognitives (e.g. Cauchoix & Chaine, 2016; Huebner et al., 2018; Morand-Ferron et al., 2015; Thornton et al., 2014) et de la préférence femelle pour ces capacités mâles (Shaw et al., 2019; Smith et al., 2015; Cauchard et al., 2017; Preiszner et al., 2017) dans le milieu naturel. Les résultats de ces études sont encore très inconsistants et leur approche ne considère généralement que l'effet de la sélection naturelle ou de la sexuelle séparément. De façon générale, les résultats de cette thèse révèlent que la sélection intersexuelle pourrait jouer un rôle important en interagissant avec la sélection naturelle et en modifiant les patrons d'évolution de la cognition prédits lorsque cette dernière agit seule (Chapitre IV). Ainsi, pour comprendre les relations entre les capacités cognitives, le comportement (e.g. choix de partenaire, approvisionnement) et l'aptitude des individus, il parait nécessaire de prendre en considération l'effet de ces deux forces (Cauchoix & Chaine, 2016; figure 3).

D'autre part, nos résultats suggèrent que le choix de partenaire sexuel pourrait permettre de maintenir de la diversité cognitive dans certains contextes au sein des populations. D'une part, nous avons démontré que dépendamment de leurs propres caractéristiques, les femelles diamants mandarins diffèrent dans leurs préférences pour les capacités cognitives mâles (Chapitre II et III) et d'autre part, que cette diversité peut être maintenue à l'échelle évolutive dans des environnements où les contraintes environnementales sont élevées (Chapitre IV). Particulièrement, des stratégies cognitives alternatives pourraient être maintenues à travers le choix de partenaire chez les mâles et les femelles lorsque les individus ont peu de temps pour s'approvisionner et choisir un partenaire sexuel et lorsque les coûts associés à la production et au maintien de bonnes capacités cognitives sont élevés (Chapitre IV). En nature, le Diamant mandarin est une espèce granivore très prédatée et vie dans un environnement aride qui fluctue de façon drastique.. Les femelles produisent leurs couvées en fonction de la disponibilité en nourriture et en eau donc en fonction de la quantité de précipitations (Zann, 1996) et les mâles participent grandement à la construction du nid, au temps de couvé, à l'approvisionnement et la protection des petits jusqu'à maturité. Ces conditions changeantes et très imprévisibles peuvent limiter le temps dont les femelles disposent pour échantillonner des partenaires potentiels (Magnhagen, 1991). Nos résultats suggèrent que le Diamant mandarin semble être un modèle particulièrement intéressant pour étudier le rôle du choix de partenaire dans l'évolution de la cognition (Healy et al., 2010. Dépendamment de la région, certaines populations peuvent être contraintes à vivre dans des conditions plus difficiles que d'autres (Zann, 1996). Ainsi, comparer l'avantage adaptatif des capacités cognitives et l'importance de la préférence sexuelle pour ces traits dans différentes populations pourrait permettre de mieux comprendre l'interaction entre sélection naturelle et sexuelle sur l'évolution de la cognition chez les oiseaux.

Capacités cognitives et bénéfices directs et indirects

Les résultats de cette thèse révèlent l'existence de préférence sexuelle pour des performances cognitives mâles, de relations entre la préférence sexuelle des femelles et leurs caractéristiques et mettent en évidence l'importance du contexte environnemental pour comprendre le rôle du choix de partenaire sur l'évolution de la cognition. Cependant, aucune mesure de bénéfices directs/indirects ni d'héritabilité n'a été relevée. Pourtant, ces points restent indispensables pour démontrer que le choix de partenaire affecte l'évolution de la cognition. Dans le chapitre IV, inspirés des espèces monogames à soin biparental, nous avons présupposé que les femelles obtenaient des bénéfices directs plus ou moins important en fonction des capacités cognitives de leur partenaire (i.e. approvisionnement des petits par le père). Dans ce contexte, nous avons trouvé que la sélection intersexuelle devrait favoriser l'évolution de bonnes capacités cognitives dans de nombreux contextes environnementaux même lorsqu'à priori la sélection naturelle favorise les mâles possédant de moins bonnes capacités cognitives. Cela dit, il est tout à fait possible que chez d'autres espèces, particulièrement des espèces où le mâle ne participe pas à l'élevage des jeunes et ne transfère que son sperme, les capacités cognitives ne représentent qu'un signal honnête pour les femelles pour juger de la qualité génétique du mâle. Dans ce cas, la sélection sexuelle pourrait souvent agir contre la sélection naturelle comme c'est le cas pour l'évolution d'un grand nombre de caractères sexuels secondaires ornementaux. En évaluant à la fois les bénéfices directs et indirects que la femelle retire en s'appariant avec un mâle plus intelligent, il serait intéressant d'investiguer le rôle du choix de partenaire pour des espèces qui varient dans leur système d'appariement. Il serait également pertinent d'étudier ce phénomène chez des espèces en conflit sexuel important pour explorer les cas où les capacités cognitives sont favorisées par le choix de partenaire, mais défavorisées par la compétition entre mâles. Par exemple, en agissant de façon antagoniste, les sélections intra et intersexuelle pourraient limiter l'évolution d'une même habilité cognitive ou alors favoriser l'évolution de différentes habilités cognitives.

Limites

Dans le chapitre II et III, il est probable que nous ayons sous-estimé les mesures de répétabilité de la plasticité comportementales des mâles et de la préférence des femelles pour les différents traits. D'une part, la plasticité comportementale mâle est mesurée dans un contexte de forte fréquence dépendance. Le gain perçu par un individu focal est fortement affecté par le comportement des trois autres mâles présents dans le groupe. Dans ce contexte, il est possible que notre mesure de plasticité comportementale d'un essai à l'autre ne reflète pas de façon optimale la capacité réelle des mâles à ajuster leur comportement. Pour vérifier si la plasticité comportementale est répétable chez le Diamant mandarin, il faudrait diminuer la force de la fréquence dépendance (Barou Dagues, Hall & Giraldeau, 2020; Morand-Ferron et al., 2010) en diminuant la densité d'individus dans le dispositif. D'autre part, la consistance de la préférence femelle, lorsque l'on se base sur le temps passé par la femelle face aux différents mâles, peut être affectée par sa motivation, sa réceptivité (Jennions & Petrie, 1997), sa naïveté sexuelle (Ryan et al., 2009) et comme nous l'avons vu, par d'autres caractéristiques associées aux contraintes lors du choix. En éliminant les femelles non actives dans le test de choix de partenaire, nous avons limité les biais de motivation et de réceptivité. Cela, dit, augmenter la durée d'observation et du test de choix ainsi que le nombre d'essais pourrait permettre d'obtenir des mesures plus fiables de consistance de préférence femelle. Par ailleurs, le principe d'estimer la répétabilité de la préférence femelle à l'échelle de la population peut être discuté. Par exemple, si toutes les femelles expriment une forte préférence consistante pour un trait, la répétabilité de la préférence pour ce trait sera faible. De la même manière, si certaines femelles expriment une forte préférence consistante pour un trait, mais que d'autres n'ont pas de préférence pour ce trait (i.e. choix aléatoire), la répétabilité de leur préférence sera faible aussi. Par exemple, plus les femelles ont une préférence similaire dans la population, moins leur préférence va être répétable. Il est donc possible que cet estimé ne soit pertinent que lorsque la sélection est forte et linéaire. De plus, un test de préférence initial (i.e. avant l'observation des mâles dans le contexte d'approvisionnement social) aurait permis de confirmer que la plasticité dans les tactiques d'approvisionnement des mâles est utilisée comme critère sur lequel les femelles se basent dans le contexte de choix de partenaire.

Dans le chapitre II et III, la composition des groupes de mâles a pu influencer la préférence des femelles pour les différentes capacités cognitives mâles. En effet, plus les mâles varient sur la base d'un trait plus les femelles peuvent les discriminer sur la base de ce trait. Nous avons vu que les mâles n'étant ni répétables dans leur plasticité comportementale, ni performants de la même manière dans les 4 tests psychométriques. Dans ce contexte, il est difficile de penser que l'on puisse composer les groupes avant de faire observer les mâles par les femelles et de contrôler ainsi la moyenne et la variance des capacités mâles présentées. En contrôlant statistiquement pour la variance de plasticité entre les mâles du même groupe et pour l'identité du groupe de mâle présenté aux femelles, nous avons démontré que ces effets étaient mineurs (Chapitre II). Par parcimonie, nous avons choisi de ne pas inclure les 4 variances de performances cognitives mâles dans les sélections de modèles de préférence pour les différentes performances cognitives mâles (Chapitre III), mais nous avons contrôlé pour l'identité du groupe de mâles présentés aux femelles. Un moyen d’améliorer le protocole serait de présenter tous les groupes de mâles à toutes les femelles et d’estimer la préférence des femelles sur la base des capacités cognitives de tous ces mâles.

Perspectives

Pendant ma thèse, j’ai pu mettre en évidence l’importance du choix de partenaire dans l’évolution de la cognition. Néanmoins, ce rôle peut dépendre des capacités cognitives mâles considérées, des caractéristiques des femelles et de l’environnement dans lequel ce choix était fait. Dans les sections suivantes, je présente des pistes de recherches que j’explore actuellement.

La plasticité comportementale et les traits sexuels secondaires reflètent-ils différentes capacités cognitives mâles?

Si les femelles expriment des préférences pour différentes capacités cognitives, il est possible que différents traits permettent d’identifier des mâles possédant ces capacités. De nombreuses études se sont intéressées aux mécanismes cognitifs associés à la qualité du chant. Par exemple, des individus plus performants dans une tâche de résolution de problème, de contrôle inhibiteur et d’apprentissage spatial avaient respectivement des chants plus complexes, des répertoires de chant plus grands et des phases de chant plus longues (Boogert et al., 2008; Boogert, Anderson et al., 2011; Farrell et al., 2011; mais voir DuBois et al., 2018; Sewall et al., 2013). Néanmoins, les mécanismes cognitifs impliqués dans les comportements de danse et dans l’expression de plasticité comportementale sont encore peu connus (Barou Dagues, Hall & Giraldeau, 2020). Dans cette thèse, nous avons mesuré la plasticité dans les comportements d’approvisionnement, les comportements de cour, et 4 performances cognitives chez les mâles. Nous explorons actuellement ces questions en prédisant un lien positif entre la plasticité comportementale et la performance en contrôle inhibiteur et un lien positif entre les comportements de danse et la performance en apprentissage moteur progressif.

Les mâles sont-ils plus attirés par des femelles plus performantes cognitivement?

Chez le Diamant mandarin nous avons démontré que certaines capacités cognitives femelles étaient associées à la préférence de certaines capacités mâles. Le choix de partenaire des femelles pourrait ainsi contribuer à l’évolution des capacités cognitives femelles via l’estimation des traits mâles (Ryan et al., 2009). Cela dit, les mâles peuvent se montrer sélectifs dans leur choix de partenaire et démontrer des préférences pour certains traits femelles. Par exemple, les mâles peuvent rejeter ou accepter de courtiser une femelle, choisir de courtiser certaines femelles plutôt que d'autres, ou encore courtiser de façon plus importante certaines femelles plutôt que d'autres (Edward & Chapman, 2011). Chez le Diamant mandarin, les mâles préfèrent les femelles qui ont reçu des suppléments de nourriture (Jones et al., 2001) et qui ont des becs plus jaunes (Burley & Coopersmith, 1987). Chez une espèce cousine, le Moineau du Japon (*Lonchura striata domestica*), les mâles ajustent leur chant en fonction de la femelle présentée et au cours des interactions avec la même femelle (Heinig et al., 2014) tandis que chez le Jardinier satiné (*Ptilonorhynchus violaceus*), les mâles ajustent l'intensité de leur comportement de cour en fonction de la réponse de la femelle (Patricelli et al., 2002). Cependant, aucune étude n'a encore examiné l'idée que les mâles puissent aussi exprimer des préférences pour des femelles possédant de meilleures capacités cognitives en ajustant leur comportement de danse. Nous explorons actuellement cette question chez le Diamant mandarin grâce à des données recueillies durant ce projet de thèse.

Évolution de capacités cognitives spécialisées par sélection naturelle et sexuelle

Les résultats du chapitre IV indiquent que les facteurs environnementaux devraient fortement affecter la force et la direction de la sélection naturelle et sexuelle dans l'évolution de la cognition. La première étape serait d'examiner cette question en réalisant une méta-analyse sur le lien entre certains facteurs environnementaux (i.e. taux de prédation, durée de la saison de reproduction ou disponibilité en nourriture) et les relations observées entre les capacités cognitives mâles, leur succès d'appariement, le succès reproducteur de leur couple et le système d'appariement chez des populations sauvages. Par exemple, il serait intéressant de tester si un faible taux de prédation, une longue saison de reproduction et une grande disponibilité en nourriture permettent d'expliquer la présence de fortes relations positives entre les capacités cognitives, le succès d'appariement et le succès reproducteur des individus indépendamment de l'espèce et du système d'appariement. À l'inverse, ces relations pourraient s'inverser ou s'annuler chez les espèces où le taux de prédation est élevé, la saison de reproduction très courte et la disponibilité en nourriture faible.

D'autre part, les résultats de cette thèse suggèrent l'existence de préférences femelles pour différentes capacités cognitives mâles indépendantes. Dans le chapitre IV, notre modèle nous permet de prédire l'évolution d'une seule capacité cognitive mâle par sélections naturelle et sexuelle. Cependant, il est possible que ces patrons changent lorsqu'on considère deux capacités cognitives mâles indépendantes l'une de l'autre. En utilisant la même démarche que dans le chapitre IV, il serait possible d'implémenter une 2^{e} capacité cognitive mâle qui permettrait aux plus performants d'obtenir un autre type de bénéfice (e.g. meilleur territoire, meilleure stratégie de défense contre les prédateurs) et de prédire l'évolution de ces deux capacités par sélection naturelle et sexuelle au sein des populations. Si chaque capacité cognitive mâle apporte des bénéfices différents aux femelles qui expriment une préférence pour ces capacités, la sélection sexuelle pourrait maintenir une diversité cognitive dans un grand nombre de contextes environnementaux. L'une de ces capacités pourrait fournir des bénéfices directs alors que l'autre pourrait fournir des bénéfices indirects aux femelles. Il serait ainsi possible de prédire les environnements où ces deux capacités se maintiennent dans la population et les environnements où une capacité prendrait le dessus sur l'autre.

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Annexes

Chapitre II

Tableau A1. Données brutes relevées dans l’expérience producteur-chapardeur.

Individual	Sex	Order of treatment	Treatment	SeedTreatment	FlockMaleFemale	FlockFemale	TrialNumByTreatment	NumProducerEvent	NumScroungerEvent	NumProducerScroungerEvent	ProportionOfWellProduced	NumSeedEatenProduce	NumSeedEatenScrounge	TotalNumSeedEaten	ProportionOfSeedEatenProduce	MaleProducerScroungerRepetition
O6	F	DA	DISP	5	G1GB	GB	1	8	6	14	0.5714	7	10	17	0.4118	A
O5	F	DA	DISP	5	G1GB	GB	2	0	3	3	0.0000	0	2	2	0.0000	A
O13	F	DA	DISP	5	G1GB	GB	3	3	0	3	1.0000	12	0	12	1.0000	A
O7	F	DA	DISP	5	G1GB	GB	4	8	0	8	1.0000	13	0	13	1.0000	A
O15	F	AD	AGRÉ	10	G2GA	GA	1	2	3	5	0.4000	4	9	13	0.3077	A
O14	F	AD	AGRÉ	10	G2GA	GA	2	2	3	5	0.4000	8	7	15	0.5333	A
O17	F	AD	AGRÉ	10	G2GA	GA	3	1	1	2	0.5000	5	3	8	0.6250	A
O16	F	AD	AGRÉ	10	G2GA	GA	4	8	0	8	1.0000	10	0	10	1.0000	A
O17	F	AD	AGRÉ	10	G2GA	GA	5	4	0	4	1.0000	16	0	16	1.0000	A
O16	F	AD	AGRÉ	10	G2GA	GA	6	6	0	6	1.0000	7	0	7	1.0000	A
O14	F	AD	AGRÉ	10	G2GA	GA	7	2	4	6	0.3333	2	10	12	0.1667	A
O15	F	AD	AGRÉ	10	G2GA	GA	8	6	2	8	0.7500	10	3	13	0.7692	A
O7	F	DA	DISP	5	G1GB	GB	5	12	0	12	1.0000	9	0	9	1.0000	A
O13	F	DA	DISP	5	G1GB	GB	6	8	0	8	1.0000	8	0	8	1.0000	A
O5	F	DA	DISP	5	G1GB	GB	7	2	2	4	0.5000	8	3	11	0.7273	A
O6	F	DA	DISP	5	G1GB	GB	8	2	10	12	0.1667	4	8	12	0.3333	A
O13	F	DA	DISP	5	G1GB	GB	9	2	1	3	0.6667	9	1	10	0.9000	A
O6	F	DA	DISP	5	G1GB	GB	10	2	6	8	0.2500	3	9	12	0.2500	A
O7	F	DA	DISP	5	G1GB	GB	11	6	3	9	0.6667	7	3	10	0.7000	A
O5	F	DA	DISP	5	G1GB	GB	12	2	4	6	0.3333	2	7	9	0.2222	A
O14	F	AD	AGRÉ	10	G2GA	GA	9	0	3	3	0.0000	0	5	5	0.0000	A
O15	F	AD	AGRÉ	10	G2GA	GA	10	2	4	6	0.3333	2	9	11	0.1818	A
O16	F	AD	AGRÉ	10	G2GA	GA	11	9	0	9	1.0000	11	0	11	1.0000	A
O17	F	AD	AGRÉ	10	G2GA	GA	12	3	2	5	0.6000	10	6	16	0.6250	A
O16	F	AD	AGRÉ	10	G2GA	GA	13	5	0	5	1.0000	6	0	6	1.0000	A
O17	F	AD	AGRÉ	10	G2GA	GA	14	0	4	4	0.0000	0	14	14	0.0000	A
O15	F	AD	AGRÉ	10	G2GA	GA	15	5	2	7	0.7143	9	4	13	0.6923	A
O14	F	AD	AGRÉ	10	G2GA	GA	16	0	3	3	0.0000	0	7	7	0.0000	A
O5	F	DA	DISP	5	G1GB	GB	13	1	6	7	0.1429	0	11	11	0.0000	A
O7	F	DA	DISP	5	G1GB	GB	14	6	2	8	0.7500	10	3	13	0.7692	A
O6	F	DA	DISP	5	G1GB	GB	15	1	9	10	0.1000	4	11	15	0.2667	A
O13	F	DA	DISP	5	G1GB	GB	16	4	1	5	0.8000	9	2	11	0.8182	A
O13	F	DA	DISP	5	G1GB	GB	17	4	0	4	1.0000	9	0	9	1.0000	A
O6	F	DA	DISP	5	G1GB	GB	18	4	5	9	0.4444	6	5	11	0.5455	A
O5	F	DA	DISP	5	G1GB	GB	19	1	6	7	0.1429	2	9	11	0.1818	A
O7	F	DA	DISP	5	G1GB	GB	20	3	0	3	1.0000	9	0	9	1.0000	A
O14	F	AD	AGRÉ	10	G2GA	GA	17	2	2	4	0.5000	7	2	9	0.7778	A
O15	F	AD	AGRÉ	10	G2GA	GA	18	1	3	4	0.2500	4	5	9	0.4444	A
O17	F	AD	AGRÉ	10	G2GA	GA	19	3	1	4	0.7500	13	4	17	0.7647	A
O16	F	AD	AGRÉ	10	G2GA	GA	20	7	0	7	1.0000	15	0	15	1.0000	A
O17	F	AD	DISP	5	G2GA	GA	1	1	3	4	0.2500	4	5	9	0.4444	A
O15	F	AD	DISP	5	G2GA	GA	2	2	4	6	0.3333	7	5	12	0.5833	A
O16	F	AD	DISP	5	G2GA	GA	3	7	0	7	1.0000	6	0	6	1.0000	A

O14	F	AD	DISP	5	G2GA	GA	4	2	2	4	0.5000	4	1	5	0.8000	A
O7	F	DA	AGRÉ	10	G1GB	GB	1	1	1	2	0.5000	5	2	7	0.7143	A
O5	F	DA	AGRÉ	10	G1GB	GB	2	0	4	4	0.0000	0	10	10	0.0000	A
O6	F	DA	AGRÉ	10	G1GB	GB	3	2	4	6	0.3333	4	8	12	0.3333	A
O13	F	DA	AGRÉ	10	G1GB	GB	4	1	0	1	1.0000	6	0	6	1.0000	A
O13	F	DA	AGRÉ	10	G1GB	GB	5	2	0	2	1.0000	11	0	11	1.0000	A
O6	F	DA	AGRÉ	10	G1GB	GB	6	1	3	4	0.2500	6	6	12	0.5000	A
O5	F	DA	AGRÉ	10	G1GB	GB	7	1	1	2	0.5000	8	3	11	0.7273	A
O7	F	DA	AGRÉ	10	G1GB	GB	8	3	0	3	1.0000	14	0	14	1.0000	A
O14	F	AD	DISP	5	G2GA	GA	5	3	2	5	0.6000	8	1	9	0.8889	A
O17	F	AD	DISP	5	G2GA	GA	6	3	5	8	0.3750	6	6	12	0.5000	A
O15	F	AD	DISP	5	G2GA	GA	7	2	7	9	0.2222	4	11	15	0.2667	A
O16	F	AD	DISP	5	G2GA	GA	8	6	0	6	1.0000	11	0	11	1.0000	A
O15	F	AD	DISP	5	G2GA	GA	9	3	4	7	0.4286	4	4	8	0.5000	A
O16	F	AD	DISP	5	G2GA	GA	10	6	0	6	1.0000	13	0	13	1.0000	A
O14	F	AD	DISP	5	G2GA	GA	11	1	2	3	0.3333	5	2	7	0.7143	A
O17	F	AD	DISP	5	G2GA	GA	12	4	2	6	0.6667	17	2	19	0.8947	A
O6	F	DA	AGRÉ	10	G1GB	GB	9	1	3	4	0.2500	1	7	8	0.1250	A
O13	F	DA	AGRÉ	10	G1GB	GB	10	4	0	4	1.0000	11	0	11	1.0000	A
O7	F	DA	AGRÉ	10	G1GB	GB	11	3	1	4	0.7500	10	1	11	0.9091	A
O5	F	DA	AGRÉ	10	G1GB	GB	12	1	1	2	0.5000	7	3	10	0.7000	A
O5	F	DA	AGRÉ	10	G1GB	GB	13	2	1	3	0.6667	5	3	8	0.6250	A
O7	F	DA	AGRÉ	10	G1GB	GB	14	5	0	5	1.0000	12	0	12	1.0000	A
O13	F	DA	AGRÉ	10	G1GB	GB	15	3	1	4	0.7500	12	2	14	0.8571	A
O6	F	DA	AGRÉ	10	G1GB	GB	16	1	3	4	0.2500	6	8	14	0.4286	A
O16	F	AD	DISP	5	G2GA	GA	13	5	1	6	0.8333	8	1	9	0.8889	A
O14	F	AD	DISP	5	G2GA	GA	14	2	4	6	0.3333	3	5	8	0.3750	A
O17	F	AD	DISP	5	G2GA	GA	15	2	2	4	0.5000	5	2	7	0.7143	A
O15	F	AD	DISP	5	G2GA	GA	16	2	6	8	0.2500	4	8	12	0.3333	A
O17	F	AD	DISP	5	G2GA	GA	17	3	3	6	0.5000	8	5	13	0.6154	A
O15	F	AD	DISP	5	G2GA	GA	18	2	4	6	0.3333	4	7	11	0.3636	A
O14	F	AD	DISP	5	G2GA	GA	19	1	4	5	0.2000	2	5	7	0.2857	A
O16	F	AD	DISP	5	G2GA	GA	20	9	0	9	1.0000	12	0	12	1.0000	A
O13	F	DA	AGRÉ	10	G1GB	GB	17	5	0	5	1.0000	28	0	28	1.0000	A
O6	F	DA	AGRÉ	10	G1GB	GB	18	3	3	6	0.5000	1	11	12	0.0833	A
O7	F	DA	AGRÉ	10	G1GB	GB	19	1	1	2	0.5000	5	2	7	0.7143	A
O5	F	DA	AGRÉ	10	G1GB	GB	20	0	2	2	0.0000	0	7	7	0.0000	A
B9	M	DA	DISP	5	G1GB	G1	1	4	0	4	1.0000	10	0	10	1.0000	A
B8	M	DA	DISP	5	G1GB	G1	2	4	3	7	0.5714	6	3	9	0.6667	A
B10	M	DA	DISP	5	G1GB	G1	3	5	5	10	0.5000	9	8	17	0.5294	A
B5	M	DA	DISP	5	G1GB	G1	4	4	3	7	0.5714	6	2	8	0.7500	A
B11	M	AD	AGRÉ	10	G2GA	G2	1	4	0	4	1.0000	17	0	17	1.0000	A
B6	M	AD	AGRÉ	10	G2GA	G2	2	2	2	4	0.5000	8	6	14	0.5714	A
B13	M	AD	AGRÉ	10	G2GA	G2	3	3	2	5	0.6000	7	5	12	0.5833	A
B12	M	AD	AGRÉ	10	G2GA	G2	4	2	5	7	0.2857	0	11	11	0.0000	A
B12	M	AD	AGRÉ	10	G2GA	G2	5	3	4	7	0.4286	6	7	13	0.4615	A
B13	M	AD	AGRÉ	10	G2GA	G2	6	1	2	3	0.3333	5	2	7	0.7143	A
B11	M	AD	AGRÉ	10	G2GA	G2	7	0	5	5	0.0000	0	10	10	0.0000	A
B6	M	AD	AGRÉ	10	G2GA	G2	8	5	2	7	0.7143	11	6	17	0.6471	A
B8	M	DA	DISP	5	G1GB	G1	5	1	4	5	0.2000	2	7	9	0.2222	A
B5	M	DA	DISP	5	G1GB	G1	6	4	5	9	0.4444	11	3	14	0.7857	A
B9	M	DA	DISP	5	G1GB	G1	7	7	0	7	1.0000	14	0	14	1.0000	A
B10	M	DA	DISP	5	G1GB	G1	8	6	2	8	0.7500	9	4	13	0.6923	A
B5	M	DA	DISP	5	G1GB	G1	9	2	9	11	0.1818	1	12	13	0.0769	A
B10	M	DA	DISP	5	G1GB	G1	10	4	3	7	0.5714	9	5	14	0.6429	A
B8	M	DA	DISP	5	G1GB	G1	11	1	8	9	0.1111	0	9	9	0.0000	A
B9	M	DA	DISP	5	G1GB	G1	12	7	1	8	0.8750	11	1	12	0.9167	A
B6	M	AD	AGRÉ	10	G2GA	G2	9	0	5	5	0.0000	0	9	9	0.0000	A

B11	M	AD	AGRÉ	10	G2GA	G2	10	2	3	5	0.4000	5	6	11	0.4545	A
B12	M	AD	AGRÉ	10	G2GA	G2	11	3	3	6	0.5000	6	5	11	0.5455	A
B13	M	AD	AGRÉ	10	G2GA	G2	12	3	4	7	0.4286	7	4	11	0.6364	A
B13	M	AD	AGRÉ	10	G2GA	G2	13	1	3	4	0.2500	2	6	8	0.2500	A
B12	M	AD	AGRÉ	10	G2GA	G2	14	2	4	6	0.3333	3	7	10	0.3000	A
B6	M	AD	AGRÉ	10	G2GA	G2	15	2	4	6	0.3333	5	9	14	0.3571	A
B11	M	AD	AGRÉ	10	G2GA	G2	16	3	4	7	0.4286	2	7	9	0.2222	A
B10	M	DA	DISP	5	G1GB	G1	13	5	1	6	0.8333	8	1	9	0.8889	A
B9	M	DA	DISP	5	G1GB	G1	14	4	0	4	1.0000	7	0	7	1.0000	A
B5	M	DA	DISP	5	G1GB	G1	15	5	4	9	0.5556	9	4	13	0.6923	A
B8	M	DA	DISP	5	G1GB	G1	16	1	5	6	0.1667	4	8	12	0.3333	A
B9	M	DA	DISP	5	G1GB	G1	17	5	2	7	0.7143	10	2	12	0.8333	A
B8	M	DA	DISP	5	G1GB	G1	18	0	6	6	0.0000	0	8	8	0.0000	A
B10	M	DA	DISP	5	G1GB	G1	19	2	4	6	0.3333	4	6	10	0.4000	A
B5	M	DA	DISP	5	G1GB	G1	20	3	4	7	0.4286	5	3	8	0.6250	A
B12	M	AD	AGRÉ	10	G2GA	G2	17	4	1	5	0.8000	4	4	8	0.5000	A
B6	M	AD	AGRÉ	10	G2GA	G2	18	1	5	6	0.1667	0	15	15	0.0000	A
B11	M	AD	AGRÉ	10	G2GA	G2	19	3	2	5	0.6000	9	4	13	0.6923	A
B13	M	AD	AGRÉ	10	G2GA	G2	20	2	2	4	0.5000	5	5	10	0.5000	A
B6	M	AD	DISP	5	G2GA	G2	1	1	4	5	0.2000	3	6	9	0.3333	A
B11	M	AD	DISP	5	G2GA	G2	2	1	2	3	0.3333	2	3	5	0.4000	A
B13	M	AD	DISP	5	G2GA	G2	3	4	4	8	0.5000	4	4	8	0.5000	A
B12	M	AD	DISP	5	G2GA	G2	4	2	2	4	0.5000	4	4	8	0.5000	A
B10	M	DA	AGRÉ	10	G1GB	G1	1	4	0	4	1.0000	16	0	16	1.0000	A
B8	M	DA	AGRÉ	10	G1GB	G1	2	2	2	4	0.5000	6	9	15	0.4000	A
B9	M	DA	AGRÉ	10	G1GB	G1	3	2	1	3	0.6667	4	2	6	0.6667	A
B5	M	DA	AGRÉ	10	G1GB	G1	4	2	4	6	0.3333	0	7	7	0.0000	A
B8	M	DA	AGRÉ	10	G1GB	G1	5	0	4	4	0.0000	0	10	10	0.0000	A
B5	M	DA	AGRÉ	10	G1GB	G1	6	0	4	4	0.0000	0	11	11	0.0000	A
B10	M	DA	AGRÉ	10	G1GB	G1	7	5	2	7	0.7143	7	8	15	0.4667	A
B9	M	DA	AGRÉ	10	G1GB	G1	8	3	2	5	0.6000	8	1	9	0.8889	A
B12	M	AD	DISP	5	G2GA	G2	5	4	3	7	0.5714	10	6	16	0.6250	A
B6	M	AD	DISP	5	G2GA	G2	6	3	7	10	0.3000	4	10	14	0.2857	A
B11	M	AD	DISP	5	G2GA	G2	7	2	3	5	0.4000	7	3	10	0.7000	A
B13	M	AD	DISP	5	G2GA	G2	8	3	1	4	0.7500	3	1	4	0.7500	A
B11	M	AD	DISP	5	G2GA	G2	9	6	2	8	0.7500	12	4	16	0.7500	A
B13	M	AD	DISP	5	G2GA	G2	10	2	1	3	0.6667	3	0	3	1.0000	A
B12	M	AD	DISP	5	G2GA	G2	11	4	1	5	0.8000	10	2	12	0.8333	A
B6	M	AD	DISP	5	G2GA	G2	12	4	7	11	0.3636	9	7	16	0.5625	A
B9	M	DA	AGRÉ	10	G1GB	G1	9	3	0	3	1.0000	10	0	10	1.0000	A
B10	M	DA	AGRÉ	10	G1GB	G1	10	4	1	5	0.8000	10	1	11	0.9091	A
B5	M	DA	AGRÉ	10	G1GB	G1	11	3	4	7	0.4286	1	9	10	0.1000	A
B8	M	DA	AGRÉ	10	G1GB	G1	12	0	3	3	0.0000	0	4	4	0.0000	A
B5	M	DA	AGRÉ	10	G1GB	G1	13	2	1	3	0.6667	4	1	5	0.8000	A
B9	M	DA	AGRÉ	10	G1GB	G1	14	2	0	2	1.0000	9	0	9	1.0000	A
B8	M	DA	AGRÉ	10	G1GB	G1	15	2	0	2	1.0000	4	0	4	1.0000	A
B10	M	DA	AGRÉ	10	G1GB	G1	16	2	2	4	0.5000	10	4	14	0.7143	A
B13	M	AD	DISP	5	G2GA	G2	13	2	3	5	0.4000	7	4	11	0.6364	A
B12	M	AD	DISP	5	G2GA	G2	14	3	3	6	0.5000	11	4	15	0.7333	A
B6	M	AD	DISP	5	G2GA	G2	15	2	6	8	0.2500	4	7	11	0.3636	A
B11	M	AD	DISP	5	G2GA	G2	16	4	1	5	0.8000	7	1	8	0.8750	A
B6	M	AD	DISP	5	G2GA	G2	17	3	7	10	0.3000	3	8	11	0.2727	A
B11	M	AD	DISP	5	G2GA	G2	18	2	6	8	0.2500	5	9	14	0.3571	A
B12	M	AD	DISP	5	G2GA	G2	19	4	2	6	0.6667	10	2	12	0.8333	A
B13	M	AD	DISP	5	G2GA	G2	20	4	0	4	1.0000	12	0	12	1.0000	A
B9	M	DA	AGRÉ	10	G1GB	G1	17	1	2	3	0.3333	6	3	9	0.6667	A
B5	M	DA	AGRÉ	10	G1GB	G1	18	1	2	3	0.3333	3	3	6	0.5000	A
B10	M	DA	AGRÉ	10	G1GB	G1	19	3	3	6	0.5000	0	6	6	0.0000	A

B8	M	DA	AGRÉ	10	G1GB	G1	20	2	1	3	0.6667	7	3	10	0.7000	A
O12	F	DA	DISP	5	G2GD	GD	3	NA	NA	NA	NA	NA	NA	NA	NA	B
O9	F	DA	DISP	5	G2GD	GD	4	6	0	6	1.0000	13	0	13	1.0000	B
O12	F	DA	DISP	5	G2GD	GD	5	4	1	5	0.8000	9	0	9	1.0000	B
O3	F	AD	AGRÉ	10	G1GC	GC	1	4	3	7	0.5714	4	8	12	0.3333	B
O2	F	AD	AGRÉ	10	G1GC	GC	2	3	0	3	1.0000	12	0	12	1.0000	B
O11	F	AD	AGRÉ	10	G1GC	GC	3	0	4	4	0.0000	0	9	9	0.0000	B
O4	F	AD	AGRÉ	10	G1GC	GC	4	4	1	5	0.8000	14	2	16	0.8750	B
O11	F	AD	AGRÉ	10	G1GC	GC	5	3	2	5	0.6000	10	6	16	0.6250	B
O4	F	AD	AGRÉ	10	G1GC	GC	6	2	2	4	0.5000	11	4	15	0.7333	B
O2	F	AD	AGRÉ	10	G1GC	GC	7	3	0	3	1.0000	14	0	14	1.0000	B
O3	F	AD	AGRÉ	10	G1GC	GC	8	3	2	5	0.6000	12	4	16	0.7500	B
O9	F	DA	DISP	5	G2GD	GD	6	8	2	10	0.8000	17	2	19	0.8947	B
O12	F	DA	DISP	5	G2GD	GD	7	4	2	6	0.6667	14	5	19	0.7368	B
O12	F	DA	DISP	5	G2GD	GD	10	1	2	3	0.3333	5	4	9	0.5556	B
O9	F	DA	DISP	5	G2GD	GD	11	8	2	10	0.8000	9	3	12	0.7500	B
O2	F	AD	AGRÉ	10	G1GC	GC	9	5	1	6	0.8333	6	1	7	0.8571	B
O3	F	AD	AGRÉ	10	G1GC	GC	10	0	4	4	0.0000	0	8	8	0.0000	B
O4	F	AD	AGRÉ	10	G1GC	GC	11	5	0	5	1.0000	16	0	16	1.0000	B
O11	F	AD	AGRÉ	10	G1GC	GC	12	4	2	6	0.6667	16	4	20	0.8000	B
O4	F	AD	AGRÉ	10	G1GC	GC	13	9	0	9	1.0000	16	0	16	1.0000	B
O11	F	AD	AGRÉ	10	G1GC	GC	14	1	3	4	0.2500	2	6	8	0.2500	B
O3	F	AD	AGRÉ	10	G1GC	GC	15	0	3	3	0.0000	0	8	8	0.0000	B
O2	F	AD	AGRÉ	10	G1GC	GC	16	2	4	6	0.3333	0	7	7	0.0000	B
O9	F	DA	DISP	5	G2GD	GD	16	3	3	6	0.5000	4	5	9	0.4444	B
O12	F	DA	DISP	5	G2GD	GD	17	3	0	3	1.0000	9	0	9	1.0000	B
O12	F	DA	DISP	5	G2GD	GD	18	4	0	4	1.0000	9	0	9	1.0000	B
O9	F	DA	DISP	5	G2GD	GD	18	5	6	11	0.4545	7	10	17	0.4118	B
O2	F	AD	AGRÉ	10	G1GC	GC	17	1	3	4	0.2500	0	7	7	0.0000	B
O3	F	AD	AGRÉ	10	G1GC	GC	18	1	3	4	0.2500	4	10	14	0.2857	B
O11	F	AD	AGRÉ	10	G1GC	GC	19	1	3	4	0.2500	6	7	13	0.4615	B
O4	F	AD	AGRÉ	10	G1GC	GC	20	3	0	3	1.0000	8	0	8	1.0000	B
O11	F	AD	DISP	5	G1GC	GC	1	2	0	2	1.0000	6	0	6	1.0000	B
O3	F	AD	DISP	5	G1GC	GC	2	5	4	9	0.5556	3	8	11	0.2727	B
O4	F	AD	DISP	5	G1GC	GC	3	7	0	7	1.0000	19	0	19	1.0000	B
O2	F	AD	DISP	5	G1GC	GC	4	3	0	3	1.0000	6	0	6	1.0000	B
O9	F	DA	AGRÉ	10	G2GD	GD	3	0	4	4	0.0000	0	10	10	0.0000	B
O12	F	DA	AGRÉ	10	G2GD	GD	4	3	0	3	1.0000	8	0	8	1.0000	B
O12	F	DA	AGRÉ	10	G2GD	GD	5	3	1	4	0.7500	6	3	9	0.6667	B
O9	F	DA	AGRÉ	10	G2GD	GD	6	0	4	4	0.0000	0	13	13	0.0000	B
O2	F	AD	DISP	5	G1GC	GC	5	2	2	4	0.5000	5	1	6	0.8333	B
O11	F	AD	DISP	5	G1GC	GC	6	4	0	4	1.0000	10	0	10	1.0000	B
O3	F	AD	DISP	5	G1GC	GC	7	0	6	6	0.0000	0	11	11	0.0000	B
O4	F	AD	DISP	5	G1GC	GC	8	6	1	7	0.8571	17	3	20	0.8500	B
O3	F	AD	DISP	5	G1GC	GC	9	6	5	11	0.5455	4	12	16	0.2500	B
O4	F	AD	DISP	5	G1GC	GC	10	2	1	3	0.6667	5	2	7	0.7143	B
O2	F	AD	DISP	5	G1GC	GC	11	1	1	2	0.5000	5	0	5	1.0000	B
O11	F	AD	DISP	5	G1GC	GC	12	3	0	3	1.0000	9	0	9	1.0000	B
O9	F	DA	AGRÉ	10	G2GD	GD	9	2	3	5	0.4000	4	12	16	0.2500	B
O12	F	DA	AGRÉ	10	G2GD	GD	10	3	1	4	0.7500	14	1	15	0.9333	B
O12	F	DA	AGRÉ	10	G2GD	GD	15	1	1	2	0.5000	4	2	6	0.6667	B
O9	F	DA	AGRÉ	10	G2GD	GD	16	0	4	4	0.0000	0	11	11	0.0000	B
O4	F	AD	DISP	5	G1GC	GC	13	5	0	5	1.0000	14	0	14	1.0000	B
O2	F	AD	DISP	5	G1GC	GC	14	2	0	2	1.0000	7	0	7	1.0000	B
O11	F	AD	DISP	5	G1GC	GC	15	2	1	3	0.6667	5	1	6	0.8333	B
O3	F	AD	DISP	5	G1GC	GC	16	8	4	12	0.6667	13	10	23	0.5652	B
O11	F	AD	DISP	5	G1GC	GC	17	5	2	7	0.7143	8	4	12	0.6667	B
O3	F	AD	DISP	5	G1GC	GC	18	10	2	12	0.8333	14	4	18	0.7778	B

O2	F	AD	DISP	5	G1GC	GC	19	4	0	4	1.0000	11	0	11	1.0000	B
O4	F	AD	DISP	5	G1GC	GC	20	5	1	6	0.8333	15	2	17	0.8824	B
O12	F	DA	AGRÉ	10	G2GD	GD	17	3	0	3	1.0000	9	0	9	1.0000	B
O9	F	DA	AGRÉ	10	G2GD	GD	18	1	3	4	0.2500	5	14	19	0.2632	B
B11	M	DA	DISP	5	G2GD	G2	1	4	0	4	1.0000	10	0	10	1.0000	B
B6	M	DA	DISP	5	G2GD	G2	2	7	3	10	0.7000	13	5	18	0.7222	B
B13	M	DA	DISP	5	G2GD	G2	3	4	1	5	0.8000	12	1	13	0.9231	B
B12	M	DA	DISP	5	G2GD	G2	4	2	2	4	0.5000	10	4	14	0.7143	B
B9	M	AD	AGRÉ	10	G1GC	G1	1	2	2	4	0.5000	11	4	15	0.7333	B
B8	M	AD	AGRÉ	10	G1GC	G1	2	1	3	4	0.2500	8	8	16	0.5000	B
B10	M	AD	AGRÉ	10	G1GC	G1	3	5	3	8	0.6250	10	8	18	0.5556	B
B5	M	AD	AGRÉ	10	G1GC	G1	4	0	2	2	0.0000	0	8	8	0.0000	B
B8	M	AD	AGRÉ	10	G1GC	G1	5	1	4	5	0.2000	10	2	12	0.8333	B
B5	M	AD	AGRÉ	10	G1GC	G1	6	2	2	4	0.5000	9	2	11	0.8182	B
B9	M	AD	AGRÉ	10	G1GC	G1	7	2	2	4	0.5000	6	4	10	0.6000	B
B10	M	AD	AGRÉ	10	G1GC	G1	8	4	0	4	1.0000	17	0	17	1.0000	B
B12	M	DA	DISP	5	G2GD	G2	5	4	2	6	0.6667	8	3	11	0.7273	B
B13	M	DA	DISP	5	G2GD	G2	6	4	1	5	0.8000	9	1	10	0.9000	B
B11	M	DA	DISP	5	G2GD	G2	7	3	1	4	0.7500	9	2	11	0.8182	B
B6	M	DA	DISP	5	G2GD	G2	8	2	4	6	0.3333	7	2	9	0.7778	B
B6	M	DA	DISP	5	G2GD	G2	9	5	0	5	1.0000	16	0	16	1.0000	B
B11	M	DA	DISP	5	G2GD	G2	10	4	2	6	0.6667	8	3	11	0.7273	B
B12	M	DA	DISP	5	G2GD	G2	11	2	2	4	0.5000	7	2	9	0.7778	B
B13	M	DA	DISP	5	G2GD	G2	12	3	0	3	1.0000	11	0	11	1.0000	B
B5	M	AD	AGRÉ	10	G1GC	G1	9	3	2	5	0.6000	6	4	10	0.6000	B
B10	M	AD	AGRÉ	10	G1GC	G1	10	3	3	6	0.5000	4	6	10	0.4000	B
B8	M	AD	AGRÉ	10	G1GC	G1	11	2	5	7	0.2857	0	12	12	0.0000	B
B9	M	AD	AGRÉ	10	G1GC	G1	12	3	2	5	0.6000	12	6	18	0.6667	B
B10	M	AD	AGRÉ	10	G1GC	G1	13	2	5	7	0.2857	7	5	12	0.5833	B
B9	M	AD	AGRÉ	10	G1GC	G1	14	3	1	4	0.7500	8	2	10	0.8000	B
B5	M	AD	AGRÉ	10	G1GC	G1	15	1	3	4	0.2500	0	10	10	0.0000	B
B8	M	AD	AGRÉ	10	G1GC	G1	16	2	4	6	0.3333	0	9	9	0.0000	B
B13	M	DA	DISP	5	G2GD	G2	13	4	1	5	0.8000	9	2	11	0.8182	B
B12	M	DA	DISP	5	G2GD	G2	14	6	2	8	0.7500	11	3	14	0.7857	B
B6	M	DA	DISP	5	G2GD	G2	15	5	2	7	0.7143	8	1	9	0.8889	B
B11	M	DA	DISP	5	G2GD	G2	16	7	1	8	0.8750	8	1	9	0.8889	B
B12	M	DA	DISP	5	G2GD	G2	17	4	2	6	0.6667	7	3	10	0.7000	B
B6	M	DA	DISP	5	G2GD	G2	18	3	7	10	0.3000	4	8	12	0.3333	B
B11	M	DA	DISP	5	G2GD	G2	19	6	3	9	0.6667	8	4	12	0.6667	B
B13	M	DA	DISP	5	G2GD	G2	20	3	0	3	1.0000	13	0	13	1.0000	B
B9	M	AD	AGRÉ	10	G1GC	G1	17	3	0	3	1.0000	13	0	13	1.0000	B
B8	M	AD	AGRÉ	10	G1GC	G1	18	0	9	9	0.0000	0	9	9	0.0000	B
B10	M	AD	AGRÉ	10	G1GC	G1	19	1	3	4	0.2500	5	3	8	0.6250	B
B5	M	AD	AGRÉ	10	G1GC	G1	20	3	5	8	0.3750	7	10	17	0.4118	B
B10	M	AD	DISP	5	G1GC	G1	1	0	7	7	0.0000	0	10	10	0.0000	B
B8	M	AD	DISP	5	G1GC	G1	2	4	4	8	0.5000	2	8	10	0.2000	B
B9	M	AD	DISP	5	G1GC	G1	3	7	1	8	0.8750	19	1	20	0.9500	B
B5	M	AD	DISP	5	G1GC	G1	4	4	2	6	0.6667	9	3	12	0.7500	B
B6	M	DA	AGRÉ	10	G2GD	G2	1	0	5	5	0.0000	0	12	12	0.0000	B
B11	M	DA	AGRÉ	10	G2GD	G2	2	3	0	3	1.0000	9	0	9	1.0000	B
B13	M	DA	AGRÉ	10	G2GD	G2	3	2	0	2	1.0000	10	0	10	1.0000	B
B12	M	DA	AGRÉ	10	G2GD	G2	4	1	3	4	0.2500	0	12	12	0.0000	B
B12	M	DA	AGRÉ	10	G2GD	G2	5	1	1	2	0.5000	10	1	11	0.9091	B
B6	M	DA	AGRÉ	10	G2GD	G2	6	1	2	3	0.3333	9	2	11	0.8182	B
B11	M	DA	AGRÉ	10	G2GD	G2	7	5	1	6	0.8333	10	2	12	0.8333	B
B13	M	DA	AGRÉ	10	G2GD	G2	8	0	2	2	0.0000	0	7	7	0.0000	B
B8	M	AD	DISP	5	G1GC	G1	5	8	3	11	0.7273	15	4	19	0.7895	B
B5	M	AD	DISP	5	G1GC	G1	6	3	5	8	0.3750	5	7	12	0.4167	B

B10	M	AD	DISP	5	G1GC	G1	7	8	1	9	0.8889	15	1	16	0.9375	B
B9	M	AD	DISP	5	G1GC	G1	8	8	1	9	0.8889	11	2	13	0.8462	B
B9	M	AD	DISP	5	G1GC	G1	9	1	0	1	1.0000	1	0	1	1.0000	B
B10	M	AD	DISP	5	G1GC	G1	10	6	3	9	0.6667	10	4	14	0.7143	B
B5	M	AD	DISP	5	G1GC	G1	11	4	1	5	0.8000	9	0	9	1.0000	B
B8	M	AD	DISP	5	G1GC	G1	12	4	2	6	0.6667	10	5	15	0.6667	B
B11	M	DA	AGRÉ	10	G2GD	G2	9	2	2	4	0.5000	8	0	8	1.0000	B
B13	M	DA	AGRÉ	10	G2GD	G2	10	1	0	1	1.0000	6	0	6	1.0000	B
B12	M	DA	AGRÉ	10	G2GD	G2	11	2	2	4	0.5000	4	4	8	0.5000	B
B6	M	DA	AGRÉ	10	G2GD	G2	12	2	3	5	0.4000	6	9	15	0.4000	B
B13	M	DA	AGRÉ	10	G2GD	G2	13	3	0	3	1.0000	15	0	15	1.0000	B
B12	M	DA	AGRÉ	10	G2GD	G2	14	0	5	5	0.0000	0	11	11	0.0000	B
B6	M	DA	AGRÉ	10	G2GD	G2	15	4	3	7	0.5714	3	7	10	0.3000	B
B11	M	DA	AGRÉ	10	G2GD	G2	16	6	1	7	0.8571	12	1	13	0.9231	B
B5	M	AD	DISP	5	G1GC	G1	13	2	2	4	0.5000	1	2	3	0.3333	B
B9	M	AD	DISP	5	G1GC	G1	14	3	1	4	0.7500	9	1	10	0.9000	B
B8	M	AD	DISP	5	G1GC	G1	15	3	2	5	0.6000	11	2	13	0.8462	B
B10	M	AD	DISP	5	G1GC	G1	16	8	0	8	1.0000	7	0	7	1.0000	B
B9	M	AD	DISP	5	G1GC	G1	17	5	2	7	0.7143	8	2	10	0.8000	B
B5	M	AD	DISP	5	G1GC	G1	18	6	1	7	0.8571	11	2	13	0.8462	B
B10	M	AD	DISP	5	G1GC	G1	19	8	2	10	0.8000	13	3	16	0.8125	B
B8	M	AD	DISP	5	G1GC	G1	20	5	4	9	0.5556	5	8	13	0.3846	B
B6	M	DA	AGRÉ	10	G2GD	G2	17	2	3	5	0.4000	3	6	9	0.3333	B
B11	M	DA	AGRÉ	10	G2GD	G2	18	2	1	3	0.6667	11	1	12	0.9167	B
B12	M	DA	AGRÉ	10	G2GD	G2	19	0	4	4	0.0000	0	11	11	0.0000	B
B13	M	DA	AGRÉ	10	G2GD	G2	20	1	0	1	1.0000	6	0	6	1.0000	B
O10	F	DA	DISP	5	G1GE	GE	1	1	5	6	0.16667	4	9	13	0.3077	C
O8	F	DA	DISP	5	G1GE	GE	2	6	1	7	0.85714	8	1	9	0.8889	C
O18	F	DA	DISP	5	G1GE	GE	4	1	0	1	1.0000	0	0	0	0.0000	C
O18	F	DA	DISP	5	G1GE	GE	6	NA	NA	NA	NA	NA	NA	NA	NA	C
O10	F	DA	DISP	5	G1GE	GE	8	6	2	8	0.7500	21	4	25	0.8400	C
O8	F	DA	DISP	5	G1GE	GE	9	6	0	6	1.0000	16	0	16	1.0000	C
O18	F	DA	DISP	5	G1GE	GE	10	3	0	3	1.0000	10	0	10	1.0000	C
O10	F	DA	DISP	5	G1GE	GE	12	3	1	4	0.7500	10	1	11	0.9091	C
O18	F	DA	DISP	5	G1GE	GE	13	4	0	4	1.0000	5	0	5	1.0000	C
O8	F	DA	DISP	5	G1GE	GE	14	3	1	4	0.7500	3	3	6	0.5000	C
O8	F	DA	DISP	5	G1GE	GE	15	7	2	9	0.7778	9	4	13	0.6923	C
O18	F	DA	DISP	5	G1GE	GE	16	3	0	3	1.0000	6	0	6	1.0000	C
O10	F	DA	DISP	5	G1GE	GE	17	6	3	9	0.6667	9	4	13	0.6923	C
O10	F	DA	DISP	5	G1GE	GE	20	4	3	7	0.5714	3	4	7	0.4286	C
O8	F	DA	DISP	5	G1GE	GE	21	3	2	5	0.6000	13	3	16	0.8125	C
O18	F	DA	DISP	5	G1GE	GE	22	3	1	4	0.7500	3	2	5	0.6000	C
O18	F	DA	AGRÉ	10	G1GE	GE	1	2	2	2	1.0000	2	7	9	0.2222	C
O10	F	DA	AGRÉ	10	G1GE	GE	2	2	5	7	0.2857	5	11	16	0.3125	C
O8	F	DA	AGRÉ	10	G1GE	GE	3	0	4	4	0.0000	0	15	15	0.0000	C
O8	F	DA	AGRÉ	10	G1GE	GE	6	2	2	4	0.5000	3	4	7	0.4286	C
O10	F	DA	AGRÉ	10	G1GE	GE	7	4	3	7	0.5714	5	7	12	0.4167	C
O18	F	DA	AGRÉ	10	G1GE	GE	8	1	4	5	0.2000	0	12	12	0.0000	C
O8	F	DA	AGRÉ	10	G1GE	GE	9	4	1	5	0.8000	20	2	22	0.9091	C
O18	F	DA	AGRÉ	10	G1GE	GE	11	2	1	3	0.6667	7	4	11	0.6364	C
O10	F	DA	AGRÉ	10	G1GE	GE	12	2	1	3	0.6667	15	0	15	1.0000	C
O10	F	DA	AGRÉ	10	G1GE	GE	13	2	6	8	0.2500	0	5	5	0.0000	C
O18	F	DA	AGRÉ	10	G1GE	GE	14	1	2	3	0.3333	0	6	6	0.0000	C
O8	F	DA	AGRÉ	10	G1GE	GE	16	3	1	4	0.7500	9	6	15	0.6000	C
O8	F	DA	AGRÉ	10	G1GE	GE	18	3	2	5	0.6000	11	6	17	0.6471	C
O18	F	DA	AGRÉ	10	G1GE	GE	19	2	2	4	0.5000	0	12	12	0.0000	C
O10	F	DA	AGRÉ	10	G1GE	GE	20	2	3	5	0.4000	7	11	18	0.3889	C
B9	M	DA	DISP	5	G1GE	G1	1	2	2	4	0.5000	5	1	6	0.8333	C

B8	M	DA	DISP	5	G1GE	G1	2	1	3	4	0.2500	1	5	6	0.1667	C
B10	M	DA	DISP	5	G1GE	G1	3	7	0	7	1.0000	20	0	20	1.0000	C
B5	M	DA	DISP	5	G1GE	G1	4	2	1	3	0.6667	4	0	4	1.0000	C
B8	M	DA	DISP	5	G1GE	G1	5	3	4	7	0.4286	6	5	11	0.5455	C
B5	M	DA	DISP	5	G1GE	G1	6	7	0	7	1.0000	13	0	13	1.0000	C
B9	M	DA	DISP	5	G1GE	G1	7	6	0	6	1.0000	11	0	11	1.0000	C
B10	M	DA	DISP	5	G1GE	G1	8	6	1	7	0.8571	14	2	16	0.8750	C
B5	M	DA	DISP	5	G1GE	G1	9	4	1	5	0.8000	9	0	9	1.0000	C
B10	M	DA	DISP	5	G1GE	G1	10	10	1	11	0.9091	7	1	8	0.8750	C
B8	M	DA	DISP	5	G1GE	G1	11	1	4	5	0.2000	4	4	8	0.5000	C
B9	M	DA	DISP	5	G1GE	G1	12	2	2	4	0.5000	2	3	5	0.4000	C
B10	M	DA	DISP	5	G1GE	G1	13	7	2	9	0.7778	4	3	7	0.5714	C
B9	M	DA	DISP	5	G1GE	G1	14	5	0	5	1.0000	11	0	11	1.0000	C
B5	M	DA	DISP	5	G1GE	G1	15	3	0	3	1.0000	7	0	7	1.0000	C
B8	M	DA	DISP	5	G1GE	G1	16	2	3	5	0.4000	7	4	11	0.6364	C
B9	M	DA	DISP	5	G1GE	G1	17	4	1	5	0.8000	11	1	12	0.9167	C
B8	M	DA	DISP	5	G1GE	G1	18	3	4	7	0.4286	9	9	18	0.5000	C
B10	M	DA	DISP	5	G1GE	G1	19	6	0	6	1.0000	7	0	7	1.0000	C
B5	M	DA	DISP	5	G1GE	G1	20	2	0	2	1.0000	10	0	10	1.0000	C
B10	M	DA	AGRÉ	10	G1GE	G1	1	3	1	4	0.7500	10	2	12	0.8333	C
B8	M	DA	AGRÉ	10	G1GE	G1	2	1	3	4	0.2500	6	9	15	0.4000	C
B9	M	DA	AGRÉ	10	G1GE	G1	3	3	0	3	1.0000	4	0	4	1.0000	C
B5	M	DA	AGRÉ	10	G1GE	G1	4	3	0	3	1.0000	9	0	9	1.0000	C
B8	M	DA	AGRÉ	10	G1GE	G1	5	3	2	5	0.6000	12	1	13	0.9231	C
B5	M	DA	AGRÉ	10	G1GE	G1	6	4	0	4	1.0000	2	0	2	1.0000	C
B10	M	DA	AGRÉ	10	G1GE	G1	7	2	3	5	0.4000	1	12	13	0.0769	C
B9	M	DA	AGRÉ	10	G1GE	G1	8	0	1	1	0.0000	0	3	3	0.0000	C
B9	M	DA	AGRÉ	10	G1GE	G1	9	1	3	4	0.2500	0	5	5	0.0000	C
B10	M	DA	AGRÉ	10	G1GE	G1	10	5	1	6	0.8333	15	5	20	0.7500	C
B5	M	DA	AGRÉ	10	G1GE	G1	11	3	0	3	1.0000	6	0	6	1.0000	C
B8	M	DA	AGRÉ	10	G1GE	G1	12	2	4	6	0.3333	7	8	15	0.4667	C
B5	M	DA	AGRÉ	10	G1GE	G1	13	2	2	4	0.5000	5	3	8	0.6250	C
B9	M	DA	AGRÉ	10	G1GE	G1	14	3	1	4	0.7500	2	2	4	0.5000	C
B8	M	DA	AGRÉ	10	G1GE	G1	15	2	4	6	0.3333	5	9	14	0.3571	C
B10	M	DA	AGRÉ	10	G1GE	G1	16	6	0	6	1.0000	20	0	20	1.0000	C
B9	M	DA	AGRÉ	10	G1GE	G1	17	NA	NA	NA	NA	NA	NA	NA	NA	C
B5	M	DA	AGRÉ	10	G1GE	G1	18	1	0	1	1.0000	6	0	6	1.0000	C
B10	M	DA	AGRÉ	10	G1GE	G1	19	7	0	7	1.0000	35	0	35	1.0000	C
B8	M	DA	AGRÉ	10	G1GE	G1	20	1	1	2	0.5000	10	4	14	0.7143	C
B9	M	DA	AGRÉ	10	G1GE	G1	21	NA	NA	NA	NA	NA	NA	NA	NA	C
O34	F	DA	DISP	5	G3GG	GG	1	5	1	6	0.833333333	6	2	8	0.75	A
O28	F	DA	DISP	5	G3GG	GG	2	2	2	4	0.5	9	3	12	0.75	A
O30	F	DA	DISP	5	G3GG	GG	3	9	3	12	0.75	12	4	16	0.75	A
O25	F	DA	DISP	5	G3GG	GG	4	8	0	8	1	16	0	16	1	A
O26	F	AD	AGRÉ	10	G4GH	GH	1	5	3	8	0.625	7	6	13	0.538461538	A
O33	F	AD	AGRÉ	10	G4GH	GH	2	3	4	7	0.428571429	0	12	12	0	A
O29	F	AD	AGRÉ	10	G4GH	GH	3	4	0	4	1	16	0	16	1	A
O27	F	AD	AGRÉ	10	G4GH	GH	4	2	3	5	0.4	1	2	3	0.333333333	A
O33	F	AD	AGRÉ	10	G4GH	GH	5	2	2	4	0.5	7	1	8	0.875	A
O29	F	AD	AGRÉ	10	G4GH	GH	6	2	2	4	0.5	8	4	12	0.666666667	A
O27	F	AD	AGRÉ	10	G4GH	GH	7	13	1	14	0.928571429	10	3	13	0.769230769	A
O26	F	AD	AGRÉ	10	G4GH	GH	8	2	4	6	0.333333333	0	13	13	0	A
O30	F	DA	DISP	5	G3GG	GG	5	5	1	6	0.833333333	13	3	16	0.8125	A
O25	F	DA	DISP	5	G3GG	GG	6	3	2	5	0.6	9	5	14	0.642857143	A
O34	F	DA	DISP	5	G3GG	GG	7	4	2	6	0.666666667	9	4	13	0.692307692	A
O28	F	DA	DISP	5	G3GG	GG	8	7	2	9	0.777777778	15	1	16	0.9375	A
O25	F	DA	DISP	5	G3GG	GG	9	5	2	7	0.714285714	14	3	17	0.823529412	A
O30	F	DA	DISP	5	G3GG	GG	10	4	2	6	0.666666667	13	1	14	0.928571429	A

O28	F	DA	DISP	5	G3GG	GG	11	1	4	5	0.2	5	4	9	0.555555556	A
O34	F	DA	DISP	5	G3GG	GG	12	2	3	5	0.4	5	5	10	0.5	A
O29	F	AD	AGRÉ	10	G4GH	GH	9	2	1	3	0.666666667	12	1	13	0.923076923	A
O26	F	AD	AGRÉ	10	G4GH	GH	10	1	5	6	0.166666667	0	8	8	0	A
O33	F	AD	AGRÉ	10	G4GH	GH	11	2	4	6	0.333333333	0	11	11	0	A
O27	F	AD	AGRÉ	10	G4GH	GH	12	6	2	8	0.75	10	1	11	0.909090909	A
O27	F	AD	AGRÉ	10	G4GH	GH	13	13	2	15	0.866666667	11	3	14	0.785714286	A
O29	F	AD	AGRÉ	10	G4GH	GH	14	2	4	6	0.333333333	2	4	6	0.333333333	A
O26	F	AD	AGRÉ	10	G4GH	GH	15	3	4	7	0.428571429	0	15	15	0	A
O33	F	AD	AGRÉ	10	G4GH	GH	16	2	5	7	0.285714286	0	10	10	0	A
O34	F	DA	DISP	5	G3GG	GG	13	4	3	7	0.571428571	10	3	13	0.769230769	A
O28	F	DA	DISP	5	G3GG	GG	14	4	2	6	0.666666667	8	3	11	0.727272727	A
O25	F	DA	DISP	5	G3GG	GG	15	2	1	3	0.666666667	10	2	12	0.833333333	A
O30	F	DA	DISP	5	G3GG	GG	16	5	0	5	1	18	0	18	1	A
O25	F	DA	DISP	5	G3GG	GG	17	5	1	6	0.833333333	14	1	15	0.933333333	A
O34	F	DA	DISP	5	G3GG	GG	18	1	2	3	0.333333333	5	6	11	0.454545455	A
O30	F	DA	DISP	5	G3GG	GG	19	10	1	11	0.909090909	11	1	12	0.916666667	A
O28	F	DA	DISP	5	G3GG	GG	20	5	2	7	0.714285714	6	4	10	0.6	A
O33	F	AD	AGRÉ	10	G4GH	GH	17	0	5	5	0	0	10	10	0	A
O27	F	AD	AGRÉ	10	G4GH	GH	18	6	3	9	0.666666667	3	8	11	0.272727273	A
O26	F	AD	AGRÉ	10	G4GH	GH	19	2	6	8	0.25	3	8	11	0.272727273	A
O29	F	AD	AGRÉ	10	G4GH	GH	20	4	1	5	0.8	14	4	18	0.777777778	A
O33	F	DA	DISP	5	G4GH	GH	1	5	5	20	0.25	17	4	21	0.80952381	A
O27	F	DA	DISP	5	G4GH	GH	2	6	1	7	0.857142857	9	0	9	1	A
O29	F	DA	DISP	5	G4GH	GH	3	3	1	4	0.75	13	2	15	0.866666667	A
O26	F	DA	DISP	5	G4GH	GH	4	5	3	8	0.625	10	6	16	0.625	A
O30	F	AD	AGRÉ	10	G3GG	GG	1	3	3	6	0.5	4	5	9	0.444444444	A
O34	F	AD	AGRÉ	10	G3GG	GG	2	1	4	5	0.2	5	14	19	0.263157895	A
O25	F	AD	AGRÉ	10	G3GG	GG	3	1	2	3	0.333333333	8	4	12	0.666666667	A
O28	F	AD	AGRÉ	10	G3GG	GG	4	0	4	4	0	0	12	12	0	A
O25	F	AD	AGRÉ	10	G3GG	GG	5	4	1	5	0.8	14	2	16	0.875	A
O28	F	AD	AGRÉ	10	G3GG	GG	6	1	3	4	0.25	4	5	9	0.444444444	A
O30	F	AD	AGRÉ	10	G3GG	GG	7	6	1	7	0.857142857	18	4	22	0.818181818	A
O34	F	AD	AGRÉ	10	G3GG	GG	8	0	4	4	0	0	16	16	0	A
O27	F	DA	DISP	5	G4GH	GH	5	7	2	9	0.777777778	13	1	14	0.928571429	A
O29	F	DA	DISP	5	G4GH	GH	6	4	0	4	1	13	0	13	1	A
O26	F	DA	DISP	5	G4GH	GH	7	2	4	6	0.333333333	4	7	11	0.363636364	A
O33	F	DA	DISP	5	G4GH	GH	8	3	3	6	0.5	9	2	11	0.818181818	A
O26	F	DA	DISP	5	G4GH	GH	9	3	6	9	0.333333333	4	11	15	0.266666667	A
O33	F	DA	DISP	5	G4GH	GH	10	4	0	4	1	15	0	15	1	A
O27	F	DA	DISP	5	G4GH	GH	11	4	2	6	0.666666667	12	0	12	1	A
O29	F	DA	DISP	5	G4GH	GH	12	3	2	5	0.6	7	3	10	0.7	A
O34	F	AD	AGRÉ	10	G3GG	GG	9	1	4	5	0.2	4	8	12	0.333333333	A
O30	F	AD	AGRÉ	10	G3GG	GG	10	4	2	6	0.666666667	7	4	11	0.636363636	A
O28	F	AD	AGRÉ	10	G3GG	GG	11	1	1	2	0.5	5	2	7	0.714285714	A
O25	F	AD	AGRÉ	10	G3GG	GG	12	1	2	3	0.333333333	5	3	8	0.625	A
O28	F	AD	AGRÉ	10	G3GG	GG	13	0	3	3	0	0	8	8	0	A
O25	F	AD	AGRÉ	10	G3GG	GG	14	3	1	4	0.75	7	5	12	0.583333333	A
O34	F	AD	AGRÉ	10	G3GG	GG	15	1	4	5	0.2	3	6	9	0.333333333	A
O30	F	AD	AGRÉ	10	G3GG	GG	16	2	2	4	0.5	6	5	11	0.545454545	A
O29	F	DA	DISP	5	G4GH	GH	13	5	0	5	1	13	0	13	1	A
O26	F	DA	DISP	5	G4GH	GH	14	0	8	8	0	0	9	9	0	A
O33	F	DA	DISP	5	G4GH	GH	15	5	1	6	0.833333333	13	1	14	0.928571429	A
O27	F	DA	DISP	5	G4GH	GH	16	8	0	8	1	13	0	13	1	A
O27	F	DA	DISP	5	G4GH	GH	17	8	0	8	1	9	0	9	1	A
O33	F	DA	DISP	5	G4GH	GH	18	4	1	5	0.8	10	2	12	0.833333333	A
O29	F	DA	DISP	5	G4GH	GH	19	5	0	5	1	14	0	14	1	A
O26	F	DA	DISP	5	G4GH	GH	20	4	3	7	0.571428571	8	3	11	0.727272727	A

O30	F	AD	AGRÉ	10	G3GG	GG	17	7	2	9	0.777777778	7	6	13	0.538461538	A
O34	F	AD	AGRÉ	10	G3GG	GG	18	1	2	3	0.333333333	0	4	4	0	A
O28	F	AD	AGRÉ	10	G3GG	GG	19	2	2	4	0.5	9	2	11	0.818181818	A
O25	F	AD	AGRÉ	10	G3GG	GG	20	3	1	4	0.75	11	1	12	0.916666667	A
B20	M	DA	DISP	5	G3GG	G3	1	3	3	6	0.5	5	8	13	0.384615385	A
B16	M	DA	DISP	5	G3GG	G3	2	5	3	8	0.625	8	3	11	0.727272727	A
B33	M	DA	DISP	5	G3GG	G3	3	4	3	7	0.571428571	6	3	9	0.666666667	A
B36	M	DA	DISP	5	G3GG	G3	4	5	4	9	0.555555556	9	4	13	0.692307692	A
B15	M	AD	AGRÉ	10	G4GH	G4	1	2	1	3	0.666666667	11	2	13	0.846153846	A
B34	M	AD	AGRÉ	10	G4GH	G4	2	1	2	3	0.333333333	6	3	9	0.666666667	A
B18	M	AD	AGRÉ	10	G4GH	G4	3	0	5	5	0	0	12	12	0	A
B35	M	AD	AGRÉ	10	G4GH	G4	4	2	0	2	1	8	0	8	1	A
B18	M	AD	AGRÉ	10	G4GH	G4	5	0	2	2	0	0	16	16	0	A
B15	M	AD	AGRÉ	10	G4GH	G4	6	5	3	8	0.625	12	3	15	0.8	A
B35	M	AD	AGRÉ	10	G4GH	G4	7	5	4	9	0.555555556	1	7	8	0.125	A
B34	M	AD	AGRÉ	10	G4GH	G4	8	4	3	7	0.571428571	1	7	8	0.125	A
B36	M	DA	DISP	5	G3GG	G3	5	4	3	7	0.571428571	10	4	14	0.714285714	A
B20	M	DA	DISP	5	G3GG	G3	6	3	5	8	0.375	8	7	15	0.533333333	A
B33	M	DA	DISP	5	G3GG	G3	7	8	2	10	0.8	7	1	8	0.875	A
B16	M	DA	DISP	5	G3GG	G3	8	2	6	8	0.25	3	6	9	0.333333333	A
B16	M	DA	DISP	5	G3GG	G3	9	4	3	7	0.571428571	9	5	14	0.642857143	A
B33	M	DA	DISP	5	G3GG	G3	10	8	1	9	0.888888889	7	0	7	1	A
B20	M	DA	DISP	5	G3GG	G3	11	5	4	9	0.555555556	13	8	21	0.619047619	A
B36	M	DA	DISP	5	G3GG	G3	12	3	5	8	0.375	5	8	13	0.384615385	A
B34	M	AD	AGRÉ	10	G4GH	G4	9	1	3	4	0.25	0	9	9	0	A
B18	M	AD	AGRÉ	10	G4GH	G4	10	2	2	4	0.5	9	3	12	0.75	A
B15	M	AD	AGRÉ	10	G4GH	G4	11	5	2	7	0.714285714	10	4	14	0.714285714	A
B35	M	AD	AGRÉ	10	G4GH	G4	12	3	3	6	0.5	1	9	10	0.1	A
B18	M	AD	AGRÉ	10	G4GH	G4	13	4	2	6	0.666666667	8	4	12	0.666666667	A
B35	M	AD	AGRÉ	10	G4GH	G4	14	4	1	5	0.8	10	0	10	1	A
B34	M	AD	AGRÉ	10	G4GH	G4	15	2	5	7	0.285714286	5	10	15	0.333333333	A
B15	M	AD	AGRÉ	10	G4GH	G4	16	5	0	5	1	18	0	18	1	A
B33	M	DA	DISP	5	G3GG	G3	13	6	1	7	0.857142857	8	0	8	1	A
B36	M	DA	DISP	5	G3GG	G3	14	8	2	10	0.8	19	1	20	0.95	A
B20	M	DA	DISP	5	G3GG	G3	15	2	5	7	0.285714286	2	9	11	0.181818182	A
B16	M	DA	DISP	5	G3GG	G3	16	1	6	7	0.142857143	0	10	10	0	A
B16	M	DA	DISP	5	G3GG	G3	17	7	2	9	0.777777778	10	3	13	0.769230769	A
B20	M	DA	DISP	5	G3GG	G3	18	0	5	5	0	0	8	8	0	A
B36	M	DA	DISP	5	G3GG	G3	19	9	1	10	0.9	15	1	16	0.9375	A
B33	M	DA	DISP	5	G3GG	G3	20	3	0	3	1	6	0	6	1	A
B34	M	AD	AGRÉ	10	G4GH	G4	17	3	4	7	0.428571429	0	9	9	0	A
B15	M	AD	AGRÉ	10	G4GH	G4	18	6	0	6	1	9	0	9	1	A
B35	M	AD	AGRÉ	10	G4GH	G4	19	9	2	11	0.818181818	4	8	12	0.333333333	A
B18	M	AD	AGRÉ	10	G4GH	G4	20	1	2	3	0.333333333	9	0	9	1	A
B34	M	DA	DISP	5	G4GH	G4	1	4	6	10	0.4	1	10	11	0.090909091	A
B18	M	DA	DISP	5	G4GH	G4	2	4	1	5	0.8	9	2	11	0.818181818	A
B15	M	DA	DISP	5	G4GH	G4	3	11	0	11	1	18	0	18	1	A
B35	M	DA	DISP	5	G4GH	G4	4	8	1	9	0.888888889	7	1	8	0.875	A
B33	M	AD	AGRÉ	10	G3GG	G3	1	4	2	6	0.666666667	4	2	6	0.666666667	A
B20	M	AD	AGRÉ	10	G3GG	G3	2	1	2	3	0.333333333	7	11	18	0.388888889	A
B16	M	AD	AGRÉ	10	G3GG	G3	3	1	0	1	1	10	0	10	1	A
B36	M	AD	AGRÉ	10	G3GG	G3	4	0	1	1	0	0	4	4	0	A
B20	M	AD	AGRÉ	10	G3GG	G3	5	1	4	5	0.2	0	9	9	0	A
B33	M	AD	AGRÉ	10	G3GG	G3	6	4	0	4	1	10	0	10	1	A
B36	M	AD	AGRÉ	10	G3GG	G3	7	3	1	4	0.75	11	3	14	0.785714286	A
B16	M	AD	AGRÉ	10	G3GG	G3	8	0	3	3	0	0	13	13	0	A
B15	M	DA	DISP	5	G4GH	G4	5	5	0	5	1	18	0	18	1	A
B34	M	DA	DISP	5	G4GH	G4	6	4	4	8	0.5	6	8	14	0.428571429	A

B18	M	DA	DISP	5	G4GH	G4	7	4	1	5	0.8	7	2	9	0.777777778	A
B35	M	DA	DISP	5	G4GH	G4	8	4	1	5	0.8	11	3	14	0.785714286	A
B35	M	DA	DISP	5	G4GH	G4	9	3	1	4	0.75	4	2	6	0.666666667	A
B18	M	DA	DISP	5	G4GH	G4	10	4	0	4	1	18	0	18	1	A
B15	M	DA	DISP	5	G4GH	G4	11	5	0	5	1	15	0	15	1	A
B34	M	DA	DISP	5	G4GH	G4	12	4	1	5	0.8	5	4	9	0.555555556	A
B16	M	AD	AGRÉ	10	G3GG	G3	9	1	2	3	0.333333333	10	5	15	0.666666667	A
B36	M	AD	AGRÉ	10	G3GG	G3	10	3	2	5	0.6	6	4	10	0.6	A
B20	M	AD	AGRÉ	10	G3GG	G3	11	2	3	5	0.4	9	7	16	0.5625	A
B33	M	AD	AGRÉ	10	G3GG	G3	12	4	3	7	0.571428571	8	6	14	0.571428571	A
B33	M	AD	AGRÉ	10	G3GG	G3	13	NA	NA	NA	NA	NA	NA	NA	NA	A
B16	M	AD	AGRÉ	10	G3GG	G3	14	2	3	5	0.4	9	8	17	0.529411765	A
B36	M	AD	AGRÉ	10	G3GG	G3	15	8	2	10	0.8	18	6	24	0.75	A
B20	M	AD	AGRÉ	10	G3GG	G3	16	0	4	4	0	0	19	19	0	A
B33	M	DA	AGRÉ	10	G3GG	G3	17	7	0	7	1	12	0	12	1	A
B18	M	DA	DISP	5	G4GH	G4	13	10	2	12	0.833333333	13	1	14	0.928571429	A
B35	M	DA	DISP	5	G4GH	G4	14	6	4	10	0.6	3	6	9	0.333333333	A
B34	M	DA	DISP	5	G4GH	G4	15	4	3	7	0.571428571	4	3	7	0.571428571	A
B15	M	DA	DISP	5	G4GH	G4	16	5	1	6	0.833333333	15	2	17	0.882352941	A
B34	M	DA	DISP	5	G4GH	G4	17	2	1	3	0.666666667	0	0	0	0	A
B15	M	DA	DISP	5	G4GH	G4	18	6	1	7	0.857142857	14	1	15	0.933333333	A
B35	M	DA	DISP	5	G4GH	G4	19	4	3	7	0.571428571	2	3	5	0.4	A
B18	M	DA	DISP	5	G4GH	G4	20	4	0	4	1	13	0	13	1	A
B36	M	AD	AGRÉ	10	G3GG	G3	18	5	1	6	0.833333333	12	0	12	1	A
B20	M	AD	AGRÉ	10	G3GG	G3	19	2	3	5	0.4	11	2	13	0.846153846	A
B33	M	AD	AGRÉ	10	G3GG	G3	20	3	2	5	0.6	9	1	10	0.9	A
B16	M	AD	AGRÉ	10	G3GG	G3	21	3	3	6	0.5	6	8	14	0.428571429	A
B18	M	DA	DISP	5	G4GG	G4	1	6	1	7	0.857142857	12	1	13	0.923076923	B
B15	M	DA	DISP	5	G4GG	G4	2	3	1	4	0.75	6	1	7	0.857142857	B
B35	M	DA	DISP	5	G4GG	G4	3	4	4	8	0.5	6	6	12	0.5	B
B34	M	DA	DISP	5	G4GG	G4	4	2	2	4	0.5	3	1	4	0.75	B
B20	M	AD	AGRÉ	10	G3GH	G3	1	1	3	4	0.25	0	10	10	0	B
B36	M	AD	AGRÉ	10	G3GH	G3	2	1	3	4	0.25	1	9	10	0.1	B
B16	M	AD	AGRÉ	10	G3GH	G3	3	2	3	5	0.4	9	4	13	0.692307692	B
B33	M	AD	AGRÉ	10	G3GH	G3	4	2	1	3	0.666666667	11	1	12	0.916666667	B
B33	M	AD	AGRÉ	10	G3GH	G3	5	5	0	5	1	7	0	7	1	B
B16	M	AD	AGRÉ	10	G3GH	G3	6	2	3	5	0.4	10	4	14	0.714285714	B
B20	M	AD	AGRÉ	10	G3GH	G3	7	0	4	4	0	0	14	14	0	B
B36	M	AD	AGRÉ	10	G3GH	G3	8	0	2	2	0	0	7	7	0	B
B34	M	DA	DISP	5	G4GG	G4	5	5	2	7	0.714285714	7	1	8	0.875	B
B35	M	DA	DISP	5	G4GG	G4	6	3	3	6	0.5	7	5	12	0.583333333	B
B18	M	DA	DISP	5	G4GG	G4	7	3	1	4	0.75	12	1	13	0.923076923	B
B15	M	DA	DISP	5	G4GG	G4	8	4	1	5	0.8	10	2	12	0.833333333	B
B15	M	DA	DISP	5	G4GG	G4	9	5	3	8	0.625	9	2	11	0.818181818	B
B18	M	DA	DISP	5	G4GG	G4	10	3	4	7	0.428571429	3	4	7	0.428571429	B
B34	M	DA	DISP	5	G4GG	G4	11	10	3	13	0.769230769	7	5	12	0.583333333	B
B35	M	DA	DISP	5	G4GG	G4	12	1	3	4	0.25	5	5	10	0.5	B
B36	M	AD	AGRÉ	10	G3GH	G3	9	6	4	10	0.6	8	11	19	0.421052632	B
B20	M	AD	AGRÉ	10	G3GH	G3	10	1	3	4	0.25	7	6	13	0.538461538	B
B33	M	AD	AGRÉ	10	G3GH	G3	11	5	2	7	0.714285714	9	1	10	0.9	B
B16	M	AD	AGRÉ	10	G3GH	G3	12	2	2	4	0.5	9	0	10	0.9	B
B16	M	AD	AGRÉ	10	G3GH	G3	13	3	3	6	0.5	6	12	18	0.333333333	B
B33	M	AD	AGRÉ	10	G3GH	G3	14	3	3	6	0.5	0	6	6	0	B
B36	M	AD	AGRÉ	10	G3GH	G3	15	2	6	8	0.25	0	12	12	0	B
B20	M	AD	AGRÉ	10	G3GH	G3	16	0	4	4	0	0	12	12	0	B
B35	M	DA	DISP	5	G4GG	G4	13	2	2	4	0.5	3	4	7	0.428571429	B
B34	M	DA	DISP	5	G4GG	G4	14	0	4	4	0	0	13	13	0	B
B15	M	DA	DISP	5	G4GG	G4	15	5	0	5	1	15	0	15	1	B

B18	M	DA	DISP	5	G4GG	G4	16	3	0	3	1	13	0	13	1	B
B34	M	DA	DISP	5	G4GG	G4	17	4	2	6	0.666666667	9	5	14	0.642857143	B
B35	M	DA	DISP	5	G4GG	G4	18	1	4	5	0.2	2	6	8	0.25	B
B18	M	DA	DISP	5	G4GG	G4	19	9	0	9	1	20	0	20	1	B
B15	M	DA	DISP	5	G4GG	G4	20	7	0	7	1	12	0	12	1	B
B33	M	AD	AGRÉ	10	G3GH	G3	17	4	1	5	0.8	5	0	5	1	B
B16	M	AD	AGRÉ	10	G3GH	G3	18	2	2	4	0.5	11	4	15	0.733333333	B
B20	M	AD	AGRÉ	10	G3GH	G3	19	1	1	2	0.5	7	3	10	0.7	B
B36	M	AD	AGRÉ	10	G3GH	G3	20	5	5	10	0.5	6	10	16	0.375	B
B16	M	DA	DISP	5	G3GH	G3	1	2	5	7	0.285714286	5	7	12	0.416666667	B
B33	M	DA	DISP	5	G3GH	G3	2	6	1	7	0.857142857	5	1	6	0.833333333	B
B20	M	DA	DISP	5	G3GH	G3	3	2	7	9	0.222222222	3	11	14	0.214285714	B
B36	M	DA	DISP	5	G3GH	G3	4	8	3	11	0.727272727	15	3	18	0.833333333	B
B35	M	AD	AGRÉ	10	G4GG	G4	1	NA	NA	NA	NA	NA	NA	NA	NA	B
B18	M	AD	AGRÉ	10	G4GG	G4	2	2	0	2	1	15	0	15	1	B
B15	M	AD	AGRÉ	10	G4GG	G4	3	3	1	4	0.75	10	1	11	0.909090909	B
B34	M	AD	AGRÉ	10	G4GG	G4	4	2	0	2	1	12	0	12	1	B
B34	M	AD	AGRÉ	10	G4GG	G4	5	3	1	4	0.75	2	3	5	0.4	B
B15	M	AD	AGRÉ	10	G4GG	G4	6	7	0	7	1	13	0	13	1	B
B18	M	AD	AGRÉ	10	G4GG	G4	7	3	0	3	1	10	0	10	1	B
B35	M	AD	AGRÉ	10	G4GG	G4	8	4	1	5	0.8	9	4	13	0.692307692	B
B20	M	DA	DISP	5	G3GH	G3	5	3	6	9	0.333333333	6	5	11	0.545454545	B
B36	M	DA	DISP	5	G3GH	G3	6	10	0	10	1	18	0	18	1	B
B16	M	DA	DISP	5	G3GH	G3	7	1	4	5	0.2	0	4	4	0	B
B33	M	DA	DISP	5	G3GH	G3	8	4	0	4	1	3	0	3	1	B
B33	M	DA	DISP	5	G3GH	G3	9	4	0	4	1	9	0	9	1	B
B16	M	DA	DISP	5	G3GH	G3	10	6	1	7	0.857142857	17	1	18	0.944444444	B
B36	M	DA	DISP	5	G3GH	G3	11	4	2	6	0.666666667	14	2	16	0.875	B
B20	M	DA	DISP	5	G3GH	G3	12	1	6	7	0.142857143	4	9	13	0.307692308	B
B18	M	AD	AGRÉ	10	G4GG	G4	9	1	3	4	0.25	4	6	10	0.4	B
B35	M	AD	AGRÉ	10	G4GG	G4	10	1	4	5	0.2	0	9	9	0	B
B34	M	AD	AGRÉ	10	G4GG	G4	11	1	3	4	0.25	5	8	13	0.384615385	B
B15	M	AD	AGRÉ	10	G4GG	G4	12	5	1	6	0.833333333	9	3	12	0.75	B
B15	M	AD	AGRÉ	10	G4GG	G4	13	3	1	4	0.75	8	1	9	0.888888889	B
B34	M	AD	AGRÉ	10	G4GG	G4	14	6	1	7	0.857142857	13	2	15	0.866666667	B
B35	M	AD	AGRÉ	10	G4GG	G4	15	2	1	3	0.666666667	6	1	7	0.857142857	B
B18	M	AD	AGRÉ	10	G4GG	G4	16	3	1	4	0.75	11	4	15	0.733333333	B
B20	M	DA	DISP	5	G3GH	G3	13	3	7	10	0.3	3	8	11	0.272727273	B
B36	M	DA	DISP	5	G3GH	G3	14	9	2	11	0.818181818	21	3	24	0.875	B
B33	M	DA	DISP	5	G3GH	G3	15	3	2	5	0.6	8	2	10	0.8	B
B16	M	DA	DISP	5	G3GH	G3	16	2	2	4	0.5	6	4	10	0.6	B
B36	M	DA	DISP	5	G3GH	G3	17	7	2	9	0.777777778	9	2	11	0.818181818	B
B20	M	DA	DISP	5	G3GH	G3	18	2	7	9	0.222222222	3	12	15	0.2	B
B16	M	DA	DISP	5	G3GH	G3	19	3	2	5	0.6	12	2	14	0.857142857	B
B33	M	DA	DISP	5	G3GH	G3	20	4	0	4	1	8	0	8	1	B
B34	M	AD	AGRÉ	10	G4GG	G4	17	2	1	3	0.666666667	6	1	7	0.857142857	B
B15	M	AD	AGRÉ	10	G4GG	G4	18	3	0	3	1	18	0	18	1	B
B35	M	AD	AGRÉ	10	G4GG	G4	19	1	2	3	0.333333333	4	8	12	0.333333333	B
B18	M	AD	AGRÉ	10	G4GG	G4	20	4	1	5	0.8	11	1	12	0.916666667	B

Tableau A2. Données brutes relevées dans l’expérience de choix de partenaire sexuelle qui représentent le temps (s) passé par chaque femelle devant chacun des quatre mâles préalablement observés.

Individual	Flock	Trial	Mâles G2			
			B6	B11	B12	B13
O14	GA	1	0	42.371941	35.5480474	22.0800115
		2	37.8804359	21.9916373	3.15621992	36.9717069
O15	GA	1	2.99352007	0	49.6254107	47.3810692
		2	0	0	0	100
O16	GA	1	100	0	0	0
		2	0	0	100	0
O17	GA	1	100	0	0	0
		2	0	0	100	0
			Mâles G1			
			B5	B8	B9	B10
O7	GB	1	62.6012793	7.24034657	14.7796936	15.3786805
		2	0	40.7010679	0	59.2989321
O5	GB	1	3.23019381	42.0897961	11.5491892	43.1308209
		2	29.1767171	35.8464556	23.923434	11.0533933
O6	GB	1	0	0	100	0
		2	0	100	0	0
O13	GB	1	8.03980533	54.208714	25.0713925	12.6800882
		2	31.1326629	18.0644601	6.38873521	44.4141417
			Mâles G1			
			B5	B8	B9	B10
O2	GC	1	59.6247058	10.4064004	5.44126091	24.5276328
		2	0	0	23.078111	76.921889
O3	GC	1	12.9632872	0	0	87.0367128
		2	1.12663205	46.9123871	0	51.9609809
O11	GC	1	9.59394453	50.4029125	24.0507766	15.9523664
		2	83.6155449	16.3840773	0.00037784	0
			Mâles G2			
			B6	B11	B12	B13
O12	GD	1	0	0	99.8147878	0.18521217
		2	0	0	100	0
			Mâles G1			
			B5	B8	B9	B10
O8	GE	1	0	100	0	0
		2	97.2399035	0	0	2.76009651
O10	GE	1	70.8971092	0	0	29.1028908
		2	0	0	100	0
			Mâles G4			
			B15	B18	B34	B35
O26	GF	1	30.3137851	29.0780796	39.5860692	1.02206608
		2	0	0	26.186827	73.813173
O33	GF	1	0	0	100	0
		2	0	0	100	0
O29	GF	1	100	0	0	0
		2	100	0	0	0
O27	GF	1	23.6983902	4.3090792	65.2309079	6.76162267
		2	0	1.44643464	98.5535654	0
			Mâles G3			
			B16	B20	B33	B36
O34	GG	1	0	0	0	100
		2	9.08344531	87.0239356	3.89261906	0
O28	GG	1	24.6043938	33.3311735	29.9050215	12.1594111
		2	7.75725066	2.5942706	74.4808433	15.1676354
O30	GG	1	74.8833843	0	10.152566	14.9640497
		2	1.27845511	34.0955356	60.382478	4.24353124
O25	GG	1	0	0	100	0
		2	35.8558565	38.2757847	0	25.8683588

Chapitre III

Tableau A3. Données brutes relevées lors des tests psychométriques. AVscore, MSscore, SLscore et ICscore représentent respectivement le nombre d'essai de chaque individu dans les tâches d'apprentissage associatif, moteur progressif, spatiale et de contrôle inhibiteur.

IndF	Sexe	Groupe	AVscore	MSscore	SLscore	ICscore	BodyCondition
O6	F	GB	44	20	4	NA	0.418212669
O13	F	GB	48	NA	NA	NA	-0.185184787
O7	F	GB	26	15	5	8	0.768866972
O15	F	GA	60	5	5	3	-0.148672907
O14	F	GA	17	7	9	2	0.018452173
O17	F	GA	10	NA	NA	NA	0.172832374
O16	F	GA	16	7	7	17	0.004592833
O12	F	GD	54	20	NA	NA	0.672162585
O3	F	GC	28	5	4	7	0.358311148
O2	F	GC	16	7	7	2	0.347509255
O11	F	GC	60	NA	NA	NA	0.361406240
O10	F	GE	14	NA	NA	NA	0.106224530
O8	F	GE	43	13	4	10	-0.297520310
B9	M	G1	25	7	4	3	0.852550446
B8	M	G1	19	18	4	3	0.280516081
B10	M	G1	21	5	1	2	-0.458207709
B5	M	G1	12	7	8	3	0.186181722
B12	M	G2	37	9	9	2	0.320544566
B13	M	G2	34	5	3	10	-0.657621376
B11	M	G2	39	5	5	8	-0.836993136
B6	M	G2	11	15	2	4	-0.306200248
O34	F	GG	NA	15	NA	NA	1.594884041
O28	F	GG	18	11	7	3	-1.585431803
O30	F	GG	10	5	5	6	-0.612741681
O25	F	GG	15	5	NA	9	-1.823339392
O26	F	GH	44	5	7	NA	-0.970882111
O33	F	GH	41	15	6	3	-1.427826471
O29	M	GH	26	20	6	NA	-0.396929269
O27	F	GH	10	13	6	5	-0.740658112
B36	M	G3	10	20	4	3	1.587555529
B16	M	G3	19	11	7	2	-0.689187158
B33	M	G3	31	9	7	2	0.420990507
B20	M	G3	60	20	NA	NA	2.486352278
B15	M	G4	37	11	4	3	0.324528171
B18	M	G4	NA	NA	NA	NA	-0.202485966
B35	M	G4	45	15	1	NA	0.057208317

Tableau A4. Scores de préférence des femelles pour les différentes performances cognitives mâles dans la tâche d'apprentissage associatif (PrefAL), moteur progressif (PrefMS), spatiale (PrefSL) et de contrôle inhibiteur (PrefIC).

IndF	Groupe	PrefAL	PrefMS	PrefSL	PrefIC
O6	GB	100	50.35247	51.36577	100
O6	GB	85.87133	100	51.36577	100
O13	GB	88.68552	76.12115	50.65072	98.17869
O13	GB	83.73395	55.31184	50.30655	93.62056
O7	GB	78.36493	52.55892	76.20194	97.79108
O7	GB	88.66404	65.20673	29.73609	91.48258
O15	GA	92.56245	59.72251	66.91032	70.27918
O15	GA	91.14525	47.79755	34.95696	100
O14	GA	96.78579	55.22033	67.26515	73.56208
O14	GA	77.83083	68.23111	37.67144	78.76279
O17	GA	50.41338	100	24.11645	57.02646
O17	GA	96.4581	68.67853	100	42.70194
O16	GA	50.41338	100	24.11645	57.02646
O16	GA	96.4581	68.67853	100	42.70194
O12	GD	96.44826	68.63985	99.87953	42.80806
O12	GD	96.4581	68.67853	100	42.70194
O3	GC	87.83357	42.49582	25.92314	87.49846
O3	GC	88.13275	68.95288	32.96059	92.53657
O2	GC	77.96705	53.30492	71.41717	96.47697
O2	GC	92.75464	43.40887	23.308	88.9513
O11	GC	88.43926	73.93628	50.21298	97.70868
O11	GC	72.08866	58.48676	92.03155	100
O10	GE	75.55566	47.7254	75.23056	95.8198
O10	GE	100	50.35247	51.36577	100
O8	GE	85.87133	100	51.36577	100
O8	GE	69.97284	50.10332	97.65088	99.60355
O34	GG	35.45626	100	58.47556	74.56378
O34	GG	93.73529	94.84315	83.61826	95.30964
O28	GG	67.93471	77.21516	88.67647	77.20402
O28	GG	58.22246	63.19351	93.21337	66.41597
O30	GG	46.9083	67.47712	93.78626	65.45644
O30	GG	73.98002	72.02732	91.81961	76.63252
O25	GG	62.56462	54.46301	100	63.85379
O25	GG	64.32657	86.64099	82.05312	80.45953