UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PERSONNALITÉ ET COMMUNICATION PAR CRIS D'ALARME CHEZ LE TAMIA RAYÉ, *TAMIAS STRIATUS*, EN MILIEU NATUREL

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN BIOLOGIE

PAR

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MAI 2018

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
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REMERCIEMENTS

J'ai pu effectuer ce doctorat grâce au soutien financier du Fonds de Recherche du Québec - Nature et technologies et de la Fondation UQAM, et via les subventions de recherche de mon superviseur D. Réale du Conseil de recherches en sciences naturelles et en génie du Canada et de la Chaire de recherche du Canada en écologie comportementale. J'ai également bénéficié de financements de la National Geographic Society et de l'Animal Behavior Society, ainsi que du Centre de la Science de la Biodiversité du Québec, de l'Association for the Study of Animal Behaviour, de la Royal Society of Biology et de l'International Society for Behavioral Ecology.

Merci à Conservation de la Nature Canada de nous avoir permis de constituer nos sites d'études au sein de la Réserve Naturelle des Montagnes Vertes.

Évidemment, je remercie infiniment Denis Réale, mon superviseur, qui m'a accueillie dans son laboratoire et m'a permis de réaliser le projet qui me plaisait. Cette aventure a été des plus plaisante et enrichissante grâce à sa gentillesse, sa gaieté, son engouement, sa confiance, sa bienveillance et son soutien, ainsi qu'à son immense savoir scientifique. Pour tout ça, merci Denis ! Merci aussi à Carolyn Hall d'avoir révisé l'anglais de mes manuscrits, mais aussi pour tous les bons moments partagés avec la famille Réale Hall, ce fût un vrai bonheur de voir grandir Ava.

Un grand merci à mon cosuperviseur Dany Garant, qui m'a apporté son expertise et un regard extérieur d'une grande valeur à plusieurs moments primordiaux de mon

doctorat. Même si je n'en ai surement pas assez profité, j'ai grandement apprécié les retours toujours très constructifs et utiles que tu as apporté à mon projet.

Je tiens aussi à remercier tous les professeurs qui ont accepté d'évaluer mon projet, en tant que proposition de recherche ou d'examen de synthèse et finalement ce document de thèse : en plus de mes superviseurs, merci à Frédérique Dubois, William Vickery, Jean-François Giroux, Pierre-Olivier Montiglio et James Hare.

Je remercie toutes les personnes impliquées dans le projet tamias, que ce soit les professeurs Murray Humphries et Fanie Pelletier ou tous les étudiants et assistants. Un immense merci aux équipes de terrain de 2012 à 2015 qui ont apporté leur aide pour le suivi à long terme et pour la réalisation de mon projet. Je ne pourrais hélas pas détailler les qualités exceptionnelles des personnes que j'ai pu rencontrer durant mon doctorat, mais je tiens au moins à les remercier pour leur précieuse aide sur le terrain ou durant les analyses, ou encore pour leur inaltérable soutien : merci infiniment à Manuelle Landry-Cuerrier et Melanie Dammhahn, mais aussi à Laurence Puillet, ainsi qu'à Pierre-Olivier Montiglio et Samantha Patrick. Merci bien sûr à Jeanne Clermont, ma fabuleuse assistante, étudiante, collaboratrice et amie. Ma gratitude est immense envers Gabrielle Dubuc Messier et Caroline Grou, qui m'ont apporté énormément de bonheur au cours de mes années de doctorat. Pour les bons moments partagés et les discussions passionnantes, merci aussi aux étudiants du labo Réale, Morgan Dutilleul, Elouana Gharnit, Tristan Juette, Joël Jameson et Raphaëlle Mercier-Gauthier, et du labo Giroux, Anik Panetier Lebeuf et Cécile Girault. Merci à Jean-François Giroux de m'avoir permis de découvrir ses travaux de recherche.

J'ai pu réaliser mon doctorat grâce à la formation et l'expérience inestimables que j'ai pu acquérir auparavant. Un grand merci à Pierre Jouventin, Marc de Dinechin, Sami Hassani, Steve Dobson, Francesco Bonadonna, Anna Nesterova et Jérôme Mardon, ainsi qu'à Torben Dabelsteen et Will Cresswell, qui m'ont permis de réaliser de beaux projets de recherche. Je remercie aussi mon futur superviseur de postdoctorat,

Dominique Berteaux, pour ces précieux conseils de fin de doctorat et pour les belles opportunités qu'il m'a offertes pour le futur.

J'ai la chance de pouvoir compter sur l'amitié inconditionnelle que m'offre Brigitte Planade, mais aussi Sandra Lai et Leïla Turki. Merci d'être là !

Merci à ma famille étendue, Catherine et Daniel Aubert, ainsi qu'à François Aubert et Violaine Louineau, pour leur soutien et d'accepter nos choix de vie.

C'est grâce à mon père Christian Couchoux et à ma sœur Christelle Couchoux que j'ai toujours pu concrétiser mes rêves, même s'ils m'ont mené à des milliers de km d'eux. Merci d'être là, tout le temps, depuis toujours.

Ce doctorat n'aurait tout simplement pas pu être réalisé sans la présence, la patience, l'aide et le soutien quotidien de Maxime Aubert. Merci pour tout, et peut être surtout de partager avec moi cette passion pour la nature. Une pensée à nos trois dondons, Sloubi, Pitchou et Nala, qui ont égayé ma fin de doctorat tout en me faisant me poser de nouvelles questions sur la complexité des comportements des rongeurs !

Et finalement, la réalisation de ce doctorat a bien sûr été possible grâce à tous les tamias des sites MV1 et MV4, qui m'ont apporté non seulement de belles données mais aussi énormément de bonheur, en dépit des heures passées à les chercher et à les attendre. Parmi tant d'autres, une pensée spéciale à Mauve-Mauve et gros Mauve-Mauve, et bien sûr à Pas d'queue/crémeux/Blanc-Orange, qui m'ont offert des moments d'observation délectables mais qui ont aussi grandement participé à augmenter le nombre de questions que je me posais sur le sens de la communication par cris d'alarme chez les tamias…

"*The love for all living creatures is the most noble attribute of man.*"

— Charles R. Darwin

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RÉSUMÉ

Les organismes vivants doivent continuellement prendre des décisions pour faire face à la variation de leur environnement naturel, et l'écologie comportementale s'intéresse particulièrement aux comportements des individus en lien avec leur environnement social et physique. Récemment, de nombreuses études ont montré l'existence de différences de comportements constantes entre les individus d'une même population, ce qui a grandement modifié notre façon d'appréhender la variation comportementale. En effet, l'étude de la variation intraspécifique au sein des populations naturelles s'inscrit plus généralement dans le cadre de l'écologie évolutive, et permet d'appréhender les causes et les conséquences de la diversité biologique. L'intégration de cette approche individuelle à l'étude des comportements permet alors d'obtenir une compréhension plus complète de la diversité comportementale.

La plupart des animaux interagissent de manière quotidienne aussi bien avec leurs conspécifiques qu'avec les composantes physiques de leur environnement. Chez les espèces sociales, mais aussi chez les espèces dites solitaires, les individus peuvent ainsi agir de manière négative avec leurs conspécifiques via des comportements compétitifs agressifs, ou bien avoir un impact positif en les prévenant par exemple de la présence d'un danger via la communication par cris d'alarme. Les comportements exprimés en contextes de compétition pour l'accès aux ressources et de risque de prédation sont ainsi largement étudiés et primordiaux, étant reliés à l'aptitude phénotypique des individus. Dans ces deux contextes, les caractéristiques de l'environnement social et physique jouent un rôle majeur sur les comportements exprimés, et la variation individuelle peut également affecter les décisions des individus.

L'objectif général de cette thèse de doctorat est d'étudier les effets des différentes sources de variation, environnementale et individuelle, sur les comportements d'agressivité et d'émission et de réception de cris d'alarme chez les tamias rayés (*Tamias striatus*), en milieu naturel.

Les études intégrant la variation individuelle au sein des systèmes de communication étant encore très limitées ou quasi inexistantes dans le cas de la communication par signaux d'alarme, le chapitre I présente tout d'abord l'intérêt d'explorer ces questions chez les animaux et les plantes. Cette contribution originale propose ainsi de lier la personnalité animale et la communication volatile chez les plantes, qui sont deux sujets d'intérêt élevés en écologie et en évolution.

Le chapitre II montre ensuite les effets de la variation environnementale et individuelle (et leur interaction) sur l'issue de plus de 2000 interactions agonistiques naturelles observées dans la population de tamias étudiée. L'intégration des différents niveaux de variation naturelle auxquels les individus sont confrontés a ainsi permis de mettre en avant les rôles conjoints des effets environnementaux et individuels sur les décisions agressives des individus.
Dans le chapitre III, une approche méthodologique novatrice est présentée pour mesurer les comportements d'émission individuels en milieu naturel. L'utilisation de micros espions a ainsi permis l'enregistrement efficace de vocalisations de qualité chez les tamias équipés, mais aussi de récolter différents sons utiles pour étudier d'autres thématiques en écologie.
Le chapitre IV présente ensuite des résultats sur les différences individuelles d'émission de cris d'alarme. Au delà des études récentes montrant que les individus diffèrent de manière constante dans leur émission de signaux acoustiques en contextes agressifs ou de reproduction, cette étude montre que la propension à émettre des cris en situation de risque de prédation peut également représenter la personnalité des individus.
Le chapitre V s'intéresse finalement au lien entre personnalité et communication au niveau de la réponse des individus aux signaux. Une expérience de repasse de cris d'alarme, réalisée sur le terrain, a ainsi montré que les individus répondent aux cris selon leur propre tendance à prendre des risques, mais aussi selon celle des émetteurs. Les individus semblent ainsi considérer les cris d'individus peu téméraires comme étant moins fiables, puisqu'ils émettraient potentiellement plus de fausses alarmes.
Des analyses futures permettront également de chercher à identifier si la personnalité des individus peut se refléter dans leurs signaux acoustiques, et intègrera plus globalement différentes mesures de comportements de prise de risque à lier à l'émission de cris.

Cette étude est ainsi une des premières à s'intéresser à et à montrer l'existence de différences individuelles dans les comportements d'émission et de réponse aux cris d'alarme, et a démontré plus globalement l'intérêt d'étudier les comportements agressifs et anti-prédateurs en milieu naturel en intégrant les différentes sources de variation environnementale et individuelle.

Mots-clés : Communication sonore, Cris d'alarme, Personnalité animale, Variation individuelle, Plasticité comportementale, Comportements agonistiques, Comportement anti-prédateurs, *Tamias striatus.*

ABSTRACT

Living organisms constantly make decisions to cope with variation in their natural environment, and behavioural ecology especially studies behaviours expressed by individuals in relation to their social and physical environment. Recent studies have greatly modified how we consider behavioural variation, as individuals from a same population have been shown to differ consistently in their behaviour. The study of intra-specific variation within natural populations is also of major interest for evolutionary ecology, to understand the causes and consequences of biological diversity. By integrating this individual-based approach to the study of behaviours we can thus obtain a more comprehensive understanding of behavioural diversity.

Most animals interact with conspecifics and the physical features of their environment on a daily basis. In social species, but also in so-called solitary ones, individuals can interact in a negative way with their conspecifics, through aggressive behaviours. They can also have a positive impact on their conspecifics when they warn them of danger through alarm communication. The behaviours expressed in both contexts of competition for access to resources and predation risk are extensively studied, being fundamentally linked to individuals' fitness. In both contexts, the social and physical characteristics of the environment play a major role on the behaviours expressed, and individual variation can also have an impact on individuals' decisions.

The general objective of this thesis is to study the effects of environmental and individual variation on aggression and alarm calling behaviours of eastern chipmunks (*Tamias striatus*), in a natural system.

Studies integrating individual variation to communication systems being still limited and even scarcer for alarm signalling, chapter I first presents the interest of exploring these questions in animals and plants. This original contribution suggests linking animal personality and volatile communication in plants, two research topics of major current interest in ecology and evolution.
Chapter II then shows the effects of environmental and individual variation (and their interaction) on the outcome of more that 2,000 natural agonistic interactions observed in the studied population of eastern chipmunks. The integration of the different levels

of natural variation encountered by individuals allowed us to highlight the combined effects of environmental and individual effects on individuals' aggressive decisions.
In chapter III, an innovative methodological approach is presented to measure the daily natural sound emissions of individuals in the wild. The use of spy mics fitted on chipmunks allowed us to efficiently record their individual vocalisations, but also to monitor different sounds useful for other questions in ecology.
Chapter IV then presents results on individual differences in emission of alarm calls. This study shows that individuals can differ consistently in their production of acoustic signals not only in aggressive or mating contexts, as shown recently, but also in a context of predation risk. The tendency to emit alarm calls can thus reflect an aspect of an individual's personality.
Finally, chapter V investigates a link between personality and communication in individuals' response to signals. A playback experiment of alarm calls implemented in the field demonstrated that individuals respond to calls according to their own risk-taking tendency, but also to the boldness of the caller. Individuals thus seem to consider calls from shy individuals as being less reliable, as these individuals would produce more false alarms.
Future analyses will investigate if a signal of personality can be reflected in the acoustic characteristics of the calls, and will more broadly include different measures of risk-taking behaviours to link to the emission of calls.

This study is thus one of the first to investigate and show the existence of individual differences in alarm calls emission and response, and has more broadly demonstrated the relevance of studying aggressive and antipredator behaviours in a natural system by integrating different sources of environmental and individual variation.

Keywords: Vocal communication, Alarm calls, Animal personality, Individual variation, Behavioural plasticity, Agonistic behaviours, Antipredator behaviours, *Tamias striatus.*

INTRODUCTION

Les thématiques de recherche abordées dans cette thèse sont ancrées dans le domaine de l'écologie comportementale, étant centrées sur l'étude de la variation des comportements des individus en lien avec leur environnement naturel. Cette thèse s'inscrit aussi de manière plus générale dans le cadre de l'écologie évolutive, puisqu'elle s'intéresse à la variation intraspécifique au sein de populations naturelles et apporte ainsi des informations sur les causes et les conséquences de la diversité biologique. L'introduction de cette thèse a pour but principal d'aborder la variation des comportements exprimés par les animaux au sein de leur environnement social et physique, en contextes de compétition pour l'accès aux ressources et de risque de prédation. Je m'intéresse tout particulièrement à la variation des comportements de communication par cris d'alarme, sans toutefois en détailler tous les aspects qui se trouvent avant tout dans l'article de synthèse présenté dans le premier chapitre. Je présenterai ensuite les quatre autres chapitres qui structurent la thèse, et décrirai le système d'étude ayant permis de répondre aux questions soulevées dans cette thèse.

0.1 Comportements et influence environnementale

Les organismes vivants sont confrontés à de nombreux facteurs environnementaux et doivent continuellement prendre des décisions. Ces décisions sont à considérer d'un point de vue évolutif, afin de comprendre comment certains comportements permettent aux individus de faire face à la variation environnementale et ainsi de maximiser leur aptitude phénotypique (en terme de survie et de reproduction, Dill 1987 ; Dukas 1998 ; Dall et al. 2004). Il est d'ailleurs largement reconnu que les

comportements des animaux peuvent être exprimés de manière très plastique en réponse aux facteurs déterminants de l'environnement social et physique (Komers 1997 ; West-Eberhard 2003 ; Alcock 2009 ; Snell-Rood 2013). En effet, la plupart des animaux interagissent de manière quotidienne aussi bien avec leurs conspécifiques qu'avec les composantes physiques de leur environnement. L'environnement social est ainsi une composante majeure de l'environnement auquel est confronté un individu, aussi bien chez les espèces sociales que chez les espèces dites solitaires (Dall et al. 2004 ; Frank 2007 ; Matessi et al. 2010 ; Wilkinson et al. 2010 ; Dingemanse & Araya-Ajoy 2015). Les interactions sociales revêtent ainsi différentes formes et peuvent générer tout un gradient de comportements, depuis les comportements agressifs jusqu'aux comportements coopératifs (Krause & Ruxton 2002). L'accès aux ressources (nourriture ou partenaires), qui est une activité primordiale aux espèces vivantes, peut notamment générer des comportements qui affectent négativement l'aptitude phénotypique des individus. Les individus peuvent ainsi entrer en compétition avec leurs conspécifiques et interagir de manière agressive afin d'accéder à des ressources limitées comme la nourriture (Wilson et al. 2009, 2011b ; Bergmüller & Taborsky 2010 ; Hardy & Briffa 2013). Les individus peuvent toutefois aussi avoir un impact positif sur la survie de leurs conspécifiques, notamment en les prévenant de la présence d'un danger via la communication par cris d'alarme (Hollén & Radford 2009). Dans ces deux contextes sociaux, les caractéristiques de l'environnement physique jouent également un rôle majeur sur les comportements exprimés, comme elles peuvent affecter le niveau d'agressivité des individus (e.g., distance à leur territoire) et grandement moduler le risque de prédation perçu (i.e., caractéristiques de l'habitat comme le couvert végétal, Ferrari et al. 2009 ; Bednekoff & Blumstein 2009). Je me suis ainsi interessée à la variation des comportements agonistiques et de communication par cris d'alarme, qui sont exprimés par les individus en relation avec les informations qu'ils acquièrent sur leurs conspécifiques et leur environnement physique.

0.1.1 Comportements agressifs et conflits

En tentant d'accéder à des ressources primordiales mais limitées tels qu'un partenaire, un territoire ou de la nourriture, les individus sont amenés à entrer en conflit avec leurs conspécifiques (Wilson et al. 2009, 2011b ; Bergmüller & Taborsky 2010). Lors d'interactions sociales, les comportements d'un individu dépendent ainsi de l'environnement social créé par les comportements de l'individu avec lequel il interagit (Moore et al. 1997 ; Wolf et al. 1998 ; Wilson et al. 2009 ; Santostefano et al. 2016). Les décisions individuelles peuvent alors être complexes, étant affectées par divers facteurs de l'environnement social et physique (Dugatkin & Dugatkin 2007). Les comportements agressifs exprimés par les individus lors de conflits agressifs sont ainsi largement étudiés dans le cadre de la théorie des conflits. Les prédictions faites par les modèles ancrés dans la théorie des jeux suggèrent ainsi que les compétiteurs adoptent des comportements hautement plastiques, qui dépendent du contexte (Maynard Smith & Price 1973 ; Parker 1974 ; Smith 1974; Enquist & Leimar 1983). Les individus compétiteurs devraient ainsi ajuster leur comportement en fonction des informations qu'ils détiennent sur leurs capacités à se battre, selon leurs potentiels de détention des ressources (RHP, Parker 1974 ; Johnstone 2001 ; Peake & McGregor 2004). L'asymétrie qui existe entre les compétiteurs peut alors être utilisée pour prédire le vainqueur d'un conflit, notamment au niveau de la force physique des individus (e.g., via des caractères sexuels secondaires surdéveloppés comme des cornes ou des bois, ou la taille/masse des individus, Arnott & Elwood 2009). L'âge et le sexe des individus jouent également un rôle sur la capacité des individus à vaincre un opposant (Maynard Smith & Parker 1976 ; Arnott & Elwood 2009). Les facteurs externes de l'environnement affectent aussi l'issue d'un combat, de sorte que les individus se trouvant à proximité de leur territoire devraient se montrer plus agressifs afin d'assurer la défense de leurs ressources (Davies 1978). Les comportements d'agression exprimés lors d'interactions agonistiques sont donc avant tout considérés comme étant plastiques et dépendants du contexte.

0.1.2 Comportements anti-prédateurs et communication par cri d'alarme

Les individus réagissent également de manière plastique dans un contexte de risque de prédation. Lors de leurs activités quotidiennes, la plupart des animaux sont en effet confrontés au risque de prédation, qui est créé et modulé par l'environnement physique (e.g., proximité des prédateurs, structure de l'habitat, conditions climatiques, Yasué et al. 2003 ; Verdolin 2006 ; Beauchamp 2015). Pour assurer leur survie, les individus doivent ainsi réaliser des compromis en adoptant des comportements qui favorisent la réalisation de fonctions primordiales comme l'approvisionnement, mais aussi la détection de prédateurs (McNamara & Houston 1987 ; Verdolin 2006 ; Cresswell 2008 ; Sansom et al. 2009). Les comportements anti-prédateurs sont particulièrement intéressants car ils sont affectés par l'environnement physique, et également exprimés en contexte social (Appendice A : Clermont et al. 2017) dans le cas de la communication par cris d'alarme. De nombreuses espèces d'oiseaux et de mammifères, et certaines espèces d'amphibiens, signalent ainsi la présence d'un danger pressenti via des signaux vocaux (Klump & Shalter 1984 ; Hollén & Radford 2009 ; Zuberbühler 2009). Les cris d'alarme revêtent différentes fonctions, et sont notamment utilisés pour prévenir les conspécifiques de la présence d'un prédateur (Macedonia & Evans 1993 ; Caro 2005 ; Blumstein 2007). Les signaux peuvent également être modulés selon la spécificité du risque perçu, ou encore les caractéristiques individuelles des émetteurs et des récepteurs. Chez certaines espèces, le système de communication est dit référentiel (Blumstein 1999), car les cris d'alarme produits sont spécifiques au type de prédateur rencontré, différenciant le plus souvent les prédateurs terrestres et les prédateurs aériens (Seyfarth et al. 1980 ; Blumstein & Arnold 1995 ; Manser et al. 2002 ; Kirchhof & Hammerschmidt 2006 ; Frederiksen & Slobodchikoff 2007). Les signaux peuvent également véhiculer des informations concernant l'imminence du danger (Blumstein 1995 ; Blumstein & Armitage 1997 ; Manser 2001 ; Manser et al. 2002). Les cris d'alarme sont également dirigés vers différents types de conspécifiques (apparentés ou non) et pour différentes

raisons (amener les conspécifiques à secourir l'émetteur, maintenir un niveau d'alerte général élevé pour augmenter la détection au retour du prédateur ou encore amener les conspécifiques à se protéger eux mêmes du danger ; Bonenfant 1996). La sélection de parentèle (Hamilton 1964) permet en particulier d'expliquer que les signaux d'alarme peuvent évoluer s'ils confèrent un avantage adaptatif (i.e., survie) aux individus apparentés à l'émetteur, créant ainsi un avantage sélectif indirect. Cependant, bien que cette hypothèse évolutive repose sur une reconnaissance entre individus (Falls 1982 ; Stoddard 1996 ; Tibbets & Dale 2007), rares sont les études qui s'intéressent à la complexité de la communication par cris d'alarme en intégrant les différences d'émission et de réponse aux signaux au niveau individuel (Hare 1998 ; Blumstein et al. 2004 ; Blumstein & Munos 2005 ; Randall et al. 2005 ; Sproul et al. 2006 ; Matrosova et al. 2009 ; Pollard 2011). L'approche individuelle pourrait pourtant apporter des informations importantes sur la variation des comportements exprimés en contexte social. Le concept de personnalité animale a en effet mis en évidence l'existence de différences de comportements constantes entre individus d'une même population, notamment au niveau de leur agressivité et de leur prise de risque (Wilson et al. 1994 ; Réale et al. 2007).

0.2 Variation interindividuelle de comportements

Au cours des deux dernières décennies, la variation intraspécifique a ainsi été progressivement considérée par les écologistes (Bolnick et al. 2011) et a changé notre vision et notre compréhension de nombreux processus écologiques et évolutifs (Dall et al. 2004 ; Réale et al. 2007 ; Stamps et al. 2010 ; Wolf & Weissing 2012 ; Dall et al. 2012). De nombreuses études ont particulièrement montré l'existence de différences de comportements constantes entre les individus d'une même population (Gosling & John 1999 ; Gosling 2001 ; Sih et al. 2004 ; Réale et al. 2007 ; Smith & Blumstein 2008 ; Réale et al. 2010), ce qui a grandement modifié notre façon d'appréhender la variation comportementale. Cette approche individuelle a en effet mis en évidence

que les comportements individuels ne sont pas entièrement plastiques, car les individus ne peuvent pas exprimer toute l'amplitude de variation d'un trait observé au niveau de la population (Sih et al. 2004 ; Réale et al. 2007 ; Duckworth 2010). Face à une même situation, les individus diffèrent dans leur réaction, ce qui reflète leurs différences de personnalité. Ces différences individuelles de comportements se manifestent notamment dans la tendance à l'exploration des individus, leur niveau d'agressivité ou encore dans leur prise de risque (Réale et al. 2007). Les traits de personnalité ont souvent une composante génétique et peuvent ainsi être héritables (van Oers et al. 2004 ; Réale et al. 2000 ; Dingemanse et al. 2002) et leur maintien peut être expliqué de manière adaptative (Wilson 1998 ; Dall et al. 2004 ; Réale et al. 2007 ; Wolf et al. 2007). Plusieurs traits de personnalité sont également souvent reliés entre eux pour former des syndromes comportementaux (Sih et al. 2004). Les traits comportementaux sont aussi liés à différentes stratégies d'histoire de vie (i.e., survie et succès reproducteur : Réale et al. 2007 ; Smith & Blumstein 2008 ; Quinn et al. 2009, et productivité : Biro & Stamps 2008) ainsi qu'à différents traits physiologiques (métaboliques, endocrinologiques ; voir par exemple Koolhaas et al. 1999 ; Careau et al. 2008). Le concept de syndrome de train de vie ("POLS : Pace of Life Syndrome", Réale et al. 2010), prédit ainsi les liens entre ces trois types de traits. Des individus proactifs, qui sont téméraires (enclins à prendre des risques), agressifs et présentant des patrons d'exploration superficiels, auraient par exemple une vie courte, associée à une reproduction précoce. En situation de stress, ils montreraient une réactivité élevée au niveau du système nerveux sympathique (rythme cardiaque élevé par exemple) mais faible au niveau de l'axe hypothalamo-hypophysaire-surrénalien ("HPA : Hypothalamic-Pituitary-Adrenal" ; production faible d'hormones du stress comme les corticostéroïdes, Koolhaas et al. 1999 ; Montiglio et al. 2012a). L'importance des liens entre les traits comportementaux et la réaction au stress ("coping style") en milieu naturel est toutefois reconsidérée, puisqu'il existerait plutôt deux axes découplés (Koolhaas et al. 2010 ; Ferrari et al. 2013). La personnalité d'un individu affecte ainsi de nombreux aspects de sa propre vie et on peut se demander

quel serait l'impact des différences interindividuelles sur les décisions des animaux interagissant avec des conspécifiques. Comme discuté ci-dessus, l'environnement social est en effet une composante importante de l'environnement d'un individu, et des travaux récents cherchent à évaluer les relations qui existent entre la personnalité et les interactions sociales (Webster & Ward 2011). Le contexte social pourrait être un facteur prédominant pour expliquer l'existence de différences interindividuelles de comportement (Réale & Dingemanse 2010 ; Dingemanse & Araya-Ajoy 2015 ; von Merten et al. 2017), et celles-ci pourraient par exemple être maintenues par le biais de la spécialisation de niches sociales (Bergmüller & Taborsky 2010 ; Montiglio et al. 2013). Une approche par réseaux sociaux, dans laquelle les liens unissant les différents individus sont pris en compte, indique également que les différences comportementales interindividuelles pourraient affecter l'aptitude phénotypique des autres individus et leur répartition dans la population (Croft et al. 2009 ; Krause et al. 2010 ; Wilson et al. 2013 ; Aplin et al. 2013).

Une emphase est donc mise sur la recherche des mécanismes liant les différences de personnalité et les interactions sociales et cette thèse cherche à estimer l'effet de la variation individuelle d'une part sur les comportements agonistiques et d'autre part sur les comportements de communication par cris d'alarme.

0.2.1 Personnalité et interactions agonistiques

Bien que les comportements agressifs exprimés en contexte agonistique soient reconnus comme étant très plastiques (voir ci-dessus), des différences individuelles de comportement peuvent toutefois exister. Des études récentes montrent en effet que les individus peuvent différer de manière constante dans leur niveau d'agressivité (Réale et al. 2007 ; Dzieweczynski & Leopard 2010 ; Burtka & Grindstaff 2013 ; Blumstein et al. 2013), et le maintien de ces différences est également suggéré par des modèles théoriques (Wolf & Weissing 2010 ; Dall et al. 2004 ; Wolf et al. 2007, 2008). Les deux approches, considérant la plasticité des comportements agressifs

d'une part et la constance des comportements individuels d'autre part, doivent donc être intégrées pour expliquer de manière plus complète la variation des comportements agressifs (Wilson et al. 2011a ; Briffa et al. 2015).

0.2.2 Personnalité et communication par cris d'alarme

La personnalité des individus pourrait aussi grandement influencer leurs comportements de prise de risque dans un contexte de communication par cris d'alarme, au niveau de l'émission et de la réponse aux signaux. En effet, des modèles théoriques récents indiquent un lien possible entre l'évolution des systèmes de communication et la personnalité, via l'existence de différences individuelles dans la production et l'interprétation des signaux (McNamara et al. 2009 ; Botero et al. 2010 ; Wolf et al. 2011). Botero et al. (2010) montrent en effet que les individus d'une population peuvent utiliser des stratégies de communication différentes, via un polymorphisme dans l'émission et la réponse aux signaux, qui peuvent être maintenues et coexister par sélection fréquence-dépendante (leur modèle se base en particulier sur les "badges de statut" qui permettent aux individus de communiquer de façon visuelle leur agressivité, Johnstone & Norris 1993 ; Pärt & Qvarnstöm 1997). Un même scénario pourrait exister pour la communication par cris d'alarme, de sorte que l'émission de signaux serait affectée par des caractéristiques de la personnalité des individus, et notamment leur propension à prendre des risques. Cette information pourrait alors être utilisée par les individus récepteurs pour estimer la fiabilité des individus émetteurs (Hare & Atkins 2001 ; Blumstein et al. 2004 ; Pollard 2011) et ajuster leurs réponses en conséquence (Hare & Atkins 2001 ; Wolf et al. 2013), en combinaison avec leurs propres tendances à prendre des risques. D'autres modèles théoriques suggèrent en effet que la constance des comportements (i.e., personnalité) évolue de paire avec la réceptivité des individus aux signaux et leur fiabilité à signaler (McNamara et al. 2009 ; Wolf et al. 2011). Le cadre théorique permet donc de considérer que les individus devraient prendre en compte les différences de

comportements de leurs conspécifiques pour prendre leurs décisions. Amy et al. (2010) suggèrent ainsi que les réseaux de communication peuvent être mieux compris en incluant les caractéristiques individuelles spécifiques comme la personnalité.

0.3 Personnalité et plasticité comportementale

En contexte d'interactions agonistiques ou de communication par cris d'alarme, la plasticité et la constance des comportements ne sont donc absolument pas antagonistes (Dingemanse et al. 2010). Ces deux approches devraient plutôt être étudiées de manière conjointe, afin de mieux appréhender les différents aspects de la variation des comportements au sein des populations animales naturelles. L'approche individuelle amenée par le concept de personnalité animale adopte avant tout l'approche utilisée par la génétique quantitative, qui vise à évaluer les différentes sources de variation qui peuvent affecter les traits (Réale et al. 2007 ; Dingemanse et al. 2010 ; Dingemanse & Araya-Ajoy 2015 ; Brommer & Class 2017). L'intégration des effets environnementaux et des effets individuels permet également d'accéder à un autre niveau de variation, qui est l'existence de différences individuelles de normes de réaction (Nussey et al. 2007 ; Dingemanse et al. 2010). Dans le cadre d'une approche de norme de réaction individuelle, on peut en effet considérer que les individus diffèrent non seulement au niveau de leurs comportements moyens (i.e., personnalités, à l'échelle interindividuelle), mais également dans leur tendance à répondre à un changement environnemental, qu'il soit social ou physique (i.e., différences individuelles de plasticité, à l'échelle intraindividuelle, Réale & Dingemanse 2010 ; Dingemanse & Wolf 2013 ; Briffa et al. 2015). Une relation négative entre la proactivité des individus et leur niveau de plasticité/réceptivité est attendue (Coppens et al. 2010), avec par exemple des individus plus agressifs qui auraient moins tendance à répondre de manière plastique à un changement dans leur environnemental social (Dingemanse et al. 2010 ; Dingemanse & Araya-Ajoy 2015). Il manque cependant des évidences empiriques pour soutenir ces prédictions en

milieu naturel (Hall et al. 2017), en partie car l'intégration des différents niveaux de variation des comportements n'est encore que rarement implémentée. Pour évaluer ces différents niveaux, de nombreuses données doivent en effet être récoltées, avec un grand nombre d'individus observés dans différentes conditions des gradients environnementaux (Martin et al. 2011 ; van de Pol 2012 ; Dingemanse & Araya-Ajoy 2015). Cela requiert donc de mesurer les comportements des individus en conditions naturelles, afin de mesurer la variation pertinente à laquelle les animaux sont confrontés en milieu naturel.

0.4 Structure et objectifs de la thèse

Cette thèse a ainsi pour but d'étudier les effets des différentes sources de variation, environnementales et individuelles, sur les comportements d'agressivité et d'émission et de réception de cris d'alarme chez les tamias rayés (*Tamias striatus*), en contexte naturel. Je présente ici cinq chapitres, qui font ou feront l'objet d'un article scientifique. Trois des chapitres répondent à différents objectifs principaux de la thèse, alors qu'un chapitre est consacré à la présentation des idées de cette thèse, élargies aux signaux d'alarme utilisés par les animaux et les plantes, et qu'un chapitre présente une méthodologie d'enregistrement des cris individuels. La Figure 0.1 illustre les thématiques abordées dans la thèse et les relations étudiées.

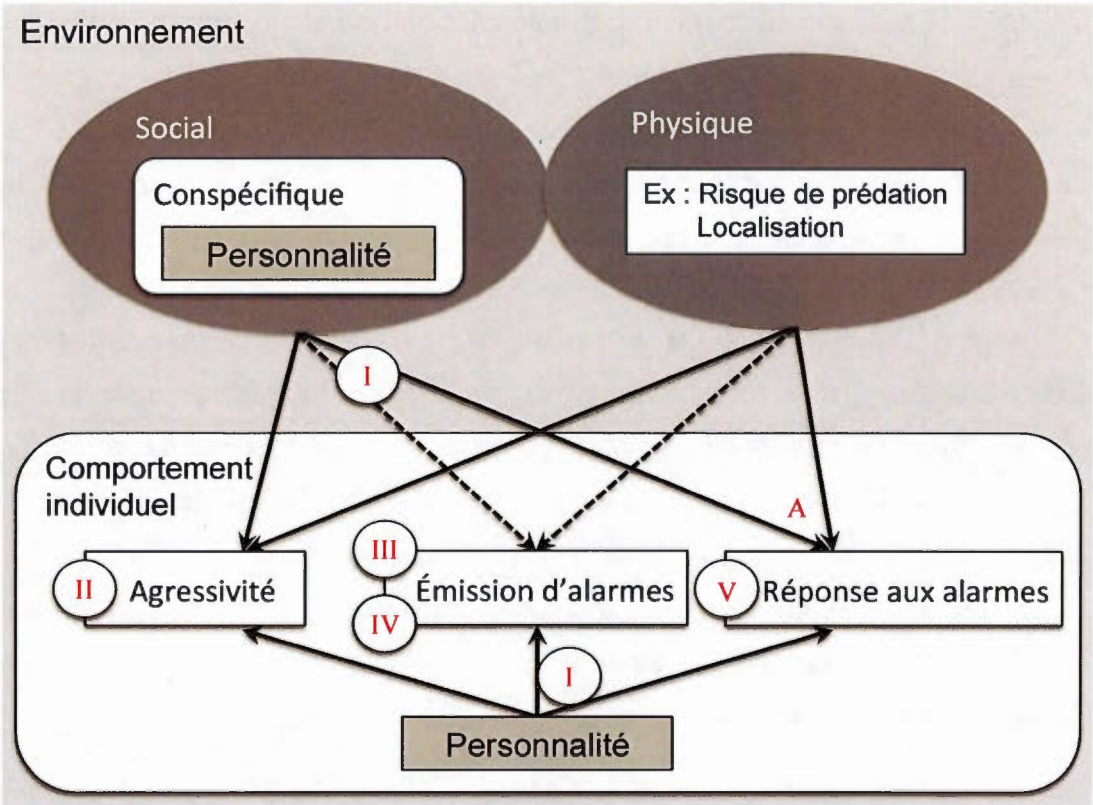

Figure 0.1 Illustration du contexte général dans lequel s'inscrit la thèse et des différentes relations abordées. Les comportements d'un individu sont étudiés en lien avec son environnement social et physique, qui vont influencer ses prises de décisions. Les comportements d'agressivité et de communication par cris d'alarme (émission et réception), sont ainsi dépendants de caractéristiques environnementales, mais peuvent aussi être influencés par la personnalité des individus. C'est ce que je cherche à évaluer dans cette thèse, via cinq chapitres dont les numéros I à V apparaissent dans le schéma aux niveaux des thèmes étudiés. L'article présenté en Appendice A (représenté par la lettre A sur le schéma) teste l'effet de l'environnement social et physique sur la réponse aux cris d'alarme. Les flèches pleines indiquent les relations testées dans cette thèse, alors que les flèches pointillées indiquent les relations attendues mais restant à tester via des analyses futures pour évaluer la variation des comportements d'émission de cris d'alarme.

Le chapitre I présente ainsi l'idée générale de cette thèse qui est d'étudier la variation des comportements d'émission et de réception de signaux d'alarme en lien avec des différences individuelles de comportements de prise de risque. Il propose ainsi des perspectives de recherche sur l'existence de différents niveaux de variation

individuelle dans les comportements de communication par alarme aussi bien chez les animaux que chez les plantes. Cet article représente une contribution d'intérêt général en écologie, en proposant de lier la personnalité animale et la communication volatile chez les plantes, qui sont deux sujets d'intérêt élevé dans les recherches actuellement menées en écologie et en évolution.

Le chapitre II explore ensuite les effets de la variation environnementale et individuelle sur l'issue d'interactions agonistiques dans la population de tamias étudiée. On peut ainsi s'attendre à trouver des effets des contextes social et physique, comme prédit par la théorie, mais aussi à ce que les individus diffèrent de manière constante dans leur agressivité et donc dans leur tendance à gagner un conflit. L'existence de variation individuelle de plasticité est aussi explorée, en supposant que tous les individus de la population ne réagissent pas de la même façon à un changement environnemental.

Dans le chapitre III, je présente une approche méthodologique novatrice qui permet de mesurer les comportements d'émission individuels en milieu naturel. L'étude démontre tout d'abord la validité et l'efficacité de la méthode pour enregistrer les vocalisations naturelles des tamias, ainsi que la qualité des enregistrements, en comparaison avec l'enregistrement de vocalisations réalisé durant une saison avec une méthode standard de suivi et d'expérimentation. L'utilité de cette technique est également démontrée pour étudier d'autres thématiques en écologie, notamment pour mesurer les patrons d'activité des individus ou leur environnement sonore.

Le chapitre IV présente ensuite des résultats sur les différences individuelles d'émission de cris, provoqués en simulant un risque de prédation. On peut en effet s'attendre à ce que tous les individus ne réagissent pas de la même façon à un risque similaire, et que la propension à émettre des cris en réponse aux tests soit répétable. La tendance à émettre des cris d'alarme représenterait alors la personnalité des

individus, d'autant plus si ce comportement est constant entre différents contextes. L'émission de cris en situation de risque pourrait également être liée de manière négative à la proactivité des individus, ce qui est exploré en utilisant l'exploration comme indice de personnalité des individus.

Enfin, le chapitre V présente les résultats d'une expérience de repasse de cris d'alarme réalisée sur le terrain, et basée sur l'enregistrement et la préparation préalable de cris d'alarme de différents individus. Cette expérience permet d'évaluer la variation de réponse aux cris d'alarme des récepteurs selon leur familiarité aux émetteurs, et surtout selon leur propre niveau de témérité et celui des émetteurs. D'éventuelles différences individuelles d'utilisation de l'information sociale peuvent aussi être quantifiées.

0.5 Modèle d'étude et mesures comportementales

J'étudie le tamia rayé (*Tamias striatus*), un Sciuridé que l'on retrouve principalement dans les forêts mixtes-décidues de l'Est de l'Amérique du Nord (Elliott 1978 ; Snyder 1982). Les tamias constituent d'excellents modèles pour répondre aux questions de recherche soulevées dans cette thèse, étant de petits rongeurs terrestres diurnes (Snyder 1982) qui recherchent leur nourriture principalement autour de leur terrier et défendent activement leur territoire par des comportements agressifs, ce qui donne lieu à des interactions agonistiques d'intensité variable (Dunford 1970 ; Elliott 1978 ; Yahner 1978 ; Aniskowicz & Vaillancourt 1979 ; Getty 1981 ; Snyder 1982 ; Clarke & Kramer 1994). Les tamias sont également confrontés quotidiennement au risque de prédation durant leur recherche de nourriture (Elliott 1978), constituant une proie pour divers prédateurs terrestres (Otter 1994) et aériens (Snyder 1982). Afin de détecter la présence d'un éventuel prédateur, les individus adoptent ainsi des comportements anti-prédateurs tels que la vigilance (Lima & Dill 1990 ; Otter 1994 ; McAdam & Kramer 1998). Comme de nombreuses espèces de rongeurs et en

particulier de Sciuridés, les tamias rayés émettent également des cris d'alarme quand il ressentent la présence d'un danger (Macedonia & Evans 1993 ; Blumstein & Armitage 1997 ; Shelley & Blumstein 2005 ; Blumstein 2007 ; Pollard & Blumstein 2012 ; McRae 2012). Leur système de communication par cris d'alarme est de type référentiel, différents cris étant spécifiques au type de prédateur rencontré (Burke da Silva et al. 1994 ; Weary & Kramer 1995). Les individus semblent ainsi produire une salve de notes à basse fréquence (en dessous des 5 kHz) appelées "chuck" quand ils ont détecté un prédateur aérien ("chucking"), et une série de notes à plus haute fréquence (entre 3 et 15 kHz) nommées "chip" ("chipping") sous le risque de prédation d'un prédateur terrestre (Burke da Silva et al. 1994). Ils émettent également des cris composés de notes multiples, mais non répétés en salve, les "trill", quand ils sont poursuivis par un prédateur (Dunford 1970 ; Elliott 1978 ; Burke da Silva et al. 1994 ; Weary & Kramer 1995 ; obs. pers.). Les chuck et les chip, émis même après le départ du prédateur, semblent être destinés aux conspécifiques qui augmentent leur niveau de vigilance à l'entente de ces cris d'alarme (Weary & Kramer 1995 ; Bonenfant 1996 ; Baack & Switzer 2000) et pourraient aussi servir à dissuader le prédateur de chasser dans la zone (Burke da Silva 1993 ; Bonenfant 1996). Bonenfant (1996) indique que les trill servent à surprendre et dissuader le prédateur, alors que Burke da Silva et al. (2002) estiment qu'ils sont utilisés par les individus pour prévenir leur descendance de la présence d'un danger, suggérant qu'ils aient pu évoluer par sélection de parentèle. Ce type de sélection pourrait en effet jouer un rôle dans l'évolution et le maintien des cris d'alarme chez les tamias rayés, car la dispersion biaisée en faveur des mâles crée une structure génétique spatiale où les femelles vivent à proximité de leurs apparentées (Elliott 1978 ; Loew 1999 ; Chambers & Garant 2010 ; Bergeron et al. 2011 ; Messier et al. 2012). Les caractéristiques des cris sont également conformes aux contraintes imposées par Hamilton (1964) pour la prédiction de leur évolution (un coût relativement faible pour l'émetteur déjà alerté et un avantage important pour les récepteurs). Bien qu'étant une espèce considérée comme solitaire, les tamias interagissent de manière

quotidienne avec leurs conspécifiques. Ce modèle d'étude est également intéressant car les individus sont facilement capturés et marqués individuellement pour les observations sur le terrain (Elliott 1978), et le suivi des individus sur plusieurs années est possible car la longévité moyenne de ces petits mammifères est de l'ordre de 3 à 4 ans en milieu naturel (Snyder 1982). De plus, des études menées au sein de la même population de tamias ont mis en avant l'existence de différences individuelles dans les comportements d'exploration et de docilité des tamias (Montiglio et al. 2012a ; St-Hilaire et al. 2017).

0.5.1 Suivi de la population

Les travaux de terrain effectués dans la population à l'étude se déroulent de début mai jusqu'au milieu de l'automne, durant la période d'activité en surface des tamias. Ceux-ci émergent en effet des terriers durant le printemps, après avoir passé un hiver en torpeur (Scott & Fisher 1972 ; French 2000 ; Landry-Cuerrier et al. 2008), subsistant grâce à la consommation de graines des arbres à production cyclique (arbres à paisson) accumulées et stockées dans leur terrier l'année précédente (Thomas 1974 ; Elliott 1978 ; Landry-Cuerrier et al. 2008). L'étude est effectuée dans le sud du Québec au sein de la Réserve Naturelle des Montagnes Vertes de Conservation de la Nature Canada, en Estrie (45°06.785'N; 72°26.078'O). Les sites d'étude sont établis au sein d'une forêt décidue semi-ouverte où l'érable à sucre (*Acer saccharum*) et le hêtre Américain (*Fagus grandifolia*) dominent. Ce projet de recherche fait partie d'une étude à long terme prolifique et multithématique sur l'écologie évolutive de cette espèce, menée depuis 2005. Nous avons mis en place trois nouveaux sites d'étude en 2012, et les données récoltées pour cette étude proviennent de deux sites constitués de grilles d'échantillonnage de 260 x 260 m et de 340 x 260 m. Au sein des grilles, les individus sont capturés de façon régulière, à l'aide de pièges de type Longworth appâtés avec du beurre d'arachide. Les captures permettent de marquer systématiquement les individus pour identification future,

avec des bagues d'oreille en métal (et pour certains un transpondeur unique sous-cutané). Pour ce projet, des fils ou des rubans de couleur ont aussi été apposés sur les bagues pour la reconnaissance à distance et permette la réalisation d'observations (Fig. 0.2, Landry-Cuerrier 2008 ; Shonfield 2010). Durant la capture nous déterminons également le sexe et le statut reproducteur des individus ainsi que leur masse (ce qui permet également de déterminer leur classe d'âge, adulte ou juvénile, Bergeron et al. 2013). Nous prélevons également un poinçon dans l'oreille à la première capture pour les analyses génétiques. Les animaux peuvent aussi facilement être équipés de colliers spécifiques, comme des colliers émetteurs (Holohil Systems Ltd., model PD-2C) utilisés pour trouver les terriers individuels par télémétrie (Landry-Cuerrier et al. 2008). Des tests comportementaux sont également réalisés lors des captures, comme le test de docilité, qui permet de mesurer la réaction de stress d'un individu à la manipulation (en mesurant sa durée d'immobilité dans le sac de contention, Montiglio et al. 2012a) ou le test d'arène ("open-field test", Archer 1973 ; Krebs 1970), qui permet de mesurer les comportements d'exploration d'un individu face à un nouvel environnement (pour des détails sur la réalisation de ce test chez les tamias voir Martin & Réale 2008a,b ; Montiglio et al. 2010, 2012a).

0.5.2 Mesures comportementales spécifiques au projet

Pour ce projet, des observations et tests comportementaux spécifiques ont également été réalisés au sein du suivi de la population. Afin de faciliter l'observation de ces petits mammifères très actifs, j'ai utilisé des placettes de nourrissage en disposant des graines à différentes localisations situées à environ 10 m des terriers de chacun des individus suivis. Durant les observations, le ou les observateurs se situent à un emplacement préalablement déterminé (favorisant la visibilité) situé à environ 10 m dans la direction opposée du terrier. Aux placettes, les interactions agonistiques survenant entre tamias identifiés sont enregistrées (via des observations directes et des caméras vidéos), ainsi que les comportements anti-prédateurs des individus. Afin

de mesurer les différences individuelles d'émission de cris d'alarme, j'ai réalisé des tests simulant l'attaque de prédateurs (via des lancers de chapeaux simulant l'attaque d'un rapace ; MacWhirter 1992 ; Mateo 1996 ; Hare 1998 ; Hare & Atkins 2001 ; Warkentin et al. 2001 ; Sloan et al. 2005 ; Sloan & Hare 2006 ; Digweed & Rendall 2009 ; Thompson & Hare 2010 ; et la poursuite mimant l'attaque d'un prédateur terrestre; Burke da Silva et al. 1994, 2002 ; Blumstein & Armitage 1997 ; Dill & Houtman 1989 ; McRae 2012), en plus d'équiper les individus avec des micros espions. L'effet de la personnalité sur les réponses des individus aux cris a été testé via une expérience de repasse de cris d'alarme préalablement enregistrés sur le terrain. Tous les détails de ces méthodes se trouvent dans les chapitres concernés, et d'autres mesures qui n'ont pas encore été exploitées seront évoquées en conclusion.

Figure 0.2 Illustration des codes couleurs individuels utilisés pour la reconnaissance des tamias à distance, permettant la réalisation d'observations comportementales. De

gauche à droite et de bas en haut : Rose-Mauve, Jaune-Jaune, Mauve-Rouge et Lime-Bleu. Photos : Charline Couchoux.

CHAPITRE I

INDIVIDUAL VARIATION IN ANIMAL AND PLANT ALARM COMMUNICATION

Charline Couchoux, Richard Karban & Denis Réale

Manuscrit en révisions comme *Ideas and Perspectives* dans *Ecology Letters.*

Dans ce chapitre, nous nous intéressons aux comportements de défense et de signaux d'alarme utilisés par les animaux et les plantes face au risque de prédation et d'herbivorie. La réponse des individus au risque pourrait être liée à leur degré d'investissement dans différentes fonctions reliées à leur aptitude phénotypique, qui sont elles-mêmes soumises à d'importants compromis évolutifs déterminés par des différences de stratégies d'histoire de vie. L'existence de variation individuelle de susceptibilités pourrait alors affecter l'émission et la réponse aux signaux et ainsi apporter de nouvelles perspectives pour l'étude de la variation des stratégies de communication par signaux d'alarme aussi bien chez les animaux que chez les plantes. Nous proposons ainsi d'explorer ces questions via une approche individuelle intégrée aux cadres d'étude offerts par la génétique quantitative et la personnalité animale. Nous détaillons des hypothèses de recherche pouvant être testées via l'observation et l'expérimentation de comportements d'émission et de réponse aux signaux, et s'appuyant sur un cadre analytique basé sur la décomposition de la variance. Nous suggérons tout d'abord que l'étude des différences individuelles de comportements de défense chez les plantes pourrait apporter des informations sur leur écologie évolutive. Nous montrons également que les comportements d'alarme des animaux et des plantes devraient être abordés via une perspective individuelle afin de mieux appréhender les différentes sources de variation à l'origine de la complexité des systèmes de communication par signaux d'alarme.

Mots-clés : Comportement de défense, Communication par signaux d'alarme, Communication végétale, Différences individuelles constantes, Personnalité animale, Prise de risque, Compromis, Histoire de vie.

1.1 Abstract

Animals and plants both deal with risk from predation and herbivory, leading them to use similar defensive behaviours and alarm signalling. The way individuals perceive and respond to risk could be influenced strongly by their investment and trade-offs in fitness-related functions, driven by differences in life-history strategies. Individual variation in risk susceptibilities could thus be expected to affect both animal and plant signalling and response to signals, offering new perspectives to study variation in alarm communication strategies. We present here a unified individual approach based on the frameworks offered by quantitative genetics and animal personality. We detail hypotheses that could be tested using observational and experimental designs of signalling and responses to signals, and an analytical framework based on variance decomposition. We first suggest that considering consistent individual differences in plant defence behaviours could give insight into plant evolutionary ecology. We also emphasise that studying alarm behaviour from an individual perspective in both animals and plants is crucial to shed light on the sources of variation that generate complexity in alarm communication systems.

Keywords: Behavioural defence, Alarm communication, Plant signalling, Herbivore-induced plant volatile, Consistent individual differences, Animal personality, Risk-taking, Trade-off, Life history.

1.2 Introduction

Most organisms face a major trade-off: eating while avoiding being eaten (Lima 1985). Predation has widely shaped animal behaviour (Lima & Dill 1990; Caro 2005; Verdolin 2006; Tollrian et al. 2015), while herbivory has led plants to respond to biotic stressors (Baldwin & Schultz 1983; Rhoades 1983; Karban & Baldwin 1997; Arimura et al. 2011; Heath et al. 2014). The trade-offs between growth (or reproduction) and defence (or survival) constitute major selective constraints that have shaped the evolution of various animals' and plants' antipredator/herbivore defences (Rangeley & Godin 1992; Lima 1998; Koricheva 2002; Yoshida et al. 2004; Boege & Marquis 2005; Lind et al. 2013; Cardenas et al. 2014). Despite differences in the way animals and plants deal with attack risk (Karban et al. 2016), their defensive strategies have evolved analogously and they share strikingly similar constitutive (i.e., passive) defences (Fig. 1.1). They also both use cost-effective plastic strategies (Karban et al. 1997) by inducing active defences only under conditions of risk (Fig. 1.1; Harvell 1990; Karban & Baldwin 1997; Dicke 1999; Agrawal et al. 2002; Tollrian et al. 2015). In particular, both animals and plants release organic compounds under risk of attack, and these chemicals can spread throughout the environment through their dispersive (airborne or waterborne) properties. In this way valuable information about risk is made available to others and can constitute alarm cues (Lönnstedt & McCormick 2011).

Animals transmit alarm signals via many different pathways to communicate the risk of predation (Meuthen et al. 2014), including visual and acoustic signals (Ydenberg & Dill 1986; Klump & Shalter 1984; Smith 1992; Bradbury & Vehrencamp 1998; Caro 2005; Hollén & Radford 2009) but also chemical signals (i.e., alarm

Constitutive defences are constantly present in organisms to prevent attacks from occurring. Permanent **(A) structural defences**, such as thick integuments (Fig. 1.1.1: a-c) or sharp extensions (d-h), represent highly deterrent physical barriers. Some specialised structures even contain irritants (i,j), and **(B) biochemicals** are even more developed in many species to make them unpalatable, toxic or even poisonous (k-q). **(C) Visual displays** protect species through aposematic coloration that signals unprofitability (r), and some organisms exploit those patterns to be identified as nonedible or dangerous (s-v). Others mimic the presence of a competitor or a predator (w-y), while some conceal themselves (z-ac). **(D) Protective mutualism** is used as an indirect defence, being a permanent association between living organism (ad,ae).

Figure 1.1.1 Examples of constitutive defences

A: Hardened carapaces, elytra and waxy cuticles protect *Limulidae* (a), *Coleoptera* (b), and *Ilex aquifolium* (c). Spines are developed in *Acanthaster planci* (d), *Echidna* (e) and *Cactaceae* (f), while *Carissa bispinosa* (g) has thorns and *Rosacea* (h) prickles. Hairs of many caterpillars (i) and trichomes of *Urtica dioica* (j) are urticating. **B**: *Hapalochlaena* octopuses (k), *Pitohui* birds (l) and *Nycticebus* (m) contain harmful toxins. Chemical content in monarchs *Danaus plexippus* (n), *Acacia* (o) (tannin) and *Nicotiana* (p) (nicotine) are unpalatable, while *Ricinus communis* (q) is highly poisonous. **C**: *Phyllobates*' (r) vivid colours signal their toxicity, and aposematic colours are shared and thus reinforced by mullerian mimicry in monarchs (n) and viceroys *Limenitis archippus* (s) or in plants *Gentiana lutea* (t, left) and *Veratrum album* (t, right). Through batesian mimicry, colour patterns of harmless *Lampropeltis* snakes (u, left) imitate the colours of venominous *Micruroides* snakes (u, right), and *Boraginaceae* plants (v, left) show the white patterns of thorny *Asteraceae* (v, right). *Passiflora* (w) plants deter *Heliconius* from laying by mimicking their eggs, *Paspalum paspaloides* (x) plants show dark flecks mimicking infestation from aphids, and *Papilio canadensis* (y) caterpillars show deflective eyespots. *Phasmatodea* (z), *Uroplatus* geckos (aa) or *Podargidae* birds (ab) are camouflaged through cryptic coloration and morphology. *Lithops* (ac) plants resemble surrounding pebbles. **D**: *Lybia* crabs (ad) are defended by mutualistic stinging sea anemones carried in their claws, and *Acacias* (ae) are protected by mutualistic *Pseudomyrmex* ants sheltered in domatias.

Induced defences allow instant response to a threat, through **(A) structural** modifications (Fig. 1.1.2: a-d) or **(B) aversive substances** (innocuous or harmful). Animals can bleed (e,f) or expel deterrent oral secretions (g,h) or anal fluids that are repulsive (i,j), toxic (k), or confusing (l,m). Sticky substances (n-p) and electric discharges (q) also ward off predators. Plants exude substances than trap or repel herbivores (r-t), and rapidly become indigestible or toxic (*Acacia* and *Nicotiana*, Fig. 1.1.1: o,p) and produce HIPVs (u, see text). Some compounds may additionally serve as conspecifics alarm signals (m,n,q,u, see text). **(C) Visual displays** allow some animals to instantly blend with their environment (v) or to mimic threatening predators (w). **(D) Protective mutualism** can also be induced (see text).

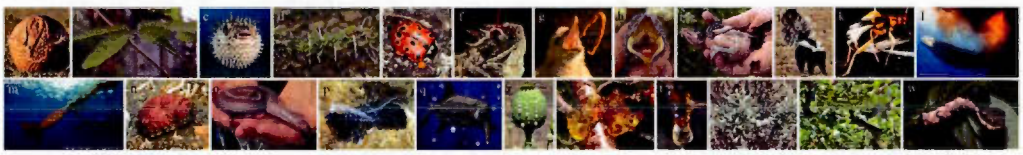

Figure 1.1.2 Examples of induced defences

A: When attacked, *Tolypeutes* species (a) turn into a ball, while *Mimosa pudica* (b) close in through thigmonasty, and *Diodontidae* (c) blow up to erect spines while the length of *Acacias*' (d) thorn's increase with grazing intensity. **B**: *Coccinellidae* (e) exude a noxious fluid ("reflex-bleeding") and *Phrynosoma* lizards (f) squirt blood from their eyes. Attackers are repelled by birds' vomit containing foul stomach oils in *Procellaridae* (g) or secondary metabolites (initially sequestered by insect prey from host plants) in nestlings *Coracias garrulus* (h). Cuckoo chicks (*Clamator glandarius*) (i) release foul-scented liquid feces (that may turn brood parasitism into mutualism), and *Mephitidae* use a malodorous spray (j). *Carabidae* (k) spray boiling poisonous fluids, while the anal syrup expelled by *Kogia breviceps* (l) or the ink squirted by *Cephalopoda* species (m) create concealing clouds. *Haliotis tuberculata* (n) excrete obscuring mucus from respiratory pores, *Myxinidae* (o) produce slime that can choke predatory fishes, *Holothuroidea* (p) eject tubules to entangle predators, and *Mormyridae* (q) produce harmful electric current. *Papaver somniferum* (r) exude sticky latex to mire insects, while many trees produce gummosis (s) and resin (t) that trap attackers. *Artemisia tridentata* (u) produce repelling chemicals. **C**: When disturbed, some *Chamaeleonidae* (v) change their skin coloration to match their background, while *Hemeroplanes ornatus* caterpillars (w) puff up to resemble a snake.

Figure 1.1 Box 1. Comparison of defences in animals and plants (Photo credits in Annex A).

pheromones, Smith 1992; Chivers & Smith 1998; Verheggen et al. 2010; Leonhardt et al. 2016). Plants also use such chemical signals by releasing herbivore-induced plant volatiles (HIPVs) in response to feeding damage (Karban 2008; Heil & Karban 2010; Heil 2014). Over the last decade, the production of volatile substances by plants has been considered a behaviour just as alarm pheromone release in animals (Karban 2008). Responses of plants to the actions of herbivores or to substances emitted by conspecifics are indeed now widely considered as behaviours (Karban 2008) and we will not debate this notion here. Considering behavioural decisions of plants from an adaptive point of view (Waser & Price 1998; Karban 2008; Dicke 2009; Metlen et al. 2009) has brought considerable insights to plant ecology and evolution. Major breakthroughs have particularly arisen from investigating plant strategies in foraging (considering game theory, McNickle et al. 2009; Louâpre et al. 2012; McNickle et al. 2013) and competitive contexts (considering kin recognition, Bais et al. 2006; Dudley & File 2007). Plants are even considered to show a form of intelligence (Trewavas 2002; Baluška & Mancuso 2007; Baluška et al. 2010), by demonstrating learning and memory capacities (Trewavas 2005, 2009; Ali et al. 2013; Affifi 2013). Although animals and plants have traditionally been studied independently, their ecology and evolution are undeniably based on the same general theories (Agrawal et al. 1999; Lankinen & Karlsson Green 2015). Adopting a more unified approach highlighting their similarities (see Fig. 1.1, and below) generates questions that could be investigated in both groups (Begon et al. 1996; Waser & Price 1998; Karban 2008) and thus could provide explanations to the broad phenomenon of communication in living organisms.

There is, however, a topic that has changed our conception of animal behaviour and ecology over the last two decades that needs to permeate the field of plant ecology: individual variation. Considering individual variation has presented new applications for ecologists, for example individual niche specialisation (Bolnick et al. 2003), individual heterogeneity in life-history strategies (Réale et al. 2007, 2010; Smith &

Blumstein 2008; Quinn et al. 2009; Biro & Stamps 2008), or animal personality and behavioural syndrome (Wilson et al. 1994; Sih et al. 2004; Réale et al. 2007; Wolf & Weissing 2012). The study of animal personalities has shown that behavioural differences among individuals are clearly important and widespread in animals. This approach, broadly based on a quantitative genetic framework, along with behavioural plasticity, provides a more complete understanding of the variation in behavioural traits observed in animal populations (Réale et al. 2007; Dingemanse et al. 2010; Brommer & Class 2017). Despite some quantitative genetics work that considers individual variation in plant traits (Roach & Wulff 1987; Wolf et al. 1998; Agrawal et al. 2001; Muir 2005; Mutic & Wolf 2007; Andersson 2014; Costa e Silva et al. 2017), the existence of individual variation for plant behaviour and ecology has been overlooked. We suggest that plant biologists adopt an individual-based approach to investigate consistent behavioural differences among individuals over time and across situations (i.e., personality, Dall et al. 2004; Réale et al. 2007). More specifically, we propose that individual differences in risk-sensitivities (i.e. risk taking or boldness; Wilson et al. 1994; Réale et al. 2007), which are themselves associated with different life-history strategies (Réale et al. 2010), could affect alarm signalling about risk from predation and herbivory. We therefore draw a parallel between alarming behaviours of both animals and plants and highlight how the concept of individual variation could be applied to alarm communication in both groups.

1.3 Alarm communication as defence behaviour in animals and plants

Communication allows organisms to fulfil major fitness-related functions such as reproduction (for mate or pollinator attraction, Hill 1991; Sutherland & Vickery 1993; Johansson & Jones 2007; Schiestl 2010; Das et al. 2013; Leonard & Francis 2017), but also survival, with defence against attackers through passive or active defence signalling. The release of alarm signals by individuals perceiving a risk has intrigued evolutionary biologists for decades, as signallers appear to compromise their own

survival to benefit others. Intensive research on alarm signalling has been carried out not only for animals (Maynard Smith 1965), but also for plants since the 1983 discussion of "talking trees" (Baldwin & Schultz 1983; Rhoades 1983). Plant alarm signalling is now well accepted: many plants use volatile signals released by attacked neighbours to activate their own defences (Heil & Karban 2010; Heil 2014; Karban et al. 2014a). However, the literatures on plant and animals alarm communication remain isolated from each other. Furthermore, the literature on animals is also largely separated, with independent research on alarm calling (mainly in birds and mammals, Klump & Shalter 1984; Macedonia & Evans 1993), on alarm pheromones in terrestrial systems (mainly in insects, Blum 1969), and on alarm pheromones in aquatic systems (mainly in fishes and aquatic invertebrates, Smith 1992; Laforsch et al. 2006; but see the broad review on alarm pheromones from Verheggen et al. 2010).

Here we wish to stimulate a more united approach to alarm communication, and further suggest why and how individual variation should be integrated with alarm communication for both animals and plants. We first present a succinct overview of the major functions of alarm signalling, which are by no means mutually exclusive. We draw a parallel between behaviours found in both animals and plants to highlight that although alarm communication is studied independently in different taxa, the fundamentals remain the same.

First of all, alarm signals can be directed at oneself. Due to their particular modularity, plants can directly benefit from emitting volatile alarm signals to trigger and coordinate systemic resistance in unattacked parts (Karban et al. 2006; Heil & Silva Bueno 2007; Frost et al. 2008; Rodriguez-Saona et al. 2009; Shiojiri et al. 2009; Heil & Karban 2010; Heil 2010). Such volatile intra-plant communication might be less costly and faster than vascular signalling (Farmer 2001; Orians 2005; Karban et al. 2006; Heil 2009; Shiojiri et al. 2009; Heil & Karban 2010). In sessile marine invertebrates and aphids, alarm pheromones also provide self-benefits since they can

elicit defence responses in clonal neighbours (Howe & Sheikh 1975; Roitberg & Myers 1978).

Alarm signals can be directed at attackers (Bergstrom & Lachmann 2001), as individuals can gain direct benefits by releasing aversive substances at these attackers (see Fig. 1.1.2), but also by indicating that they have perceived the predator. Alerted prey are difficult to catch (Trivers 1971; Dunford 1977) and induced plants are likely to already host herbivorous competitors and to contain higher levels of chemical defenses (De Moraes et al. 2001); as such, alarm signals can deter predators and herbivores (Woodland et al. 1980; Hasson 1991; Caro 1995; Zuberbühler et al. 1999). Alarm calling in rodents (Blumstein 2007) can, for instance startle, distract or deter the predator, increasing the prey's chances of escaping (Sherman 1985; Shelley & Blumstein 2005; Digweed & Rendall 2009). Although alarm calling can be dangerous (Sherman 1977), the predator's preference for non-alarming individuals can provide direct benefits to callers (Kareksela et al. 2013). HIPVs are commonly avoided by many insects and thus can also protect a plant from herbivore attacks (Kessler & Baldwin 2001; De Moraes et al. 2001; Heil 2008; Heil & Karban 2010; Hatano et al. 2015; Veyrat et al. 2016; El-Sayed et al. 2016), although their production also comes with ecological costs since HIPVs attract some herbivores (Heil 2008; El-Sayed et al. 2016). Attackers also avoid areas filled with alerted individuals (Zuberbühler et al. 1999), especially when neighbours join in a mobbing chorus of contagious alarm calls (Curio 1978; Sherman 1985; Uster & Zuberbühler 2001; Krams et al. 2009; Deng et al. 2016) or of HIPVs (Zakir et al. 2013).

Plants also release alarm signals directed at "bodyguards", to induce indirect defences through tritrophic interactions (Dicke & Sabelis 1988; Turlings et al. 1990; Arimura et al. 2005; Halitschke et al. 2008; Heil 2008; Dicke 2009; Mumm & Dicke 2010; Dicke 2015; Blande 2017). HIPVs attract the predators and parasitoids of herbivores (Dicke & Sabelis 1988; Turlings et al. 1990; Dicke & van Loon 2000; Kessler &

Baldwin 2001; Dicke 2009; Kessler & Heil 2011), and even insectivorous birds (Amo et al. 2013; Mäntylä et al. 2017). These associations with predators may benefit terrestrial plants (Kessler & Baldwin 2001), or marine plants that attract crabs or fishes that feed on their marine herbivores (Coleman et al. 2007). Animals can also attract bodyguards, using the "attract the mightier predator" strategy (Curio 1978): threatened aphids and treehoppers respectively produce chemical and acoustic alarms that increase the effectiveness of their protective ants (Nault et al. 1976; Morales et al. 2008). When they are attacked, some marine organisms also protect themselves by releasing bioluminescence signals that constitute dissuasive "burglar alarms": the attackers will spit out the prey as the shining trail could attract their own top predators (Burkenroad 1943; Abrahams & Townsend 1993; Fleisher & Case 1995; Haddock et al. 2010). In a similar way, alarm signals attracting further predators can create competition disrupting the predation event (Chivers et al. 1996; Lönnstedt & McCormick 2015).

Intuitively, alarm signals are directed at conspecifics to warn them of danger. In many species of animals and plants, individuals indeed respond to alarm signals, although this observation only suggests the intent of the responder, not the signaller (Smith 1992; Karban 2008; Heil & Karban 2010; Dicke & Baldwin 2010; Karban et al. 2014a). Animals respond with anti-predation behaviours, such as vigilance and flight in birds and mammals (Blumstein 2007; Hollén & Radford 2009), or retraction in coral polyps (Goddard et al. 2006). Plants show anti-herbivore defences by inducing defences or priming protection against upcoming herbivore attacks (Conrath et al. 2006; Kost & Heil 2006; Himanen et al. 2010). Altogether, alarm signallers gain advantage from the alertness and priming of their neighbours as they can further compel attackers to look elsewhere, through mobbing (Curio 1978) and associational resistance (Himanen et al. 2010; Morrell & Kessler 2017). In wasps, emitters of alarm pheromones can recruit conspecifics that will attack the threat (Landolt et al. 1999). Signallers can also benefit from inducing neighbours' HIPVs emissions, which

further increases the recruitment of natural enemies (Choh et al. 2004; Kobayasi & Yamamura 2007). The increase of survival of warned mates (Hogstad 1995) and familiar neighbours is also beneficial through mate protection and reciprocal altruism (Trivers 1971; Krams et al. 2006). However, the alarms are not necessarily primarily intended for intra- or inter-specific receivers. Alarms may be by-products of the attack that receivers perceive by eavesdropping on the available information and use to increase their fitness (Bradbury & Vehrencamp 1998; Karban 2008; Schmidt et al. 2008).

Alarm signals may also be directed at kin, as kin selection theory predicts that the costs associated with alarm signal production would be overcome by benefits to the signaller's kin (Hamilton 1964). Alarm signalling can thus be adaptive if it promotes survival of offspring (Blumstein et al. 1997) and collateral kin, creating direct and indirect fitness for the signaller (Maynard Smith 1965; Sherman 1985). Alarm calls of rodents are for instance directed towards relatives (Dunford 1977; Sherman 1977, 1985; Blumstein et al. 1997; Blumstein 2007), as are alarm pheromones of aphids (Wu et al. 2010). Plants have not yet been shown to be able to emit preferentially toward relatives, but sagebrush (*Artemisia tridentata*) do respond more intensely to HIPVs emitted by more closely related clipped neighbours (Karban et al. 2013). In animals, individuals are also more responsive to alarms from kin, as shown through playback of alarm calls in superb fairy-wrens (*Malurus cyaneus*, Colombelli-Négrel & Evans 2017) and in African elephants (Loxodonta Africana, McComb et al. 2000; O'Connell-Rodwell et al. 2007). In fish, although individuals show antipredator behaviours in response to involuntary damage-released alarm pheromones from conspecifics, the influence of kin selection remains to be proven to explain the evolution of these chemical cues (Chivers et al. 2007; Meuthen et al. 2014).

Alarm signals are thus widely and similarly used among the different kingdoms to exchange risk-based information, both at the intra- and at the inter-specific levels.

Most of these studies though focus on the overall, adaptive plastic response of animals or plants to the risk of predation or herbivory, but they rarely consider among-individual variation in that response and the potential evolutionary consequences of such variation. We will now consider individual variation beyond its value for kin recognition, to see how its integration into alarm communication systems could provide insights into their ecology and evolution.

1.4 Individual variation in behaviour

1.4.1 The individual approach applied to plant behaviours

Individual variation is the raw material for selection and evolution, and thus studying individual trait variation within natural populations is of major interest for evolutionary ecology. Recent research highlighted that individuals within a population should not be considered as equivalent entities by ecologists (Herrera & Bazaga 2011), because intra-specific variation can impact ecological dynamics (Bolnick et al. 2003, 2011; Violle et al. 2012) and have implications on the whole community and ecosystem (Clark et al. 2010; Raffard et al. 2017). Over the last two decades, the individual-based approach has prompted a reconsideration of the view that animal behavioural traits are limitlessly plastic and that all individuals within a population could express an adaptive behavioural response to an environmental change, and thus led behavioural ecologists to move beyond the "golden mean" (Wilson et al. 1994; Sih et al. 2004; Réale et al. 2009). Individual behavioural variation is, thus, now considered as an important aspect of the ecology and the evolution of wild populations. The development of research on animal personality has revealed extensive evidence of consistent among-individual differences in behavioural traits (Wilson et al. 1994; Gosling 2001; Réale et al. 2007; Bell et al. 2009; Wolf & Weissing 2012; Dall et al. 2012).

In plants, intra-specific variation has long been considered obvious (Karban 1992), and Briggs (1997) distinguished "intrinsic" (fixed and heritable) individual differences from those that are "developmental" (due to age for instance) and "environmentally induced" (caused by environmental phenotypic plasticity). However, only a few studies have investigated individual variation as an important population attribute (Albert et al. 2011). This might be related to the ambiguous nature of the notion of individuality in plants (Clarke 2011), since identifying an individual in the field is more difficult than for animals because many plants are clonal. For example the Pando aspen forest (*Populus tremuloides*) spreading over 100 acres is actually one clone or individual (DeWoody et al. 2008). However, rather than being an important impediment to using the individual approach on plants, clonal propagation could actually provide great advantages to experimentally separate the different sources of variation affecting a trait's phenotypes. For instance, in *Labiatae* individuals differed consistently in their fecundity (e.g., in number of inflorescences) over the years (Herrera 1991). In *Kalmia latifolia*, the production of nectar also varied among individuals and was linked to their fitness, but these individual differences were not repeatable over years (Real & Rathcke 1991). In fact, individual variation in plants has been studied primarily to investigate its impact on the other members of the community that experience this variation. For instance, individual oaks (*Quercus robur*) vary consistently in their phenology between years, and this has been linked to their herbivore loads (Crawley & Akhteruzzaman 1988). Several studies also linked plant genetic diversity to communities of associated arthropods (Fritz 1995; Wimp et al. 2005; Bangert et al. 2005; Johnson et al. 2006; Zytynska et al. 2011). Variation in defensive traits can also structure the community of insects or fungi that plants interact with (Poelman et al. 2008; Sthultz et al. 2009), and among-individual variation in growth and fecundity can promote tree diversity in forests (Clark et al. 2010).

Intraspecific variation in plants has informed studies at different community levels, and, although still limited (Sih et al. 2012), research on animal personality has started to investigate the effects of behavioural individual differences on trophic dynamics such as predator-prey interactions (Belgrad & Griffen 2016; Start & Gilbert 2017). Animal personality could shape animal-plant interactions through individual variation in seed dispersal by foraging animals (Zwolak 2017) and through the level of aggressiveness of ant colonies that protect their mutualistic tree (Marting et al. 2018). Beyond investigating the effects of behavioural individual variation on trophic dynamics, we suggest that plant biologists begin by studying the existence of variation and its causes and consequences to gain insights into plant evolutionary ecology. Plant behavioural plasticity could thus be studied through the individual-based approach that has been applied effectively to animals.

1.4.2 Trade-offs and life-history strategies

Using similar approaches for both animals and plants makes good sense as they are both confronted with important trade-offs. These trade-offs partly explain the maintenance of individual differences within a population: they influence living organisms in their life history strategies, with potentially equivalent fitness outcomes (Dall et al. 2004; Wolf et al. 2007; Biro & Stamps 2008; Smith & Blumstein 2008; see Dingemanse & Réale 2013 for a review on the other causes of variation). Trade-offs are present among different life-history traits (Stearns 1992; Roff 1992), and plant species differ in their life histories along a fast-slow, or pace-of-life, continuum similar to that described for animals (Stearns 1983; Gaillard et al. 2016; Salguero-Gómez et al. 2016); species at different latitudes or altitudes generally show different levels of pace-of-life (Wikelski et al. 2003; Hille & Cooper 2015). Differences in pace-of-life could be further linked to physiological traits (Ricklefs & Wikelski 2002) and behavioural traits (Réale et al. 2010), and these associations could be studied at species, population, and individual levels (Réale et al. 2010). The rationale behind

including physiological and behavioural traits into the general fast-slow continuum is that these traits play a functional role on life-history decisions, with their variance explained by trade-offs between life-history tactics (Stamps 2007; Wolf et al. 2007; Réale et al. 2010). As a result, we should expect that all these traits form a pace-of-life syndrome (POLS, Réale et al. 2010). Plant behaviour, and more specifically alarm communication used as defence against herbivory, could thus provide a very appropriate model to test the POLS hypothesis.

Plants have limited time and energy for their growth and reproduction, and they also have to defend themselves against herbivores (Agrawal et al. 2010; Dicke & Baldwin 2010; Lucas-Barbosa et al. 2011; Pierik et al. 2014). Investment in defences, thus, often comes with costs in fitness components linked to growth and reproduction (Koricheva 2002; Brönmark et al. 2012; Neilson et al. 2013; Blande 2017; Cerrudo et al. 2017; Karban 2017). Certain plants for instance invest in vertical growth to counteract low light conditions, but at the expense of efficiently inducing defences against herbivory (McGuire & Agrawal 2005; Karban 2008, 2016). We should thus expect a pace-of-life syndrome relating resistance to herbivory, and life history: if resistance to herbivores is costly to produce, then fast plants showing fast growth, early reproduction and possibly short life, should also show lower investment in resistance against herbivory compared to slower plants. In support to that hypothesis, Kempel et al. (2011) have shown the existence of a trade-off between constitutive and induced defence in plants, and that fast growing plants species do not show as much constitutive defence as slow growing ones. Within a species, the POLS may be found between individuals that favour a fast growth and individuals that favour a longer life.

1.4.3 Direct and indirect effects on alarm communication

Animal personality traits, such as risk-taking behaviours, have been shown to have a genetic component and to be heritable (van Oers et al. 2004; Réale et al. 2007; Dingemanse et al. 2002). Since plant resistance and susceptibility to herbivory is

known to have a genetic component (Karban 1992; O'Reilly-Wapstra et al. 2004; Johnson & Agrawal 2005; Sthultz et al. 2009), we can expect individual behavioural variation in the way plants deal with the previously mentioned trade-offs. Moreover, important intra-specific or genetic variation exists in the production of HIPVs (Kessler & Baldwin 2001; Degen et al. 2004; Wu & Baldwin 2010; Dicke & Baldwin 2010; Hare 2011; Moore et al. 2014), both quantitatively and qualitatively (Karban et al. 2014b). Agrawal et al. (2002) found genetic variation in induction of chemical defence in wild radish (*Raphanus raphanistrum)*, and higher plasticity levels associated with fitness costs in the absence of herbivory. In the Portuguese laurelcherry (*Prunus lusitanica*), basal levels of defensive secondary metabolites also show differences at the among-populations level, and this intraspecific variation is heritable (Pardo et al. 2016). For these and other species, individual differences in plant defence behaviour and alarm communication can be investigated within a quantitative genetic framework.

The study of communication in animals and plants is particularly amenable to the general approach used in quantitative genetics: the study of indirect genetic effects (Wolf et al. 1998; Bijma 2010). An individual's phenotype is directly affected by its own genotype (i.e., direct genetic effects), but also by the genotypes of others that are part of its social environment (Wolf et al. 1998; Agrawal et al. 2001). These common indirect genetic effects can help explain how complex phenotypes can evolve through the simultaneous influences of genetics and the environment (Agrawal et al. 2001; Costa e Silva et al. 2017; Schneider et al. 2017), with environment in this case being gene expression in a conspecific. The effects of social influences have for instance been well studied through maternal effects in animals (Mousseau & Fox 1998) and plants (Roach & Wulff 1987), and through interactions among other, unrelated, conspecifics (Wolf et al. 1998; Muir 2005) or heteropecifics (Campobello et al. 2015). In *Arabidopsis thaliana* and *Sedum album*, the fitness-related traits of individuals interacting with competitive neighbours are affected not only by their own genotypes

but also by the genetic characteristics of their competitors (Mutic & Wolf 2007; Andersson 2014). Indirect genetic effects are thus important for many evolutionary processes from kin selection to community structure (see above the effects of plant individual variation on arthropod community), and interacting phenotypes need to be considered when an individual phenotype is influenced by its interaction with conspecifics (Moore et al. 1997; Agrawal et al. 2001; Bleakley et al. 2010) or heterospecifics (Campobello et al. 2015). Although it is recognized that indirect genetic effects influence behaviours expressed in communication contexts (Moore et al. 1997; Bleakley et al. 2010; Bailey et al. 2018), empirical examples scarcely exist in animals, and, to the best of our knowledge, none exist for plant communication. In a few arthropod species, individuals are affected by the genotypes of their conspecifics in contexts of social chemical communication and courtship displays (D'Ettorre & Moore 2008; Kent et al. 2008; Hoefler et al. 2009), but we do not know any work on the role of indirect genetic effects in contexts of alarm communication. To complement the approach used in quantitative genetics, it is useful to investigate individual variation in behavioural phenotypes expressed by individuals interacting with conspecifics or heterospecifics. This is especially interesting because social interactions are widely affected by animal personalities (Bergmüller & Taborsky 2010; Aplin et al. 2013; Montiglio et al. 2013) and could even be one of the main drivers explaining their existence (Réale & Dingemanse 2010; Dingemanse & Araya-Ajoy 2015; von Merten et al. 2017). Here, we suggest using this individual perspective to study alarm communication in a context of risk in both animals and plants.

1.5 An individual approach to study alarm communication

Above we have shown that animals and plants share similar alarm signalling systems and that an individual approach to the evolutionary ecology of behaviours could provide fruitful information in plants as it did for animals, especially for defensive

chemical signalling. We now formalize a framework that could be applied to both animals and plants to question whether individual variation in risk sensitivity could influence both communication signals and responses to them.

1.5.1 Individual variation in alarm signals emission and response

Researchers recently developed theoretical models that demonstrated the possible coevolution of communication and personality, through individual differences in the production and the interpretation of signals (Botero et al. 2010; McNamara et al. 2009; Wolf et al. 2011). Although this link was investigated in a context of agonistic interactions, featuring individuals signalling their quality (fighting abilities) through ornaments (i.e., badges of status), it could potentially be applicable to the joint evolution of personality and alarm signals.

Although individuals can emit alarm signals depending on the presence of relatives or preferentially respond to their signals (see above), their alarm behaviours may not be entirely plastic. As argued previously, the proximate cause of individual variation in defence signalling could be physiological constraints, through the existence of intrinsic individual variation in sensitivities. For instance, animal signalling behaviours expressed in aggressive or reproductive contexts are influenced by individuals' physiological sympathetic system reactivity. Bolder individuals repeatedly emit more aggressive or social signals (Hollander et al. 2008; Guillette & Sturdy 2011; Akçay et al. 2014; Friel et al. 2016) or sing more often (Crino et al. 2010). In a context of risk, alarm signalling could be linked to an individual's physiological stress responses via the Hypothalamic-Pituitary-Adrenal (HPA) axis, reflected in the production of glucocorticoids in animals (Blumstein et al. 2006). Bolder individuals, that show lower stress responses (Clary et al. 2014), could have higher thresholds for both emission of alarm signals and response to the signals. At the opposite, highly risk-sensitive, shy individuals would have lower thresholds of

emission and would more often emit alarm signals in response to unthreatening environmental stimuli (Hare & Atkins 2001; Searcy & Nowicki 2005; Pollard 2011).

The ultimate causes of the existence of individual differences in alarm signalling in both animals and plants could be related to the predictions made within the POLS framework (Réale et al. 2010, see above). Low risk-sensitive individuals, that maximize immediate reproduction and invest less in defensive behaviours (i.e., fast pace-of-life), would be less prone to react to stressful situations with alarm signals. At the other extreme, highly risk-sensitive individuals, that allocate more energy to defence for immediate survival and future reproduction (i.e., slow pace-of-life), would tend to produce more alarm signals. Individuals could then consistently differ in their propensity and/or intensity to signal under identical stresses. Individuals that tend to produce "false alarms" could also gain some benefit, because plants' unfounded HIPVs can attract natural enemies of future herbivores (Shiojiri et al. 2010; Yamauchi et al. 2015), and false alarm calls can deter naïve predators from hunting in presumed occupied areas (besides providing foraging and mating opportunities when produced intentionally to deceive conspecifics, Munn 1986; Bro-Jørgensen & Pangle 2010). Overall, it is relevant to investigate plasticity of signalling and the constraints that exist at the individual level to gain insights into the evolution of the signals.

Individual variation in risk sensitivities could not only affect individuals' tendency to signal risk, but also constrain their response to alarm signals received and thus mediates the interpretation of social information. In Trinidadian guppies (*Poecilia reticulate*, Brown et al. 2014) and eastern chipmunks (*Tamias striatus*, Couchoux et al. 2018), individuals that receive alarm signals respond according to their level of boldness, with shyer individuals expressing stronger anti-predator responses than bolder ones. In plants, individuals with a low threshold in their response to HIPVs preferentially invest in defence and show strong responses to alarm signals, and thus could be considered to be highly risk-sensitive (i.e. error management framework:

Orrock et al. 2015). Assuming that defence activation is a costly process, such a defensive strategy could be compatible with a slow pace-of-life (Réale et al. 2010). In the context of risk it is thus important to consider both facets of alarm communication, the propensity to signal, the sensitivity to respond to the signal, and their potential interaction.

Considering that individuals could differ in their propensity to emit alarm signals, and consequently in their reliability to signal the presence of a threat, we need to come back to the idea of plasticity. Receivers could also plastically adjust their response according to the specific behavioural characteristics of the signaller of the alarm. In chipmunks (Couchoux et al. 2018), the alarms of potentially low-accuracy shy signallers elicit less intense reactions in receivers (Hare & Atkins 2001; Pollard 2011), allowing them to maximise resource acquisition against potentially unecessary defence. Plants avoid inducing defence in response to foreign HIPVs that are less likely to indicate true damage (Moreira et al. 2015), and thus may also be able to evaluate the reliability of a signal. Receivers could adjust their response based on two possible (and not mutually exclusive) mechanisms: 1) the recognition of the signaller and previous experiences with it (i.e., learned response) or 2) the evaluation of relevant characteristics directly decoded from the signal itself (i.e., alarm calls' acoustic features; or HIPVs' chemotypes, which vary among individuals and are similar among close relatives, Karban et al. 2014b). Features of the signal itself prevail for chipmunks, as individuals respond to the personality of both familiar and unfamiliar signallers (Couchoux et al. 2018). In this case, we should expect an association between the characteristics of the signal and those of the signaller (i.e., personality or life-history tactics). Such plastic responses would thus not require any complex cognitive capacities, contrary to a learned response, and could be examined in plants.

1.5.2 Estimating and analysing sources of individual variation in alarm communication

We will now describe several experimental or observational designs that can permit the analyses of the different sources of individual variation in alarm communication in animals and plants. Different hypotheses could thus be tested, allowing us to obtain information on signaller/receiver dynamics from which ecological or evolutionary inferences can be made.

Alarm communication signals and responses to those signals, like other traits, are characterised by a population mean and a phenotypic variance (Allegue et al. 2016). With an individual approach, we are interested in the reasons underlying this individual variation, because of their biological importance (i.e., trait selection, phenotypic plasticity in response to changes in physical and social environments). We can estimate the among- and within-individual variance components in the same mixed-effect model, by including various fixed effects that are potentially responsible for differences among individuals (e.g., sex, age, light, soil nitrogen, body condition, etc.), and the identity of each individual (animal or plant) as random effects to evaluate individual phenotypic deviations from the mean (Allegue et al. 2016; Table 1.1). Within-individual variance, or residual variance, can include both the effects of unmeasured environmental effects on the phenotype (i.e., phenotypic plasticity) and measurement errors (which can be evaluated by including the IDs of two independent observers that measured the same trait, see e.g., Dubuc Messier et al. 2017).

Table 1.1 Sources of phenotypic variation in alarm communication of animals and plants. When emission of alarm signals or responses to these signals are measured several times on each individual, mixed-effect models can help decompose the multiple sources of phenotypic variance for these traits into unique variance components. Here we present the different types of models of decomposition of variance –from the simplest to the most complex– and the (co)variance components they provide[1].

	Type of trait	Type of random effects	Components[2, 3]
1	Signal (*s*)	Signaller (*S*) ID	V_{sSi}, V_{sSw}
2	Response to signal (*r*)	Receiver (*R*) ID	V_{rRi}, V_{rRw}
3	Signal	Signaller + Receiver IDs	V_{sSi}, V_{sRi}, V_{sSw}, V_{sRw}
4	Response to signal	Signaller + Receiver IDs	V_{rRi}, V_{rSi}, V_{rRw}, V_{rSw}
5	Signal + response to signal	Signaller + Receiver IDs	$\begin{bmatrix} V_{sSi} & Cov_{sSi,sRi} & Cov_{sSi,rRi} & Cov_{sSi,rSi} \\ & V_{sRi} & Cov_{sRi,rRi} & Cov_{sRi,rSi} \\ & & V_{rRi} & Cov_{rRi,rSi} \\ & & & V_{rSi} \end{bmatrix}$ $\begin{bmatrix} V_{sSw} & Cov_{sSw,sRw} & Cov_{sSw,rRw} & Cov_{sSw,rSw} \\ & V_{sRw} & Cov_{sRw,rRw} & Cov_{sRw,rSw} \\ & & V_{rRw} & Cov_{rRw,rSw} \\ & & & V_{rSw} \end{bmatrix}$
6	Signal + environmental factor F[4,5]	Signaller + Receiver IDs	Variance in intercepts: VI_{sSi}, VI_{rRi}, VI_{sRw}, VI_{rRw} Variance in slopes: VS_{sSi}, VS_{rRi}, VS_{sSw}, VS_{rRw}

[1]. Other types of designs and models can be implemented, where some individuals are only signallers and others only receivers, in which case the matrices of variance and covariance will be simpler than the ones provided by model #5.
[2]. V_{sSi} = among-individual variance in intensity of signal; V_{rRi} = among-individual variance in intensity of response to signals; V_{sRi} = among-individual variance in receiver's ability to trigger intense signals from others; V_{rSi} = among-individual variance in signaller's ability to trigger responses by others.
[3]. V_{sSw} = within-individual variance in intensity of signal; V_{rRw} = within-individual variance in intensity of response to signals; V_{sRw} = within-individual variance in receiver's ability to trigger intense signals from others; V_{rSw} = within-individual variance in signaller's ability to trigger responses by others.
[4]. F could for example be level of risk in animals, or the intensity of herbivory pressure in plants.
[5]. For simplicity we have chosen to represent only signalling and response to signal, but more complex models such as #4 or 5 can be run with the inclusion of an environmental effect either on signallers, or receivers, or both.

To measure individual variation in emission of alarm signals and in response to signals, repeated behavioural records should be obtained for different individuals. In plants, modularity could even permit the simultaneous measurement of the reactions

of different tissues as repeated measures, thus easily increasing the number of samples used to estimate intra-individual variation. Individual signalling behaviours (e.g., occurrence/duration of the alarm call, quantity of chemical volatiles emitted) could be measured during simulated attacks (e.g., predation risk simulated by throwing a hat over rodents, Hare 1998; Hare & Atkins 2001, herbivory risk simulated by clipping plants leaves, Karban et al. 2000). Individual response to signals could be measured by repeatedly recording the behavioural defence reaction of receivers (e.g., vigilance level, Hare & Atkins 2001; Couchoux et al. 2018, proportion of leaves damaged on the receiver branch at the end of the season, Karban et al. 2013) in response to alarm signals from varying signallers (e.g., playback experiment of alarm calls, Couchoux et al. 2018, transfer of volatile cues, Karban et al. 2010, 2013). Those measures could also be taken under variable risk conditions (e.g., at varying locations, by inducing more or less clipping damage), to measure potential individual differences in behavioural reaction norms (i.e., differences in individuals' plasticity, Dingemanse et al. 2010). With these data, it is then possible to run mixed models (Dingemanse & Dochtermann 2013) that provide different information on both the consistency of signalling and responses to the signals (see Fig. 1.2 for an illustration).

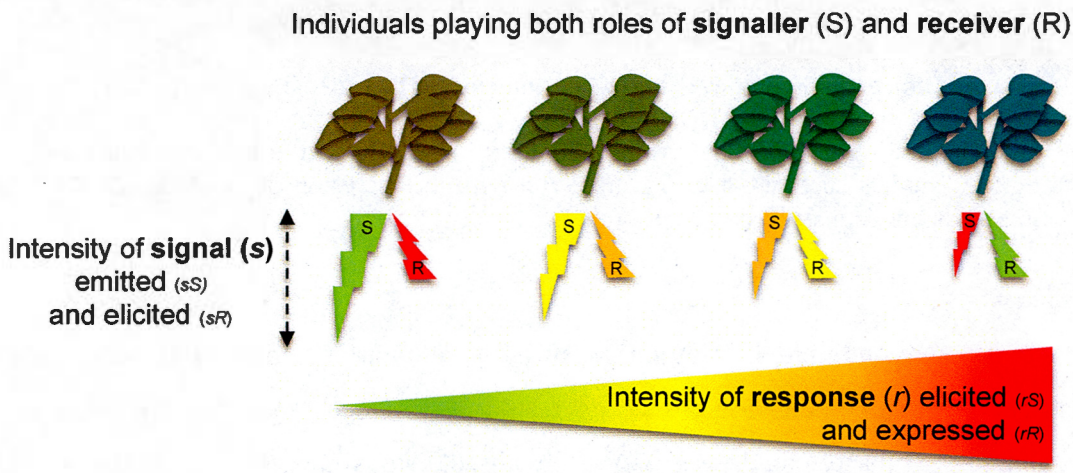

Figure 1.2 Experimental or observational designs to study sources of individual variation in emission and response to alarm signals. Four different plant individuals (which could alternatively be animals) are represented with four different colours and ordered from left to right according to their level of boldness, from the shyest/highly risk-sensitive individuals to the boldest/least risk-sensitive individuals. The downward and upward lightning symbols respectively represent the emission (*S*) and reception (*R*) of alarm signals by the individuals. The size of the lightning symbols represents the frequency/intensity of the signal (*s*) that an individual emits as signaller (*sS*) and elicits in others as receiver (*sR*). The colour of the lightning symbol represents the magnitude of the response (*r*) that an individual elicits in others as signaller (*rS*) and expresses to other's signals as receiver (*rR*), with an increase in magnitude from green to red. Note that the repeatability in individuals' behaviour is not represented here, but could be reflected in repeated lines of more or less similar signalling behaviours (representing different measurements made repeatedly on the different individuals). Here, individuals differ both in their emission (V_{sSi}) and in their response (V_{rRi}) to the signal: from the shyest (left) to the boldest (right) individuals, there is a decrease both in the magnitude (here the size) of the emitted signal (*S*, downward lightning symbol) and in the magnitude of response (here the colour intensity) to the signal received (*R*, upward lightning symbol). This also indicates a positive covariance between an individuals' intensity to signal and its intensity of reaction to signals ($Cov_{sSi,rRi}$). Individuals also vary in the intensity of response that they elicit as signallers (V_{rSi}): downward lightning symbols (*S*) increase in colour intensity from left to right, so that signals from bolder signallers elicit stronger responses. Moreover, this negatively covaries both with individuals' signal intensity ($Cov_{sSi,rSi}$) and intensity of response to a signal ($Cov_{rRi,rSi}$): there is an overall association among more intensely coloured and smaller downward lightning symbols (*S*) and less intensely coloured upward lightning symbols (*R*). There are, however, no individual differences in the intensity of the signal elicited in others by receivers (no V_{sRi}): all the upward lightning symbols (*R*) have the same size. It is thus possible to use mixed models to decompose phenotypic (co)variance in both signalling and response to signal (see text for more details).

In the simplest situations (Table 1.1, #1 and 2) we need several replicated measures of signalling (#1) or responses to signal (#2) for the focal individual. The ID of the signallers (#1) or receivers (#2) can then be included as a random effect in each model, and the variance can be decomposed in among-individual (*i*) variance V_{sSi} (#1, where *s* and *S* respectively stand for signalling and signaller) or $V_{rRi,}$ (#2, *r:* response to a signal, *R*: receiver), and the corresponding within-individual (*w*) variance V_{sSw} (#1) or V_{rRw} (#2). We can then calculate the trait's repeatability (Réale et al. 2007),

which can provide an upper bound to the trait's heritability (Boake 1989) and helps evaluate the individual parts of the variance on which selection can operate (see below Table 1.1, #6 for other more appropriate ways of studying this aspect). With repeatability estimates we can evaluate how consistently individuals behave over the study period, expecting that some individuals would systematically signal (#1) or respond to signal (#2) more intensely than others, independently of the receiver or the signaller (see Fig. 1.2). For generalisation of the results, the behaviours of the focal individuals can be measured with all the different receivers and signallers tested (Fuller & Hahn 1976; Couchoux et al. 2018).

When signalling is measured several times in each signaller and we know the identity of the different receivers for each signaller (Table 1.1, #3), it is possible to evaluate whether: 1) signallers differ consistently in their signalling (i.e., V_{sSi}, same as situation #1), and 2) receivers differ consistently in how they trigger the signals from others (i.e., V_{sRi}). In this case, experimental or observational designs that allow the signaller to signal for particular receivers permit one to test the hypothesis that the strength of a signal depends on the receiver's features. Although we would expect a null V_{sRi} (see Fig. 1.2) in alarm communication, where the signal is not directed toward a specific individual but rather towards a group of neighbours, it may exist in one-on-one communication systems such as in a mating or agonistic context (Maynard Smith & Parker 1976; Enquist & Leimar 1983). A positive V_{sRi} would indicate that preferential signalling could depend not only on receivers-signallers' relatedness (see above) but also on receivers' behavioural characteristics, which would be a new finding. This would more broadly allow one to test whether eavesdropping or active intra and interspecific communication are at play in animal and plant communication.

Similarly, when the response to signals is measured several times for each receiver and we know the identity of the signallers for each receiver (Table 1.1, #4), it is

possible to evaluate whether: 1) receivers differ consistently in how they respond to signals (i.e., V_{rRi}, same as situation #2) and 2) signallers differ consistently in how they trigger a response in others (i.e., V_{rSi}, see Fig. 1.2). We could thus test if, and for what reasons, individuals differ in how much their signals influence the response of other individuals. This would be of interest if receivers could respond differentially to signallers differing in their reliability, according to individual features such as their behavioural profile (e.g., Couchoux et al. 2018).

When both signalling and response to signals are recorded in each individual and when every individual is tested with several other signallers or receivers (Table 1.1, #5), it is possible to run a bivariate mixed model (Hadfield 2010; Dingemanse & Dochtermann 2013) to obtain two (co)variance matrices among and within individuals, for both signal and response. We thus obtain estimates of variance components similar to the ones obtained in models #1 to 4, but also different components of covariance. With $Cov_{sSi,rRi}$ we get information on the relationship between an individual's signalling intensity and the intensity of its reaction to signals (see Fig. 1.2). This would reflect a behavioural syndrome (Sih et al. 2004) for alarm communication behaviours, with individuals' risk sensitivity being reflected in both their overall signalling and response behaviours, and individual positions along this syndrome may be associated with the slow-fast life-history continuum (i.e. high signalling and high response to signals related to low risk-taking and a slow pace-of-life; see above). Then $Cov_{sSi,rSi}$ corresponds to the covariance between an individual's signalling intensity and its ability as a signaller to trigger a response from receivers (see Fig. 1.2). This information is crucial to test whether bold individuals that would signal only under high risk are more influential, as their signal would generate more valid information on the risk of predation (Couchoux et al. 2018). Similarly, $Cov_{rRi,rSi}$ represents the covariance between the intensity of an individual's reaction to signals and its ability as a signaller to trigger a response from

receivers (see Fig. 1.2). An individual's level of reaction to signals could also reflect its boldness (Couchoux et al. 2018), and be negatively linked to the level of reaction it triggers in receivers. $Cov_{sRi,rSi}$ is the covariance between an individual's ability to trigger the signals from others when receiver and its ability to trigger a response in others when signaller. This provides some information on how central certain individuals are, being influential both as receivers and as signallers. It would also be relevant to investigate these effects in species for which social networks are already known, and especially for studies that have highlighted the influence of personality on individuals' social roles among networks (Matessi et al. 2010; Aplin et al. 2013). As reactive individuals have been shown to form stronger and more stable associations with a greater number of individuals (Aplin et al. 2013), these types of individuals could be more influential in alarm signalling contexts. $Cov_{sSi,sRi}$ corresponds to the covariance between an individual's signalling intensity and its ability as a receiver to trigger signals produced by others. In relation to the previous covariance, the shyest individuals, those that would signal most often, would be more strongly associated with other individuals and therefore more influential. This relationship could then only reflect the differential roles of individuals in social networks depending on their behavioural profiles. Alternatively, this information could test for the hypothesis related to the reciprocity of communication; for example, signallers could refrain themselves from giving alarm signals when in presence of cheaters that are not reciprocating, preventing the cheaters from benefitting from their signalling without paying the cost of signalling themselves. This would imply advanced cognitive capacities and that signalling is intentional and not merely a consequence of physiological constraints as argued previously (i.e., individual differences in intrinsic sensitivities and risk perception). Overall, this relation may also provide information on whether communication is targeted towards some specific individuals or if signals are eavesdropped (Peake 2005). Finally, $Cov_{sRi,rRi}$ reflects the relationship between an individual's ability to trigger signals from others

and its propensity to respond to signals, which could be similar to the previous one: shy individuals would respond strongly to signals and would be highly influential in the alarm system. If alarm signalling and response to signal are indeed linked to individual differences in risk-taking and more broadly to differences in pace-of-life along the slow-fast life-history continuum (see above), we expect most of these covariance components to be positively correlated. In an alarm communication context, if VsR_i is null, we also expect $Cov_{sRi,rSi}$, $Cov_{sSi,sRi}$ and $Cov_{sRi,rRi}$ to be null. However it may not be the expectation for other communication systems such as mating, or agonistic interactions.

The within-individual covariance matrix indicates the same types of relationships, but the covariance components reflect combined plastic responses to both signaller and receivers to the same (unmeasured) changes in environmental effects. For example, a positive $Cov_{sSw,rRw}$ would indicate that when an individual, for some unknown reason, is producing more intense signals relative to the average level of signalling, this individual is also reacting strongly to signals from others during that particular time. Note that with this design, measurement errors may be part of the within-individual covariance estimated.

The individual approach can be extended to many other situations and questions. For example, by adding a fitness trait to model #5 we can obtain a direct estimate of selection happening on both signalling and response to the signal (while removing the potential noise occurring at the within-individual level). The incorporation of a relatedness or relationship matrix (from a pedigree or genomic polymorphism information) can also allow estimating direct, maternal or other indirect genetic effects of signals and responses to them (Wilson et al. 2010). Although the individual approach has been used for other types of social interactions in animals (Wilson et al. 2009; Wilson et al. 2011) and plants (Muir 2005; Mutic & Wolf 2007), we do not know of any study that has used it, either at the phenotypic or genetic level, to study

alarm communication in animals or plants, with the exception of our study on response to alarm calls in chipmunks (Couchoux et al. 2018). Furthermore, we could also test more specific hypotheses related to alarm communication by including different fixed effects. Including the coefficient of inbreeding, or individual heterozygosity, in the model could test the effect of inbreeding. Information on age, sex, kinship, microhabitat, or geographical distance between signallers and receivers, could test for hypotheses related to kin selection, or specific environmental effects, on the intensity of alarm communication. We could also directly test for the effects of personality traits such as boldness, expecting that more risk-sensitive individuals (investing more in defence) would signal more often or more intensely and would respond more to the signal. Finally, inclusion of life-history traits would permit us to test whether individual plants with a high growth and a short life may invest less in the production of costly HIPVs compared to individuals with a slower growth and a longer life.

When the different individual measures are recorded under environmental changes, a different model (Table 1.1, #6) allows us to estimate the variation in plastic signalling or response as a function of the environmental effect *F*, both at the among- (intercepts, *VI*) and within- (slopes, *VS*) individual levels (Table 1.1, #6). For example, it could be possible to experimentally test whether individual plants differ in the sensitivity of their alarm communication to temporal changes in parameters such as nitrogen, water, or herbivory pressures. In animals, individuals may differ in their plastic adjustment to varying levels of perceived risk. Further details on these designs applicable to both animals and plants can be found in Dingemanse and Dochtermann (2013).

1.6 Conclusion

Alarm signalling is a widespread mode of communication, being used as a defensive behaviour in both animals and plants when a risk of attack is perceived. We have

highlighted similarities in the behavioural defences of animals and plants, and demonstrated how the same evolutionary pressures, especially trade-offs, could lead to individual variation in both groups. In particular, the frameworks offered already by quantitative genetics and by animal personality could allow investigation of individual variation in plant behavioural traits and give insight into plant evolutionary ecology. Adopting an individual-based approach is also relevant to study defence behaviours that could be linked to life-histories strategies in both groups, and more broadly to behaviours that are expressed under social influence. We detailed how this perspective could be applied to alarm communication in both animals and plants, presenting hypotheses that could be tested using strong experimental designs and an existing analytical framework. This framework, however, is not restricted to alarm communication and could easily be extended to other systems of communications. Moreover, although we focused on plant defence behaviours in a context of risk from herbivory, the existence of individual variation in other plant behaviours could also be considered. Plant individual strategies in foraging and competitive contexts may vary and could relate to individual differences found in exploration, sociality and aggressiveness in animals, which are some components of their personality. This could provide general insights into plant evolutionary ecology and also help generalise the study of the causes and consequences of individual variation in organisms.

1.7 Acknowledgments

Funding was provided by a research team grant from the Fonds de Recherche du Québec - Nature et Technologies (FRQNT) to D.R. (and Dany Garant, Murray Humphries and Fanie Pelletier), by a Discovery grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) (D.R.) and by a Canada Research Chair (D.R.). C.C. was supported by a scholarship from the FRQNT and through grants from the UQAM, and by a National Geographic Young Explorers grant and a

Student Research grant from the Animal Behavior Society. We thank Anne Charmantier, Jeanne Clermont and Claire Doutrelant for valuable comments on the initial proposal or some parts of the manuscript. We thank the doctoral program at the UQAM for allowing PhD students to broaden their knowledge and horizons with the course "examen de synthèse", that led C.C. to discover and be immersed in the fascinated literature on plant behaviour and communication. This course, implemented by William Vickery and Jean-François Giroux, was the starting point of this *Ideas and Perspectives* paper.

CHAPITRE II

ENVIRONMENTAL EFFECTS AND INDIVIDUAL CONSISTENCY SHAPE AGONISTIC INTERACTIONS IN WILD CHIPMUNKS

Charline Couchoux, Dany Garant, Maxime Aubert & Denis Réale

Manuscrit en révisions dans *Behavioral Ecology*.

Dans ce chapitre, nous étudions les comportements agressifs exprimés par les animaux lorsqu'ils se retrouvent en compétition pour l'accès à des ressources limitées. L'issue des interactions agressives est largement prédite par la théorie des conflits, qui suppose que les compétiteurs adoptent des stratégies agressives plastiques qui dépendent du contexte social et ainsi de leurs potentiels de détention des ressources (RHP). Les individus pourraient toutefois aussi différer de manière constante dans leurs stratégies agressives, comme l'agressivité est une composante importante de la personnalité d'un individu. Il apparait alors nécessaire d'intégrer les approches s'intéressant à la plasticité et à la constance des comportements agressifs au sein d'un même cadre analytique, tout en considérant l'existence potentielle de différences individuelles de plasticité en réponse aux changements environnementaux. Nous avons testé ces hypothèses chez un petit Sciuridé territorial, le tamia rayé (*Tamias striatus*), en observant les interactions agonistiques naturelles survenant entre différents individus à des emplacements supplémentés en nourriture situés à différents distances de leurs terriers. Les analyses suggèrent que l'issue d'un conflit est partiellement expliquée par des différences en RHP. Les individus les plus gros et les plus âgés, ainsi que les propriétaires des territoires, avaient ainsi une plus grande probabilité de gagner les conflits. La probabilité de victoire était aussi dépendante de l'identité des deux compétiteurs, ce qui suggère des différences individuelles constantes d'agressivité. Les individus variaient également dans leurs tendances à répondre à une variation de l'environnement. L'utilisation d'une approche intégrative permet ainsi de mettre en avant les effets conjugués du contexte et de la variation individuelle sur les interactions (agressives) sociales.

Mots-clés : Comportement agonistique, Propension à la victoire, Personnalité, Différences individuelles constantes, Plasticité comportementale, Système naturel.

2.1 Abstract

Animals often aggressively interact when they compete over limited resources, and the outcome of a contest is largely predicted by contest theory. Competitors are thus assumed to adopt aggressive strategies dependent on the social context, with plastic responses based on their resource holding potential (RHP). Individuals may, however, also show consistent differences in aggressive strategies, as aggressiveness is an important component of an individual's personality. It is thus necessary to integrate both concepts to assess plasticity and consistency of aggressive behavior using a single analytical framework, and also to consider potential variation in individuals' plasticity in response to environmental changes. We tested these hypotheses in a small territorial mammal, the Eastern chipmunk (*Tamias striatus*), by observing natural agonistic interactions occurring among individuals competing for food resources supplied at different distances from their burrows. Our analyses suggest that the outcome of a contest can partially be explained by differences in RHP. Larger and older individuals, as well as territory owners, had a higher probability of winning contests. Variation in the probability of winning was also dependent on the identity of the two competitors, suggesting that individuals consistently differed in their aggressiveness. Furthermore, we found that individuals also varied in their responsiveness to environmental variation. Using an integrative approach thus highlights the roles of both context-specific and individual variation in shaping social agonistic interactions.

Keywords: Aggressive behavior, Probability of winning, Personality, Consistent individual differences, Behavioral plasticity, Natural system.

2.2 Introduction

Social interactions constitute strong evolutionary forces on animals that interact cooperatively or aggressively with conspecifics (Krause & Ruxton 2002). Social conflicts appear when individuals compete over limited resources such as mates, food, or territories (Wilson et al. 2009, 2011a; Bergmüller & Taborsky 2010), and often result in the expression of aggressive behaviors (Hardy & Briffa 2013). The outcome of direct aggression, or agonistic contests, has important implications for fitness-related traits (Lindström et al. 1990; Renison et al. 2002), and it is thus essential to identify the factors driving the probability of winning these contests.

Contest theory predicts that the expression of aggressive behaviour should be contingent on the competitors' fighting ability (Maynard Smith & Price 1973; Smith 1974; Enquist & Leimar 1983), as individuals have different resource holding potential (RHP, Parker 1974). The decision to be aggressive or not is highly plastic and depends on self-assessment and assessment of the opponent (i.e., indirect effects, Wilson et al. 2009; Santostefano et al. 2016). Determinants of individual RHP involve intrinsic factors, including physical characteristics (e.g., weaponry or body size), but also age and sex (Maynard Smith & Parker 1976; Arnott & Elwood 2009). In many species, larger or heavier contestants have a higher chance of winning contests (Arnott & Elwood 2009), as do older individuals (Murie & Harris 1978; Kemp 2000; Wilson et al. 2011b), and males (Wilson 1992). Extrinsic factors concerning the spatial and temporal occurrence of contests are also important in determining RHP of individuals (Dugatkin & Dugatkin 2007). For example, animals fighting in their own territory generally win contests (Davies 1978). The prior-residency/occupancy effect also suggests that an individual has an advantage over

defending resources and winning ensuing fight, when it is the first to discover them (Snell-Rood & Cristol 2005).

Despite the ability of individuals to express context-specific aggression levels, empirical evidence has recently revealed that individuals from the same population consistently vary in their aggressiveness, among other aspects of their personality (Réale et al. 2007; Dzieweczynski & Leopard 2010; Burtka & Grindstaff 2013; Blumstein et al. 2013). Moreover, recent theoretical models suggest that a continuum of fixed strategies, including fighting strategies (Wolf & Weissing 2010), can be maintained through negative frequency-dependent selection and explain the evolution of animal personality (Dall et al. 2004; Wolf et al. 2007, 2008). Social interactions have also been suggested to play a crucial role in generating individual behavioral variation (Réale & Dingemanse 2010; Bergmüller & Taborsky 2010; Montiglio et al. 2013; von Merten et al. 2017). Agonistic interactions should therefore be studied by integrating the individual-based approach into a contest theory framework, as they could both predict the outcome of aggressive contests (Wilson et al. 2011a; Briffa et al. 2015).

Plasticity and consistency of aggressive behavior are not mutually exclusive (Dingemanse et al. 2010) and individuals can vary not only in their average behavioral state (i.e., personality differences, at the among-individual scale) but also in their tendency to show behavioral variation (i.e., differences in behavioral plasticity, at the within-individual scale; Réale & Dingemanse 2010; Briffa et al. 2015). In a social context, social responsiveness or social competence (Taborsky & Oliveira 2012; Wolf & McNamara 2013) can then be assessed by modelling individuals' propensity to adjust their aggressive behavior according to a change in their physical or social environment (e.g., location or opponent phenotype, Briffa et al. 2015; Dingemanse & Araya-Ajoy 2015). Although animals have to deal frequently with these potentially important sources of variation in the wild, they are often

minimized in experimental studies (Briffa et al. 2015). Staged encounters might not only prevent physical environmental variation and reduce the potential diversity of features in the opponent, but they might also represent situations that do not exist in nature. Studies conducted in the wild are thus also required (Briffa et al. 2015), with repeated measures of individual behaviors across a relevant range of environmental contexts (e.g., with at least 40 individuals and 1,000 observations, van de Pol 2012).

In this study, we performed multiple observations of naturally occurring agonistic interactions in a free-ranging population of individually-marked eastern chipmunks (*Tamias striatus*). We were thus able to measure behavioral variation in aggression at different levels, to assess: 1) if fighting outcome depended on the resource holding potential of the contestants, as predicted by contest theory; 2) if individuals consistently differed in their probability of winning across a range of physical and social environmental contexts, as would be expected if they showed different aggressive personalities; and finally 3) if and how individuals differed in their aggressive response to environmental changes, assessed by the plasticity of their aggressive behaviour. Addressing these questions in chipmunks is particularly relevant, as these small diurnal ground-dwelling Sciurids are central-place foragers that actively compete for patchy resources. Individuals aggressively defend their territory around their burrow through agonistic interactions with neighboring conspecifics (Aniskowicz & Vaillancourt 1979; Getty 1981). Interestingly, in this territorial species and others, it has often been claimed that proximity to the territory is the key factor to predict the victor of a contest (Dunford 1970; Elliott 1978; Dobson 1982; Harper & Batzli 1997, but see Kemp & Wilkund 2004). We however expected to find personality effects on chipmunks' aggression, as individuals of this species show consistent variation for other behavioral traits (e.g., exploration, docility, Montiglio et al. 2012; St-Hilaire et al. 2017). Our study thus offers the opportunity to disentangle how the outcome of agonistic contests can be predicted by both theory-

related context-specific effects and by differences in personality in a territorial species.

2.3 Material and Methods

2.3.1 Study system

Eastern chipmunks are found mostly in mixed-deciduous forests of Eastern North American (Elliott 1978). As part of a long-term project (started in 2005) investigating the evolutionary ecology of this species in Southern Québec, Canada (45°06.785'N; 72°26.078'W), we routinely trapped free-ranging individuals on two study sites (separated by approximately 1 km, consisting of 260 x 260 m and 340 x 260 m flagged grids). During capture, we recorded each individual's body mass, sex and age (i.e., adult or juvenile). We also marked individuals with metal ear tags (National Band and Tag Corp.), on which we attached colored vinyl flagging pieces for individual recognition from a distance. We located individual burrows either using visual observation or radio telemetry. Each burrow location was assigned to an individual after observing it at least twice at the same location within a week, and its coordinates were recorded to the nearest meter within our sampling grids.

2.3.2 Field observations of agonistic interactions

We recorded agonistic interactions that occurred among individual chipmunks through observations performed over 3 field seasons, in September 2012 (over 6 days), from June through September 2013 (16 days) and from June through August 2014 (39 days). To facilitate observations of these very active rodents, we attracted them to temporary feeding patches consisting of a handful of sunflower seeds mixed with leaves on the ground and located approximately 10 m away from each individual's burrow. Behaviors were recorded by observers placed 10 m away in the

direction opposite the burrow, and by cameras opportunistically set at the feeding patches (attached to the nearest tree).

For each dyadic interaction we noted: the precise location of the feeding patch (to the nearest meter, using grid coordinates), the identity of the individual who was first observed foraging at the feeding patch and the identity of the individual who arrived second, the role of each individual as attacker or defender (depending on who initiated the attack, i.e., who first jumped on the other), and the identity of the individual who ended up at the feeding patch and ate at least one seed, who was scored as the winner of the contest. The contests were classified in different categories of increasing intensity from: 1) avoidance (the individual at the patch either retreated or was avoided by the new comer); 2) tolerance (the two individuals both foraged at the feeding patch without showing any agonistic display); 3) chase (one individual briefly chased the other on a distance shorter than 2 m from the feeding patch, followed by a quick return of one of the competitors); 4) pursuit (one of the individual pursued the other for a long time and at distances longer than 2 m away from the feeding patch); and 5) struggle (both competitors engaged in an intense physical attack and rolled on the ground). We considered that an individual won the contest when it was either avoided by the other individual or when it returned first at the feeding patch after a chase, a pursuit or a struggle. Tolerant interactions were not considered further in the analyses, as none of the individuals could be identified as the winner of the contest.

We collected in total 2,713 dyadic interactions on the two study sites (n = 1,689 and n = 1,024, respectively), mostly at the feedings patches (n = 2,664; with 49 interactions being observed on other sporadic occasions) and mainly in 2014 (n = 2,443; 2012: n = 97; 2013: n = 173). Overall, 1,606 interactions were recorded from visual observations and 1,107 from videos.

2.3.3 Statistical analyses

2.3.3.1 Data preparation and transformation of variables

We removed from our analyses interactions featuring an individual that could not be identified with certainty (i.e., absence of colored flags) or for which the burrow location was unknown (or, for one observation, way outside of the grid), but we kept individuals with only one observation (as in Wilson et al. 2011b) to increase statistical power (Martin et al. 2011). We calculated the Euclidian distance between the feeding patch and the two competitors' burrows. As individuals can change burrows between years and during the active season, for each observation we assigned to each individual the burrow most recently occupied. Similarly, for each observation, individuals were assigned an age class (adult or juvenile) and a mean mass value measured during the season of interest. As each observation consists of a dyad of individuals, and to avoid pseudoreplication in analyses, for each dyadic interaction we randomly assigned one individual as being the focal, and the other as being the opponent (Wilson et al. 2011b). This allowed modeling the variation in propability of winning of the focal individual, according to characteristics of both individuals.

We analyzed 2,297 interactions for 68 different individuals assigned as focals, from whom we recorded 33.78 ± 34.36 (mean ± SD; range: 1-158) interactions, with 5.06 ± 3.68 (mean ± SD; range: 1-15) different opponents, at 3.84 ± 3.55 (mean ± SD, range: 1-17) different locations. Among those 68 focal individuals, 33 were males and 35 were females, and 50 were adults and 18 were juveniles (the individuals were observed only at one age-class, as the only three individuals that were re-observed in 2014 were already adults in 2013). The sample included 70 different individuals considered either as focal or opponent: 65 individuals were represented in both roles, while three individuals were included only as focal, and two only as opponent.

We were thus able to measure many individuals across an ecologically relevant range of environmental contexts. However, sampling from non-experimental field studies can preclude observations of individuals over the whole range of environmental contexts, as individuals are often naturally non-randomly distributed over environmental gradients (van de Pol & Wright 2009; Dingemanse et al. 2010). This natural heterogeneity needs to be taken into account to reliably estimate plasticity, especially within an individual reaction norm framework (Schielzeth & Forstmeier 2009; Dingemanse et al. 2010). The within-individual centering approach suggested by van de Pol and Wright (2009) allows separating sources of among- and within-individual variance, as among-individual variance could simply reflect differences in the environment experienced by individuals. Preliminary data exploration suggested that this method was indeed required for our study, as we detected individual differences in the distances at which individuals were observed interacting from their burrow (Annex B: Fig. B1, Table B1). Distances to the focal and to the opponent burrow were thus each separated into two new variables: we first calculated for each individual the mean value of the distances at which it was observed from its burrow during contests (thereafter referred to as the mean distance to the burrow) and then calculated the deviation of each observation from the mean individual distance (thereafter referred to as the deviation distance to the burrow). We were thus able to separate the effect of mean distance to each competitor's burrow on the focal probability of victory at the among-individual level, and individuals' plastic probability of victory in response to a change in their own environmental gradient of distances, at the within-individual level.

In order to control for scaling problems and to ensure the convergence of the models, individual mass was standardized. The original value (x_i) was thus subtracted by the mean of the variable ($\bar{x}_i$) and divided by its standard deviation (σ_x), so that $Z_x = \frac{x_i - \bar{x}_i}{\sigma_x}$ (Schielzeth 2010).

2.3.3.2 Testing the effects of RHP on the probability of winning

To model the probability of the focal individual winning (with contest outcome being either 0 = lost or 1 = won), according to the focal and the opponent's RHP and to individual effects, we used generalized linear mixed effect models, with a binomial error distribution, implemented in the package ''lme4'' (Bates et al. 2015) in R. 3.1.3. (R Development Core Team 2013). Model selection consisted in sequentially dropping each non-significant effect (at $\alpha = 0.05$) to reach a reduced final model. This selection procedure was also validated by reduced AICs of the models successively selected.

To test whether fighting ability (or RHP) of the contestants predicted the outcome of a contest, we included the following fixed effects, for both the focal individual and the opponent: Z-score for mass, mean distance to the burrow and deviation distance to the burrow, as well as age and sex (references levels in models were respectively set for juveniles and females). We also included the order of arrival of the focal individual at the feeding patch (reference set for 1st arrival).

2.3.3.3 Estimating individual variation in the probability of winning

To estimate if an individual's probability of winning reflects its aggressiveness during a contest, we preliminary tested for the independence of a focal individual's probability of victory and its propensity to initiate the fight. A chi-square test was performed on a reduced data set containing information on the focal individual's probability of winning and its role as attacker or defender (n = 1,833 observations with 68 individuals).

To test whether individuals intrinsically differed in their probability of winning a contest we included the identity of both the focal (ID_F) and the opponent (ID_O) as random effects. This allowed us to partition the overall phenotypic variance (V_P) into

among-focal-individual (V_F) and among-opponent-individual (V_O) variance, and within-individual (i.e., residual) variance (V_R). We thus estimated for the final model both the repeatability in the likelihood of the focal ID to defeat its adversary (proportion of V_P due to V_F), and of the opponent ID to lose a contest to the focal (proportion of V_P due to V_O). As the roles of focal individuals and opponents were randomly assigned to each individual in the dyad, we expect that their effects will be mirrored and therefore highly correlated (Wilson et al. 2011b), and that repeatability estimates will be similar. To calculate repeatability estimates and their significance, we used the method of Nakagawa and Schielzeth (2010) for non-Gaussian data. The expected existence of a mirror effect in these random effects was graphically represented using individual best linear unbiased predictors (BLUPs, Pinheiro & Bates 2000) of intercepts, and further confirmed through a correlation test (all correlation tests implemented were Pearson's, or Spearman's correlations when variables were not normally distributed).

The repeatability of an individual's probability of winning was illustrated by correlating the percentage of victory of a focal individual when it arrived 1st and 2nd at the feeding patch (and the significance of the correlation was also tested). The percentages were calculated based on a reduced dataset considering only individuals with at least 10 observations (n = 2,249 observations with 53 individuals), in order to obtain more reliable estimates of individual probability of winning.

2.3.3.4 Testing for individual differences in plasticity

We implemented a reaction norm approach to test whether focal individuals differed in their plasticity of the probability of winning a contest (Nussey et al. 2007; Dingemanse et al. 2010; Dingemanse & Araya-Ajoy 2015). This statistical method, also reduces type I errors and provides appropriate estimates of variance (Schielzeth & Forstmeier 2009; Martin et al. 2011). Consequently, when models included

significant individual random slopes, we recalculated repeatability estimates (Martin et al. 2011), keeping the structure that allows covariance between intercepts and slopes (see below).

In separate final models, we included individual random slopes for fixed effects previously found to be significant, to test whether focal individuals varied in their plasticity to win across a gradient of physical and social environmental characteristics: deviation from the mean distance of the focal to its burrow, deviation from the mean distance of the opponent to its burrow, and opponent mass and age variation. To further investigate the effect of social environment, we also tested the responsiveness of the focal individual to the aggressiveness of its opponent. Aggressiveness of the opponent was measured as the percentage of victory of each individual considered as a focal. Aggressiveness was thus measured from different dyadic interactions than the ones analyzed in the model. As the calculation of proportions is highly dependent on sample sizes, we ran this analysis based on a reduced dataset, by selecting only contests in which both individuals were observed at least 10 times as focal individuals (retaining 2 194 observations involving 53 different individuals playing both roles of focal and opponent). This new variable was included as a fixed effect, and other fixed effects were adjusted to the new dataset (we recalculated Z-scores for mass, but also the mean and deviation of distance to the burrows of the competitors).

Random slopes were included for both the focal individual and the opponent (except for the opponent's aggressiveness), because the individual mirror effect that is expected for intercepts (i.e., elevation) should also be reflected in slopes. For instance, individuals who always win independently of the characteristics of the physical or social environment should always elicit defeat in the focal individuals when they are opponents. We tested the significance of the random slope terms by comparing models with and without them, while keeping the same structure of fixed effects.

2.3.3.5 Linking individual aggressiveness and plasticity

Using different model covariance structures, we then investigated if an individual's level of aggressiveness was linked to its plasticity in aggressiveness. For each model evaluating the effect of random slopes, we tested the significance of a structure allowing the covariance between the individual intercepts and slopes. We also included mirror effects, with random slopes for both focal and opponent, and interpreted the correlation estimate when the covariance structure was selected. To further confirm and represent the existence of such a covariance effect, we extracted and correlated both individual predictors (BLUPs) of intercepts and slopes at the individual level (BLUPs of slopes measure individual plasticity in response to an environmental gradient, Nussey et al. 2007). We did not further relate individual measures of plasticity among them or to individual characteristics, as using BLUPs for subsequent analyses should be avoided, as they do not carry individual errors and can lead to erroneous interpretations (Houslay & Wilson 2017).

2.3.4 Ethics statement

All captures and manipulations were carried out in accordance with the guidelines of the Canadian Council on Animal Care and protocols were approved through the Université du Québec à Montréal (CIPA permit #760) and the Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques du Québec (SEG permits #2014-04-22-103-05-S-F).

2.4 Results

2.4.1 Victory partially explained by RHP

Probability of winning a contest increased significantly with the mass of the focal individual (Table 2.1, Fig. 2.1a). Mass of the opponent also had a significant negative effect on the focal's probability of winning (Table 2.1, Fig. 2.1b). Adults had a higher

probability of winning than juveniles and individuals had more chance to win when they encountered a juvenile (Table 2.1). The sex of the competitors, however, had no effect on the probability of winning a contest (Table 2.1).

Table 2.1 Results from generalized linear mixed-effect model (binomial error distribution) on probability of winning an agonistic contest in eastern chipmunks (n = 2,297 observations, with 68 focal individuals and 67 individual opponents).

Fixed effects[a]	Estimate	SE	z value	P	Random effects	Variance
Intercept	0.20	0.82	0.24	0.81	ID Focal	1.80
Mass Focal	1.40	0.36	3.95	< 0.001	ID Opponent	2.36
Mass Opponent	-1.14	0.37	3.09	0.002	Residual	$\pi^2/3$
Age Focal	1.62	0.75	2.15	0.031		
Age Opponent	-1.70	0.80	2.12	0.034		
Mean distance burrow Focal	-0.038	0.006	5.98	< 0.001		
Mean distance burrow Opponent	0.032	0.006	5.08	< 0.001		
Deviation distance burrow Focal	-0.037	0.004	9.35	< 0.001		
Deviation distance burrow Opponent	0.036	0.004	9.39	< 0.001		

[a]Removed after model selection: Sex Focal (z = 0.19, P = 0.85), Sex Opponent (z = 0.23, P = 0.66) and Arrival order Focal (z = 0.08, P = 0.56). AIC decreased from the starting model to the final model as follows: 1663.8 (starting model), 1661.9 (without Sex Focal), 1660.1 (without Sex Opponent) and 1658.4 (final model without Arrival order Focal). Mass of both competitors were Z-transformed. Juvenile and female were respectively considered as references for age and sex. SE = standard error.

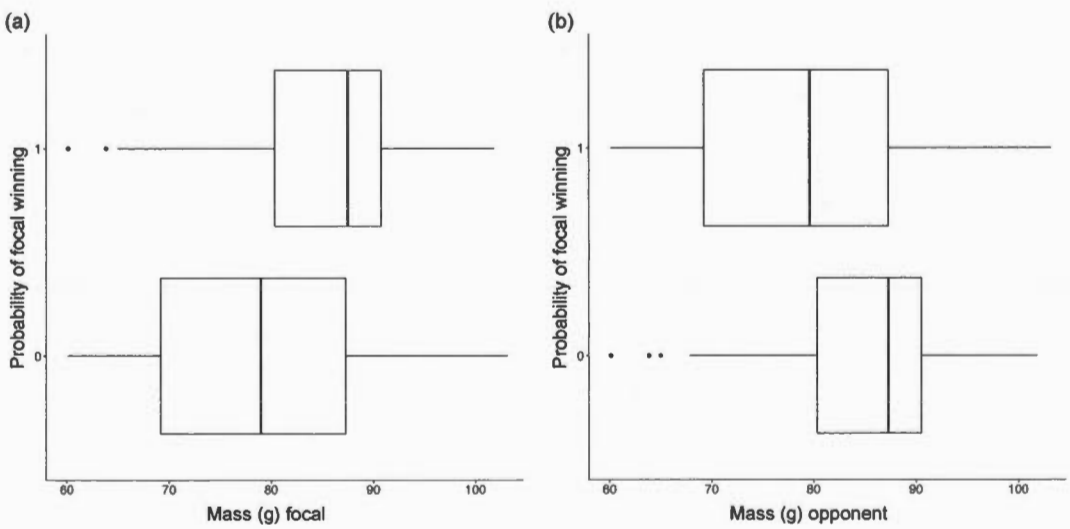

Figure 2.1 Boxplots based on raw data showing the outcome of the aggressive contests (Lose = 0 or Win = 1, n = 2,297 observations) for the focal individual depending on (a) its mass and (b) the mass of its opponent. Boxplots show medians,

first and third quartiles (middle, upper and lower border respectively). Whiskers represent the variability outside the upper and lower quartiles and points represent outliers. For convenience of interpretation we reversed the axes orientation of the boxplots, so that the dependent variable is represented on the y-axis.

We found significant negative relationships between the probability of winning and the distance to an individuals' burrow, both at the among- and at the within-individual levels (Table 2.1, Fig. 2.2). At the among-individual level, this indicates that individuals that were involved in interactions closer to their burrow (low values of mean distance to the focal burrow) had more chance to win than individuals that were involved in interactions further away from their burrow (Fig. 2.2a). At the intraindividual level, this implies that focal individuals showed plasticity in their probability of winning according to the distance to their burrow (deviation distance to their burrow), with individuals winning more when they were involved in contests closer to their burrow (Fig. 2.2c). We also found a significant opposite effect of the distance to the burrow of the opponent (Table 2.1). Focal individuals had more chance to win when they encountered an opponent that was at a greater distance from its burrow (high values of mean distance to the burrow of the opponent, Fig. 2.2b). The distance to the opponent burrow also affected victory at the within-individual level: an opponent relatively far from its burrow was subject to more wins by the focal individual (high values of deviation distance to the opponent burrow, Fig. 2.2d). There was no significant effect of the order of arrival at the feeding patch on the probability of winning the contest (Table 2.1).

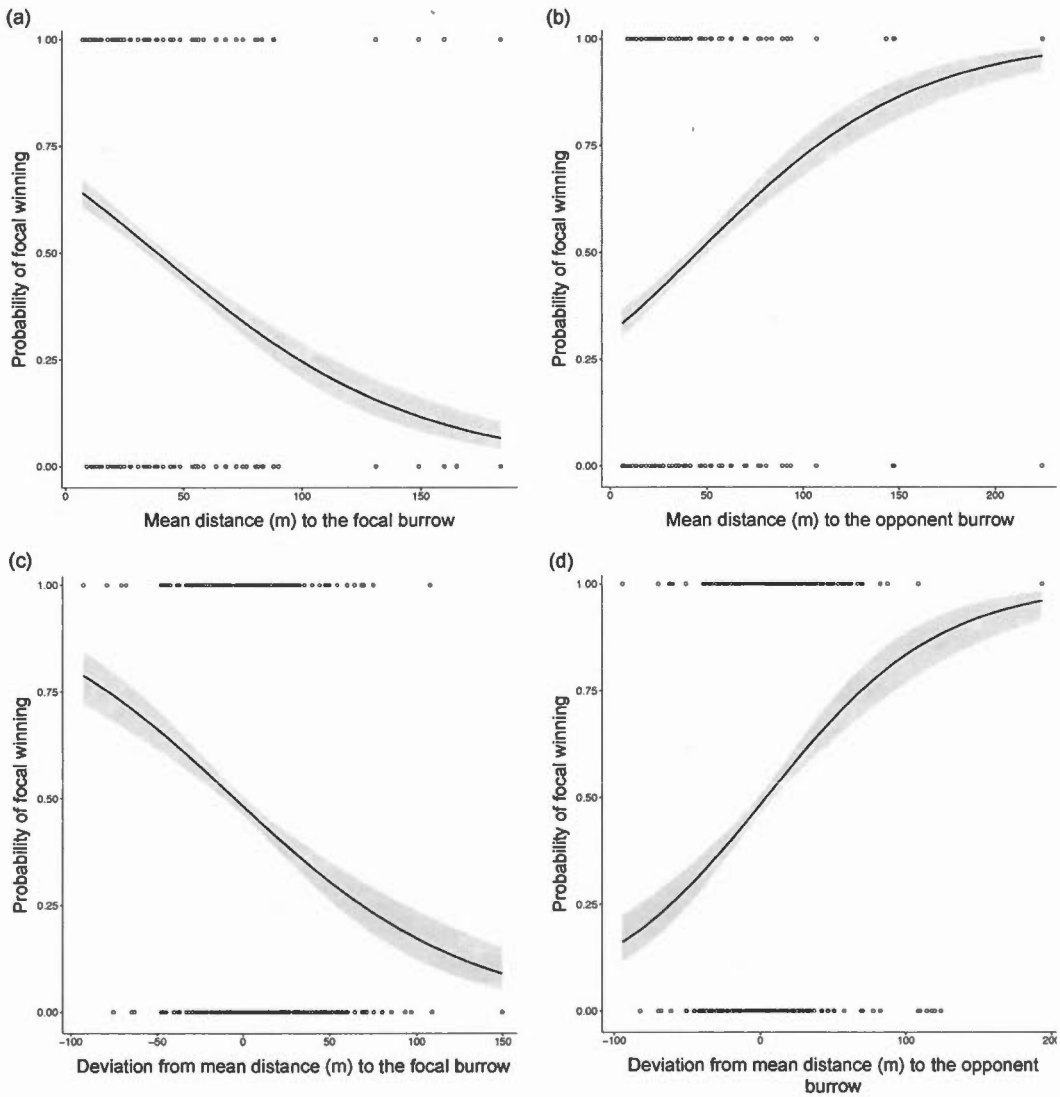

Figure 2.2 Logistic graphs showing the predicted probability of victory for the focal individual (n = 2,297 observations) depending on the mean distance at which (a) the focal and (b) the opponent interacted from their burrow, and on the deviation from the mean distance from (c) the focal and (d) the opponent burrow. Dots represent the data points and the curved solid lines represent the fitted logistic regressions from simplified models including only the effect of interest. The light grey area represents the standard error associated with each fitted regression.

2.4.2 Victory explained by consistency in individual aggressive behaviours

We first found that an individual's probability of winning a contest was highly dependent on its capacity to initiate the attack ($\chi^2_1 = 1461.60$, df = 1, $P < 0.001$). Then, once body mass and age differences were taken into account, the variation in the probability of winning was still explained by the identity of the focal individual (Table 2.1, $R = 0.24$, LRT: $\chi^2_1 = 93.11$, $P < 0.001$), and by the opponent identity ($R = 0.31$, LRT: $\chi^2_1 = 115.97$, $P < 0.001$). We further confirmed this expected mirror effect with the strong negative correlation between an individual's predicted probability of winning when it is focal ($BLUP_{Focal}$) and its tendency to elicit victory in the focal when it is opponent ($BLUP_{Opponent}$, Pearson correlation: $r = -0.83 \pm 95\%$ CI [-0.89: -0.74], t = 11.91, $P < 0.001$, Annex B: Fig. B2). The lack of effect of arrival order and the repeatability of a focal individual's probability of winning is illustrated by a strong significant correlation between the percentages of victory of a focal individual when it arrives 1st and 2nd at the feeding patch (Spearman correlation: $\rho = 0.77$, S = 5762.50, $P < 0.001$, Fig. 2.3).

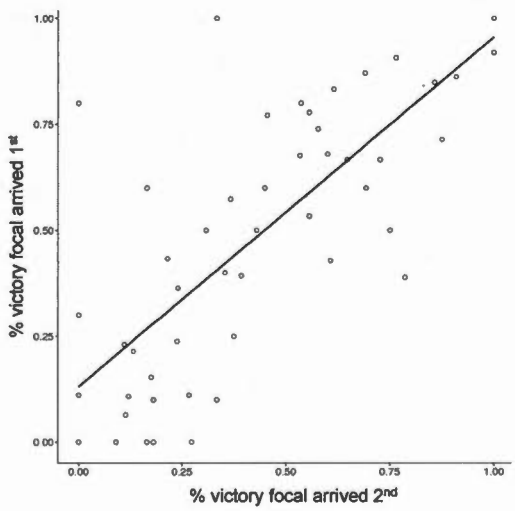

Figure 2.3 Correlation based on raw data showing the consistency in an individuals'

probability of winning a contest when it arrives 1st and 2nd at the feeding patch (n = 2,249 observations with 53 individuals). Open circles represent the data points and the solid line represents the fitted regression estimated from a linear model (used only for representation as the non-normality of the data required to use a non-parametric test).

2.4.3 Victory modulated by individual variation in plasticity

Individuals varied significantly in their plasticity of winning in response to a change in environmental factors tested (Table 2.2). All the mirror effects tested were significant (see details below) and therefore retained in the final random structures of the different models (Table 2.2). Covariance between individuals' intercepts and slopes was significantly different from 0 and retained only for aggressiveness of the opponent (Table 2.2, see details below and Annex B: Table B2).

Table 2.2 Results from the reaction norm approach testing the existence of individual variation in slopes for the probability of winning according to different environmental factors.

Random structure retained	**Focal slopes**			**Opponent slopes**		
	χ^2	P	R	χ^2	P	R
$(1 \mid ID_F) + (0 + DistB_F \mid ID_F) + \mathit{(1 \mid ID_O) + (0 + DistB_O \mid ID_O)}$	27.72	< 0.001	0.26	25.63	< 0.001	0.31
$(1 \mid ID_F) + (0 + DistB_O \mid ID_F) + \mathit{(1 \mid ID_O) + (0 + DistB_F \mid ID_O)}$	30.94	< 0.001	0.24	52.71	< 0.001	0.27
$(1 \mid ID_F) + (0 + Mass_O \mid ID_F) + \mathit{(1 \mid ID_O) + (0 + Mass_F \mid ID_O)}$	20.14	< 0.001	0.22	20.02	< 0.001	0.29
$(1 \mid ID_F) + (0 + Age_O \mid ID_F) + \mathit{(1 \mid ID_O) + (0 + Age_F \mid ID_O)}$	12.23	0.002	0.26	17.95	< 0.001	0.33
$(Aggr_O \mid ID_F) + \mathit{(1 \mid ID_O)}$	18.23	< 0.001	0.52		NA	0.15

ID_F: identity Focal; ID_O: identity Opponent; $DistB_F$: Deviation from the mean distance to the focal burrow; $DistB_O$: Deviation from the mean distance to the opponent burrow; $Mass_O$: Mass of the opponent; Age_O: Age class of the opponent; $Aggr_O$: Aggressiveness of the opponent; see the text for details on the transformations of the different variables. Mirror effects are indicated in italics, and the results that allowed retaining the best covariance structures can be found in Table B2.

The LRT (Likelihood Ratio Test values) indicate the significance of the individual random slopes, through a comparison of a model containing the individual random effect (with a covariance structure) and the final binomial mixed model (presented in Table 2.1, that did not include any random slopes).

Repeatabilities (R) for ID_F and ID_O were recalculated using the same references but with the inclusion of the different significant random slopes with a covariance structure (even if non-significant, as it ensured the stability of the models).

We found significant individual differences in slopes for the focal probability of winning according to the deviation distance to its burrow and to that of its competitor

(Table 2.2, Fig. 2.4). Both of these effects were also reflected in significant random slopes for the opponent (Table 2.2). Individual slopes in the probability of victory also differed significantly as a function of mass, age, and aggressiveness of the opponent (Table 2.2, Annex B: Fig. B3). The mirror effect also still existed with significant random slopes for mass and age of the opponent (Table 2.2). Probability of victory was thus independent of the opponent features for some individuals, while it was highly sensitive to these features for others (Fig. B3).

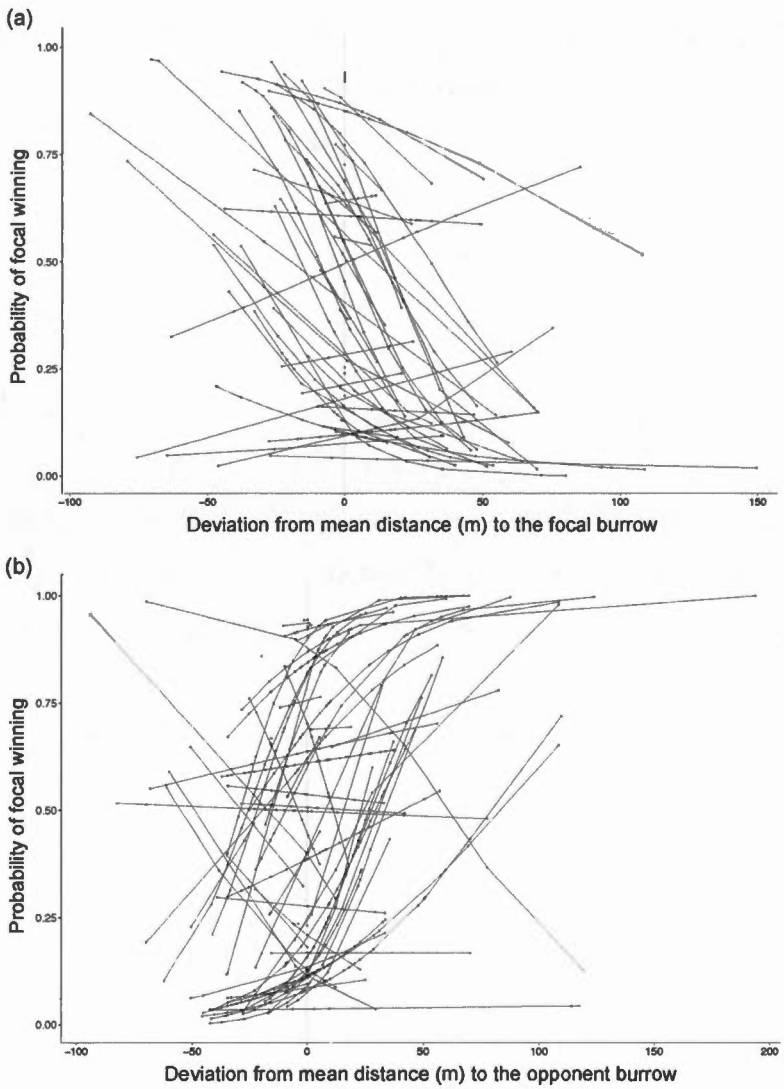

Figure 2.4 Representation of predicted individual random slopes for the probability of victory of the focal depending on the deviation from the mean distance to (a) its burrow and (b) to the opponent's burrow (n = 2,297 observations). Slope predictions were extracted from simplified mixed models including only the effect of interest as a fixed effect and as random slope for the focal. Dots represent the different deviation distances at which focals were observed interacting. The slight vertical grey dotted line indicates the mean individual distance to the focal (a) or the opponent's (b) burrow.

Including a covariance between individual (both focal and opponent) intercepts and slopes did not improve the models significantly, except for the model that included random slopes for the opponent's aggressiveness (see Annex B: Table B2).). In this latter model, individual intercepts and slopes were negatively correlated (Table B2): less plastic individuals in response to the aggressiveness of the opponent had a low probability of winning at the intercept (see Annex B: Fig. B4).).

2.5 Discussion

Using the analytical framework suggested by Wilson et al. (2011a), we empirically showed that the outcome of dyadic agonistic interactions among eastern chipmunks is dependent both on plastic assessment strategies, as predicted by contest theory, and on individual variation, as suggested by personality studies. Moreover, we showed that individuals varied in their plastic response to environmental changes. We thus showed that observed variation in contest outcome arises from among- and within-individual sources of variance, which emphasizes that plasticity and consistency in aggressive behavior are not necessarily antagonistic and need to be investigated and integrated within a same framework.

We found that the outcome of agonistic interactions in chipmunks is partly dependent on assessment of RHP, as predicted by contest theory (Arnott & Elwood 2009). We showed that the absolute body mass of the contestants represented their physical

fighting ability, as chipmunks had a greater chance to win when they were relatively heavier and when they encountered opponents that were relatively lighter (Wilson et al. 2011a). Body size can represent an advantage in terms of physical strength to ensure access to and defend resources, such as food or reproductive partners (Jenssen et al. 2005; Safryn & Scott 2000; Sacchi et al. 2009). The use of real dyadic interactions allowed us to thoroughly explore these morphological effects, which is more difficult in experimental studies that may use unrealistically matched pairs (Briffa et al. 2015). Asymmetry in RHP between the contestants is also related to age, as we found that adults had a higher probability of victory than juveniles (Murie & Harris 1978; Kemp 2000; Wilson et al. 2011b). Older individual chipmunks thus seem to show higher competitive abilities over food than juveniles (as found in foraging doves, *Columba livia,* Sol et al. 1998), likely due to experience. Contrary to what has been shown in great tits (*Parus major*, Wilson 1992), and red deer (*Cervus elaphus*, Wilson et al. 2011b), males were not more likely to win a contest than females, which was somehow expected in a species with negligible sexual dimorphism.

As expected, we found an effect of the location of the contest on the probability of victory of the focal individual. In insects and rodents, for instance, territory owners indeed win most of their contests against intruders (Peixoto & Benson 2012; Dunford 1970; Harper & Batzli 1997). Here we investigated the effects of the distances to each chipmunk's most recent burrow on the probability of winning both at the among- and at the within-individual levels, and found similar effects. These two effects can, however, be interpreted in different ways. The general expected effect of ownership is depicted at the within-individual level: an individual far from its burrow sees a decrease in its probability of winning. An individual also has a higher probability of winning when it encounters an opponent that is relatively far from its own burrow. Individuals thus respond plastically to a change in location, and win when closer to their territory. This effect could be explained by the fact that territory owners have

interest in defending their resources and because they may gain an advantage from being familiar with the physical and social environmental features associated to their territory (Sacchi et al. 2009). At the among-individual, however, individuals were first found to interact on average at different distances from their burrow. The repeatable distance at which individuals interacted is thus a component of their behavior and may represent their consistent levels of territoriality. Individuals' territoriality, or propensity to defend an area (Burt 1943), could then reflect their personality, especially as we then found that individuals that are on average observed closer to their burrow tend to win more. In such a territorial species, the level of aggressiveness of an individual is thus reflected both by its tendency to stay close to its burrow (to patrol its territory and defend its resources from intruders, Sacchi et al. 2009), and by its ability to win a contest. Separating variance components at the among- and within-individual levels can thus bring information on both plasticity and consistency of territorial behaviors.

We found that the individual who first discovered the resources did not gain any advantage in defending them, as the order of arrival at the feeding patch did not affect an individual's probability of winning. The lack of such prior-occupancy advantage (Snell-Rood & Cristol 2005) may be explained by the individual effect that supplants it, as we found repeatability in an individual's probability of winning a contest.

As found for instance in field crickets (*Gryllus campestris*), green swordtails (*Xiphophorus helleri*) and red deer (Santostefano et al. 2016; Wilson et al. 2011a,b), individual chipmunks show consistency in their probability of winning a dyadic agonistic interaction. The opponent's probability of losing a contest to the focal was also repeatable, as expected from the random assignment of each competitor to each role (Wilson et al. 2011b). Individuals with high intercepts for victory as focals thus have low intercept values for focal victory as opponents, because a factor that predisposes an individual to win when it is focal also predisposes it to induce defeat

in the focal when it is itself considered as the opponent (Wilson et al. 2011a,b). In a natural system where chipmunks were observed freely interacting with competitors, we thus found that the probability of winning, which is highly associated with the propensity to attack, partly reflects the aggressive aspect of an individual's personality. Some individuals were always more or less aggressive and prone to winning contests independently of the distance to their burrow, which somewhat challenges the classical view considering that, in territorial species, victory is predominantly explained by the status of ownership of an individual (Dunford 1970; Elliott 1978; Dobson 1982; Harper & Batzli 1997). However, some individuals may actually win more often only because they fight with non-aggressive individuals, as their territoriality may prevent them from encountering conspecifics of varying aggressiveness in the population. This seemed to happen in our system, as we found repeatability in the level of aggressiveness of the opponents encountered by the focal individuals (although to a lower extent than the distance to the burrow, see Annex B: Fig. B5, Table B3). An individual's aggressiveness, here reflected by its capacity to win, is therefore somehow modulated by the variation in the features of the conspecifics it interacts with. Individuals could actually choose or be constrained to specific environmental conditions depending on their personality. Recent research suggests that individuals can show phenotypic segregation in their physical and social environments, through non-random distribution or association with social partners (Montiglio et al. 2013; Montiglio et al. 2016).

Finally, we also found that individuals differed in their plasticity, as they were more or less responsive in their probability of victory depending on environmental changes (Nussey et al. 2007; Dingemanse et al. 2010; Dingemanse & Wolf 2013; Briffa et al. 2015). We will not interpret individual differences in reaction norms for each effect specifically, as we only wanted to test for overall variation in plasticity. Also, the new repeatability estimates only confirmed an overall effect of individual variation at the intercepts, and the random slopes of the opponents ensured the use of robust models

and only acted as mirrored effects. Individuals thus differed not only in their average probability of winning a contest, but also in the extent to which they respond to environmental features (Briffa et al. 2015). Some individuals, graphically represented with weak slopes, therefore show highly consistent aggressive behaviors regardless of the physical or social characteristics of the environment (and then contribute to an increase of repeatability estimates). In contrast, other individuals, represented with inclined slopes, are less consistent as they show aggressive responses that are more dependent on the environmental factors (they will then decrease repeatability estimates). Theoretical models predict that a mixture of socially unresponsive and responsive individuals can coexist, as consistent individual differences in aggressiveness can actually select for plastic individuals and vice-versa (McNamara et al. 2009; Wolf et al. 2011; Wolf & McNamara 2013; Dingemanse & Wolf 2013).

We also found that an individual's level of behavioral plasticity (or social responsiveness) when it encounters individuals of different levels of aggressiveness is positively linked to its own average level of aggressiveness. More plastic individuals thus seem to be the more aggressive ones, while it is usually expected that more aggressive individuals do not respond to their social context (high intercepts and weak slopes, Dingemanse et al. 2010; Dingemanse & Araya-Ajoy 2015). The expected negative relationship between proactivity (i.e., high boldness, aggressiveness and activity) and plasticity (Coppens et al. 2010), however, remains to be supported empirically in the wild (Hall et al. 2017). In superb fairy-wrens (*Malurus cyaneus*) for instance, individuals with different exploration levels did not differ in their responsiveness to simulated territorial intrusion (Hall et al. 2017). Moreover, our data are not based on the observation of aggressive behaviors per se, but on the probability of winning, so this result may reflect a statistical constraint as individuals who tend to always win (identified as the more aggressive ones) may have more chance to show plasticity than those who are more inclined to lose most of their fights (Auld et al. 2010). We, however, only found a significant covariance

between intercepts and slopes for aggressiveness of the opponents, and not for the other effects, so that this result may be meaningful. It should also be added that we could not detect the existence of a quadratic effect (e.g., if individuals with extreme personalities may be the less plastic) by testing these linear structures of covariance. The covariance between personality and social responsiveness thud needs to be further investigated using a multivariate approach, that would also allow to link aggressiveness to other behavioral and life-history traits. Indeed, the outcome of aggressive contests can highly influence fitness in both a positive and a negative way. On one hand, more aggressive competitors can gain access to a greater amount of resources such as food and mates and therefore increase their survival and their reproduction (Harris & Siefferman 2014). On the other hand, territorial behaviors and high levels of aggressiveness can be costly as they can cause both a loss of time/opportunities and an increased risk of injury (Sacchi et al. 2009). A further step could then be to couple our dataset to measures of reproduction and survival in our studied population, which could give insight into the evolutionary implications of individual aggressive behaviors.

2.6 Conclusion

To conclude, aggressive social interactions measured in a natural system are determined by among- and within-individual variation, which can be thoroughly studied within a same framework. The outcome of an aggressive contest depends on environmental contexts, as predicted by contest theory, but also on individual behavioral consistency, as highlighted by animal personality. Behavioral plasticity and consistency are even further emphasized through a reaction norm approach. This integrative approach could thus shed light on decision-making during conflicts and on the role played by personality in social interactions.

2.7 Acknowledgments

The study was supported by a research team grant from the Fonds de Recherche du Québec - Nature et Technologies (FRQNT) to D.G., D.R. (and Murray Humphries, Fanie Pelletier), by Discovery grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) (D.G., D.R.) and by a Canada Research Chair (D.R.). C.C. was supported by a scholarship from the FRQNT and through grants from the UQAM, and by a National Geographic Young Explorers grant and a Student Research grant from the Animal Behavior Society.

We thank the Green Mountains Nature reserve of the Nature Conservancy of Canada (CNC) for allowing us to access the study sites, as well as all the people that helped in the field to maintain the long-term project over the last 10 years. We especially thank Béatrice Carrier, Jeanne Clermont and Brigitte Planade who helped collected this specific data, and Melanie Dammhahn for suggesting to use cameras to collect more data. We are also grateful to Pierre-Olivier Montiglio and Samantha Patrick for their help in creating individual random slopes figures in R.

CHAPITRE III

SPYING ON SMALL WILDLIFE SOUNDS USING AFFORDABLE COLLAR-MOUNTED MINIATURE MICROPHONES: AN INNOVATIVE METHOD TO RECORD INDIVIDUAL DAYLONG VOCALISATIONS IN CHIPMUNKS

Charline Couchoux, Maxime Aubert, Dany Garant & Denis Réale

Scientific Reports, 2015. *5*, 10118 (doi: 10.1038/srep10118).

Dans ce chapitre, nous mettons en avant le rôle majeur des avancées technologiques qui permettent à la communauté scientifique d'accéder à de nouveaux champs de recherche. L'étude de la communication sonore peut particulièrement bénéficier des progrès technologiques en matière d'équipement d'enregistrement, et il est évident que les signaux acoustiques émis par les animaux pourraient être davantage compris en suivant de manière quotidienne les émissions des individus en milieu naturel. Cette approche serait notamment pertinente dans le contexte actuel d'intégration de la variation individuelle au sein des questions de recherche en écologie évolutive. Nous montrons ici que l'existence d'enregistreurs miniaturisés opérationnels rend cette approche possible, puisque ces appareils peuvent facilement être utilisés comme enregistreurs de données embarqués en les apposant sur des petits animaux sauvages. Les enregistrements acoustiques de 24 h réalisés par les micros espions ont permis de récolter une grande quantité de vocalisations de qualité chez les tamias rayés équipés. Les données obtenues apportent ainsi des informations beaucoup plus détaillées sur leur communication sonore qu'avec l'enregistrement classique réalisé via un microphone directionnel durant une saison de terrain. Les enregistrements permettent également de mesurer les patrons d'activité des individus et d'avoir accès à de longs enregistrements de battements cardiaques au repos, et même d'identifier des évènements durant lesquels les individus se grattent et des couinements émis par les jeunes avant leur émergence du terrier maternel.

Mots-clés : Technique d'enregistrement, Microphones miniatures, Communication acoustique, Suivi individuel continu, Petite faune sauvage.

3.1 Abstract

Technological advances can greatly benefit the scientific community by making new areas of research accessible. The study of animal vocal communication, in particular, can gain new insights and knowledge from technological improvements in recording equipment. Our comprehension of the acoustic signals emitted by animals would be greatly improved if we could continuously track the daily natural emissions of individuals in the wild, especially in the context of integrating individual variation into evolutionary ecology research questions. We show here how this can be accomplished using an operational tiny audio recorder that can easily be fitted as an on-board acoustic data-logger on small free-ranging animals. The high-quality 24 h acoustic recording logged on the spy microphone device allowed us to very efficiently collect daylong chipmunk vocalisations, giving us much more detailed data than the classical use of a directional microphone over an entire field season. The recordings also allowed us to monitor individual activity patterns and record incredibly long resting heart rates, and to identify self-scratching events and even whining from pre-emerging pups in their maternal burrow.

Keywords: Recording technique, Miniature microphones, Acoustic communication, Continuous individual tracking, Small wildlife.

3.2 Introduction

New research questions become increasingly accessible through technological breakthroughs, particularly for the study of animal vocal communication. In the past few years, for instance, the development and successful use of new bioacoustic technologies based on microphone arrays have allowed researchers to record the sounds produced by wildlife and relate this to their ecology and habitat (Blumstein et al. 2011; Mennill et al. 2012). Since most ecologists cannot, unfortunately, turn themselves into micro-electrotechnicians, it appears most interesting to monitor the continuous development of cutting-edge devices in areas distant from our field of expertise, as sometimes an inventive but simple deviation of an apparatus from its primary purpose (see for instance the ingenious use of "burrowscopes", Boland et al. 2005) can make a significant difference for an entire field of research. Miniaturisation of the equipment, in particular, makes it more and more possible to observe undisturbed animal behaviour in detail for multiple individuals (Rutz & Troscianko 2013). Indeed, whereas non-invasive methods that are performed from a remote location (Blumstein et al. 2011; Mennill et al. 2012) are preferred whenever possible, it becomes necessary to equip the animal with a monitoring device when research questions are based at the individual level.

This is particularly interesting considering the generalised growing interest in individual differences (Bolnick et al. 2003) that have led scientists to rethink and adapt their approach in many research areas. In the field of evolutionary ecology, there is thus a need to better integrate and understand among-individual differences in behavioural tendencies within natural populations (i.e., animal personality, Réale et al. 2007; Réale et al. 2010; Wolf & Weissing 2012). For instance, the study of vocal communication systems would highly benefit from focusing on among-individual differences, which can be monitored through on-board acoustic data-loggers. However, thus far such devices have been developed to fit specific species

characteristics (marine mammals, Johnson et al. 2009, or bats, Hiryu et al. 2007), and they are either too big to be used on small terrestrial animals (Leong et al. 2003; Lynch et al. 2013) or they are not readily available for deployment in the wild (Anisimov et al. 2014).

To overcome these limitations, we suggest using an "off-the-shelf" professional miniaturised audio recorder device that is commercially available (approx. 300 $) and that can be easily and readily used to monitor free-ranging small animal sound emissions for 24 continuous hours at a time (frequency range from 100 to 10,000 Hz). The Edic-mini Tiny A31 model (http://ts-market.com/products/models/1198/), the world's smallest digital audio recorder (weight = 6 g; Guinness World Records holder), is developed by the Russian company TS-Market (http://www.ts-market.com/) specialised in the design and the manufacture of professional miniature audio and video devices. Through a simple re-packaging with a lighter protective encasing (i.e., shape-adapted), we were able to design a system mounted into a collar to fit small animals (eastern chipmunks, *Tamias striatus*) weighing 100 g or more (Fig. 3.1, Annex C: Fig. C1 and Methods section). The technological advances made in the world of espionage thus allow to spy on the vocal emissions of individuals from natural populations.

In this methodological study, we show the validity and the efficiency (in terms of both quantity and quality) of this affordable, operational and robust miniaturised audio recorder device compared to the classical use of a directional microphone for recording emissions from focal individuals. We also present several types of research questions that could be addressed using the spy microphones.

Figure 3.1 A collar-mounted spy microphone for recording individual sound emissions in free-ranging chipmunks. Two individual chipmunks equipped with the device for a recording of 24 h in natural conditions. Photos by C. Couchoux.

3.3 Results

3.3.1 Validity and efficiency of recording with spy microphones

The spy microphone devices proved to be extremely robust and wild-proof since they were retrieved without any damage, despite being subject to rough conditions by chipmunks that spend part of their time underground in the narrow tunnels of the burrow.

The number of calls recorded at different times of the day with the spy microphones reflected the number of calls recorded throughout the field season with the directional microphone (Fig. 3.2a, Spearman rank-correlation test: $\rho = 0.80$, $S = 56.56$, $P = 0.002$, $n = 10$). We also found a positive relationship between the proportion of the different types of calls recorded with the two methods, although the small period over which the spy microphones have been used and the small number of call types prevented us from finding a significant association between the two methods (see details on the types of calls in Burke da Silva et al. (1994); Fig. 3.2b). This indicates that the spy microphones could easily replace more standard techniques for some research protocols in bioacoustics.

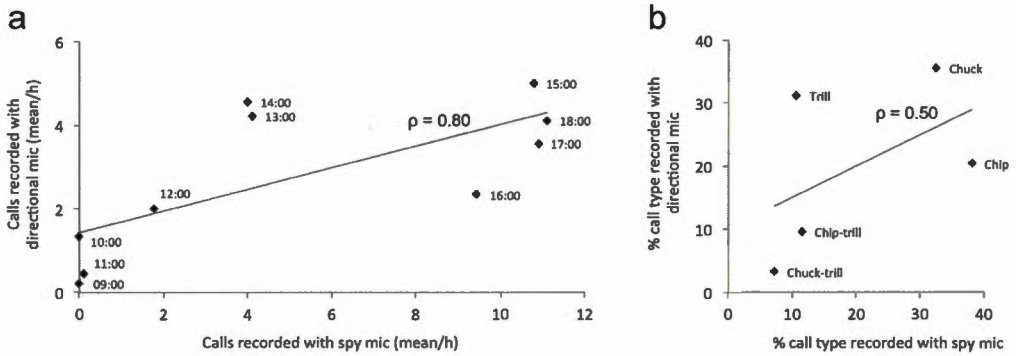

Figure 3.2 Test of the validity of the recording method: recording data are similar for the recordings made with the spy microphones (24 h) and with the classic manual recording (directional microphone; entire field season). (a) Comparison of the mean number of calls recorded through the two techniques, considering the time of the day (the different points represent the mean number of calls recorded at different times of the day, for the corresponding hour). (b) Comparison of the percentage of call types recorded using the two techniques. Mean number of calls and percentage of call types were calculated based on the emissions of nine individuals followed during the field season and equipped with the spy microphones on the same day and at the same site.

Spy microphones were highly efficient at recording calls while human observers were absent from the area, and their recording performances became even more compelling when considering the reduced recording effort needed to obtain the data. They allowed us to record 450 calls during the first 12 h of recording for the 9 equipped individuals. In comparison, surveying the same 9 individuals with classical methodology (directional microphone) for 176 h throughout the field season allowed us to record manually only 250 of their calls. Since our study was performed on chipmunks that are solitary and therefore emit calls to their conspecifics at a distance, we are highly confident that we could differentiate the calls emitted by the collared individuals from those emitted by conspecifics, especially since the sound captured at the throat of the animal was extremely loud. Studies in which individuals tend to aggregate to vocalise might first need to measure the loudness of the sounds expected at standardised distances through tests and observations (see also the use of a specific device for this purpose in Anisimov et al. 2014).

Using spy microphones therefore increased the sample size by a factor of 3.43 ± 2.30 (mean ± SD) for each of the studied individuals (Fig. 3.3). Furthermore, in terms of sampling effort, we recorded 4.35 ± 3.98 (mean ± SD) calls per hour with spy microphones compared to only 0.16 ± 0.13 per hour with the directional recording technique (paired Wilcoxon signed rank test, V = 2, P = 0.012, n = 9), and calls recorded with the spy microphone represented 80.91 ± 32.74% (mean ± SD) of all the calls collected for each individual.

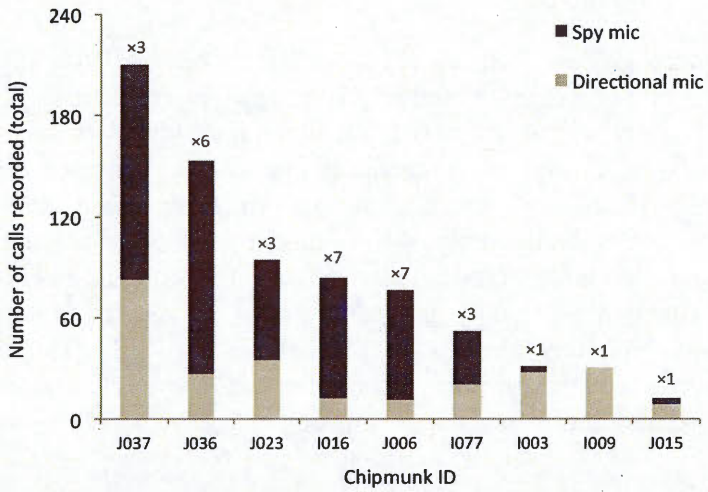

Figure 3.3 Representation of the spy microphone's high efficiency to record a great quantity of calls, by comparison to the quantity of calls recorded through the directional microphone. Illustration of the raw number of calls (without considering the sampling effort) recorded with the two techniques, showing the high proportion of the sample size due to calls recorded with the spy microphones. Numbers above each bar indicate the increase in individual sample size allowed with the recordings from the spy microphones.

With spy microphones, the recording is captured on the throat of the animal, which produces clear signals that sound like those recorded in lab conditions (Fig. 3.4). Ideally, the frequency of the sound recorded should not exceed 11 kHz so that all of the acoustic characteristics of the sounds can be retrieved (the maximum sampling

frequency is 22 kHz as it was designed to record human voice, see the manual for further details on the acoustic characteristics of the device).

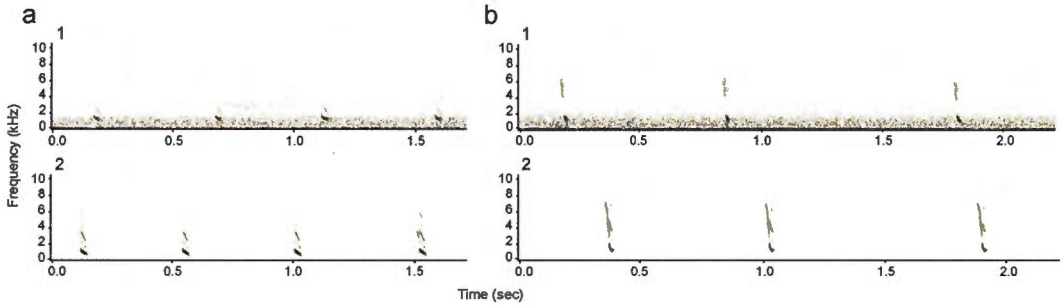

Figure 3.4 Sound spectrograms of low frequency "chuck" calls emitted in a bout, illustrating the high quality of recordings obtained from spy microphones. (a,b) Comparison of four "chuck" calls recorded for two different individuals (a and b) with the directional microphone (a1 and b1, recordings chosen for being of high quality) and with the spy microphones (a2 and b2, raw recordings not submitted to any filter). The grey scale represents the intensity of the sounds, so that louder sounds appear darker. The sounds recorded with the directional microphone contain a certain level of background noise (fuzzy lighter grey in spectrograms a1 and b1, mainly caused by windy conditions), which overlaps with the calls and could affect the acoustic measurements, whereas the vocalisations recorded with the spy microphones are very clean and not affected by interference noise.

3.3.2 Beyond vocalisations: individual heart rate, activity patterns, self-scratching events and whining

The 24 h continuous recording allowed by the spy microphone device also revealed other sounds that could be identified and analysed in different research contexts. Spy microphones could be particularly well suited to monitoring the activity and time budget of individuals (Lynch et al. 2013). In chipmunks, above ground foraging activities would induce more noisy recordings compare to periods of relative inactivity (e.g., an individual resting in its burrow) and this variation in decibel level can be quantified through variation in grey intensity in the spectrogram (Fig. 3.5a; measured with the software ImageJ, Schneider et al. 2012). Activity patterns can then be estimated at different periods of the day to compare the behaviour of different

individuals (Fig. 3.5b) or to estimate the mean activity level for a population (Fig. 3.5c). The activity budget could also be established in even more detail, as we can easily identify other sounds on a spectrogram (e.g., self-scratching events, Annex C: Fig. C2a,b). Resting heart rates can also be measured through the recordings. These were mostly accessible during the night portion of the recording, but several were also obtained during the day, when chipmunks appeared to be resting (Fig. C2c). Other interesting sounds are also recognisable, such as whining that seemed to be emitted by pre-emerging pups in the burrow of their mother (Fig. C2d, Annex C: Supplementary Audio A1).

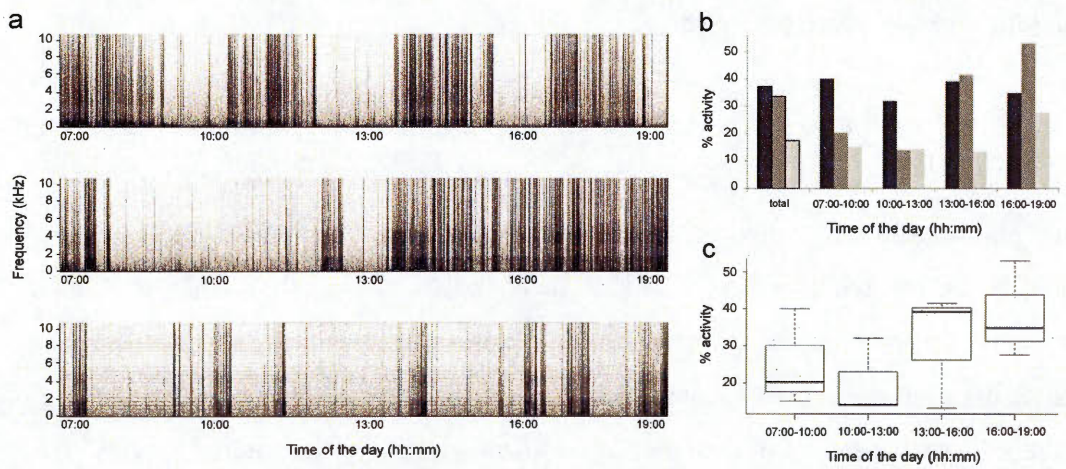

Figure 3.5 Illustration of the potential to monitor individual activity levels through the use of noises produced by and around the chipmunk. (a) Large view spectrograms representing activity patterns of three different individual chipmunks between 7:00 am and 7:00 pm. (b) The activity levels measured and compared for the three individuals illustrated in (a) (individuals from top to bottom in (a) are represented from left to right in (b) from darker to lighter grey bars), for the total 12 h of recording and for each separated period of 3 h. The percentage of activity for different times of the day is estimated based on grey intensity indices measured on the spectrograms (the percentage is calculated as the value of grey intensity for the measured period divided by the maximum value of intensity possible (for black)). (c) Population activity levels at different periods of the day (here based on the values estimated in b, for the three individuals).

3.4 Discussion

The simultaneous recording of several individuals allowed by this method represents an obvious advantage for efficient data recording. This technique is especially appealing to record the emissions from individuals that are difficult to observe/detect in the field or for those located at the edges of a study area, making it easier to sample the complete range of individual behaviours. It will also allow a more detailed investigation of the information encoded in the calls by facilitating repeated recordings of vocalisations. Equipping each individual several times during the season would allow one to acquire a sufficient quantity of calls to investigate intra- and inter-session variation in the vocalisations.

The spy microphones also recorded a wider spectrum of the chipmunks' call diversity than the traditional technique. The more natural conditions in which the recordings are made with this method allowed us to record several "chip" calls, which are usually hard to record when following focal individuals, as they emit "trill" calls in response to human presence (Fig. 3.2b). Recording continuous individual behaviour could thus allow one to record vocalisations that are rarely elicited and therefore obtain a better measure of the complete vocal repertoire of the studied species.

Sounds recorded with the spy microphones are extremely pure and can therefore be easily analysed for acoustic measurements, and such quality could be particularly interesting for researchers interested in harmonics. The quality of recording also provides surrounding sounds with a good quality, which could then permit the determination of the soundscapes of an animal's environment (Blumstein et al. 2011) (see Annex C: Fig. C3 for examples of bird songs recorded and Annex C: Supplementary Audio A2 - sound of Canadian geese).

The daylong recordings performed by the on-board devices could also be used to monitor individual activities in detail (Lynch et al. 2013). This technique would allow researchers interested in time budgets to monitor individuals simultaneously and efficiently, especially for small animals that are difficult to track continuously in the field.

During the inactive phases of the individuals, the quality of the recordings produced exceptional data as we were able to obtain resting heart rate measurements without the more common highly invasive techniques such as surgery and implantation of monitors (Valance et al. 2008; Kostelanetz et al. 2009). These can be used as actual resting heart rate to compare them with heart rate under stress to measure different processes such as coping styles (Koolhaas et al. 2010).

The quantity of self-scratches that occurred throughout the day for the equipped individuals could be used to estimate their parasite load, as previous studies showed that grooming behaviours are related to ectoparasite loads (Cotgreave & Clayton 1994; ter Hofstede & Fenton 2005).

The recordings retrieved from the devices set on females before pup emergence all contained whining, which clearly seemed to be emitted by pups in the maternal burrow. These sounds could be useful to assess maternal care, mother-offspring relationship or to study the ontogeny of the calls in species where pups are inaccessible before emergence from burrows.

Obviously, the spy microphones could also be used for bigger animals in concert with some other devices such as accelerometers (Anisimov et al. 2014), GPS or radio transmitters (Lynch et al. 2013) to gather complementary data along with the recording of sounds.

In summary, these spy microphones are highly efficient tiny audio recorders that are readily available and can be easily used as on-board acoustic data loggers to survey the behaviour of free-ranging small animals.

3.5 Methods

3.5.1 Setting the on-animal device on chipmunks

The collar-mounted devices were successfully fitted and recovered on 21 chipmunks, during summers 2013 (5) and 2014 (respectively 9 and 7 on two different study sites), as part of a long-term project that investigates the evolutionary ecology of this species in a deciduous forest in Southern Québec, Canada.

Chipmunks in this population regularly wear collars for a long period (they are equipped with collar-mounted radio transmitters to find their burrows and thermo-sensors to monitor their torpor activity during winter, Landry-Cuerrier et al. 2008) but the spy microphone device is a bit bigger and heavier (5.5 g vs 2.2–4.1 g for the other devices, which represents 4.9–6.2% of the body mass of the chipmunks tested). We thus retrieved the device as soon as the recording was finished to limit the impact on chipmunks. We put the collars on as many individuals as possible during a day, then did not return to the site for the next 24 hours to ensure our presence did not affect the recordings. We returned to the site on the third day to capture the individuals and recover the devices. When active above ground chipmunks can be easily captured, which allowed us to limit the time that they spent with the collar. Fitting a collar only takes a minute for an experienced handler and does not require any anaesthesia. After the handling, we monitored the behaviour of the equipped individuals to ensure that they supported the device and that they returned to their natural activities, such as foraging or grooming, until they reached their burrow (see examples of individuals equipped with the device and that performed such natural behaviours in Annex C:

Supplementary Videos V1a,b, V2 & V3). This monitoring also allowed us to make sure that individuals had safely reached their burrow if they needed further time to recover. To increase our probability of retrieving the collars on the third day, we performed targeted trapping at the individual burrows and added Sherman traps that are bigger than the Longworth traps (30.5 × 9.5 × 7.5 cm vs 14 × 6.5 × 8.5 cm) and that individuals equipped with collars seem to prefer.

All captures and manipulations were carried out in accordance with the guidelines of the Canadian Council on Animal Care and the protocols were approved through the Université du Québec à Montréal (permit CIPA #0512-760-0513) and the Québec Ministry of Sustainable Development, Environment, Wildlife and Parks (permit SEG #2014-04-22-103-05-S-F).

Spy microphones can also be used to record vocalisations when they are not set on chipmunks, as they are easier to handle than a directional shotgun microphone plus a recorder. With this method of recording sounds are not missed by delays in pressing start/stop on the recorder and there is no need to change batteries, which would be the case for daylong recording using traditional methods.

3.5.2 Audio recording analyses

We present here the data from the recordings done on nine eastern chipmunks that were equipped with the device (Fig. 3.1; see Annex C: Fig. C1 for further illustrations of the device), on the same day (22 June 2014) and at the same site. The first 12 h (7:00 am–7:00 pm) of the 24 h audio recordings were visually inspected for identification of the sounds recorded (software AVISOFT-SAS Lab Pro, through a 10 seconds view, and FFT-length = 1024).

The validity and the efficiency of recording with the spy microphones were assessed through a comparison with the recordings made on the same individuals throughout the field season using a shotgun directional microphone (Sennheiser ME67/K6 connected to a Marantz PMD661 portable recorder; on 23 days, from 6 June to 20 August 2014, 176 hours of presence on the site for recording). Non-parametric correlations tests (for small sample sizes) were implemented to compare the efficiency of recording between the two methods.

3.5.3 Spy microphone specificities & settings.

The recorder has several acoustic features and recording options that can be found in the operational manual (http://ts-market.com/upload/iblock/db4/Operational%20Manual%20Tiny.pdf). We chose the 600 h rechargeable version of the device that allows the maximum amount of recording time. The programming of the device is quite straightforward, being done through a firmware accessible on the device once the USB connection is established. The recording settings were chosen to record with the highest quality and capacity of recording, by choosing a recording format without any compression and selecting the highest sampling frequency (22 kHz).

When retrieving the recordings, done using the USB connection, sections can be chosen for downloading. For a 24 h recording, two separate files of 12 h must be downloaded. The battery can be recharged in a few hours.

We chose to use the timer recording option to schedule the 24 h recording at 7:00 am the day after the capture (after synchronising the clock on the device with that of the computer), to ensure that the chipmunks had recovered from the manipulation and to therefore obtain meaningful behavioural data. There is also a VAS mode available on the device that records only those sounds that are above a defined threshold.

3.5.4 Design of the wild-proof collar-mounted spy microphone.

In order to mount the spy microphone into a collar that could be fitted on chipmunks (Fig. 3.1), we removed the heavy rectangular-shaped metal case (Annex C: Fig. C1a1,2) that protects the circuit (containing the data logger and the microphone) and battery (Fig. C1a2-4, circuit: green and black part, battery: silver part). For this purpose, the device can be ordered unglued in the case, allowing you to fashion it your own way. After carefully removing the device from the case (Fig. C1a), the tiny metal spring (Fig. C1a3,4) was cautiously removed as its only purpose is to hold the device inside the case. The little white square pad that is attached to the battery (Fig. C1a4, visible on the left part of the battery) was left in place as it insulates the battery from the circuit to avoid a short-circuit. There is also a tiny white switch above the plug connection (Fig. C1a,1,3,4) that can be used to turn the recording on and off. For our purpose we only used the programming function of the recorder so the switch was always set on the 'off' position (switch set on the left, closest to the microphone) and it was no longer accessible once assembled. The device was then set in a light protective case made of a large tube of heat-shrink (Fig. C1b, the heat-shrink is the transparent envelope (1) that after being heated slightly with a flame takes the shape of the material it covers (2-4)). The heat-shrink was cautiously sealed at the extremities (Fig. C1b2-4) by pressing the warm open sides of the tube with tweezers (Fig. C1b2) so that dust, earth, or water could not enter the device. Then some openings were created (with a box cutter) in front of the plug connection and the microphone (Fig. C1b3, result seen in Fig. C1d3). To individually identify the spy microphones (crucial for unmistakable simultaneous setting and recovery of the different devices on multiple individuals), a label bearing the device number was placed on top of the heat-shrink encased device (Fig. C1c1,). Figure C1c shows how the collar was then mounted using another (transparent) wide heat-shrink tube to encase the device (1) and to hold a smaller heat-shrink tube (black) that allowed the passage of a ty-rap (2), that served as the collar. The shape of the collar (that fits the

study animal's neck) was obtained by curving the (black) heat-shrink tube (again with heat, Fig. C1c3) and by stuffing FIMO (green matter in Fig. C1c4) in-between the device and the (black) heat-shrink tube receiving the ty-rap. The holes were also sealed to prevent the animal from grabbing the device. The shape of the collar was adapted to suit the animal's neck by simply fastening the extremities of the ty-rap together (with the green wire, Fig. C1d1-4). Two additional heat-shrink tubes (red) were added on each side of the ty-rap to protect the animal's neck (Fig. C1d1-5).

Finally, the open extremities of the second large heat-shrink (that stayed open with the FIMO, Fig. C1d1) were covered with resistant tape (black electrical tape, Fig. C1d2-5). The holes made in front of the microphone and the plug were left open, to allow programming using the USB cable (Fig. C1d3). Figure C1d3 shows the final version of the collar-mounted spy microphone that could then be used successively on different chipmunks. The entire device weighed 5.5 g. Once the device was programmed, a supplementary piece of tape was added to cover the microphone and plug entrances (Fig. C.1d4). The device was then ready to use (Fig. C1d5) on a free-ranging animal. Once the device was retrieved we remove the tape in front of the plug openings to download the data (Fig. C1d3). Before fitting the device on the next animal, the ty-rap was changed and a new piece of tape was placed to cover the plug (Fig. C1d4). The device could be shaped differently to fit the requirements of other species (see e.g., in Anisimov et al. 2014).

3.6 Acknowledgments

The study was supported by a research team grant from the Fonds de Recherche du Québec - Nature et Technologies (FRQNT) to D.G., D.R. (and Murray Humphries, Fanie Pelletier), by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grants (D.G., D.R.) and by a Canada Research Chair program (D.R.). C.C. was supported by a scholarship from the FRQNT and through grants

from the Université du Québec à Montréal, and by a National Geographic Young Explorers grant and a Student Research grant from the Animal Behavior Society that allowed the purchase of the recording devices. We thank the Green Mountains Nature reserve of the Nature Conservancy of Canada (CNC) for allowing us to access the study sites. We are particularly grateful to Carolyn Hall for her thorough English-editing and also to Caroline Grou for her insightful comments on the manuscript. We also thank Manuelle Landry-Cuerrier and Melanie Dammhahn for their useful advice on the design of the collars, as well as all the people that helped in the field.

CHAPITRE IV

ALARM CALLING AS A PERSONALITY TRAIT: INDIVIDUAL CHIPMUNKS VARY CONSISTENTLY IN THEIR PROPENSITY TO COMMUNICATE PREDATION RISK

Charline Couchoux, Dany Garant & Denis Réale

Manuscrit en préparation pour soumission à *Biology Letters.*

Dans ce chapitre, nous nous intéressons à la communication, qui joue un rôle majeur dans la vie des animaux. L'échange d'informations a des conséquences importantes pour l'aptitude phénotypique des individus en contextes de territorialité, de choix de partenaire ou de défense contre les prédateurs. Au sein d'un intérêt grandissant pour la variation individuelle des comportements exprimés sous influence sociale, des modèles théoriques récents ont suggéré l'existence d'un lien entre communication et personnalité. La personnalité peut ainsi générer de la variation au sein des stratégies de communication, notamment via l'utilisation de signaux acoustiques en contexte social (i.e., pour la cohésion, l'agression ou la reproduction). Cependant, un tel lien empirique n'a pas encore été démontré en ce qui concerne les cris d'alarmes produits en contexte de risque de prédation. L'existence de différences individuelles de tendances à la prise de risque pourrait pourtant créer de la variation dans les tendances individuelles à émettre des cris d'alarme. Nous avons montré que les tamias rayés (*Tamias striatus*) soumis à des simulations d'attaque de prédateurs aériens et terrestres diffèrent en effet de manière constante dans leur propension à émettre des cris d'alarme, et ce même à travers les contextes. L'émission de cris d'alarme représente ainsi un aspect de la personnalité des tamias, et semble également être liée de manière négative à leur niveau de proactivité (i.e., exploration). Des analyses futures seront cependant nécessaires pour confirmer l'existence d'une covariance entre la propension à produire des alarmes et d'autres traits de personnalité comme la témérité. Des différences individuelles de perceptions du risque pourraient ainsi créer d'importantes variations dans les stratégies individuelles d'émission de cris d'alarme,

et ainsi expliquer la production de fausses alarmes qui a une incidence globale sur les systèmes de communication.

Mots-clés : Communication acoustique, Cris d'alarme, Comportement antiprédateur, Personnalité animale, Variation individuelle.

4.1 Abstract

Communication plays a predominant role in animals' life, as it is used in many fitness-related contexts such as territoriality, mating or defence against predators. As part of an increasing interest in individual variation in behaviours expressed under social influence, recent theoretical models have suggested a link between communication and personality. The implications of personality for generating variation in communication strategies have been empirically highlighted for acoustic signals used in social contexts (i.e., for cohesion, aggression or reproduction), but they have not yet been investigated for alarm calls produced in a predation risk context. Individual differences in risk-taking tendencies, could, however, create variation in individuals' tendencies to produce alarm calls. By subjecting wild chipmunks (*Tamias striatus*) to simulated attacks of aerial and terrestrial predators, we showed that individuals consistently differ in their propensity to emit alarm calls, both within and across contexts. Alarm calling thus represents an aspect of chipmunks' personality. We also found a tendency for a negative relationship between emission and proactivity (i.e., exploration), but future analyses will be required to confirm that alarming covaries with other personality traits such as boldness. Intrinsic individual differences in risk-perception may thus create important variation in alarm calling strategies, and could explain the production of false alarm signals that impact an entire alarm communication system.

Keywords: Acoustic communication, Alarm calling, Antipredator behaviour, Animal personality, Individual variation.

4.2 Introduction

Many living organisms exchange information in various ecological and social contexts such as territoriality, mating, parental care, or defence against predators. Communication is thus essentially ubiquitous and intimately linked to individual fitness (Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). Animal communication has been widely studied, from many different perspectives, but it is only recently that consistent individual differences have been suggested to play an important role in generating variation in communication strategies (Akçay et al. 2014). Indeed, behaviours expressed in social contexts are increasingly reconsidered using an individual-based approach, as the social environment has been recently suggested to play an important role in the evolution and maintenance of animal personality (Bergmüller & Taborsky 2010; Montiglio et al. 2013; Dingemanse & Araya-Ajoy 2015; von Merten et al. 2017). In particular, communication strategies could be linked to personality, as suggested by recent theoretical models that predict the natural emergence of consistent individual differences in the production and interpretation of the signals, and their evolutionary stable maintenance via frequency-dependent selection (McNamara et al. 2009; Botero et al. 2010; Wolf et al. 2011). A few empirical tests have considered visual signals displayed in aggressive contexts (Matessi et al. 2010), but also acoustic signals.

Recent studies have suggested that personality reflected in acoustic signalling may play an important role in shaping social interactions in social mammals. Chaverri and Gillam (2015) showed the existence of consistent individual differences in the calling behaviours of the Spix's disc-winged bat (*Thyroptera tricolor*), while the production of vocalisations in highly social domestic pigs (*Sus scrofa domestica*) is also

repeatable and linked to different personality traits (Friel et al. 2016). The implications of personality for acoustic communication have also been highlighted in reproductive and aggressive contexts. In passerine birds for instance, individuals differ in their production of songs (Naguib et al. 2010; Amy et al. 2010; Akçay et al. 2014) and mobbing calls (Hollander et al. 2008; Guillette & Sturdy 2011), with more proactive, faster explorers or more aggressive, individuals producing more songs or calls. The proximate causes of a relationship between vocalizing and personality could lie in differential individual reactivity of the sympathetic nervous system (Guillette & Sturdy 2011). In singing mice (*Scotinomys teguina*), more proactive individuals that sang more often were indeed the ones with high sympathetic system reactivity (Crino et al. 2010). From an ultimate perspective, the maintenance of diverse communicative strategies in social groups may contribute to the evolution of social roles (Chaverri & Gillam 2015; for details on the notion of social niche specialisation see Bergmüller & Taborsky 2010; Montiglio et al. 2013). Individual variation in sexual signals such as singing activity will also be favoured when individuals pair not only based on signal quality (Naguib et al. 2010) but also assortatively based on behavioural profiles (Both et al. 2005).

Although individual differences in risk-taking tendencies represent an important personality trait (Wilson et al. 1994; Réale et al. 2007), linking personality and communication in a predation risk context have somehow been overlooked (Matessi et al. 2010). Many species however emit acoustic alarm signals when they perceive the presence of a danger (Klump & Shalter 1984; Hollén & Radford 2009; Zuberbühler 2009), and the production of "false alarms" (i.e., signals given in response to innocuous stimulations) is common in birds and mammals (Haftorn 2000; Beauchamp & Ruxton 2005). Although the production of such irrelevant signals is supposedly dependent on individuals' "threshold of excitation" (Hare & Atkins 2001), "jumpiness" (Searcy & Nowicki 2005) or "skittishness" (Pollard 2011), consistent individual differences in the propensity to emit alarm calls has never yet been truly

investigated. An individual's tendency to utter an alarm call could however depend on its intrinsic risk perception and stress response reactivity, with individual variation in physiology as the proximate causes of this variation. Different thresholds of emission are linked to the production of stress hormones (Bercovitch et al. 1995; Blumstein et al. 2006), while stress hormones concentrations show consistent individual differences (Smith et al. 2012) and are linked to individual variation in proactivity level (Clary et al. 2014). The propensity to emit alarm calls could thus vary predictably among individuals, and be linked to individuals' personality profiles. Less proactive, overly risk-sensitive, individuals would then produce high levels of stress hormones and have low thresholds for emitting alarm calls, and could thus be expected to emit alarm calls more frequently in response to unthreatening environmental stimuli.

The maintenance of such variation in alarm signalling behaviours could ultimately be due to differential life-history strategies and investment in fitness-related functions, following the predictions made within the POLS framework (Réale et al. 2010). While more proactive bold individuals would allocate more energy to rapid growth and early reproduction (Biro & Stamps 2008), thus trading off foraging against investment in defence and immediate survival (Wolf et al. 2007), other less proactive, highly risk-sensitive, individuals would invest more in defence for immediate survival and future reproduction (Réale et al. 2010). Differential investment in defensive functions could thus be reflected in different tendencies to sense risk and thus in an individual's propensity to produce alarm signals in response to situations with varying levels of threat. In addition, although alarm calling can be risky in the presence of a predator (Sherman 1977), it does not necessarily generate high costs as alerted prey are generally difficult to catch (Trivers 1971; Elliott 1978; Burke da Silva et al. 1994) and non-alarming individuals are sometimes preferred (Kareksela et al. 2013). Although emitting alarms in the absence of a real threat could also impose important energetic costs, these are hard to evaluate and consequently not well known

(Mondor & Roitberg 2003; Blumstein 2007). In fact, costs of emission of alarm calls are thought to be low (Blumstein 2007; Zachau & Freeberg 2012), although secretion of alarm pheromones in aphids can have fitness costs that are age-dependent (Mondor & Roitberg 2003). The "better safe than sorry" concept (Haftorn 2000) also suggests that even if the emission of false alarms is associated with a foraging cost (since the signaller interrupts its activity to call), it could be balanced by high costs of missing the detection of highly dangerous threats (Zachau & Freeberg 2012). Hypothetically, overabundant alarm signalling may also prove beneficial as a pronouncement of vigilance or pursuit-deterrent signal (similar to tail flagging displays in California ground squirrels, *Otospermophilus beecheyi*, Putman & Clark 2015) to advertise alertness to predators and potentially prevent them from hunting in the area (Sherman 1985; Zuberbühler et al. 1999; Krams et al. 2009). All these explanations could thus justify the maintenance of overly-risk sensitive individuals that often produce false alarms.

In this study, we measured variation in individuals' tendency to emit alarm calls in free-ranging eastern chipmunks (*Tamias striatus*) subjected to repeated simulated aerial and terrestrial predation risks. We were thus able to investigate 1) if individuals consistently differed in their tendency to produce alarm calls under a similar risk of predation; 2) if individuals showed consistent differences between contexts, and 3) if individuals' propensity to call was linked to a known personality trait (i.e., exploration). Chipmunks are suitable candidates to answer these questions as they are ground-dwelling Sciurids that spend most of their time foraging under the risk of predation from diverse terrestrial and aerial predators (Elliott 1978; Snyder 1982; Otter 1994). They produce different types of alarm calls (Elliott 1978; Burke da Silva et al. 1994; Weary & Kramer 1995) under perceived risk, and individuals have been shown to vary in their level of stress hormones (i.e., faecal glucocorticoid metabolites, Montiglio et al. 2015) and in different aspects of their behaviours (e.g., exploration, docility; Montiglio et al. 2012a; St-Hilaire et al. 2017).

4.3 Material and Methods

We studied a population of eastern chipmunks in a deciduous forest in Southern Québec, Canada (45°06.785'N; 72°26.078'W). Trapping allowed us to mark individuals with coloured vinyl flagging pieces on their metal ear tags (National Band and Tag Corp.) for individual recognition from a distance, and to subject individuals to open-field tests (for details on the implementation of these tests in chipmunks see Martin & Réale 2008a,b; Montiglio et al. 2010, 2012a). We performed simulations of predator attacks opportunistically over 2 field seasons, in August and September 2012 (over 9 days), and from May to October 2013 (32 days). The tests were performed on sporadic encounters with recognizable individuals, upon release from capture or when individuals where observed at temporary feeding patches (for details on the feeding patches see Couchoux et al. 2017).

Simulation of an aerial attack consisted of throwing a hat from concealment above the targeted individual (Hare 1998; Hare & Atkins 2001; Sloan & Hare 2006; Digweed & Rendall 2009; Thompson & Hare 2010). To simulate a terrestrial predatory threat, an experimenter pursued the targeted chipmunk while running over a few meters, until the individual reached refuge (Burke da Silva et al. 1994, 2002; Blumstein & Armitage 1997; Dill & Houtman 1989; McRae 2012). During each test, we noted whether the targeted individual emitted alarm calls. The tests were repeated on each individual during the entire summer, for a total of 235 tests performed on 27 different individuals (107 tests were performed in 2012 and 128 in 2013, with 115 aerial predator tests and 120 terrestrial predator tests). The individuals were on average each tested 8.70 times (± 7.36 s.d.; range: 1-22). Twenty-four individuals were tested 4.79 ± 3.49 times [range: 1-10] employing an aerial predator model, while 24 individuals were tested 5.00 ± 3.87 times [range: 1-13] employing the terrestrial predator paradigm.

To estimate individual consistency in the propensity to emit alarm calls (with emission being either 0 = no emission or 1 = emission), we used linear mixed effect models, with a binomial error distribution, implemented in the package ''lme4'' (Bates et al. 2015) in R. 3.1.3. (R Development Core Team 2013). Individual identity was included as a random effect, and the repeatability of emission and its significance were estimated with the package "rptR" (with both PQL method and logitlink and MCMC method, Nakagawa & Schielzeth 2010). Individuals with only one observation were kept in the analyses as excluding them can reduce statistical power (Martin et al. 2011). We present the simplest model, not including any fixed effect, as preliminary analyses showed that repeatability estimates were similar when including confounding effects. In the same way, the estimates were similar when using the quantity of calls emitted instead of the propensity to call.

To investigate if individuals showed consistent differences in emission across contexts, we calculated their percentages of emission in both contexts of predation risk. As proportions are highly dependent on sample sizes, we calculated these percentages based on a reduced dataset considering only individuals with at least 2 observations per context (n = 226 observations with 18 individuals). We then performed a Spearman correlation test (as percentage data were not normally distributed and the sample size was relatively small) between an individual's percentage of calls emitted in each context.

Finally, we examined if the propensity to call was linked to a personality trait known in our population with a Spearman correlation test between an individual's percentage of emission during the predation tests and its level of exploration in the open-field tests. The percentages were also calculated based on a reduced dataset considering only individuals with at least 2 tests and using only the first 10 tests performed on each individual (as complementary analyses showed evidence of habituation; n = 163 observations with 18 individuals). As individual exploration scores have already been

shown to be significantly repeatable in our population, we directly used the number of lines crossed to quantify exploration during the duration of the test (1 min and 30 s; see Montiglio et al. 2010, 2012a). For individuals that were measured twice (individuals get a maximum of two tests in their lifetime as they habituate, Montiglio et al. 2010), we used the mean value of this score as an index of exploration.

4.4 Results

Probability to emit alarm calls during predator tests was significantly repeatable (Repeatability estimates (on link scale) for PQL method: $R = 0.16 \pm 95\%$ CI [0.01; 0.28], $P = 0.001$; for MCMC method: $R = 0.17 \pm 95\%$ CI [0.06; 0.47]). We also found a significant positive correlation between an individual's percentage of emission during aerial predation tests and terrestrial predation tests (Spearman correlation test: $\rho = 0.71$, $S = 130.01$, $P = 0.004$, Fig. 4.1).

An individual's propensity to emit alarm calls was non-significantly related to its exploration score, but there was a trend indicating that individuals emitting more often showed more thorough exploration patterns in the open-field tests (i.e., lower number of lines crossed, Spearman correlation test: $\rho = -0.38$, $S = 1341.30$, $P = 0.11$, Fig. 4.2).

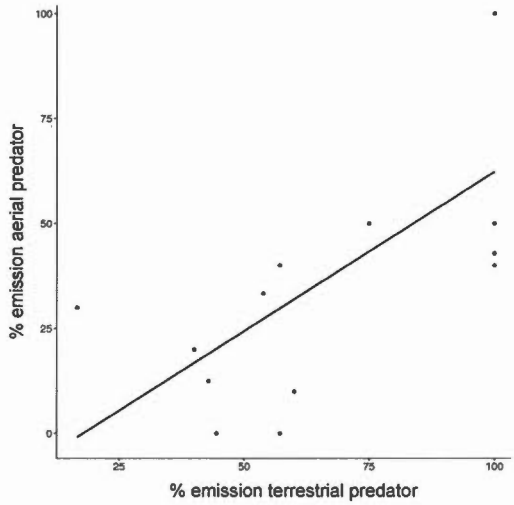

Figure 4.1 Correlation based on raw data showing the consistency in an individuals' propensity to call in tests simulating an aerial and a terrestrial attack (n = 226 observations with 18 individuals). Dots represent the individual data points and the solid line represents the fitted regression estimated from a linear model (used only for representation as we used a non-parametric test).

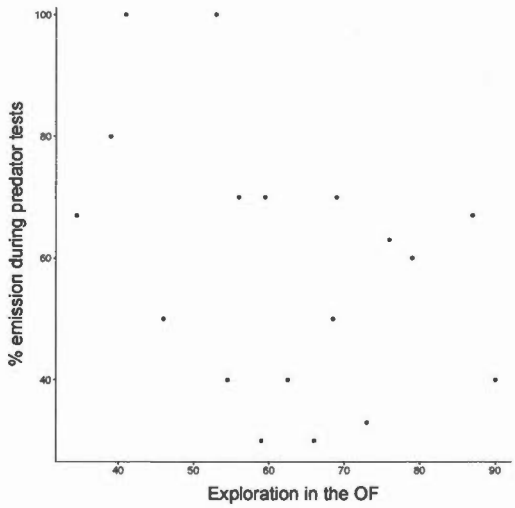

Figure 4.2 Correlation based on raw data showing a negative tendency for individuals with a high propensity to emit alarm calls to show more thorough exploration patterns in the open-field tests (n = 163 observations with 18 individuals). Exploration in the open-field (OF) is represented by the mean number of lines crossed by the individual during the tests.

4.5 Discussion

This study showed that the propensity to produce alarm calls under predation risk is consistent among individuals and across contexts, and suggests that alarm calling can be considered as an aspect of chipmunk personality. Although we did not find a significant relationship between the emission of calls and another personality trait (i.e., exploration), the trend observed followed the expected prediction that less proactive individuals (here the individuals with a thorough exploration) would be the ones that emit more often. These results suggest considerable promise in applying the individual-based approach to communication behaviours, as individual variation may constitute an important part of variation in communication systems.

As found in a few species of mammals (Chaverri & Gillam 2015; Friel et al. 2016) and birds (Hollander et al. 2008; Naguib et al. 2010; Amy et al. 2010; Guillette & Sturdy 2011; Akçay et al. 2014), acoustic signalling can thus reflect an individual's personality. Here we show that individuals consistently vary in their emission of vocalizations in a context of predation risk, as has often been suggested but never tested (Hare & Atkins 2001; Searcy & Nowicki 2005; Pollard 2011). We suggest that these individual differences in emission of alarm calls are due to underlying physiological constraints arising from differential investments in fitness-related functions subjected to trade-offs (e.g., growth/foraging and antipredator behaviours, Lima 1998). Individual variation in sensitivity to risk would thus be reflected in individual differences in risk-perception and stress response, so that some individuals would tend to have low thresholds of perceived risk and would produce alarm calls even in the absence of a predator. Concretely, some individuals are easily alerted by non-threatening environmental stimuli and can for instance emit alarm calls over falling leaves (pers. obs.). At the extreme opposite, individuals who have high thresholds of risk perception would tend to signal the presence of a danger only when it is imminent. Although the emission of false alarms can be intentional in some

species, assuming a deceptive function to gain a foraging advantage (Munn 1986; Møller 1988; Wheeler et al. 2009; Hollén & Radford 2009; Satischandra et al. 2010; Flower 2011) or mating opportunities (Bro-Jørgensen & Pangle 2010), in many species it may be the byproduct of individuals' intrinsic risk-sensitivities.

The existence of such individual variation in the emission of alarm calls has particularly important consequences from the receiver point of view, as signallers may thus differ in their reliability to signal a threat (Hare & Atkins 2001; Blumstein et al. 2004). In chipmunks, we recently reported that receivers seem to consider the reliability of the signallers based on their personality, as they respond more intensely to alarm calls from bold signallers (Couchoux et al. 2017). Future analyses will employ multivariate modelling to integrate measures of boldness (i.e., risk-taking tendencies), in addition to other personality traits such as exploration tested here, to confirm that an individual's proactivity is negatively linked to its propensity to produce alarm calls. The physiological constraints that would link emission of alarm calls and personality could also be further investigated by quantifying the mean and variation levels of glucocorticoid metabolites extracted from faeces collected from individual chipmunks (Montiglio et al. 2012b, 2015).

The propensity to emit alarm calls can depend on many factors, such as individual characteristics and environmental features (Townsend et al. 2012). A next research step will thus integrate both consistent individual variation and plastic decisions into the same analytical framework (Dingemanse et al. 2010), to get a more complete overview of the variation in chipmunks' emission of alarm calls. Differences in emission of alarm calls can indeed depend on the signaller's age, as juveniles would presumably produce more false alarms than adults (Hare & Atkins 2001), due to differential basal excitation levels (Hollén & Radford 2009) and their inability to properly recognize real dangers (Seyfarth et al. 1980; Robinson 1981; Hollén et al. 2008). The social environment can also affect an individual's probability to emit

alarms, especially in relation to kin selection that predicts variation in emission depending on the presence of descendant offspring and collateral kin (Maynard Smith 1965; Sherman 1977; Shields 1980; Blumstein et al. 1997; Blumstein 2007). Several species of ground squirrels for instance warn their kin in the presence of a potential predator (Dunford 1977; Wilson & Hare 2006; Matrosova et al. 2009). In chipmunks, the "trills" emitted by fleeing individuals also seem to be directed to relatives, as females, which tend to live close to their female kin (Elliott 1978; Messier 2012), emit these alarm calls more often than males (Burke da Silva et al. 1994, 2002). The physical environment can also modify individuals' risk perception through habitat characteristics (e.g., closed versus open habitat, see for instance Clermont et al. 2017), and therefore influence the likelihood of alarm call emission.

4.6 Conclusion

The production of alarm calls in the context of predation risk is repeatable, and consistent individual differences are maintained across contexts. Alarm calling is thus a personality trait, and further analyses could reveal that an individual's tendency to emit is also negatively related to its proactivity (i.e., exploration, boldness). Overly risk-sensitive shy individuals could thus be the ones that often "cry wolf", so that individual behavioural variation may have an important impact on the reliability of the information transmitted in alarm communication systems.

4.7 Acknowledgments

The study was supported by a research team grant from the Fonds de Recherche du Québec - Nature et Technologies (FRQNT) to D.G., D.R. (and Murray Humphries, Fanie Pelletier), by Discovery grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) (D.G., D.R.) and by a Canada Research Chair (D.R.). C.C. was supported by a scholarship from the FRQNT and through grants

from the UQAM, and by a National Geographic Young Explorers grant and a Student Research grant from the Animal Behavior Society.

We thank the Green Mountains Nature reserve of Nature Conservancy of Canada (CNC) for allowing us to access the study sites, as well as all the people that helped in the field to maintain the long-term project over the last 10 years. We especially thank Maxime Aubert, Béatrice Carrier, Jeanne Clermont and Brigitte Planade who helped collected these specific data.

CHAPITRE V

SIGNALER AND RECEIVER BOLDNESS INFLUENCE RESPONSE TO ALARM CALLS IN EASTERN CHIPMUNKS

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Behavioral Ecology, 2017 (doi: 10.1093/beheco/arx152).

Dans ce chapitre, nous nous intéressons à l'utilisation de l'information sociale, dont les individus tirent de nombreux bénéfices. Répondre à un signal d'alarme permet par exemple à un individu de maximiser sa survie sous le risque de prédation. Les individus devraient toutefois considérer la fiabilité de l'information, afin d'adopter des comportements antiprédateurs qui ne compromettraient pas inutilement leur acquisition de nourriture. La personnalité des individus pourrait avoir un effet global sur la prise de décisions des récepteurs, comme la variation individuelle de tendance à prendre des risques (i.e., témérité) pourrait affecter non seulement la perception du risque des récepteurs mais aussi la fiabilité des émetteurs. Des modèles théoriques récents suggèrent en effet une coévolution possible entre personnalité et communication. Grâce à une expérience de repasse, nous avons montré que les tamias rayés (*Tamias striatus*) répondent aux cris d'alarme selon leur propre niveau de témérité (représenté par des différences individuelles constantes de vigilance basale) et qu'ils augmentent leur niveau de vigilance à l'entente de cris d'émetteurs téméraires potentiellement considérés comme étant plus fiables. De plus, les récepteurs prennent en compte la témérité des émetteurs indépendamment de leur propre niveau de témérité et de leur niveau de familiarité aux récepteurs, ce qui suggère qu'ils décodent cette information directement des vocalisations. Les effets de la variation individuelle de comportements sur la perception et l'interprétation de l'information sociale

pourraient ainsi avoir des répercussions sur les signaux utilisés dans de nombreux contextes.

Mots-clés : Signaux d'alarme, Communication sonore, Information sociale, Personnalité animale, Variation individuelle, Comportement antiprédateur.

5.1 Abstract

Using social information can benefit individuals in many ways. Responding to alarm signals can, for instance, maximize survival under predation risk. However, foraging individuals should consider the reliability of such risk-based information to balance antipredator behavior and resource acquisition. Receiver decisions could depend on personality effects, as individual variation in risk-taking tendencies (i.e., boldness) could not only affect receiver perception of the signaled threat but also signaler reliability. Recent theoretical models support the possibility of coevolution between personality and communication strategies. Using a playback experiment, we show that wild eastern chipmunks (*Tamias striatus*) respond to alarm calls according to their own boldness level (measured as consistent individual differences in basal vigilance) and that they increase their vigilance response to bolder callers potentially considered as more reliable. Further, receivers respond to the callers' boldness regardless of their own boldness and independently of their familiarity level with callers, therefore decoding this information from vocalizations. Such effects of individual behavioral variation on the perception and interpretation of social information could apply to signals used in a variety of ecological contexts.

Keywords: Alarm signaling, Vocal communication, Social information, Animal personality, Individual variation, Antipredator behavior.

5.2 Introduction

Individuals can enhance decision-making by using social information (Danchin et al. 2004; Dall et al. 2005). In various ecological contexts such as mating, foraging, and predator avoidance, individuals benefit from using information acquired from others to assess and respond to their environment and thus maximize their fitness (Giraldeau et al. 2002; Dall et al. 2005). Assessing sexual signals can for instance improve reproductive success in the context of mate choice (Andersson 1994). In a foraging context, individuals can also use social information to enhance their foraging efficiency and thus their long-term survival (by observing other individuals' discovery of resources or through information exchange; Ward & Zahavi 1973; Danchin et al. 2004; Dall et al. 2005), but they also need to constantly trade off resource acquisition against safety. Many animals therefore engage in antipredator behaviors that can maximize short-term survival under predation risk (Lima & Dill 1990). Responding to alarm signals from conspecifics can therefore be highly beneficial for immediate survival (Blumstein 2007). However, although paying attention to trustworthy signals is worthwhile (Searcy & Nowicki 2005), using socially acquired information can become costly if the reliability of the signal is not ensured (Giraldeau et al. 2002). Responsive behaviors therefore remain adaptive only if they are adjusted to the accuracy of the signals. Devoting less importance to social information that comes from unreliable signalers becomes critical to optimize the trade-off between antipredator behavior and resource acquisition (Pollard 2011). This is highly relevant for alarm communication systems in which the accuracy of the information transferred regarding risk depends greatly on the signalers' capacity to accurately evaluate the presence of a danger (Pollard 2011).

The discrimination of unreliable signalers has been reported in a few alarm-call systems of social mammals, by testing differences in response to callers that differ in their reliability. Reliability was classically considered in relation to familiarity

(through social relationship and spatial proximity to the receiver, Hare 1998; O'Connell-Rodwell et al. 2007; Hollén & Radford 2009) and age (less reliable juveniles are expected to be ignored, Blumstein & Daniel 2004; Hollén & Radford 2009), or even modified through artificial manipulation (Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004). The reliability of public information can also be assessed using the number of signalers asserting that a threat is present (Sloan & Hare 2008). Although receivers would ideally adjust their response to signalers of varying reliability (Pollard 2011), the origin of variation in signaler reliability in natural alarm communication systems remains largely unclear (Hare & Warkentin 2012). This is central, however, to our understanding of why, how and when individuals use social information and how they interpret it. It is thus worth considering that an individual's propensity to emit alarm calls could depend not only on the presence of kin (Maynard-Smith 1965; Blumstein et al. 1997) or on its social status (Fuong et al. 2015), but also on its intrinsic stress response and risk-sensitivity. Low thresholds of emission are linked to high production of stress hormones (high stress reaction along the HPA axis, Blumstein et al. 2006), and alarm signals emitted by overly risk-sensitive individuals should particularly arouse suspicion in receivers as they could be false alarms produced in reaction to unthreatening environmental stimuli, due to individuals' "skittishness" (Pollard 2011), "jumpiness" (Searcy & Nowicki 2005) or "low threshold of excitation" (Hare & Atkins 2001). Receivers could thus truly adjust their responses to the so-called personality of the signalers, as inherent individual risk-taking profiles are known to vary consistently within a population, along a shyness-boldness continuum (Wilson et al. 1994; Réale et al. 2007).

The concept of animal personality (Réale et al. 2007) has recently shed light on many aspects of animal evolutionary ecology (Wolf & Weissing 2012) through its individual-based approach, and consistent individual differences in behavior could be closely linked to intrinsic physiological constraints (POLS concept, Réale et al. 2010).

In a stressful risky situation, less proactive shy individuals would respond with high concentration of stress hormones (Clary et al. 2014), and these high risk-sensitive individuals could be expected to have low thresholds of reaction for emission of alarm signals and for response to the alarms. Personality could thus be one of the critical drivers of variation in responses to signals, an idea strengthened by recent theoretical models which highlight how personality and communication can coevolve (McNamara et al. 2009; Botero et al. 2010; Wolf et al. 2011). Polymorphism in communication strategies is predicted to naturally emerge for both signalers and receivers, and the existence of individual variation in the production and interpretation of signals could maintain consistent individual differences in behavior (Botero et al. 2010). Behavioral consistency could also be favored by individual differences in responsiveness and reliability (McNamara et al. 2009; Wolf et al. 2011). Boldness, one of the most commonly studied personality traits, could thus play a significant role in differential response to alarm signals. Receivers' reaction could be affected by their own boldness, but also be adjusted to the boldness of the alarm signalers, as shy signalers may appear less reliable. Personality could therefore affect individuals' decisions not only through their tendency to use the available social information (Amy et al. 2010; Kurvers et al. 2010) but also through their interpretation of the signals, which could depend on both their own personality and that of the signaler.

In this study, we examine variation in receivers' reaction to conspecific alarm calls beyond any expected effect of familiarity, to determine whether the boldness of the receiver and that of the alarm caller affect these reactions. We also investigate if individuals' boldness influences the degree to which individuals plastically use social information on caller boldness, while assessing if the estimation of such information depends on the receiver's familiarity with the caller. To test these hypotheses, we conducted a field playback experiment with a free-ranging population of individually-marked eastern chipmunks (*Tamias striatus*). Our playback experiment integrated

multiple levels of natural individual variation, as we repeatedly measured the reaction of several receivers to alarm calls from different callers varying in boldness and in their level of familiarity to the receiver. This design offers the opportunity to disentangle the complexity of social information use and interpretation in a natural alarm communication system.

5.3 Material and Methods

5.3.1 Study system

Eastern chipmunks are ground-dwelling Sciurids (Elliott 1978) generally considered as solitary, but they produce different types of alarm calls (Elliott 1978; Burke da Silva et al. 1994) that elicit antipredation vigilance in conspecifics (Weary & Kramer 1995). The alarm communication system in this species may have evolved through kin selection (Maynard-Smith 1965; Burke da Silva et al. 2002), as female kin show spatial clustering (Elliott 1978; Messier 2012). Chipmunks also show consistent individual differences in behaviors (e.g., exploration, docility), which are linked to many facets of their life-history strategies (Montiglio et al. 2012a; Dammhahn et al. 2017).

The study was conducted on two sites, separated by approximately 1 km, in a deciduous forest in Southern Québec, Canada (45°06.785'N; 72°26.078'W). Free-ranging chipmunks were identified and sexed through trapping, and we attached colored flags on their ear tags for recognition from a distance. To facilitate observations, individuals were attracted at temporary feeding patches (supplied with a handful of sunflower seeds mixed with leaves on the ground) established 10 m away from their burrows (previously found using visual observation and radio-telemetry), while observers were placed 10 m away, in the direction opposite to the burrow.

5.3.2 Field recording and selection of alarm calls

We based our playback experiment on "chucking" calls, which are typically emitted in response to aerial threats and consist of low frequency notes repeated within a calling bout (see Fig. 5.1b and Burke da Silva et al. 1994). These vocalizations, along with occasional flight-associated multi-note calls ("trills", Burke da Silva et al. 1994), were primarily elicited under simulated aerial predation risk by experimentally throwing a hat above a foraging individual (see Fig. 5.1a and Hare 1998; Hare & Atkins 2001), and recorded using a directional microphone (Sennheiser ME67/K6, protected by a Rycote Windshield kit 7) connected to a portable digital recorder (Marantz PMD661, sampling frequency of 96 kHz, with Sennheiser HD 280 Pro headphones to monitor the audio recording). From these original recordings, we first selected 20 calls from 15 callers (three calls were recorded in 2013 and 17 in 2014) through a screening process (using Avisoft-SASLab Pro version 5.0) maximizing 1) the playback experiment's crossed design (Fig. 5.1c, to consider only calls from individuals present as potential receivers in 2015), 2) the number of callers with two calls available (ensuring that differential responses to calls would relate to callers' characteristics and not to the context of recording of the calls) and 3) calls with high signal-to-noise ratios (for a broadcast with the most natural effect). We further supplemented this sample by retaining three calls recorded (in 2014) with a digital voice recorder (Olympus VN-702PC, sampling frequency of 48 kHz), for a total of 23 calls recorded during aerial-predator simulations (at a distance of 7.89 ± 1.95 (mean ± s.d.) meters, range: 5-11). Calls naturally emitted were also derived from 10 recordings made with the directional microphone during opportunistic encounters with calling individuals (two calls were recorded in 2013 and eight in 2014, at a distance of 9.88 ± 5.64 (mean ± s.d.) meters, range: 4-20), and from three recordings made in 2014 from video cameras positioned at 3.33 ± 1.53 (mean ± s.d.) meters [range: 2-5] from the feeding patches (Sony HDR CX220 and CX240, sampling frequency of 48 kHz). Thirty-six calls from 20 callers were thus available for

playback (including 16 callers with two calls and four with one call; using each recording technique for callers of varying personalities).

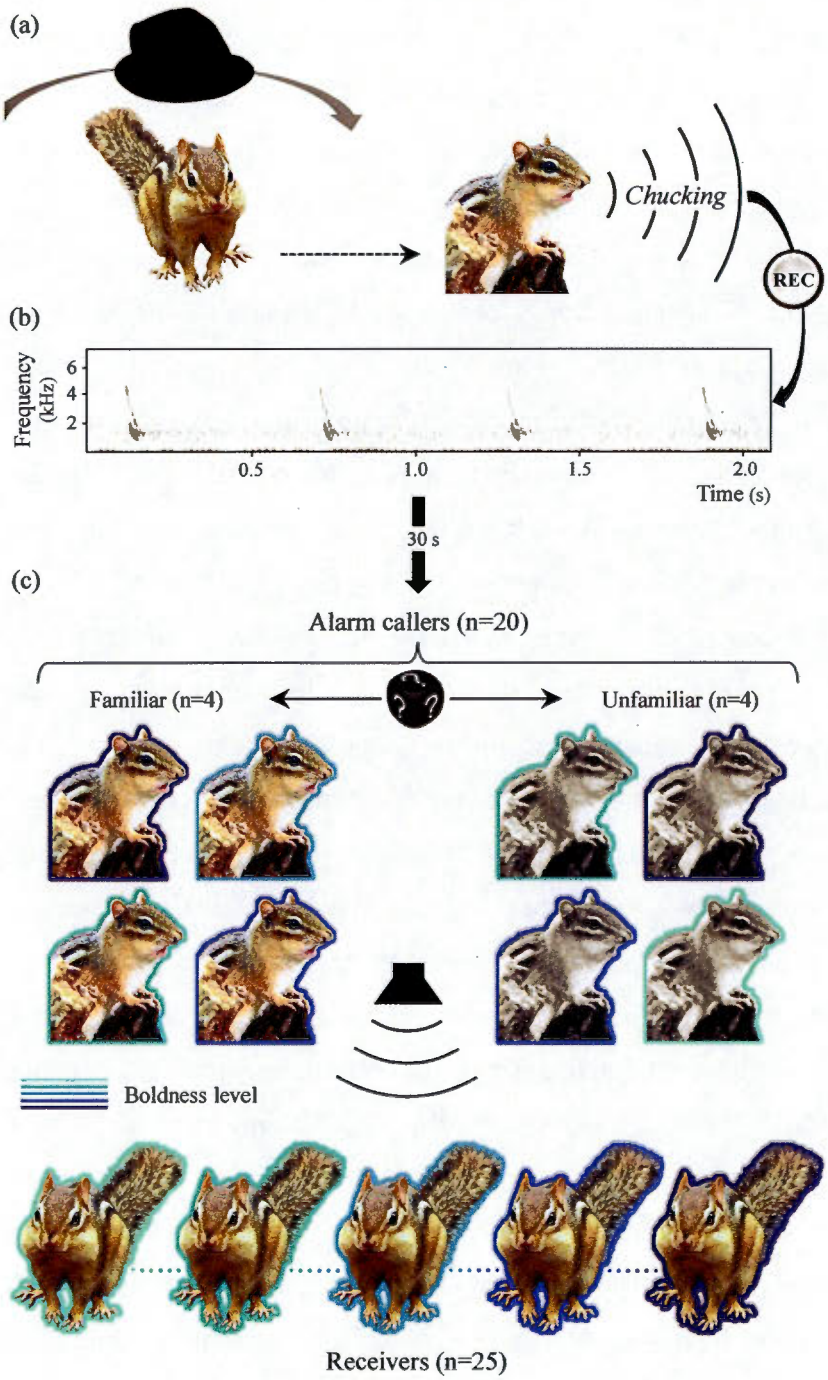

Figure 5.1 Main steps used to implement the field playback experiment. (a) Simulation of aerial predator attack for recording of elicited chucking alarm calls. (b) Acoustical preparation of 30-s calling sequences for playback. (c) Playback design for broadcast of multiple callers' calls randomly assigned to multiple receivers. Callers and receivers varied in their boldness (color code is similar to the one used in Fig. 5.2) and in their level of familiarity.

5.3.3 Acoustical preparation of calling sequences

We prepared the 36 calls for playback as chucking sequences lasting 30 s (Fig. 5.1b), following Weary & Kramer (1995) and to allow consistent comparison of receivers response (natural chucking bouts emitted during 129 hat tests for instance lasted on average (± s.d.) 186.34 ± 215.49 s, median = 98, range: 3-600, and 100 contained on average (± s.d.) 2.65 ± 2.68 trills, range: 1-16). To retain as much individual variation as possible, we kept the trills naturally contained within the chucking bouts (21/36 calls contained on average (± s.d.) 3.67 ± 3.12 trills, range: 1-13, which accounted for 0.81% ± 0.76 (mean ± s.d.) of the 30 s bout, range: 0.10-2.91%). For nine calls that originally lasted less than 30 s (19.98 ± 5.29 (mean ± s.d.) seconds, range: 14-28, which belonged to individuals of varying personalities), we selected a chucking portion (of 7.27 ± 4.83 (mean ± s.d.) seconds, range: 2-13.5) and repeated it on average (± s.d.) 1.78 ± 1.30 times [range: 1-4] right after the cut, insuring smooth and inaudible transitions during broadcast, and keeping the chucking bout's first and last four seconds natural. This type of procedure is commonly implemented for playback experiments (Weary & Kramer 1995; Hare & Atkins 2001; Blumstein & Daniel 2004) and should not have damaged any individuality encoded in the vocalizations as chipmunks tend to emit similar notes in a calling bout (Burke da Silva et al. 1994), and internote intervals were consistently preserved (Frommolt et al. 2003). We also improved the quality of the sequences with a gentle High Pass Filter (set at 0.63 ± 0.03 (mean ± s.d.) kHz, range: 0.6-0.7) which only attenuated low frequencies (through a smooth transition), allowing to get rid of background noise while ensuring that chucking notes at lowest frequencies were not cut off (we confirmed that

chucking frequencies as low as 300 Hz were still preserved, both at the hearing and through acoustic measurements applied in Avisoft). For convenience of playback control we made the calling sequences start and end with two seconds and one minute of silence respectively, and they were further down-sampled to 48 kHz for broadcast compatibility through the digital caller (Foxpro Scorpion X1B). Based on previous work (Weary & Kramer 1995; Emmering & Schmidt 2011) and on the experience of observers, the volume of the calls was calibrated to reach a natural loudness of 50 dB SPLA (mean ± s.d. = 49.51 ± 3.58, range: 40-52.5) at five meters from the source, using a digital sound level meter (Nady DSM-1, calibrated by the manufacturer).

5.3.4 Playback experiment procedure

We ran the playback experiment from 18 June to 10 July 2015, over 20 fieldwork days during which we performed 9.65 ± 3.59 (mean ± s.d.) trials per day [range: 3-16], alternating sites every other day to limit potential habituation to playbacks. A period of at least five hours separated trials performed on a same individual, and we also maximized the distance between two successive trial locations (to avoid testing individuals that may have heard calls from the previous playback). Twenty-five receivers (12 and 13 individuals on each site, 16 females and nine males) received a total of 193 playback trials, being each tested 7.72 ± 1.77 (mean ± s.d.) times [range: 3-9], every 2.3 ± 1.7 (mean ± s.d.) days [range: 0.2-7]. Seventeen individuals played both roles of receivers and callers, as three individuals among the 20 selected alarm callers (10 individuals from each site, 12 females and eight males) disappeared (either dispersed or died) once we started the experiment. Eight other individuals, from which we had acquired behavioral data in 2014, were added as receivers. Only adults were considered in the experiment, and individuals' sex was included in the analyses.

Receivers were exposed to calls from both familiar and unfamiliar callers (precluding their own calls; Fig. 5.1c), allowing to test if they would respond to callers' personality: 1) only for familiar callers, thus potentially assessing this information

through acoustic individual recognition associated with social assessment of callers' behaviors; or 2) for both familiar and unfamiliar callers, thus decoding this information directly from the calls. We considered individuals as familiar when they lived on the same site and most assuredly knew each other through natural encounters (C. Couchoux unpublished field observations from 2014, wherein individuals: 1) engaged in agonistic interactions, or 2) used the same feeding patch, or 3) lived at a close range [~50 m]). Unfamiliar individuals lived on our two different sites and therefore did not know each other (chipmunks have dispersal distance smaller than 1 km; Messier et al. 2012). Each receiver was intended to receive eight calls that were randomly selected beforehand, four calls from familiar callers (random assignment performed for nine receivers having more than four neighbors, the average (± s.d.) being at 4.44 ± 0.82, range: 3-7), and four calls from unfamiliar callers (Fig. 5.1c). To increase the power to detect any possible personality effect for unfamiliar callers, we selected them among the six (out of 10) callers from the other site with the most extreme calling behaviors during aerial-predator simulations (based on the 129 hat tests mentioned above, Fig. 5.1a). For each receiver, we thus randomly selected two (out of three) callers that tended to call for short duration and two (out of three) callers that called for longer duration. As most callers had two calling sequences (16/20), one of them was randomly selected for each playback trial. For each receiver, we then randomly assigned the calls' playback order and reassessed it every evening before the next fieldwork day, among the remaining possibilities. The familiarity treatment was reassigned if chosen three times in a row or more than three times during the first four trials, to ensure that if individuals were to disappear they would have received at least one call from each treatment by their third trial and two of each by their fourth. While four individuals disappeared prematurely, with two individuals that received five trials and two that received three trials, 21 individuals received their eight planned calls, among which nine even got a ninth one (preferentially selected among familiar callers; total of 95 familiar and 98 unfamiliar treatments).

A playback trial consisted in measuring the vigilance reaction of a foraging individual (as the amount of time spent in alert posture, with the head raised) in response: 1) to a 30-s control "soundscape" playback, and (upon subsequent return of the individual) 2) to a 30-s alarm call playback (Fig. 5.1, Weary & Kramer 1995; Baack & Switzer 2000). The control playbacks allowed us not only to confirm that responses were elicited by alarm calls (and not just by the playback apparatus or by the presence of observers nearby), but also to obtain repeated measures of individual basal vigilance that could reflect differential individual risk-taking tendencies (i.e., boldness). We also opportunistically performed 35 separate soundscape tests that were not followed by an alarm call playback (or in five cases by one that was aborted due to the arrival of a conspecific), both to prevent receivers from associating our presence with the broadcast of calls and to gather supplementary observations to estimate the consistency of individuals' basal vigilance (17/25 individuals received on average (± s.d.) 2.06 ± 1.09 of these tests, range: 1-4). Control playbacks consisted of four soundscape sequences of sufficient quality that were derived from recordings of neutral surrounding forest sounds made on our study sites using the directional microphone. They were also subjected to a higher High Pass Filter (set at 1.6 kHz, as it was possible here to remove as much background noise as possible without risking damage to meaningful low-frequency sounds) and to an addition of identical silence sections, and were further down-sampled to 48 kHz. We calibrated their broadcasting volume to reach a natural effect (preliminary setting it to match the volume of the surrounding sounds heard simultaneously in the forest) and we randomly assigned one sequence to each playback trial.

To implement a playback trial, we first filled the feeding patch before the targeted individual's arrival, and perpendicularly installed the digital caller (Foxpro Scorpion X1B) five meters away from the middle point between feeding and observation spots (randomly choosing either left or right side, so calls would not always come from the same direction). We then started the trial once the foraging individual had made at

least one return to the burrow with loaded cheek pouches (Weary & Kramer 1995), and after ascertaining the absence of potentially disruptive conspecifics (within a ~10 m visibility radius). The trial was performed in blind conditions: one experimenter (J.C.) was responsible for planning and playing back the sequences, which were renamed with neutral codes within the remote control (Foxpro TX-9) and on the playbacks' field plan, while the other experimenter (C.C.) was in charge of measuring (with a stopwatch) individual's vigilance during the playbacks and for setting up a backup video camera at the observation spot (useful to later confirm manual measurements if visibility conditions were not optimal). During each playback we also accounted for confounding variables (habitat characteristics, wind, social environment, see details in Clermont et al. 2017). The 20 callers had their calls broadcast 9.65 ± 4.45 (mean ± s.d.) times [range: 3-15], and each of the 36 calling sequences was played back 5.36 ± 0.40 (mean ± s.d.) times [range: 1-11] (the 12 callers' sequences played back on both sites being broadcast more often). On the other hand, the four soundscape sequences were each played back 57.00 ± 3.83 (mean ± s.d.) times [range: 52-60] during 228 tests.

5.3.5 Statistical analyses

To analyze repeated individual measurements of vigilance, we used linear mixed models in R. 3.1.3. (R Development Core Team 2013) with the REML method in package "lme4" (Bates et al. 2015). To most accurately model vigilance variation, we included environmental fixed effects as confounding variables (see Clermont et al. 2017) and we ran preliminary models investigating the effects of individual random slopes along with potentially meaningful interactions (random slope models allow to reduce type I errors and to obtain the most appropriate estimates of variance, Schielzeth & Forstmeier 2009). To reach a minimal final model, we sequentially dropped each nonsignificant effect by comparing models lacking the different terms using likelihood ratio tests (LRT). The LRT *P*-values ($\alpha = 0.05$) were also

corroborated with 95% bootstrapped confidence intervals calculated for the fixed effects' estimates (Bates et al. 2015). We removed nonsignificant random slopes from the model, but kept nonsignificant random effects to avoid potential statistical issues related to the nonindependence of data with repeated measures from the same individual. The models were checked and validated for normality, homogeneity and nonindependence of their residuals through graphical visualizations.

We modeled the variation of individuals' basal vigilance (converted to 60 s) during the 228 control playbacks (for the 25 receivers) and from 28 focal observations performed in 2014 on the three individuals that were only considered as callers. The 256 focal observations lasted on average (± s.d.) 59.15 ± 7.33 seconds, [range: 20-90], and the 28 individuals were each observed on average (± s.d.) 9.14 ± 2.59 times [range: 3-14], every 2.2 ± 2.3 (mean ± s.d.) days [range: 1 minute-13 days]. Random effects included date and individual identity. The starting model included Z-scores for tree cover and number of neighbors as confounding environmental fixed effects (see Clermont et al. 2017), as well as a categorical measure of disturbance (yes or no) resulting from the occurrence of wind or from the presence of conspecifics. We also controlled for a potential habituation effect due to our presence by including the observation's number, which was transformed by subtracting 1 and divided by its standard deviation to set the reference for the first observation. Preliminary models showed nonsignificant individual random slopes for the observation's number (LRT: $\chi^2_2 = 3.08$, $P = 0.21$). After estimating a significant repeatability for the individual random effect (through a LRT comparing the model with and without it, Nakagawa & Schielzeth 2010), we extracted individual best linear unbiased predictors (BLUPs, Pinheiro & Bates 2000) as measures of consistent individuals' basal vigilance level. We further used the reverse of these values (-BLUPs) as scores of individual boldness (highest values are thus for bold individuals, which have low values of basal vigilance).

We analyzed the variation of individuals' vigilance response to conspecifics' alarms calls during the 193 30-s alarm call playbacks, for the 25 receivers (considering the focal chipmunk as still being vigilant when it fled from the feeding patch, see Clermont et al. 2017). Random effects included date and individual identity of both receiver and alarm caller. As in the model for basal vigilance, Z-scores for tree cover, number of neighbors and trial's number were included as confounding fixed effects. Categorical wind intensity (none, low, high, see Clermont et al. 2017) and level of disturbance (none, low or high number of disturbance events from neighbors) were however kept separated for this model (as we specifically made disturbance events rare by trapping intruders). To test our effects of interest, we included: receiver-callers' familiarity, included in interaction with the pair's sex combination; receiver's and caller's personality (using scores of boldness extracted from the model of basal vigilance); an interaction between the boldness of both receiver and caller; and an interaction between the caller's boldness and its familiarity with the receiver. We preliminary tested and removed receivers' random slopes for the trial's number (LRT: $\chi^2_2 = 0.45$, $P = 0.80$), along with the interaction between the trial's number and receiver's boldness (LRT: $\chi^2_1 = 0.54$, $P = 0.46$), as well as callers' random slopes for the trial's number (LRT: $\chi^2_2 = 0.67$, $P = 0.71$), along with the interaction between the trial's number and the caller's boldness (LRT: $\chi^2_1 = 0.54$, $P = 0.46$). Non-significant receivers' random slopes for callers' boldness were also removed from subsequent analyses (LRT: $\chi^2_2 = 0.68$, $P = 0.71$).

5.3.6 Ethics statement

All captures and manipulations were carried out in accordance with the guidelines of the Canadian Council on Animal Care and the protocols were approved through the Université du Québec à Montréal (CIPA permit #760) and the Québec Ministry of Sustainable Development, Environment, Wildlife and Parks (SEG permits #2014-04-22-103-05-S-F and #2015-05-12-106-05-S-F).

5.4 Results

5.4.1 Repeatable basal vigilance as a measure of boldness

Basal vigilance levels, primarily measured during multiple control soundscape playbacks, consistently differed among individuals (repeatability estimated at 22.34% with mixed models, LRT: $\chi^2_1 = 24.38$, $P < 0.001$, Table 5.1a). We therefore extracted and further used -BLUPs values as individual boldness scores (Fig. 5.2a), with individuals with the lowest basal vigilance levels being considered as taking greater risks and classified as the bolder ones.

Table 5.1 Results from linear mixed-effect models on vigilance in eastern chipmunks during (a) control and (b) alarm call playbacks.

(a) Basal vigilance model							
Fixed effects[a]	Estimate	95% CI	χ^2	df	*P*	Random effects	Variance
Intercept	18.88	15.87: 21.93				**Individual**	**16.89**
Disturbance	1.90	-0.28: 4.00	3.01	1	0.083	Date	4.22
Observation number	-3.22	-4.41: -2.02	19.27	1	<0.001	Residual	54.49
[a]Removed from the model after LRT: Number of neighbors ($\chi^2_1 = 1.69$, $P = 0.194$) and Tree cover ($\chi^2_1 = 2.38$, $P = 0.123$). The effect of interest is in **bold**.							
(b) Vigilance response model							
Fixed effects[b]	Estimate	95% CI	χ^2	df	*P*	Random effects	Variance
Intercept	17.01	14.97: 18.97				Receiver ID	9.05
Wind	1.90	0.77: 3.14	9.52	1	0.002	Caller ID	7.49
Number of neighbors	1.80	0.32: 3.24	5.41	1	0.020	Date	1.23
Trial number	-3.81	-4.98: -2.58	24.15	1	<0.001	Residual	53.27
Boldness receiver	-0.62	**-1.08: -0.14**	6.83	1	**0.009**		
Boldness caller	0.51	**0.04: 0.99**	4.19	1	**0.041**		
[b]Removed from the model after LRT: Tree cover ($\chi^2_1 = 0.02$, $P = 0.877$), Disturbance ($\chi^2_1 = 0.10$, $P = 0.753$), **Boldness receiver*Boldness caller** ($\chi^2_1 = 0.18$, $P = 0.667$), **Sex combination*Familiarity** ($\chi^2_3 = 1.62$, $P = 0.655$), Sex combination ($\chi^2_3 = 3.06$, $P = 0.382$), **Familiarity*Boldness caller** ($\chi^2_1 = 1.21$, $P = 0.272$) and **Familiarity** ($\chi^2_1 = 0.001$, $P = 0.972$). Effects of interest are in **bold**.							

5.4.2 No familiarity effect on response to alarm calls

The playback experiment revealed that vigilance during the 30-s alarm call playbacks was not significantly affected by the receiver's familiarity with the alarm caller (Table 5.1b). Moreover, calls received from familiar females (potentially related in our system) did not elicit higher vigilance levels (no interaction between the receiver-caller's sex combination and their familiarity, Table 5.1b).

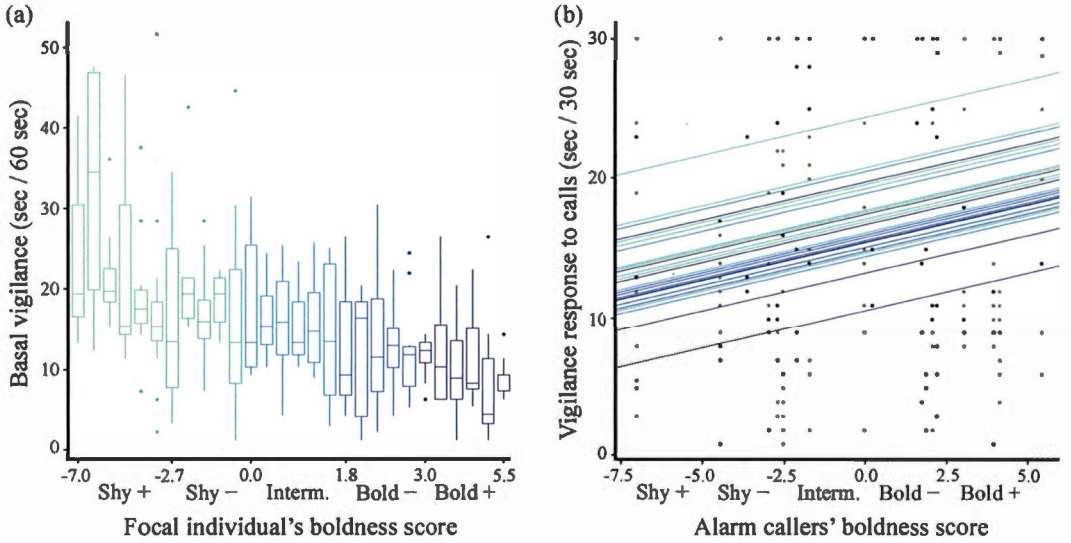

Figure 5.2 Boldness as a driver of risk-taking reaction in chipmunks. (a) Boxplot representing individuals' consistent differences in basal vigilance (n = 256). Individuals (n = 28) are ordered according to their boldness score (-BLUPs), with an increase in blue darkness from shyer to bolder individuals (Interm. = Intermediate). Boxplots show medians, first and third quartiles (middle, upper and lower hinge respectively). (b) Scatterplot illustrating variation in vigilance response to 30-s alarm call playbacks (n = 193). Receivers (n = 25) have their boldness represented using the same colors as in (a), and their intercepts were extracted from the final model not including receiver's boldness (which otherwise encompasses a part of individual variation). Individual slopes of vigilance response used the slope estimate for the population, as there was no significant interaction between receiver's and caller's boldness. Black and grey points represent response to familiar (n = 95) and unfamiliar (n = 98) callers respectively.

5.4.3 Overall effects of boldness on the interpretation of alarm calls

Receivers' vigilance response to alarm calls was significantly negatively affected by their own boldness score: the shyest individuals (with high levels of basal vigilance/low values of -BLUPs, represented in light blue in Fig. 5.2a) reacted the most strongly to alarm calls (Table 5.1b, with high levels of vigilance response, as reflected in Fig. 5.2b by intercepts of lighter blue lines being higher than intercepts of darker blue lines).

Receivers also significantly increased their vigilance level in response to alarm calls from bolder alarm callers (Table 5.1b, Fig. 5.2b). By randomly playing back one of two different calls for most callers (16/20), we ensured that differential reactions were due to the individual characteristics of the callers and not only to the context of recording of their calls.

5.4.4 An unconditional use of the social information

Receivers used the social information provided by the alarm caller's boldness independently of their own boldness (nonsignificant interaction between the receiver's and caller's boldness; Table 5.1b, Fig. 5.2b). In addition, familiarity between the receiver and the caller did not affect the receiver's response to the caller's boldness (nonsignificant interaction between familiarity and caller's boldness, Table 5.1b, Fig. 5.2b).

5.5 Dicussion

Using a carefully designed field playback experiment that integrated multiple levels of natural individual variation, we showed that personality affects the interpretation of social information in eastern chipmunks. Receivers adapted their response to alarm calls based on their own tendency to take risk, but also on the risk-taking behavioral profile of the signaler. This result reinforces the importance of considering individual variation in response to signals. Our results emphasize that behavioral tendencies represent important characteristics of individuals.

Our results showed that receivers did not react more intensely towards calls from familiar neighbors or potential relatives (Fig. 5.3). This suggests that familiar signals are not considered to be more reliable or to represent more imminent danger, in contrast to what has been reported for some social mammals (Hare 1998; O'Connell-Rodwell et al. 2007, but see Blumstein & Daniel 2004; Hare & Warkentin 2012).

Familiarity may convey less valuable information on the imminence of the threat in more spatially dispersed territorial species such as chipmunks. However, alarm calls could still have evolved to be directed primarily towards relatives, as preferential response given to their calls may not be required in cases where the population/species displays spatial clustering of relatives. Moreover, granting more importance to every neighbor or relative is not necessarily a beneficial strategy if these individuals vary in their intrinsic call reliability depending on their personality.

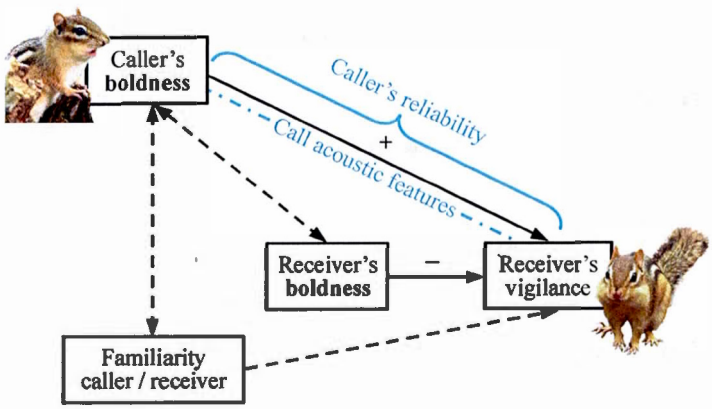

Figure 5.3 Main findings arising from the playback experiment, and their implications for underlying relationships. The effects on receiver's vigilance response to alarm calls, tested through the playback experiment, are represented by black arrows, with thick arrows for significant results and thinner dashed arrows for nonsignificant ones. Double arrows represent interactions. Underlying findings are indicated in blue: the brace emphasizes how the boldness of the caller reflects its reliability, as calls from bolder individuals appeared to be judged as being more reliable by eliciting more intense reactions in the receivers; the dashed-dotted line indicates that the information on caller boldness is decoded directly from the acoustic features of the calls, as receiver reactions to the caller boldness did not depend on their level of familiarity.

In fact, we show that individuals consistently differed in their basal vigilance and that these individual differences in risk-taking behavior (i.e., boldness) play a role in the way receivers perceive and react to alarm calls. Receivers responded to calls according to their own boldness, with shyer individuals being more vigilant that bolder ones in response to alarm calls (Fig. 5.3). This suggests that, in an alarm

context, interindividual behavioral variation can constrain individuals' decisions as much as other individual characteristics such as age, sex or relationship (Hare 1998; Blumstein & Daniel 2004; Hollén & Radford 2009). Receivers use the available social information on threat detection as they increased their vigilance level towards alarm calls (Clermont et al. 2017, see also Weary & Kramer 1995; Baack & Switzer 2000), but their relative level of reaction is dependent on their own risk perception and reflects their own boldness. A receiver's response level is thus constrained by its personality, but the response can still be plastic. Personality constraints and behavioral plasticity are not mutually exclusive (Dingemanse et al. 2010), as an individual's behavioral phenotype is a combination of its unique behavioral tendencies and its responsiveness to environmental variation.

We thus found that receivers also respond plastically to the specificity of the information, as they showed reduced responsiveness towards calls from shyer individuals (Fig. 5.3). Behavioral responses are therefore adjusted to the boldness of the callers, which implies that chipmunks could assess and respond to the alarm caller's reliability (Fig. 5.3). This would suggest that the ability to assess the reliability of the signaler is not restricted to social mammals (Cheney & Seyfarth 1988; Hare 1998; Hare & Atkins 2001; Blumstein et al. 2004). More importantly, we show here for the first time that individuals can perceive information related to a signaler's personality and respond accordingly. While individuals can evaluate the quality of an alarm signal from fixed characteristics of the signaler (e.g., age or relationship level, Hollén & Radford 2009), or from its instantaneous behavior (e.g., in dwarf mongooses, *Helogale parvula*, the elevation position of an alarm caller can reflect its reliability to detect predators, Kern et al. 2017), we showed here that they can also respond to a signaler's intrinsic behavioral characteristics (i.e., risk-taking profile; though the proximate basis of that assessment is presently unknown).

In other contexts, individuals respond to the reliability of the social information by observing social foraging cues from conspecifics. In barnacle geese (*Branta leucopsis*), for instance, individuals who observe other foraging individuals will ignore the social information when it is made incorrect (Kurvers et al. 2010). Also, bumble bees (*Bombus impatiens*) adjust their decisions to the social information depending on its reliability to predict a reward (Dunlap et al. 2016). Although the cost-benefit balance of evaluating the reliability of the social information seems quite profitable in a foraging context, responding to all alarm calls may appear more optimal in an alarm context. The "better-safe-than-sorry" strategy - or "adaptive gullibility" - may indeed prevail in risky situations, given the potential fatal cost of not responding to a genuine alarm (Wiley 1994; Searcy & Nowicki 2005; Beauchamp 2010). However, individuals would limit feeding opportunities by responding to erroneous alarm signals, and should thus reduce time-consuming antipredator behaviors if the social information eliciting them is untrustworthy (Hare & Atkins 2001; Searcy & Nowicki 2005). We show that, just as the vigilance response to alarm calls is predicted to decrease in a group with a high rate of false alarms (Beauchamp & Ruxton 2007), the same holds true at the individual level: vigilance also decreased in response to shyer alarm callers more prone to cry wolf because of their high level of risk-sensitivity.

We further found that the receivers all showed "social competence" (Taborsky & Oliveira 2012), as individuals of different boldness similarly adjusted their response to the social information provided by the alarm caller's boldness (Fig. 5.3). Although it has been shown in some situations that shyer individuals are more prone to plastically adjust their behavior to the behaviors of conspecifics (Harcourt et al. 2009; Kurvers et al. 2010), in an alarm context plastic responses may be selected for and considered adaptive since receivers may benefit from placing less trust in individuals that are overly risk-sensitive.

In addition, we found that receivers did not need to know the callers to evaluate their reliability (as in Cheney & Seyfarth 1988; Hare & Atkins 2001), as they adjusted their vigilance level to the boldness of both familiar and unfamiliar callers. This implies that the assessment of callers' risk-taking tendencies is not necessarily based on social experience, and that cues about caller's boldness could be decoded directly from the vocalizations (Fig. 5.3). The signals could indeed convey information on the tendency of an individual to take risks, especially since alarm calls can encode information about the situation's riskiness (Hollén & Radford 2009) or urgency (Manser 2001). Acoustic characteristics could thus be modulated by the individuals' levels of excitation, which are intrinsically related to stress physiological constraints. Individual variation in sympathetic system reactivity (see POLS concept, Réale et al. 2010) could particularly affect the rate of emission of repetitive calls such as chucking, in the same way it affects heart rate (more proactive individuals have high sympathetic response reflected in high heart rates, Montiglio et al. 2012a). A next research step will be to explore this possibility in chipmunks, as they seem to produce chucking at variable rates and are more responsive to chucking played at higher rates (Weary & Kramer 1995). The presence of trills within chucking bouts also requires further investigation, as these calls are thought to signal highly threatening situations (Burke da Silva et al. 1994) and could be predominantly emitted by overly risk-sensitive individuals.

5.6 Conclusion

The social environment is a crucial component of an individual's environment and the use of social information can greatly impact decision-making, not only in group-living species but also in so-called solitary species, such as chipmunks, which interact with conspecifics on a daily basis. The integration of personality traits to social networks increasingly sheds light on our understanding of complex social behaviors (Aplin et al. 2013) and here we showed that individual variation in behavior can play

a significant role in the perception and interpretation of alarm signals. The individual-based approach, which takes into account widespread interindividual behavioral differences, has brought considerable insights in many research areas (Réale et al. 2007; Réale et al. 2010; Wolf et al. 2012) and could help us understand variation in alarm communication strategies. Studies using playback experiments should thus carefully consider behavioral variation for individuals chosen as receivers and signalers. We advocate the integration of individual behavioral variation in studies of alarm communication systems as personality could broadly affect the way animals communicate about danger in both solitary and social species. Considering individual variation emphasizes the ability of animals to perceive and respond accurately to social information in many ecological contexts.

5.7 Funding

The study was supported by a research team grant from the Fonds de Recherche du Québec - Nature et Technologies (FRQNT) to D.G., D.R. (and Murray Humphries, Fanie Pelletier), by Discovery grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) (D.G., D.R.) and by a Canada Research Chair (D.R.). C.C. was supported by a scholarship from the FRQNT and through grants from the UQAM, and by a National Geographic Young Explorers grant and a Student Research grant from the Animal Behavior Society. J.C. was supported by an Undergraduate Summer Research Award from NSERC and a Biodiversity Science Discovery award from the Quebec Center for Biodiversity Science.

5.8 Acknowledgements

We thank the Green Mountains Nature reserve of the Nature Conservancy of Canada (CNC) for allowing us to access the study sites, as well as all the people that helped in the field to maintain the long-term project over the last 10 years. We are also

grateful to Arnaud Béchet, Anne Charmantier, Christelle Couchoux, Carolyn Hall, Joël Jameson, Rupert Marshall, James Hare and an anonymous reviewer for useful comments on previous versions of the manuscript. We also thank Torben Dabelsteen, Élise Huchard and Rupert Marshall for their advice on the experimental design, and Raimund Specht for his advice on Avisoft's acoustic settings.

5.9 Data accessibility

Analyses reported in this article can be reproduced using the data provided by Couchoux et al. (2017).

CONCLUSION

L'étude de la variation des traits s'insère dans le cadre de l'écologie évolutive, et l'écologie comportementale cherche particulièrement à comprendre et expliquer la variation des traits phénotypiques de type comportemental, en lien avec l'environnement des individus. Bien que les traits comportementaux aient largement été appréhendés à travers leur grande diversité et leur plasticité, des études récentes ont bouleversé le domaine et amené un changement majeur dans la manière d'étudier la variation comportementale, via l'approche individuelle (Wilson et al. 1994 ; Sih et al. 2004 ; Réale et al. 2007 ; Wolf & Weissing 2012). Il est maintenant évident que les individus d'une même population ne peuvent plus être considérés comme équivalents, et cela nous amène à repenser de nombreuses thématiques largement étudiées à l'échelle de la population. La prise en compte de la variation individuelle peut notamment apporter des informations primordiales à la compréhension des comportements exprimés en contexte social (Aplin et al. 2013 ; Dingemanse & Araya-Ajoy 2015 ; Montiglio et al. 2013 ; von Merten et al. 2017), qui sont directement influencés par les caractéristiques des individus. Cette thèse s'insère ainsi dans ce cadre de recherche, en cherchant à étudier les différents niveaux de variation, environnementale et individuelle, qui affectent les comportements des animaux en milieu naturel. J'ai ainsi exploré les sources de variations pouvant expliquer les comportements agressifs des individus lors d'interactions agonistiques, et leurs comportements d'émission et de réponse aux cris d'alarme. Via une approche intégrative, j'ai pu évaluer si ces comportements majeurs, qui sont étroitement liés à la survie des individus, peuvent être expliqués aussi bien par la variation environnementale que par la variation individuelle.

6.1 Contributions

Les études intégrant la variation individuelle au sein des systèmes de communication étant encore très limitées ou quasi inexistantes dans le cas de la communication par signaux d'alarme, j'ai tout d'abord présenté dans le chapitre I (voir Fig. 0.1 : I) une synthèse expliquant l'intérêt d'explorer ces questions, chez les animaux comme chez les plantes. Les nouvelles perspectives de recherche proposées, sur l'existence de variation individuelle dans les comportements de communication par signaux d'alarme chez différents organismes, permettraient ainsi d'intégrer des thématiques d'intérêt majeur pour de nombreux écologistes. Cette étude vise ainsi à contribuer à rassembler des recherches récentes et prolifiques jusqu'alors étudiées de manière séparée, en mettant en avant les liens possibles entre la personnalité animale et la communication volatile chez les plantes. Cet article de synthèse représente également une contribution très originale de mon doctorat, puisqu'au delà de faire office d'introduction à mon sujet de thèse il intègre aussi des sujets de recherche découverts et détaillés lors du cours "examen de synthèse" du programme de doctorat à l'UQAM.

La contribution importante apportée par le chapitre II (Fig. 0.1 : II) se situe en partie dans l'analyse de plus de 2000 interactions agonistiques récoltées en milieu naturel. Cette approche observationnelle a ainsi permis d'intégrer les niveaux de variation naturelle auxquels les individus sont confrontés au quotidien, ce qui donne des informations réalistes sur les facteurs environnementaux et individuels pouvant affecter les décisions agressives des individus. Ce jeu de données a également permis de mesurer les différences individuelles de normes de réaction, qui est un sujet novateur et encore peu étudié via des comportements mesurés en milieu naturel. Cette étude a de plus permis d'apporter un test empirique aux perspectives de recherche formulées par Wilson et al. (2011a) et Briffa et al. (2015), suggérant une intégration des prédictions de la théorie des jeux, et de la variation individuelle dans un même cadre conceptuel et analytique. L'utilisation d'une approche intégrative permet en

effet de mettre en avant les rôles conjoints des effets environnementaux et individuels sur les décisions prises par les individus en contexte social.

La méthode d'enregistrement novatrice présentée en chapitre III (Fig. 0.1 : III) constitue en elle même un apport original de cette thèse, étant issue d'idées directement liées à l'approche globale utilisée, soit le suivi individuel des animaux en conditions naturelles. L'utilisation de cette méthode a pu être concrétisée grâce aux échanges d'idées avec mes collaborateurs et au soutien d'un organisme de vulgarisation. Au delà de l'apport indéniable de cette méthode pour l'enregistrement individuel des vocalisations des petits animaux en milieu naturel et pour l'enregistrement d'autres types de données, sa publication a également permis des retombées importantes pour la visibilité de mon projet. Le sujet des micros espions ayant grandement éveillé l'intérêt des médias et des organismes de vulgarisation, cela a permis à mon projet d'avoir un impact important au niveau du transfert de connaissances. La méthode a également avant tout été utilisée pour récolter des données permettant de répondre à un des objectifs de la thèse, qui est de mesurer les différences individuelles d'émission de cris d'alarme. Je reviendrai sur ces aspects dans la partie analyses futures de cette conclusion, comme ces données n'ont hélas pas encore pu être analysées.

Le chapitre IV (Fig. 0.1 : IV) apporte des informations essentielles sur la variation individuelle des comportements d'émission de cris d'alarme. Cette étude montre en effet que les individus diffèrent de manière constante dans leur propension à émettre des cris lors de la simulation d'évènements de prédation, et que ces différences individuelles sont maintenues entre les contextes. Les individus qui émettent le plus souvent des cris semblent également être les moins proactifs (durant les tests d'arène), mais cette tendance devra être confirmée par des analyses ultérieures, notamment en utilisant des mesures de comportements de prise de risque (i.e., témérité) plus pertinentes au contexte de risque de prédation. Ces résultats démontrent l'importance

de considérer les comportements individuels au sein des systèmes de communication, et pas seulement les comportements moyens à l'échelle de la population. Les individus semblent donc bien varier dans leur perception du risque et ces différences individuelles de sensibilités amèneraient certains individus à émettre plus de fausses alarmes. Ces résultats ont ainsi des répercussions importantes sur notre compréhension de la valeur des informations transmises et de l'interprétation des signaux.

Le chapitre V (Fig. 0.1 : V) constitue une contribution majeure de cette thèse, car il présente des questions novatrices sur les causes de la variation qui existe au sein des systèmes de communication, en montrant pour la première fois que les individus répondent aux cris d'alarme selon leur propre personnalité mais aussi selon celle des émetteurs, en considérant comme moins fiables les cris d'individus peu téméraires qui émettraient plus de fausses alarmes. Cette étude fait ainsi suite au chapitre précédent, en testant explicitement l'impact de la variation de comportement des émetteurs sur la réponse apportée aux signaux. Les résultats apportés par ce chapitre impliquent ainsi des répercussions larges sur notre compréhension de la perception et l'interprétation de l'information sociale chez les animaux, notamment car les individus semblent détecter la personnalité des émetteurs directement dans leurs signaux vocaux. L'originalité et l'intérêt de cette étude repose également sur l'utilisation d'une expérience de repasse d'apparence simple mais complexe à réaliser, ayant intégré de nombreux niveaux de variation individuelle et étant basée sur des cris enregistrés l'année précédente.

6.2 Perspectives et analyses futures

Les résultats présentés dans cette thèse apportent ainsi des informations importantes sur les effets de la variation environnementale et individuelle sur les comportements agonistiques et de communication par cris d'alarme. De nombreuses pistes semblent

toutefois encore à explorer pour élucider certains aspects et pour répondre à des objectifs de la thèse non présentés dans ce document. Des données ont ainsi été récoltées et pourront être analysées dans un futur proche, afin de répondre aux questions présentées ci-dessous.

Tout d'abord, cette thèse s'intéressait initialement plus largement aux comportements agressifs et aux comportements antiprédateurs des tamias, à lier à leur communication sonore. En effet, les tamias émettent également des cris d'avertissement/de dissuasion ou de menace en contextes agonistique et de territorialité (Digweed & Rendall 2009 ; Dabelsteen & Pedersen 1990). Les cris de type chip et "chip-trill" peuvent ainsi également être entendus lors d'interactions agonistiques entre tamias (Dunford 1970 ; Yahner 1978 ; Burke da Silva et al. 1994 ; obs. pers.), et être utilisés par les individus défendant leur territoire (Dunford 1970 ; obs. pers). Je ne rentrerai pas ici dans les détails des hypothèses liées à la variation individuelle attendue de ces cris, mais elle pourra être explorée car de nombreux cris ont été enregistrés. Une complication survenue lors de la réalisation de cette thèse est liée à la complexité insoupçonnée du système de communication sonore des tamias. Au vu des milliers d'enregistrements sonores réalisés sur le terrain, le système de cris des tamias semble en effet bien plus diversifié que celui décrit par les études passées (Dunford 1970 ; Elliott 1978 ; Burke da Silva et al. 1994 ; Weary & Kramer 1995). Le fait d'avoir axé notre étude des cris au niveau individuel, en enregistrant de manière répétée les cris des individus (et en utilisant les micros espions), semble en effet révéler que les caractéristiques acoustiques des cris, ainsi que leur fonction et leur utilisation dans différents contextes, soient beaucoup plus complexes et imbriquées que ce qui a été précédemment avancé. Ces variations pourraient notamment refléter des différences individuelles de communication.

Au delà de la variation individuelle de propension à émettre des cris, un objectif s'est donc rajouté au plan de thèse initial afin d'explorer la diversité individuelle des types

de cris utilisés. Les milliers d'observations réalisées semblent en effet indiquer que certains individus émettraient une plus ou moins grande diversité de cris à travers les contextes. Je planifie ainsi d'utiliser des méthodes statistiques multivariées telles que les analyses de redondance (RDA; Borcard et al. 1992 ; Legendre & Legendre 1998 ; Borcard et al. 2011), largement utilisées en écologie des communautés (Makarenkov & Legendre 2002 ; Legendre et al. 2005), afin de quantifier si la diversité des types de cris émis est lié à différents facteurs environnementaux et surtout à l'identité des individus émetteurs. La variation individuelle pourrait alors jouer un rôle sur la complexité du répertoire vocal utilisé par les différents individus, en plus d'affecter la structure acoustique des cris (voir ci-dessous).

Un des objectifs non présenté dans cette thèse, mais évoqué en chapitre V, concerne les informations qui peuvent être encodées dans les vocalisations. Les signaux sonores peuvent être affectés par de nombreuses caractéristiques intrinsèques ou extrinsèques à l'individu et ainsi contenir de nombreuses informations (Blumstein & Munos 2005 ; Blumstein et al. 2013b ; Charlton et al. 2009 ; Briefer & McElligott 2011). Les cris de nombreuses espèces contiennent par exemple un signal d'identité (voir par exemple Charrier et al. 2001 ; Bee et al. 2001 ; Kennedy et al. 2009 ; Couchoux & Dabelsteen 2015) et ceci a été particulièrement bien mis en évidence chez les Sciuridés (Blumstein & Armitage 1997 ; Blumstein & Munos 2005 ; Schneiderová & Policht 2011 ; Matrosova et al. 2009 ; Digweed et al. 2012). Chez les tamias, bien que les caractéristiques intrinsèques aux individus pourraient être encodées dans leurs cris, cela n'a encore jamais été étudié. Grâce aux milliers de vocalisations enregistrées je pourrai ainsi effectuer la caractérisation acoustique des cris via le logiciel Avisoft (i.e., paramètres temporels, structuraux, de fréquence et d'amplitude), et ainsi chercher à confirmer si les cris des tamias sont individualisés. J'utiliserai des analyses discriminantes permettant d'identifier une combinaison linéaire de facteurs acoustiques pour caractériser les différences entre individus (Nelson & Marler 1990 ; Yorzinsky et al. 2006 ; Charlton et al. 2011 ; Hoffmann et al.

2012). Comme évoqué précédemment, la tâche sera compliquée par le fait que les types de cris ne soient en fait pas clairement définis (avec l'existence de nombreux cris intermédiaires aux chuck, chip et trills), mais je chercherai justement à définir les cris par leurs caractéristiques acoustiques et non par une discrimination visuelle arbitraire. Des analyses préliminaires ont permis de différencier dans un premier temps les cris formés d'éléments uniques (e.g., chuck) ou émis en salve (e.g., chucking) ainsi que les cris dits composés (plusieurs notes successives accolées, e.g., trill). Les chip, chuck (ou l'intermédiaire appelé "chup" ; émis de manière unique ou en salve) ainsi que les trill, chip-trill, "chuck-trill" et "chup-trill" (cris composés) sont alors uniquement différenciés sur des bases acoustiques.

L'analyse acoustique des cris de tamias permettrait également, et avant tout, d'identifier un potentiel signal de personnalité encodé dans les cris, ce que suggère les résultats de l'expérience de repasse présentée en chapitre V. On pourrait s'attendre à ce que les cris d'alarme (et notamment les chucking utilisés dans l'expérience de repasse) puissent fournir de l'information sur les tendances à la prise de risque des individus, notamment car les cris d'alarme semblent pouvoir encoder des informations sur la dangerosité ou l'urgence d'une situation (Hollén & Radford 2009 ; Manser 2001). La réactivité du système sympathique des individus pourrait par exemple avoir une influence sur leur rythme d'émission de cris (nombre de notes dans une salve, formant le cri), comme elle affecte par exemple leur rythme cardiaque et la réaction des individus à la manipulation (Réale et al. 2007 ; Montiglio et al. 2012a). L'émission de trills (ou de manière plus générique, de cris de type composé) mélangés aux chuck pourrait également signaler l'état d'excitation des individus, comme ces cris seraient utilisés dans des situations de menace extrêmes (Burke da Silva et al. 1994). Des analyses pourront être faites dans un future très proche, via les 36 cris utilisés pour la repasse de cris d'alarme et pour lesquels les caractéristiques acoustiques ont déjà été mesurées. J'examinerai ainsi le lien entre le niveau de témérité des individus (estimé via les mesures de vigilance basale) et leur rythme

d'émission de cris émis sous forme de salve (e.g., via le nombre d'éléments, l'intervalle de temps entre les éléments), ainsi qu'avec la quantité de cris composés contenus dans la salve.

Comme évoqué précédemment, l'utilisation des micros espions avait pour but premier d'estimer les variations individuelles d'émission de cris. Ce but doit encore être atteint, car 11 enregistrements de 24 h doivent encore être analysés afin de détecter et de comptabiliser les cris émis par les individus équipés. Bien que j'aurais souhaité pouvoir rééquiper les individus afin de mesurer la répétabilité de leur tendance à émettre de plus ou moins grandes quantités de cris, cela n'a pas été possible pour des raisons logistiques. Le nombre de cris enregistrés pour des individus équipés sur un même site semble toutefois très variable, et pourra être relié à la propension à émettre (ou à la durée des cris émis) en contexte de simulation de prédation. D'autres données sur les émissions de cris durant la capture et lors du test d'arène serviront également à mesurer les différences individuelles d'émission dans différents contextes. Les résultats présentés en chapitre IV seront également complétés avec des données supplémentaires récoltées en 2014, et en intégrant l'effet de mesures environnementales sur la tendance des individus à émettre des cris (flèches pointillées en Fig. 0.1), comme les caractéristiques de l'habitat (Frechette 2007) et la présence de voisins apparentés (Sherman 1977 ; Dunford 1977 ; Wilson & Hare 2006 ; Burke da Silva et al. 1994, 2002). Je chercherai également à lier la tendance à émettre des individus avec leur témérité. Ceci permettrait de confirmer que les individus qui prennent le moins de risque (les moins téméraires) seraient moins fiables (chapitre V : Couchoux et al. 2017) car ils auraient tendance à émettre plus souvent des cris d'alarme, même en situation non liée à un risque réel. Le lien potentiel sous-jacent entre la quantité d'hormones de stress produites et l'émission de cris (Bercovitch et al. 1995 ; Blumstein et al. 2006) chez les tamias pourrait même faire l'objet d'un projet ultérieur, puisque les niveaux de glucocorticoïdes peuvent être extraits des fèces récoltées durant la capture des individus (Montiglio et al. 2012b, 2015).

Le niveau de témérité des individus sera estimé grâce à de nombreuses mesures de comportements anti-prédateurs réalisées sur le terrain. Comme évoqué au début de cette partie, un des objectifs initiaux de cette thèse était également de mesurer les comportements anti-prédateurs des individus de manière répétée, afin d'estimer leur personnalité en conditions naturelles (Ferrari 2010 ; Couchoux & Cresswell 2012). En utilisant les placettes de nourrissage, j'ai ainsi pu mesurer le niveau de vigilance des individus durant leur recherche de nourriture, et également mesurer leurs distances de fuite à l'approche d'un humain (Blumstein 2003 ; Garamszegi et al. 2009 ; Stankowich & Blumstein 2005 ; Blumstein 2006 ; Carrete & Tella 2010 ; Ward et al. 2004 ; Keyel et al. 2012 ; Petelle et al. 2013). En utilisant la même approche analytique que celle présentée dans les chapitres de cette thèse (modèle mixtes), je pourrais ainsi évaluer la répétabilité des comportements de prise de risque des individus, tout en prenant en compte la variation environnementale (voir Appendice A : Clermont et al. 2017). Afin de vérifier l'existence d'un syndrome comportemental liant les traits de personnalité chez les tamias (Sih et al. 2004 ; Montiglio et al. 2012a) et d'évaluer plus généralement les liens entre différents traits comportementaux prédits par le POLS (Réale et al. 2010), j'effectuerai également des analyses en modèles mixtes multivariés pour estimer la covariance entre les traits. J'intégrerai ainsi les mesures comportementales effectuées en conditions non restreintes (prise de risque et mesures d'agressivité individuelles), et les mesures plus expérimentales issues de la capture (docilité et temps de latence à sortir du piège) et des tests d'arène (Martin & Réale 2008a,b ; Montiglio et al. 2010, 2012a). Je pourrais alors vérifier si les profils de proactivité des tamias se reflètent en effet par une covariance positive entre une prise de risque élevée, une faible docilité, une exploration superficielle d'un nouvel environnement et une forte agressivité. Ultimement, l'analyse pourrait également intégrer des traits d'histoire de vie (e.g., âge à la première reproduction, taille de portée) afin de vérifier plus largement les prédictions du POLS (Montiglio et al. 2014, 2015).

6.3 Conclusion générale

Cette thèse a ainsi mis en évidence l'importance d'étudier les différentes sources de variation qui peuvent affecter les comportements des individus, pour obtenir une vision plus complète de la complexité des comportements exprimés en situation agonistique et lors de l'émission et de la réception de cris d'alarme. En conditions naturelles, les animaux répondent ainsi de manière plastique à leur environnement social et physique, mais sont aussi contraints par des différences de personnalités intrinsèques, et peuvent même différer dans leur réceptivité aux changements environnementaux. J'espère finalement que cette étude pourra encourager de nouvelles recherches visant l'intégration des différentes sources de variations pour comprendre les comportements des individus en milieu naturel.

ANNEXE A

INFORMATION SUPPLÉMENTAIRE POUR LE CHAPITRE I

Photo credits for Figure 1.1.1:

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a: Mark Payne-Gill, b: giphy.com, c: Dave Fleetham, d: Wenfei Tong, e: Remy Ware, f: National Geographic Wild, g: Siman Wagen, h: D. Parejo et al. 2012, i: Daniela Canestrari, j: Skeeze, k: Eisner & Aneshansley, l: Caters, m: Richard Hermann, n: taxateca.com, o: phys.org, p: Robert Pillon, q: OpenCage, r: Toni Kutchan, s: Roger Griffith, t: André Karwath, u: lhseeds.com, v: dailypicksandflicks.com, w: Daniel Janzen.

ANNEXE B

INFORMATION SUPPLÉMENTAIRE POUR LE CHAPITRE II

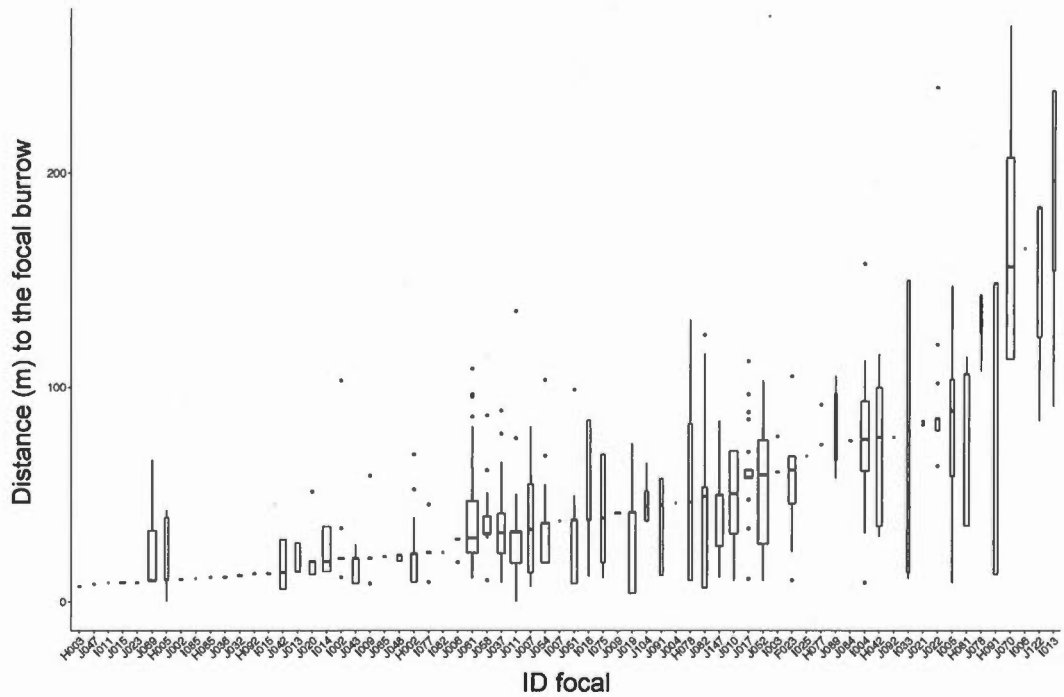


Figure B1 Boxplot of individual distance separating the food patch and the burrow over the whole sample of agonistic interactions. Individuals differed consistently in the distances at which they interacted from their burrow, suggesting the need to use the within-individual centering method. Boxplots show medians, first and third quartiles (middle, upper and lower border respectively). Whiskers represent the variability outside the upper and lower quartiles and points represent outliers. The width of the boxes is adjusted to the sample size available for each individual.

Table B1 Results from linear mixed-effect models on distance to the burrow for the focal and for the opponent, confirming the existence of individual variation and the need to use the within-individual centering method.

Dependent variable	Random effect	Variance	Repeatability	LRT	*P*
Distance burrow Focal	ID Focal	1411.4	0.72	2094.9	< 0.001
	Residual	547.9			
Distance burrow Opponent	ID Opponent	1530.1	0.75	2190.7	< 0.001
	Residual	507.5			

LRT = Likelihood Ratio Tests performed between each model containing the individual random effect and the equivalent null model. Exact LRT values were extracted using the package RLRsim in R.

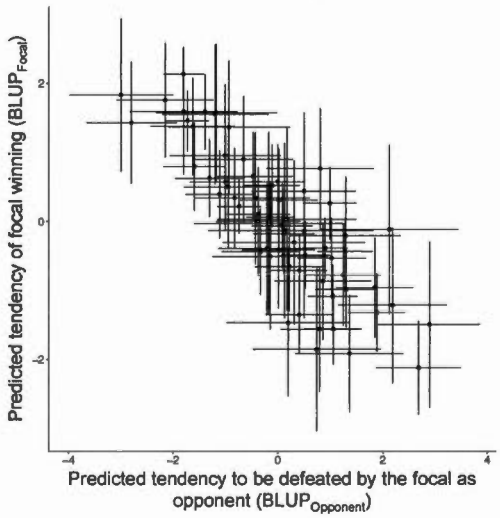


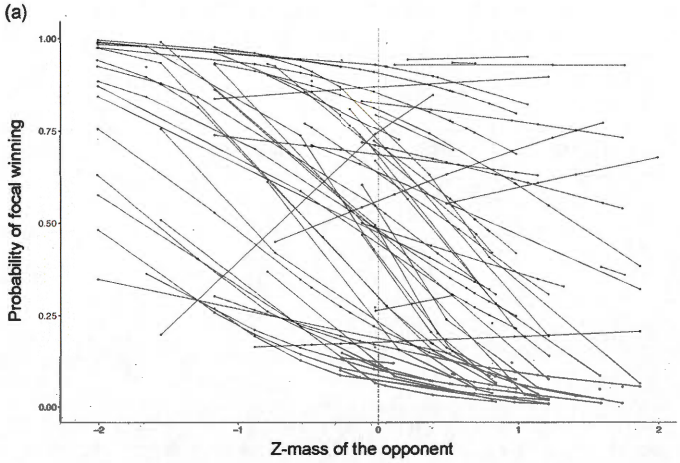
Figure B2 Correlation between an individual's predicted tendency to win as focal and its predicted tendency to be defeated by the focal when it is considered as opponent (BLUPs of intercepts were extracted from the best binomial mixed model for ID focal and ID opponent entered as random factors, n = 2,297 observations with 65 individuals playing both roles of focal and opponent). Black dots represent the BLUP individual values, with vertical and horizontal lines representing the associated standard errors for $BLUP_{Focal}$ and $BLUP_{Opponent}$ respectively.

Table B2 Results from binomial mixed-effect models testing individual random slopes for the probability to win according to different physical and social environmental effects.

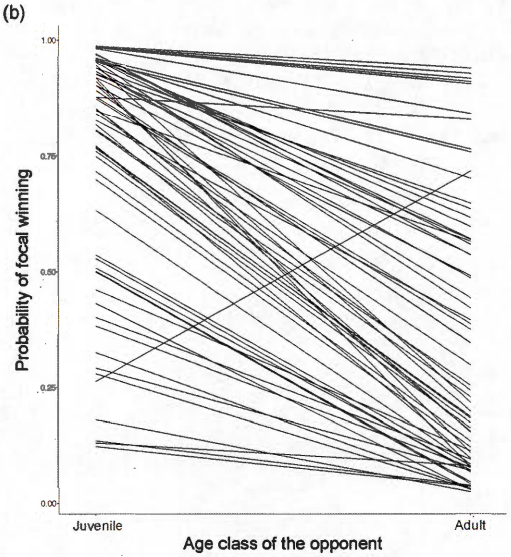
Individual random slopes	No Cov / Cov ID_F	No Cov / Cov *ID_O*	Both Cov / Cov ID_F	Both Cov / Cov *ID_O*	Cor intercept / slope ID_F	Cor *intercept / slope ID_O*
	LRT (χ^2; *P*)					
$DistB_F$	0.82; 0.37	0.36; 0.55	0.55; 0.46	1.00; 0.32	0.33	0.22
$DistB_O$	0.05; 0.82	2.19; 0.14	2.17; 0.14	0.04; 0.85	-0.06	-0.41
$Mass_O$	2.17; 0.14	3.07; 0.08	3.60; 0.06	2.70; 0.10	0.55	0.60
Age_O	1.81; 0.18	2.77; 0.10	4.16; 0.04	3.20; 0.07	-0.65	-0.66
$Aggr_O$	13.93; < 0.001	NA	NA	NA	-0.86	NA

Cov: covariance between individual intercept and slope; ID_F: identity Focal; ID_O: identity Opponent; Cor: Correlation; $DistB_F$: Deviation from the mean distance to the focal burrow; $DistB_O$: Deviation from the mean distance to the opponent burrow; $Mass_O$: Mass of the opponent; Age_O: Age class of the opponent; $Aggr_O$: Aggressiveness of the opponent; see the text for details on the transformation of the different variables.
Mirror effects are indicated in italic, and used the opposite effect (*$DistB_O$*, *$DistB_F$*, *$Mass_F$* and *Age_F*).
Random structure of the models: Model no covariance = (1 | ID_F) + (0 + Effect | ID_F) + *(1 | ID_O)* + *(0 + Effect | ID_O)*; Model covariance ID_F = (Effect | ID_F) + *(1 | ID_O)* + *(0 + Effect | ID_O)*; Model covariance *ID_O* = (1 | ID_F) + (0 + Effect | ID_F) + *(Effect | ID_O)*; Model both covariance = (Effect | ID_F) + *(Effect | ID_O)*.

(a)


Probability of focal winning
1.00
0.75
0.50
0.25
0.00
-2
-1
0
1
2
Z-mass of the opponent

(b)


Probability of focal winning
1.00
0.75
0.50
0.25
0.00
Juvenile
Adult
Age class of the opponent

(c)

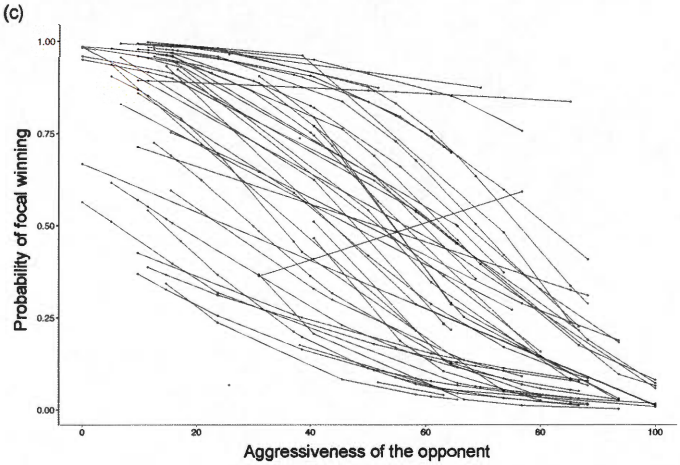

Probability of focal winning
1.00
0.75
0.50
0.25
0.00
0
20
40
60
80
100
Aggressiveness of the opponent

Figure B3 Representation of predicted individual random slopes for the probability of victory of the focal depending on the opponent's (a) mass (Z-score of the average mass), (b) age, and (c) aggressiveness. Slopes predictions were extracted from simplified mixed models including only the effect of interest as a fixed effect and as random slope for the focal (with (a) and (b): n = 2,297 observations with 68 focal individuals and (c): n = 2,194 observations with 53 focal individuals). The model including the opponent's aggressiveness (c) was run on a reduced data set, using only individuals observed at least 10 times as focal individuals. Dots in (a) and (c) represent the different values of the characteristics of the opponents encountered by the focals.

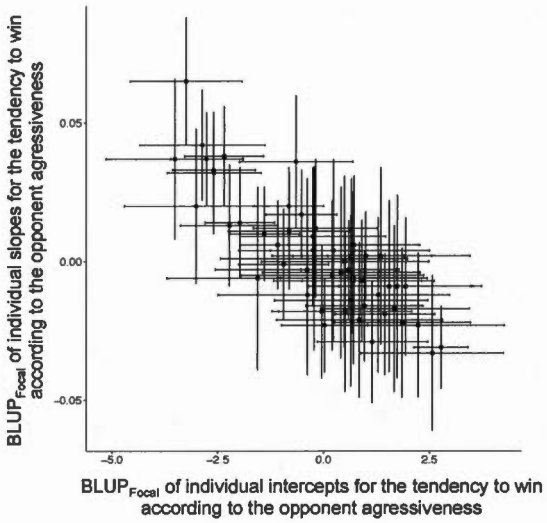


Figure B4 Correlation between an individual's predicted slope and intercept for the tendency to win according to the aggressiveness of the opponent. BLUPs of intercepts and slopes were extracted from the binomial mixed model including focal random slope for the opponent aggressiveness, with a covariance structure between intercepts and slopes (n = 2,194 observations with 53 focal individuals). Black dots represent the BLUP values, with vertical and horizontal lines representing the standard errors for $BLUP_{Focal}$ of slopes and $BLUP_{Focal}$ of intercepts respectively.

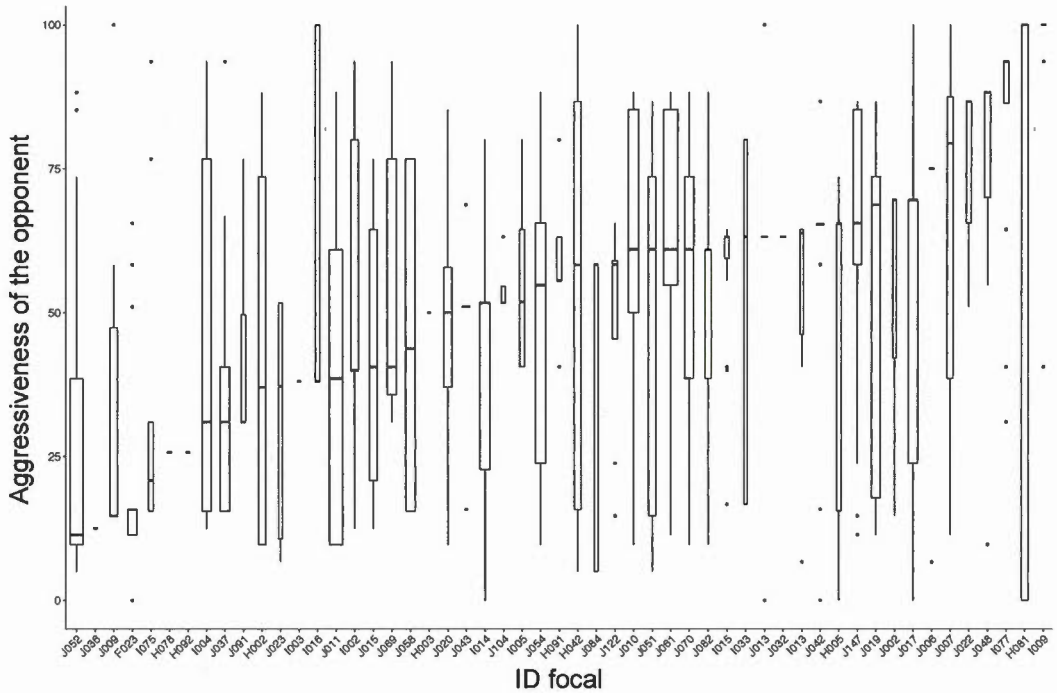


Figure B5 Boxplot showing the existence of individual differences in the percentage of victory of the opponents encountered by the focals, suggesting that the probability to win of focals is constrained by their social environment. Boxplots show medians, first and third quartiles (middle, upper and lower border respectively). Whiskers represent the variability outside the upper and lower quartiles and points represent outliers. The width of the boxes is adjusted to the sample size available for each individual.

Table B3 Results from linear mixed-effect model on percentage of victory of the opponents encountered by the focals, showing the existence of individual variation in the focal tendency to encounter opponents of different levels of aggressiveness.

Dependent variable	Random effect	Variance	Repeatability	LRT	*P*
% victory opponent	ID Focal	191.4	0.23	364.64	< 0.001
	Residual	629.7			

LRT = Likelihood Ratio Tests performed between a model containing the individual random effect and the equivalent null model. Exact LRT values were extracted using the package RLRsim in R.

ANNEXE C

INFORMATION SUPPLÉMENTAIRE POUR LE CHAPITRE III

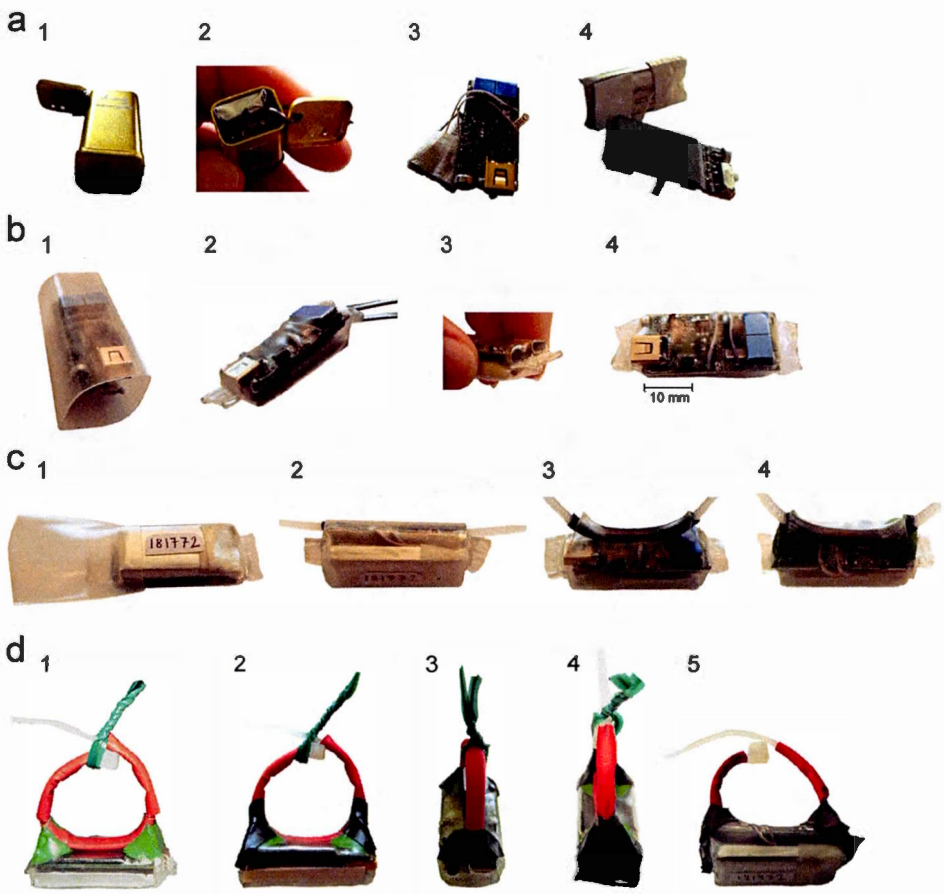


Figure C1 Illustration of the different steps implemented to design the spy microphone device into a wearable collar-mounted device for small mammals (details in the Methods section).

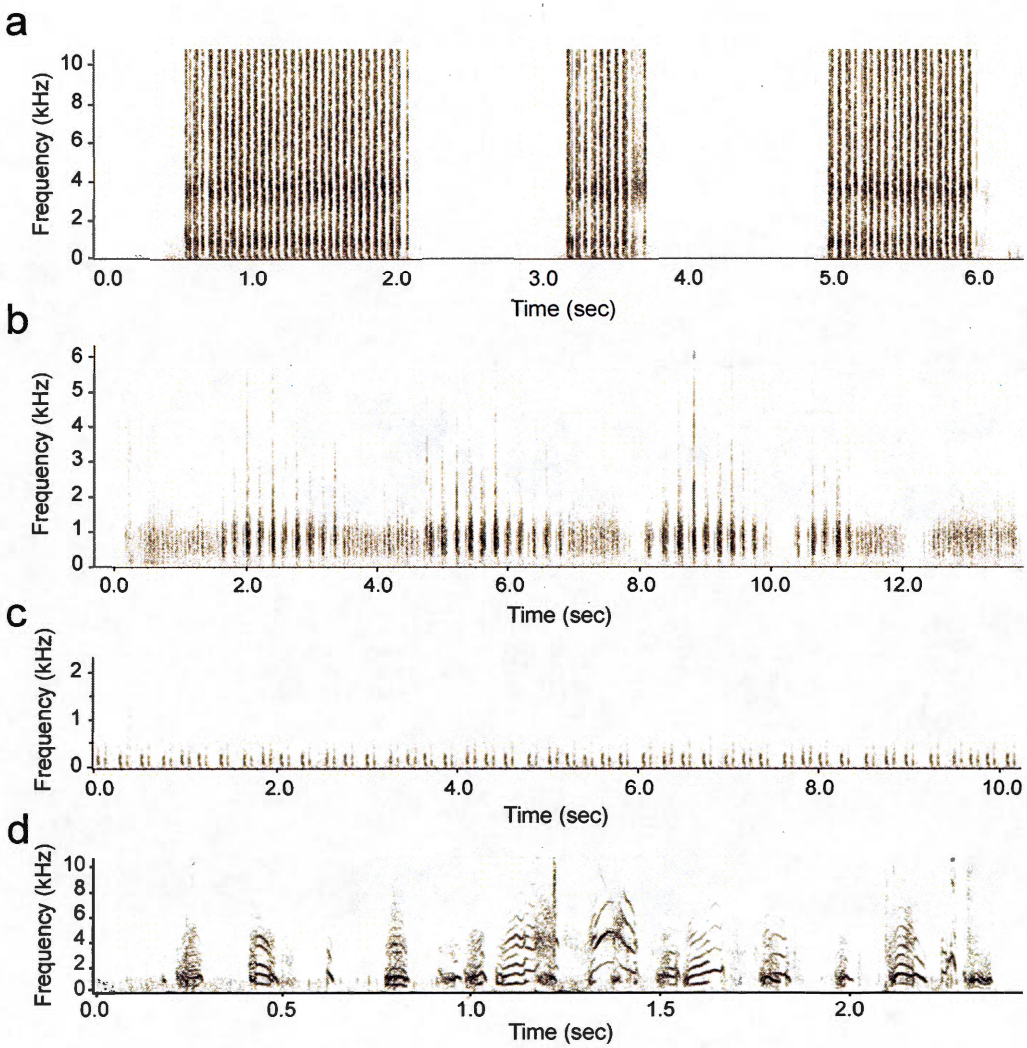


Figure C2 Spectrograms showing different behavioral data that could be estimated through the spy microphone recordings. (a,b) Representation of two different scratching sequences. (c) Illustration of a high quality resting heart rate. (d) Example of whining recorded in a female burrow before pups emergence.

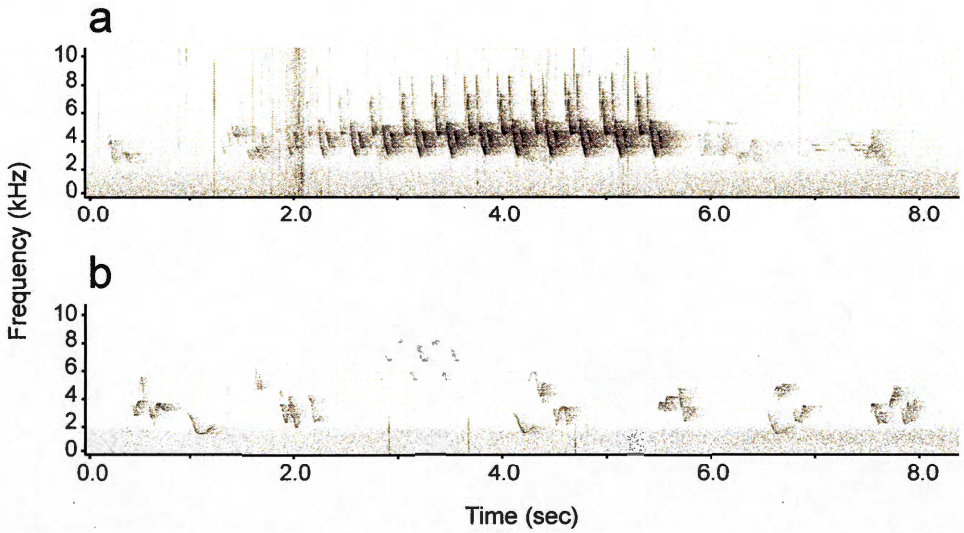


Figure C3 Sound spectrograms illustrating the possibility of recording the soundscapes of the equipped individuals. In the recording we can recognise (a) an ovenbird (*Seiurus aurocapilla*) and (b) a red-eyed vireo (*Vireo olivaceus*).

Contenu Audio et Vidéo supplémentaire, accessible en ligne : https://www.nature.com/articles/srep10118#supplementary-information

Supplementary Audio Recording A1: Illustration of the soundscape recorded by a chipmunk equipped with the recording device: sounds of Canadian geese passing flying over the canopy.

Supplementary Audio Recording A2: Example of some whinings recorded by a female chipmunk equipped with the recording device, sounding like emissions from pre-emerging pups in the maternal burrow.

Supplementary Video V1: Example of an individual chipmunk equipped with the recording device, attending to its natural activities such as (a) feeding on a beech nut and (b) grooming.

Supplementary Video V2: Example of an individual chipmunk equipped with the recording device, attending to its natural activities such as foraging under windy conditions, along with scratching events.

Supplementary Video V3: Example of an individual chipmunk equipped with the recording device, returning to its burrow.

APPENDICE A

ASSESSING ANTI-PREDATOR DECISIONS OF FORAGING EASTERN CHIPMUNKS UNDER VARYING PERCEIVED RISKS: THE EFFECTS OF PHYSICAL AND SOCIAL ENVIRONMENTS ON VIGILANCE

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Behaviour, 2017. *154*(2), 131-148 (doi: 10.1163/1568539X-00003414).

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Behaviour 154 (2017) 131–148

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Assessing anti-predator decisions of foraging eastern chipmunks under varying perceived risks: the effects of physical and social environments on vigilance

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Accepted 12 November 2016; published online 19 November 2016

Abstract

Animals foraging under risk have to trade-off resource acquisition and predator avoidance. Environmental factors can modulate the level of risk and should thus influence the expression of anti-predator behaviours such as vigilance. In this study, we investigated the effects of physical and social environments on eastern chipmunks' (*Tamias striatus*) vigilance, by varying the perceived risk through playback experiments of alarm calls and neutral environmental sounds, and by integrating habitat and weather characteristics, as well as neighbour density. Chipmunks showed higher levels of vigilance when foraging in more open habitats, under high wind conditions, when they heard alarm calls and when surrounded by a high neighbour density. The effects of wind intensity and neighbour density on vigilance were also stronger during the broadcast of alarm calls rather than neutral sounds. Our results emphasize how both the physical and social environments can modify risk perception and therefore risk-taking decisions of foraging individuals.

Keywords

predation risk perception, anti-predator behaviour, social monitoring, vigilance, playback experiment, alarm call, eastern chipmunk.

1. Introduction

Prey spend most of their time searching for food and avoiding predators. However, these two activities are often conflicting, as foraging is a risky activity during which animals expose themselves to predators (Lima & Dill,

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DOI 10.1163/1568539X-00003414

1990; Lima, 1998; Eklov & Halvarsson, 2000). Predation risk therefore limits resource acquisition (Sih, 1980; McNamara & Houston, 1987; Cresswell, 2008). In many animal species, individuals make decisions and adjust their behaviour according to a prior assessment of the level of risk. To maximize fitness, foraging animals often trade-off starvation against predation risks by engaging in anti-predator behaviours like vigilance (McNamara & Houston, 1987; Verdolin, 2006; Cresswell, 2008; Sansom et al., 2009). Vigilance is usually described as periods during which foraging individuals raise their head to detect an approaching predator or competitor (Loughry & McDonough, 1988; Otter, 1994; Trouilloud et al., 2004; Beauchamp, 2015). Different environmental factors can increase the level of risk of a given situation and can thus influence how animals trade-off between exposure and foraging.

The physical environment surrounding the animal can affect its perception of the level of risk (Verdolin, 2006; Beauchamp, 2015). Habitat characteristics can greatly influence anti-predator behaviour (Lima & Dill, 1990; Enstam & Isbell, 2002; Ferrari et al., 2009; Bednekoff & Blumstein, 2009; Beauchamp, 2015). Verdolin's (2006) meta-analysis on foraging and predation risk trade-offs showed that the habitat structure can indicate the risk of predation for a prey. Open habitats are typically associated with fewer refuges (McAdam & Kramer, 1998; Martin & Réale, 2008a), and their lower structural complexity can increase predator captures (Longland & Price, 1991; Landry-Cuerrier, 2008). Herbaceous plant cover also modifies the perceived level of risk of many species (Arenz & Leger, 1997; Mahan & Yahner, 1999; Blumstein & Daniel, 2002; Ebensperger & Hurtado, 2005; Bednekoff & Blumstein, 2009; Ferrari et al., 2009) and high risk is often associated with low cover (Verdolin, 2006; Beauchamp, 2015). Other aspects of the physical environment, such as weather conditions, can influence risk perception (Yasué et al., 2003; Beauchamp, 2015). For example, high wind could create background noise that reduces an individual's ability to detect an approaching predator (Hilton et al., 1999; Yasué et al., 2003; Quinn et al., 2006) thus increasing perceived risk (Quinn et al., 2006) and vigilance level (Beauchamp, 2015), as shown in some species that were observed to engage in less foraging activities under such conditions (Yasué et al., 2003; Hayes & Huntly, 2005; Fairbanks & Dobson, 2007).

The social context in which foraging animals are located can also influence risk perception. For example, many species communicate with alarm

calls when facing predation risks (Klump & Shalter, 1984; Blumstein, 2007; Hollén & Radford, 2009; Zuberbühler, 2009). Vigilance increases when hearing an alarm call as this signal can reflect the presence of a predator (Weary & Kramer, 1995; Bonenfant, 1996; Hare, 1998; Baack & Switzer, 2000; Blumstein et al., 2004). In addition to being used for predator detection, vigilance behaviour can also serve for conspecific monitoring (Hirsch, 2002; Kutsukake, 2007; Gaynor & Cords, 2012; Beauchamp, 2015). Several studies conducted on social species assessed the effect of group size on vigilance and found that individuals usually decrease their level of vigilance as group size increases (reviewed in Beauchamp, 2015), because of the dilution and/or the predator detection effects (Lima & Dill, 1990; Beauchamp, 2015). However, this is not always the case: for example, Favreau et al. (2010) found that eastern grey kangaroos' (*Macropus giganteus*, a social species) level of vigilance increased with group size due to social monitoring. Conspecifics can also be seen as potential threats in a context of competition, for both social and territorial species. In such cases, vigilance increases with the number of nearby conspecifics, possibly due to food, territory or mate competition (Hirsch, 2002; Kutsukake, 2007; Beauchamp, 2015). The time allocated to foraging can thus depend on social aspects like neighbour density (Unck et al., 2009; Gaynor & Cords, 2012).

All of the effects previously discussed can alone drive changes in risk perception and vigilance, but as briefly discussed by Beauchamp (2015), additive and interactive effects are also probably very common, but not often considered. Frid's (1997) study on Dall's sheep (*Ovis dalli dalli*) is one example showing that risk factors can have interactive effects on vigilance: the effect of group size depended on the level of predation risk created by the proximity to a refuge. When sheep were far from cliffs, vigilance increased as group size decreased, but when they were closer, the effect of group size on vigilance was either weak or absent (Frid, 1997).

In this study, we assessed the effects of both physical and social environments on risk perception by measuring vigilance behaviour in a wild population of eastern chipmunks (*Tamias striatus*). Eastern chipmunks are solitary and diurnal rodents observed in most of Eastern North American forests (Elliot, 1978; Snyder, 1982). They are central-place foragers that defend territories and resources through agonistic interactions with neighbouring individuals (Dunford, 1970; Elliot, 1978). When foraging, chipmunks use vigilance as an anti-predator behaviour to assure quick predator detection

(Lima & Dill, 1990; Otter, 1994; McAdam & Kramer, 1998), by raising their head while foraging (Otter, 1994; Trouilloud et al., 2004). When in presence of a predator (or of another risk), they often escape and seek refuge in their burrow, or under rocks, plants or woody debris, and can emit context-specific calls of differing acoustic structures (Burke da Silva et al., 1994). For example, when facing an aerial threat, they produce 'chucks'; low frequency calls repeated in bouts (Burke da Silva et al., 1994). The function of these calls is still unclear, though the hypotheses of kin selection (Burke da Silva, 2002) and predator deterrence (Bonenfant, 1996) are favoured, but chipmunks do become more vigilant when hearing calls of surrounding individuals (Weary & Kramer, 1995; Bonenfant, 1996; Baack & Switzer, 2000).

More specifically, we conducted playback experiments by broadcasting either sounds of a neutral environment or eastern chipmunks' alarms calls, in order to mimic situations associated with different levels of risk. We investigated the effects of these two different contexts on vigilance, along with the potential effects of the surrounding environment such as the characteristics of the habitat, wind intensity, and the density of neighbours. We expect an effect of the physical environment on chipmunks' vigilance: chipmunks should be more vigilant when they are foraging in more open habitats, where tree and herbaceous plant covers are low. Vigilance should also increase when wind intensity is high. Moreover, the social environment should also affect chipmunks' vigilance, so that individuals would become more vigilant when hearing conspecifics' alarm calls. Foraging individuals should also show higher levels of vigilance under a high density of neighbour, as an expected result of social monitoring. Finally, we also expect to observe an increase in vigilance caused by joint effects of the physical and social environments. The effects of covers, wind intensity and number of neighbours should be stronger when chipmunks hear alarm calls (higher level of risk) than natural sounds.

2. Material and methods

2.1. Study site and monitoring

This study took place in the Nature Conservancy of Canada (NCC) Green Mountains Nature Reserve, in the Mount Sutton, QC, Canada (45°06.785′N, 72°26.078′W). The study site consists of a deciduous forest dominated by sugar maples (*Acer saccharum*) and American beech (*Fagus grandifolia*),

which are both mast-producing trees and food sources for chipmunks (Elliot, 1978). As part of a long-term project on this site, chipmunks are regularly captured during each field season (from May to September), sexed and marked with ear tags and coloured flags for individual identification. Individual burrows were located through visual observations and radio-telemetry.

In order to facilitate the observation of foraging chipmunks, we set up a feeding patch supplied with sunflower seeds (i.e., each patch was filled for seven non-consecutive days on average, during the time of observation), at 10 m from each individual burrow (distance determined to make visual observations possible without interfering with chipmunks' natural behaviours). We observed chipmunk foraging behaviour at 10 m from the feeding patch, in the direction opposite to the burrow. Habitat characteristics were evaluated within a circle of an approximate radius of 10 m, with the feeding patch in the middle: we estimated the proportion of space occupied by tree trunks at breast height (for tree cover) and by herbaceous plants (for herbaceous plant cover). The average covers, estimated on the 24 feeding patches where the observations took place, were of 35% for tree cover (range 10–60%) and of 53% for herbaceous plant cover (range 10–90%).

For the estimation of neighbour density, we counted the number of individuals living at a distance of 20 m and less from the feeding patch (excluding the focal individual), so that only immediate neighbours foraging in the same area were considered. We determined chipmunks' geographical location using trapping data from the whole population. We calculated the centroid of each individual's home range by taking the average of every captures' coordinates, but we used only 51 of the 77 chipmunks captured on the site which had at least five captures (individual number of captures ranging from 5 to 31). The average number of neighbours surrounding a chipmunk was 1 (range 0–3) and we used this measure as an indicator of a chipmunk intra-specific competition on his territory.

2.2. Playback experiment

During the months of June and July 2015, while focal individuals were foraging at the feeding patch associated with their burrow, we ran playback tests using a FOXPRO Scorpion digital game caller by successively playing back two different recordings that each lasted 30 s: (1) neutral natural environmental sounds, which we call a soundscape and (2) an alarm call (chucking bouts with occasional trills) that was recorded during natural or simulated

predation events during the 2014 field season. The sounds that were broadcasted were selected among 4 different recordings of soundscapes and 36 recordings of alarm calls emitted by one of 20 different individuals (i.e., the callers). All recordings were prepared using AVISOFT-SAS Lab Pro version 5.0.

A total of 25 focal chipmunks were tested on average 9 times (range 3–12) with soundscapes and on average 8 times (range 3–9) with different alarm calls (a given chipmunk never heard the same alarm call twice). We made sure each chipmunk received calls from neighbours and from unknown individuals living on a different study grid, to diversify the degree of relatedness between the caller and the focal individual. Three individuals present at the beginning of the field season, when the study design was established, disappeared afterwards during the season (either dispersed or died), and therefore could not be used as focal individuals. In total, we performed 193 tests during which we broadcasted alarm calls (the 36 different recordings were played 5 times on average (range 1–11)) and 228 tests with soundscapes (the 4 different recordings were played 57 times on average (range 52–60)). To limit possible habituation effect, chipmunks usually received only one alarm call playback every two days, but in 28 occasions (out of the 193 alarm call playbacks) individuals received two alarm calls on the same day (with at least 5 h separating the two tests). On average, time between alarm call playbacks was 2 days and 8 h (minimum of 5 h and a maximum of 7 days).

We measured the time spent vigilant by focal individuals during the 30-s playback and for 30 s following the playback, for a total of 60 s, for each soundscape and alarm call test. We considered a chipmunk to be vigilant every time it stopped foraging and raised its head. Some chipmunks escaped during alarm call playbacks (for 58 of the 193 alarm call playbacks). For those individuals, time spent vigilant during the escape was considered as maximal, as they were observed to be still vigilant, but just further away from the feeding patch. Therefore, in those cases, time spent vigilant was equal to the time of the escape plus the time spent vigilant when back at the feeding patch, or of 60 s when they did not come back to the feeding patch. Even if we are losing some variability by approximating time spent vigilant when chipmunks escaped, this variable seems to fairly represent risk taking during the playback, which is what we were interested in within the scope of this study.

During each playback, we evaluated wind intensity (no wind, low wind or high wind intensity), based on an estimation of the perception of the wind gusts in the canopy that produced relatively low or high background noise. We did not consider other aspects of the weather as the experiment was conducted on a short time period (mid-June to mid-July), during which the temperature is relatively stable, and we did not collect data during rainy days.

2.3. Statistical analysis

Data analysis was performed using version 3.2.2 of the software R (R Development Core Team, 2013). We standardized percent tree cover and percent herbaceous plant cover to adjust scaling problems and help interpret model estimates (by z-transforming them, i.e., $z = \frac{x-\bar{x}}{\sigma_x}$, where x is the uncorrected measure of the variable, and σ_x is the standard deviation of the variable; Schielzeth, 2010). The variation of time spent vigilant during each 60-s test was analysed with a linear mixed model (function 'lmer' from package 'lme4', using REML, Bates et al., 2015). The model was checked and validated for normality, homogeneity and non-independence of its residuals based on a visual exploration of residuals plotted against fitted values, qq-plots, and histograms. We tested for the significance of the following fixed effects: tree cover, herbaceous plant cover, wind intensity (categorical variable: no wind, low wind or high wind intensity), number of neighbours, playback type (categorical variable: soundscape or alarm call), as well as second-order interactions of playback type with tree cover, herbaceous plant cover, wind intensity and with number of neighbours. We also included as potentially confounding variables the sex of the focal individual, to control for possible sex differences in vigilance (Beauchamp, 2015), as well as the individual's test number, to control for potential habituation to the tests. The 95% confidence intervals associated with the fixed effects' estimates, presented in Table 1, were calculated using bootstrap (function 'confint'). Model selection was performed using Likelihood Ratio Tests (LRT) (function 'drop1' with the option test = 'Chisq'), where the full model is compared with models missing each of every term (for this part models were fitted by 'Maximum Likelihood'). In this way, non-significant terms (at $\alpha = 0.05$) were successively removed one by one based on the LRT values. Chipmunk identity, date and recording identification number (because each recording was played more than once) were added to the model as random effects, to control for

Table 1.
Results of the starting and final linear mixed models explaining time spent vigilant (in s) in eastern chipmunks of Mount Sutton, QC, Canada ($N = 421$) and Likelihood Ratio Tests (LRT).

	Model			LRT		
	Estimate (95% C.I.)	SE	t	χ^2	df	$p_r(>\chi^2)$
Starting model						
(Intercept)	22.70 (16.10: 29.34)	3.43	6.63			
TC	−1.76 (−3.64: 0.09)	0.99	−1.78	3.52	2	0.172
HPC	0.05 (−1.76: 1.85)	0.91	0.05	0.02	1	0.992
WI/low	−0.62 (−3.63: 2.57)	1.59	−0.39	30.69	4	<0.001
WI/high	1.35 (−3.08: 5.97)	2.31	0.59			
PT	9.25 (3.02: 15.53)	3.20	2.90	49.79	6	<0.001
NN	0.51 (−1.84: 2.90)	1.22	0.42	10.53	2	0.005
Focal individual sex	2.99 (−1.16: 7.23)	2.19	1.36	2.01	1	0.156
Individual's test number	−0.89 (−1.18: −0.57)	0.15	−5.87	21.29	1	<0.001
PT × TC	0.04 (−2.39: 2.42)	1.25	0.03	0.01	1	0.927
PT × HPC	0.00 (−2.49: 2.51)	1.23	0.00	0.02	1	0.902
PT × WI/low	4.93 (0.47: 9.18)	2.23	2.21	17.10	2	<0.001
PT × WI/high	12.64 (6.46: 18.48)	3.07	4.12			
PT × NN	5.23 (2.01: 8.49)	1.67	3.13	9.83	1	0.002
Final model						
(Intercept)	23.90 (17.51: 30.31)	3.30	7.24			
TC	−2.13 (−3.97: −0.32)	0.93	−2.28	5.21	1	0.022
HPC						
WI/low	−0.52 (−3.56: 2.64)	1.58	−0.33	30.7	4	<0.001
WI/high	1.24 (−3.25: 5.80)	2.30	0.54			
PT	9.31 (3.05: 15.49)	3.16	2.95	50	4	<0.001
NN	0.45 (−1.74: 2.71)	1.14	0.40	11.6	2	0.003
Focal individual sex						
Individual's test number	−0.91 (−1.20: −0.60)	0.15	−5.97	23	1	<0.001
PT × TC						
PT × HPC						
PT × WI/low	4.83 (0.42: 9.12)	2.21	2.18	17.5	2	<0.001
PT × WI/high	12.67 (6.61: 18.60)	3.05	4.16			
PT × NN	5.24 (2.22: 8.27)	1.53	3.43	10.7	1	0.001

Percent tree cover and percent herbaceous plant cover were z-transformed. Wind intensity, none was considered as the reference for wind intensity in the model. Playback type, soundscape was considered as the reference for playback type in the model. Focal individual sex, female was considered as the reference for focal individual sex in the model. Abbreviations: TC, tree cover; HPC, herbaceous plant cover; WI, wind intensity; PT, playback type; NN, number of neighbours.

unmeasured factors and pseudoreplication. Model selection therefore also consisted in testing the significance of each random effect, using LRTs between models with and without each random effect.

3. Results

The final best model explaining chipmunks' vigilance during each 60-s test (for both soundscapes and alarm calls) contained tree cover, wind intensity, number of neighbours, playback type, individual's test number, playback type in interaction with wind intensity and playback type in interaction with number of neighbours (Table 1).

We first found an effect of the physical environment: chipmunks increased their vigilance when tree cover was lower (Table 1 and Figure 1), but there was no significant effect of herbaceous plant cover (Table 1). Vigilance did

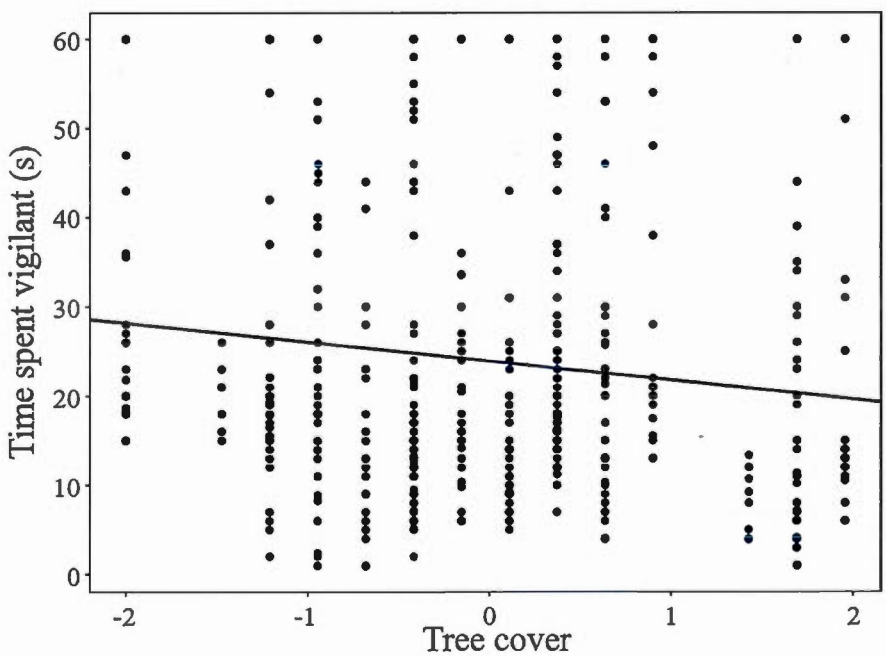

Figure 1. Time spent vigilant during playbacks as function of tree cover (z-transformed percent tree cover) in eastern chipmunks of Mount Sutton, QC, Canada. Time spent vigilant (in s) is for the complete 60-s test. The solid line shows the linear regression predicted by the final model. The intercept was estimated at wind intensity = none and playback type = soundscape.

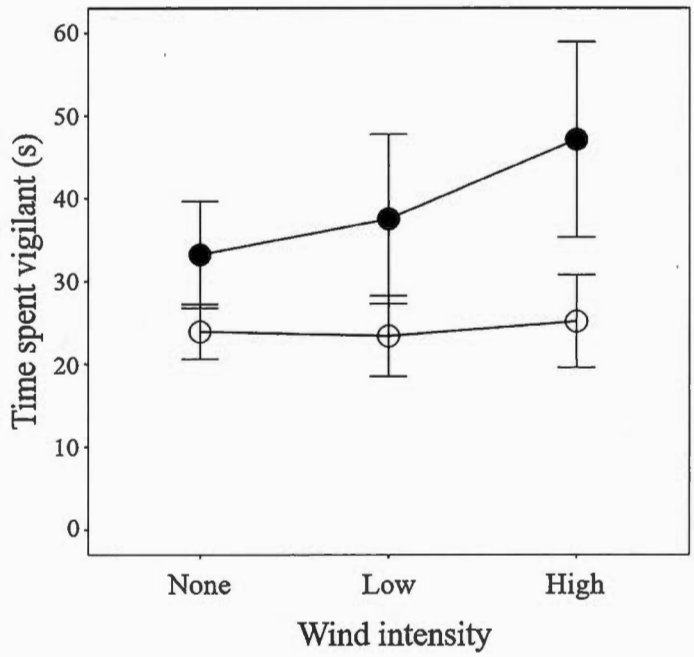

Figure 2. Predicted time spent vigilant during playbacks of soundscapes (open circles) and alarm calls (filled circles) as function of wind intensity in eastern chipmunks, with respective standard errors. Time spent vigilant (in s) is for the complete 60-s test.

increase when wind intensity was high compared to when there was no or low wind, as shown by the LRT results in Table 1, although this effect seemed to be driven by an interactive effect (as wind intensity lost its significance when it was also considered in interaction with playback type, as we will see below).

We also found an effect of the social environment: individuals were significantly more vigilant when hearing the playback of an alarm call compared to a soundscape (Table 1). Furthermore, chipmunks observed in habitats with higher neighbour density were more vigilant than those living in a habitat with fewer neighbours (Table 1), but as for wind intensity, the effect of the number of neighbours seemed to be driven by an interactive effect, as we will see below.

We found combined effects of the physical and social environments: the interaction between wind intensity and playback type was significant; the effect of wind intensity was more pronounced when chipmunks heard alarm calls than soundscapes (Table 1 and Figure 2). The interactions between

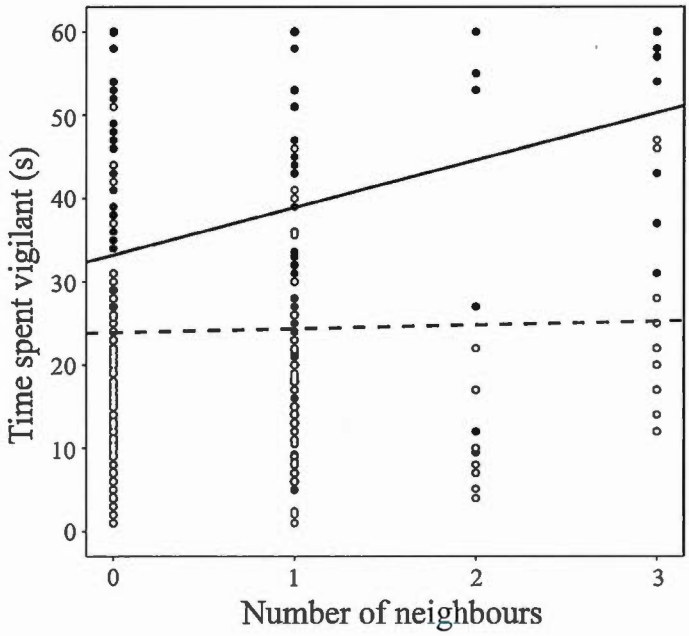

Figure 3. Time spent vigilant during playbacks of soundscapes (open circles) and alarm calls (filled circles) as function of number of neighbours in eastern chipmunks. Time spent vigilant (in s) is for the complete 60-s test. The dotted line and the solid line show the linear regressions predicted by the final model for soundscapes and alarm calls respectively. Intercepts were estimated at wind intensity = none.

playback type and tree cover, and between playback type and herbaceous plant cover were however not significant (Table 1).

We found combined effects of different aspects of the social context: the interaction between number of neighbours and playback type was significant (Table 1 and Figure 3). Chipmunks surrounded by a larger number of neighbours reacted more strongly to alarm calls than chipmunks with a lower number of neighbours, whereas it was not the case for soundscapes.

As for the confounding variables, we found no significant effect of the focal individual's sex (Table 1), and vigilance decreased significantly with the number of tests conducted on an individual (Table 1).

Finally, the three random effects, chipmunk identity (LRT: $\chi^2 = 43.83$, df = 3, $p < 0.001$; $V_{ID} = 10.32$), date (LRT: $\chi^2 = 13.83$, df = 1, $p < 0.001$; $V_{date} = 12.01$) and the recording identification number (LRT: $\chi^2 = 11.45$, df = 1, $p < 0.001$; $V_{rec} = 21.92$), were all significant. The best model also

included significant individual random slopes for the playback type (LRT: $\chi^2 = 8.87$, df $= 2$, $p = 0.012$; $V_{\text{slope}} = 12.47$), however, this aspect will not be discussed as this is not within the scope of this paper.

4. Discussion

Our study reveals that both physical and social environments modified eastern chipmunks' anti-predator decisions. These results emphasize the importance of considering both of these types of environments when studying the vigilance behaviour of a territorial prey species, as also shown by a few studies conducted on social species (see Hirsch, 2002; Kutsukake, 2007; Favreau et al., 2010, 2015; Gaynor & Cords, 2012).

We first showed that tree cover can explain chipmunks' level of vigilance, therefore confirming that open habitats are associated with a higher level of perceived predation risk for this species, as suggested in previous studies (Otter, 1994; Mahan & Yahner, 1999; Martin & Réale, 2008a). There was however no interaction between tree cover and the social environment (the hearing of alarm calls), suggesting that the effect of tree cover on chipmunks' vigilance do not depend on their perception of the level of risk. Also, the lack of effect of herbaceous plant cover on chipmunks' vigilance can be explained in two different ways: this type of cover may not be perceived as a protection against predators and therefore does not affect chipmunks' perception of the level of risk. Alternatively, a more complex measurement of the herbaceous plant cover may be needed to account more precisely for the variation that might be perceived by chipmunks. In many species, cover serves as a protection against predators by increasing the complexity of the habitat and thus decreasing the chances of being caught (Longland & Price, 1991; Landry-Cuerrier, 2008). We would expect to find a more important effect of cover on vigilance in habitats where it is highly variable among patches, for example in managed and fragmented forests (see Mahan & Yahner, 1999 for example).

The level of risk perceived by foraging chipmunks also seemed to be affected by wind conditions. Wind could indeed affect an individual's ability to identify the direction from which a possible threat is approaching (Hilton et al., 1999; Beauchamp, 2015): foraging individuals may not be able to rely on their hearing to detect a predator and should thus compensate by increasing their vigilance under such conditions. A previous study by Fairbanks &

Dobson (2007) found no effect of wind speed on the vigilance of foraging Colombian ground squirrels (*Spermophilus columbianus*), in an open habitat. This suggests that the effect of wind is much more important in forested habitats where gusts of wind going through the canopy create a lot of background noise. Our results also underline the importance of wind on the behaviour of species communicating with alarm calls. Hayes & Huntly (2005) found that wind attenuates pure tones, creates more background noise and therefore decreases the effectiveness of alarm call communication for pikas (*Ochotona princeps*). This could also be a plausible explanation for the pattern we observed in chipmunks' foraging behaviours. It could also explain why the individuals are less active under inclement weather, which might affect the effectiveness of their communication system (Clermont, pers. obs.). Interestingly, we found interactive effects between risk factors as vigilance was more affected when chipmunks were hearing alarm calls than when hearing natural sounds, meaning that the hearing of an alarm call in combination with wind is necessary to trigger higher vigilance levels. Rabin et al. (2006) found that California ground squirrels (*Spermophilus beecheyi*) living near wind turbines, which are very noisy, were more vigilant than those living further away, and they were even more vigilant when hearing playbacks of conspecifics alarm calls, as for our chipmunks. In a windy or noisy environment, individuals face higher predation threat and should become more vigilant to compensate for the loss, deterioration or even misinformation of auditory cues.

As for the effect of the social context, alarm calls increased chipmunks' perception of the level of predation risk (as previously shown by Weary & Kramer, 1995; Bonenfant, 1996; Baack & Switzer, 2000). The alarm calls used in this experiment, which were emitted by chipmunks during natural or simulated predation events, seemed to be interpreted as cues signalling the presence of a predator. We also confirmed that vigilance can serve for both predator detection and social monitoring (Hirsch, 2002) as chipmunks foraging in habitats with a greater neighbour density were more vigilant than individuals foraging near no or fewer neighbours. However, this increase in vigilance only happened when chipmunks heard an alarm call, as chipmunks' basal vigilance level (i.e., during soundscapes) did not increase with the density of neighbours: this represents an example of interactive effects of the social environment (Frid, 1997). To explain the variation in anti-predator behaviours in a more realistic way, it might indeed be important to account

for interactions that might exist between the different predation risk factors, as suggested by Frid (1997). Being in a larger group often reduces individual predation risk and there is thus often a reduction of individual vigilance as there are more group members (Lima & Dill, 1990; Beauchamp, 2015). In our study system, however, conspecifics are also competitors (chipmunks are rodents that actively defend their territory or food patches through agonistic interactions; Dunford, 1970; Elliot, 1978), and this social aspect led to an increase in vigilance when individuals had more neighbours. Therefore, when foraging, chipmunks must assure that no competitors are around to get access to the same resources. If they have no or few neighbours, they can afford to invest more energy/time in foraging than in social monitoring. But, as neighbour density increases, they should spend more time being vigilant to protect the resources they are exploiting. Hirsch (2002) suggested that in cases where predator detection is the primary function of vigilance behaviour, vigilance should decrease as neighbour density increases, as predicted by the dilution and detection effects (Beauchamp, 2015). The Argentinian brown capuchin monkeys (*Cebus apella*) that he studied however increased their vigilance with increasing neighbour density, and because predation had a weaker effect on their vigilance, he concluded that vigilance served mainly for social monitoring for this species. We obtained a similar effect of neighbour density, but also an effect of predation expressed through the effects of the physical environment and the hearing of alarm calls, suggesting that social monitoring and vigilance for predator detection are not mutually exclusive and could possibly be performed at the same time. A second possible explanation as to why more vigilant chipmunks were those with more neighbours could be that individuals are non-randomly distributed among habitats. Indeed, it is likely that individuals with different levels of vigilance (or different personalities, sensu Réale et al., 2007) vary in their habitat use (Boon et al., 2008; Martin & Réale, 2008b; Dingemanse et al., 2010) and occupy territories with different chipmunk densities. In our case, chipmunks that are more sensitive to predation and more receptive to alarm calls could be the ones choosing to live in habitats that are denser, as a greater number of individuals in an area increases the probability to detect an approaching predator (Bednekoff & Lima, 1998).

In conclusion, chipmunks seem to trade-off foraging and anti-predator decisions by perceiving risks through both their physical and social environments. Our study reflects how vigilance serves for both predator detection

and social monitoring for a territorial species, and highlights the importance of considering the different aspects of the environment as well as interactive factors to understand the decisions made by animals foraging under varying risk.

Acknowledgements

We thank Murray Humphries, Manuelle Landry-Cuerrier and all members of the lab from the MacDonald campus of McGill University for their help and useful advices during the project, as well as all the people who helped in the field over the last 10 years. We also thank Will Cresswell and an anonymous reviewer for thoughtful and constructive comments which helped us to improve the manuscript. We are also grateful to the Green Mountains Nature reserve of Nature Conservancy of Canada (NCC) for allowing us to access the study sites. The study was supported by a research team grant from the Fonds de Recherche du Québec — Nature et Technologies (FRQNT) to D.G., D.R. (and Murray Humphries, Fanie Pelletier), by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grants (D.G., D.R.) and by a Canada Research Chair program (D.R.). J.C. was supported by an NSERC Undergraduate Summer Research Award (USRA) as well as a Quebec Center for Biodiversity Science (QCBS) Biodiversity Science Discovery award. C.C. was supported by a scholarship from the FRQNT and through grants from the Université du Québec à Montréal (UQAM), and by a National Geographic Young Explorers grant.

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