UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DIFFÉRENCES INDIVIDUELLES ET PLASTICITÉ PHÉNOTYPIQUE DANS LA DÉFENSE DU NID ET EFFETS SUR LE SUCCÈS REPRODUCTEUR CHEZ LA BERNACHE DU CANADA (*BRANTA CANADENSIS*)

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AVANT-PROPOS

Ce mémoire est composé d'une introduction générale rédigée en français, de deux chapitres rédigés sous forme d'article scientifique en anglais, et d'une conclusion générale rédigée en français. Les deux chapitres seront soumis pour publication dans des périodiques scientifiques. J'ai fait l'expérimentation et les analyses nécessaires aux deux articles, que j'ai aussi rédigés. Je suis première auteure pour ces deux articles, suivi de mon co-directeur, Denis Réale, et de mon directeur, Jean-François Giroux. Au Chapitre 1 s'ajoute Mari-Ève Lindsay (3^{e} auteure) qui a participé avec nous à l'élaboration des questions de recherche et de la méthodologie pour ce chapitre, ainsi qu'à la collecte des données en 2015.

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RÉSUMÉ

Les comportements de défense du nid augmentent la probabilité de survie des jeunes dans le nid, mais diminuent la probabilité de survie du parent qui défend sa couvée. Les parents devraient donc ajuster l'intensité de leurs comportements de défense selon la qualité de leur couvée, afin de maximiser le ratio entre les bénéfices liés à leur succès reproducteur et les coûts liés à leur survie. Ainsi, la plasticité phénotypique dans la défense du nid dépendrait de la valeur de leur couvée (taille et date de ponte qui influence la survie des jeunes). Effectivement, les oiseaux nicheurs les plus défensifs sont généralement ceux qui ont pondu le plus d'œufs et le plus tôt dans la saison de nidification. Plusieurs études en écologie comportementale montrent des différences individuelles répétables dans les comportements de défense du nid à travers le temps et les situations (différences de personnalité). La présence de différentes stratégies d'histoire de vie, et une coévolution entre les traits comportementaux et d'histoire de vie pourraient aussi expliquer l'association entre ces traits. Les différences individuelles et la plasticité phénotypique seraient ainsi les deux mécanismes à l'origine de la variation dans les comportements de défense du nid, mais leur rôle respectif n'a pas été clairement décrit. Aussi, les individus des couples chez différentes espèces sont parfois appariés de manière homogame selon leur personnalité, ce qui a des conséquences positives sur leur succès reproducteur. L'objectif de cette maîtrise était d'analyser les sources de la variation observée dans les comportements de défense du nid d'une espèce aux soins biparentaux, la bernache du Canada (*Branta canadensis*), au sein d'une population établie dans le sud du Québec. Pour le premier chapitre de cette maîtrise, nous avons estimé la répétabilité des comportements de défense du nid chez les femelles et les mâles pour déterminer l'importance des différences individuelles dans ces comportements. Nous avons ensuite étudié l'association entre les comportements de défense du nid et deux traits d'histoire de vie, la taille et la date de ponte, aux niveaux inter- et intra-individuel (entre les années). Cette approche hiérarchisée permet de mieux comprendre les rôles respectifs des différences persistantes entre les individus et de la plasticité phénotypique pour expliquer l'association entre les traits. Pour ce faire, nous avons utilisé des données récoltées lors d'approches répétées au nid de plusieurs couples durant trois années. Nous avons trouvé une très forte répétabilité des comportements chez les deux sexes ; une grande partie de la variation résultait donc de différences inter-individuelles persistantes. Au niveau inter-individuel, l'intensité de défense du nid des femelles n'était pas associée

aux traits d'histoire de vie, mais les mâles les plus défensifs étaient appariés aux femelles qui en moyenne étaient les plus fécondes. Au niveau intra-individuel/inter-couvées, ni les mâles ni les femelles n'ajustaient leur comportement à la taille et à la date de ponte d'une année à l'autre. Cependant, à l'intérieur de chaque saison de nidification, les femelles étaient plus défensives lors des tests effectués près de la date d'éclosion des œufs, et faisaient donc preuve de plasticité phénotypique à court-terme. Pour le deuxième chapitre de cette maîtrise, nous avons déterminé le patron d'appariement des couples selon l'intensité de leur défense du nid, et testé l'effet du niveau d'homogamie sur le succès reproducteur. Les données ont été analysées à l'aide de modèles mixtes bivariés pour déterminer la covariance entre les traits (comportements de la femelle et du mâle). Nous avons trouvé que les couples étaient appariés de manière homogame selon l'intensité de leur défense du nid, suggérant un rôle de la personnalité dans le choix du partenaire. Cependant, le niveau d'homogamie des couples n'affectait pas leur succès reproducteur. Les mécanismes expliquant l'évolution de l'homogamie selon la personnalité pour cette population restent donc à identifier. Mon projet de maîtrise contribue ainsi au domaine de l'écologie comportementale en apportant des pistes pour mieux comprendre l'évolution des soins parentaux et le maintien des différences de personnalité dans les populations animales.

Mots clés : appariement, date de ponte, défense du nid, différences inter-individuelles, homogamie, personnalité, plasticité phénotypique, succès reproducteur, taille de ponte

INTRODUCTION GÉNÉRALE

0.1 Défense du nid

La prédation des nids est le facteur qui limite le plus le succès reproducteur des espèces d'oiseaux nichant au sol (Ricklefs 1969). Un comportement de défense visant à réduire la vulnérabilité du nid face aux prédateurs a donc évolué chez ces espèces (Montgomerie & Weatherhead 1988). De plus, ce comportement s'insère dans la théorie de l'investissement parental proposée par Trivers en 1972. Selon cette théorie, un comportement représente un investissement parental s'il augmente l'aptitude, c'est à dire les chances de survie et de reproduction, de la progéniture aux dépends de celle du parent (ex : survie ou reproduction ultérieure).

Montgomerie et Weatherhead (1988) ont défini les comportements de défense du nid comme étant des comportements qui réduisent la probabilité qu'un prédateur nuise au déroulement de la nidification ou détruise le contenu d'un nid, mais qui augmentent aussi la probabilité de blessures ou de mort du parent qui défend son nid. Effectivement, un lien entre l'intensité des comportements de défense et le succès d'éclosion du nid a déjà été démontré chez plusieurs espèces d'oiseaux (Andersson et al. 1980; Greig-Smith 1980; Blancher & Robertson 1982; Sjöberg 1994). Les individus nicheurs font donc face à un compromis entre la perte du contenu de leur nid et leur survie jusqu'au prochain épisode de nidification (Montgomerie & Weatherhead 1988). Un niveau de défense du nid optimal qui maximise l'aptitude des parents sera donc avantagé (Curio et al. 1884; Montgomerie & Weatherhead 1988; Redondo 1989).

0.2 Personnalité animale et plasticité phénotypique

Au cours des dernières décennies, l'étude de la personnalité en comportement animal a reçu beaucoup d'attention, en raison de ses implications dans le domaine de l'écologie et de l'évolution (Réale et al. 2007; Wolf & Weissing 2010; Sih et al. 2012). La personnalité animale se définit par la présence de comportements répétables au cours du temps et entre les situations, qui peuvent être causées par des différences génétiques ou développementales (Dall et al. 2004; Sih et al. 2004; Réale et al. 2007; Bell et al. 2009). Ces différences de personnalité peuvent par exemple affecter les réactions des individus face à des changements dans leur environnement, et avoir des répercussions sur la dynamique d'une population (Dall et al. 2004). Les différents traits de personnalité couramment étudiés sont la témérité (réaction d'un individu face au risque), l'exploration (réaction d'un individu face à une nouvelle situation), l'activité (niveau d'activité général d'un individu), l'agressivité (réaction agonistique d'un individu face à un conspécifique) et la sociabilité (réaction d'un individu face à la présence ou l'absence d'un conspécifique) (Réale et al. 2007). Ces différents traits de personnalité peuvent être reliés entre eux, et former des syndromes comportementaux (Sih et al. 2004).

Les traits de personnalité influencent aussi l'aptitude, et plus particulièrement le succès reproducteur (Dingemanse et al. 2004; Dingemanse & Réale 2005; Smith & Blumstein 2008; Quinn et al. 2009). Il y a aussi une composante génétique à la personnalité, puisque les traits de personnalité peuvent être héritables (van Oers et al. 2005; Réale et al. 2007; Quinn et al. 2009). Plusieurs explications adaptatives ont été proposées pour expliquer le maintien des différences de personnalité dans les populations (Réale & Dingemanse 2010; Dingemanse & Wolf 2010; Dingemanse & Réale 2013). Aussi, le maintien de ces différences pourrait même être expliqué par la

sélection sexuelle, plus précisément par le choix du partenaire de reproduction qui serait non-aléatoire (Schuett et al. 2010).

Il existe également un lien entre les traits de personnalité et les traits d'histoire de vie (Wolf et al. 2007; Biro & Stamps 2008; Smith & Blumstein 2008; Quinn et al. 2009; Réale et al. 2009; Réale et al. 2010). Ce lien pourrait s'expliquer par la présence de différences individuelles constantes dans les stratégies d'histoire de vie (Wolf et al. 2007; Biro & Stamps 2008). En raison du compromis entre longévité et succès reproducteur, les individus sujets à une forte mortalité à l'âge adulte seraient plus investis dans leur reproduction actuelle comparativement aux individus sujets à une faible mortalité, qui attendent des bénéfices de leur reproduction future (Rickelfs 1977; Zammuto 1986). Les traits de personnalité peuvent être inclus dans le syndrome de train de vie (« POLS : Pace of Life Syndrome »), qui stipule que des individus au train de vie rapide, c'est-à-dire qui ont une vie courte, qui se reproduisent pour la première fois à un âge précoce et qui ont un taux de croissance élevé, seraient aussi agressifs, téméraires, très actifs et des explorateurs qualifiés de superficiels, pour ainsi maximiser leur reproduction actuelle (Réale et al. 2010). Les individus au train de vie lent, qui vivent plus longtemps, qui se reproduisent pour la première fois plus tard dans leur vie et qui ont un taux de croissance plus faible, seraient peu agressifs, timides, peu actifs, mais des explorateurs approfondis (Réale et al. 2010). Ces différentes stratégies favorisent l'existence et le maintien de différences inter-individuelles dans les comportements (Wolf et al. 2007; Biro & Stamps 2008; Réale et al. 2010). La méta-analyse de Smith et Blumstein (2008) a montré que les individus plus téméraires avaient un succès reproducteur élevé, mais un faible taux de survie, comparés aux individus timides, qui eux avaient un succès reproducteur faible sur le long-terme mais vivaient plus longtemps.

Les traits de personnalité peuvent cependant être flexibles et être ajustés suite à des changements environnementaux ou à d'autres changements de condition. On parle de plasticité phénotypique lorsqu'un phénotype varie selon les conditions environnementales (Komers 1997; Piersma & Drent 2003). Par exemple, les bernard-l'hermites (*Pagurus bernhardus*) font preuve de plasticité en ajustant leur comportement en fonction du risque de prédation (Briffa et al. 2008). De plus, les individus capables de montrer de la plasticité dans leurs comportements ont souvent un avantage sélectif (Piersma & Drent 2003; Nussey et al. 2005).

Les différences de personnalité et la plasticité phénotypique peuvent ainsi expliquer la variation observée dans les comportements, mais la compréhension de ce qui génère cette variation serait facilitée en utilisant une approche hiérarchisée des différents niveaux impliqués. La variation phénotypique doit ainsi être décomposée aux niveaux inter- et intra-individuel (van de Pol & Wright 2009; Brommer 2013; Dingemanse & Dochtermann 2013).

0.3 Défense du nid, personnalité et plasticité

Afin de faciliter la compréhension des rôles de la personnalité et de la plasticité phénotypique dans la défense du nid, les causes de la variation dans ces comportements seront étudiées à différents niveaux, comme illustré par la Figure 0.1.

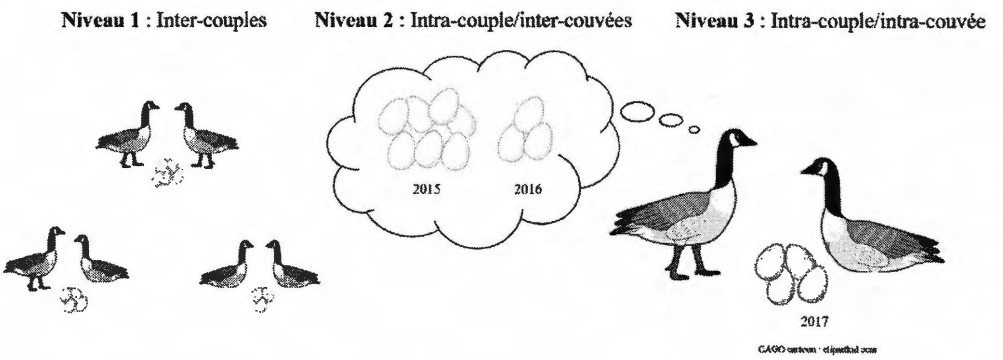

Figure 0.1. Les différents niveaux impliqués dans l'analyse des comportements de défense du nid. Le niveau 1, inter-couples, permet de déterminer le rôle des différences persistantes entre les couples (causées par des différences génétiques ou développementales). Le niveau 2, intra-couple/inter-couvées, permet d'expliquer la variation inter-couvées au niveau intra-couple causée par des changements de condition, et par exemple la capacité des individus à ajuster l'intensité de leurs comportements selon leur taille et date de ponte. Le niveau 3, intra-couple/intra-couvée, permet de déterminer si les individus ajustent leurs comportements à des changements de condition à court-terme, à l'intérieur d'une même saison de nidification (par exemple des changements dans le stade de développement des œufs).

D'abord, les individus au sein d'une même espèce peuvent différer dans leur intensité de défense du nid en raison de différences persistantes qui leur sont propres (Niveau 1 : inter-couples). L'intensité de la défense du nid peut premièrement dépendre du sexe de l'individu, si par exemple il y a dimorphisme sexuel et que les coûts associés à la défense sont plus faibles pour l'individu le plus gros (Svagelj et al. 2012), si le niveau de certitude d'apparentement d'une couvée diffère entre le mâle et la femelle, ou encore si la probabilité de nicher à nouveau diffère entre les sexes (Montgomerie & Weatherhead 1988; Redondo 1989). De plus, des études récentes ont montré la présence de différences inter-individuelles répétables, et donc de personnalité, dans les comportements de défense du nid (Kontiainen et al. 2009; Redmond et al. 2009; Burkta

& Grindstaff 2013; Møller & Nielsen 2014; Vrubleska et al. 2015; Arroyo et al. 2017). Ces différences pourraient être expliquées par des différences génétiques, des effets maternels, ou encore par des effets environnementaux permanents (Réale et al. 2007). Il est aussi important de noter que ce qui est de l'ordre des différences constantes entre individus et de la plasticité phénotypique dépend de l'échelle temporelle de l'étude. La variation dans les comportements résultant de la plasticité phénotypique peut être interprétée comme résultant de différences constantes entre individus si la durée de l'effet causant la variation dépasse la durée de l'étude.

Les couples peuvent faire preuve de plasticité et ajuster leurs comportements à des changements environnementaux ou d'autres changements de conditions (Niveau 2 : intra-couple/inter-couvées). En effet, un couple ayant une taille de nichée plus élevée sera avantagé en défendant son nid plus intensément, ou en prenant plus de risques, puisque les coûts restent équivalents peu importe le nombre d'œufs ou de jeunes à défendre dans le nid. On s'attendrait donc à observer un lien entre la taille de nichée et l'intensité des comportements de défense du nid (Montgomerie & Weatherhead 1988; Redondo 1989), ce qui a été confirmé par plusieurs études (Knight & Temple 1986a; Sjöberg 1994; Albrecht & Klvaňa 2004; Quillfeldt et al. 2005; Kontiainen et al. 2009; Svagelj et al. 2012), mais réfuté par d'autres (Redmond et al. 2009; Klvaňová et al. 2011; Burtka & Grindstaff 2013). Cette variation dans les comportements en fonction de la taille de ponte pourrait cependant être en partie expliquée par des différences de conditions persistantes entre les individus. Comme précédemment discuté, des différences de personnalité pourraient être reliées à des différences de stratégies d'histoire de vie, ce qui expliquerait l'association entre les comportements de défense du nid et les traits d'histoire de vie. Ceci justifierait pourquoi certains individus pondent un plus grand nombre d'œufs (la taille de ponte est un trait plastique, mais aussi répétable, Sheldon et al. 2003; McCleery et al. 2004) et sont plus agressifs (la variation serait dans ce cas expliquée au niveau inter-individuel).

Chez les oiseaux nidifuges, la relation entre le degré d'investissement parental et la taille de ponte n'est pas toujours claire puisque les parents ne nourrissent pas directement leurs jeunes (Winklers & Walters 1983). Cependant, les individus de ces espèces s'investissent autrement que par le nourrissage (notamment par l'incubation des œufs ou la protection des jeunes contre les prédateurs et compétiteurs). La taille de nichée pourrait donc avoir un effet sur le niveau d'investissement parental. Par exemple, la survie des oisons et le comportement des parents d'oies des neiges (*Anser caerulescens atlanticus*) sont influencés par la taille de ponte : plus la nichée est grande, plus la survie des oisons est assurée, plus les parents sont dominants lors de rencontres avec d'autres parents (Lepage et al. 1998). Chez les bernaches du Canada (*Branta canadensis*), Sjöberg (1994) a trouvé que les femelles ayant pondu un plus grand nombre d'œufs étaient légèrement plus attachées à leur nid. Encore une fois, il n'est pas clair dans ces études si la variation dans les comportements est expliquée par des différences persistantes entre les individus et/ou par de la plasticité phénotypique en réponse au changement de taille de nichée.

Aussi, des jeunes qui quittent le nid tard dans la saison ont une probabilité de survie jusqu'à la prochaine année plus faible que ceux qui quittent le nid plus tôt (Curio et al. 1984; Pilotte et al. 2014). Dans ce cas, les parents devraient montrer des comportements plastiques et défendre davantage leur progéniture si celle-ci quitte le nid plus tôt (Montgomerie & Weatherhead 1988). Effectivement, plusieurs ont observé des comportements de défense plus intenses lorsque la date de ponte était plus hâtive (Kontiainen et al. 2009; Redmond et al. 2009; Klvaňová et al. 2011; Møller & Nielsen 2014). La capacité d'une femelle à pondre plus tôt et à défendre son nid pourrait aussi être due à des différences individuelles persistantes (la date de ponte est un trait plastique, mais aussi répétable, Sheldon et al. 2003; McCleery et al. 2004; Clermont et al. 2018).

La valeur résiduelle de reproduction d'un individu diminuant avec son âge (Pianka & Parker 1975), les individus devraient modifier leurs comportements en vieillissant. Pugesek (1983) a observé une augmentation de l'intensité de la défense du nid avec l'âge chez les goélands de Californie (*Larus californicus*). Møller et Nielsen (2014), qui ont suivi des femelles d'autours des palombes (*Accipiter gentilis*) tout au long de leur vie, ont trouvé que l'investissement des mères dans la reproduction (date de ponte, taille de ponte, nombre de jeunes) augmentait d'abord avec l'âge puis diminuait (dû à la senescence), de manière que les femelles d'âge intermédiaire étaient celles qui s'investissaient le plus. C'était également le cas avec les comportements de défense du nid : les femelles d'âge intermédiaire étaient les plus agressives (Møller & Nielsen 2014).

De plus, la capacité d'une femelle à pondre beaucoup d'œufs ou d'un individu à être attentif à son nid est souvent reliée à son expérience ; par exemple les bernaches du Canada les plus expérimentées (c'est-à-dire celles qui se sont déjà reproduites) sont celles qui réussissent le mieux à se nourrir, qui ont le plus de réserves et qui conséquemment investissent le plus dans leur nidification (Aldrich & Raveling 1983). En effet la probabilité de survie des jeunes augmente avec l'expérience des parents qui connaissent mieux les comportements des prédateurs. Il devient donc moins couteux pour ceux-ci d'augmenter l'intensité de leurs comportements de défense (Montgomerie & Weatherhead 1988). L'âge d'un individu, qui reflète son expérience, est donc important à considérer lorsqu'on étudie un aspect de la nidification puisque les individus plus vieux et plus expérimentés (jusqu'au point où ils font face aux effets de la senescence) pondent généralement plus tôt et ont de plus grandes tailles de ponte que les plus jeunes (Hamann & Cooke 1987).

Finalement, la plasticité phénotypique pourrait expliquer la variation observée dans les comportements de défense du nid à l'intérieur d'un même évènement de

reproduction (Niveau 3 : intra-couple/intra-couvée). En effet, plusieurs ont suggéré que l'intensité avec laquelle les parents défendent leur nid augmente avec l'âge des jeunes (de la ponte jusqu'à l'envol des poussins) possiblement parce que le potentiel de nouvelle nidification devient plus faible plus les jeunes vieillissent et la nichée devient donc plus précieuse plus elle vieillit (Barash 1975; Andersson et al. 1980; Blancher & Robertson 1982; Curio et al. 1984; Montgomerie & Weatherhead 1988; Redondo 1989; Albrecht & Klvaňa 2004; Brown & Brown 2004; Osiejuk & Kuczyński 2007; Redmond et al. 2009; Svagelj et al. 2012). Cependant, comme Knight et Temple (1986b) l'ont suggéré, cet effet peut être confondu avec un effet d'habituation à l'observateur dans le cas d'observations répétées : les parents peuvent perdre leur peur de l'observateur et se montrer plus agressifs après plusieurs observations.

0.4 Appariement et succès reproducteur

L'intensité des comportements de défense du nid a parfois été liée au succès de la nichée. Par exemple, Kontiainen et al. (2009) ont trouvé un meilleur recrutement des jeunes de parents de personnalité extrême (plus agressifs) chez la chouette de l'Oural (*Strix uralensis*). Cependant, le lien entre la personnalité et le succès reproducteur n'est pas toujours clair. Par exemple, Burtka et Grindstaff (2013) et Redmond et al. (2009) n'ont pas trouvé de liens entre l'intensité des comportements de défense du nid et la taille de la nichée. Chez les espèces à soins biparentaux, les traits des deux parents sont importants pour déterminer le succès reproducteur. On dit qu'un appariement est homogame lorsque que les couples sont formés d'individus qui présentent des phénotypes similaires (Jiang et al. 2013). Jiang et al. (2013) ont observé une corrélation moyenne de 0.28 pour différents traits chez des espèces appartenant à différents groupes taxonomiques. L'homogamie pourrait être observée si les individus similaires sont contraints à s'apparier, par exemple chez les espèces monogames les couples sont souvent formés d'individus du même âge (Black & Owen 1995; Jiang et al. 2013).

L'homogamie pourrait aussi possiblement résulter de conflits intra-sexe lors du choix du partenaire (Jiang et al. 2013). Par exemple, si les femelles les plus grosses sont les plus fécondes, les mâles entreront en compétition pour ces femelles. Un mode d'appariement homogame résultera de cette préférence si les mâles les plus gros sont aussi ceux qui arrivent à accéder et à défendre ces femelles (Jiang et al. 2013). Certaines combinaisons de traits pourraient aussi être plus compatibles génétiquement, ce qui pourrait rendre l'homogamie un choix adaptatif si c'est la combinaison du même trait qui apporte un avantage (Schuett et al. 2010; Schuett et al. 2011). L'effet de l'homogamie dans les traits morphologiques comme la coloration ou la taille sur le succès reproducteur a déjà été beaucoup étudié (Jiang et al. 2013), comparativement aux traits pour lesquels la répétabilité est plus petite que 1 (comme les traits comportementaux). De plus, pour ces traits dits labiles, des effets environnementaux communs aux membres des couples et des erreurs de mesure pourraient mener à la corrélation des traits homologues chez les individus en couple (Class et al. 2017).

C'est seulement récemment qu'on a commencé à regarder les liens entre la personnalité, l'appariement et le succès reproducteur (Schuett et al. 2010). Des études ont montré qu'un appariement de personnalité homogame avait un effet positif sur le succès reproducteur (Buadev et al. 1999; Dingemanse et al. 2004; Both et al. 2005; Sinn et al. 2006; Schuett et al. 2011; Gabriel & Black 2012; Ariyomo & Watt 2013; Kralj-Fišer et al. 2013; Harris & Siefferman 2015; Burtka & Grindstaff 2015; Montiglio et al. 2016). Par exemple, Gabriel et Black (2012) ont trouvé que les couples de geai de Steller (*Cyanocitta stelleri*) formés d'individus similaires dans leur comportement d'exploration et leur tendance à prendre des risques initiaient leur nid plus tôt et avaient un meilleur succès d'envol des jeunes. Both et al. (2005) ont quant à eux trouvé que les couples homogames de mésanges charbonnières (*Parus major*) aux comportements extrêmes (soit les couples d'explorateurs les plus approfondis et les couples d'explorateurs les plus superficiels) produisaient les jeunes en meilleure

condition à l'envol. Par contre, le type de personnalité avantagé chaque saison dans cette population varie en fonction de l'abondance de nourriture (Dingemanse et al. 2004). Schuett et al. (2011) ont aussi trouvé que la personnalité et la combinaison de traits de personnalité au sein des couples avaient un effet sur la condition des jeunes. Selon eux, l'homogamie peut avoir d'importants effets sur le succès reproducteur dû à la réduction des conflits parentaux reliés à l'investissement parental. Finalement, Burtka et Grindstaff (2015) ont trouvé qu'une asymétrie dans l'intensité des comportements de défense du nid au sein des couples de merles bleus de l'Est (*Siala sialis*) diminuait le succès reproducteur, ce qui suggère un certain avantage de l'homogamie.

0.5 Système à l'étude

Les bernaches du Canada forment des couples qui durent pour la vie, mais seule la femelle incube les œufs (Bellrose 1976). Cependant, les deux individus du couple défendent le nid (Bellrose 1976; Sjöberg 1994; Pannetier-Lebeuf & Giroux 2014). Pour cette espèce qui niche au sol, la prédation est une cause de perte de nid importante (Bellrose 1976; Bruggink et al. 1994). Puisque c'est une espèce longévive, les parents devraient rarement risquer leur vie pour sauver leur couvée, puisque la femelle peut facilement en pondre une autre dans les années qui suivent (Miller et al. 2007). Un lien entre les comportements de défense et le succès reproducteur a déjà été suggéré chez l'espèce. Miller et al. (2013) ont trouvé un faible effet de la taille de ponte sur les comportements de défense : les femelles avec un plus grand nombre d'œufs retournaient à leur nid plus rapidement que les autres suite à la perturbation. Sjöberg (1994) a quant à lui trouvé que les femelles qui ont fui plus tard à l'approche d'un humain étaient celles qui avaient pondu le plus d'œufs (il n'a cependant pas trouvé d'effet de l'âge ni de la date de ponte sur la distance de fuite des femelles). Cependant, dans ces deux études, les relations ont été analysées au niveau phénotypique ; on ne

peut donc pas savoir si elles sont expliquées par des différences inter-individuelles persistantes, ou par la plasticité phénotypique. Sjöberg (1994) a aussi trouvé un effet du stade de développement des œufs sur les distances de fuite : les femelles fuyaient plus tard plus près de l'éclosion. Finalement, Sjöberg (1994) et Miller et al. (2013) ont trouvé que les comportements de défense du nid étudiés étaient en partie expliqués par des différences inter-individuelles répétables chez les femelles.

La population à l'étude niche sur les îles de Varennes (45°40′N, 73°27′W), sur le fleuve St-Laurent, à 15 km au Nord-Est de la ville de Montréal. Les bernaches s'y sont établies au début des années 1990 (Giroux et al. 2001), et depuis la population a cru exponentiellement (Pannetier-Lebeuf & Giroux 2014). Le site d'étude est constitué de quatre îles voisines (total de 111.5 ha) couvertes majoritairement d'herbes et d'arbustes et connectées par des marais. Différents mammifères et oiseaux se nourrissent d'œufs et de jeunes bernaches sur les îles, avec comme espèce de mammifère la plus commune le vison d'Amérique (Pannetier-Lebeuf & Giroux 2014). Chaque année, les bernaches arrivent sur les sites de nidification à la mi-mars et nichent durant les mois d'avril et de mai (Beaumont et al. 2013). Comme l'ont montré Pannetier-Lebeuf et Giroux (2014), le succès d'éclosion est élevé pour cette population, sauf lors d'inondations liées au niveau du fleuve. Il était de 78% en 2015 et de 73% en 2016, mais de 25% en 2017 dû aux importantes inondations printanières. De plus, Fontaine (2016) a trouvé que la probabilité de survie des jeunes avant l'envol était meilleure lorsque la taille de la couvée était plus élevée et lorsque la date d'éclosion était plus hâtive.

0.6 Objectifs et hypothèses

Ce projet de recherche vise à mieux comprendre la variation observée dans les comportements de défense du nid des bernaches du Canada. Ainsi, le premier objectif

du premier chapitre de ce projet était de déterminer le rôle des différences inter-individuelles persistantes dans les comportements de défense du nid des bernaches du Canada. Le deuxième objectif était d'étudier l'association entre les comportements de défense du nid des mâles et des femelles et deux traits d'histoire de vie, la taille et la date de ponte, aux niveaux inter- (différences inter-individuelles persistantes) et intra-individuel (ajustements des comportements selon la valeur de la couvée). Nous avons aussi regardé si les bernaches ajustaient leur comportement de défense à court-terme (durant chaque saison de nidification), selon le stade de développement des œufs. Cette approche hiérarchisée permet de mieux comprendre les rôles respectifs des différences persistantes entre les individus et de la plasticité phénotypique pour expliquer la variation comportementale et l'association entre les traits. Les prédictions pour ce chapitre étaient les suivantes :

1) Il existe des différences persistantes entre les individus dans les comportements de défense du nid, qui se reflètent lors des tests d'approche au nid.

2) Au niveau inter-individuel, les individus qui en moyenne défendent leur nid intensément sont aussi ceux qui en moyenne ont de grandes tailles de ponte et qui pondent le plus tôt.

3) Au niveau intra-individuel/inter-couvées, les individus ajustent leur niveau de défense à la valeur de leur couvée ; ce niveau de défense diminue avec la date de ponte et augmente avec sa taille, d'une saison de nidification à l'autre.

4) Au niveau intra-individuel/intra-couvée, le niveau de défense augmente avec le stade de développement des oeufs.

Dans le deuxième chapitre, nous avons étudié le patron d'appariement entre les individus des couples selon l'intensité de leur défense du nid, et testé l'effet du niveau d'homogamie sur le succès reproducteur. Voici les prédictions pour ce deuxième chapitre :

1) Les couples sont formés d'individus qui défendent leur nid avec une intensité similaire (patron d'appariement homogame).

2) Le niveau d'homogamie dans la défense du nid affecte le succès reproducteur ; les couples formés d'individus les plus similaires ont un meilleur succès reproducteur.

CHAPITRE I

PLASTICITY, STATE-DEPENDENCY, AND INDIVIDUAL CONSISTENCY IN CANADA GOOSE NEST DEFENSE BEHAVIOR

Jeanne Clermont, Denis Réale, Mari-Ève Lindsay & Jean-François Giroux

1.1 Abstract

Breeding birds are thought to adjust their nest defense intensity to fitness benefits associated with their current reproduction. They should thus be more defensive when they nest early in the season, when they produce larger clutches or as their young get older. Beyond these plastic changes, consistent among-individual differences in nest defense behavior may have coevolved with slow-fast life history strategies, leading to associations among traits at the individual level. Separating the mechanisms at the origin of behavioral phenotypic variation is essential to understand the determinants and evolution of parental care. During three breeding seasons, we investigated whether variation in Canada goose (*Branta canadensis*) nest defense resulted from individual short-term plastic adjustments to reproductive stage, adjustments to brood value across breeding seasons, or from long-term among-individual and pace-of-life differences. We thus estimated the among- and within-individual relationships between nest defense, clutch size, and laying date. Female and male nest defense behaviors were

repeatable in time (R = 0.74 and 0.69 on the short term). At the among-individual level, we found no significant association between female nest defense and life history traits, but the more defensive males were mated with the more fecund females. Female and male nest defense was not adjusted to annual variation in laying date nor in clutch size. However, females adjusted their nest defense within each breeding season and became more defensive when approaching egg hatching. Thus, Canada goose nest defense behavior is stable and to some extent independent of reproductive effort.

Keywords: among-individual differences, clutch size, laying date, nest defense, pace-of-life, personality

1.2 Introduction

Nest defense is a parental behavior that increases survival probability of young in the nest, but simultaneously reduces parent survival and the probability of breeding in the future (Montgomerie & Weatherhead 1988). Nest defense could be adjusted to maximize benefits associated with reproduction, while minimizing costs associated to survival. As such, nest defense would be a highly labile trait varying according to changes in benefits and costs associated with parental investment. First, labile plastic adjustments of nest defense could happen in the short-term, within each breeding season. For example, many studies have shown that nest defense becomes more intense as young in the nest get older (Brown & Brown 2004; Osiejuk & Kuczyński 2007; Redmond et al. 2009; Svagelj et al. 2012). This possibly occurs because both the parental investment needed to replace a lost clutch and the probability that eggs will hatch increase with time (Andersson et al. 1980; Montgomerie & Weatherhead 1988; Redondo 1989).

Plastic adjustments of nest defense could further occur across breeding seasons with changes in brood value. These plastic adjustments would thus be state-dependent,

and they could explain the relationship between the intensity of nest defense and life history traits like laying date and clutch size, which themselves generally covary (Klomp 1970). First, birds encountering poorer environmental conditions lay eggs later in the season and produce smaller clutches (Daan et al. 1990; Brommer et al. 2002; Brommer et al. 2012). The environmental variables affecting laying date and clutch size could further affect nest defense, resulting in the covariation of these traits. Secondly, laying date affects fledging date, which in turn reduces survival and the probability of recruitment in the population (Curio et al. 1984; Verhulst et al. 1995). Parents should thus defend their nest more intensely if their offspring are expected to leave the nest early in the season (Montgomerie & Weatherhead 1988). This hypothesis was supported by the observed negative relationship between the intensity of defense and laying date (Kontiainen et al. 2009; Redmond et al. 2009; Klvaňová et al. 2011; Møller & Nielsen 2014). Furthermore, a pair with a larger clutch size would benefit from a more intense defense as costs to the parents' survival remain the same, no matter the number of eggs or young in the nest. A positive relationship between nest defense intensity and clutch size should thus be observed (Knight & Temple 1986a; Sjöberg 1994; Kontiainen et al. 2009; Svagelj et al. 2012). Individual plastic adjustments of nest defense behavior to laying date and clutch size would then result in significant phenotypic associations between nest defense and these life history traits.

Finally, variation in nest defense could be explained on the long-term by among-individual differences that could be genetic, developmental, and/or related to differences in life history strategies. Behavioral traits have been shown to covary with both life history and physiological traits (Biro & Stamps 2008; Careau et al. 2008; Smith & Blumstein 2008; Réale et al. 2009; Réale et al. 2010; Ferrari et al. 2013; Careau et al. 2015). First, short-lived individuals should be more committed to their current reproduction compared to long-lived ones, who can expect benefits from future reproduction (Ricklefs 1977; Zammuto 1986). This negative relationship between

lifespan and reproduction could further explain the association between life history traits and behavior, if individuals are consistent in their life history strategies (Wolf et al. 2007; Biro & Stamps 2008). Consistent individual differences in life history traits can directly affect reproductive parameters like laying date and clutch size (Sheldon et al. 2003; McCleery et al. 2004). More generally, coevolution among life history, physiological, and behavioral traits may be the result of long-term correlational selection pressures (Réale et al. 2010). According to the pace-of-life syndrome (POLS), individuals qualified as "fast" over the fast-slow pace-of-life continuum should be those that have a shorter lifespan but a higher growth rate, a more precocious reproduction and fewer reproductive events but a greater number of young per event (Réale et al. 2010). The differences between the life history strategies of fast and slow individuals can further explain personality (i.e. repeatable differences in behavior in time and across contexts: Réale et al. 2007). Indeed, fast individuals should also be bolder and more aggressive to maximize lifetime reproductive success (Réale et al. 2010). Consistent individual differences have been observed in nest defense behavior (Kontiainen et al. 2009; Redmond et al. 2009; Burtka & Grindstaff 2013; Møller & Nielsen 2014; Arroyo et al. 2017). Covariation between this behavior and other individually consistent traits like clutch size and laying date could thus be explained by consistent among-individual differences rather than (or in addition to) plastic adjustments to variation across years.

There are thus different sources of variation in nest defense: 1) long-term individual differences and coadaptation between life-history and behavior (pace-of-life syndrome), 2) state-dependent plastic adjustments to parental investment changing over the years (plasticity among-years), and 3) labile phenotypic adjustments to short-term changes in costs/benefits related to reproductive stages (plasticity within-years), which are associated with different ecological or evolutionary mechanisms. It is thus essential to separate their effects to better understand both the determinants and the

evolutionary potential of parental nest defense. Indeed, only among-individual variation can underpin genetic variation that can matter for trait evolution. In fact, most studies that found significant relationships between nest defense and reproductive value (e.g. laying date and clutch size), or repeatable among-individual differences in nest defense, did not try to disentangle the effects of these different sources of variation. This is probably because repeated measures of the traits of interest on the same individuals are required to determine whether trait associations at the phenotypic level are explained by consistent individual differences or phenotypic plasticity (Dingemanse & Dochtermann 2013). One exception is the study of Brommer et al. (2014) who found that phenotypic covariation between boldness displayed during defense, clutch size, and timing of reproduction resulted solely from within-individual covariation of traits across years in female tawny owls (*Strix aluco*).

The objective of this study was to determine the mechanisms generating variation in nest defense behavior of Canada goose (*Branta canadensis*) pairs. Canada goose is a bi-parental care species that mate for life with both parents defending their nest but only females incubating the eggs (Sjöberg 1994). We analyzed the variance in nest defense behavior and its association with clutch size and laying date in pairs of individually marked females and males over a three-year period. We used mixed models and within-individual centering of variables, a method that allows the partitioning of phenotypic correlations into among- and within-individual correlations (van de Pol & Wright 2009; Dingemanse et al. 2010). Relying upon a 15-year dataset of nest monitoring, we first measured female repeatability in clutch size and laying date, as these traits need to be individually consistent to further covary with nest defense at the among-individual level. We then measured repeatability in female and male nest defense and assessed variation explained at 1) the among-individual level caused by genetic or developmental effects, 2) the within-individual/among-year level caused by state-dependent effects, and 3) the within-individual/within-year level (residuals)

caused by short-term plastic adjustments or measurement errors. We investigated the effect of long-term pace-of-life syndrome among-individual differences by looking at among-individual associations between nest defense, clutch size, and laying date. We predicted that more defensive individuals would also be those with the greater brood values (greater clutch size and earlier laying date). Secondly, we investigated the state-dependency (or integrated plasticity) of nest defense among years by looking at within-individual (among-year) associations between nest defense and both clutch size and laying date. We predicted that individuals' nest defense would covary with clutch value, being more defensive in years where more eggs are laid earlier in the season. Thirdly, we assessed the importance of short-term labile adjustments of nest defense to changes in reproductive stage within each breeding season (plasticity within-years). We predicted that individuals would become more defensive as young get older.

1.3 Methods

1.3.1 Study system

We studied a Canada goose population nesting on the Varennes islands (45° 40′ N, 73° 27′ W) located on the St. Lawrence River, 15 km northeast of the city of Montreal, Quebec, Canada. The study site comprised four islands connected by marshes (total area of 111 ha). Geese usually arrive on the breeding grounds around mid-March and nest during the months of April and May (Beaumont et al. 2013). Pannetier-Lebeuf and Giroux (2013) showed that geese of this population were assorted based on age. More details on the study area and the population can be found in Pilotte et al. (2014).

1.3.2 Nest monitoring and banding

Each year since 2003, three systematic nest searches were conducted on the Varennes islands. At each nest, we determined the identity of the parents, and counted and marked the eggs. The date at which the first egg was laid (laying date) was calculated using different methods depending on the stage of the nest when discovered. If only one egg was found, we assumed it had been laid earlier that day and the laying date was identified as the date of nest discovery. If a nest was found with more than one egg but still during laying, we calculated the laying date by subtracting the current date by the number of eggs laid multiplied by 1.5 knowing that the egg-laying interval in Canada geese is 1.5 days (Cooper 1978). To obtain the laying date of nests found during incubation, we used the hatching date (based on an incubation period of 27 days, starting the day when the last egg was laid, Cooper 1978). Due to lack of precision, we did not use laying dates of nests found during incubation and with an unknown hatching date. At hatching and just before nest departure, goslings were counted and marked with a unique numbered web-tag (Pilotte et al. 2014).

Individuals have been banded and sexed by cloacal examination during annual mass captures occurring at the end of June or beginning of July (Pilotte et al. 2014). Plastic neck-collars with a unique code were fitted to adult females with a brood patch, and on all individuals already marked with a web-tag. Based on their plumage, geese were aged as hatching-year (HY) or after hatching-year (AHY, yearlings and 2+ year-old birds). Exact age of birds observed during this study was calculated for individuals with known hatching year (banded as HY or as AHY previously marked with a web-tag). A minimum age was estimated for the other individuals assuming that they started breeding at 2 years of age (Pilotte et al. 2014).

1.3.3 Nest defense behavior

During three breeding seasons (2015-2017), we quantified nest defense behavior of pairs with neck-collared females by performing nest approaches during the incubation period. Not all males were banded and marked with a neck-collar. Our goal was to perform three approaches per season per pair (one at the beginning, one at the midpoint, and one towards the end of the incubation period). We aimed to obtain sufficient replicates while minimizing habituation, and to observe the same pairs each year. We were able to perform 336 approaches (77 in 2015, 159 in 2016, and 100 in 2017). Males were temporarily absent during 21 of these approaches and we therefore measured their behavior during 315 approaches. We studied the behavior of 112 pairs among which 40 were tested during 2 breeding seasons and 3 during 3 seasons. Females and males were tested on average 3.0 ± 1.4 (mean ± SD) [range 1:8] and 3.0 ± 1.5 [range 1:7] times, respectively. Male identity based on neck-collars was available for 40 pairs. We found only two occurrences of mate change between years in these pairs (5%), possibly associated with male death. For these 40 pairs, we found no significant difference between female and male age (paired t-test: $t = 0.60$ $df = 38$, $P = 0.55$), which confirms an assortative mating based on age (Pannetier-Lebeuf & Giroux 2013). We assumed that females paired with males of unknown identity remained together for the duration of the study and used the age of the paired female as a surrogate for the age of unbanded males.

Approaches started at 40 meters from the nest as measured with a GPS. Before performing the approach, we estimated the male distance to the nest. During the approach, we noted the reaction distance of the male and female as the distance between the observer and the nest at the exact moment when individuals reacted. We considered that the male reacted when it stood up, moved (if it was already standing up), or started to whistle or vocalize. We considered that the female reacted when it

stood up on the nest, moved away from the nest, or started to whistle or vocalize. If individuals moved, we noted if it was toward or away from the observer or the nest, and at which distance they went from the nest. We also noted if individuals vocalized, whistled, performed head pumping, shook their head, opened their wings, or flew towards the observer. The observer stayed 30 seconds at the nest and then walked back to the starting point, waited for four minutes and noted the distance individuals were from the nest. All distances except reaction distances were visually estimated. Reaction distances were estimated by dropping an object when the geese react and by counting steps (of approximately 1 meter) when going back to the starting point at the end of the test. All distances were categorized (see below).

We categorized behavior into nine variables: 1) reaction distance, 2) reaction (i.e. for females: whether the female moved towards the observer, stayed on the nest or moved away from the nest, and to which distance, for males: the distance from the nest to which the male moved), 3) vocalization, 4) whistling, 5) head pumping, 6) head shaking, 7) wing opening, 8) flying toward observer, and 9) position after approach. We used a 10th variable for males which was the starting position. The number of categories for each variable was determined to have a similar number of occurrences in each category (Annexe A). Finally, we calculated the number of days elapsed between the beginning of laying and the date when each test was conducted.

1.3.4 Statistical analyses

All analyses were performed using R version 3.2.2 (R Development Core Team 2013). We used nonmetric multidimensional scaling (NMDS), an ordination technique that does not assume linear relationships among variables which can be of different distributions (McCune & Grace 2002), using the vegan package (Oksanen et al. 2016). It was used to obtain a nest defense score for females and males separately based on

the ordinal and binomial variables noted for each test. We assessed NMDS stress values, which should be lower than 0.2 to provide an appropriate and interpretable ordination space (McCune & Grace 2002).

We analyzed variation in female and male NMDS scores and association with life history traits using linear mixed models (lme4 package, using Restricted Maximum Likelihood (REML), Bates et al. 2015). We z-transformed all variables included in models to a mean of zero and a standard deviation of one to adjust scaling problems and to facilitate interpretation of model estimates (Schielzeth 2010). We tested for the significance of random and fixed effects by performing Likelihood Ratio Tests (LRT) between models with and without each effect. LRT *P*-values ($\alpha = 0.05$) of fixed effects were corroborated with 95% bootstrapped confidence intervals (Bates et al. 2015). Models were checked and validated for normality, homogeneity, and non-independence of their residuals based on a visual exploration of residuals plotted against fit values, qqplots, and histograms.

Firstly, we performed linear mixed models for clutch size and laying date to estimate repeatability in these traits. Repeatability represents the proportion of variance attributed to differences among individuals (Bell et al. 2009; Nakagawa & Schielzeth 2010). Repeatability was calculated using variance values extracted directly from the output of a model that analyzed 1,531 nesting attempts of 667 marked females (average of 2.3 ± 1.7 [range 1:11] observations per female) between 2003 and 2017 for which we knew both the laying date and clutch size (and thus not only females considered in the behavioral tests). We included female age as a fixed effect and female identity (ID) and year as random effects in both models. We also tested for an interaction between female age and ID (i.e. random slopes) in both models, to test whether the relationships between age and clutch size and age and laying date were similar among females.

In the female and male nest defense linear mixed models, we used the random effect structure described in Araya-Ajoy et al. (2015) to calculate the repeatability at different temporal scales. We thus included two random effects in both models: the individual identity (ID) and a combination of ID and year (ID_year). This was used to denote a period, here breeding season, during which multiple observations of individuals occur (Araya-Ajoy et al. 2015). This would also allow separating variation into the three levels of interest: 1) variance among-individuals (ID), 2) variance within-individual/among-years (ID_year), and 3) variance within-individual/within-year (residuals). Using these variance values, we estimated repeatability in male and female nest defense on the long-, intermediate-, and short-term. Long-term repeatability (R_{lt}) was calculated as the ratio of among-individual variance in the trait divided by the sum of all the variance components (i.e. among-individual variance, within-individual/among-year variance, and within-individual/within-year or residual variance). Intermediate-term repeatability (R_{it}) was calculated as the ratio of within-individual/among-year variance over all variance components, and short-term repeatability (R_{st}) as the ratio of the sum of within-individual/among-year variance and among-individual variance over all of the variance components (Araya-Ajoy et al. 2015).

We used the within-individual centering method described by van de Pol and Wright (2009) to determine association between nest defense and life history traits at the among-individual and within-individual/among-year levels. For each female, we calculated mean clutch size and mean laying date across all known reproductive events since 2003 (a high value of mean laying date means the female laid its eggs late in the season). We then calculated the deviation from the individual's mean value for both variables for each observation. A positive deviation from female mean clutch size indicates that more eggs were laid than average, while a negative deviation from female mean laying date implies eggs were laid earlier than average. Including both female

means and deviations from female means as fixed effects in mixed models allows us to differentiate the effect of the trait on defense occurring at the among- (means) and within-individual (deviations) levels (van de Pol & Wright 2009; Dingemanse et al. 2010). The among-individual level represents long-term associations between the behavior and the life history traits caused by genetic or developmental effects (among-individual variation), whereas the within-individual level represents the plastic response of the trait to annual changes in that life history trait (within-individual/among-year variation). Both female and male nest defense full models included the following fixed effects: female mean clutch size, deviation from female mean clutch size, female mean laying date, and deviation from female mean laying date. In addition, number of days elapsed since laying at the date the test was performed allowed us to test for a potential labile adjustment of the intensity of nest defense depending on the stage of development of the eggs (within-individual/within-year variation). Finally, individual age was also included as a covariate. We also tested for interactions between age and female mean clutch size, and age and female mean laying date, to assess whether the relationship between nest defense and female mean clutch size and laying date varied in relation to goose age. However, these interactions were not significant in both models and will not be further discussed.

1.3.5 Ethics statement

Animal handling methods were approved by the UQAM Animal Care Committee (#578 and #716) and conformed to guidelines of the Canadian Council for Animal Care.

1.4 Results

1.4.1 Ordination of nest defense behavior

We used NMDS of two dimensions to reduce stress (0.12 for the analysis of the 9 female variables, and 0.17 for the analysis of the 10 male variables). From a visual analysis of both NMDS, we concluded that the first dimensions were representative of the level of nest defense for both females and males, with higher scores corresponding to higher levels of defense (Annexe B). This was also confirmed by the greater correlation coefficients between NMDS scores and behavioral variables for the first dimension than the second one for both sexes (Annexe C). For female scores on the first NMDS dimension (hereafter called female nest defense scores), greater values corresponded to tests where females stayed at the nest during the whole approach, whistled, and opened their wings, whereas lower values corresponded to tests where females left their nest early during the approach and vocalized. For male scores on the first NMDS dimension (hereafter called male nest defense scores), greater values corresponded to tests where males reacted early during the approach, moved towards the observer or the nest, and whistled, whereas lower values corresponded to tests where males stayed away from the observer and the nest during the whole approach.

1.4.2 Clutch size and laying date repeatability

Random effects ID and year were significant in both clutch size and laying date models (LRT for clutch size model: ID: $\chi^2 = 61.87$, df = 1, $P < 0.001$, year: $\chi^2 = 38.69$, df = 1, $P < 0.001$, LRT for laying date model: ID: $\chi^2 = 83.65$, df = 1, $P < 0.001$, year: $\chi^2 = 755.79$, df = 1, $P < 0.001$). Variances of the clutch size model were 0.21 for ID, 0.04 for year, and 0.72 for residuals. Respective values for the laying date model were 0.18, 0.34, and 0.43. Clutch size and laying date repeatability estimates were thus 0.22 and

0.19, respectively. Female age had a significant effect on both clutch sizes and laying dates (Table 1.1). Older females laid more eggs earlier in the breeding season.

Table 1.1. Effect of female age on clutch size and laying date of Canada geese nesting on the Varennes islands, Quebec, Canada. Clutch size and laying date linear mixed models included female ID and year as random effects. Number of observations = 1531.

	Clutch size model					***Laying date model***				
Fixed effect	Estimate	95% CI	χ^2	df	*P*	Estimate	95% CI	χ^2	df	*P*
(Intercept)	-0.02	-0.15: 0.10				0.16	-0.15: 0.47			
AGE	**0.23**	**0.17: 0.28**	**58.89**	**1**	**<0.001**	**-0.15**	**-0.20: -0.11**	**38.74**	**1**	**<0.001**

AGE: female age. Significant fixed effects are in bold.

The interaction between the random effect female ID and age in the clutch size model was not significant (LRT: $\chi^2 = 0.50$, df = 2, $P = 0.779$). This indicates that the relationship between age and clutch size was similar among females and that the variable female mean clutch size correctly depicted among-female fecundity differences in the nest defense model. On the other hand, the interaction between the random effect female ID and age in the laying date model was slightly significant (LRT: $\chi^2 = 6.10$, df = 2, $P = 0.047$). Although females might be somewhat different in the way they change their laying date as they become older, we consider that female mean laying date correctly represented among-female differences in laying date in the nest defense model.

1.4.3 Variation in nest defense behavior

Random effects ID and ID_year were significant in both female and male nest defense models (LRT for female model: ID: $\chi^2 = 17.82$, df = 1, $P < 0.001$, ID_year: $\chi^2 = 29.04$, df = 1, $P < 0.001$, LRT for male model: ID: $\chi^2 = 15.77$, df = 1, $P < 0.001$, ID_year: $\chi^2 = 13.24$, df = 1, $P < 0.001$). Variance estimates of the female nest defense model were 0.47 for ID (among-individual variation), 0.26 for ID_year (within-individual/among-

year variation), and 0.25 for residuals (within-individual/within-year variation). We thus found a long-term repeatability R_{lt} of 0.48, an intermediate-term repeatability R_{it} of 0.26, and a short-term repeatability R_{st} of 0.74 for female nest defense scores. In the male nest defense model, variance estimates were respectively 0.46, 0.25, and 0.32 for the random effects ID, ID_year, and residuals. Male nest defense scores repeatability was estimated to be 0.45 in the long-term, 0.24 in the intermediate-term, and 0.69 in the short-term.

Female nest defense scores increased significantly with the number of days elapsed since the beginning of laying (Table 1.2, Figure 1.1; within-individual/within-year variation). There were no long- or intermediate-term effects of clutch size and laying date (i.e. no effect of female mean and deviation from female mean; among-individual and within-individual/among-year variations), nor of age on female nest defense scores (Table 1.2).

Table 1.2. Relationships between individual characteristics of female and male Canada geese and their nest defense behavior. Female and male nest defense linear mixed models included individual ID and ID_year as random effects. Number of observations = 336 and 315 for females and males respectively.

	Female nest defense model					***Male nest defense model***				
Fixed effect	Estimate	95% CI	χ^2	df	*P*	Estimate	95% CI	χ^2	df	*P*
(Intercept)	-0.02	-0.18: 0.14				-0.06	-0.22: 0.11			
Mean_CS	0.08	-0.10: 0.27	0.80	1	0.370	**0.19***	**0.002: 0.37**	**3.89**	**1**	**0.049**
Dev_CS	0.01	-0.11: 0.14	0.04	1	0.840	-0.04	-0.18: 0.10	0.37	1	0.549
Mean_LD	-0.05	-0.22: 0.13	0.30	1	0.586	0.06	-0.11: 0.24	0.49	1	0.486
Dev_LD	-0.10	-0.23: 0.02	2.73	1	0.099	-0.10	-0.23: 0.04	1.93	1	0.164
NDL	**0.12***	**0.04: 0.20**	**9.51**	**1**	**0.002**	0.06	-0.03: 0.15	1.33	1	0.250
AGE	-0.04	-0.21: 0.12	0.28	1	0.595	0.10	-0.07: 0.23	1.87	1	0.172

AGE: individual age. Female mean clutch size (Mean_CS) and laying date (Mean_LD) were used to test for long-term among-individual nest defense associations caused by genetic or developmental effects. Deviations from female mean clutch size (Dev_CS) and laying date (Dev_LD) were used to test for within-individual/among-year nest defense associations caused by state-dependent effects. Number of days elapsed since laying (NDL) was used to test for short-term labile adjustments of nest defense to reproductive stage varying within a breeding season. Significant fixed effects are in bold.

*The estimate for number of days elapsed since laying in the female nest defense model containing only this significant fixed effect is 0.13 (95% CI = 0.06: 0.21, $\chi^2 = 12.86$, $df = 1$, $P < 0.001$). The estimate for female mean clutch size in the male nest defense model containing only this significant fixed effect is 0.20 (95% CI = 0.04: 0.37, $\chi^2 = 6.10$, $df = 1$, $P = 0.014$).

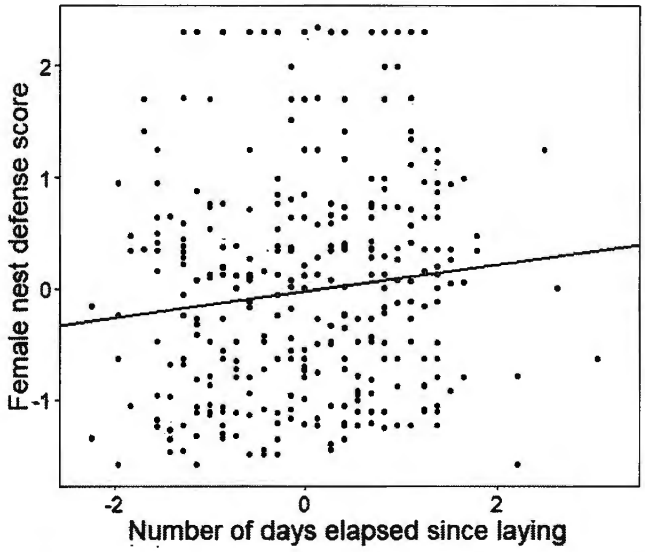

Figure 1.1. Female nest defense score in relation to the number of days elapsed since egg laying at the date the test was performed (N = 336). Variables are z-transformed. Mean number of days elapsed since laying (0 for z-transformed variable) corresponds to 22 days ± 7.2 (mean ± SD).

Male nest defense scores were positively associated with female mean clutch size (Table 1.2, Figure 1.2; among-individual variation). There was no effect of deviation from female mean clutch size (within-individual/among-year variation), laying date (female mean and deviation from female mean; among-individual and within-individual/among-year variations), age, or the number of days elapsed since the beginning of laying (within-individual/within-year variation) on male nest defense scores.

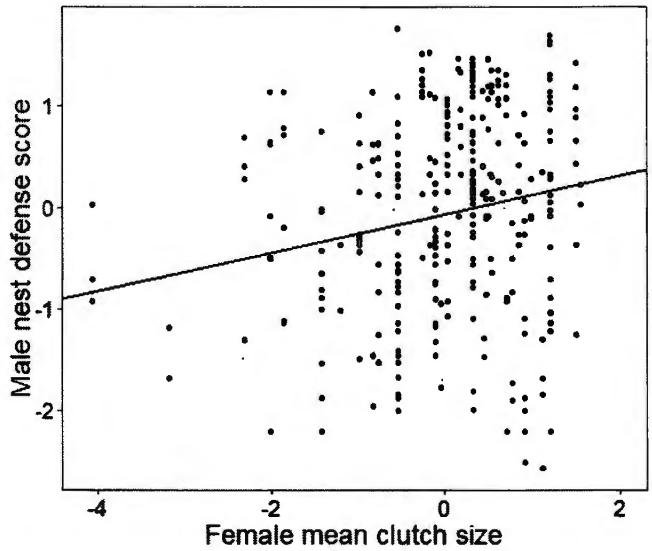

Figure 1.2. Male nest defense score in relation to female mean clutch size (N = 315). Variables are z-transformed. Mean female clutch size (0 for z-transformed variable) corresponds to 5.6 eggs ± 1.1 (mean ± SD).

1.5 Discussion

In this study, we aimed to determine the mechanisms responsible for the variation in female and male Canada goose nest defense behavior. We thus partitioned this variation at three levels: 1) the among-individual level caused by genetic or developmental effects leading to among-individual differences, 2) the within-individual/among-year level caused by state-dependent plastic adjustments to brood value varying across years, and 3) the within-individual/within-year level resulting from labile short-term adjustments or measurement errors. First, we found consistent individual differences in both female and male nest defense at every level and time scale. Both female and male nest defense behavior were repeatable (0.24 – 0.74) indicating that some individuals were being consistently more defensive than others. These individual differences could result from genetic or developmental effects. Female nest defense was however not associated with clutch size and laying date at the

among-individual and within-individual/among-year levels, but it was plastically adjusted to the stage of development of the eggs in the short-term (within each breeding season). On the other hand, male nest defense varied with clutch size at the among-individual level, but not at the within-individual/among-year level. It was not associated to laying date at both levels. Our results demonstrate the importance of partitioning variance at the different levels to better understand what ecological and evolutionary mechanisms generate variation in parental behavior.

Canada goose clutch size and laying date were moderately repeatable (0.19 – 0.22). Large residual variance in clutch size indicates that much of the variation in this trait could not be explained by consistent individual differences nor by year. However, it varied with female age, with older females laying more eggs, as expected in geese (Hamann & Cooke 1987). Clutch size could further be related to differences in female body condition that are not individually consistent across breeding seasons nor related to specific years. For laying dates, contrary to clutch size, a large proportion of variation was explained by the study year (see below) and female age, as expected again in geese (Hamann & Cooke 1987), but important unexplained residual variation remained.

At the among-individual level, the most defensive females were not necessarily laying larger clutch sizes compared to less defensive females (i.e. no effect of Mean_CS on female nest defense, Table 1.2). Our results do not fit with hypotheses of the POLS framework, which considers that the most fecund females trade-off between lifespan and reproduction and should therefore invest more in their current reproduction and be more aggressive (Réale et al. 2010). Sjöberg (1994) and Miller et al. (2013) found phenotypic association between the intensity of female nest defense and clutch size in Canada geese. Still, we cannot say whether this phenotypic association was explained by among-individual differences or phenotypic plasticity as

variation was not partitioned between the among- and within-individual levels in these studies. The relationship between age and clutch size was similar among females confirming that female mean clutch size correctly depicted among-female fecundity differences in our nest defense model.

For males, we found a significant effect of female mean clutch size on their nest defense intensity. The most defensive males were thus mated with the most fecund females. Differences in life history strategies used to explain covariation between fecundity and behavior is less intuitive for males as they do not bear the costs of egg production and incubation. However, having a larger number of young could be costly for their survival if larger families are more vulnerable to predation or hunting. Furthermore, it has also been proposed that sexual selection can maintain individual consistency in behavior through non-random mate choice, and that a behavioral trait can serve as an honest signal of quality (Schuett et al. 2010). For example, females of different species have shown a preference for bold and aggressive males during mate selection (Schuett et al. 2010). If the quality of a Canada goose male is determined by its ability to defend a nest (and possibly a nesting territory or a food patch), and that the quality of a female is determined by its fecundity, this could result in non-random mating of the most defensive males with the most fecund females, and consequently the less defensive males with the less fecund females. It should indeed be beneficial for females to mate with defensive males (that are consistent in their behavior) as it could allow them to focus entirely on egg laying and incubation (rather than defense) with reduced disturbance. In fact, during the pre-laying period, male geese are much more vigilant than females which spend more time feeding (Gauthier & Tardif 1991). It is also possible that females mated with the more defensive males have access to better food resources and are less disturbed by predators and competitors, allowing them to lay more eggs. Brommer et al. (2015) also discussed how males can influence their mate's reproduction through their behavior (e.g. mating behavior, food

provisioning). Overall, our results suggest Canada goose fecundity was not significantly linked to female personality, but it was to male personality.

Still at the among-individual level, we found no significant association between both female and male nest defense and laying date (i.e. no effect of Mean_LD on nest defense, Table 1.2). The most defensive individuals were thus not necessarily those laying earlier in the season. Sjöberg (1994) also failed to find a clear relationship between female nest defense intensity and laying date. As discussed by Browne et al. (2007), laying date in birds depends mainly on annual variation in weather conditions, as well as female characteristics, and not very much on male characteristics. Even though we found some individual repeatability in female Canada goose laying date, and in addition to being explained by the age of the female, laying date seems to be a highly labile trait dependent on environmental variation (as it usually does, Charmantier et al. 2008; Balbontin et al. 2009). Indeed, laying date in this population was shown to be plastically adjusted to spring temperatures that vary among years (Clermont et al. 2018). The important plasticity of this trait to environmental variation could explain why it is not clearly related to nest defense at the among-individual level, in both sexes. Because females might be slightly different in the way they change their laying date when aging, further investigations are needed to better understand how aging effects on laying date affect the among-individual association between nest defense and laying date.

At the within-individual/among-year level, neither female nor male nest defense behaviors were related to changes in state (here clutch size and laying date, i.e. no effect of Dev_CS or Dev_LD on nest defense, Table 1.2). This contradicts hypotheses from parental investment theory that proposes parents should adjust the intensity of their nest defense to the value of their clutch, and therefore be more defensive when more eggs are laid and when eggs are laid earlier in the season

(Montgomerie & Weatherhead 1988). Indeed, individual consistency in behavior may result in limited plasticity (Bell 2007). Nest defense being very consistent, it is possible that Canada geese do not adjust it to variation in clutch size and laying date. Still, we found significant within-individual/among-year variation in nest defense (significant variance of the random effect ID_year), meaning Canada goose nest defense varied with other factors varying among years. First, reproductive effort of previous years (rather than the one of the current year) could affect the intensity of nest defense. For example, previous reproductive effort was shown to affect feeding behavior in eastern grey kangaroos (*Macropus giganteus*) (Gélin et al. 2013) and migration decisions in black brant geese (*Branta bernicla nigricans*) (Sedinger et al. 2011). Also, varying winter or spring climatic conditions that may further affect body condition could cause parents to invest more or less in nest defense, independently of their investment in clutch size and laying date.

Lastly, at the within-individual/within-year level, we found that females (but not males) became more defensive during tests performed at dates closer to hatching (significant effect of NDL on female nest defense, Table 1.2). Females thus plastically adjusted their nest defense to short-term (within-breeding season) variation in the value of their clutch. This is in accordance with the parental investment theory, as the benefits of defending a nest become greater as young get older (Montgomerie & Weatherhead 1988). However, Knight and Temple (1986b) suggested that the seasonal increase in nest defense could be an artifact of methodology resulting from repeated measurements on the same individuals. We reject this possibility as the geese that we studied are used to human presence in urban and sub-urban regions and are being submitted to repeated visits during nest monitoring. The remaining residual variance in female and male nest defense behavior suggests an adjustment of nest defense to other factors varying within the breeding season (e.g. environmental conditions), or measurement errors.

1.6 Conclusion

In conclusion, Canada goose nest defense intensity is stable in time, and to some extent independent of reproductive effort. However, Canada goose males that defended their nest most intensely were paired with the most fecund females, and females plastically adjusted their nest defense to short-term changes in clutch value within each breeding season. Our study shows how an association between traits at the phenotypic level can be partitioned into association at the among- and within-individual levels, which allows us to better understand (co)variation of traits that can result from both among-individual differences and phenotypic plasticity. As a final note, our study demonstrated the importance of studying nest defense in both sexes even in species where only females incubate eggs, as both sexes can invest in nest defense.

CHAPITRE II

ASSORTATIVE MATING BY NEST DEFENSE INTENSITY IS NOT RELATED TO REPRODUCTIVE SUCCESS IN CANADA GEESE

Jeanne Clermont, Denis Réale & Jean-François Giroux

2.1 Abstract

Individuals consistently differ in their behavior, and such personality differences can further predict fitness. For biparental care species, the behavior of both parents can impact reproductive success. In fact, behavioral similarity within pairs has been shown to provide adaptive advantages for many species. In this study, we tested for assortative mating in 112 pairs of nesting Canada geese with respect to nest defense behavior, an individually consistent trait. We used a bivariate mixed model to provide unbiased estimates of assortative mating correlations. We also tested the effect of assortative mating on reproductive success and predicted greater success for pairs positively assorted. We found that pairs of Canada geese were formed of individuals showing similar nest defense intensities, suggesting that personality may play a role in mate selection. The behavior of an individual also covaried with the behavior of its mate between successive tests. However, similarity in nest defense intensity did not result in

higher reproductive success. The non-adaptive mechanisms that led to assortment based on personality in this goose population remain to be identified.

Keywords: assortative mating, bivariate mixed model, nest defense, personality, reproductive success

2.2 Introduction

Individual consistency in behavioral traits such as aggressiveness and boldness has been demonstrated for many animal species (see review by Réale et al. 2007). Terms like personality, temperament, and behavioral syndromes are often used to refer to individual differences in behavior that are repeatable over time and across contexts (Sih et al. 2004; Réale et al. 2007; Bell et al. 2009). Furthermore, personality differences can explain fitness variation in a population (Dingemanse & Réale 2005; Smith & Blumstein 2008; Réale et al. 2009). For example, exploration behavior in great tits (*Parus major*) has been related to nest success, fledging size and condition, and offspring survival (Dingemanse et al. 2004; Both et al. 2005). There is also a genetic basis behind personality, as behavioral traits can be heritable (van Oers et al. 2005; Réale et al. 2007; Quinn et al. 2009). If certain personality types are associated with greater reproductive success, then why are personality differences maintained in a population? Fluctuating selection related to changes in environmental conditions in time and space is one explanation (Dingemanse et al. 2004; Boon et al. 2007). Other adaptive mechanisms have been proposed to explain the maintenance of among-individual differences (Réale & Dingemanse 2010; Dingemanse & Wolf 2010; Dingemanse & Réale 2013), one of them being the link between personality traits and life-history trade-offs (Wolf et al. 2007; Biro & Stamps 2008; Réale et al. 2010).

One particular explanation comes from sexual selection, and more precisely from non-random mate choice (Schuett et al. 2010). Because of the moderate to high

repeatability of these traits, females could use behavior (e.g. boldness, exploration) as an honest signal of male quality. For example, highly explorative male zebra finches (*Taeniopygia guttata*) produced offspring that were in better body condition compared to males with limited exploratory tendencies (Schuett et al. 2011). If only females of a certain personality can access higher quality males, non-random mate choice could further maintain personality traits (Schuett et al. 2010). Non-random mate choice and intra-sexual conflicts could thus lead to different patterns of assortment based on different phenotypes, and thus to positive or negative correlations between traits of mated individuals. Furthermore, assortative mating is a type of non-random assortment where individuals select mates based on phenotypic similarity to themselves (Jiang et al. 2013). It could have evolved if fitness depends on mate similarity or if similar mates are constrained to be paired. An example is the age-assortative mating in monogamous species (Black & Owen 1995; Jiang et al. 2013). Assortative mating could also reduce sexual conflict over the provisioning of parental care, which could further be beneficial to reproductive success (Schuett et al. 2011). Most studies on assortative mating have been conducted on fixed traits (e.g. size, Choudhury et al. 1996; Jiang et al. 2013) rather than labile traits like behavior, where trait repeatability is generally moderate (Bell et al. 2009), and for which environmental effects (e.g. weather condition or food availability) can lead to covariation of homologous traits between mated individuals (Class et al. 2017).

Assortative mating based on different personality traits has been shown to be adaptive for many species (e.g. Both et al. 2005; Schuett et al. 2011; Gabriel & Black 2012; Ariyomo & Watt 2013; Burtka & Grindstaff 2015; Montiglio et al. 2016). For example, Gabriel and Black (2012) found that Steller's jay (*Cyanocitta stelleri*) pairs composed of individuals similar in exploration and willingness to take risks initiated their nest earlier and had a better fledging success, but not in every year of their study. In guppies (*Poecilia reticulate*), each parent's boldness did not directly affect brood

size, but parturition success was greater in couples formed of individuals with similar degree of boldness (Ariyomo & Watt 2013).

In this study, we assessed assortative mating with respect to nest defense behavior in a biparental care monogamous species, the Canada goose (*Branta canadensis*), and tested whether reproductive success increased with similarity in nest defense between the two sexes. We have previously shown important personality differences in nest defense in both females and males, and found that the more defensive males were mated with the more fecund females (Chapter 1). Kontiainen et al. (2009) also found that offspring recruitment was best explained by nest defense aggressiveness of Ural owl (*Strix uralensis*) mothers. However, this is not always the case. Neither Redmond et al. (2009) nor Burtka and Grindstaff (2013) found a significant effect of nest defense on nesting success. For species where both parents defend the nest, it is important to consider the phenotype of both individuals of a pair to predict its effect on reproductive success. This is true especially in monogamous species that mate for life and stay together throughout the annual cycle. For example, pairs of barnacle geese (*Branta leucopsis*) are formed of individuals similar in age and size, and the most assorted pairs have the highest reproductive success (Black & Owen 1995; Choudhury et al. 1996). In their study, Burtka and Grindstaff (2015) found that pairs of eastern bluebirds (*Sialia sialis*) that mated assortatively by aggressiveness and those where males were more aggressive than females produced more fledglings than pairs where females were more aggressive than males.

To test whether Canada geese mated assortatively according to their aggressiveness to defend their nest against a human intruder, we used a Bayesian bivariate mixed modelling approach. This method has been shown to correctly account for short-term environmental effects that can inflate the estimation of assortative mating, as it can decompose covariation between female and male traits into different

levels, i.e. the among-pair level or the assortative mating covariation, and the common environment and residual covariations (Class et al. 2017). We predicted a positive assortative mating at the among-pair level, and thus that the most defensive females would be paired with the most defensive males. We further assessed the selective advantage of assortative mating by testing the effect of assortative mating by nest defense behavior on four reproductive success proxies: clutch size, laying date, number of young leaving the nest, and juvenile pre-fledging apparent survival. We predicted that assorted pairs would have a greater reproductive success than non-assorted pairs.

2.3 Methods

2.3.1 General methods

We conducted this study between 2015 and 2017 on a series of islands located on the St. Lawrence River (45° 40′ N, 73° 27′ W), 15 km northeast of the city of Montreal, Quebec, Canada. Annual nest monitoring of Canada geese allowed us to obtain laying date, clutch size, and number of young leaving each nest. At hatching and just before nest departure, goslings were marked with a unique numbered web-tag (Pilotte et al. 2014). See Chapter 1 and Clermont et al. (2018) for more information on nest monitoring.

We also conducted banding operations just before fledging (late June/early July), when juveniles were at least 40 days old. Plastic neck-collars with a unique code were fitted to adults already marked with a web-tag and to adult females with a brood patch. Based on their plumage, geese were aged as hatching-year (HY, i.e. juveniles) or after hatching-year (AHY, yearlings and 2+ year-old birds). Exact age of birds observed during this study was calculated for individuals with known hatching year (banded as HY or as AHY previously marked with a web-tag). A minimum age was

approximated for the other individuals assuming that they started breeding at 2 years of age (Pilotte et al. 2014). A pre-fledging apparent survival status was later attributed to each juvenile that was web-tagged at hatching; it received a survival status of 1 if it was recaptured (during the banding operations of its hatching year or of subsequent years), and of 0 if it was never recaptured. See Pilotte et al. (2014) and Clermont et al. (2018) for more information on banding operations.

During incubation, we performed nest approaches to characterize the intensity of nest defense by both parents of pairs with females marked with a neck-collar. Not all males were banded. We used the age of the paired female as a surrogate for the age of unbanded males, as Canada geese mate assortatively by age (Pannetier-Lebeuf & Giroux 2013; Chapter 1). During each nest approach, we measured the distance between the observer and the nest when individuals first reacted, whether the geese stayed near or at the nest, moved towards the observer, or moved away from the nest. We estimated the distance at which the geese moved from the nest, noted if they vocalized, whistled, performed head pumping, shook their head, opened their wings, or flew towards the observer. We finally estimated the distance to the nest of both males and females after the approach. Each of these behaviors were then categorised. See Chapter 1 for more details on nest approaches and on the different categories for each behavior. The goal was to perform up to three nest approaches per pair per year and to observe the same pairs every year. Repeating measurements each year instead of measuring a pair only once a year greatly increases statistical power needed to assess assortative mating (Class et al. 2017).

2.3.2 Statistical analyses

All analyses were performed using version 3.2.2 of the R software (R Development Core Team 2013). We first used nonmetric multidimensional scaling (NMDS, Oksanen

et al. 2016) with the behavior categorical variables noted during each nest approach to obtain a nest defense score for each female and male separately, and thus characterize the level of defense at each test with one variable per sex (higher scores were associated with a greater level of nest defense). For further details on how these nest defense scores were obtained, see Chapter 1.

We used a Bayesian bivariate mixed modelling approach to estimate variance of female and male nest defense scores and covariance components at different hierarchical levels, using the package MCMCglmm (Markov-chain Monte-Carlo generalized linear mixed models, Hadfield 2010). Particularities of Bayesian mixed models and MCMCglmm are detailed by Wilson et al. (2010) and Houslay and Wilson (2017). All traits in the models were centered at their mean value and standardised to units of 1 phenotypic standard deviation, which makes easier to fit the model (Houslay & Wilson 2017). As shown by Class et al. (2017), bivariate mixed models provide the best unbiased estimates of assortative mating correlations. We used scores from tests where both female and male were present.

For both male and female nest defense scores, we included as fixed effects the number of days elapsed between the beginning of laying and the date when the test was performed to control for a potential effect of egg developmental stage on intensity of nest defense (Chapter 1). We also included the confounding variable year to correct for annual variation. We further included female age and male age for nest defense scores. We used the random effect structure described in Araya-Ajoy et al. (2015) to allow quantification of (co)variation at different hierarchical levels (i.e. within and among years), and the calculation of repeatability at these different temporal scales. We thus included two random effects: pair identity (pair_ID) and a combination of pair_ID and year (pair_ID_year). This was used to indicate a period (here breeding seasons), within which multiple observations of pairs' nest defense were assessed (Araya-Ajoy et al.

2015). This random effect structure allows to control for short-term effects common to both individuals in a pair (like weather conditions, food availability, or reproductive effort varying across years) that can inflate the estimation of assortative mating (Class et al. 2017). Covariation between female and male behavior was thus assessed at 3 levels: 1) at the among-pair level (random effect pair_ID), i.e. the assortative mating covariation or the ''true'' association between female and male behavior, 2) at the within-pair/among-year level (random effect pair_ID_year) that depicts the association between female and male behavior caused by common short-term effects varying across years, and 3) at the residual within-pair level, depicting the residual association between female and male behavior caused by plastic adjustments to short-term effects varying across tests within each year, or by measurement errors (Class et al. 2017).

In this model, we used a prior distribution of parameters with variance (parameter V) equal to 1 as all variables were scaled, divided by the number of random effects in the model (here 3 including residuals) and a degree of belief "nu" equal to the order of the prior matrices, i.e. 2 (bivariate model), for both the R and G structures (see Hadfield 2010 and Wilson et al. 2010). We validated the priors by testing models with different "nu" (e.g. nu = 0.1, nu = 1, nu = 3), which did not affect the results of the posterior distributions. The two traits were assumed to follow a Gaussian distribution. We used a burn-in of 2000, for five million iterations with a thinning interval of 1000 to produce chains of low posterior autocorrelations, which were assessed using the function autocorr. We used the mode of posteriors and 95% Highest Posterior Density (measure of 95% credible interval (CRI) used to assess significance, which does not significantly differ from zero when overlapping zero, Hadfield 2010). We removed non-significant fixed effects and ran the model again to obtain (co)variance components. To estimate the proportion of variance attributed to differences among individuals (Bell et al. 2009; Nakagawa & Schielzeth 2010), long- and short-term repeatabilities were calculated using posterior distribution of variances,

and by dividing the variance of interest by the total variance. Recall that the distinction between equations for long- and short-term repeatabilities is that the short-term repeatability equation includes the variance among-individual (associated with random effect pair_ID) and the variance within-individual/among-year (associated with random effect pair_ID_year) in the numerator, thus depicting short-term among-individual consistency in behavior (Araya-Ajoy et al. 2015). The long-term repeatability equation only includes the variance among-individuals, thus depicting more permanent consistent individual differences in behavior (Araya-Ajoy et al. 2015). Both equations include the sum of among-individual (pair_ID), within-individual/among-year (pair_ID_year) and residual variances in the denominator. Correlations presented in Table 2.2 were calculated from (co)variance matrices to allow easier interpretation of results, following the formula $r_{X,Y} = C_{X,Y} / \sqrt{(V_X \times V_y)}$, where $C_{X,Y}$ is the covariance between the two traits X and Y, and V_X and V_Y represents the variance of X and Y, respectively.

To test for the effect of assortative mating on reproductive success, we performed univariate mixed models using MCMCglmm, with as proxies of reproductive success, clutch size, laying date, number of young leaving the nest, and juvenile pre-fledging apparent survival status. For these analyses, we only retained data for the nests where parent nest defense was assessed. For the models on number of young leaving the nest and juvenile pre-fledging apparent survival status, we only used data of young hatched in 2015 and 2016 because a very small number of nests succeeded in 2017 due to unusually high water levels of the St. Lawrence River and a concomitant widespread flooding of nests.

In the five models, we tested for the significance of fixed effects female and male nest defense scores to test for the effect of (each) parent behavior on nesting success. We used the nest defense scores of the first nest approach performed the year

of the observation, because only one nest defense score had to be considered for each year/breeding event, and nest defense was shown to be very repeatable within years (Chapter 1). We also included the quadratic forms of these variables to test for non-linear effects. To test for the effect of assortative mating by nest defense intensity on reproductive success (and thus the combined effect of female and male behavior), we included the interaction between female and male nest defense scores (as in Schuett et al. 2011). We also included the confounding variables female age and hatching year. As a random effect, we included pair_ID in the four models. In the juvenile pre-fledging apparent survival status model, we did not include the identity of the nest as a second random effect due to the low number of nest repeats per pair; it was thus impossible to differentiate parental from brood effects (see Results). We used the same model particularities described above for the bivariate model and assessed significance of fixed effects using 95% CRI of posterior modes. For the juvenile pre-fledging apparent survival status model, we used a categorical distribution (a Gaussian distribution was used in all other models) and a prior where the residual variance was fixed (Hadfield 2010). Means are presented ± SD.

2.3.3 Ethics statement

Animal handling methods were approved by the UQAM Animal Care Committee (#578 and #716) and conformed to guidelines of the Canadian Council for Animal Care.

2.4 Results

2.4.1 Association between female and male nest defense

We measured nest defense behavior in 112 Canada goose pairs that were tested on average 3.0 ± 1.5 [range 1:7] times. We used a total of 315 female and male nest

defense scores, and 38 of the 112 pairs were tested during more than one breeding season.

In the female and male nest defense bivariate mixed model containing all fixed effects, we found a significant increase in nest defense score with the number of days elapsed since the beginning of laying (credible intervals (CRI) of estimates excluded zero for both traits, Table 2.1). Nest defense scores were significantly higher in 2016 and 2017 compared to 2015, but they did not vary significantly with goose age (Table 2.1). To assess (co)variances, we thus used a model containing only number of days elapsed since laying and year as fixed effects for both variables.

Table 2.1. Estimates of fixed effects included in the Bayesian bivariate mixed model explaining female and male nest defense scores of the southern Quebec (Canada) Canada goose population, between 2015 and 2017. Pair_ID and pair_ID_year were included as random effects (N = 315). All estimates are shown with their 95% credible interval (CRI, between brackets). Significant fixed effects are in bold.

Trait	Fixed effect	Estimate
Female nest defense	Intercept	-0.29 [-0.64, -0.08]
	NDL	**0.15 [0.07, 0.23]**
	Age	-0.01 [-0.21, 0.12]
	Year (2016)	**0.45 [0.09, 0.75]**
	Year (2017)	**0.58 [0.18, 0.87]**
Male nest defense	Intercept	-0.45 [-0.71, -0.16]
	NDL	**0.12 [0.04, 0.21]**
	Age	0.04 [-0.14, 0.18]
	Year (2016)	**0.34 [0.03, 0.68]**
	Year (2017)	**0.85 [0.44, 1.14]**

NDL: number of days elapsed since the beginning of laying, Age: individual age.

We found a positive and significant covariance between female and male nest defense scores among pairs that yielded a correlation of 0.61 (Table 2.2, Figure 2.1). However, the covariance within-pair/among-years (i.e. caused by common

environmental effects like weather conditions or food availability) was not significant (Table 2.2). Female and male nest defense scores also covaried from one test to another within each breeding season as we also found a small positive but significant residual within-pair covariance between traits (Table 2.2).

Table 2.2. Among-pair, within-pair/among-year, and residual within-pair covariances/correlations between female and male Canada goose nest defense scores estimated from a Bayesian bivariate mixed model including pair_ID and pair_ID_year as random effects (N = 315). The among-pair covariance (i.e. pair_ID) depicts assortative mating by nest defense, while the within-pair/among-year covariance (i.e. pair_ID_year) depicts assorted adjustment within a pair caused by common environmental effects like weather conditions or reproductive effort that varied among years. The residual within-pair covariance depicts plastic, combined, adjustments of nest defense within each breeding season or measurement errors. All estimates are shown with their 95% CRI (between brackets).

Level	Covariance	Correlation
Among-pair	0.26 [0.09, 0.44]	0.61 [0.32, 0.83]
Within-pair/among-year	0.05 [-0.06, 0.17]	0.22 [-0.22, 0.63]
Residual within-pair	0.05 [0.004, 0.09]	0.14 [0.02, 0.30]

Fixed effects included in the model are presented in bold in Table 2.1.

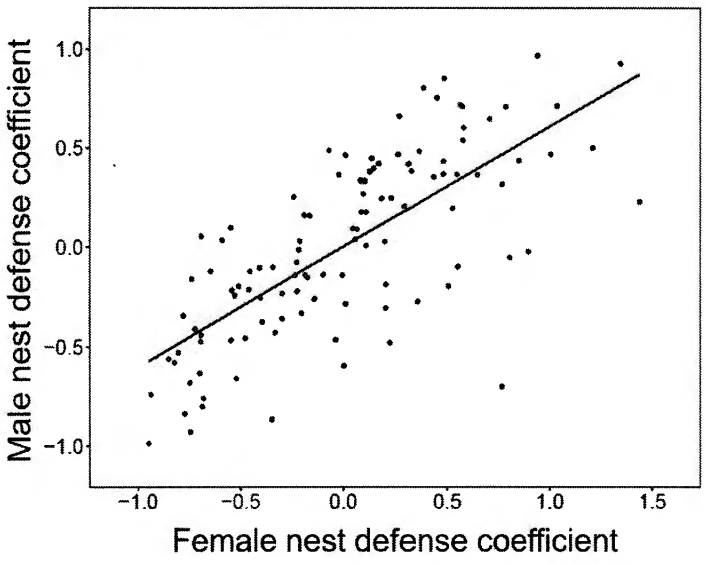

Figure 2.1. Among-pair association between female and male nest defense for the 112 studied Canada goose pairs nesting in Southern Quebec (Canada), depicting assortative mating. Here we show the relationship between female and male nest defense using posterior modes of the random effect pair_ID (i.e. individual coefficients at the among-pair level) estimated from the Bayesian bivariate mixed model of female and male nest defense scores (N = 315) with pair_ID and pair_ID_year as random effects.

A large amount of variation in female and male nest defense scores was explained at the among-individual level (random effect pair_ID), and both were repeatable with respective repeatabilities of 0.73 and 0.65 on the short-term and of 0.52 and 0.45 on the long-term (Table 2.3).

Table 2.3. Among-individual (V_I), within-individual/among-year (V_{IY}) and residual (VR) variances, and long- (R_{LT}) and short-term repeatabilities (R_{ST}) of female and male Canada goose nest defense scores estimated from a Bayesian bivariate mixed model including pair_ID and pair_ID_year as random effects (N = 315). All estimates are shown with their 95% CRI (between brackets).

Trait:	**Female nest defense**	**Male nest defense**
Variance		
V_I	0.47 [0.27, 0.72]	0.36 [0.21, 0.63]
V_{IY}	0.23 [0.11, 0.40]	0.20 [0.08, 0.37]
V_R	0.26 [0.21, 0.31]	0.32 [0.26, 0.41]
Repeatability		
R_{LT}	0.52 [0.34, 0.65]	0.45 [0.26, 0.58]
R_{ST}	0.73 [0.66, 0.81]	0.65 [0.56, 0.74]

Fixed effects included in the model are presented in bold in Table 2.1.

2.4.2 Effect of assortative mating on reproductive success

We used 147 observations of clutch size and laying date, and 100 observations of number of young leaving the nest (see Methods). For the juvenile pre-fledging apparent survival status model, we used data of 329 web-tagged young from 72 nests of 69 pairs (thus only three pairs had more than one nest (different years) in this dataset, justifying why we did not use nest identity as a second random effect). Of these young, 116 (35%) were captured during banding operations.

In all models, the interaction between female and male nest defense scores was not significant (CRI including zero, Table 2.4). In the clutch size model, the age of the female was the only significant fixed effect, with older females laying more eggs (Table 2.4). In both the laying date and juvenile pre-fledging apparent survival status models, only the fixed effect year was significant (Table 2.4). Finally, in the number of young leaving the nest model, we found that male nest defense score was the only significant fixed effect, with the number of young leaving the nest increasing with male nest defense score (Table 2.4).

Variances for the random effect pair_ID as well as residual variance indicated most variation was not explained by the fixed effects included in the models, and that unexplained among-pair reproductive success differences remained (Table 2.4).

Table 2.4. Estimates of fixed effects included in the Bayesian univariate mixed models explaining Canada goose clutch size (N = 147 nests), laying date (N = 147 nests), number of young leaving the nest (N = 100 nests), and juvenile pre-fledging apparent survival status (N = 329 web-tagged young), and variances for random effects pair_ID (V_P) and residuals (V_R). The interaction between female and male nest defense scores depicts combined effects of these traits (i.e. the effect of assortative mating) on each reproductive success proxy. All estimates are shown with their 95% CRI (between brackets). Significant fixed effects are in bold.

Model:	**Clutch size**	**Laying date**	**Number of young leaving the nest**	**Pre-fledging apparent survival**
Fixed effect		Estimate		
Intercept	-0.11 [-0.45, 0.20]	1.12 [0.93, 1.31]	-0.03 [-0.37, 0.26]	-2.34 [-3.33, -1.20]
FND	0.003 [-0.22, 0.23]	-0.02 [-0.15, 0.12]	-0.19 [-0.47, 0.19]	-0.67 [-1.59, 0.19]
MND	0.11 [-0.12, 0.33]	-0.04 [-0.16, 0.11]	**0.29 [0.01, 0.63]**	-0.18 [-1.13, 0.68]
FND^2	-0.01 [-0.20, 0.22]	0.03 [-0.10, 0.15]	-0.03 [-0.33, 0.23]	0.33 [-0.53, 1.03]
MND^2	0.08 [-0.15, 0.25]	-0.06 [-0.17, 0.06]	0.08 [-0.16, 0.38]	-0.04 [-0.81, 0.82]
FND*MND	-0.10 [-0.23, 0.13]	-0.005 [-0.12, 0.10]	0.10 [-0.12, 0.38]	-0.06 [-0.94, 0.49]
Age	**0.21 [0.006, 0.38]**	-0.11 [-0.22, 0.01]	-0.01 [-0.23, 0.21]	0.13 [-0.41, 0.72]
Year (2016)	0.25 [-0.11, 0.70]	**-1.98 [-2.18, -1.72]**	0.02 [-0.30, 0.51]	**1.49 [0.40, 2.79]**
Year (2017)	-0.06 [-0.45, 0.44]	**-0.91 [-1.20, -0.69]**	-	-
Random effect		Variance		
pair_ID	0.20 [0.07, 0.50]	0.12 [0.04, 0.23]	0.26 [0.06, 0.72]	0.95 [0.93, 5.69]
residuals	0.70 [0.48, 0.99]	0.23 [0.14, 0.33]	0.55 [0.30, 1.03]	0.50 (fixed)

FND: female nest defense, MND: male nest defense, Age: female age. Variances are those from models containing all fixed effects.

2.5 Discussion

For biparental care bird species, the behavior of both partners can determine nesting success. It has been shown that pairs assorted by personality have the greatest reproductive success (e.g. Schuett et al. 2011; Burtka & Grindstaff 2015), as behavioral

similarity/complementarity can reduce sexual conflicts and increase fitness (Schuett et al. 2010; Schuett et al. 2011). In this study, we found that Canada geese paired assortatively based on the intensity of their nest defense behavior, with the more defensive females paired with more defensive males (significant and positive covariation between female and male nest defense intensity at the among-pair level). The assortative mating correlation we observed (0.61) is much larger than what it is usually measured for behavioral traits. Jiang et al. (2013) calculated mean values of 0.35 for behavioral traits (all taxa considered) and 0.25 for birds (all trait categories considered). Assortative mating based on phenotypes like age and size has been already established in geese. Moreover, Black et al. (2007) suggested that geese might also show a preference for mates with a personality like their own. Our results suggest that personality could indeed play an important role in mate selection in geese, in addition to other individual attributes like age and size.

Several mechanisms can explain assortative mating in birds. First, individuals might actively select mates with characteristics like their own (Jiang et al. 2013, but similar individuals could also be constrained to be paired, see below). Secondly, they could plastically adjust their phenotype to their partner's phenotype (Dingemanse & Araya-Ajoy 2015). This last option was suggested by Choudhury et al. (1992) to explain assortative mating in barnacle geese based on body size. As most other studies, we did not assess goose personalities before pairing (see Schuett et al. 2010 for a review). Our results, however, indicate that Canada geese may pair assortatively based on personality. First, the covariation between nest defense intensity of paired individuals was significant at the among-pair level rather than at the within-pair/among-year level. Shared short-term effects varying across breeding seasons on the covariation between the two partners' traits were negligible. Therefore, mated individuals did not show similar nest defense adjustments to shared changes in environmental or body conditions across years. Second, our repeatability estimates

were high, both on the long- and the short-term. Bell et al. (2009) found that repeatabilities usually fall around 0.37 for behavioral traits. Our high repeatability scores may be explained by the fact that we used a synthetic NMDS score for each test, which removed part of the stochastic variance associated with each behavioral variable used in the analysis. Nevertheless, individual Canada geese differed consistently in nest defense behavior, and these differences were maintained over the long-term. Considering that Canada geese mate for life (Sjöberg 1994), our results suggest that it is unlikely that assortative mating may arise from geese adjusting their behavior after pairing. However, we cannot discard the possibility that geese may adjust their behavior to their partner's just after they pair, and then stay consistent for the rest of their life.

On the short-term within each breeding season, Canada geese matched the level of nest defense of their partner from one test to another as indicated by significant, although weak, positive covariation between female and male nest defense intensity at the residual within-pair level. Indeed, parents can respond to changes in their partner's level of parental care behavior (see McNamara et al. 1999; McNamara et al. 2003). Individuals could either match their mate's level of parental care or compensate for a reduction of parental care by their partner (Johnstone & Hinde 2006). Matching should be favoured when parents have partial information regarding clutch value or need. An increase in parental care by one parent could be interpreted by the other as the brood needing more care (Johnstone & Hinde 2006). Environmental effects varying within and across days could also cause partners' behavior to positively covary from one test to another. Both parents spend much time at the nest, and they must experience similar conditions. For example, a stressful event happening one morning could cause both parents to be more defensive during a test performed later the same day. However, despite all our efforts to standardise the test, our nest approach might have been perceived differently by the members of a pair, which, consequently, might have

affected their intensity of nest defense. Thus, significant residual within-pair covariation could also be caused by measurement errors (Class et al. 2017).

Both males and females became significantly more defensive as eggs developed. This is consistent with the parental investment theory as the probability that eggs will hatch increase with time (Montgomerie & Weatherhead 1988). In Chapter 1, we also found this effect on female nest defense, but not on male nest defense. However, the bivariate model combining both female and male nest defense scores used in the present paper might provide more information needed to detect this effect in males.

Homogamy is assumed to have evolved because mating with similar individuals has selective advantages (Both et al. 2005; Jiang et al. 2013; Ariyomo & Watt 2013; Burtka & Grindstaff 2015). We did not observe any selective advantage of being assorted by personality in Canada geese (i.e. absence of significant interaction between female and male nest defense scores on reproductive success). However, male nest defense intensity did affect the number of young that left the nest in 2015 and 2016. In Chapter 1, we found that the most defensive males were paired with the most fecund females, but here we did not observe a significant relationship between male nest defense and clutch size. The two analyses were different; in Chapter 1 we partitioned the association between male nest defense intensity and clutch size at the among- and within-individual levels and included female clutch sizes since 2003 to determine each female's mean fecundity. Here, we only looked at the phenotypic association between the two traits during three breeding seasons. The observed effect of male nest defense intensity on the number of young leaving the nest confirms the link between male nest defense and female fecundity (Chapter 1).

The remaining question is thus how assortative mating by personality could have evolved in this population if there is no adaptive advantage. Canada geese became established on our study site only in the early 1990s (Giroux et al. 2001), and differences between current and past environmental conditions (on previous sites) may explain why we did not observe any adaptive advantage for assortative mating. Additionally, pairs could benefit from being assorted in ways that are not related to the proxies of reproductive success that we studied. For example, pairs behaving similarly may be better at accessing the best food patch and thus produce young in better condition. Both et al. (2005) and Schuett et al. (2011) found that pairs assorted by their exploratory capacity produced offspring in better condition.

Jiang et al. (2013) further proposed three non-adaptive mechanisms to explain the evolution of assortative mating. The first mechanism is allochronic isolation. Individuals of similar personalities may have been constrained to be paired through temporal segregation if, for instance, arrival dates on the sites where pair formation occurs depends on personality. This cannot be verified as we do not have individual specific movement data for the Canada geese that we studied. The second mechanism is spatial segregation that would require trait-related habitat matching (see Edelaar et al. 2008; Nicolaus & Edelaar 2018). In other words, individuals of similar personalities could occupy similar types of habitats (e.g. wintering grounds) and thus be more likely to encounter, socialise, and pair. Again, we do not have the data to confirm this hypothesis. Thirdly, assortative mating could be a by-product of intra-sexual competition and inter-sexual conflict. For example, males may prefer more fecund females, and fecundity may be linked to female personality. If only males of a certain personality can access the most fecund females, then assortative mating by personality could arise. We did find an association between male personality and female fecundity, but not between female personality and fecundity (Chapter 1). Other traits could still be involved in mate selection and lead to assortative mating by personality. Lastly, the

strong level of assortative mating in our population (much larger than what is usually observed, see Jiang et al 2013) and thus the low variability in the level of assortment might also explain why we did not observe a selective advantage for assortative mating by personality: the variance among-pairs in assortative mating in the population may be too low to allow the establishment of a link between assortment and fitness.

To conclude, we have shown that pairs of Canada geese are formed of similar individuals based on their level of nest defense, and that personality might play an important role in mate selection. However, similarity in nest defense intensity did not result in higher reproductive success for the three years we studied. Thus, assortative mating in this population seems to be non-adaptive and results from other features of the mating system.

CONCLUSION GÉNÉRALE

Afin de réduire la vulnérabilité du nid face aux prédateurs, les oiseaux adoptent des comportements de défense. L'intensité de la défense du nid peut varier selon le contexte, par exemple selon la valeur de la couvée, et elle peut même varier d'un individu à l'autre (différences de personnalité). L'objectif principal de cette maîtrise était d'expliquer la variation dans la défense du nid des bernaches du Canada nichant sur les îles de Varennes. Plus précisément, au premier chapitre de cette maîtrise, nous avons étudié les rôles des différences persistantes entre les individus (causées par des différences génétiques ou développementales), des ajustements plastiques qui dépendent de la condition variant d'une année à l'autre (taille et date de ponte), et des ajustements à court-terme (stade de développement des œufs) pour expliquer la variation observée dans le comportement des femelles et des mâles entre 2015 et 2017. Au deuxième chapitre de cette maîtrise, nous avons regardé le patron d'appariement des couples selon l'intensité de leur défense du nid. Nous avons aussi regardé si le degré d'homogamie des couples selon ce comportement affectait leur succès reproducteur.

Au Chapitre 1, nous avons trouvé d'importantes différences inter-individuelles dans la défense du nid chez les deux sexes, avec des répétabilités allant jusqu'à 0.74 à court-terme ce qui est plus élevé que ce qui est généralement observé pour des traits comportementaux (0.37; Bell et al. 2009). Bien que la défense du nid des femelles n'était pas associée à la taille ni à la date de ponte au niveau inter-individuel, nous avons trouvé que les mâles les plus défensifs étaient en couple avec les femelles qui en moyenne étaient les plus fécondes. Effectivement, une femelle en couple avec un mâle

très défensif peut potentiellement avoir accès à de meilleurs sites d'alimentation et de nidification, se nourrir davantage et être moins dérangée lors de la nidification, ce qui lui permettrait de pondre un plus grand nombre d'œufs. Aussi, l'association entre le comportement du mâle et la fécondité de la femelle pourrait s'expliquer par un choix du partenaire non-aléatoire. Les femelles de différentes espèces montrent une préférence pour des mâles plus téméraires et agressifs (Schuett et al. 2010). Si la qualité d'un mâle dépend de sa personnalité, et celle de la femelle de sa fécondité, les mâles les plus défensifs devraient être appariés avec les femelles les plus fécondes. La défense du nid chez les deux sexes n'était pas associée à la date de ponte au niveau inter-individuel. La date de ponte est en effet un trait très plastique, qui est ajusté aux conditions environnementales variant d'une année à l'autre (Clermont et al. 2018). Par contre, ni les femelles ni les mâles n'ont ajusté leur défense du nid d'une année à l'autre selon leur taille et leur date de ponte (niveau intra-individuel/inter-couvées), ce qui invalide la théorie de l'investissement parental qui propose que les parents devraient ajuster l'intensité de leur défense à la qualité de leur couvée (Montgomerie & Weatherhead 1988). Cependant, les femelles ont ajusté leur défense à court-terme, en étant plus défensives lors des tests effectués plus près de la date d'éclosion des œufs (niveau intra-individuel/intra-couvée).

Les résultats de ce premier chapitre montrent bien l'importance d'étudier la variation aux différents niveaux impliqués, pour mieux comprendre les mécanismes évolutifs et écologiques qui génèrent la variation dans les comportements parentaux (plasticité phénotypique et différences inter-individuelles persistantes). Aussi, chez les espèces aux soins biparentaux, il est important d'étudier les comportements des deux individus des couples. Pourtant, les études faites sur des espèces où seule la femelle incube les œufs, mais où les deux parents défendent le nid, comme chez les Anatidés, ont très peu considéré les comportements de défense des mâles par rapport à celui des femelles (par exemple Sjöberg 1994; Quillfeldt et al. 2005; Osiejuk & Kuczyński 2007;

Miller et al. 2013). Nous montrons pourtant que le comportement des mâles bernaches du Canada est lié au succès reproducteur. Notre analyse simultanée des comportements des femelles et des mâles contribuent ainsi à une meilleure compréhension des comportements de défense du nid pour de telles espèces.

D'autres facteurs qui n'ont pas été considérés dans ce projet de maîtrise pourraient générer de la variation dans la défense du nid. En effet, la visibilité et l'accessibilité d'un nid prédit souvent son risque de prédation (Ricklefs 1969; Colombelli-Négrel & Kleindorfer 2009). Plusieurs ont trouvé que les parents dont le nid était mieux camouflé que la moyenne s'investissaient moins dans la défense de leur nid puisque les bénéfices associés à la défense d'un nid bien camouflé sont plus faibles (Montgomerie & Weatherhead 1988; Albrecht & Klvaňa 2004; Miller et al. 2007; Miller et al. 2013). Les caractéristiques du nid pourraient ainsi être un effet de l'environnement auquel les parents peuvent s'ajuster d'une année à l'autre (niveau intra-individuel/inter-couvées), en étant par exemple plus défensif les années où le nid est moins bien camouflé. Par contre, il serait aussi possible que la localisation du nid, et donc certaines de ses caractéristiques comme son camouflage, résultent de caractéristiques individuelles constantes.

Les individus pourraient également différer dans leur capacité à ajuster leur comportement aux changements environnementaux ou de conditions. On observerait alors des différences inter-individuelles de normes de réaction (ou encore de différences inter-individuelles de pente), où la relation entre le trait de personnalité étudié et l'environnement diffère selon les individus (Nussey et al. 2007; Dingemanse et al. 2010; van de Pol 2012; Dingemanse & Wolf 2013). Par exemple, Kontiainen et al. (2009) ont trouvé que les chouettes de l'Oural (*Strix uralensis*) différaient dans leur degré de plasticité dans leurs comportements de défense selon la disponibilité des ressources. Betini et Norris (2012) ont quant à eux trouvé que les comportements de

défense du nid d'hirondelles bicolores (*Tachycineta bicolor*) étaient ajustés en fonction de la température, et ce plus particulièrement chez les individus les plus agressifs. Cependant, rares sont les études qui ont testé des différences de normes de réaction avec des comportements de soins parentaux (Westneat et al. 2011). Chez les bernaches, les individus pourraient par exemple différer dans le degré de plasticité de leur défense du nid selon le stade de développement des œufs. Cette hypothèse pourrait être facilement testée avec les données récoltées pour cette maîtrise.

Suite à ce projet, il serait intéressant de continuer de tester les hypothèses du POLS (voir Réale et al. 2010) chez les bernaches du Canada, lorsque des données comportementales, de reproduction à long-terme et de survie seront disponibles pour les mêmes individus. On pourrait par exemple se demander si les individus qui ont été les plus défensifs tout au long de leur vie ont une probabilité de survie plus faible comparativement aux individus les moins défensifs. De plus, ces individus à plus faible longévité ont-ils un succès reproducteur à vie qui équivaut celui des individus qui ont vécu plus longtemps? Effectivement, les animaux font face à un compromis entre longévité et reproduction ; les individus à faible longévité devraient ainsi être plus investis dans leur reproduction actuelle pour maximiser leur succès reproducteur à vie (Ricklefs 1977; Zammuto 1986). Ces individus au train de vie rapide devraient aussi être plus téméraires et agressifs (Réale et al. 2010). Réale et al. (2009) ont par exemple montré que les mâles mouflons d'Amérique (*Ovis canadensis*) les plus dociles vivaient plus longtemps et bénéficiaient d'un succès reproducteur plus élevé plus tard dans leur vie. Par contre, la témérité était corrélée négativement à la docilité. Avec les résultats de ce projet de maîtrise, on pourrait penser que les mâles les plus défensifs, qui ont aussi un meilleur succès reproducteur (puisqu'ils sont appariés aux femelles les plus fécondes), font face à ce compromis entre survie et reproduction. Ils devraient donc vivre moins longtemps que les mâles moins défensifs qui ont un succès reproducteur plus faible à chaque évènement de reproduction.

Au Chapitre 2 de cette maîtrise, nous avons trouvé que les bernaches étaient appariées selon l'intensité de leur défense du nid. Ainsi, les femelles les plus défensives étaient en couples avec les mâles les plus défensifs. Puisque la défense du nid est un trait très répétable et que les individus des couples montrent des intensités de défense du nid similaires sur le long-terme, la personnalité semble donc jouer un rôle dans le choix du partenaire pour cette population. De plus, la sélection sexuelle et plus précisément le choix du partenaire non-aléatoire serait un des mécanismes favorisant les différences de personnalité (Schuett et al. 2010). Puisque les traits de personnalité sont en partie héritables (van Oers et al. 2005; Réale et al. 2007; Quinn et al. 2009), l'homogamie dans la défense du nid (un trait fortement répétable suggérant son héritabilité) pourrait ainsi contribuer au maintien des différences de personnalité chez les bernaches du Canada qui nichent sur les îles de Varennes.

Les individus en couple ont aussi montré des niveaux de défense du nid similaires à l'intérieur d'un même événement de nidification, d'un test à l'autre. Effectivement, les parents pourraient répondre aux changements de comportements de leur partenaire (Johnstone & Hinde 2006). Si un individu augmente l'intensité de ses soins parentaux, son partenaire pourrait déduire que la couvée nécessite plus d'attention et augmenter son propre niveau de soin. Les parents pourraient aussi répondre de manière semblable à des effets environnementaux communs. Pour tester cette hypothèse, il faudrait mesurer différentes variables environnementales qui varient d'un test à l'autre, et voir si les réponses des deux parents à ces changements sont les mêmes. Mais la corrélation entre les comportements des femelles et des mâles des couples au niveau intra-individuel/intra-couvée pourrait aussi résulter d'erreurs de mesure, puisque les deux individus des couples ont été observé en même temps (Class et al. 2017).

Nous avons aussi montré dans ce chapitre que le niveau de similarité dans la défense du nid entre les individus des couples n'avait pas d'effet sur le succès reproducteur (taille de ponte, date de ponte, nombre de jeunes quittant le nid et survie apparente des jeunes avant l'envol). Les avantages adaptatifs de l'homogamie, s'ils existent, restent donc à identifier pour cette espèce. Il serait par exemple intéressant de regarder si l'homogamie dans la défense du nid a un effet sur la condition corporelle des jeunes. Effectivement, la similarité des personnalités des parents influence ce trait chez d'autres espèces (Both et al. 2005; Schuett et al. 2011). Cependant, l'homogamie pourrait tout de même évoluer sans qu'il n'y ait d'avantage adaptatif. Jiang et al. (2013) ont notamment proposé des mécanismes pour expliquer la présence d'homogamie non-adaptative dans les populations. Les individus similaires pourraient entre autre être contraints à s'apparier. Effectivement il se pourrait que les individus de personnalités différentes aient aussi des préférences en terme d'utilisation de l'habitat (i.e. « matching habitat choice », Edelaar et al. 2008; Nicolaus & Edelaar 2018). Ainsi les individus aux personnalités similaires auraient plus de chance de se rencontrer et de s'apparier. Il serait fort intéressant de déterminer les contraintes qui mèneraient à l'homogamie dans le système d'appariement des bernaches. Cela nécessiterait cependant de faire des observations individuelles au moment même de l'appariement.

Pour la suite de ce projet sur la personnalité des bernaches, nous pourrions étudier d'autres traits comportementaux, comme les comportements de défense sur les sites de nourrissage juste avant la nidification, ou après celle-ci lors de l'élevage des jeunes. On pourrait par la suite voir si ces différentes mesures comportementales sont reliées entre elles (formant ainsi un syndrome comportemental, Sih et al. 2004), et si l'appariement est également homogame pour ces autres traits. De plus, d'autres mesures de comportement pourraient être mesurées indépendamment chez la femelle et le mâle des couples pour éviter les erreurs de mesure qui pourraient mener à la covariation de traits homologues chez les membres des couples (voir Class et al. 2017).

Par exemple, on pourrait mesurer l'agressivité en main lors de la manipulation (lors des captures pendant le baguage de masse), comme on le fait souvent dans les études de personnalité (voir Dubuc-Messier et al. 2017).

En conclusion, les bernaches du Canada montrent des différences individuelles persistantes dans leur défense du nid. Les mâles les plus agressifs sont appariés aux femelles les plus fécondes, et les femelles deviennent de plus en plus défensives plus les œufs se développent. Les couples sont formés d'individus montrant des niveaux de défense du nid similaires, mais l'homogamie ne semble pas avoir d'effet sur le succès reproducteur. Ce projet de maîtrise contribue ainsi au domaine de l'écologie comportementale en apportant des pistes pour mieux comprendre l'évolution des soins parentaux et le maintien des différences de personnalité dans les populations animales.

ANNEXE A

DESCRIPTION OF EACH BEHAVIORAL VARIABLE RECORDED DURING CANADA GOOSE NEST APPROACHES

	Categorisation of female nest defense		Categorisation of male nest defense	
Variable	Category	Description	Category	Description
starting position*			1	located 1-5 m from the nest
			2	located 6-10 m from the nest
			3	located > 10 m from the nest
reaction distance	0	stayed on the nest ("no reaction")	1	reacted when observer at 0-2 m from the nest
	1	reacted when observer at 1-2 m from the nest	2	reacted when observer at 3-5 m from the nest
	2	reacted when observer at 3-5 m from the nest	3	reacted when observer at 6-10 m from the nest
	3	reacted when observer at 6-10 m from the nest	4	reacted when observer at 11-15 m from the nest
	4	reacted when observer at 11-15 m from the nest	5	reacted when observer at 16-29 m from the nest
	5	reacted when observer at 16-40 m from the nest	6	reacted when observer at 30-40 m from the nest
reaction	0	moved towards the observer	1	moved to 1-5 m from the nest
	1	stayed on the nest		
	2	moved 1-5 m away from the nest	2	moved to 6-10 m from the nest
	3	moved 6-10 m away from the nest	3	moved to > 10 m from the nest
	4	moved > 10 m away from the nest		
vocalization	0	not performed	0	not performed

	1	performed	1	performed
whistling	0	not performed	0	not performed
	1	performed	1	performed
head pumping	0	not performed	0	not performed
	1	performed	1	performed
head shaking	0	not performed	0	not performed
	1	performed	1	performed
wing opening	0	not performed	0	not performed
	1	performed	1	performed
flying toward observer	0	not performed	0	not performed
	1	performed	1	performed
position after approach	1	located on the nest	1	located 1-5 m from the nest
	2	located 1-5 m from the nest		
	3	located 6-10 m from the nest	2	located 6-10 m from the nest
	4	located 10-20 m from the nest	3	located > 10 m from the nest
	5	located > 20 m from the nest		

*This variable was not used to categorise female nest defense, as females were always located on their nest at the beginning of the approach.

ANNEXE B

SUPPLEMENTARY FIGURES: FEMALE AND MALE NEST DEFENSE NMDS ANALYSIS

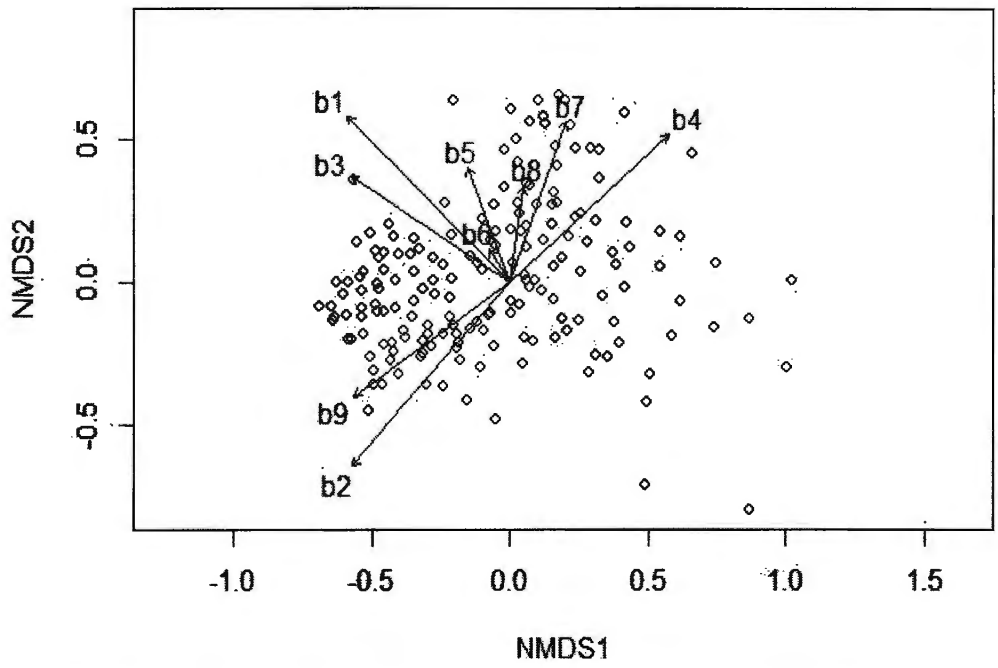

Figure 1. Female nest defense NMDS scores with dots representing the position of each test and arrows the vectors for each variable. b1: reaction distance, b2: reaction, b3: vocalization, b4: whistling, b5: head pumping, b6: head shaking, b7: wing opening, b8: flying toward observer, b9: position after approach.

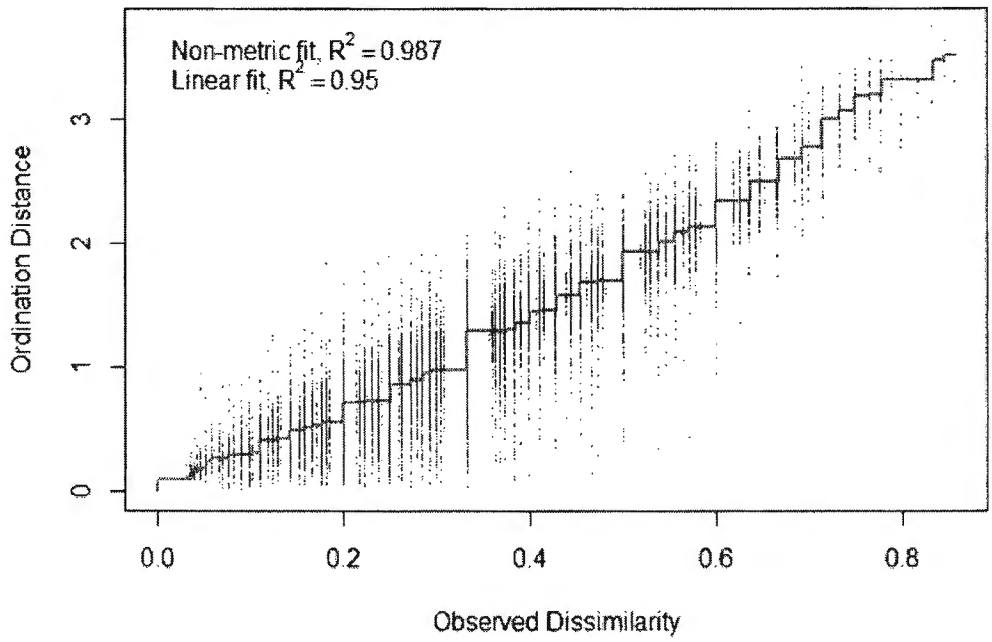

Figure 2. Female NMDS stressplot. Stressvalue = 0.12.

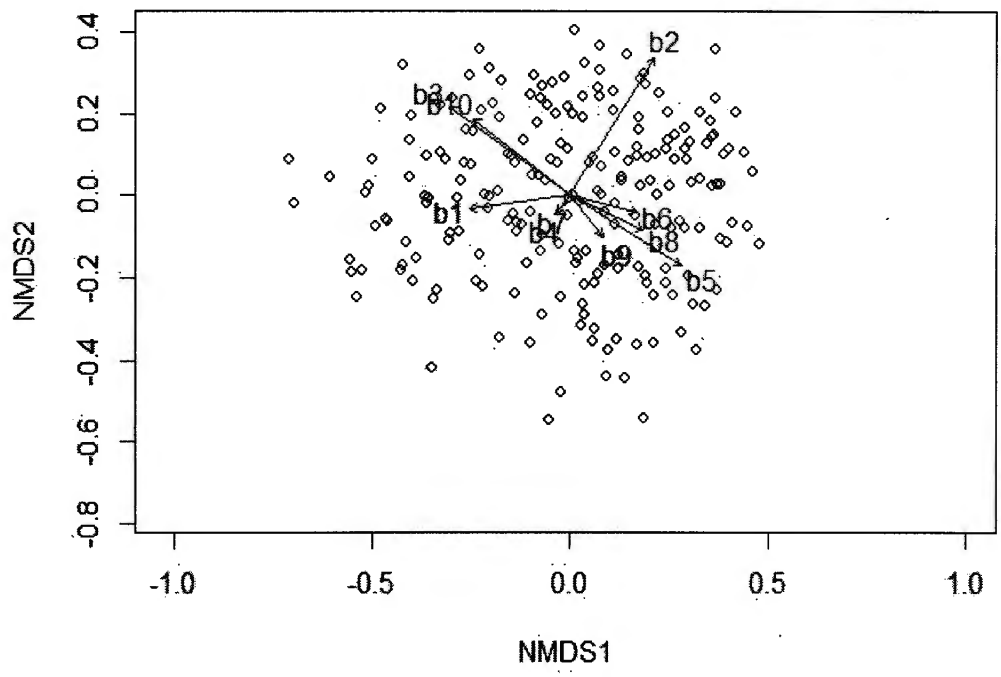

Figure 3. Male nest defense NMDS scores with dots representing the position of each test and arrows the vectors for each variable. b1: starting position, b2: reaction distance, b3: reaction, b4: vocalization, b5: whistling, b6: head pumping, b7: head shaking, b8: wing opening, b9: flying toward observer, b10: position after approach.

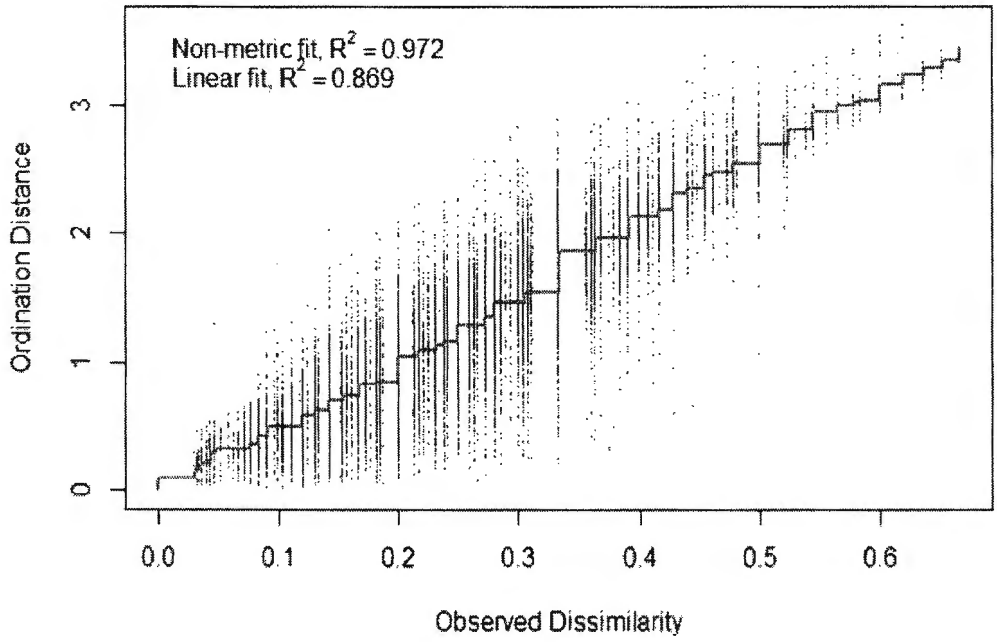

Figure 4. Male NMDS stressplot. Stressvalue = 0.17.

ANNEXE C

CORRELATIONS BETWEEN BEHAVIORAL VARIABLES AND THE 2 NMDS DIMENSIONS FOR FEMALE AND MALE NMDS ANALYSES

Sex	Behavioral variable*	NMDS dimension	r	t	df	*P*
Female	Reaction distance	1	-0.78	-22.77	334	< 0.001
	Reaction distance	2	-0.42	-8.45	334	< 0.001
	Reaction	1	-0.79	-23.33	334	< 0.001
	Reaction	2	0.48	9.99	334	< 0.001
	Position after approach	1	-0.69	-17.51	334	< 0.001
	Position after approach	2	0.26	4.89	334	< 0.001
Male	Starting position	1	-0.60	-13.36	313	< 0.001
	Starting position	2	-0.05	-0.88	313	0.38
	Reaction distance	1	0.65	14.99	313	< 0.001
	Reaction distance	2	0.69	16.99	313	< 0.001
	Reaction	1	-0.79	-23.17	313	< 0.001
	Reaction	2	0.38	7.35	313	< 0.001
	Position after approach	1	-0.65	-15.07	313	< 0.001
	Position after approach	2	0.33	6.31	313	< 0.001

*See Annexe A.

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