UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFETS DE LA PERSONNALITÉ SUR LA SPÉCIALISATION INDIVIDUELLE DE NICHE CHEZ LE TAMIA RAYÉ (*TAMIAS STRIATUS : SÉLECTION, UTILISATION DE L'HABITAT ET RÉGIME ALIMENTAIRE*

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DÉDICACE

À mon frère.

« C'est quoi la formule des *bolds* ? »

Mehdi Gharnit

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RÉSUMÉ

Au sein d'une espèce, les individus ont longtemps été considérés comme équivalent écologiquement par les biologistes. Les différences comportementales entre individus sont largement décrites, mais sont restées jusqu'à très récemment interprétées comme du bruit statistique autour d'une moyenne. De plus, le comportement est encore perçu comme un trait plus plastique dans son expression que d'autres traits morphologiques, physiologiques ou écologiques. Au cours du XX^{e} siècle, le concept de personnalité, provenant de la psychologie et du schéma du « Big Five », a été réadapté en biologie animale afin de comprendre comment et pourquoi la variation interindividuelle se maintient et évolue au sein des populations naturelles. Un nombre croissant d'études rapporte la présence de différences de comportements entre les individus qui sont stables dans le temps et héritables. Il a récemment été proposé que les traits de personnalité auraient coévolué avec des traits d'histoire de vie et des traits physiologiques. Les empiristes sont aujourd'hui encouragés à étudier comment l'utilisation différenciée des ressources, et leurs hétérogénéités spatiale et temporelle agissent sur les mécanismes d'évolution du comportement.

De même, on recense de manière exponentielle que les individus se distinguent dans leurs traits écologiques. La spécialisation individuelle de niche écologique est répandue au sein d'une large gamme de taxons et d'écosystèmes. Les individus varient dans l'utilisation de nombreuses dimensions écologiques : dans leurs comportements de recherche alimentaire, de sélection des ressources alimentaires, dans leur environnement social et dans les dimensions structurelle, spatiale et temporelle de l'habitat. D'un point de vue évolutif, un individu devrait utiliser des conditions écologiques dans lesquelles il performe le mieux en fonction de son phénotype, morphologique, physiologique, mais aussi comportemental. Bien que certaines études aient montré l'implication de traits de personnalité au niveau de patrons de dispersion, d'utilisation d'habitat et de stratégie de recherche alimentaire, ces liens manquent encore d'un cadre global solide et d'un suivi à long-terme.

L'objectif principal de ce doctorat est de vérifier comment la variabilité comportementale interindividuelle (*c.-à-d.* personnalité) est impliquée dans la spécialisation individuelle de niche écologique. Une population d'un petit rongeur sauvage, le tamia rayé (*Tamias striatus*) a été suivie de 2012 à 2018 dans le sud du Québec (Estrie, Canada). Nous avons démontré une structuration spatiale importante

des traits comportementaux ainsi que des différences entre les individus dans l'utilisation du microhabitat autour de leur terrier, site d'hivernage et de reproduction. Selon leur profil d'exploration, les individus différaient aussi dans leurs patrons d'activités quotidiens et leur niche temporelle. Enfin, l'exploration des individus est impliquée dans la spécialisation du régime alimentaire, différemment chez mâles et femelles. Nous avons mis en évidence que la variabilité temporelle des ressources du milieu et la dynamique de population conditionnent de manière importante la spécialisation de niche au niveau de la population, mais également au niveau individuel.

Cette thèse de doctorat s'inscrit dans le large champ de la compréhension de la fonction adaptative de la personnalité et tente d'apporter une part de réponse quant aux mécanismes intrinsèques et environnementaux qui maintiennent la variation interindividuelle. La mise en place de ce cadre conceptuel global est un enjeu majeur en écologie, à la fois pour améliorer nos connaissances sur (i) l'évolution de la niche écologique individuelle et (ii) les origines de la variation individuelle qui mène à la divergence phénotypique et génétique entre populations/espèces.

Mots clés : Spécialisation individuelle, personnalité, sélection d'habitat, activité, spécialisation alimentaire, hétérogénéité environnementale, *Tamias striatus*.

ABSTRACT

Within a species, individuals have long been considered ecologically equivalent by biologists. Behavioural differences between individuals are widely described but have been regarded as statistical noise until recently. In addition, behaviour is still seen as a more plastic trait than other morphological, physiological or ecological traits. During the twentieth century, the concept of personality, from psychology and the "Big Five", has been rehabilitated in animal biology. This framework helps to understand how and why variation between individuals is maintained and evolves within natural populations. An increasing number of studies report the presence of behavioral differences between individuals that are consistent over time and heritable. Recently, it has been proposed that personality traits may have coevolved with life-history traits and physiological traits. Empiricists now focus on how resource utilization affects the mechanisms of behaviour's evolution in spatial and temporal heterogeneous contexts.

Similarly, there is exponential evidence that individuals differ in their ecological traits. Individual ecological niche specializations are widespread within a wide range of taxa and ecosystems. Individuals differentiate their utilization of many niche dimensions: in their foraging strategies, in their diet, in their social environment and in structural, spatial and temporal dimensions of the habitat. From an evolutionary point of view, an individual should use ecological conditions in which he performs better according to his morphological, physiological but also behavioural phenotype. Albeit some studies showed that personality traits are involved in dispersal patterns, habitat use, and foraging strategy, yet, few have studied these long-term and multi-dimensional links.

The main objective of this thesis was to assess how interindividual behavioural variability (i.e., personality) translates into individual niche specialization. We monitored a population of a free-ranging rodent, the eastern chipmunk (*Tamias striatus*) from 2012 to 2018 in southern Quebec (Estrie, Canada). We showed that individuals are highly spatially structured in their behavioural phenotypes and that they differed in the micro-habitat use around their burrow. According to their exploration profile, individuals also varied in their daily activity patterns and their temporal niche. Finally, variation among-individuals in exploration is involved in the individual diet specialization. We found that yearly fluctuation in resource abundance

and population dynamic highly modulate niche specialization at the population level but also at the individual level.

This study is part of the broad field of understanding the adaptive function of animal personality and provides insights about intrinsic and environmental mechanisms that maintain the interindividual variation. Nurturing this global conceptual framework is a major challenge in ecology to improve our knowledge of (i) the evolution of the individual ecological niche and (ii) the origins of the individual variation that can lead to phenotypic and genetic divergence between populations/species.

Keywords: individual specialization, personality, habitat selection, activity, diet specialization, environmental heterogeneity, *Tamias striatus.*

CHAPITRE I

INTRODUCTION

1.1 La spécialisation de niche écologique

1.1.1 Les premiers concepts

Les travaux les plus influents sur la notion de niche écologique émergent dans le cadre de l'étude des communautés. Ils ont pour but de comprendre la répartition des espèces à l'échelle biogéographique (*ex.* biomes), de prédire leur abondance dans un milieu donné ou la réponse des populations aux fluctuations environnementales (Levins, 1968; May et Arthur, 1972). Au sens de Grinnell (1917), les variables environnementales caractérisent les dimensions de la niche d'un organisme (« niche spatiale »). Elton (1927) offre une approche dans laquelle les attributs fonctionnels spécifiques définissent la niche écologique, son rôle dans l'écosystème (*ex.* détritivore, pollinisateur, *etc.* Devictor *et al.*, 2010). Hutchinson (1957) représente la niche écologique d'une espèce comme un hypervolume à *n* dimensions qui reflètent l'ensemble des relations entre un organisme et son environnement biotique et abiotique. Ainsi, la niche *fondamentale* d'une espèce équivaut à l'ensemble des conditions abiotiques dans lesquelles elle peut survivre et se reproduire tandis que les interactions biotiques du milieu la restreignent à remplir une niche *réalisée* (Hutchinson, 1957).

Au cours de ces mêmes décennies émergent les premiers modèles de variation de niche de Van Valen (1965) et d'évolution de largeur de niche (Roughgarden, 1972,

1974) qui conduit à des spécialisations de niche. La spécialisation écologique correspond à la réduction de l'amplitude de la niche occupée par une espèce, par son adaptation à un sous-ensemble de ses environnements possibles (Poisot *et al.*, 2011). Par une étude empirique chez un lézard du genre *Anolis,* Roughgarden (1974) introduit deux composantes qui subdivisent la largeur de niche totale (TNW : *Total Niche Width*) : une composante interindividuelle (BIC : *Between-Individual Component*) et une composante intra-individuelle (WIC : *Within-Individual Component*). La variation de ces deux paramètres participe selon les conditions à l'augmentation ou la réduction de l'espace de niche totale occupé par une espèce (Figure 1.1).

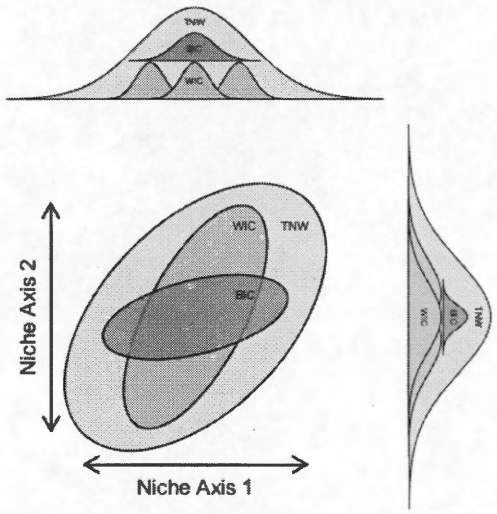


Figure 1.1 Visualisation des sous-composantes de l'espace de niche totale (TNW) : la composante interindividuelle (BIC) et intra-individuelle (WIC) sur deux axes de la niche écologique, telles que TNW = BIC + WIC. Deux processus peuvent modifier la largeur de niche totale : une augmentation de la BIC (individus spécialisés et différenciés, axe 1) ou une hausse du WIC (individus généralistes, axe 2). Pour des raisons de clarté, sur ce schéma WIC + BIC < TNW (adapté d'Ingram *et al.*, 2018).

1.1.2 Les causes écologiques et évolutives de la spécialisation de niche

Au cours du XX^{e} siècle, les forces qui façonnent la taille d'une niche populationnelle sont des sujets centraux dans la compréhension de la coexistence et la répartition des espèces. Depuis Darwin, la compétition demeure la force évolutive considérée comme la plus importante sur la réduction de niche d'une espèce. Selon la théorie de l'exclusion compétitive, deux espèces doivent se différencier sur l'axe d'une ressource qu'elles exploitent en commun pour pouvoir coexister (Alley, 1982; Armstrong et McGehee, 1980; Diamond, 1973; Hardin, 1960; Pianka, 1981). Van Valen (1965) suppose notamment que la relâche de la compétition interspécifique permet l'accroissement de la TNW d'une espèce et que l'augmentation de la BIC en est le processus principal. Ce postulat est basé sur l'idée que les contraintes morphologiques, physiologiques ou cognitives individuelles limitent la largeur de niche individuelle (WIC, Araújo *et al.*, 2007; Bolnick *et al.*, 2007, 2010). Cependant, l'augmentation de la BIC comme de la WIC suppose une plasticité dans l'utilisation des ressources, mais à notre connaissance, peu d'études se sont penchées sur la plasticité de niche individuelle (*ex.* Villegas-Ríos *et al.*, 2018). Les changements dans les positions de niches individuelles sous plus largement étudiés, notamment sous l'effet de la compétition intraspécifique (Bolnick, 2001; Holbrook et Schmitt, 1992; Svanbäck et Bolnick, 2005, 2007; Zanden *et al.*, 2010; Pagani-Núñez *et al.*, 2016). La prédation peut également confiner ou déplacer la niche d'une espèce, par exemple lorsqu'un prédateur est restreint à un type d'habitat, les proies peuvent converger vers d'autres types d'habitat (Werner *et al.*, 1983).

À une échelle évolutive, Poisot et al. (2011) soulignent que l'évolution de la spécialisation dépend de l'interaction entre les contraintes adaptatives des individus (*ex.* pléiotropie), leurs traits d'histoire de vie (*ex.* dispersion) et les caractéristiques de l'environnement (*ex.* complexité, prédictibilité). L'hétérogénéité de l'habitat devrait favoriser la spécialisation (Hanski, 1983; Kassen, 2002; Jasmin et Kassen, 2007)

alors que la fluctuation temporelle des ressources devrait avantager les espèces généralistes (Poisot *et al.*, 2011, 2012). Selon le contexte écologique, ces forces s'opposent et préviennent la mise en place d'adaptations locales et l'évolution de la spécialisation. Ainsi, certaines études ont présenté de solides évidences d'une performance écologique supérieure des spécialistes (*ex.* succès reproducteur, Golet *et al.*, 2000), tandis que d'autres n'ont trouvé aucune différence entre spécialistes et généralistes (*ex.* survie et succès reproducteur, Woo *et al.*, 2008).

Les recherches sur la niche écologique ont évolué dans la seconde moitié du siècle. Les concepts de variation de niche de Van Valen et Roughgarden introduisent une nouvelle approche dans l'analyse de la spécialisation : l'importance de la composante individuelle dans les modifications de la niche d'une espèce. À une échelle proximale, les études sont nombreuses reportant la covariation entre les traits morphologiques et l'utilisation des ressources (Baker, 1979; Diamond, 1978; Ineich *et al.*, 2006; Smith, 1987). Cependant, de nombreuses questions restent sans réponse : quels mécanismes dirigent les changements de la WIC (individus spécialistes/généralistes) et de la BIC ? Les spécialisations individuelles sont-elles adaptatives, c'est-à-dire, accentuent-elles les différences en termes de survie et de reproduction entre les individus spécialistes *versus* généralistes (mais voir les systèmes hôte/parasite, Kaltz et Shykoff, 1998; Via, 1984) ? Sont-elles héritables ? Ces spécialisations sont-elles constantes à travers les contextes ? Puisque la sélection naturelle agit au niveau individuel, la variation interindividuelle de l'utilisation des ressources est un prérequis obligatoire à l'évolution de la niche d'une espèce.

1.2 Vers une prise en compte des différences interindividuelles

1.2.1 La spécialisation individuelle de niche

Depuis les quarante dernières années, le postulat selon lequel les individus d'une même population ne sont pas écologiquement équivalents s'impose de manière importante en biologie évolutive (Wilson, 1994, 1998). Des différences phénotypiques interindividuelles peuvent découler de la sélection naturelle et affecter de nombreux processus écoévolutifs (Bolnick *et al.*, 2011; Kingsolver *et al.*, 2001; Smith et Blumstein, 2007; Wolf et Weissing, 2010). De même, on recense de manière exponentielle que les individus se distinguent dans leurs traits écologiques. De multiples exemples empiriques existent sur la spécialisation individuelle au sein d'une large gamme de taxons et d'écosystèmes et pour diverses dimensions de niches (Araújo *et al.*, 2011; Bolnick *et al.*, 2003; Ingram *et al.*, 2018). L'augmentation significative des études sur la spécialisation individuelle de niche s'observe réellement dans les années 90s (voir figure 1.2).

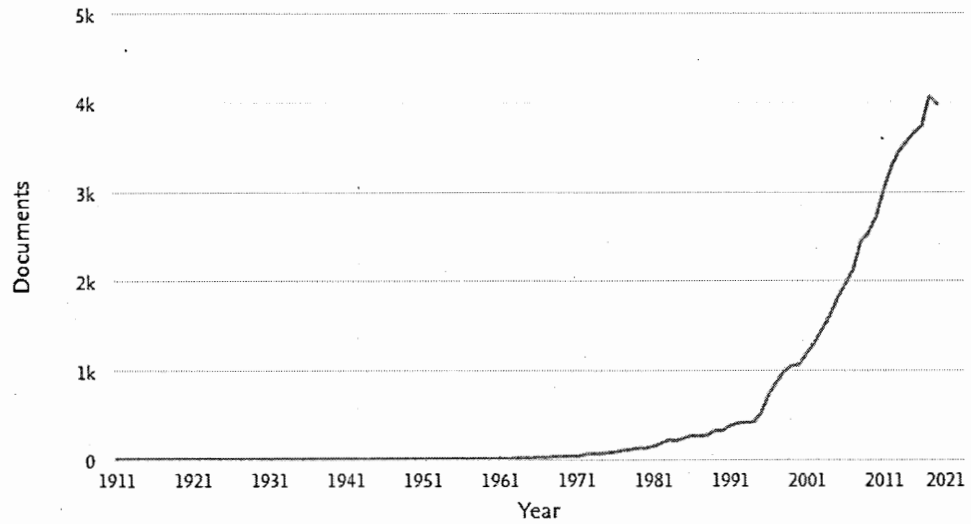


Figure 1.2 Nombre d'études par année dont le titre, les mots-clés ou le résumé contiennent les mots « individual & niche & specialization », ou « individual & variation resource & use », ou « individual & habitat & use », ou « individual & variation & diet », entre 1911 et 2018. Statistiques descriptives issues du site Scopus.

On recense des différenciations interindividuelles dans l'utilisation de dimensions abiotiques et spatiales de l'habitat (Bourke *et al.*, 1997; Clobert *et al.*, 2009; Fodrie *et al.*, 2015; Spiegel *et al.*, 2015). On les observe aussi pour des comportements de recherche alimentaire et pour la diète (Araújo *et al.*, 2007; Bolnick et Paull, 2009; Estes *et al.*, 2003; Giller et Greenberg, 2015; Haage *et al.*, 2017; Han *et al.*, 2016; Woo *et al.*, 2008). Enfin, on décèle des différences d'utilisation de l'environnement social (Bergmüller et Taborsky, 2007; Carter *et al.*, 2014; Croft *et al.*, 2005; Lusseau *et al.*, 2006; Réale et Dingemanse, 2010). Ces spécialisations doivent se distinguer d'un changement de niche ontogénique (*c.-à-d.* facteur âge) et d'un polymorphisme discret, qu'il soit sexuel ou trophique (*c.-à-d.* morphe particulier ou disponibilité variable des ressources). La variation entre individus dans l'utilisation d'une ressource peut refléter les différences individuelles de capacités morphologiques (*ex.*

locomotion, vitesse, taille de mâchoire), physiologiques (*ex.* conditions de digestion, détoxification) ou cognitives (*ex.* innovation, mémoire spatiale, apprentissage) (Bolnick *et al.*, 2003; Araújo *et al.*, 2011). Ces facteurs intrinsèques interagissent avec les mêmes forces écologiques qui s'exercent au niveau de la niche d'une espèce (*ex.* hétérogénéité spatiale des ressources, prédation et compétition interspécifique, Araújo *et al.*, 2011). Cependant, la compétition intraspécifique est susceptible d'accroître significativement la BIC et donc la TNW (Bolnick, 2001; Evangelista *et al.*, 2014; Holbrook et Schmitt, 1992; Svanbäck et Bolnick, 2005, 2007).

D'un point de vue évolutif, un individu devrait utiliser des conditions écologiques dans lesquelles il performe le mieux en fonction de son phénotype (*ex. Matching habitat choice*, Edelaar *et al.*, 2008). La supériorité adaptative (survie, reproduction) d'un phénotype spécialisé dans un environnement donné peut renforcer à son tour la covariance entre le phénotype et le génotype de l'individu dans cet environnement (corrélation génotype-environnement, figure 1.3). Ainsi, une spécialisation phénotypique pourrait avoir coévolué de manière étroite avec certaines conditions écologiques. Ce processus demeure à la base de la sélection divergente se produisant au sein ou entre des populations (Senar *et al.*, 2006; Bolnick *et al.*, 2009). Chez les pinsons de Darwin, l'exemple le plus connu, il mène à la spéciation et à la radiation adaptative (Grant et Grant, 2006). Toutefois, les bénéfices d'une spécialisation individuelle peuvent varier en fonction des stratégies utilisées par les conspécifiques (sélection fréquence-dépendante, Beauchamp *et al.*, 1997; Rueffler *et al.*, 2006b) et de l'hétérogénéité spatiale et temporelle (sélection fluctuante, Le Cœur *et al.*, 2015; Quinn *et al.*, 2009).

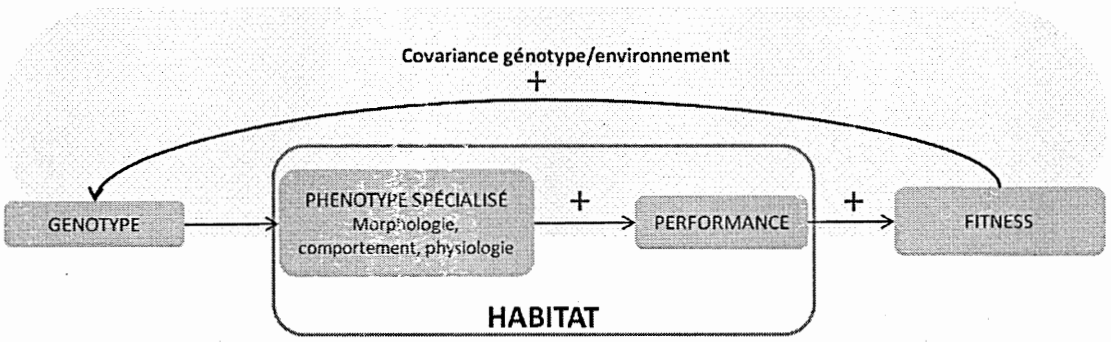


Figure 1.3 Lorsqu'un phénotype spécialisé dans un habitat donné confère une performance et une fitness élevée, il y a possiblement évolution de la covariance génotype/environnement. L'habitat peut ici refléter les nombreuses dimensions d'une niche écologique et représenter aussi bien l'utilisation de l'habitat abiotique, trophique ou social d'un individu.

Un second constat peut être souligné : l'essentiel de l'étude sur la relation entre traits et niche écologique concerne des traits morphologiques (Ferry-Graham *et al.*, 2002). En revanche, les chercheurs ont négligé le rôle adaptatif du comportement dans la sélection ou l'utilisation des multiples dimensions de la niche écologique individuelle. Une raison de cette omission viendrait du fait que les comportements sont souvent considérés comme très plastiques et moins sujets aux divergences génétiques (Dall *et al.*, 2012). Jusqu'à récemment, le comportement est resté une sorte de mécanisme transitoire plastique entre traits fonctionnels (morphologie) et spécialisation (*ex.* stratégie de recherche alimentaire, Svanbäck et Eklöv, 2006; Werner et Sherry, 1987).

1.2.2 La spécialisation comportementale

L'étude de la spécialisation individuelle de niche écologique se focalise sur la variation individuelle pour des traits écologiques ayant une importance dans

l'interaction entre l'individu et son milieu biotique et abiotique. Les individus se spécialisent également au niveau de leur phénotype comportemental, et dont le rôle écologique est non négligeable. Pourtant, on a longtemps considéré les différences comportementales interindividuelles comme des déviations par rapport aux stratégies optimales (Magurran, 1986). Depuis quelques décennies, le rôle adaptatif de ces différences comportementales est devenu plus clair. Elle ont notamment des conséquences sur la dynamique des populations (*ex.* dispersion, Cote et Clobert, 2007; Cote *et al.*, 2010a, 2010b), la transmission de pathogènes (Barber et Dingemanse, 2010; Sih *et al.*, 2018), sur les traits d'histoire de vie (Boon *et al.*, 2007, 2008; Réale *et al.*, 2009; Stamps, 2007), ou sur les processus écosystémiques (Mittelbach *et al.*, 2014; Sih *et al.*, 2012; Wolf et Weissing, 2012). On appelle personnalité ou tempérament ces différences comportementales constantes, dans le temps et entre les situations (Réale *et al.*, 2007). La corrélation entre plusieurs traits comportementaux, constante chez les individus à travers différentes situations devient alors un syndrome comportemental (Sih *et al.*, 2004). Cinq comportements sont majoritairement étudiés : la réaction face à un environnement nouveau ou risqué (témérité), ou face à des objets nouveaux (néophobie), l'exploration d'un milieu nouveau, l'activité générale, la sociabilité et l'agressivité relatives à un contexte social (Réale *et al.*, 2007). Depuis les dernières années, d'autres traits ont été ajoutés à cette liste et l'étude de la personnalité correspond à la dimension répétable de tout trait comportemental.

Les causes proximales des différences comportementales individuelles peuvent être de nature physiologique (*ex.* réponse au stress, Koolhaas *et al.*, 1999; taux métabolique, Careau *et al.*, 2008; Sih *et al.*, 2015; activité neuroendocrinienne, Ellis *et al.*, 2006; Koolhaas *et al.*, 2010). Selon le modèle du style de gestion du stress (*coping style*), contrairement aux individus réactifs, les proactifs sont très rapides dans leur exploration, très agressifs et téméraires. Ces proactifs montreraient une plus faible réactivité de leur axe hypothalamo-hypophyso-surrénalien, associé à une faible sécrétion de cortisol (*c.-à-d.* réactivité au stress, Montiglio *et al.*, 2012, mais voir

Ferrari *et al.*, 2013). Plus récemment, on a montré que les conditions sociales (Laskowski et Pruitt, 2014; Modlmeier *et al.*, 2014), l'hétérogénéité spatiale (Dubuc-Messier, 2017) et temporelle (Le Cœur *et al.*, 2015) pouvaient renforcer les traits de personnalité.

Dall et ses collaborateurs (2012) proposent un rapprochement incontournable de trois sous-domaines étudiés en écologie, réunis sous le terme de « spécialisation comportementale ». Le premier concerne la division du travail chez certaines espèces d'insectes. Le second se rapporte à la spécialisation individuelle de niche écologique. Enfin le troisième regroupe les recherches sur la personnalité animale. La mise en place de ce cadre conceptuel global est un enjeu majeur en écologie, à la fois (i) pour démontrer l'implication du comportement dans les différences d'utilisation des ressources et (ii) pour penser les conséquences en termes de valeur adaptative de la variation comportementale. Les empiristes sont encouragés à étudier comment l'utilisation différenciée des ressources agit sur les mécanismes d'évolution du comportement (Dingemanse et Wolf, 2010; Pearish *et al.*, 2013; Réale et Dingemanse, 2010; Wolf et Weissing, 2010).

1.3 Objectifs et structure de l'étude

1.3.1 Relier personnalité et spécialisation individuelle de niche

Dans les sections précédentes, j'ai présenté une série de postulats. Premièrement, les interactions biotiques et abiotiques façonnent la manière dont les espèces sélectionnent et utilisent les ressources du milieu à une échelle évolutive. Deuxièmement, la variation individuelle est impliquée dans l'évolution de la niche d'une espèce, puisqu'elle reste la matière première de la sélection naturelle. Troisièmement, les individus diffèrent en termes d'utilisation des conditions écologiques : ils choisissent celles dans lesquelles ils performent le mieux en fonction

de leurs caractéristiques phénotypiques. Enfin, les preuves de la spécialisation individuelle de niche sont nombreuses mais peu d'études ont soulevé la question de l'implication de la personnalité dans ce phénomène.

L'objectif principal de ce doctorat est de vérifier comment la variabilité comportementale interindividuelle (*c.-à-d.* personnalité) est impliquée dans la spécialisation individuelle de niche écologique. Par une approche empirique sur une population naturelle d'un petit rongeur sauvage, le tamia rayé (*Tamias striatus*), j'ai mesuré la variation individuelle de trois traits comportementaux susceptibles d'être impliqués dans la spécialisation d'utilisation des ressources : la témérité (prise de risque), la docilité en main et l'exploration d'un milieu nouveau. La docilité est généralement négativement corrélée à une forte agressivité et à une témérité élevée (Réale *et al.*, 2010; St-Hilaire *et al.*, 2017). Elle est également associée à une exploration lente/minutieuse dans un nouvel environnement (Montiglio *et al.*, 2012). Des études précédentes sur la même population ont révélé que les tamias différaient de manière répétable dans leur exploration, variant d'une exploration lente/ approfondie à une exploration rapide/superficielle (Montiglio *et al.*, 2010, 2012) et dans leur docilité face à la manipulation (St-Hilaire *et al.*, 2017).

1.3.2 Modèle d'étude

Le tamia rayé est un rongeur diurne de la famille des Sciuridés. Son habitat s'étend du nord-est au sud-est de l'Amérique du Nord dans des forêts mixtes de hêtres et d'érables et des forêts de chênes. L'essentiel de ses activités extérieures est centré autour d'un terrier (Kramer et Nowell, 1980), site de reproduction, d'hivernage et d'émergence des jeunes (Elliott, 1978; Yahner, 1978a). Des études précédentes ont évalué la surface du domaine vital du tamia rayé à un espace relativement circulaire d'environ 4500 m^2 autour du terrier principal (Elliott, 1978; Bowers, 1995). Cependant, lors de période de reproduction, certains trajets des mâles peuvent atteindre des distances de 200 mètres (Montiglio, 2009). Bien que territorial et

solitaire, les interactions sociales sont nombreuses chez cet animal, de même que les chevauchements entre territoires (Getty, 1981; Yahner, 1978b). Il stocke dans son terrier des quantités importantes de graines essentielles pour survivre à l'hiver qu'il passe en semi-torpeur (Humphries *et al.*, 2002, 2003). Dans le sud du Québec (Estrie, Canada), les tamias se nourrissent principalement de graines de hêtre d'Amérique (*Fagus grandifolia*), d'érable rouge (*Acer rubrum*) et d'érable à sucre (*Acer saccharum,* Snyder, 1982). Au printemps, les individus recherchent activement les bulbes d'herbacées éphémères telles que l'érythrone d'Amérique (*Erythronium americanum*) et la Claytonie de Caroline (*Claytonia caroliniana*). Occasionnellement, ils peuvent consommer des champignons, des petits invertébrés (limaces, insectes) et des œufs ou oisillons de petits passériformes (Elliott, 1978).

Sur notre zone d'étude, la dynamique de population du tamia dépend fortement du cycle de la production de graines de hêtres et d'érables (Humphries *et al.,* 2002; Bergeron *et al.,* 2011*c)*. Les femelles entrent en œstrus une fois par an, à la fin de l'hiver ou à la fin du printemps, dépendamment de ces événements de paisson se produisant tous les deux ans (figure 1.5). L'émergence de nombreux juvéniles à l'automne au moment de la paisson des hêtres et au printemps suivant une paisson de hêtre, conduit à l'augmentation régulière de la densité de population (Bergeron *et al.*, 2011c). L'absence de reproduction, en dehors de ces périodes, et le vieillissement de la population se traduisent par un déclin de la population.

Le tamia rayé offre un modèle idéal à l'étude de la spécialisation comportementale et écologique. Son mode de vie offre à la fois un contexte de compétition spatiale adéquat qui pourrait motiver la différenciation de l'utilisation des ressources entre les individus. Il offre aussi un contexte de variabilité temporelle des ressources qui dicte la dynamique de population et potentiellement l'intensité de la spécialisation individuelle et populationnelle (voir section 1.3.2).

1.3.3 Hypothèses et prédictions

Je me suis intéressée à trois dimensions majeures de la niche écologique : (i) la sélection de l'habitat, (ii) l'utilisation de l'habitat et (iii) la sélection des ressources alimentaires.

J'ai d'abord testé dans le chapitre II si les phénotypes comportementaux étaient structurés au niveau spatial à partir de leur localisation de terrier, site principal de reproduction et d'élevage des jeunes. De plus en plus d'études empiriques rapportent que la variation individuelle dans la témérité et l'exploration est impliquée dans des différences de patrons de dispersion (Cote *et al.*, 2010a; Cote et Clobert, 2007), de préférences et d'utilisation d'habitat (Boyer *et al.*, 2010; Kobler *et al.*, 2011; Bonnot *et al.,* 2015; Patrick *et al.*, 2014, 2017; Charmantier *et al.*, 2017). Selon la théorie de l'adéquation entre phénotype et environnement (Edelaar *et al.*, 2008; Pearish *et al.*, 2013), un individu devrait choisir un habitat dans lequel sont phénotype est avantagé. J'ai testé si les variables du microhabitat structurel et biotique autour du terrier expliquaient la structure spatiale des comportements, mais aussi de la durée de vie des individus et de leur succès de reproduction total. Je m'attendais à ce que les individus diffèrent dans leurs préférences de type d'habitat et à mettre en évidence une corrélation phénotype-environnement si la valeur adaptative individuelle était plus élevée dans l'habitat choisi.

Dans le chapitre III, j'ai évalué si les individus différaient au niveau de leur utilisation quotidienne de l'habitat. La propension intrinsèque à explorer dans un nouvel environnement devrait se refléter au niveau de les patrons quotidiens d'activité de recherche alimentaire. J'ai testé si l'exploration expliquait la variation individuelle dans le niveau d'activité quotidien, dans la structure du patron d'activité et dans l'utilisation des fenêtres temporelles d'activité matinale et crépusculaire. Je m'attendais à ce qu'une exploration plus rapide soit corrélée à un niveau d'activité plus élevé mais rythmé par de plus nombreuses phases de repos (compromis

intensité/durée). Enfin, je m'attendais à ce que les profils d'exploration, lents/minutieux *versus* rapides/superficiels se différenciaient au niveau de leur niche temporelle, conséquence potentielle de la compétition spatiale pour les ressources.

Finalement, au cours du chapitre IV, j'ai étudié si les différences d'exploration entre les individus affectaient l'utilisation de la niche alimentaire, en inspectant leurs signatures d'isotopes stables d'azote et de carbone stockés dans leurs tissus. Je m'attendais à ce que des individus plus minutieux dans leur exploration montrent un régime plus spécialiste, du fait d'une exploitation plus localisée des parcelles de nourriture. À l'inverse, des individus rapides/superficiels dans leur exploration devraient montrer une plus grande aire de recherche alimentaire et être moins sélectifs dans le choix des proies (compromis exploitation/exploration, Patrick *et al.*, 2017). De manière globale, j'ai également évalué si l'utilisation de ces dimensions variait au niveau de la population et au niveau individuel en fonction de la variabilité temporelle des conditions environnementales (densité de population et disponibilité des ressources principales).

Les trois chapitres de cette thèse m'ont permis de réunir au sein de la littérature les preuves empiriques nombreuses, mais encore isolées, qu'il existe des patrons personnalité-dépendants au sein de ces trois dimensions écologiques chez un grand nombre de taxons animaux. Ultimement, l'objectif général de ce doctorat est de participer à l'étude multidimensionnelle de la spécialisation individuelle (Ingram *et al.*, 2018) et de nourrir un cadre plus global sur les implications écoévolutives de la spécialisation comportementale.

1.3.4 Système de capture et sites d'étude

L'étude s'est déroulée sur une population de tamias rayés de 2012 à 2018 dans le sud du Québec (Canada, 45° 05'N; 72° 25'W, figure 1.4), sur trois sites consistant en des grilles rectangulaires de 7.84 ha (Site 1), 8.40 ha (Site 2) et 4 ha (Site 3). Nous avons

effectué le suivi de la population à l'aide d'un trappage quotidien pendant la période d'activité des tamias de mai à septembre, à l'aide de piège *Longworth* et appaté par une petite quantité de beurre d'arachide. Le trappage régulier a permis le marquage et la recapture des individus d'une année à l'autre, de récolter des données sur leur diète (récolte de poils), d'analyser leur sélection de terriers (méthode de localisation nocturne par télémétrie), de mesurer leur activité (méthode d'accélérométrie) et de mesurer régulièrement le phénotype des individus (masse corporelle, comportements). Nous avons mesuré les traits de comportement au cours de ces années sur un total de 719 individus (pour 10,732 captures au total).

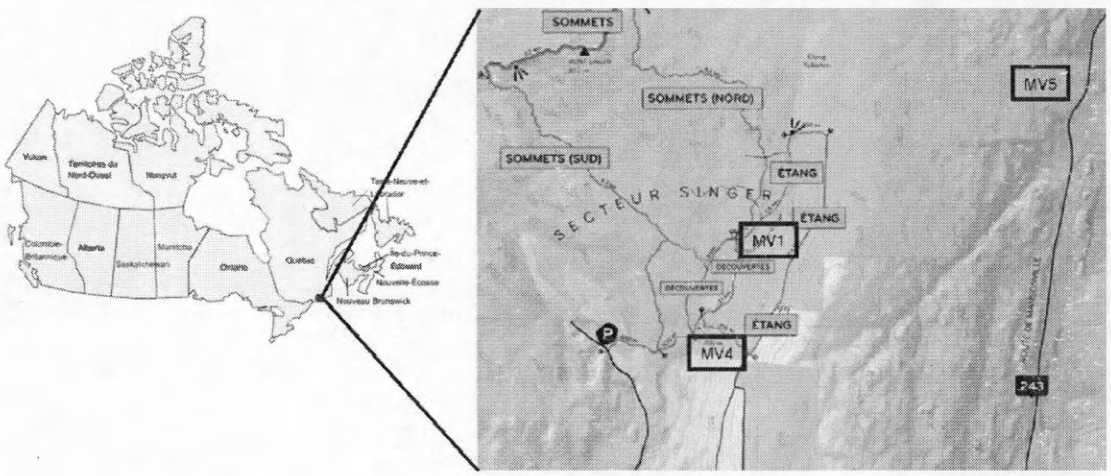


Figure 1.4 Localisation des sites des trois grilles d'échantillonnage, site 1 (MV1 : 45° 06.785'/72° 26.078'), site 2 (MV4 : 45° 06.207'/72°. 26.207') et site 3 (MV5 : 45° 07.852'/72° 23.735') dans le secteur Singer, vallée du Ruiter en Estrie (Canada).

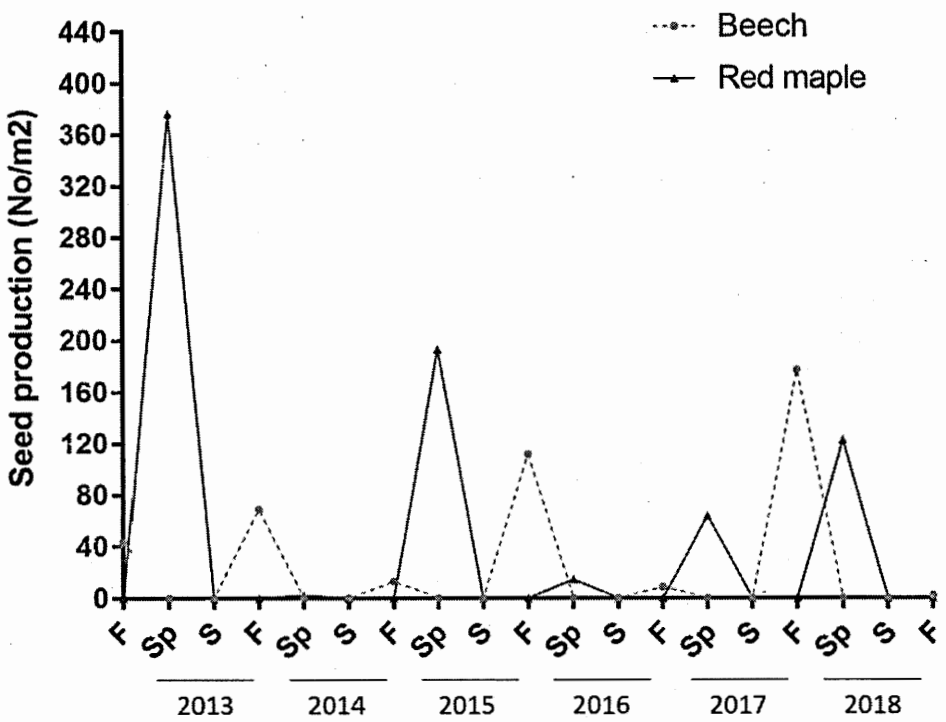


Figure 1.5 Variabilité temporelle de la production de graines du hêtre d'Amérique (*Fagus grandifolia*) et de l'érable rouge (*Acer rubrum*) sur nos trois sites d'échantillonnage (secteur Singer, vallée du Ruiter, Canada, 45° 05'N; 72° 25'W). Les hêtres produisent une plus grande quantité de graines en automne (F : *Fall*) 2013, 2015 et 2017 tandis que les *mast* d'érable rouge se produisent au printemps (SP : *spring*) de ces mêmes années. Les années 2014, 2016 et 2018 sont considérées comme des années sans paisson (ou post-paisson). Les données manquent pour l'année 2012 (Figure adaptée de Tissier *et al.*, sous presse).

CHAPITRE II

INDIVIDUAL BEHAVIOURAL VARIATION PREDICTS MICROHABITAT SPECIALIZATION IN A WILD RODENT

Gharnit Elouana, Dany Garant, Patrick Bergeron et Denis Réale.

2.1 Abstract

Dispersal and habitat selection are critical stages in the lifetime of individuals. They must make the best choices in terms of abiotic and biotic habitats in which they will live and breed. At the species-level how phenotypic variations are involved in habitat specialization has a long tradition in the literature. Niche variation results in decreasing overlap in resource use, reduces competition and enhances coexistence. More recently, ecologists focused on factors that lead to individual habitat specialization. At individual-level, morphology, physiology and life history traits are also correlated with dispersal and settlements decisions. Less documented, behaviours should drive how individuals choose a habitat and perform in this habitat. Individuals vary in risk perception, space use and habitat preferences. For instance, bold and fast explorers prefer colonize riskier habitat or invasion front and asocial dispersers have high probabilities to be found in low-density habitats. In this study, we sampled microhabitat features around 207 burrows in eastern chipmunks (*Tamias striatus*) and assessed the link between habitat use and individual variation in

exploration, boldness, handling docility, lifespan and reproductive success. We found that among-individuals behavioural differences drove habitat use specializations and structured spatial heterogeneity in lifetime fitness traits. Bold, less docile and fast/superficial explorers (i.e., proactive individuals) used closed areas in shrub layer density but with fewer refuges compared to docile, shyer/slower (i.e., reactive) individuals. Proactive individuals exhibited higher fitness in these habitats than reactive ones. Since, these patterns varied among sites and overall, both behavioural and fitness traits were highly spatially structured independently of habitat. This study brings evidence for individual behavioural-environment correlation that leads to spatially structured population. It should enhance our comprehension of coevolution of both behavioural and ecological traits variation within-species and effects on ecological processes like parasite spread, mating system and foraging dynamics.

2.2 Introduction

Among-species, variations in phenotypic traits and habitat preferences lead to habitat niche specialization, result in decreasing overlap in resource use, reduce competition and enhance the different species coexistence (Jones *et al.*, 2001; Kotler et Brown, 1999; May et Arthur, 1972; Schoener, 1974). In Darwin's finches, the best known example, it led to speciation and adaptive radiation (Grant et Grant, 2006). However, the origin of adaptive divergence among-populations and ultimately ecological speciation flows from selection on individual variation (Bolnick *et al.*, 2009; Senar *et al.*, 2006). Individual niche variation is thus a precondition to niche evolution at the species level (Roughgarden, 1972, 1974; Van Valen, 1965). Intra-specific variation in biotic and abiotic components preferences related to individual phenotypes/genotypes should also lead to individual habitat specialization. According to the matching habitat choice hypothesis (MHC) species should have evolved so that their individuals match the habitat they choose with their phenotype for traits of ecological importance (Edelaar *et al.*, 2008). For instance, young dispersers increase their fitness

by choosing a habitat similar to their native habitat, because this habitat has allowed their parents to survive and reproduce (Berteaux et Boutin, 2000; Davis et Stamps, 2004; Stamps et Davis, 2006). As a consequence, the adaptive superiority of specialized phenotypes in a habitat should reinforce the correlation between phenotype (and genotype) and habitat and evolve towards local adaptations (Edelaar *et al.*, 2008). Moreover, phenotypic-dependent habitat selection may lead to spatially structured population. The non-random spatial aggregation of individuals of similar phenotypes has important effects on ecological processes like predation, parasite spread, mating system, intraspecific cooperation and foraging dynamics (review in Farine *et al.*, 2015).

Individuals are subject to strong selective pressures to make the best choices in terms of habitats in which they will live and breed. Heterogeneous environments offer a range of available habitats within which an animal can sample and decide to settle. Individuals rely on various internal and external cues that lead to complex dispersal and settlement patterns (Clobert *et al.*, 2009; Jacob *et al.,* 2015). Extrinsic conditions such as habitat availability, competition, predation risk and social information drive settlement decisions (Doligez *et al.*, 2003). Habitat selection or degree of habitat selection depends on intrinsic individual phenotype (body condition, sex, age) and preferences (e.g., natal habitat experience, Davis et Stamps, 2004). At the individual-level, morphology, physiology, behaviours and life history traits are also correlated with dispersal and settlement decisions (review in Clobert *et al.,* 2004, 2009). The description of morphology/habitat matching has a long tradition in the literature, e.g., fin length and pelagic *vs.* benthic zone use (Bourke *et al.*, 1997). At the individual-level, morphology, physiology, behaviours and life history traits are also correlated with dispersal and settlement decisions (review in Clobert *et al.*, 2004, 2009). Less documented, consistent differences in behaviours among individuals should play important roles in habitat selection in dispersers. Individuals specialise in their behaviours across time and contexts (personality traits, Koolhaas *et al.*, 2010; Réale

et al., 2007; Sih *et al.*, 2004). Proactive individuals consistently display higher levels of exploration, boldness or aggressiveness in contrast to reactive individuals (Sih *et al.*, 2004). The predation risk is one of the most relevant criteria affecting habitat choice (DeCesare *et al.*, 2014; Lima et Dill, 1990). A reduced risk should be favoured, enhancing the survival of both parents and juveniles (Fernandez *et al.*, 1993). Risk perception may vary depending on the structural elements of the landscape and induce, for instance, boldness-dependent utilization. Shy individuals should avoid risky habitats (e.g., Seltmann *et al.*, 2014). Recently, Bonnot et al. (2015) showed that individual differences in the use of open habitats were related to individual differences in vigilance in European Roe deer (*Capreolus capreolus*). Also, propensity to explore large areas can help individuals to perform in poor/risky or heterogeneous food habitats (Charmantier *et al.*, 2017). For instance, slow/thorough explorers may be better at finding food over shorter distances than fast/superficial explorers. Recently, exploration and boldness-dependent patterns have been found in space use (Boyer *et al.*, 2010; Patrick *et al.*, 2014, 2017), dispersal (Cote *et al.*, 2010a; Cote et Clobert, 2007), and habitat preferences (Kobler *et al.*, 2011; Leclerc *et al.*, 2016; Pearish *et al.*, 2013). However, how and why personality is involved in habitat use specialization is still poorly documented, especially how it leads to spatially structured population in clustered habitats.

In this study, we assessed the link between individual behavioural differences and habitat selection in eastern chipmunk (*Tamias striatus*). We tested whether: (1) individuals aggregated depending on their personalities (exploration, boldness, and handling docility), (2) microhabitat explained behaviour-dependent spatial aggregation and (3) microhabitat explained individual lifespan and lifetime reproductive success. Because habitats are seldom environmentally and socially homogeneous, disentangling MHC from other processes can be tricky. First, MHC should be distinguished from phenotypically plastic changes in the trait (i.e., individuals adjust their phenotype to the habitat they live in), selective mortality (i.e.,

only some individuals with specific characteristics survive in a particular habitat), and direct exclusion by conspecifics (i.e., some individuals despotically use some habitats, imposing other habitats to other individuals, Edelaar *et al.,* 2008). Second, spatial autocorrelation in environmental gradients, biased spatial dispersal between sexes or among related individuals may also lead to similar heterogeneous distributions of individuals. For instance, in mammals, male-biased dispersal is widely documented (Dobson, 1982; Wolff, 1994). We expected that, according to their behavioural type, individuals chose habitats that differ in their characteristics. The matching habitat use hypothesis should be corroborated by showing that: i) microhabitat features are spatially structured, ii) habitat heterogeneity explains clusters of individuals with similar phenotypes once spatial autocorrelation in both behavioural and environmental features was accounted for, and iii) a given correlation behaviour/habitat explain a higher individual lifespan or reproductive success in this habitat compared to mismatching individuals. Despite we control for spatial autocorrelation and because individual choices depend on many factors that we were not able to control in natural conditions, our main goal is to bring some evidence that a correlation habitat/phenotype should enhance individual fitness when matching habitat use is beneficial.

2.3 Material & methods

2.3.1 Study system and study sites

The eastern chipmunk is a diurnal and territorial rodent (family: Sciuridae). They concentrate their activities around a burrow that they use solitarily and in which they store seeds for winter (Humphries *et al.*, 2002, 2012). In southern Québec (Canada), chipmunks mainly feed on spring herbaceous bulbs of American trout lily (*Erythronium americanum*) and Carolina spring beauty (*Claytonia caroliniana*) and on seeds from the dominant American beech (*Fagus grandifolia*), red maple (*Acer*

rubrum) and sugar maple (*A. saccharum,* Snyder, 1982). These tree species produce seeds in mast events every 2–3 years. Females enter oestrus once a year, either in early summer or in early spring, depending on the occurrence of an American beech tree mast in the fall (Bergeron *et al.*, 2011c).

From 2012 to 2018, we live-trapped individuals on two sites near Mansonville, in southern Québec, Canada (45° 05'N; 72° 25'W) on rectangular grids of 7.84 ha (Site 1) and 8.40 ha (Site 2) in mixed hardwood forests. We ran linear trapping transects composed of Longworth traps placed every 40 meters and alternately disposed along parallel adjacent transects. We trapped daily during the activity period of chipmunks from early May until early September baiting traps with peanut butter. Animals were marked with a single ear tag code (National Band and Tag Co., New York, KY) upon the first capture. At each capture, we recorded identity, sex, body mass and reproductive status (based on nipple size and vulva hypertrophy for females and testes position and hypertrophy for males (Bergeron *et al.*, 2011c). We considered individuals under 70 g and for which we did not have information on the cohort of birth as juveniles (Bergeron *et al.*, 2011c).

2.3.2 Individual behavioural and lifetime fitness traits

We quantified among-individual differences in exploration using a novel environment test in an open-field arena on 396 individuals. The open-field test is used frequently in personality studies (Gould *et al.*, 2009) and short tests accurately measure consistent differences in activity in a novel environment in rodents (Montiglio *et al.*, 2010, 2012). The experimental arena consists of an empty box (80 x 80 x 40 cm), deprived of any refuge, gridded at the base and placed in the middle of the trapping grid. We first placed the captured individual in an opaque tubular entrance for one minute for acclimation before the test. Exploration in the novel environment was video recorded during 90s (Montiglio *et al.*, 2010). Using The Observer XT11 software (Noldus), we later counted the number of lines crossed by an individual

during 90s, as an index of exploration or activity in a novel environment (Réale *et al.*, 2007). Tests were run during June, twice during the life of an animal, because habituation occurring by the 3rd test reduces the phenotypic variation (i.e., every chipmunk freezes until the end of the 90s; Montiglio *et al.*, 2010). We ran the two tests per individual at 1-year intervals (generally during the first and the second year of life of an individual) to obtain a phenotypic value representative of the whole individual life (Réale et Dingemanse, 2012). We calculated individual's best linear unbiased predictor (BLUPs) for exploration, once controlling for year, date, hour of the test, waiting time before the test, site, number of trials as fixed effects and chipmunk and experimenter IDs as random effects. We used a method proposed by Dingemanse et al. (2019, see Annexe A) to avoid the issue of not translating the error associated to the BLUPs in analyses (Hadfield *et al.*, 2010; Houslay et Wilson, 2017). Following the mixed model on exploration, we first simulated 1000 series of individual BLUPs using the *sim* function of the *arm* library (Gelman et Su, 2018). We then used the individual exploration BLUP mean of the 1000 estimates (see Villegas-Ríos *et al.*, 2018) as individual exploration score in subsequent analysis that vary from slow/thorough to fast/superficial exploration.

We measured boldness using an 'exit test' from the trap, at each capture. We attached a mesh bag around the entry of the trap, and recorded the latency to emerge from the trap (when the animal sticks head and anterior legs out). A test lasted 60s, and we attributed a score of 61s to animals that did not emerge from the trap before the end of the test. We used the inverse latency to emerge from the trap as an index of boldness. Boldness was measured on 693 individuals on average 9 tests times (range = 1-60) during the study period. Docility was measured by a handling-bag test after the exit test each time an animal is captured (N = 719, mean = 9 tests/ind., range = 1-55). The test was carried out during 1 min and docility was measured as the number of seconds spent immobile in the suspended mesh bag (Martin et Réale, 2008; Montiglio *et al.*, 2012).

Docility was expected to be linked to low aggressiveness, low risk-taking (Réale *et al.*, 2010; St-Hilaire *et al.*, 2017) and to low exploration measured in an open-field (Montiglio *et al.*, 2012). As we carry out these tests on many occasions, we assume having minimised errors associated with measurements and with unmeasured effects that can affect intra-individual phenotypic variation. We thus used the individual means of emergence values and docility values as its behavioural score. Using the *rptR* library (Stoffel *et al.*, 2017), we tested the repeatability of each behavioural traits using a Gaussian distribution for exploration and a Poisson distribution for handling docility and latency to emerge. Docility and inverse latency to emerge were then log-transformed to fit a Gaussian distribution and to be included in multivariate analyses (see section 2.3.5). Individual lifespan was calculated as the minimum number of days from an individual's estimated date of birth (first capture date - 44 days, Elliott, 1978) until its last capture, and varied from 295 to 1961 days in the 1st site and from 320 to 1777 days in the 2nd site. Lifetime reproductive success was calculated as the total number of juveniles assigned to an individual during its lifetime and varied from 1 to 11 juveniles in the 1st site and from 1 to 9 juveniles in the 2nd site. Assignments were done in Cervus by using microsatellite loci and captures of juveniles at their natal burrow (Bergeron *et al.*, 2011a; Peters *et al.*, 2007).

2.3.3 Microhabitat data collection

We detected individual burrows at night using radio-transmitter collars (model PD-2CT, Holohil Systems Ltd, ON, Biotracker receivers, Lotek). We identified 207 burrows (102 on site 1 and 105 on site 2), between 2012 and 2017. The eastern chipmunk is a central-place forager. Yahner (1978b) and Elliott (1978) estimated the territory size of these animals around about 24 to 30 meters of diameter around the burrow. We thus sampled the microhabitat on a circle of 20 m diameter around the main burrow entry (James et Shugart, 1970). We used a circular quadrat sampling of 10 m radius. We sampled sixteen microhabitat variables based on Landry-Cuerrier, (2008) and Mahan et Yahner (1996) to characterize ground composition and openness

of the environment (table S2.1). We counted the percentage of cover of rocks, litter, ground vegetation (herb layer), bare ground and woods; the number of shelters and logs on the ground, the density of the shrub layer and the percentage of canopy openness. Data were recorded at every meter along two 20 m perpendicular transects centered at the burrow of the individual (James et Shugart, 1970), using an ocular tube. Seven biotic variables were also recorded. Within the 10m radius circle, we exhaustively counted the total number of beech, red maple and sugar maple trees, and the number of trees in each species separated and the total number of tree species. Finally, we estimated the number of spring herbaceous bulbs of American trout lily and Carolina spring beauty from 8 quadrats sampling within circle with 0.33 m^2 hoops. All environmental variables were scaled and log-transformed to fit Gaussian distributions.

2.3.4 Moran's eigenvectors maps

To control for spatial autocorrelation, we computed Moran's eigenvectors maps (MEMs, function *dbmem*, package adespatial, Dray *et al.*, 2006) for each site, based on the distance matrix between burrows. This method extracts principal coordinates of neighbour's matrix as spatial predictors in the data structure (Borcard et Legendre, 2002). The MEMs eigenvalues are proportional to Moran's I coefficient of spatial correlation (Dray *et al.*, 2006; Legendre et Legendre, 2012). The truncation threshold of the geographic distance matrix was adjusted to the length of the longest edge of the minimum spanning tree. We obtained 29 and 31 positive MEMs on site 1 and 2, respectively. These vectors tables were then used as conditional tables in regression analysis to remove the effects of spatial structures in the data (see section 2.3.5). The first eigenvectors define large scale patterns and thus tend to describe large clusters of similar values in space, whereas the last MEMs describe smaller spatial scale variation and thus tend to define more mixed values in space (i.e., dispersion, Fig. S2.1).

2.3.5 Statistical analyses

To answer our different objectives, we used a global approach of multivariate statistical analysis to link individual phenotypes, spatial and environmental aspects. For that, we created four data tables with data collected from 2012 to 2018. Y_1 included exploration, boldness and docility and Y_2 lifespan and lifetime reproductive success of chipmunks *i*. As explicative tables, we used environmental variables X that regrouped the environmental variables around burrow *j*, and positive MEMs were regrouped into conditional table Z. Data tables were associated by the coordinates (x, y) of burrow *j* occupied by chipmunk *i*. Redundancy analysis principle (RDA, in *vegan,* Oksanen *et al.*, 2019) is based on multiple linear regressions of an explanatory data table on a response data table. We performed 3 RDAs to test our different predictions on the two sites separately:

(1) To test whether similar behavioural phenotypes were spatially aggregated without considering the environmental spatial structure, we only regressed the table Z on the table Y_1 (Model 1: $Y_1 \sim Z$).

(2) To test whether microhabitat explained the distribution of individual behavioural phenotypes, after accounting for spatial structure, we regressed the table X on the table Y1 accounting for the Z table (Model 2: $Y_1 \sim X + \text{Condition (Z)}$). We accepted a $P < 0.05$ corresponding to a constrained variation explained by the global model.

(3) To evaluate if a given correlation behaviour/habitat predicted the individual fitness, we had to control for spatial autocorrelation in both behaviours and environmental variables. For that, we use a variation partitioning approach on the global model 3: $Y_2 \sim Y_1 + X + Z$. The variation partitioning distinguishes variation equivalent to distinct fractions (and shared fractions) explained by explanatory tables (Borcard *et al.*, 1992) and that can be tested by subsequent RDAs (See Fig. S2.2). We used the function varpart (library *vegan*) and reported adjusted fractions (Peres-Neto *et al.*, 2006) of the global model to apportion the variation in fitness traits among behavioural traits, habitats variables and spatial MEMs data sets. Using

RDAs, we tested separately whether (3.1) variation in behaviours explained variation in fitness traits, while accounting for spatial structures with the model 3.1 as $Y_2 \sim Y_1 \mid Z$ (the fraction [a + d] as); (3.2) variation in habitat explained variation in fitness traits, while accounting for spatial structures with the model 3.2 as $Y_2 \sim X \mid Z$ (the fraction [b + d]); and (3.3) variation in behaviours explained variation in fitness traits, while accounting for habitat variables with the model 3.2 as $Y_2 \sim Y_1 \mid X$ (the fraction [a + f]). We followed this procedure because the direct shared variation of two (fraction d) or three tables (fraction g) is not testable with this method.

Finally, we carried out forward selections (*forward.sel*, library *adespatial*) on models 1, 2 and 3.2 to select the most significant spatial and environmental predictors of individual traits (behaviours and fitness). The threshold of variables selection was P = 0.05 and only the 5 first selected variables are shown in table 2.2 if applicable. However, because forward selection is too liberal, we used the adjusted R^2 of the global RDA model as second stopping criterion (Blanchet *et al.*, 2008) and significant predictors are in bold (table 2.2). Additionally, to describe the spatial pattern in environmental variables and microhabitats on both sites, we performed a separate RDA as $X \sim Z$ (Fig. S2.3). As missing data are not allowed in ordination analysis, we used a final N_{obs}= 146 for Y_1 and N_{obs} = 88 for Y_2 on site 1; N_{obs} = 136 for Y_1 and N_{obs} = 80 for Y_2, as an observation corresponds to an association individual/burrow.

2.4 Results

2.4.1 Behavioural traits repeatability

We found significant repeatability estimates for exploration (2012 – 2017, r = 0.41, 95 % CI = 0.34-0.59, P <0.001, N_{id}= 396, N_{obs} = 552), boldness (2012 – 2018, r = 0.09, 95 % CI = 0.04-0.12, P <0.001, N_{id} = 693, N_{obs} = 4935) and docility (2012 – 2018, r = 0.41, 95 % CI = 0.37-0.45, P <0.001, N_{id}=719, N_{obs} = 5371).

2.4.2 Behavioural spatial patterns

On both sites, behavioural traits are significantly spatially structured (Model 1, Site 1: 40 %; Site 2: 41 %, table 2.1). The forward selection showed that spatial structures are combined by large (e.g., MEM4, MEM1, table 2.2) and small patterns (e.g., MEM26, MEM31). Only considering the higher R^2_{adj} (table 2.2), behaviours are structured according to the MEM4 on site 1 and MEM1 on site 2 (Fig. 2.1). The RDA plot on site 1 illustrated that MEM4 positively covariated with docility and negatively with boldness on the axis RDA1 and to a lesser extent with exploration (Fig. 2.1). This relation means that the higher values of MEM4 are found at same burrow locations that higher values of docility but lower values of boldness and exploration (aggregated clusters). On site 2, MEM1 mainly positively covariated with boldness and negatively with docility on the axis RDA1, while exploration was explained by a very small spatial structure (MEM31 on the axis RDA2, Fig. 2.1). These relations mean that the higher values of MEM1 are found at same burrow locations that higher values of boldness but lower values of docility (aggregated clusters). On the contrary, similar exploration phenotypes do not form aggregated cluster but a dispersed spatial pattern.

2.4.3 Microhabitat use

Microhabitat features significantly explained variation in behaviours on site 1 (Model 2, 20%, Y_1: $F = 2.21$, $P < 0.001$, Fig. 2.2a) and to a lesser extent on site 2 (13%, Y_1: $F = 1.75$, $P < 0.01$, Fig. 2.2b). On site 1, shrub density (DENS), the number of shelters (SHELT) and to a lower extent the vegetation cover (VEG), abundance of mature beech trees (FRAGRA) and total number of mature trees (TOTMAT) explained the heterogeneity in behaviours (table 2.2). Fast/bold and less docile individuals were more found in habitats with a higher shrub density, vegetation cover and more beech trees compared to slow/shy and docile individuals (RDA1, Fig. 2.2a). Alternatively,

fast explorers were also found in habitat with fewer mature trees, logs and shelters (RDA2, Fig. 2.2a).

On site 2, the heterogeneity in behavioural phenotypes was better explained by the number of sugar maple trees (ACERUB), the canopy openness (CANOP) and the litter cover (LIT), and to a lower extent by the shrub density (DENS) and by the number of logs (LOGS, table 2.2). Fast/bold and docile individuals prefered habitats with a higher litter cover and canopy closure but fewer sugar maple trees and logs (RDA2, Fig. 2.2b) compared to slow/shy and less docile individuals.

2.4.4 Fitness spatial patterns

Fitness traits were spatially structured (Model 3, Site 1: 65 %; Site 2: 36 %, table 2.1) and variation partitioning of lifetime fitness traits revealed differences among sites (Fig. 2.3). First, our global model explained more variation in fitness traits on site 1 (residuals = 0.175) compared to site 2 (residuals = 0.347). Second, variation in behaviours and habitats explained about 10 and 20 times more variation in fitness traits on site 1 than on site 2. Similarly, spatial structure explained almost twice more variation in fitness traits on site 1 than site 2. We first tested the behavioural fraction (models 3.1) accounting for spatial structure in the data. Behaviours (Y_1) covaried significantly with lifetime fitness traits (Site 1: $F = 5.49$, $P < 0.001$; Site 2: $F = 3.68$, $P < 0.01$, table 2.1), even though they explained, overall, 9% and 6% of the total variation, respectively (Figs. 2.2c and 2.2d). However, once habitat variation has been accounted for (models 3.3), behaviours still explained variation in fitness traits on site 1 (7%) but not on site 2 (0 %, table 2.1). As well, microhabitat features significantly explained variation in fitness traits on site 1 (20%) but not on site 2 (2%, models 3.2, table 2.1). On site 1, the shrub density (DENS) and the rocky cover (ROC) better explained the spatial heterogeneity in fitness variation (table 2.2 and Fig. 2.2e). On site 2, the low proportion of variation explained by habitat (2%, $P = 0.153$, table 2.2) is also poorly represented by ordination on RDA axes (Fig. 2.2f).

2.4.5 Tables and figures

Table 2.1 Variation partitioning of responses tables Y_1 (exploration, boldness, handling docility) and Y_2 (lifespan, lifetime reproductive success) accounting for habitat table (X) and spatial table (MEMS, Z) and for Y1 in models 3. [1]

Y_1 (*behav.*)						
	Model	Fractions	Variation partitioning		RDAs	
			Df	$R^2_{Adj.}$	*F*	*P-value*
Site 1	(1)	MEMs (40%)	/		**2.67**	**P <0.001**
	(2)	Habitat	16	0.20	**2.21**	**P <0.001**
		Habitat | MEMs	16	0.11		
		MEMS | Habitat	29	0.16		
		Shared	/	0.09		
		Residuals	/	0.64		
Site 2	(1)	MEMs (41%)	/		**2.37**	**P <0.001**
	(2)	Habitat	16	0.13	**1.75**	**P <0.01**
		Habitat | MEMs	16	0.08		
		MEMs | Habitat	31	0.19		
		Shared	/	0.05		
		Residuals	/	0.68		
Y_2 (*fitness*)						
	Model	Fractions	Variation partitioning		RDAs	
			Df	$R^2_{Adj.}$	*F*	*P-value*
Site 1	(3)	Behav. | Habitat + MEMs	3	0.11		
		Habitat | Behav. + MEMs	10	0.22		
		MEMs | Behav. + Habitat	23	0.65		
	(3.1)	Behav. | MEMs	3	0.09	**5.49**	**P <0.001**
	(3.2)	Habitat | MEMs	10	0.20	**5.16**	**P <0.001**
	(3.3)	Behav. | Habitat	3	0.07	**3.13**	**P <0.05**
		Total Shared	/	0.06		
Site 2	(3)	Behav. | Habitat + MEMS	3	0.07		
		Habitat | Behav. + MEMS	3	0.03		
		MEMs | Behav. + Habitat	18	0.36		
	(3.1)	Behav. | MEMs	3	0.06	**3.68**	**P <0.01**
	(3.2)	Habitat | MEMs	3	0.02	1.85	P = 0.153
	(3.3)	Behav. | Habitat	3	< 0	0.93	P = 0.462
		Total shared	/	0.01		

[1] The symbol "|" precedes conditional tables for which variation is accounted for. When 2 tables were involved in the variation partitioning (model 2), we tested the fraction [a] corresponding to Habitat | MEMs. When 3 tables were involved in the variation partitioning (model 3), we tested (3.1) the fraction [a+d] corresponding to Behaviours | MEMS, (3.2) the fraction [b+d] corresponding to Habitat | MEMs and (3.3) the fraction [a+f] corresponding to Behaviours | Habitat (see Fig. S2.2). Multiple linear regressions were carried using redundancy analyses (RDAs, see *F*, *P-values*). Percentages in brackets corresponded to the variance of Y_1 explained by MEMs and based on RDAs, without considering any other variable (not adjusted). Adjusted R-squared (R^2_{Adj}, Peres-Neto *et al.*, 2006) represent the proportion of variation of Y explained by the corresponding fraction.

Table 2.2 The first five selected variables explained by global models in RDA (1) $Y_1 \sim Z$ and (2) $Y_1 \sim X$ + Conditional (Z) and (3.2) $Y_2 \sim X$ + Conditional (Z). The cumulative adjusted R^2 is given by forward selection for each variable (threshold P = 0.05) and the global R^2_{adj} is based on the global RDA model. Explanatory variables under the global R^2_{adj} threshold (in bold) can be considered as the most explanatory variables.

Models	Site	Variables	R^2_{adj} (cumulative)	F	*P-value*	Global model R^2_{adj}
(1) Y_1 (*Behav.*) ~ MEMs	Site 1	**MEM4**	**0.04**	**7.23**	**0.001**	0.25
		MEM26	**0.07**	**4.68**	**0.010**	
		MEM8	**0.09**	**5.15**	**0.007**	
		MEM11	**0.12**	**5.99**	**0.001**	
		MEM3	**0.15**	**5.76**	**0.004**	
	Site 2	**MEM1**	**0.10**	**15.98**	**0.001**	0.24
		MEM31	**0.10**	**15.98**	**0.001**	
		MEM6	**0.16**	**10.33**	**0.001**	
		MEM24	**0.18**	**4.57**	**0.003**	
		MEM30	**0.20**	**4.26**	**0.007**	
(2) Y_1 (*Behav.*) ~ Habitat	Site1	**DENS**	**0.07**	**11.46**	**0.001**	0.11
		SHELT	**0.10**	**6.71**	**0.002**	
		VEG	0.13	5.20	0.008	
		FAGGRA	0.15	4.68	0.017	
		TOTMAT	0.17	5.13	0.006	
	Site 2	**ACERUB**	**0.03**	**4.74**	**0.004**	0.08
		CANOP	**0.05**	**4.38**	**0.007**	
		LIT	**0.07**	**3.62**	**0.012**	
		DENS	0.09	4.66	0.005	
		LOGS	0.11	2.80	0.043	
(3.2) Y_2 (*fitness*) ~ Habitat	Site 1	**DENS**	**0.03**	**3.87**	**0.03**	0.20
		ROC	**0.06**	**3.25**	**0.04**	
	Site 2	ACERUB	0.06	6.48	0.007	0.02
		DENS	0.10	4.09	0.041	
		DIV	0.17	7.36	0.002	
		FAGGRA	0.21	4.45	0.027	
		ROC	0.23	3.79	0.030	

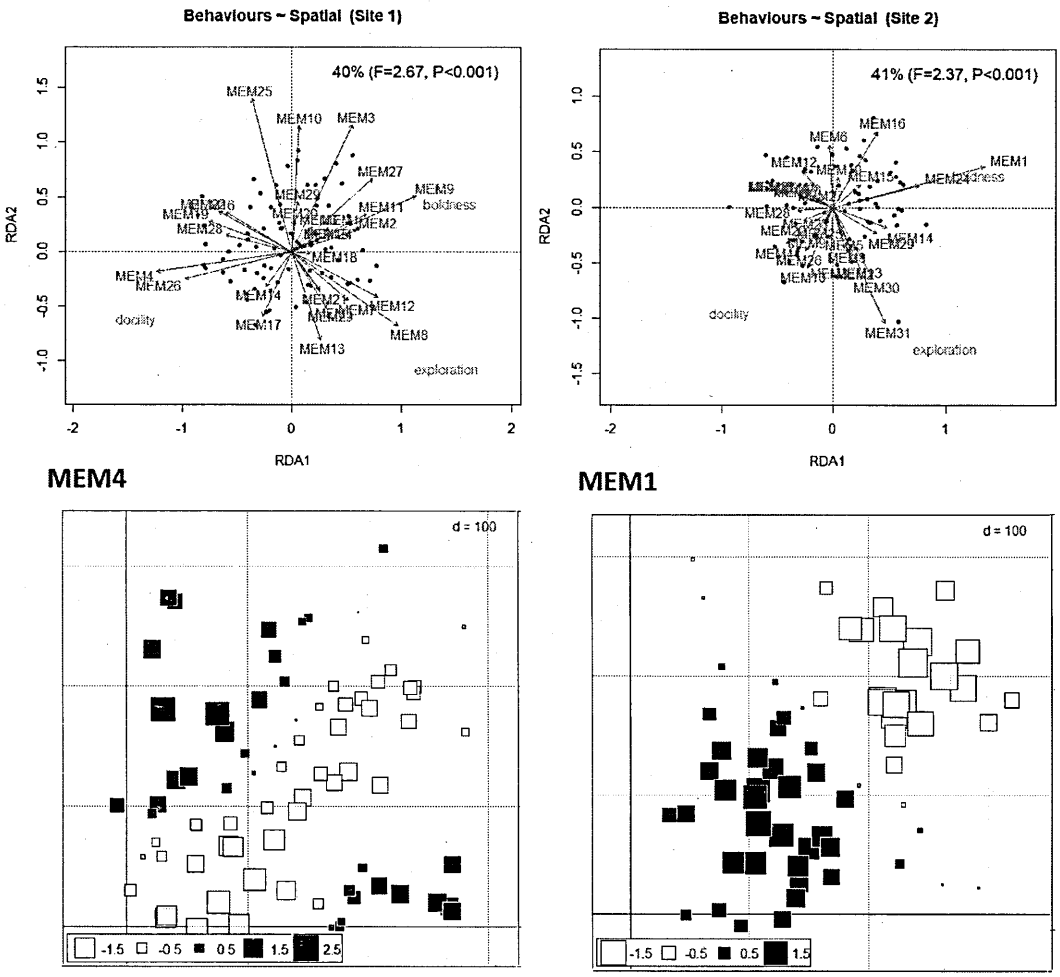
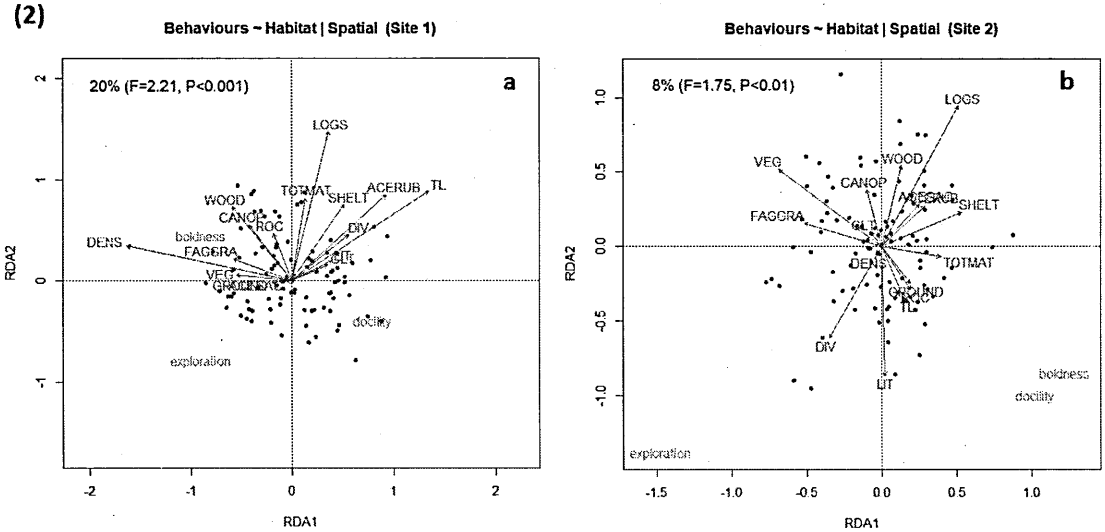


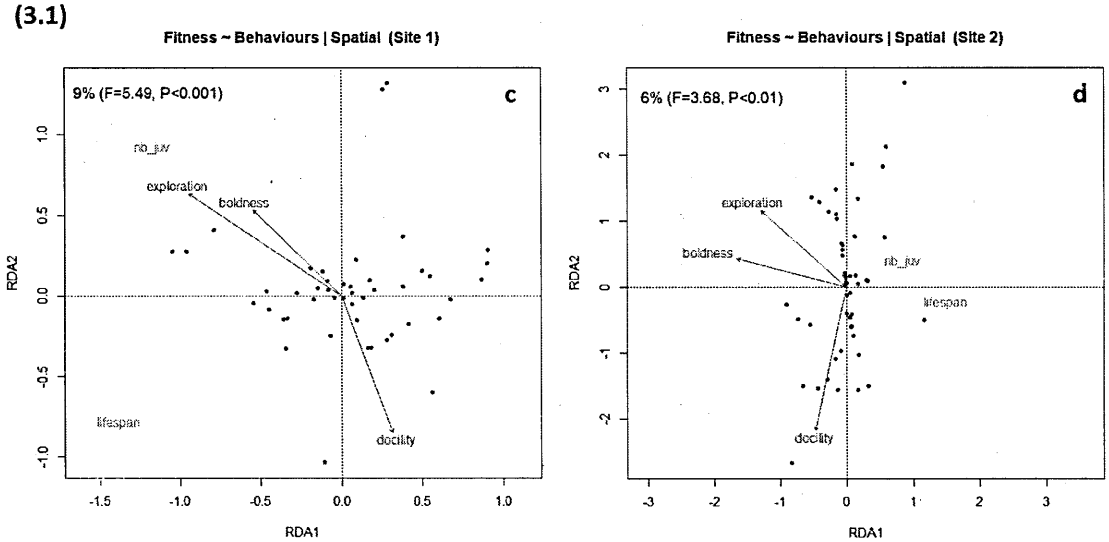
Figure 2.1 Ordination plot of the relation between the spatial table (Moran's eigenvectors' map, MEMs) and behavioural variables based on RDAs on site 1 (top left) and site 2 (top right) in southern Québec (Canada, 45° 05'N; 72° 25'W). The first selected positive MEMs (positive auto-correlation) on site 1 (bottom left) and site 2 (bottom right) represents the personality-structured patterns. MEM4 best explained how the combined phenotypes (exploration, boldness and handling docility) were structured on site 1 (R^2_{Adj} = 0.04, F = 7.23, P <0.001) and MEM1 on site 2 (R^2_{Adj} = 0.10, F = 15.98, P <0.001, table 2.2). Each square represents a burrow location; black and white squares represent higher and lower values of the MEMs respectively.

Similar behavioural phenotype tended to be aggregated in space in our populations, here, without considering environmental spatial structures.

(2)


Behaviours ~ Habitat | Spatial (Site 1)
20% (F=2.21, P<0.001)
a
LOGS
TOTMAT
SHELT
ACERUB
TL
WOOD
CANOP
ROC
DIV
boldness
DENS
FAGGRA
LIT
VEG
GROUND
docility
exploration
RDA1
RDA2
Behaviours ~ Habitat | Spatial (Site 2)
8% (F=1.75, P<0.01)
b
LOGS
VEG
WOOD
CANOP
ACERUB
SHELT
FAGGRA
TOTMAT
DENS
GROUND
ROC
TL
DIV
LIT
boldness
docility
exploration
RDA1
RDA2

(3.1)


Fitness ~ Behaviours | Spatial (Site 1)
9% (F=5.49, P<0.001)
c
nb_juv
exploration
boldness
lifespan
docility
RDA1
RDA2
Fitness ~ Behaviours | Spatial (Site 2)
6% (F=3.68, P<0.01)
d
exploration
boldness
nb_juv
lifespan
docility
RDA1
RDA2

(3.2)

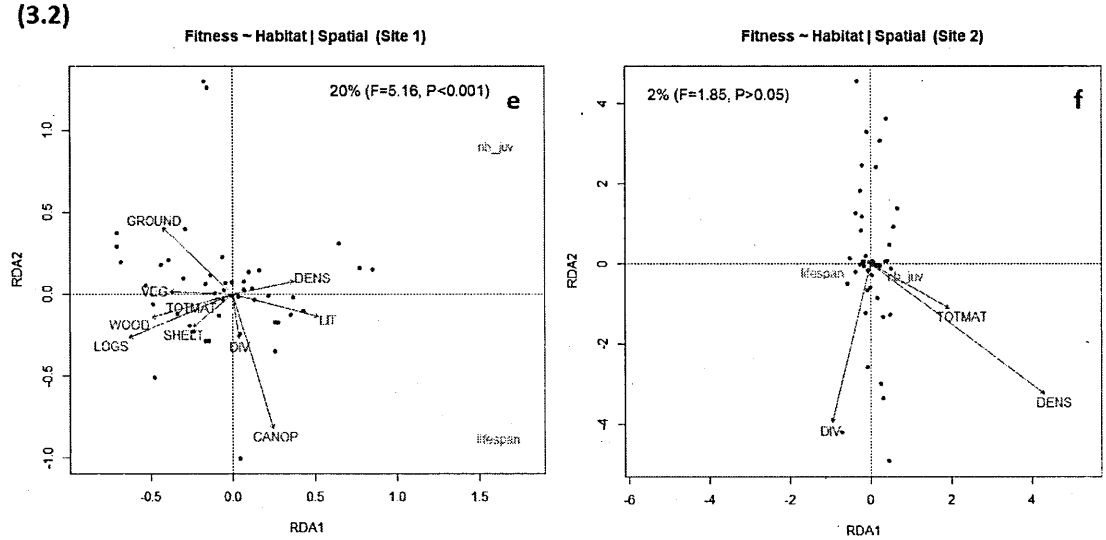

Fitness ~ Habitat | Spatial (Site 1)
20% (F=5.16, P<0.001)
e
nb_juv
GROUND
DENS
VEG
TOTMAT
LIT
WOOD
SHELT
LOGS
DIV
CANOP
lifespan
RDA1
RDA2
Fitness ~ Habitat | Spatial (Site 2)
2% (F=1.85, P>0.05)
f
lifespan
nb_juv
TOTMAT
DENS
DIV
RDA1
RDA2

Figure 2.2 Ordination plot of redundancy analyses (RDAs) tested in models (2) and (3.1) and (3.2) on site 1 (left) and site 2 (right). The model (2) assessed whether variation in habitat (see table S2.1) predicted spatial distribution of behavioural phenotypes (exploration, boldness and handling docility) accounting for spatial structures in the data. Models (3) tested whether (3.1) behaviours and (3.2) habitat predicted spatial distribution of lifetime fitness (lifespan and number of produced juveniles) accounting for spatial structures in the data (table 2.1).

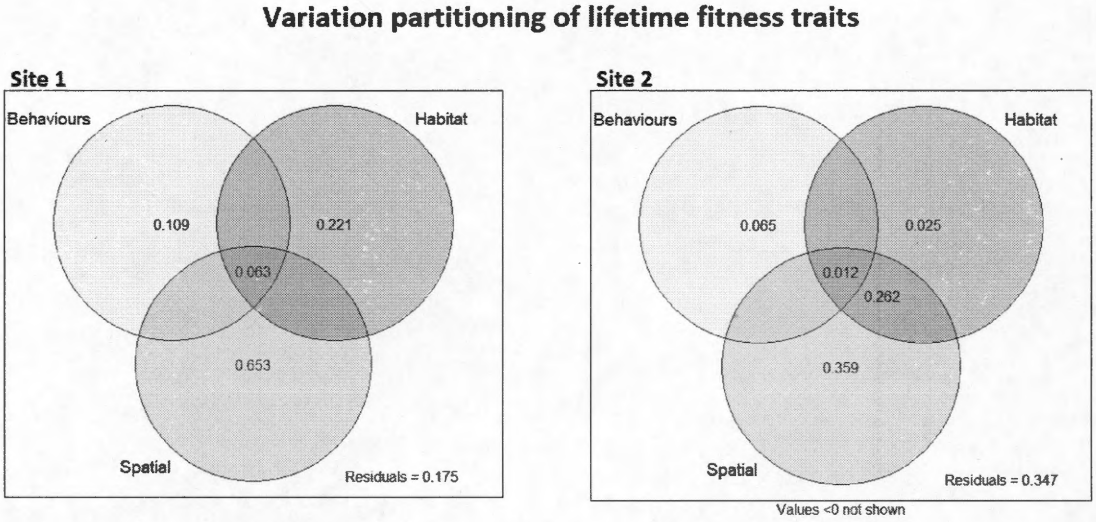


Figure 2.3 Variation partitioning of lifetime fitness traits Y_2 (lifespan and lifetime reproductive success) accounting for behaviours (Y_1: exploration, boldness and handling docility), habitat table (X) and spatial table (MEMs, Z) in eastern chipmunks (*Tamias striatus*), in southern Québec (Canada, 45° 05'N; 72° 25'W). Using RDAs, we tested whether (3.1) behaviours explained the fitness traits, accounting for spatial structures (fraction [a+d], see Fig. S2.2), (3.2) habitat explained the fitness traits, accounting for spatial structures [b+d] and (3.3) behaviours explained the fitness traits, accounting for habitat variables ([a+f], table 2.1).

2.5 Discussion

The interplay between behavioural variations and individual ecological traits is still poorly documented (Dall *et al.*, 2012; Smith et Blumstein, 2007; Wolf et Weissing, 2012) while the habitat matching theory predicts that the habitat should fit the individual phenotype to enhance performance, survival and reproduction of organisms (Edelaar *et al.*, 2008). Behavioural phenotypes should drive in a large manner how individuals perceive, choose a habitat and perform in this habitat. In return, improved ecological performance in a given habitat would reinforce the behavioural-environmental correlation (e.g., Pearish *et al.*, 2013). In this study, we found that behaviours varied with micro-habitat and lifetime fitness traits at the spatial level in eastern chipmunks. However, this relation seemed modulated according to habitat characteristics.

We found that behavioural phenotypes (exploration, boldness and handling docility) were spatially structured. A large spatial pattern described clusters of individuals, considering the three traits combined and, thusly, similar behavioural phenotypes tended to be spatially aggregated in both populations. In particular, boldness and docility exhibited larger clusters than exploration (both sites considered). Others studies have demonstrated that adjacent individuals have similar personalities. For instance, bold/fast explorers are the first to colonize an invasion front (Duckworth et Badyaev, 2007; González-Bernal *et al.*, 2014) and asocial dispersers tend to be found in low-density habitats (i.e., social niche specialization, Cote et Clobert, 2007). Aggregated patterns have also been found due to biased-interactions in social networks (Aplin *et al.*, 2013) and clustered habitat use (Torres et Read, 2009).

In our case, we showed that microhabitat features were spatially structured and explained a part of the spatial heterogeneity in behaviours. In addition to the number of beech and red maple trees, the density in shrub and herb layers, the canopy and

litter cover, the number of shelters and logs were associated with behavioural phenotypes. In other small mammals, several studies have documented preferences for dense microhabitats based on vegetation cover (Dueser et Shugart, 1978; Lagos *et al.*, 1995) or canopy closure (Manson et Stiles, 1998; Zollner et Crane, 2003). A previous study also found that the number of woody debris was the best predictor of burrow site use in a close population (Landry-Cuerrier, 2008). Chipmunks actively use woody and rocky shelters, forage under vegetation cover and mainly use logs to move quietly (personal observation; Elliott, 1978) but we found individual variation in microhabitat use. One prediction based on habitat preferences would have suggested that less risk-prone individuals should prefer 'safer' habitat (Bonnot *et al.*, 2015; Seltmann *et al.*, 2014). Interestingly, bold, docile and fast/superficial explorers (proactive types) tended to use more closed areas in shrub layer (and open canopy) but fewer woody refuges and logs compared to less docile and shyer/slower individuals. One explanation is that bolder individuals, and potentially dominant, monopolize access of the best habitats (with reduced predation risk), forcing less docile individuals to stay in riskier habitats (competitive exclusion, e.g., Alanärä *et al.*, 2001). A second explanation is that we observed the result of individual phenotypic plasticity in habitats that individuals initially did not choose. Individuals forced to stay in open habitats should reduce their boldness and exploration (minimizing time exposed to predators) compared to in safer habitats. Besides, our results suggest that proactive individuals perform well in these habitats exhibiting a longer lifespan and reproductive success than reactive individuals (Site 1, Fig. 2.2c). In particular, the shrub density predicted both spatial heterogeneities in fitness and behavior variation on site 1. Thus, the predation risk gradient appears to be a major candidate of habitat selection, denser habitats affording benefits in proactive individuals (DeCesare *et al.*, 2014).

Alternatively, matching habitat use was less supported on our second site and fitness was unrelated to habitat (Fig. 2.2f) and to behaviours (once habitat variation was

accounted for). Cote et al. (2013) also demonstrated that dissimilar habitats in predation risk modulate personality-dependent dispersal patterns. Less social individuals dispersed in low-risk habitat whereas no difference in sociality was found between non-dispersers *vs.* dispersers in high-risk habitat. Our two sites also vary in their habitats features and homogeneities: the site 2 seems more homogeneous in micro-habitat features than the site 1 (e.g., less variance on PC2, Fig. S2.4). A more homogeneous habitat should constrain the coexistence of alternative ecological specialization and thus, limit contrasting fitness outcomes among individuals related to habitat (Kassen, 2002; Poisot *et al.*, 2011). Moreover, a relatively small proportion of variation in behavioural heterogeneity was explained by habitat (8%) and still, both behavioural and fitness traits were highly spatially structured in our population independently of habitat. Possibly, we did not sample some relevant microhabitat variables on our study sites. Also, biotic factors can also predict spatial heterogeneity among behavioural phenotypes. Predation (Werner *et al.*, 1983) and social environment can affect microhabitat selection and use. For instance, Spiegel et al. (2015) found that aggressive lizards were less likely to use quadrats also used intensively by other conspecifics. One other explanation is that aggregated individuals may display more similar genotypes that distant individuals and share a heritable fitness (but see Kruuk *et al.*, 2000). We know that sex-biased dispersal occurred in chipmunks and that male disperse further away from their natal burrows than females. That results in aggregations of 'family' patches and in a genetically structured population (Dubuc-Messier *et al.*, 2012). Sex and age should also explain a part of the spatial heterogeneity among individuals.

Within the term "habitat selection", terminologies are often confusing (Hall *et al.*, 1997). To our perspective, habitat selection regroups habitat choice (and preference) and habitat use. Using ecological niche terms, habitat choice can evoke the fundamental niche of an organism, i.e., the most extended range of ecological conditions within which an individual can fit. Alternatively, habitat use may describe

the realised niche, i.e., the range of physical or biological conditions that an animal use (Hall *et al.*, 1997) and in which it actually lives after actions from external conditions (exclusion competition, availability, *etc.*). It is delicate to demonstrate the habitat choice in natural conditions but the evidence of enhanced fitness in a given habitat brings valuable information about matching habitat use and the potential maintenance of the phenotype/environment correlation. Here, we provided evidences that behavioural variation participates in ecological niche specialization. Personality-dependent habitat use should heighten the correlation between behavioural and environment at a phenotypic level but also at a genetic level, which will ultimately determine the evolutionary potential of individual variation. It helps our comprehension of how individual differences in behaviour can be generated and maintained in some natural population. Since, other environmental and social processes act in interaction to modulate specialization patterns. Intraspecific competition (Agashe et Bolnick, 2010) or dissimilarity/homogeneity in habitat features should either enhance or constrain individuals niche expansion or differentiation (Bolnick *et al.*, 2003; Roughgarden, 1972). Lastly, highlighting social and spatial/temporal environmental factors acting on personality-dependent specializations should help our comprehension of both personality and ecological traits coevolutions (Dall *et al.*, 2012).

2.6 Acknowledgments

We thank the many students and crew members who assisted with data collection on the field in the Sutton Chipmunk Project since 2012. We thank Pedro Peres-Neto for advice on our spatial analysis; the Nature Conservancy and the Réserve Naturelle des Montagnes Vertes (Estrie, Québec, Canada) for providing access to the chipmunk study sites. Financial support for this project was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), NSERC Discovery grants to

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2.7 Supplementary material

Table S2.1 Micro-habitat variables sampled around chipmunks' burrows in southern Québec (Canada, 45° 05'N; 72° 25'W). Percents were estimated on a total of four 10m-transects; Abundances of herbaceous bulbs were summed on 8 quadrats; Trees abundance are exhaustive in a 10m-diameter circle around the burrow.

Micro-habitat Variables	Unity	Range	Abbreviation
Number of mature trees	Abundance	3-40	TOTMAT
Number of species trees	Abundance	3-16	DIV
Density	Abundance TOTMAT/314 (m^2)	0.08-0.94	DENS
Number of logs	Abundance	3-22	LOGS
Number of refuges	Abundance	2-26	SHELT
Canopy openness	%	0-50	CANOP
Dead wood cover	%	0-25	WOOD
Litter cover	%	25-87.50	LIT
Vegetation cover	%	0-67.5	VEG
Bare ground cover	%	0-25	SOIL
Rocky cover	%	0-17.50	ROC
Number of mature beech trees	Abundance	0-21	FAGGRA
Number of mature Red maple trees	Abundance	0-13	ACERUB
Number of mature Sugar maple trees	Abundance	0-19	ACESAC
Number of Trout lily	Abundance	0-747	TL
Number of Carolina spring beauty	Abundance	0-390	CLT

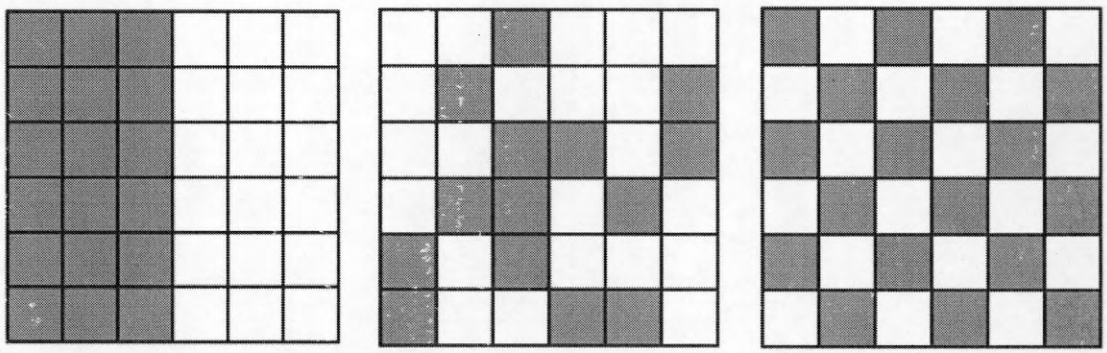

Figure S2.1 Visualisation of three examples of spatial patterns that represent Moran's eigenvectors maps (MEMs). The first eigenvector (left) defines large scale patterns and thus tend to describe large clusters of similar values in space. Intermediate eigenvector (middle) represents random spatial patterns, with a priori no spatial structure, whereas the last MEMs (right) describes smaller spatial scale variation and thus tend to define more close opposed values in space (i.e., dispersion).

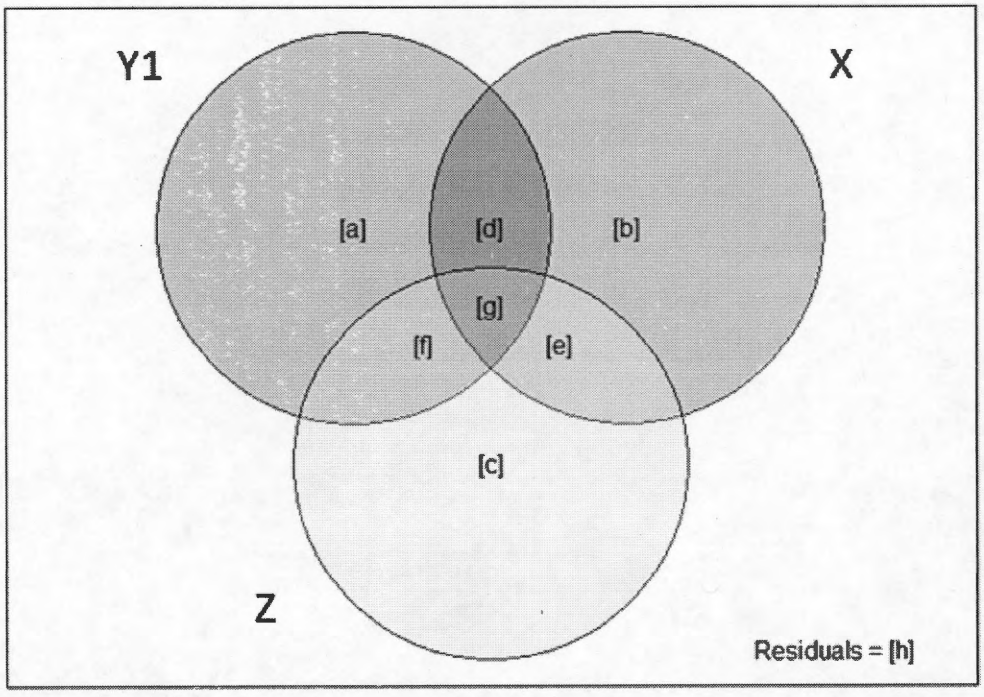

Figure S2.2 Visualisation of the fractions of a variation partitioning that can be tested by subsequent RDAs. The variation partitioning distinguishes variation equivalent to the distinct fractions (and shared fractions) explained by explanatory tables. We partitioned the variation in fitness traits (Y_2) among behavioural traits (Y_1), habitat variables (X) and spatial MEMs (Z) data sets.

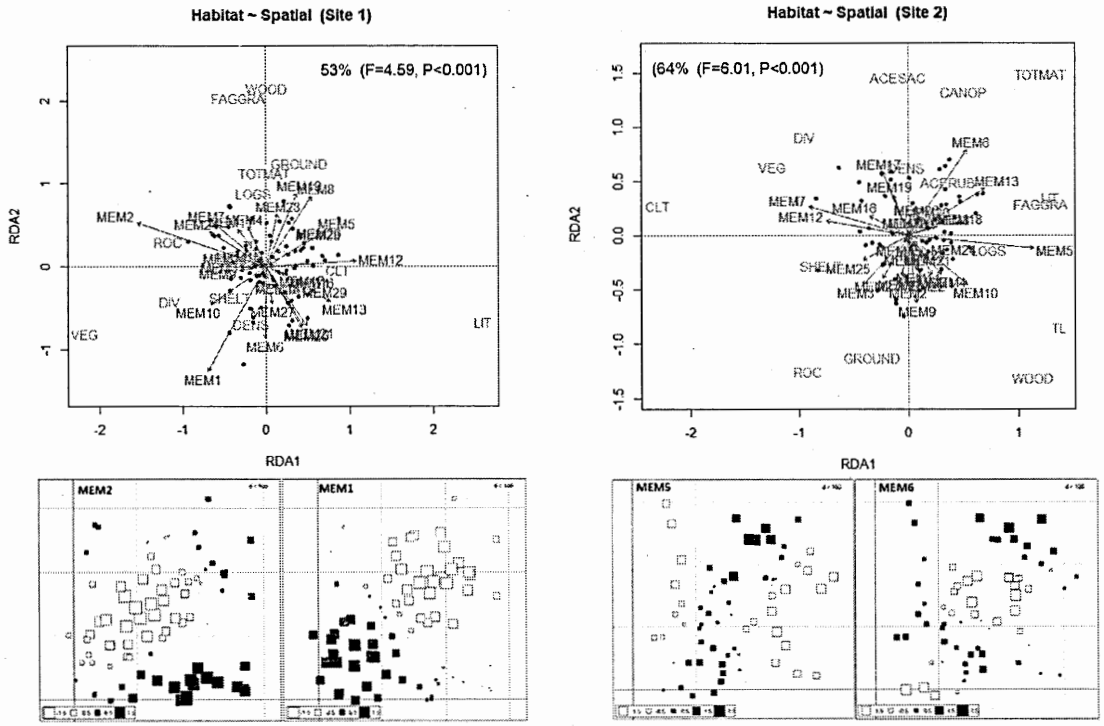

Figure S2.3 Ordination plot of the relation between spatial table (Moran's eigenvectors' map, MEMs) and environmental variables based on RDAs on site 1 (left) and site 2 (right) in southern Québec (Canada, 45° 05'N; 72° 25'W). We provided visualisations of the first selected positive MEM contributing to each axis (bottom). On site 1, MEM2 (R^2_{Adj} = 0.06, F = 9.75, P <0.001) better explained RDA1 and covariated positively with vegetation cover (VEG), tree species diversity (DIV) and rocky cover (ROC) and negatively with litter cover (LIT) and presence of Carolina spring beauty (CLT). MEM1 (R^2_{Adj} = 0.10, F = 8.29, P <0.001) better explained the RDA2 and covariated positively with density of shrub layer (DENS) and negatively with beech trees (FAGGRA), woody debris (WOOD and LOGS) and bare ground (GROUND).

On site 2, MEM5 (R^2_{Adj} = 0.10, F = 16.24, P <0.001) better explained RDA1 and covariated positively with litter cover (LIT), presence of beech trees (FRAGRA), woody debris (WOOD and LOGS) and Trout lily (TL) and negatively with vegetation cover and shelters (VEG and REF), Carolina spring beauty (CLT) and tree species diversity (DIV). MEM6 (R^2_{Adj} = 0.16, F = 9.98, P <0.001) better explained RDA2 and positively covariated with red maple trees (ACERUB and ACESAC), canopy openness (CANOP), density of shrub layer (DENS) and negatively with bare ground (GROUND), woody and rocky cover (WOOD and ROC).

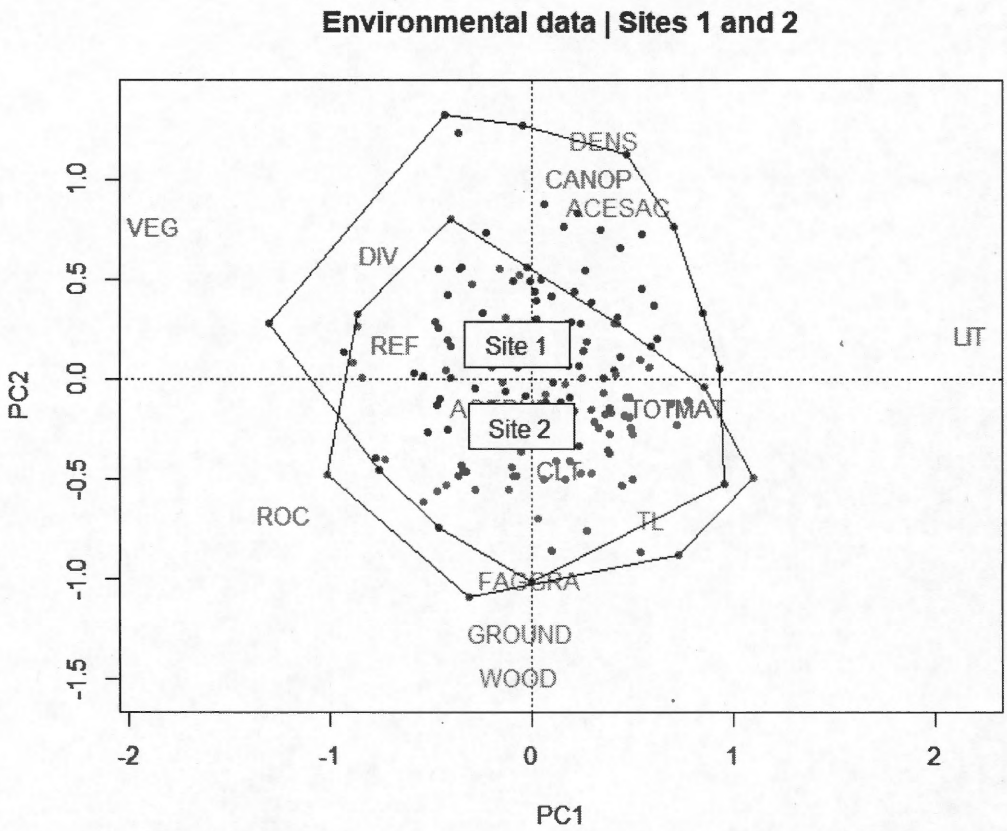

Figure S2.4 Differences in micro-habitats features (ordination axes) between site 1 and site 2 in southern Québec (Canada, 45° 05'N; 72° 25'W). Multivariate micro-habitat table (table S2.1) is constrained in a Principal Components Analysis (PC1: 15.36%; PC2: 13.48%) and niche spaces are visualized with ordihull (library *vegan*). Site 1 shows a higher variance on PC2 than site 2 and thusly contains more burrows with dense shrub layer (DENS), open canopy (CANOP) and sugar maple trees (ACESAC).

CHAPITRE III

EXPLORATION PROFILES DRIVE ACTIVITY PATTERNS AND TEMPORAL NICHE SPECIALIZATION IN A WILD RODENT

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3.1 Abstract

Individual niche specialization can have important consequences for competition, fitness, and ultimately population dynamics and ecological speciation. The temporal window and the level of daily activity are niche components that may vary with sex, breeding season, food supply, population density, and predators circadian rhythm. More recently, ecologists emphasized that traits such as dispersal and space use could depend on personality differences. Boldness and exploration have been shown to correlate with variation in foraging patterns, habitat use, and home range. Here we assessed the link between exploration, measured from repeated novel environment tests, activity patterns, and temporal niche specialization in wild eastern chipmunks (*Tamias striatus*). Intrinsic differences in exploration should drive daily activity patterns through differences in energy requirements, space use, or the speed to access resources. We used collar-mounted accelerometers to assess whether individual exploration profiles predicted: (1) daily overall dynamic body acceleration, reflecting

overall activity levels; (2) mean activity duration and the rate of activity sequences, reflecting the structure of daily activity; and (3) patterns of dawn and dusk activity, reflecting temporal niche differentiation. Exploration and overall activity levels were weakly related. However, both dawn activity and rate of activity sequences increased with the speed of exploration. Overall, activity patterns varied according to temporal variability in food conditions. This study emphasizes the role of intrinsic behavioral differences in activity patterns in a wild animal population. Future studies will help us understand how yearly seasonality in reproduction, food abundance, and population density modulate personality-dependent foraging patterns and temporal niche specialization.

3.2 Introduction

Individual niche specialization defines how individuals vary in their resource use within the same population (Bolnick *et al.,* 2003). Niche variation can reduce within-species interference and competition (e.g., diet segregation, Estes *et al.,* 2003; Kobler *et al.,* 2009; Zanden *et al.,* 2010; Araújo *et al.,* 2011; Terraube *et al.,* 2014). Furthermore, individual niche variation has important effects on individual fitness (Ceia et Ramos 2015), organisms coexistence (Bolnick *et al.,* 2003), and on population dynamics and species communities (Bolnick *et al.,* 2011). For instance, a generalist predator interacts with more prey species than a specialist predator (Snyder et Ives 2003). Individual niche variation should lead, ultimately, to adaptive divergence within and among populations (Senar *et al.,* 2006; Bolnick *et al.,* 2009; Ingram *et al.,* 2018) and is thus a prerequisite for species niche evolution (Van Valen, 1965; Roughgarden, 1972; Roughgarden, 1974). Individual differences in spatial and temporal use of resources can decrease competition (Schoener, 1974). Individuals can vary in space use and habitat preferences (Boon *et al.,* 2008; Hensley *et al.,* 2012; Spiegel *et al.,* 2015), or in daily foraging patterns (Alanärä *et al.,* 2001; Dammhahn et Almeling, 2012; Conners *et al.,* 2015). Individuals also vary in their

movement patterns, such as speed and sinuosity (Nathan *et al.,* 2008; Spiegel *et al.,* 2017), and these patterns can affect spatial and temporal foraging activities and may covary with the metabolic rate (Biro et Stamps 2010) or energy requirements (Perrigo, 1990). Yet, the interplay between behavioral differences and ecologically relevant traits like resource specialization is still poorly documented (Smith et Blumstein 2007; Dall *et al.,* 2012; Wolf et Weissing 2012).

Individuals show consistent level differences in behavioral traits, a.k.a. personality differences (Réale *et al.,* 2007) that covariate with metabolism and locomotor performance (Careau *et al.,* 2008; Galliard *et al.,* 2013; Biro *et al.,* 2018; Newar et Careau 2018). For instance, bolder individuals often display higher social rank, aggressiveness, and activity than shyer individuals (Colléter et Brown 2011; David *et al.,* 2011). Differences in boldness or exploration can explain foraging performance, habitat preference or home range use (Aplin *et al.,* 2013; Patrick *et al.,* 2014; Spiegel *et al.,* 2017). Theory predicts that speed of exploration should increase foraging activity (Toscano *et al.,* 2016), or home range size (Spiegel *et al.,* 2017). Also, bold, aggressive individuals may prefer to forage in rich but riskier environments (e.g., cities, Charmantier *et al.,* 2017), or at riskier periods during which they can meet their energetic needs at the cost of a higher mortality (Ward-Fear *et al.,* 2018; Vinne *et al.,* 2019). Furthermore, when individuals compete for access to limited resources, they can temporally modify their activity level, shift their temporal niche (Daan *et al.,* 2011; Fingerle *et al.,* 2016) or segregate foraging activities according to their social rank (Stone *et al.,* 2018). Generally, dominant individuals monopolize access to water and food sources (Lee *et al.,* 2018) or to most beneficial foraging periods (e.g., with low predation risk, Alanärä *et al.,* 2001). Food availability, intraspecific competition, predation, or population density can, therefore, interact with intrinsic individual features to affect activity and time budgets. For instance, Quinn et al. (2012) showed how predation risk interacts with starvation conditions and personality types to shape the temporal use of food patches in great tits (*Parus major*). Behavioral phenotypes

may thus affect niche specialization and vice versa. Yet, we know little about how intraspecific behavioral variation affects daily/seasonal spatial and temporal niches in natural fluctuating conditions (Spiegel *et al.,* 2017).

Recent studies have used miniaturized accelerometers to quantify animal movement and investigate various aspects of animal activity in the wild. The overall dynamic body acceleration, measured on three orthogonal axes in space, reflects above-ground activity (Williams *et al.,* 2016) and energy expenditure (Green *et al.,* 2009; Hicks *et al.,* 2017). Also, partial dynamic acceleration on separate axes captures distinct behaviors like running, resting, grooming, and foraging behaviors (e.g., prey capture events, Viviant *et al.,* 2010; Kokubun *et al.,* 2011; Wang *et al.,* 2015) and thus time-activity budgets (Shamoun-Baranes *et al.,* 2012). Accelerometry has been mainly deployed on large aquatic mammals and marine birds (Halsey *et al.,* 2009), and less on smaller animals like rodents (Hammond *et al.,* 2016; Lush *et al.,* 2016; Studd *et al.,* 2019). To our knowledge, no study has used accelerometry to analyze how consistent among-individual behavioral differences measured in experimental tests (i.e., open-field test) reflect the fine-scale time-activity budget in the wild. In this paper, we tested the link between individual exploration profiles and activity patterns in a wild eastern chipmunk (*Tamias striatus*) population, using accelerometry. We tested whether individual exploration profiles predicted: *i*) the daily Overall Dynamic Body Acceleration (thereafter ODBA), reflecting overall activity levels in natural conditions; *ii*) the mean activity bouts duration and the rate of activity sequences, reflecting the rhythmicity of daily activity; *iii*) the onset and end times of the daily activity, to assess exploration-dependent temporal-niche differentiation.

Eastern chipmunks are easily and frequently captured. They solitarily defend small territories that overlap with their neighbors. They thus interact frequently and aggressively over resources such as territory, food, or mates (Getty, 1981; Bergeron *et al.,* 2011a). Differences in time budgets among individuals reflect encounter

avoidance with neighbors and reduction in competition (Getty, 1981). Therefore, chipmunks offer an ideal spatial competition model to study niche differentiation, and we hypothesize that different behavioral profiles should display differences in their daily foraging patterns. Chipmunks show repeatable differences in their response to novel environment tests (i.e., open-field test) and vary from slow/thorough explorers to fast/superficial explorers (Montiglio *et al.,* 2010). Exploration increases with handling aggression and trappability (Montiglio *et al.,* 2012). Some studies have shown a positive correlation between velocity (Wilson *et al.,* 2006), aboveground activity (Williams *et al.,* 2016), daily energy expenditure (Elliott *et al.,* 2013), and dynamic body acceleration. We thus predict a positive relationship between the speed of exploration in the open-field test and daily ODBA, and a negative relationship between exploration and mean duration of daily activity sequences. This negative relationship should reflect an energetic trade-off between the intensity and duration of active bouts. Slower explorers should also show lower levels of activity and thus distribute their activity more homogeneously during the day.

We collected data over two consecutive years (2016 and 2017) with contrasting ecological conditions. Chipmunk reproduction and population dynamics depend heavily on a 2-year cycle beech mast (Humphries *et al.,* 2002; Bergeron *et al.,* 2011c). This mast is synchronized with a red maple mast occurring in the spring (Tissier *et al.,* in press). The red maple and American beech masting event of 2017 created striking differences in the abundance of food resources and population density: compared to a mast year, a non-mast year is characterized by low food abundance and high population density. These temporal fluctuations in ecological conditions should affect intraspecific competition intensity and thusly individual activity patterns. For instance, individual differences in dawn/dusk activity should increase at high population density in the non-mast year. Finally, we expect differences in activity between males and females. Non-mast springs coincide with lactation period in females and mating

activity occurs in late spring of mast years and males significantly increase their home range size to find a partner (Montiglio *et al.,* 2010).

3.3 Material & methods

3.3.1 Study system and study sites

The eastern chipmunk is a diurnal and territorial rodent (family: Sciuridae), feeding mostly on seeds from the dominant American beech (*Fagus grandifolia*), red maple (*Acer rubrum*) and sugar maple (*A. saccharum*). Chipmunks concentrate their activities around a burrow that they use solitarily and defend actively, and in which they store seeds for winter (Humphries *et al.,* 2002; 2012). Females enter in estrus once a year, either in early summer or in early spring, depending on the occurrence of an American beech tree mast in the fall (Bergeron *et al.,* 2011a).

From 2012 to 2017, we live-trapped individuals at two sites near Mansonville, in southern Québec, Canada (45°05'N; 72°25'W) on rectangular grids of 7.84 ha (site 1) and 8.40 ha (site 2) in mixed hardwood forests. We placed *Longworth* traps every 40 meters along 14 linear and parallel transects separated by 20 meters each. We trapped daily during the activity period of chipmunks from early May until early September baiting traps with peanut butter. Animals were marked with a single ear tag code (National Band and Tag Co., New York, KY) upon first capture. At each capture, we recorded identity, sex, body mass in a suspended mesh bag and reproductive status (based on nipple size and vulva hypertrophy for females and on testes position and hypertrophy for males (Bergeron *et al.,* 2011a).

3.3.2 Exploration tests

We quantified among-individual differences in exploration using a novel environment test in an open-field arena on 396 individuals from 2012 to 2017. Personality studies

often use the open-field test to measure exploration and activity (Réale *et al.,* 2007; Gould *et al.,* 2009) and short tests accurately measure consistent differences in activity in a novel environment in rodents (Montiglio *et al.,* 2010; 2012). The experimental arena consists of an empty white box (80 x 80 x 40 cm), deprived of any refuge, gridded at the base and placed in the middle of the trapping grid. Before the test, we placed the captured individual for one minute in an opaque tubular entrance for acclimation. Exploration in the novel environment was video recorded during 90 sec (Montiglio *et al.,* 2010). Using The Observer XT11 software (*Noldus*), we later counted the number of lines crossed by an individual during 90 sec, as an index of exploration or activity in a novel environment (Réale *et al.,* 2007). We ran two tests per individual at 1-year intervals (generally during the first and the second year of life of an individual) to obtain a phenotypic value representative of the whole individual life (Réale et Dingemanse 2012). Chipmunks habituate quickly to the open-field test by the 3rd test, which reduces the among-individual variation in exploration (i.e., every chipmunk freezes until the end of the 90 s; Montiglio *et al.,* 2010). We used the individual exploration BLUP in subsequent analysis (Villegas-Ríos *et al.*, 2018; Dingemanse *et al.*, 2019, see Annexe A) as exploration profile to reflect the slow/thorough to fast/superficial exploration gradient.

3.3.3 Acceleration measurements

We deployed neck collars with accelerometers devices (*Axy3*, 9 x 15 x 4 mm, 0.7 g, *Technosmart*; Fig. S3.1) on 36 individuals. We equipped 27 adults (13 males and 14 females) in 2016, from May 27th to July 7th, and 20 adults (10 males and 10 females) in 2017 from June 4th to June 24th. Eleven individuals were monitored in both years. The devices recorded accelerations on chipmunks over 12 days on average (Min = 7; Max = 20, $Days_{total}$ = 693). We protected accelerometers with electrical tape, set on a tie wrap collar locked by shrinkable plastic to limit neck friction and positioned below the animal head. The final weight never exceeded 4g (a maximum of 5.7% of

the mass of the smaller individual). Devices recorded the animal body accelerations at 10 Hz (i.e., 10 fix/sec) on three orthogonal axes, heave, sway and surge, which corresponded respectively to the initial z, x and y axes of the device. To obtain the daily activity, we worked on complete 24-hours temporal windows for each individual. For each day, we calculated axis dynamic acceleration for each point recording (0.10 sec) by removing the static part of the total acceleration (rolling mean of 2 seconds as in Shepard *et al.,* 2008; Elliott *et al.,* 2013). We calculated OBDA by summing absolute dynamic accelerations of the three axes for each 0.10 sec and then, by averaging the ODBA by day by individual. We removed the first and the last days of recording for each individual because they did not contain full 24-hours recordings ($Days_{final}$ = 585 days).

3.3.4 Activity structure metrics

To describe individual rhythm structure from 0:00 a.m. to 23:59 p.m., we extracted the daily rate of activity sequences and their daily mean duration for each of the 36 individuals. We obtained activity sequences by using an intermediate step. First, we used the interpeak minimum frequency method (Collins *et al.,* 2015) based on the bimodal distribution of the averaged sample ODBA (Fig. S3.2). This method determines a value corresponding to the minimum frequency of data points falling between peaks and separating clustered discrete behaviors. We obtain a threshold of 0.2, separating a low activity (ODBA < 0.2) and a high activity (ODBA > 0.2). To validate this dichotomy, we assessed visually the changes in the ODBA according to this threshold across the typical day of our sample (averaged hourly ODBA, n = 585, Fig. S3.3). Below this threshold, we observe a low nocturnal and dawn activity (00:00 a.m. to 6:00 a.m.; ODBA: μ = 0.08 ± 0.08) and a low dusk and nocturnal activity (20:00 p.m. to 23:59 p.m.; ODBA: μ = 0.08 ± 0.10, Fig. S3.3). Above this threshold, we observe a high day activity (6:00 a.m. to 20:00 p.m.; ODBA: μ = 0.30 ± 0.10).

Second, we extracted the mean ODBA per 10 min (n = 144 data/day) as a smoothing procedure. We then transformed raw ODBA data into a binary variable: we attributed a value of 1 to ODBA > 0.2 (i.e., activity) and of 0 to ODBA < 0.2 (i.e., inactivity). After a threat, active chipmunks are likely to remain motionless and to vocalize during a period of a few minutes (personal observation). This may lead to short sequences of 0s included within longer sequences of 1s. For each sequence of 1s, we thus removed sequences of 2 consecutive zeros (the equivalent of 20 min of lower activities), to keep sequences of at least 30 min as resting sequences. The sum of daily activity sequences was strongly correlated to daily ODBA ($r = 0.91$, $df = 569$, t = 52.65, $P < 0.001$). We calculated the mean duration of activity sequences and the number of activity sequences per day (i.e., the rate of activity sequences). The mean duration of activity sequences revealed a bimodal distribution varying from 0 to 1000 minutes (<1h to 16.5h) with variations around two peaks from 0 to 400 minutes and from 600 to 900 minutes.

Finally, we extracted the onset time and end time of daily activity. For each individual, we obtained the onset time of activity by summing the time corresponding to the first sequence of 0s of each day. The following sequence of 1s meant that the day activity had started. Similarly, we obtained the end time of activity by summing the time corresponding to the last sequences of 0s of each day and by subtracting this time from 24.

3.3.5 External factors and population dynamics

We determined several independent variables that could affect chipmunks' daily activity (Williams *et al.,* 2016): the number of captures per day, each capture corresponds to a maximum of two hours of immobility inside a trap; the mean daily temperature (C°) and precipitations (mm). We collected temperature and precipitations on the Environment Canada weather database, using the Sutton station (Québec, Canada, 45° 05'N; 72° 68'W) at a distance of 10 km from our site.

We calculated the average number of red maple seeds and American beech seeds collected per m^2 on both sites, in 2016 (35.7 seeds/m^2; 8.7 seeds/m^2, respectively) and in 2017 (300.7 seeds/m^2 and 177.4 seeds/m^2, respectively, see methods in Bergeron *et al.,* 2011c). There was another mast in 2015, making 2016 a non-mast year. Red maple and American beech tree masting events occurred in the spring and in the fall, respectively. We also calculated population density for each year, using the number of individuals caught at least once on the grid during that year. On site 1, we caught 66 individuals in 2016 (8.42/ha), and 40 in 2017 (5.10/ha). On site 2, we caught 70 individuals in 2016 (8.33/ha) and 36 individuals in 2017 (4.29/ha). High population density in 2016 coincided with the emergence of juveniles in May (Bergeron *et al.,* 2011c), following the spring reproduction that occurred after the 2015 mast. There was no reproduction in the summer 2016 or in the spring 2017, and thus in 2017, population density was low. Note that population density overlapped with food abundance and we could not separate their effects on activity patterns.

3.3.6 Statistical analyses

We first tested whether exploration scores predicted (1) individual ODBA (total ODBA, from 00:00 a.m. to 23:59 p.m.), (2) mean duration activity, and (3) rate of activity sequences, using linear mixed-effect models (*lmer*, R package). For each model, we included chipmunk identities (n = 36), date (n = 59), and accelerometer ID (n = 22) as random effects. We included exploration, year (2016/2017), sex, body mass (the averaged body mass corresponding to the activity recording period in June), daily capture rate, mean daily temperature and precipitations as fixed effects. We also included the interaction between year and exploration. We finally included the interaction between sex and year because sexes may differ in their activity either during the mast or the non-mast year (Montiglio *et al.,* 2012). Both mean activity duration and rate of activity sequences can increase with total activity. We thus ran models (2) and (3) controlling for the individual daily activity, i.e., the sum of activity

sequences. We transformed mean duration activity and rate of activity sequences using the Box-Cox method (function *coxboxfit*, library *geoR*, Box and Cox 1964) to fit a Gaussian distribution. We optimise the exponent (respectively, λs = -0.21; 0.53) of variable transformations following $Y' = (Y^{\lambda} - 1)/ \lambda$ (Legendre et Legendre 2012). To assess the effect of exploration on (4) onset and (5) end times of activity, we used the same fixed and random effect structures as above, except body mass and capture rate. We tested for the significance of random effects by running likelihood ratio tests that compared models with and without each random effect (LRTs). We provided 95% confidence intervals associated with fixed effects obtained with the package stats (function *confint*). The effects were not significant when 95% CI included zero.

3.4 Results

3.4.1 Day activity

Individuals ID explained 16% of the total variance in daily ODBA (Table 3.1, Fig. S3.4). Date and accelerometer ID explained significant portions of the variance in daily ODBA (Table 3.1). Daily ODBA increased with temperature and decreased with precipitations and capture rate (Table 3.1). Daily ODBA did not vary with exploration in the non-mast year (2016), but significantly decreased with it in 2017 (Exploration*Year, Fig. 3.1, Table 3.1). Daily ODBA did not vary with body mass but males and females varied in their level according to years (Table 3.1).

3.4.2 Mean Activity Duration

Mean activity duration had low repeatability (r = 0.08, Table 3.1). The mean activity duration significantly decreased with exploration (Table 3.1, Fig. 3.2A) and increased in the mast year (2017, Table 3.1). No other significant effect was found on the mean activity duration (Table 3.1).

3.4.3 Rate of Activity Sequences

Rate of activity sequences had low repeatability (r = 0.07, Table 3.1), increased with exploration (Table 3.1, Fig. 3.2B) and was significantly lower in the mast year (2017) compared to the non-mast year (2016, Table 3.1). Rate of activity sequences increased significantly with precipitation and capture rate (Table 3.1), but neither body mass nor temperature affected the rate of activity sequence (Table 3.1).

3.4.4 Dawn and dusk activities

The onset time and end time of the daily activity had medium repeatability (Onset time: r = 0.18; End time: r = 0.32, Table 3.1). We found a significant interaction between exploration and year on dawn ODBA (Table 3.1): fast/superficial explorers displayed a precocious onset time than slow/thorough explorers in the non-mast year (2016) but not in the mast year (Table 3.1, Fig. 3.3 and 3.4A). The mean effect of exploration did not affect dusk activity end time (Fig. 3.4B). Sex did not affect onset time or daily activity end time (Table 3.1). Chipmunks started dawn activity earlier but reduced significantly their dusk activity in the mast year (2017) compared to the non-mast year (Table 3.1, Fig. 3.3 and 3.4B). Precipitation did not affect dusk activity but chipmunks extended it in hotter days (Table 3.1).

3.4.5 Tables and figures

Table 3.1 Linear mixed models testing individual exploration on (1) daily Overall Dynamic Body Acceleration (total averaged ODBA from 00:00 a.m. to 23:59 p.m.); on (2) Mean activity duration; (3) Rate of activity sequences and on (4) Onset time of activity and (5) End time of activity.

	(1) Daily ODBA		(2) Mean activity duration		(3) Rate of activity sequences		(4) Onset time of activity		(5) End time of activity	
Random effects	Var	LRT (χ^2, P-value)	Var	LRT (χ^2, P-value)	Var	LRT (χ^2, P-value)	Var	LRT (χ^2, P-value)	Var	LRT (χ^2, P-value)
Chipmunk ID (*i*)	0.16	96.35 (P < 0.001)	0.08	8.08 (P < 0.01)	0.07	5.39 (P < 0.05)	0.18	20.34 (P < 0.001)	0.32	101.65 (P < 0.001)
Date	0.42	251.49 (P < 0.001)	0.09	17.26 (P < 0.001)	0.11	24.06 (P < 0.001)	0.02	3.26 (P > 0.05)	0.02	9.84 (P < 0.01)
Accelerometer ID	0.10	16.80 (P < 0.001)	0.12	17.70 (P < 0.001)	0.10	16.08 (P < 0.001)	0.36	78.17 (P < 0.001)	0.34	90.52 (P < 0.001)
Residual	0.32		0.71		0.72		0.44		0.32	
Fixed effects	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]
(Intercept)	0.19 ± (0.17)		-0.18 ± (0.09)		0.19 ± (0.14)		0.33 ± (0.22)		0.55 ± (0.23)	
Exploration	0.08 ± (0.09)	[-0.09; 0.24]	**-0.15 ± (0.05)**	**[-0.24; -0.05]**	**0.29 ± (0.07)**	**[0.16; 0.42]**	**-0.31 ± (0.11)**	**[-0.52; -0.10]**	0.17 ± (0.13)	[-0.08; 0.43]
Sex (Males)	0.09 ± (0.18)	[-0.26; 0.43]	0.08 ± (0.11)	[-0.12; 0.28]	0.00 ± (0.16)	[-0.28; 0.29]	-0.41 ± (0.23)	[-0.85; 0.04]	-0.18 ± (0.27)	[-0.69; 0.34]
Body mass	-0.04 ± (0.08)	[-0.19; 0.11]	-0.05 ± (0.05)	[-0.14; 0.03]	0.12 ± (0.07)	[-0.01; 0.24]	/	/	/	/
Year (2017)	-0.03 ± (0.22)	[-0.45; 0.39]	**0.47 ± (0.11)**	**[0.27; 0.68]**	**-0.58 ± (0.16)**	**[-0.89; -0.27]**	**-0.36 ± (0.15)**	**[-0.64; -0.06]**	**-1.15 ± (0.14)**	**[-1.43; -0.86]**
Mean temperature	**0.27 ± (0.10)**	**[0.08; 0.46]**	0.01 ± (0.04)	[-0.07; 0.09]	-0.03 ± (0.06)	[-0.16; 0.09]	-0.09 ± (0.05)	[-0.18; 0.00]	**0.09 ± (0.04)**	**[0.01; 0.18]**
Precipitations	**-0.21 ± (0.10)**	**[-0.41; -0.02]**	-0.07 ± (0.04)	[-0.15; 0.00]	**0.14 ± (0.06)**	**[0.02; 0.26]**	-0.04 ± (0.04)	[-0.13; 0.04]	-0.03 ± (0.04)	[-0.10; 0.05]
Capture rate	**-0.13 ± (0.03)**	**[-0.19; -0.08]**	-0.05 ± (0.03)	[-0.10; 0.00]	**0.09 ± (0.04)**	**[0.01; 0.17]**	/	/	/	/
Exploration * Year	**-0.18 ± (0.08)**	**[-0.35; -0.01]**	0.05 ± (0.07)	[-0.07; 0.18]	-0.13 ± (0.10)	[-0.32; 0.05]	**0.33 ± (0.11)**	**[0.07; 0.55]**	-0.01 ± (0.11)	[-0.22; 0.20]
Sex * Year	**-0.50 ± (0.19)**	**[-0.89; -0.11]**	-0.20 ± (0.15)	[-0.50; 0.08]	0.14 ± (0.21)	[-0.26; 0.57]	0.20 ± (0.24)	[-0.32; 0.66]	0.01 ± (0.24)	[-0.45; 0.47]
Daily sum of activity seq.	/	/	**0.77 ± (0.03)**	**[0.69; 0.83]**	**-0.24 ± (0.05)**	**[-0.33; -0.13]**	/	/	/	/

[1]Estimates (± standard error, SE) and 95% confidence intervals are given for fixed effects. Fixed effects included sex, body mass, daily capture rate (except on Onset and End activity times), year as a factor (2016/2017), daily mean temperature and precipitations. Significant effects are in bold when confidence intervals did not include zero. For all models, proportions of the variance explained by random effects (Var) *corresponded to* chipmunk ID, accelerometers ID and date effects. The significance of each random effect was tested by a Likelihood Test Ratio (LRT, *R* package, all Df = 1) and repeatability estimates (r) of the traits were calculated by dividing phenotypic inter-individual variance (chipmunk ID) by the total phenotypic variance.

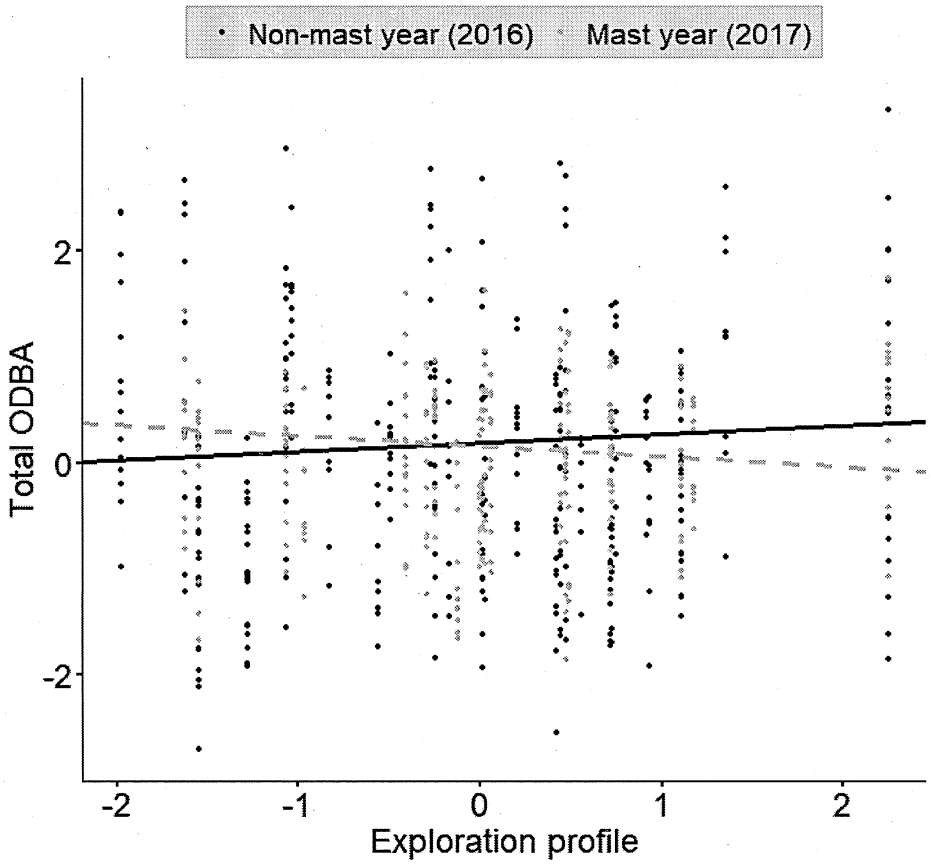

Figure 3.1 Total activity (Day ODBA, 00:00 a.m. to 23:59 p.m.) according to exploration profiles in 2016 (non-mast year, grey line) and 2017 (mast year, black line). Regression lines are provided by a linear mixed-effects model (Table 3.1). Each point represents ODBA value for one day for each individual ($Days_{total}$ = 585). Data were centered on 0 and scaled.

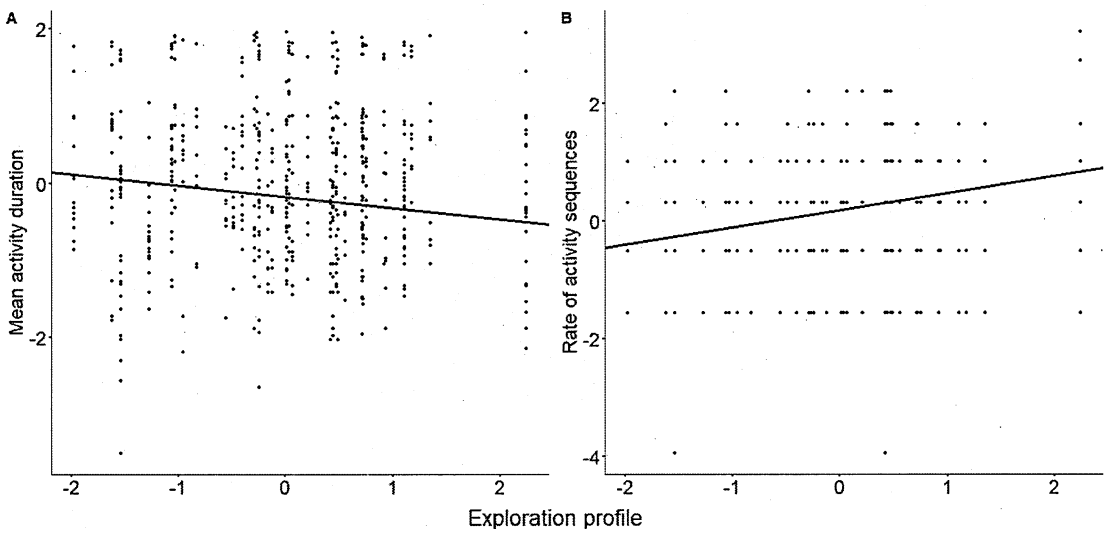

Figure 3.2 A) Mean activity duration and B) Rate of activity sequences according to exploration profiles. Regression lines are based on predictions from a linear mixed-effects model (Table 3.1). Each point represents one day for each individual ($Days_{total}$ = 585). Data were centered on 0 and scaled.

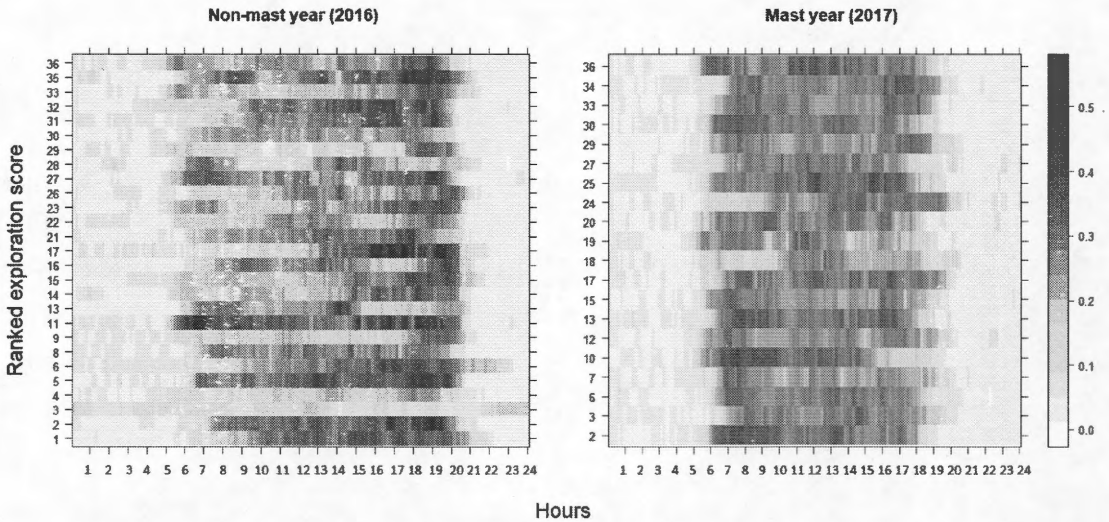

Figure 3.3 Level plot of hourly mean individual activity (yellow to red scale) in 36 eastern chipmunks, *Tamias striatus*, in southern Québec (Canada, 45° 05'N; 72° 25'W) in 2016 (non-mast year) and 2017 (mast year). Activity corresponds to the ODBA averaged over 10 min periods for each individual (all recorded days). Individuals were ranked according to their exploration profiles from 1 representing the slowest individual to 36 representing the fastest explorer.

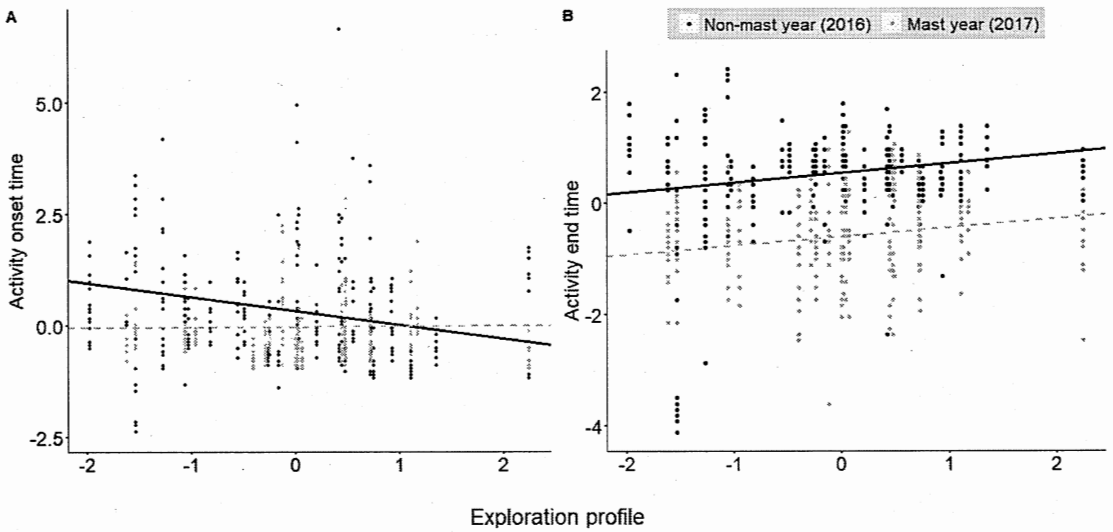

Figure 3.4 A) Individual activity onset time at dawn and B) individual activity end time at dusk according to exploration profiles in 2016 (non-mast year, black lines) and 2017 (mast year, grey lines). Regression lines are provided by a linear mixed-effects model (Table 3.1). Each point represents one day for each individual ($Days_{total}$ = 585). Data were centered on 0 and scaled.

3.5 Discussion

In this study, we tested whether among-individual differences in exploration could translate into different activity patterns and temporal niche specialization in eastern chipmunks. Fast/superficial explorers showed shorter but more frequent bouts of activity during the day and were more active at dawn than slow/thorough explorers. Additionally, we found strong differences in activity patterns between the two years: slow/thorough explorers showed stronger variation in their daily activity between the two years than fast-superficial ones. Furthermore, in mast year, chipmunks showed less robust activity rhythmicity and reduced their total daily time active. These differences indicate that chipmunks may modify their temporal ecological niche in response to changes in environmental conditions such as food abundance and population density.

As we predicted, individual differences in exploration measured in a controlled environment (open-field test) reflected differences in daily activity patterns in a natural environment. Fast explorers showed an earlier activity at dawn and more frequent and shorter activity bouts per day than slow ones. These results suggest the existence of intrinsic control of circadian rhythms and intra-day activity periodicity (ultradian rhythm) related to exploration profiles. Circadian rhythms generally synchronize with photoperiod and temperatures (Daan, 1981; Hut *et al.,* 2012). These external factors have shaped endogenous biological cycles such as melatonin production, responsible for sleeping time in many animals (Sharma 2009). However, high interindividual variability in activity rhythms and chronotypes has been described in shorebirds (Bulla *et al.,* 2016), mammals (e.g., onset times, Refinetti *et al.,* 2016; Halle, 1995) and humans (Randler *et al.,* 2017). For instance, extreme morning and evening types have been described in *Octodon degus* and were linked to morning temperature rise (Labyak *et al.,* 1997). In humans, personality-dependent *morningness* and *eveningness* also suggest a link between personalities and biological

clock rhythms (Cavallera et Giudici 2008; Randler *et al.,* 2017). Morningness was associated with short circadian cycle periods (Duffy *et al.,* 2001), and with conscientiousness, extraversion or agreeableness (Randler *et al.,* 2017). In non-humans animals, laboratory studies found that internal biological clocks regulate the rhythmicity in daily activities differently in proactive (i.e., fast/superficial explorers, aggressive and active) and in reactive (i.e., slow/thorough explorers, lowly aggressive and active) individuals. For instance, Tudorache et al. (2018) found higher activity rhythmicity in proactive zebra fish (*Danio rerio*) than reactive ones. In the Eurasian perch (*Perca fluviatilis*), Nakayama et al. (2017) found that "fast life" individuals, characterized by a high reproductive effort and earlier age at first reproduction, switched more frequently between active and inactive foraging modes than "slow life" individuals. We found, however, that fast/superficial explorers showed early chronotype only in the non-mast year. That result suggests that environmental conditions modulate chronotype expression differently according to exploration. Slow explorers showed between year plasticity in the onset of activity (they delay the onset of activity in 2016 compared to 2017), whereas fast ones did not show such plasticity. This can be explained by that individual may suffer from a predation/starvation trade-off as found in Quinn et al. (2012), accentuated in high food conditions. Chipmunks above-ground activity is related to collecting information and resources, which has some fitness benefits and costs (predation is mostly happening above ground). In a Pace-Of-Life-Syndrome hypothesis (Réale *et al.,* 2010), we could predict that slower explorers should reduce this cost and spend less time above ground than fast explorers when food is abundant. On the contrary, in low food conditions, all individuals may be forced to forage equally to maintain enough energy intakes.

Fast and slow exploring individuals differ in metabolic characteristics like daily energy expenditure (Careau *et al.,* 2015), cortisol level (Montiglio *et al.,* 2012) and stress-induced rise in temperature (Careau *et al.,* 2012). These differences may

explain the link between exploration and activity rhythms. Foraging modes may depend on energetic trade-offs: individuals or species have to trade the intensity of periods of activity with the duration of those periods (Werner et Anholt 1993; Stamps, 2007; Kurvers *et al.,* 2010). Such energetic trade-off should constrain how long an animal can display energetically costly behaviors, such as fast exploration (Careau *et al.,* 2008; Careau *et al.,* 2013). For instance, we know that sprint speed is negatively correlated to distance moved in the open field in chipmunks (Newar et Careau 2018). Short-intense periods of daily activity may help fast-exploring chipmunks save energy, although for now, we do not know the mechanism responsible for this pattern. Differences in activity structure between chipmunks varying in their speed of exploration may explain the absence of the link between exploration and overall activity levels.

As expected, activity patterns also depended on year-to-year and day-to-day variability in external conditions (temperature, precipitations). We found that activity metrics interacted in many ways with years and sex in our system. Year and sex-dependent differences in the temporal distribution of activity patterns suggest that external factors such as breeding season, resource availability and competition can modulate time and energy budget management (Careau *et al.,* 2013; Portugal *et al.,* 2016). Chipmunks showed fewer but longer bouts of activity and decreased their activity at dusk in 2017 (mast year) compared to 2016 (non-mast year). Increased bouts of activity may correspond to higher foraging activity following the 2017 red maple masting, which occurred in early May and constituted an important part of spring food sources (Elliott, 1978; Tissier *et al.,* in press). June of 2017 also coincided with a breeding season for chipmunks in Southern Québec, and during that period individuals search actively for sexual partners (Smith et Smith 1972; Pidduck et Falls 1973; Bergeron *et al.,* 2011a), which may also explain the extension of activity bouts compared to 2016. Similarly in females, the gestation and lactation

occurring at this period and which are extremely costly in mammals (Gittleman et Thompson 1988), should lead to increased foraging efforts.

Alternatively, chipmunks' activity may depend on population density (Fingerle *et al.,* 2016). The population density in spring 2016 (non-mast year) was almost twice as high as in 2017, and juveniles from the spring reproduction had emerged a few weeks before our study period. More robust rhythmicity of activity and different activity levels at dawn and dusk may be a response to direct (Getty, 1981) or indirect intraspecific competition (Schoener, 1974; Carothers et Jaksić 1984; Alanärä *et al.,* 2001; Kronfeld-Schor et Dayan 2003; Stone *et al.,* 2018). It may also result from a decrease in food availability (Moncorps *et al.,* 1997; Sereni et Einum 2015). In this study, we only have two years of data in contrasting environmental conditions, and consequently, we could not statistically separate the effects of food abundance from those of population density, or any other year-related unmeasured environmental effects. Future studies with replicated years of contrasting conditions are needed to decipher the effects of the ecological factors at the origin of this phenomenon. However, our results show some differences in plasticity in activity patterns related to ecological conditions fluctuation.

In conclusion, our study highlights a combination of intrinsic and extrinsic factors that modulate activity patterns in eastern chipmunks. We failed to show a positive relationship between exploration profile and activity levels. However, our study suggests that exploration measured in a controlled environment (open-field) reflects activity structure and chronotypes in chipmunks. We provide evidence that circadian and ultradian rhythms could play an important role in determining personality-dependent activity patterns in a wild population when few studies have examined this link in non-human animals (Randler, 2014). Given that chronotypes are heritable, and linked to hormones and neurotransmitters (Randler, 2014), investigating the link between chronotype and personality and its ecological role in modulating the level of

competition would help better understand the evolution of temporal niche specialization. Altogether, our results suggest that yearly fluctuation in environmental condition modulate the link between activity pattern and individual variation in behaviors, as well as exacerbating temporal niche differentiation. The advantages to detect robust patterns of activity with automatic locomotor-activity record systems opens new exciting research questions. Future empirical investigations will help to decipher mechanisms underlying this link (e.g., speed-accuracy and exploration-exploitation trade-offs, Patrick *et al.,* 2017; Mazza *et al.,* 2018) by describing the respective behaviors that each activity values represent (Hut *et al.,* 2012). Investigating personality-dependent specialization in ecological traits (Bolnick *et al.,* 2003) is a decisive perspective to understand how is generated and maintained individual variation in personality and life history traits (Dall *et al.,* 2012).

3.6 Acknowledgments

We thank the many students and crew members who assisted with data collection on the field in the Sutton Chipmunk Project since 2012. We particularly thank Carlo Catoni (*Technosmart*) and Manuelle Landry-Cuerrier for their precious ideas and advice about practical issues with accelerometers; Kyle Elliott and Orr Spiegel for their help on analyses. We also thank the Nature Conservancy and the Réserve Naturelle des Montagnes Vertes (Estrie, Québec, Canada) for providing access to the chipmunk study sites. Financial support for this project was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), NSERC Discovery grants to DR, PB and DG and The Fonds de Recherche du Québec – Nature et technologies (FRQNT).

3.7 Supplementary material

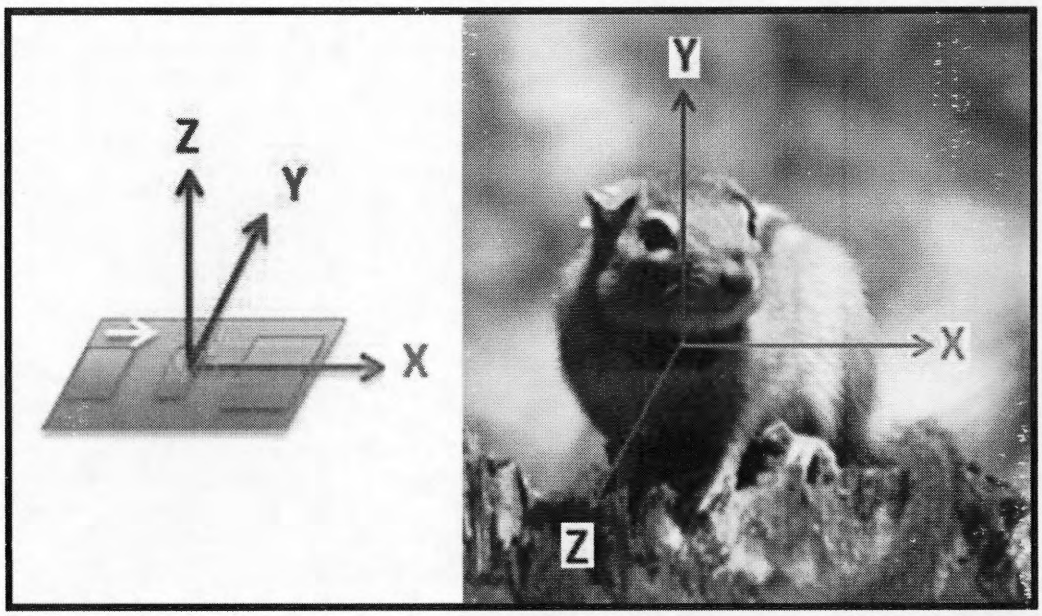

Figure S3.1 Set-up of accelerometers collars on eastern chipmunk, *Tamias striatus*. Devices recorded the animal body accelerations at 10 Hertz (i.e., 10 data/sec) on three orthogonal axes, heave, sway and surge, which corresponded respectively to the initial *z*, *x* and *y* axes of the device. Accelerometers were protected by electrical tape, set on a tie wrap collar locked by shrinkable plastic to limit neck friction and positioned below the animal head (final weight = 4 g).

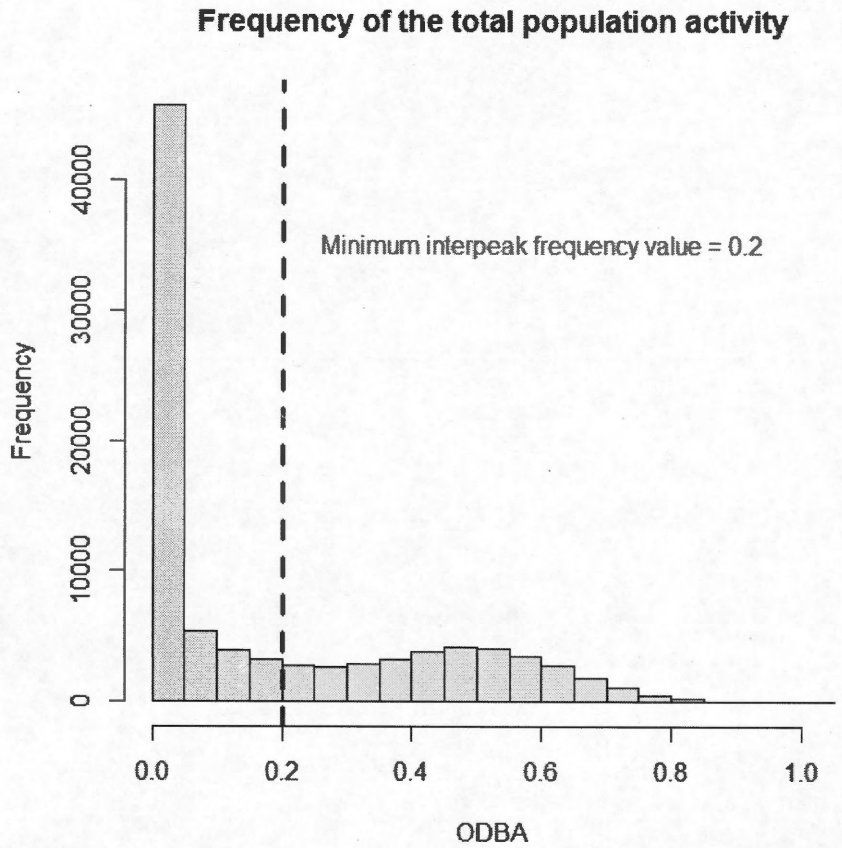

Figure S3.2 Frequencies of ODBA values (Overall Dynamic Body Acceleration) for the whole dataset. ODBA was extracted from raw data of 10 Hertz (i.e., 10 fix/sec), over 12-day periods on average for each individual (N_{id} = 36, N_{obs} = 585) in June 2016 and 2017. The minimum interpeak frequency threshold of 0.2 (red dotted line) delimitated values for low (ODBA < 0.2) and high accelerations (ODBA > 0.2).

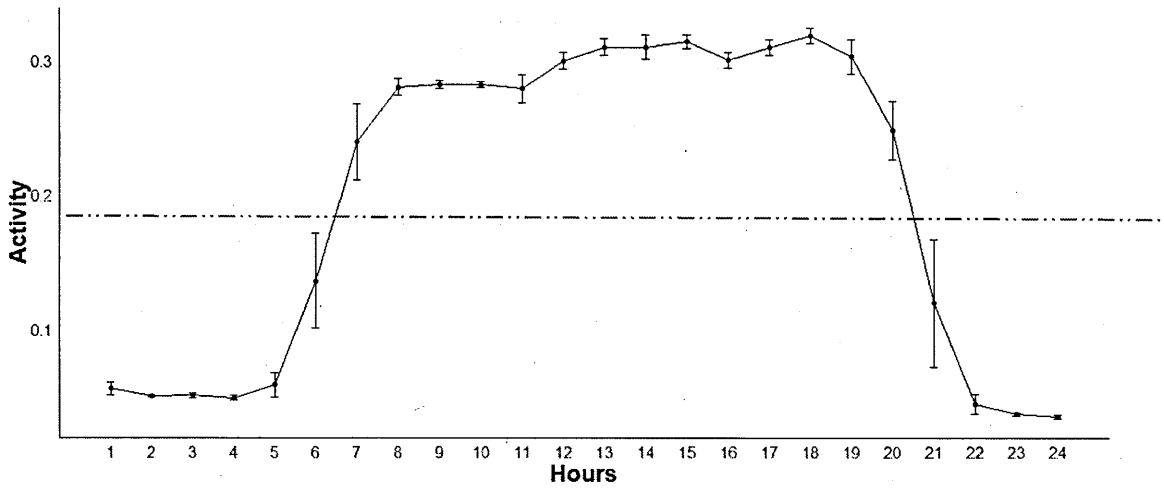

Figure S3.3 Hourly activity (Overall Dynamic Body Acceleration, ODBA, mean ± SE) in eastern chipmunk, *Tamias striatus*, in southern Québec (Canada, 45° 05'N; 72° 25'W). Below this threshold, we differentiate a low nocturnal and dawn activity (00:00 a.m. to 6:00 a.m.; ODBA: $\mu = 0.08 \pm 0.08$) and a low dusk and nocturnal activity (20:00 p.m. to 23:59 p.m.; ODBA: $\mu = 0.08 \pm 0.10$) from a high day activity (6:00 a.m. to 20:00 p.m.; ODBA: $\mu = 0.30 \pm 0.10$).

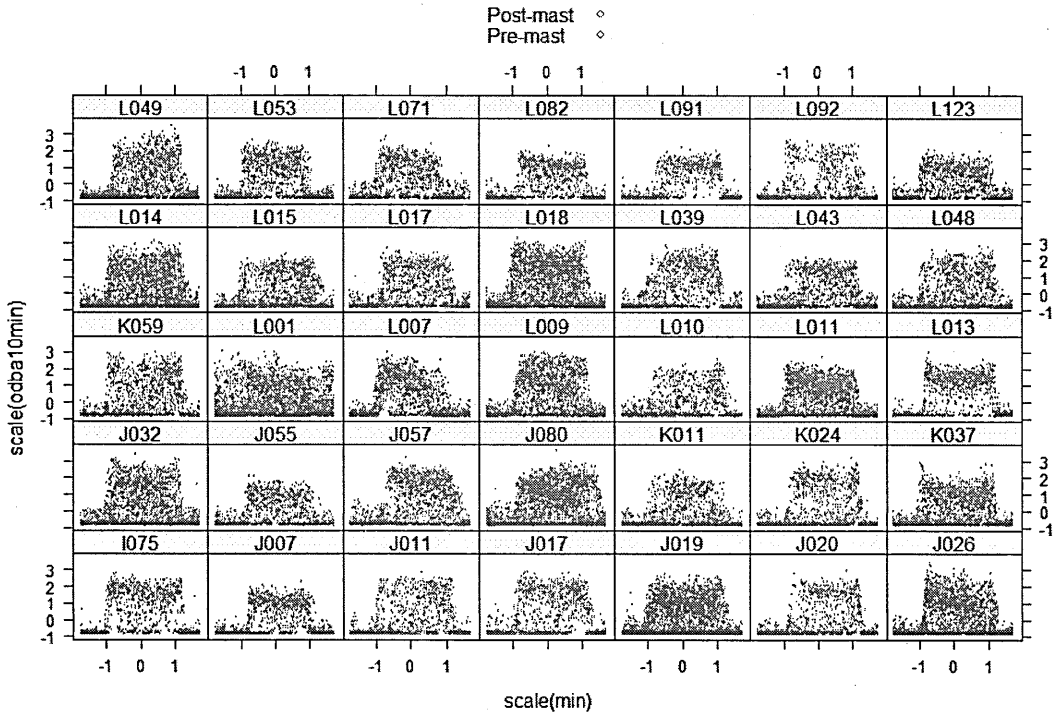

Figure S3.4 Distribution of individual typical day activity for 36 eastern chipmunks (*Tamias striatus*) in Southern Québec in 2016 (non-mast year, in blue) and 2017 (mast year, in pink). Activities were obtained from scaled ODBA values. Raw ODBA was previously smoothed by a rolling mean of 10-min and averaged by day by individual.

CHAPITRE IV

EXPLORATION PROFILES AS DETERMINANTS OF INDIVIDUAL DIET SPECIALIZATION

Elouana Gharnit, Dany Garant, Melanie Dammhahn et Denis Réale.

Cet article est en révision pour une seconde soumission dans la revue *The American Naturalist* en janvier 2020.

4.1 Abstract

Individual diet specialization (IDS) is widespread and can profoundly affect ecological and evolutionary dynamics of populations. Extrinsic factors (i.e., food abundance) and individual variation in energetic needs, morphology, or physiology have been suggested as drivers of IDS. Less investigated behavior traits like exploration and boldness may also impact foraging decisions. Specifically, variation along the exploration-gradient may lead to different aspects of spatial variation in foraging, like home range size or exploration/exploitation trade-off and may affect the diversity of resources acquired by an individual. Here we used stable carbon and nitrogen isotope values in eastern chipmunks, *Tamias striatus,* to investigate the implication of individual differences in exploration on IDS. We found that exploration phenotype, sex, and yearly fluctuations in food availability explained differences in the degree of specialization and plasticity in stable carbon and stable nitrogen. This study brings empirical evidence that consistent individual differences

in exploration can be an important driver of individual niche specialization and could affect within-species competition. Mechanisms underlying the correlation behavior/diet specialization should be assessed in future studies, in particular about exploration/exploitation and speed/accuracy trade-offs.

4.2 Introduction

At a species-level, ecological specialization to a restricted range of habitats or resources, i.e., niche differentiation, plays important evolutionary roles, favoring speciation (e.g., Darwin's finches, Werner et Sherry 1987), fast population responses to environmental changes (Poisot *et al.,* 2011) and reducing interspecific competition (Hardin 1960; Pianka 1974; Schoener 1974). Also, conspecifics are not ecologically equivalent and could use different resources within the whole niche used by the population. Van Valen (1965) formalized that individual variation is involved in the total niche width (TNW) variation. Individuals can vary in their position along a resource axis and in their range on this axis. These mechanisms respectively amplify either the Between-Individuals Component (BIC) either the Within-Individuals Component (WIC, Roughgarden, 1972, 1974), since TNW = BIC + WIC. Individual Diet Specialization (IDS) represents one major dimension of niche variation and is now widely studied and detected in many taxa (Bolnick *et al.,* 2002, 2003; Estes *et al.,* 2003; Kobler *et al.,* 2009; Zanden *et al.,* 2010; Araújo *et al.,* 2011; Terraube *et al.,* 2014). Extrinsic ecological factors such as intra- and inter-specific competition (Svanbäck et Bolnick 2005; Bolnick *et al.,* 2010), predation, and spatiotemporal heterogeneity of food availability can either increase or decrease individual specialization (Araújo *et al.,* 2011). For instance, in Eurasian perch (*Perca fluviatilis*), intraspecific competition forced individuals to specialize on different prey items, increasing the BIC and the TNW (Svanbäck et Persson 2004). On the contrary, a high population density led all individuals to generalize their diet to face competition in threespine sticklebacks (*Gasterosteus aculeatus*, Rundle *et al.,* 2003).

The Optimal Diet Theory argues that individuals differ in their ability to find, handle and digest alternative prey (Schoener, 1971). In this perspective, individuals may have a different preferred diet to optimize their energy intakes, even in a homogeneous environment (Svanbäck et Bolnick 2005). Thus, IDS largely depends on differences in individual features such as morphological or physiological traits (Roughgarden, 1972; Smallwood et Peters 1986; Ehlinger, 1990; Afik et Karasov 1995; Han *et al.,* 2016). Individual variation in behaviors should also lead to variation in resources use (e.g., foraging behaviors, Woo *et al.,* 2008; learning abilities, Haage *et al.,* 2017). Nowadays, it is increasingly admitted that individuals specialize in their behaviors across time and contexts, i.e., personality traits (Sih *et al.,* 2004; Réale *et al.,* 2007, 2010; Koolhaas *et al.,* 2010). Proactive individuals consistently display higher levels of exploration, boldness or aggressiveness in contrast to reactive individuals (Réale *et al.,* 2010). Toscano et al. (2016) have proposed five hypothetical mechanisms linking consistent among-individual behavioral differences to IDS. For instance, individuals may differ in "physiological drivers of foraging". Individuals displaying energetically expensive behaviors such as high aggressiveness or fast exploration (Biro et Stamps 2010; Careau et Garland 2012) may specialize in particular diet to meet their energetic requirements. Habitats' heterogeneity and 'spatial aspects of foraging' should also shape how individuals use habitats and resources. For instance, bold individuals should better colonize new yet poor/riskier habitats (e.g., cities, Charmantier *et al.,* 2017) and encounter different prey types. Theory predicts that fast versus slow explorers should vary in the degree of area-restricted search use (Spiegel *et al.,* 2017). The area-restricted search consists in moving fast and straight between food patches, and to move slowly and sinuously when a food item is detected (Benhamou, 1992). Fast/superficial explorers are assumed to show a low area-restricted response, favoring exploration over exploitation (Patrick *et al.,* 2017). In contrast, slow/thorough explorers take more time to acquire accurate information by favoring local exploitation of a food patch (Spiegel *et al.,* 2017). Recently, exploration and boldness-dependent patterns have

been recognized in space use (Boyer *et al.,* 2010; Patrick *et al.,* 2014, 2017), dispersal (Cote et Clobert 2007, Cote *et al.,* 2010a) and habitat preferences (Kobler *et al.,* 2011; Pearish *et al.,* 2013; Leclerc *et al.,* 2016). However, how among-individual differences in behavior translate into feeding niche specialization (Dall *et al.,* 2004, 2012), notably based on rigorous personality tests and long-term field investigation, has yet to be done.

In this study, we used repeated novel environment tests and stable isotope analyses to test for the link between food availability, exploration and individual diet specialization in a natural population of eastern chipmunks, *Tamias striatus*. Studies using stable isotopes to analyse trophic niches offer significant advantages over direct observations or fecal pellets examination (Dammhahn et Goodman 2014). For instance, stable nitrogen and carbon in hair or feathers integrate information about food assimilated over several weeks or months (Bearhop *et al.,* 2004). Stable nitrogen isotope values represent the position along the range of consumers' trophic levels (e.g., producers *vs.* primary consumers, Newsome *et al.,* 2007). Higher values reveal an increasing position along the trophic network because animal food sources exceed plant food sources by 3 to 5 δ^{15}N ‰ (Post 2002; McCutchan *et al.,* 2003). Stable carbon isotope values mainly reflect differences in ingested basal primary producers and, thus, vary with habitat-specific diversity (e.g., C3 *vs.* C4 photosynthetic plants; Newsome *et al.,* 2007). Inspecting repeated measures of individual isotopic values provides an effective way to investigate plasticity and among-individual variation in diet niche positions within the population total niche width.

Trophic niche dynamic should vary with availability of food resources in the optimal foraging theory context (Stephens *et al.,* 2019). Eastern chipmunks highly depend on a 2-3-year-long masting cycle of American beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) which constitutes their main food source and determines reproduction and winter survival (Humphries *et al.,* 2002; Bergeron *et al.,* 2011c, Tissier *et al., in*

press). In mast years, red maple and beech masting occur respectively in early spring and in fall, offering ideal ecological conditions to contrast IDS variation under low *vs.* high food availability (Yang *et al.,* 2008). First, we assessed changes in the population diet according to this temporal variability in food abundance between two mast and two non-mast years. After a mast, we expect a narrow population niche width due to the high availability of the preferred resource. During non-mast periods, rodents that would otherwise consume seeds must find alternative food sources, such as fungi or insects (Stephens *et al.,* 2019). We thus predict that the population should show a larger total niche width in these periods. The intraspecific competition over resources should be exacerbated in low food conditions, reinforcing individual specialization (Svanbäck et Bolnick 2005; Araújo *et al.,* 2011).

Second, we questioned the relationship between individual differences in exploration and diet variation in carbon and nitrogen trophic niche dimensions. In chipmunks, repeatable individual differences in exploration are linked to home range size and aboveground daily activity (Montiglio *et al.,* 2012, Chapter III). According to the exploration-exploitation trade-off described above, we predicted that fast/superficial explorers will have a generalist diet: these individuals should have access to a larger diversity of food patches (i.e., low area-restricted search) but should be less selective than slow/thorough explorers, choosing preys faster and more randomly in the environment. On the contrary, slow/thorough explorers should be diet specialists: they should have access to less diverse food patches, but should be more selective of an optimal diet, at the expense of a larger foraging area (i.e., high area-restricted search). Because we collected only one isotope sample per individual per season, we could not measure the WIC. We adopted a phenotypic-approach to test our hypotheses. We evaluated the niche width of three functional phenotypic classes within fast, intermediate and slow phenotypes groups (i.e., behavioral type). In other words, the group of slow/thorough explorers should display a narrow niche width meaning that individuals have a diet more similar between each other (smaller BIC)

compared to faster explorers.

Third, we assessed the linear relationship between exploration and isotopes values on carbon and nitrogen dimensions to verify if individuals occupied particular niche positions and varying as a function of food availability (i.e., plasticity). Because masting trees drive reproduction chipmunks, we also expected differences in diet between sexes. In pre-mast summers in southern Québec, males increase about twice their home range to find a sexual partner (Bowers *et al.,* 1990; Montiglio *et al.,* 2010) while females enter in estrus in early summer and 93 to 100% of adult females are pregnant or lactating during that period (Bergeron *et al.,* 2011a). These circumstances can influence energy requirements and prey items encountering. For instance, we can expect that females will consume more animal proteins (higher values of nitrogen) during pre-mast summers than males (Speakman, 2008).

4.3 Material & methods

4.3.1 Study system and study sites

The eastern chipmunk is a diurnal and territorial rodent (family: Sciuridae). They concentrate their activities around a burrow that they use solitarily and in which they store seeds for winter (Humphries *et al.,* 2002, 2003). Home range size has been estimated at 0.45 ha on average (Elliot, 1978) with seasonal variations up to 0.60 ha (Bowers *et al.,* 1990). From 2012 to 2016, we live-trapped individuals within three sites near Mansonville, in southern Québec, Canada (45°05'N; 72°25'W) on rectangular grids of 7.84, 8.40 and 4.00 ha (sites 1 to 3), in mixed northern hardwood forests. We ran linear trapping transects composed of Longworth traps placed every 40 meters and alternately disposed along parallel adjacent transects. We trapped daily during the activity period of chipmunks from early May until early September baiting traps with peanut butter. Animals were marked with a single ear tag code (*National*

Band and Tag Co., New York, KY) upon first capture. At each capture, we recorded identity, sex, body mass and age. We considered individuals under 70 g as juveniles (Bergeron *et al.,* 2011a, 2011c). We assigned a minimum age of 1 year to individuals caught for the first time as adults and regularly trapped thereafter. Chipmunks mostly disperse during their first year of life (Elliott, 1978) and thus have the opportunity to settle on the trapping grid. We obtained an approximate age for our period from 2013 to 2016 varying from 0 (juveniles) to 5 years old. We checked the reproductive status, based on nipple size and vulva hypertrophy for females (Bergeron *et al.,* 2011*c*) to confirm that females enter estrus once a year, in early summer in mast year and in early spring in non-mast year.

4.3.2 Red maple and American beech masting

In our system, chipmunks feed mostly on seeds from the dominant American beech, red maple and sugar maple (Snyder, 1982) in southern Québec. These tree species produce seeds in mast events every 2–3 years. In spring, eastern chipmunks mainly feed on herbaceous bulbs of American trout lily (*Erythronium americanum*) and Carolina spring beauty (*Claytonia caroliniana*, Snyder, 1982). Occasionally, they consume fungi, small invertebrates (e.g., slugs and insects, Fig. S4.1) and passerine eggs or young birds (Elliott, 1978). To quantify temporal variation in the availability of key food sources for chipmunks, we estimated red maple and American beech seed productions. We used 26 plastic buckets (with 0.06 m^2 opening) installed on two metallic poles, at 50 cm above the ground and 1 m away from the trunk of a tree. On each site, we chose 8 to 13 mature red maple trees and 13 mature American beech trees with a minimum circumference at breast height of 31 cm and uniformly distributed on the trapping grid (Bergeron *et al.,* 2011c). We collected buckets contents twice yearly, in July and October. For each tree species, we quantified the average number of nuts collected per m^2. Beech and red maple masts peaked in 2013 (64.7 nuts/m^2 and 744.6 nuts/m^2 respectively) and 2015 (91.0 nuts/m^2; 132.9 nuts/m^2).

Both species showed low seed productions in 2014 (12.8 nuts/m²; 16.8 nuts/m²) and 2016 (12.8 nuts/m²; 65.2 nuts/m²). In the following text, we use the term mast years (2013 and 2015) and non-mast year (2014 and 2016) to consider our temporal variability in food availability.

4.3.3 Exploration tests

We quantified among-individual differences in exploration using a novel environment test in an open-field arena on 396 individuals from 2012 to 2017. Personality studies often use the open-field test to measure exploration and activity (Réale *et al.,* 2007; Gould *et al.,* 2009) and short tests accurately measure consistent differences in activity in a novel environment in rodents (Montiglio *et al.,* 2010; 2012). The experimental arena consists of an empty white box (80 x 80 x 40 cm), deprived of any refuge, gridded at the base and placed in the middle of the trapping grid. Before the test, we placed the captured individual for one minute in an opaque tubular entrance for acclimation. Exploration in the novel environment was video recorded during 90 sec (Montiglio *et al.,* 2010). Using The Observer XT11 software (*Noldus*), we later counted the number of lines crossed by an individual during 90 sec, as an index of exploration or activity in a novel environment (Réale *et al.,* 2007). We ran two tests per individual at 1-year intervals (generally during the first and the second year of life of an individual) to obtain a phenotypic value representative of the whole individual life (Réale et Dingemanse 2012). Chipmunks habituate quickly to the open-field test by the 3rd test, which reduces the among-individual variation in exploration (i.e., every chipmunk freezes until the end of the 90 s; Montiglio *et al.,* 2010).

In a first linear-mixed model, we included chipmunk identity as the unique random effect on the number of lines crossed (library *rptR,* Stoffel *et al.,* 2017). We obtained a repeatability value of $r = 0.41$ (2012-2017, 95% CI = 0.27-0.52, $P < 0.001$, N= 396, N_{obs} = 552). Second, we calculated individual's best linear unbiased predictor (BLUPs) for exploration, once controlling for date, hours of the test, waiting time

before the test, site, number of trials as fixed effects and years, chipmunk and experimenter IDs as random effects. We used a method proposed by Dingemanse et al. (2019) to avoid the risk of transferring the error associated to the BLUPs into subsequent analyses (Hadfield *et al.,* 2010; Houslay et Wilson 2017). Following the mixed model on exploration, we first simulated 1000 series of individual BLUPs using the *sim* function of the *arm* library (Gelman et Su 2016). We then used the individual exploration BLUP mean of the 1000 estimates in subsequent analysis (Villegas-Ríos *et al.,* 2018; Dingemanse *et al.,* 2019) as exploration profile to reflect the slow/thorough to fast/superficial exploration gradient (Annexe A).

4.3.4 Hair samples and stable isotopes analysis

We collected hair samples from 107 adult individuals over four successive years from 2013 to 2016. Each hair-sampled individual has been tested in open-field during the study period. We sample 24, 52, 33 and 39 individuals in springs (May to June) and 27, 39, 29 and 21 individuals in summers (August to September), from 2013 to 2016 respectively. Forty-four individuals were sampled in both mast and non-mast-years. We cut recent darker hair before and after the molting in late June, close to the skin, at the same place on the right thigh. Inert hair preserves isotopes indefinitely (Bearhop *et al.,* 2004) and we assumed that the most recent hair contains information on the diet of the last weeks. Because of the difficulty of assessing hair growth rate in wild chipmunks we based our estimation on a study in rats showing a 19 day growing period in the mid-dorsal region (Johnson 1958). Samples of the main food items available (except fungi and insects) were dried until constant weight before measuring isotope values ($\delta^{15}N/\delta^{13}C$, Table S4.1). The animal food source (slugs) showed the highest $\delta^{15}N$ value. Carbon values varied among the primary producer food sources: the "spring diet" as herbaceous bulbs showed the lowest $\delta^{13}C$ values, beechnuts showed intermediate values, and both maple species showed the highest values (Fig. 4.1).

Protocol for isotopic analysis followed Dammhahn and Goodman (2014). Isotope data are presented in ‰ $\delta^{15}N$ relative to nitrogen in air or $\delta^{13}C$ relative to Pee Dee Belemnite calculated as follows: $\delta X = [(Rsample/Rstandard) - 1] \times 103$, where δX is either $\delta^{15}N$ or $\delta^{13}C$, and R is the respective $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratio. For quantification of $\delta^{15}N$ and $\delta^{13}C$, approximately 1 g of total dry hair was enclosed into tin capsules and processed through an isotope ratio mass spectrometer. We carried out mass spectrometry analyses on the 2013-14 and food sources samples at the Center for Stable Isotope Research & Analysis (KOSI) in Göttingen (Germany) using an isotope ratio mass spectrophotometer (Delta Plus, Finnigan MAT, Bremen, Germany). We carried out the analyses on the 2015-16 samples at the GEOTOP laboratories of the Université du Québec à Montréal (Montréal, Canada), using an isotope ratio mass spectrophotometer (Isoprime 100, Elementar, Vario MicroCube). Analytical precision was assessed based on three laboratory-specific working standards and ranged between -42.48 to -17.04‰ for $\delta^{13}C$ and between -0.10 to 14.95‰ for $\delta^{15}N$. To obtain non-biased niche width metrics (i.e., ellipse area, see below), we corrected raw data for laboratory effects. We used two conservative linear models with the laboratory and year of analyses as fixed effects respectively on $\delta^{15}N$ and $\delta^{13}C$ values as response variables. On GEOTOP data, we subtracted 0.57‰ in $\delta^{15}N$ and adding 0.38‰ in $\delta^{13}C$ (i.e., estimates of laboratory effect) and used these corrected isotopes values in all subsequent analyses.

4.3.5 Statistical analyses

First, we quantified the total niche width by measuring the whole population isotopic space based on the $\delta^{15}N/\delta^{13}C$ bi-plot. We calculated the posterior Bayesian 95% standard ellipse area (SEA_B, function *siberEllipses* package SIBER, Jackson *et al.,* 2011). We calculated SEA_B for each season (spring/summer) and year (mast/non-mast) separately (Table S4.2). We obtained the mode and the 95% credible intervals of each SEA_B ellipses by computing 20,000 MCMC bootstrap permutations with vague prior parameters (mu.tau = 1.0E-3; Jackson *et al.,* 2011). We tested for a

difference in size between two ellipse areas by calculating the proportion p of times that each 20,000 value of the first ellipse was smaller than each 20,000 value of the 2nd one. Thusly, the probability that the two ellipses are different was thus equivalent to $1–p$ (Jackson *et al.,* 2011).

Second, we quantified the niche width of exploration phenotypes. We created three functional classes based on exploratory scores (raw number of crosses in the open-field). To bin exploration scores into classes, we used a distance matrix based on the Ward method (i.e., maximizing inter-class distance and minimizing intra-class distance). This method allowed us to differentiate three behavioral types: slow (n = 50, Mean = 39.98 crosses/90sec ± 11.46), intermediate (n = 28, Mean = 67.24 ± 5.87) and fast explorers (n = 29, Mean = 89.67 ± 7.99, Fig. S4.2). We computed SEA_B for each behavioral type for each season and years (Table S4.2) and compared the size of their SEA_Bs using the same procedure as above. A smaller niche width indicates that individuals are more similar in their diet (i.e., small BIC) than in a larger niche. We tested for temporal changes in the total niche width and for each behavioral group by comparing SEA_B between the years and seasons (Table 4.1).

Third, to test the linear relation between exploration and isotopes values, we analyzed $\delta^{15}N$ (i.e., trophic level position) and $\delta^{13}C$ (i.e., position in the basal resources range) as a function of exploration in two linear mixed-effects models. We added sex, season (spring, summer), and type of year (Mast/Non-mast) as fixed effects. To test for plastic changes in niche position between the two food-abundance contexts, we added the interaction between exploration and year and between exploration, year and sexes because sexes may differ in their activity and energetic needs either during the mast or the non-mast year (reproduction period). We also included sites, age and body mass during the three weeks preceding hair sampling as fixed effects, as age and body mass can affect nutritional preference (Han *et al.,* 2016) and metabolic rate in rodents (Bergeron *et al.,* 2011b). Sites only weakly differed in baseline stable isotopes values

in carbon and nitrogen (Table S4.1) but we still controlled for sites in all following analyses for other potential habitat specificities. Preliminary results showed a significant triple interaction on carbon positions (Table S4.3) and a non-significant trend of the triple interaction on nitrogen positions (Fig. S4.3). We thus ran all the models on each sex separated. We finally included chipmunk identities and season-year (n = 8) as random effects to control for repeated measures and other potential unmeasured seasonal effects. To test for the significance of random effects we ran likelihood ratio tests that compare models with and without each random effect (LRTs, function *anova*). For fixed effects, we provided 95% confidence intervals with the library *stats* (function *confint*) and assumed a negligible effect when intervals crossed zero. Season-year (all $P = 1$) was not significant, we thus ran all the final models without this variable.

4.3.6 Survival analysis

We assessed whether individual $\delta^{15}N$ and $\delta^{13}C$ positions in the summer diet at year t affected survival over the next winter (year $t+1$). Recapture probabilities of adults in our system are very high (Bergeron *et al.,* 2013; Dammhahn *et al.,* 2017), and thus every resident individual not captured from one summer to the next was considered dead. We ran a generalized linear model (GLM, *package lme4, R*) to fit the binomial distribution of the survival variable (binary: 0 = dead; 1 = alive). We included years (mast/non-mast), sex, age, and the two-term interactions between isotope variables and years as fixed effects. Bergeron et al. (2013) found disruptive viability selection favouring extreme explorers in that population, and thus we controlled for the exploration score as well as its quadratic effect when testing for the effect of diet on survival. We included chipmunk identities as random effect to control for the repeated values.

All the models were run using R software (R Development Core Team 2018, version 3.5.1). We mean-centered and variance-standardized variables prior to analyses to facilitate the comparisons between effects.

4.4 Results

4.4.1 Total niche width

We expected a reduction of the population niche width after a red maple and beech masts. These periods corresponded to springs 2013 and 2015 and springs 2014 and 2016. We observed a significant reduction in niche width between 2013 and 2014 (from 2.12 to 1.42 ‰², P <0.05) and a significant increase in niche width between 2014 and 2015 (from 1.42 to 2.44 ‰², P <0.05) but no significant changes between 2015 and 2016 (from 2.44 to 2.04 ‰², P = 0.16). The total niche width significantly increased between spring and summer in mast years (2013: from 1.59 to 5.69 ‰², P <0.001; 2015: from 1.82 to 5.73 ‰², P <0.001), but did not vary between seasons in non-mast years (2014: from 1.71 to 1.3 ‰², P = 0.94; 2016: from 1.62 to 1.86 ‰², P = 0.45, Table 4.1). We thus observed a significant increase in the total niche width in summers of mast years (2013 and 2015) compared to all other periods (Fig. 4.2).

4.4.2 Behavioral classes niche width

We compared niche widths between the 3 exploration classes and the intra-class temporal changes in niche width. The isotopic niche width of the slow phenotype group were constantly smaller than those of the intermediate group (mast/non-mast, all P <0.001, Table 4.1) and of the fast/superficial explorers group (mast/non-mast, all P <0.01, Fig. 4.3). Groups of intermediate and fast/superficial explorers did not differ in their niche width neither in mast nor in non-mast years (all P ≥0.70). Both slow and fast groups significantly reduced their niche width in non-mast years (all P

<0.05), while intermediate phenotypes' group showed a constant niche width in non-mast and in mast years (Table 4.1, $P = 0.06$).

4.4.3 Individual $\delta^{15}N$ positions

We found repeatable $\delta^{15}N$ values in females ($r = 0.44$, $\chi_1^2 = 21.53$, $P < 0.001$) but not in males ($r = 0.19$, $\chi_1^2 = 1.73$, $P = 0.19$). In females ($n = 54$), body mass and age did not affect $\delta^{15}N$ positions (Table 4.2). In mast years, $\delta^{15}N$ was significantly higher than in non-mast years, especially in spring (Table 2). Stable nitrogen values varied significantly with exploration in females, but this effect was year-specific: in mast years, $\delta^{15}N$ increased significantly with exploration, but no relationship was observed in non-mast years (Fig. 4.4). In males ($n = 44$), we found a positive effect of age while body mass, season, year and the interaction between exploration and year or season and year were not significant (Table 4.2).

4.4.4 Individual $\delta^{13}C$ positions

Individual stable carbon values were not repeatable over time: We found no repeatable differences in $\delta^{13}C$ in females ($r = 0.13$, $\chi_1^2 = 1.04$, $P = 0.31$) nor males ($r = 0.22$, $\chi_1^2 = 1.98$, $P = 0.16$). Carbon values increased significantly with body mass in both sexes and with age but were not related to exploration in females (Table 4.2). Carbon values decreased significantly with exploration score in males generally as in mast years particularly, while the pattern was reversed in non-mast years (Fig. 4.5). Overall, chipmunks had higher $\delta^{13}C$ in non-mast years, especially in spring, while the opposite pattern was observed in mast years (Table 4.2).

4.4.5 Survival analysis

Winter survival increased significantly with carbon position in summer (Fig. 4.6) but not with nitrogen position (table 4.3). We found a significant linear and quadratic

effect of exploration on survival, with a lower survival for intermediate individuals (table 4.3). Age, sex, or year did not have any significant effect on survival.

4.4.6 Tables and figures

Table 4.1 Temporal comparisons of isotopic space of the total niche width (TNW) and of exploration classes (Slow, intermediate and fast explorers), across springs and summers from 2013 to 2016. The isotopic space is based on the $\delta^{15}N$ / $\delta^{13}C$ bi-plot and calculated with the posterior Bayesian 95% standard ellipse area ("SEA_B"). Differences in isotopic niche width were tested by comparing SEA_B among classes and within classes between springs and summers and between mast and non-mast years.

		Pairwise comparisons A < B	SEA_B (A) / SEA_B (B) ‰²	Proportion that SEA_B (A) < SEA_B (B)	*p-value*
Population temporal variability		2014 < 2013	1.42 / 2.12	0.991	**0.010 ***
		2016 < 2015	2.04 / 2.44	0.836	0.164
		2014 < 2015	1.42 / 2.44	0.910	**0.012 ***
		Spring 2013 < Summer 2013	1.06 / 3.85	1	**<0.001 *****
		Spring 2014 < Summer 2014	1.32 / 0.95	0.055	0.935
		Spring 2015 < Summer 2015	1.27 / 3.85	1	**<0.001 *****
		Spring 2016 < Summer 2016	1.15 / 1.17	0.547	0.453
Inter-class comparisons	Mast	Slow < Inter	1.25 / 2.86	1	**< 0.001 *****
		Slow < Fast	1.25 / 2.53	0.997	**0.003 ****
		Inter < Fast	2.86 / 2.53	0.297	0.703
	Non-mast	Slow < Inter	0.85 / 2.02	1	**< 0.001 *****
		Slow < Fast	0.85 / 1.75	1	**< 0.001 *****
		Inter < Fast	2.02 / 1.75	0.267	0.733
	Spring	Slow < Inter	1.09 / 1.40	1	**< 0.001 *****
		Slow < Fast	1.09 / 1.31	1	**< 0.001 *****
		Inter < Fast	1.40 / 1.31	0.560	0.440
	Summer	Slow < Inter	1.37 / 2.71	0.984	**0.016 ***
		Slow < Fast	1.37 / 1.81	0.929	0.071
		Inter < Fast	2.71 / 1.81	0.270	0.730
Intra-class temporal variability	Slow	Spring < summer	1.09 / 1.37	0.993	**0.007 ****
		Non-mast < Mast	0.85 / 1.25	0.951	**0.049 ***
	Inter	Spring < summer	1.40 / 2.71	0.825	0.175
		Non-mast < Mast	2.02 / 2.86	0.936	0.064
	Fast	Spring < summer	1.31 / 1.81	0.944	0.056
		Non-mast < Mast	1.75 / 2.53	0.961	**0.039 ***

Table 4.2 Linear mixed models testing individual exploration on $\delta^{15}N$ (i.e. trophic niche position, left) and on $\delta^{13}C$ (i.e. basal resources, right) isotopic values for females and males separately.

	$\delta^{15}N$				$\delta^{13}C$			
	Females (n = 54)		Males (n = 44)		Females (n = 53)		Males (n = 44)	
Fixed effects	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]
Intercept	-0.08 (± 0.17)		-0.20 (± 0.21)		0.50 (± 0.17)		0.49 (± 0.18)	
Exploration	-0.13 (± 0.10)	[-0.33; 0.06]	-0.17 (± 0.16)	[-0.47; 0.13]	0.02 (± 0.09)	[-0.15; 0.19]	**-0.30 (± 0.14)**	**[-0.55; -0.05]**
Season (Summer)	0.11 (± 0.17)	[-0.22; 0.44]	0.35 (± 0.30)	[-0.20; 0.91]	**-0.50 (± 0.20)**	**[-0.90; -0.12]**	**-0.77 (± 0.24)**	**[-1.24; -0.32]**
Year (Mast years)	**0.43 (± 0.16)**	**[0.13; 0.73]**	0.01 (± 0.27)	[-0.50; 0.56]	**-1.01 (± 0.19)**	**[-1.37; -0.66]**	**-0.74 (± 0.23)**	**[-1.17; -0.32]**
Age	0.06 (± 0.07)	[-0.09; 0.20]	**0.43 (± 0.15)**	**[0.15; 0.70]**	**0.16 (± 0.08)**	**[0.00; 0.32]**	0.11 (± 0.12)	[-0.04; 0.27]
Body mass	0.00 (± 0.08)	[-0.16; 0.16]	-0.14 (± 0.12)	[-0.37; 0.09]	**0.25 (± 0.09)**	**[0.07; 0.42]**	**0.29 (± 0.10)**	**[0.10; 0.48]**
Site (Site 2)	0.26 (± 0.21)	[-0.14; 0.66]	**0.72 (± 0.27)**	**[0.21; 1.23]**	-0.26 (± 0.18)	[-0.61; 0.08]	-0.17 (± 0.23)	[-0.60; 0.25]
Site (Site 3)	**-0.87 (± 0.30)**	**[-1.44; -0.29]**	**-1.15 (± 0.46)**	**[-2.00; -0.29]**	-0.01 (± 0.25)	[-0.49; 0.47]	**0.73 (± 0.39)**	**[0.01; 1.44]**
Season * Year	**-0.58 (± 0.24)**	**[-1.04; -0.13]**	-0.02 (± 0.41)	[-0.81; 0.74]	**1.02 (± 0.29)**	**[0.47; 1.60]**	**1.14 (± 0.34)**	**[0.68; 1.81]**
Exploration * Year	**0.56 (± 0.11)**	**[0.35; 0.77]**	0.20 (± 0.26)	[-0.28; 0.71]	-0.18 (± 0.13)	[-0.44; 0.07]	**0.57 (± 0.21)**	**[0.26; 0.82]**

[1] Estimates (± standard error, SE) and 95% confidence intervals are given for fixed effects. Intrinsic covariables included sex, age in years and body mass. Extrinsic ecological covariables included sites, seasons (spring/summer) and years (Mast/Non-mast) as well as their interaction. Site 1 and non-mast years are used as references. The exploration score is the individual average of 1000 simulations of posterior distributions of BLUPs. Significant effects are in bold when 95% confidence intervals do not cross zero.

Table 4.3 Estimates (± standard error, SE) of fixed effects from model testing the effect of the summer diet in $\delta^{15}N$ and $\delta^{13}C$ on winter survival (n = 77). Intrinsic covariables included sex, age and exploration score (linear and quadratic effects). We included the year as a factor (mast/non-mast) and its interaction with isotopes values. Non-mast year is used as reference. The exploration score is the individual average of 1000 simulations of posterior distributions of BLUPs. Significant effects are in bold when 95% confidence intervals do not cross zero.

Fixed effects	Estimate (± SE)	[95 % CI]
Intercept	0.49 (± 0.53)	
$\delta^{15}N$	0.19 (± 0.50)	[-0.82; 1.17]
$\delta^{13}C$	**1.08 (± 0.46)**	**[0.22; 2.07]**
Exploration	**1.14 (± 0.41)**	**[0.43; 2.05]**
Exploration²	**0.78 (± 0.37)**	**[0.18; 1.63]**
Sex	-0.48 (± 0.54)	[-1.55; 0.57]
Age	0.61 (± 0.36)	[-0.06; 1.38]
Years (Mast)	0.68 (± 0.57)	[-0.44; 1.82]
$\delta^{15}N$ * Years	-0.92 (± 0.61)	[-2.14; 0.28]
$\delta^{13}C$ * Years	-0.88 (± 0.60)	[-2.10; 0.27]

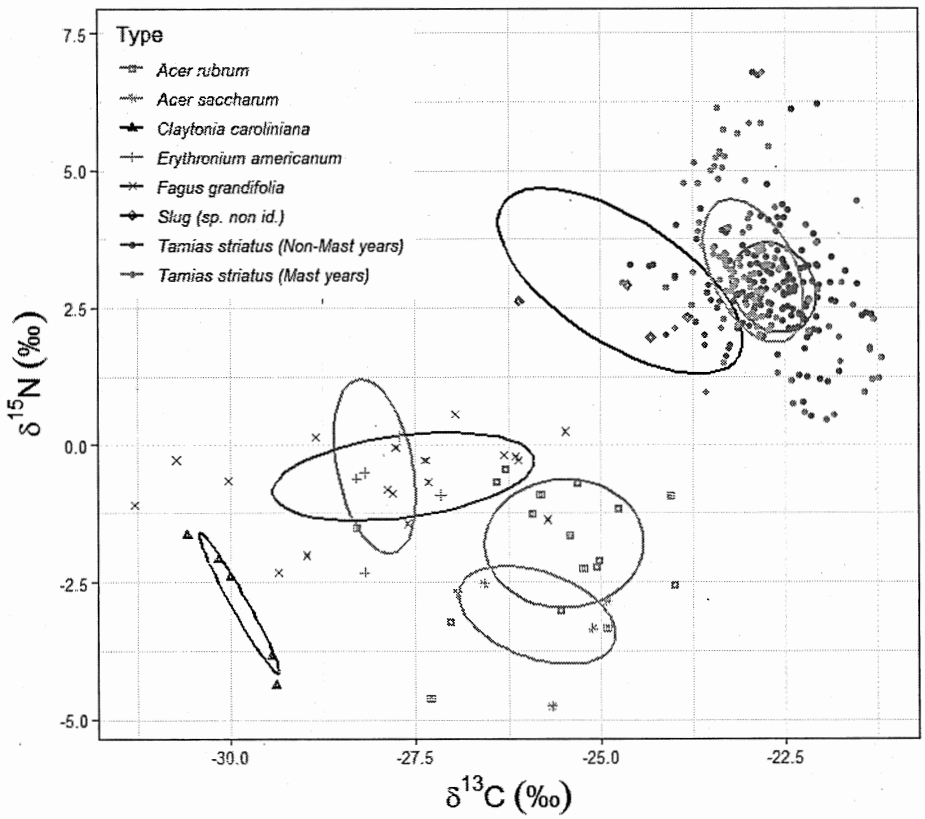

Figure 4.1 Isotopic niche space (δ^{15}N / δ^{13}C, 50% ellipse) of *Tamias striatus* (n = 107) in southern Québec (Canada, 45°05'N; 72°25'W) and the main food sources of eastern chipmunk sampled in mixed hardwood forest (see Table S4.1). Isotopes values of each sampled individuals in mast (grey circles) and non-mast years (orange circles) represent repeated measures from spring 2013 to summer 2016 (N total = 264).

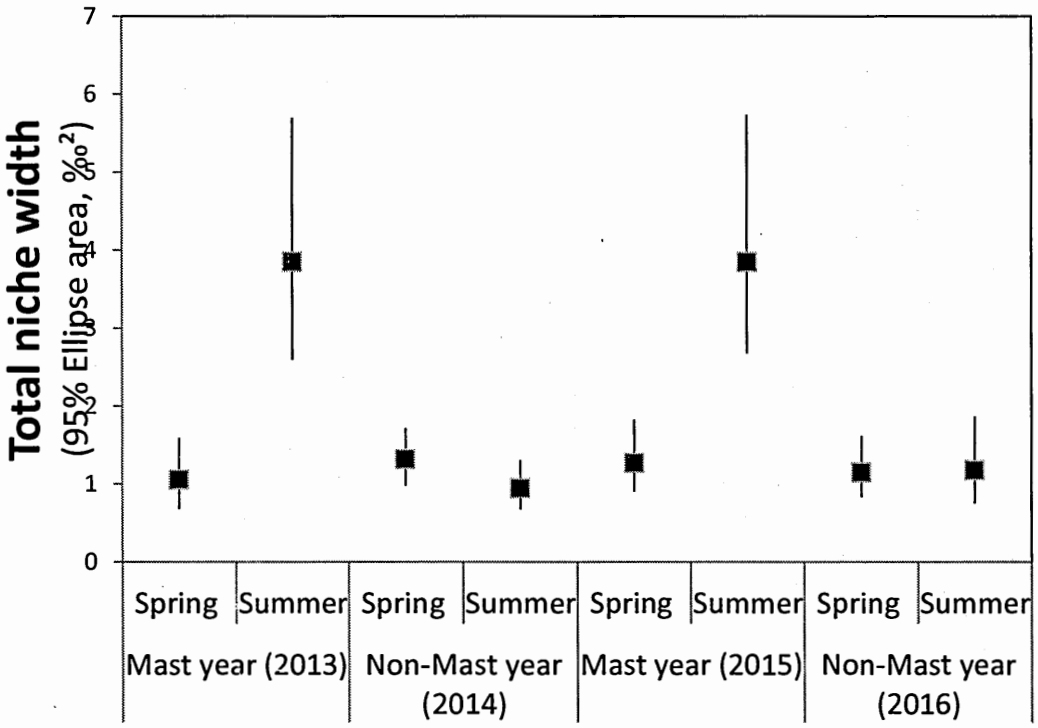

Figure 4.2 Seasonal and yearly variation of the total niche width (TNW) in eastern chipmunks (*Tamias striatus*) in southern Québec (Canada, 45°05'N; 72°25'W) for 2013 to 2016, based on 95% Bayesian standard ellipse area on $\delta^{15}N/\delta^{13}C$ bi-plot. Two beech mast events occurred in falls of 2013 and 2015. The TNW significantly increase in pre-mast summers (2013-2015) but not in non-mast years (2014-2016). The posterior modes of ellipse area (black squares) and the 95% confident intervals are provided by 20000 MCMC bootstrap permutations (Table 4.1).

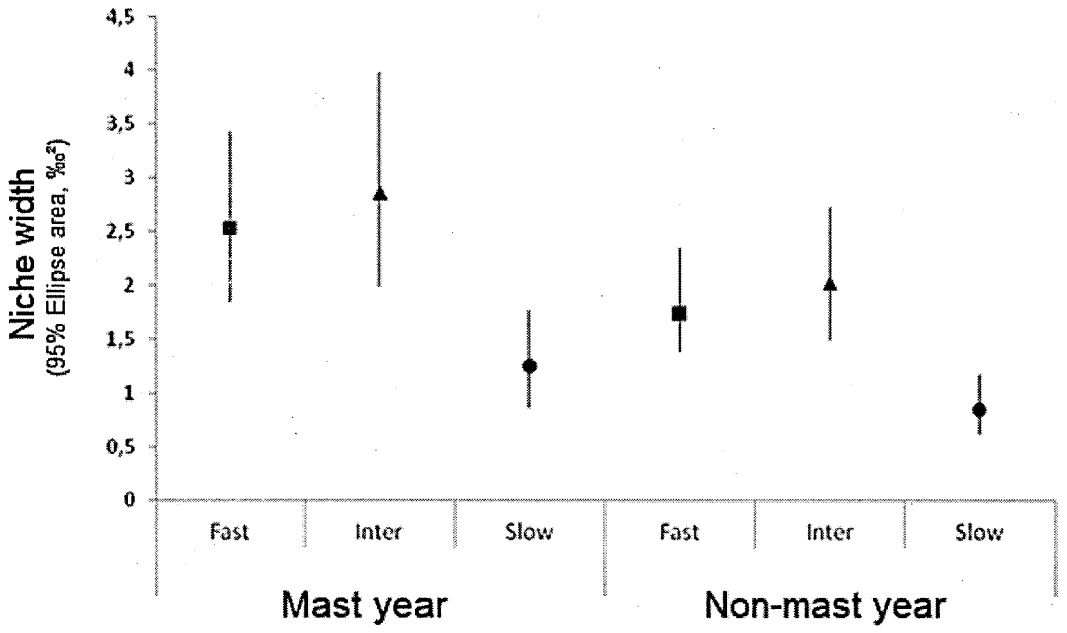

Figure 4.3 Annual feeding niche widths of three exploration classes, i.e., fast (black squares, intermediate (black triangles) and slow (black circles) explorers, in eastern chipmunks. Niche widths estimation is based on Bayesian standard ellipse areas in $\delta^{15}N/\delta^{13}C$ bi-plots for mast years (2013-2015) and non-mast years (2014-2016). The posterior modes of ellipse areas for each behavioral type' group and the 95% credibility intervals are based on 20.000 MCMC bootstrap permutations (Table 4.1).

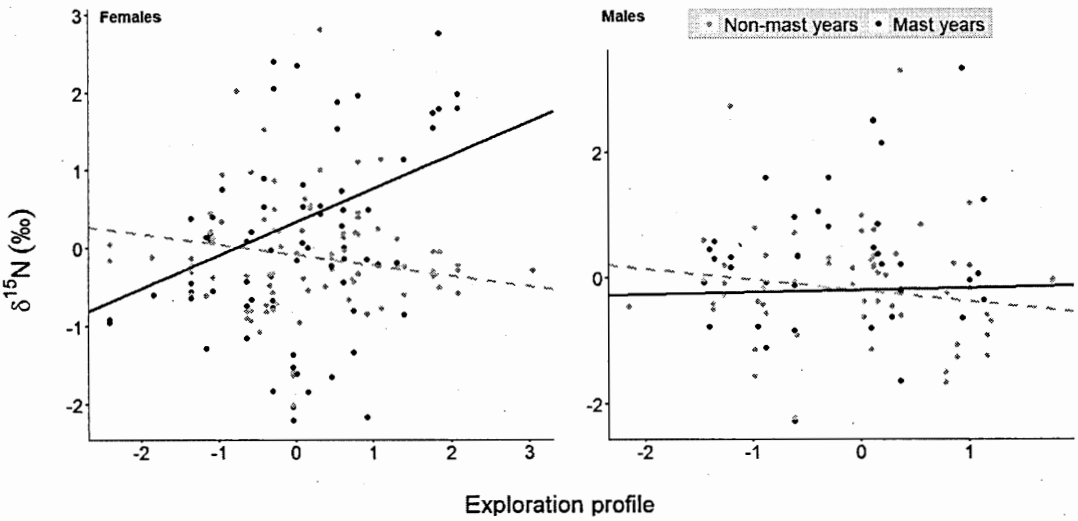

Figure 4.4 Effect of individual exploration profile on δ^{15}N in mast years (2013-2015) and non-mast years (2014-2016) in female (left) and male (right) eastern chipmunks. Stable nitrogen isotope values represent the trophic level of a consumer's diet. Regression lines are based on predictions from a linear mixed-effects model (Table 4.2). Each point corresponds to one individual isotope value. Data were centered and scaled.

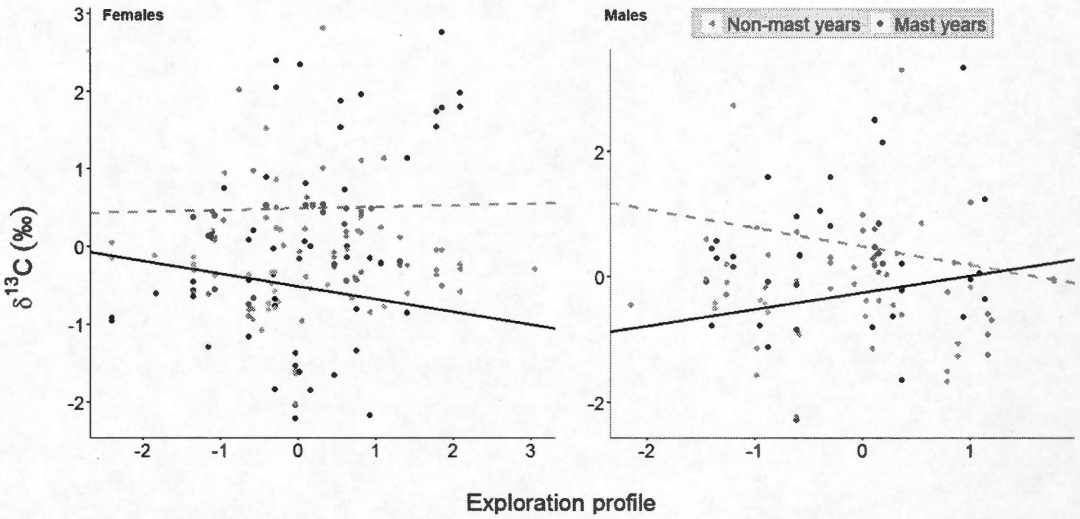

Figure 4.5 Effect of individual exploration profile on $\delta^{13}C$ in mast years (2013-2015) and non-mast years (2014-2016) in female (left) and male (right) eastern chipmunks. Stable carbon isotopes values mainly represent the basal resource use within the same trophic level of a consumer's diet. Regression lines are based on predictions from a linear mixed-effects model (Table 4.2). Each point corresponds to one individual isotope value. Data were centered and scaled.

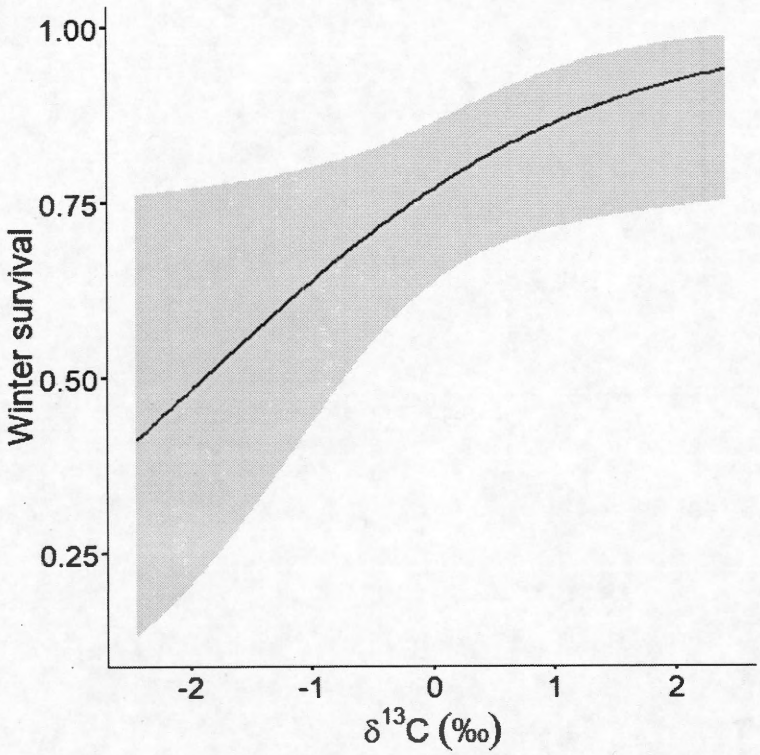

Figure 4.6 Effect of the previous summer carbon position ($\delta^{13}C$) on winter survival in eastern chipmunks (*Tamias striatus*) in southern Québec (Canada, 45° 05'N; 72° 25'W). Regression line and 95% CI (grey bands) are based on estimates of the final generalized linear mixed-effects model (see table 4.3).

4.5 Discussion

This study reports the importance of ecological conditions on the relationship between diet specialization and a personality trait in a long-term empirical study. We tested for a relationship between exploration and dimensions of the trophic niche, using stable isotopes of carbon and nitrogen. The stable isotope approach provides long-term information on the diet and helps to describe variations in both individual and population trophic niches. We found that free-ranging eastern chipmunks differed in how much they specialized in both carbon and nitrogen dimensions, depending on their exploration profile, their sex, and on the yearly fluctuation in their food resources.

Fluctuation in yearly food production affected the total niche width (TNW). During summers prior to a mast, the population significantly increased its niche width, becoming more generalist than in non-mast years. Theory predicts that the TNW should increase when either BIC or WIC also increases (Roughgarden, 1972, 1974, Van Valen, 1965). Resources availability is one major ecological cause of population and individual niche variation (Araújo *et al.,* 2011). Previous to a beech mast, the lack of preferred resource may push individuals to switch on alternative preys, as found in Stephens et al. (2019). Alternatively, a high diversity of resources (ecological opportunity) may lead to an increased TNW favoring individual specialization, each individuals foraging on different optimal diets (increasing the BIC, Gerardo Herrera *et al.,* 2008). During mast years, the diversity of prey items is reflected in chipmunk' cheek pouches (Fig. S4.1) and that seems to favor the expansion of the total trophic niche. On the contrary, the population specialized in non-mast years, following the massive production of beechnuts in fall. One explanation is that this main food source is abundantly available, even over the following year. Most individuals, especially in hoarders, should consume them, decreasing between and within diet variation (Pagani-Núñez *et al.,* 2016). Here, then,

the question was whether differences in exploration are involved in individual diet variation and in the population niche increasing.

In this study, we were not able to measure the within-individual niche width. As an alternative, we obtained phenotypes categories derived from the exploration score. As expected, we found that the group of slow individuals had a lower niche width than other phenotypes independently of the year. That indicates that slow/thorough individuals remained overall more similar in their diet (low BIC) than individuals of other groups. Exploration-dependent niche specialization should reflect a trade-off between exploration or exploitation decisions. As we suggested, slow/thorough explorers should be selective, favor familiar options (e.g., van Overveld et Matthysen, 2013), and exploitation over exploration. This result suggests than slow/thorough explorers all converge toward an optimal diet compared to other behavioral types. In contrast, fast/superficial individuals should be less choosy due to the faster exploitation of food patches than slow individuals (Spiegel *et al.,* 2017). They also may have a high probability of encountering a higher diversity of resources (1) larger foraging areas (Patrick *et al.,* 2017; Spiegel *et al.,* 2017) and (2) access to different/riskier habitats (Boon *et al.,* 2008; Minderman *et al.,* 2010).

We found clear differences in diet specialization in males and females along the nitrogen and carbon dimensions separately. Within sexes, we found individual variation in diet according to exploration profiles. Faster/superficial females exploited food sources richer in $\delta^{15}N$ in mast years than slower/thorough females or males. First, acquiring energy and nutrients, like protein and calcium, is crucial for reproduction and lactation (Speakman, 2008). For example, in several tropical rodent species, a diet richer in proteins in pregnant females compared to males and non-reproducing females indicated that pregnant females increase their trophic level by feeding on animal prey (Henry, 1997). Second, this result indicates that fast-exploring females alone switched from primary resources (e.g., seeds or nuts) to secondary

resources (e.g., small invertebrates). As expected, according to the exploration/exploitation trade-off, fast/superficial explorers may thus be more inclined to find secondary food sources than slow/thorough explorers (van Overveld et Matthysen 2010). Also, Montiglio et al. (2012) found that fast/superficial females moved further away from the center of their home range than slow/thorough females. They may have access to different habitats and prey items. In a separate study (Gharnit *et al.,* submitted, Chapter III), we showed that only slow-exploring females increased their daily activity during pre-mast summers. These results suggest that slow-exploring females may increase foraging effort and spent more time exploiting resources while fast-exploring ones switch to secondary resources (i.e., animal high protein sources) to meet energetic needs during pregnancy/lactation periods. Additionally, the trade-off between speed and accuracy in the acquisition of information (Sih et Del Giudice 2012; Mazza *et al.,* 2018) should also affect foraging decisions and drive individual differences in diet. A lower performance of fast explorers in a radial maze exploration suggests the link between exploration and the speed/accuracy trade-off (unpublished data). This mechanism may also explain the link between exploration and diet specialization.

Interestingly, only slow/thorough exploring males switch from low carbon positions in mast years to higher positions in non-mast years compared to faster explorers that showed a constant generalist diet (intermediate carbon value). This result confirms our predictions that slower/thorough individuals should be more selective on the basal resources dimension (carbon), dependently on food availability. Alternatively, fast explorers forage on a larger diversity of items, albeit this is not corroborated in females. One explanation is that opposite intrinsic and extrinsic forces modulate diet specialization among sexes: first, our results suggest that males and females specialized on distinct dimensions of the trophic niche when sex-dependent energy needs are required (i.e., lactation) and ecological opportunity allowed the BIC to increase. Second, space use mechanisms as exploration-exploitation trade-off may

explain personality-specific specialization within males and females distinctly (Patrick *et al.,* 2017). Other studies have found sex-specific diets and foraging strategies, based on temporal foraging niche differentiation, differences in habitat use, and sex-related physiological performances, in marine birds (Bearhop *et al.,* 2006; Camphuysen *et al.,* 2015; Patrick *et al.,* 2017) and mammals (Breed *et al.,* 2009). Here also, patterns of sex-specific foraging niche seem to be associated with sex-related physiological demands for reproduction and with space use variation.

Overall, in response to changes in food availability, individuals with extreme exploration phenotype were more plastic in their diet than intermediate ones. Not only did they show more changes in either nitrogen or carbon levels, but they also showed a higher niche width variation between years than intermediate individuals. This result contradicts the general view that proactive animals (i.e., bolder, faster exploring, more aggressive individuals) show lower behavioral plasticity (Koolhaas *et al.,* 2010; but see Mazza *et al.,* 2018). Nevertheless, previous studies suggesting that fast exploring individuals take less time to discover new patches and are more inclined to switch to new options when food conditions are constraining (van Overveld et Matthysen 2010; 2013). We suggest the hypothesis that eastern chipmunks are facultative generalists at the population level, because of their pulsed resources environment. However, in low food conditions, both extreme slow and fast explorers behave as facultative diet specialists, that possibly enhances their individual fitness (Bergeron *et al.,* 2013) whereas intermediate explorers are constrained as obligate generalists. We adopted the definition of 'facultative specialists' as "*individuals adapted to exploit a single food type or niche, but able to exploit other niches either opportunistically or when primary food is in short supply"* (See Table 1 in Pagani-Núñez *et al.,* 2016), whereas 'obligate generalists' forage in a broad variety of prey but are unable to develop new specialization. We also found a disruptive viability selection on exploration as Bergeron *et al.* (2013), but independently of diet. From an adaptive point of view, fluctuating selection processes, notably caused by

spatial and temporal heterogeneity, would explain why alternative strategies are maintained over time in different contexts (Dingemanse et Réale, 2005; Quinn *et al.*, 2009). Disruptive selection occurs when extreme phenotypes have a fitness advantage over intermediate phenotypes (Rueffler *et al.*, 2006a). This is consistent with the theory that generalists should perform better in unpredictable/heterogeneous conditions (in space and/or time) while predictable and/or stable environmental conditions tend to favour specialists (Büchi et Vuilleumier, 2014; Devictor *et al.*, 2008; Futuyma et Moreno, 1988; Kassen, 2002; but see Woo *et al.*, 2008). However, we did not found that a particular niche position affected winter survival but it increased with the level of carbon in an individual's summer diet, independently of the years. One explanation is that a diet composed by maple and beech seeds helps chipmunks to survive the winter, and might reflect much massive underground stocks or higher intrinsic quality of these items. In our system, slow/thorough *vs.* fast/superficial explorers may perform better when foraging on particular items according to food fluctuations but the direct consequences of the correlation behaviour/diet specialization on individual fitness remain to be tested.

We help decipher mechanisms under specialization patterns at the population and at the individual level. On a large scale, ecological opportunity drives the trophic niche variation of the population. Chipmunks became more generalist under high food conditions compared to low food conditions. At a second level, we found niche dimension specialization between males and females according to energy requirements during the reproduction period. Finally, we found inter-individual variation in diet according to exploration profiles, which can be supported by spatial foraging mechanisms involving exploitation/exploration trade-off. Exploration should highly reflect variation in resource exploitation in nature. Our study brings empirical evidence about the role of personality differences as a driver of IDS (Dall *et al.,* 2012) and its potential implication for evolutionary and ecological processes (Dall *et al.,* 2004; Patrick et Weimerskirch, 2014; Wolf et Weissing, 2010, 2012). From a

mechanistic perspective, our study provides novel information on how diet specialization/generalism is contingent on the combination of intrinsic and extrinsic factors. We stress the importance of investigating ecological and evolutionary causes and consequences of the speed-accuracy trade-off affecting exploration and exploitation of resources in wild animals (Nathan, 2008; Nathan *et al.,* 2008; Spiegel *et al.,* 2017). Niche specialization theory offers a prolific framework to study the maintenance of phenotypic and genetic variation for traits such as resources use (i.e., diet, abiotic habitat, Araújo *et al.,* 2011; Bolnick *et al.,* 2003), social traits (Bergmüller et Taborsky, 2010; Montiglio *et al.,* 2013; Réale et Dingemanse, 2010) or behavior traits (Dingemanse et Réale, 2005; Quinn *et al.,* 2009).

4.6 Acknowledgments

We thank the many students and crew members who assisted with data collection on the field in the Sutton Chipmunk Project since 2012. We also thank the Nature Conservancy and the Réserve Naturelle des Montagnes Vertes (Estrie, Québec, Canada) for providing access to the chipmunk study sites. Financial support for this project was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), NSERC Discovery grants to DR and DG, The Fonds de Recherche du Québec – Nature et technologies (FRQNT) and the German Research Foundation (DFG) for MD.

4.7 Supplementary material

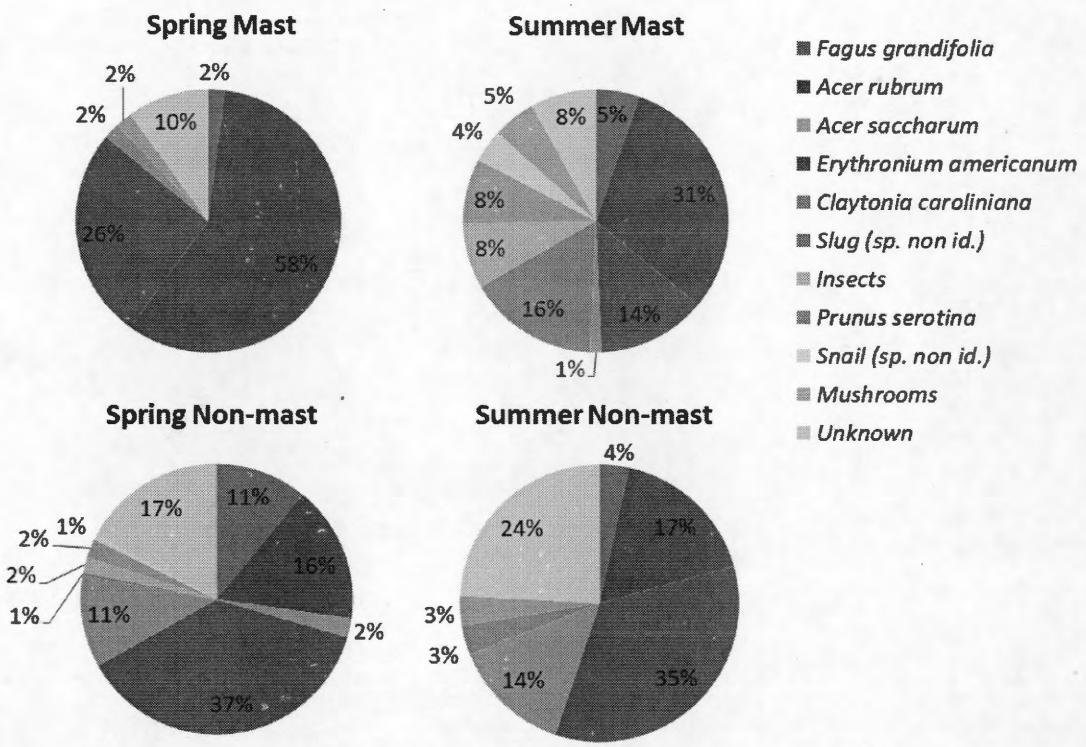

Figure S4.1 Proportion (%) of main food items gathered in chipmunk' cheek pouches (N = 516, *Individuals* = 220) for spring and summer of mast and non-mast years. In mast years, the diet is dominated by red maple (*Acer rubrum*) and the bulbs of trout lily (*Erythronium americanum*). In non-mast years, the diet consists mainly of trout lily bulbs in all seasons. Chipmunks used animal prey such as slugs, insects and snails mainly in summer of mast years. American beech seeds (*Fagus grandifolia*) are under-represented in all seasons and years. Beech seeds are mainly collected in the fall season and stocked in underground burrows.

Table S4.1 **S**table carbon ($\delta^{13}C$) and stable nitrogen ($\delta^{15}N$) isotope values (mean, min-max range in ‰) of main food sources of eastern chipmunk (*Tamias striatus*), sampled in a mixed hardwood forest in southern Québec (Canada, 45°05'N; 72°25'W). American beech and red maple were collected at three study sites (Site 1, Site 2, Site 3, respectively 7.84, 8.40 and 4.00 ha). Other sources have been mainly collected from the largest site 2 and analyzed at the KOSI laboratory (Germany).

Food items	Sites	Mean $\delta^{13}C$ (‰)	Range	Mean $\delta^{15}N$ (‰)	Range
American beech (*Fagus grandifolia*, $n = 18$)	Site 1 Site 2 Site 3	-28.03 -27.14 -28.45	(-31.29; -25.48)	-0.38 -0.57 -0.99	(-2.32; 0.55)
Sugar maple (*Acer saccharum*, $n = 5$)	Site 2	-25.84	(-26.95; -24.92)	-3.24	(-4.76; -2.53)
Red maple (*Acer rubrum*, $n = 17$)	Site 1 Site 2 Site 3	-25.49 -25.80 -25.72	(-28.29; -24.00)	-1.28 -1.72 -2.92	(-4.63; -0.45)
Carolina spring beauty (*Claytonia caroliniana*, $n = 5$)	Site 2	-29.91	(-30.59; -29.38)	-2.87	(-4.38; -1.63)
Trout lily (*Erythronium americanum*, $n = 6$)	Site 2	-28.05	(-28.75; -27.16)	-0.26	(-2.33; 2.67)
Slug (*non id.*, $n = 6$)	Site 2	-25.10	(-28.40; -23.31)	3.51	(1.96; 7.34)

Table S4.2 Descriptive statistics of seasonal and annual variations in $\delta^{15}N$ and $\delta^{13}C$ values (mean ‰, ± SD) and in niche width of eastern chipmunks (*Tamias striatus*) in southern Québec (Canada, 45°05'N; 72°25'W) for the total population and for each exploration class. The 95% Bayesian standard ellipse area modes and 95% credibility intervals are based on 20.000 MCMC bootstrap permutations (*function siberEllipses package SIBER, R*). Mast years corresponded to 2013 and 2015 and non-mast years corresponded to 2014 and 2016.

	Year	$\delta^{15}N$ (corrected, ‰ ± SD)	$\delta^{13}C$ (corrected, ‰ ± SD)	Niche width ($\delta^{15}N/\delta^{13}C$ bi-plot)	
				95% Bayesian standard ellipse area mode (‰²)	95% CI
POPULATION	Mast	3.16 ± 1.31	-22.87 ± 0.69	2.54	[2.09 ; 3.05]
	Spring	3.37 ± 1.02	-23.13 ± 0.48	1.83	[1.41 ; 2.40]
	Summer	2.95 ± 1.54	-22.59 ± 0.77	2.72	[2.11 ; 3.60]
	Non-mast	2.93 ± 0.96	-22.69 ± 0.59	1.76	[1.50 ; 2.05]
	Spring	2.90 ± 1.05	-22.49 ± 0.50	1.31	[1.06 ; 1.63]
	Summer	2.97 ± 0.80	-22.98 ± 0.60	1.52	[1.16 ; 1.96]
SLOW	Mast	2.71 ± 0.84	-22.71 ± 0.85	1.25	[0.86 ; 1.77]
	Spring	3.00 ± 0.56	-23.11 ± 0.66	1.06	[0.62 ; 1.80]
	Summer	2.42 ± 0.98	-22.30 ± 0.83	1.65	[1.04 ; 2.90]
	Non-mast	2.86 ± 0.93	-22.52 ± 0.53	0.85	[0.63 ; 1.17]
	Spring	2.78 ± 0.98	-22.32 ± 0.48	1.11	[0.74 ; 1.64]
	Summer	2.99 ± 0.88	-22.87 ± 0.43	1.08	[0.66 ; 1.94]
INTER	Mast	3.24 ± 1.49	-22.93 ± 0.66	2.86	[1.98 ; 3.99]
	Spring	3.60 ± 1.26	-23.17 ± 0.37	1.76	[1.09 ; 2.82]
	Summer	2.81 ± 1.67	-22.64 ± 0.82	3.74	[2.18 ; 6.19]
	Non-mast	2.94 ± 0.82	-22.80 ± 0.68	2.02	[1.50 ; 2.73]
	Spring	2.86 ± 0.82	-22.59 ± 0.58	1.04	[0.70 ; 1.55]
	Summer	3.03 ± 0.84	-23.03 ± 0.72	1.68	[1.09 ; 2.70]
FAST	Mast	3.44 ± 1.38	-22.93 ± 0.58	2.53	[1.84 ; 3.42]
	Spring	3.43 ± 1.02	-23.11 ± 0.43	1.14	[0.74 ; 1.79]
	Summer	3.44 ± 1.68	-22.77 ± 0.66	2.26	[1.41 ; 3.42]
	Non-mast	2.96 ± 1.07	-22.72 ± 0.54	1.75	[1.39 ; 2.34]
	Spring	3.00 ± 1.24	-22.54 ± 0.43	1.47	[1.11 ; 2.15]
	Summer	2.91 ± 0.72	-23.01 ± 0.59	1.36	[0.88 ; 2.09]

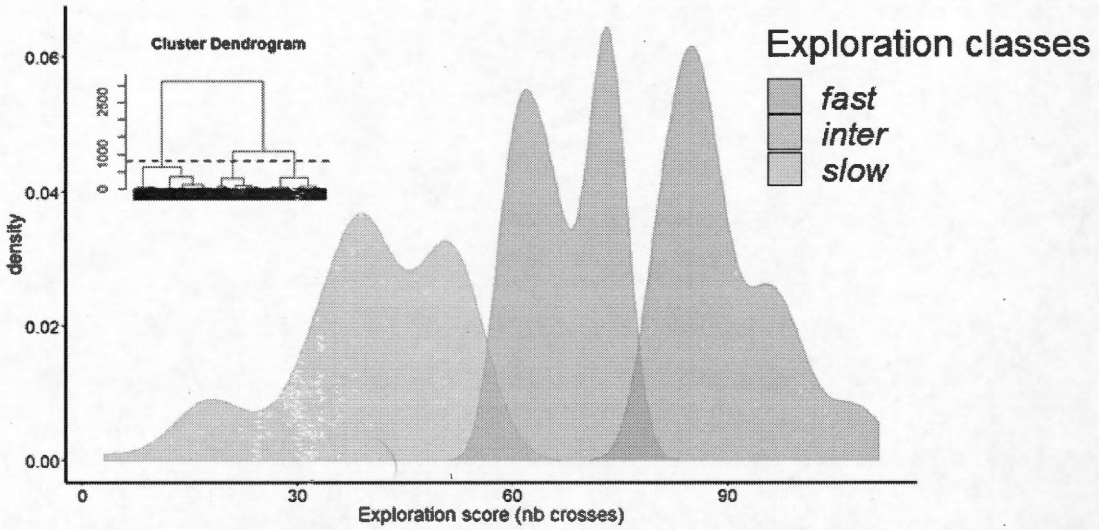

Figure S4.2 Density distributions of three exploration classes created from distance matrix (Ward.D method) and cluster dendrogram. We selected three classes maximizing inter-classes distance and minimizing intra-classes distance: a class of slower explorers (n = 50, Mean = 39.98 crosses/90sec ± 11.46), a class of medium explorers (n = 28, Mean = 67.24 ± 5.87) and a last class of faster explorers (n = 29, Mean = 89.67 ± 7.99).

Table S4.3 Linear mixed models testing individual exploration on $\delta^{15}N$ (i.e., trophic niche position, left) and on $\delta^{13}C$ (i.e., basal resources, right) isotopic values. Effect plots (library *effects*) of the triple interaction are provided below (Fig. S4.3). [1]

	$\delta^{15}N$ (n = 97)		$\delta^{13}C$ (n = 98)	
Fixed effects	Estimate (± SE)	[95% CI]	Estimate (± SE)	[95% CI]
Intercept	-0.14 ± (0.16)		0.47 ± (0.14)	
Exploration	-0.14 ± (0.10)	[-0.33; 0.06]	0.04 ± (0.09)	[-0.14; 0.21]
Season (Summer)	0.19 ± (0.16)	[-0.12; 0.49]	**-0.60 ± (0.16)**	**[-0.90; -0.30]**
Year (Mast)	**0.34 ± (0.17)**	**[0.02; 0.66]**	**-1.01 ± (0.16)**	**[-1.33; -0.70]**
Sex (Male)	0.03 ± (0.18)	[-0.31; 0.36]	0.04 ± (0.16)	[-0.26; 0.35]
Age	**0.15 ± (0.07)**	**[0.02; 0.29]**	0.12 ± (0.07)	[-0.01; 0.25]
Body mass	-0.04 ± (0.07)	[-0.17; 0.10]	**0.27 ± (0.07)**	**[0.13; 0.39]**
Site (Site 2)	**0.39 ± (0.16)**	**[0.08; 0.69]**	-0.23 ± (0.14)	[-0.49; 0.04]
Site (Site 3)	**-1.03 ± (0.24)**	**[-1.48; -0.57]**	0.23 ± (0.21)	[-0.17; 0.62]
Season * Year	-0.40 ± (0.22)	[-0.82; 0.02]	**1.05 ± (0.22)**	**[0.64; 1.48]**
Exploration * Year	**0.56 ± (0.13)**	**[0.31; 0.81]**	-0.17 ± (0.13)	[-0.42; 0.07]
Exploration * Sex	-0.01 ± (0.18)	[-0.35; 0.33]	**-0.34 ± (0.16)**	**[-0.65; -0.03]**
Year * Sex	-0.05 ± (0.23)	[-0.49; 0.40]	0.28 ± (0.22)	[-0.15; 0.70]
Exploration * Year * Sex	-0.42 ± (0.26)	[-0.91; 0.10]	**0.74 ± (0.25)**	**[0.25; 1.22]**

[1] Estimates (± standard error, SE) and 95% confidence intervals are given for fixed effects. Intrinsic covariables included sex, age in years and body mass. Extrinsic ecological covariables included sites, seasons (spring/summer) and years (Mast/Non-mast) as well as their interaction. Site 1, female and non-mast years are used as references. The exploration score is the individual average of 1000 simulations of posterior distributions of BLUPs. Significant effects are in bold when 95% confidence intervals do not cross zero.

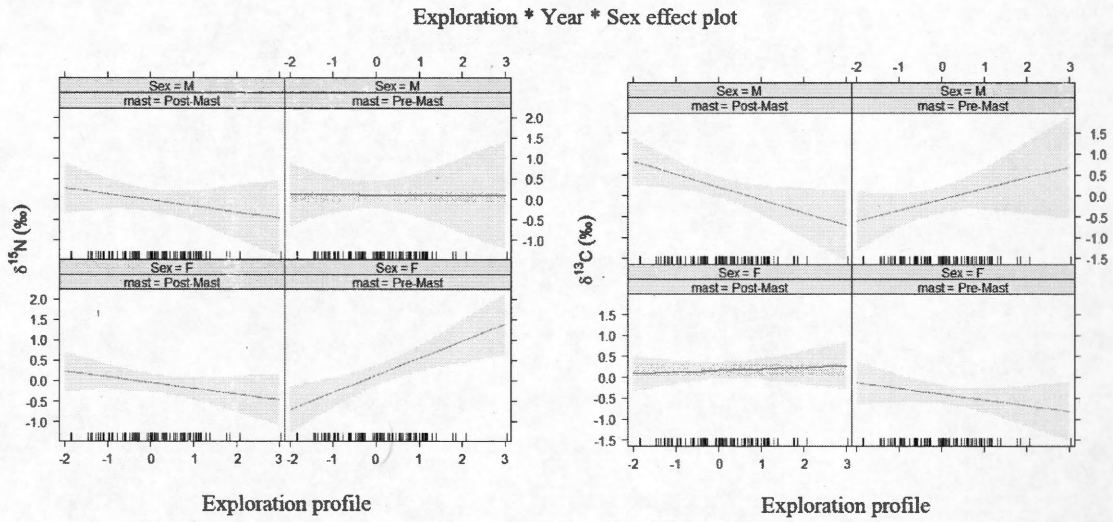

Figure S4.3 Effect plots (library *effects*) of the triple interaction Exploration * Year * Sex from global models on $\delta^{15}N$ (trophic position) and $\delta^{13}C$ (basal resource) isotopic values. Regression lines and 95% confidence intervals (blue bands) are based on predictions from linear mixed-effects models (See table S4.3).

CONCLUSION

5.1 Conclusions et implications écologiques

L'hypothèse de variation de niche (HVN) proposée par Van Valen (1965) a ouvert un champ de recherche conséquent à propos des processus menant à l'augmentation de la niche d'une population/espèce. Cette hypothèse stipule qu'une population généraliste devrait être phénotypiquement plus variable qu'une population montrant une taille de niche réduite. Selon cette hypothèse, une espèce augmente sa taille de niche totale (TNW) en (1) accroissant la taille de niche individuelle (*Within-individual component*, WIC) ou (2) en renforçant la divergence entre individus dans leur utilisation des ressources (*Between-individual component*, BIC). Depuis sa publication, de nombreux exemples empiriques ont confirmé que la variation morphologique, physiologique ou cognitive facilitait le partage des ressources (Bolnick *et al.,* 2003, 2007; Cloyed et Eason, 2017; Hamilton et Johnston, 1978; Ineich *et al.,* 2006; Roughgarden, 1974; Thornton, 2008). Les différences comportementales inhérentes aux stratégies de recherche alimentaire sont parfois associées à l'étude de la spécialisation individuelle de diète (Svanbäck et Eklöv, 2006; Werner et Sherry, 1987). Jusqu'ici, néanmoins, cela n'a que peu participé à l'étude de la variation adaptative comportementale en soi. Ce n'est que récemment qu'un effort a été accompli pour étudier les processus qui génèrent et maintiennent les traits de personnalité chez les animaux (Réale *et al.,* 2007; Sih *et al.,* 2004; Wilson, 1998).

L'objectif premier de cette thèse était de mesurer la contribution de la variation comportementale intraspécifique dans les processus de spécialisation individuelle de

niche écologique. De manière générale, j'ai tenté d'élargir le cadre de la HVN et d'améliorer notre compréhension des facteurs intrinsèques et écologiques responsables de la différenciation des individus dans leur utilisation des ressources, c'est-à-dire la composante interindividuelle (BIC) de la niche écologique populationnelle.

J'ai montré que la variation comportementale interindividuelle était impliquée dans la spécialisation individuelle au niveau de l'utilisation spatiale, temporelle et trophique de l'habitat (corrélation phénotype/environnement). L'exploration, la docilité et la hardiesse sont bien impliquées dans l'utilisation de l'habitat et la spécialisation sur plusieurs dimensions de la niche. Nous avons mis en évidence l'augmentation de la BIC dans le processus d'élargissement de niche au niveau de la population (chapitres III et IV), et des spécialisations personnalité-dépendantes dans différentes dimensions de la niche écologique. Notamment, une exploration plus rapide/superficielle des individus était à la fois liée à l'utilisation d'habitats plus denses (chapitre II), à des patrons plus rythmés de séquence activités/repos et à des fenêtres temporelles plus avancées dans la journée (chapitre III). Enfin l'exploration rapide et superficielle était associée à des niveaux trophiques plus élevés chez les femelles (chapitre IV).

À la fois au niveau individuel et populationnel, nous avons mis en lumière l'effet conjoint de facteurs intrinsèques et environnementaux importants qui modulaient l'intensité de la spécialisation écologique. Premièrement, la fluctuation temporelle des conditions environnementales affecte significativement les changements de la taille de niche totale. En accord avec l'HVN, l'augmentation de la BIC intervient lorsque la population élargit sa niche totale (temporelle : chapitre III; trophique : chapitre IV). Dans notre système d'étude, ce phénomène se produit de manière cyclique, en fonction de la production ponctuelle de graines consommées par les tamias et qui rythme drastiquement la dynamique de population (Bergeron *et al.*,

2011c). Nos résultats suggèrent alors que la diversité des ressources disponibles et la densité de population agissent sur l'augmentation de la niche totale à des périodes distinctes. Si la population se généralise au niveau de la diète lorsque les ressources principales se raréfient (été avant la paisson, chapitre IV), la niche temporelle augmente avec la densité de population en période de reproduction (printemps post-mast). De manière générale, cela suggère que l'augmentation de la BIC est une réponse à l'opportunité écologique et la compétition intraspécifique comme d'autres études l'ont montré (Araújo *et al.,* 2011; Bolnick, 2001; Gerardo Herrera *et al.,* 2008; Svanbäck et Bolnick, 2005, 2007).

Deuxièmement, nous avons souligné un effet conjoint de l'exploration et du sexe sur l'augmentation de la BIC, mais également sur la plasticité de la spécialisation (chapitres III et IV). Particulièrement, les femelles les plus rapides/superficielles dans leur exploration augmentaient leur niveau trophique (δ^{15}N) en période de reproduction (printemps de mast) tandis que les exploratrices plus minutieuses augmentaient seulement leur activité moyenne quotidienne à cette même période. Ces résultats suggèrent que ces individus adoptent deux stratégies distinctes afin de combler leurs besoins énergétiques importants en période de reproduction : i) augmenter son effort d'approvisionnement en ressources ou ii) changer son alimentation. Bergeron et al. (2013) ont montré une sélection divergente favorisant les explorateurs les plus minutieux et les plus superficiels (meilleure survie) dans une population proche. Ce résultat pourrait corroborer le fait que ces stratégies alternatives permettent le même gain de ressources et, à terme, une valeur adaptative équivalente et leur maintien dans la population. Nous n'avons pas testé les mécanismes directement à l'origine de ces spécialisations personnalité-dépendantes (Spiegel *et al.,* 2017; Toscano *et al.,* 2016). De futures études, je l'espère, permettront d'apporter des précisions sur les compromis entre exploration et exploitation (Patrick *et al.,* 2017) ou entre vitesse et précision dans l'acquisition des ressources (Mazza *et*

al., 2018; Sih et Del Giudice, 2012, Dammhahn et Réale, *non publié*) sur lesquelles nous avons bâti nos prédictions.

5.2 Implications évolutives et perspectives

Notre étude a permis d'apporter des évidences empiriques de la corrélation phénotypique comportement/environnement (Edelaar *et al.,* 2008; Pearish *et al.,* 2013) et soulève de nombreuses autres questions et pistes de recherche.

Premièrement, dans la perspective de renforcer le cadre conceptuel (écoévo) et méthodologique de la spécialisation individuelle, Bolnick et ses collaborateurs (2003, 2011) insistent sur l'importance de renseigner la répétabilité et l'héritabilité de la variation individuelle d'utilisation des ressources pour concevoir les effets écoévolutifs plus larges de la spécialisation individuelle. La supériorité adaptative d'une spécialisation écologique personnalité-dépendante peut renforcer à son tour la covariance entre le comportement et le génotype de l'individu et mener à la formation d'adaptations locales (Bolnick *et al.,* 2009). Plusieurs dimensions de niche ont montré des valeurs de répétabilité moyennes (Chapitres III et IV) ce qui suggère une base génétique de ces traits écologiques et un potentiel évolutif de ces spécialisations de niche. Dans de prochaines études, il sera nécessaire de mesurer l'avantage adaptatif (survie, reproduction) de la corrélation personnalité-habitat afin de démontrer la covariation phénotypique et génétique de la spécialisation individuelle de niche.

À l'inverse, à notre connaissance, peu d'études se sont penchées sur les mécanismes menant à la plasticité individuelle de niche, soit l'augmentation du WIC. Les changements individuels de niche sont le plus souvent décrits en fonction de la variabilité environnementale et des individus spécialistes peuvent développer de nouvelles spécialisations, dits « généralistes facultatifs » (Pagani-Núñez *et al.,* 2016; Zanden *et al.,* 2010). Certaines contraintes morphologiques ou physiologiques

peuvent limiter l'augmentation de la niche individuelle (Araújo *et al.,* 2007). Cependant, la plasticité des phénotypes (Nussey *et al.,* 2007) et des traits écologiques (Villegas-Ríos *et al.,* 2018) peut favoriser la variation de niche. De plus, il a été montré que les individus diffèrent dans leur degré de plasticité (Dingemanse *et al.,* 2012), ce qui peut mener, par conséquent, à la coexistence d'individus spécialistes et d'individus généralistes au sein de la même population (Powell et Taylor, 2017). Il est recensé de nombreux exemples sur la coexistence d'espèces spécialistes et généralistes (*ex.* Büchi et Vuilleumier, 2014). Ce type de patron mérite une attention nouvelle au niveau intrapopulationnel, à la fois au niveau théorique et empirique. L'approche statistique par les modèles linéaires à effets mixtes et les normes de réactions offre, quant à elle, un outil méthodologique adéquat (Dingemanse *et al.,* 2010; Dingemanse et Dochtermann, 2013).

Troisièmement, les études démontrant des spécialisations personnalité-dépendants se font de plus en plus nombreuses. Toutefois, peu d'entre elles ont fourni un cadre global et étudié les mêmes individus sur plusieurs dimensions à la fois. Ingram et al. (2018) encouragent l'étude de la multidimensionnalité de la spécialisation individuelle afin de mieux appréhender ses conséquences sur de nombreux aspects écoévolutifs (*ex.* dynamique de communauté et d'écosystème, spéciation, *etc.*). D'un point de vue ultime, les auteurs insistent sur le fait que seule la spécialisation multidimensionnelle a le potentiel d'agir sur le chevauchement de niche entre individus/populations et de moduler l'intensité de la compétition, la coexistence ou la divergence adaptative entre espèces. Dans notre cas, pour des raisons logistiques, relier ces trois dimensions n'a pu se faire que sur la seule année 2016. Nos résultats montrent que les profils d'exploration des individus sont associés à plusieurs dimensions de la niche écologique, elles-mêmes interreliées (Annexe B). Le suivi répété des individus sur plusieurs années et sur plusieurs axes de niches est à souhaiter pour de futures études, ce qui permettra également de mesurer la temporalité de la spécialisation individuelle et ses conséquences sur la dynamique des

populations. Des populations composées de spécialistes facultatifs ou de spécialistes obligatoires ne sont pas à même de répondre de manière équivalente aux changements environnementaux (Bolnick *et al.,* 2003; Pagani-Núñez *et al.,* 2016).

Enfin, nous avons discuté plus haut que les répercutions écologiques d'une population spatialement structurée sont nombreuses et peuvent affecter les patrons de dispersion (Cote *et al.,* 2010b), la transmission de pathogènes (Sih *et al.,* 2018), la rapidité de colonisation et d'invasion de nouveaux habitats (González-Bernal *et al.,* 2014) ou favoriser l'appariement entre partenaires sexuels de phénotypes similaires ou dissimilaires (Sih et Watters, 2005). Dans le chapitre II, nous avons démontré que les individus plus similaires au niveau de leur phénotype comportemental tendent à être plus agrégés dans l'espace. Bien que l'utilisation de microhabitats différents explique une partie de l'hétérogénéité spatiale des phénotypes comportementaux, une part importante de la variation spatiale reste inconnue. D'autres facteurs non mesurés par notre étude mériteraient notre attention. Notamment, même chez les espèces solitaires, l'environnement social est une composante importante des conditions environnementales dans lesquelles les organismes performent et entrent en compétition (*c.-à-d.,* dimension sociale de la niche écologique). Les écologistes se sont penchés plus récemment sur le lien entre les traits de personnalité et la spécialisation de niche sociale (Carter *et al.,* 2014; Laskowski et Pruitt, 2014; Réale et Dingemanse, 2010). Se comporter de manière constante et différente par rapport aux autres individus dans un groupe ou sélectionner des conditions sociales particulières décrit une spécialisation de niche sociale (Bergmüller et Taborsky, 2010; Montiglio *et al.,* 2013). Dans un groupe social coopératif, l'hypothèse prédit que si des individus interagissent de manière répétée, la constance des comportements permet de réduire la compétition directe entre les partenaires (*ex.* Laskowski et Bell, 2013) ou d'augmenter l'efficacité à effectuer une tâche (*ex.* Wright *et al.,* 2014). Aussi, Modlmeier et al. (2012) et Sih et Watters (2005) constatent un succès reproducteur supérieur des colonies d'araignées composées de phénotypes

comportementaux variés que des colonies plus homogènes. Dans ce contexte, la spécialisation de niche sociale représenterait une force évolutive et un mécanisme de maintien des traits de personnalité (Bergmüller et Taborsky, 2007, 2010; Jandt *et al.,* 2014; Réale et Dingemanse, 2010). En retour, le contexte social peut affecter l'expression des traits de personnalité (Laskowski et Pruitt, 2014; Modlmeier *et al.,* 2014). Plus généralement, je n'ai pas pris en compte d'autres dimensions de la niche biotique, telles que la compétition interspécifique et la prédation, qui pourraient aussi être échantillonnées et cartographiées. Celles-ci pourraient également expliquer la répartition spatiale des phénotypes comportementaux, et contraindre ou favoriser la spécialisation individuelle dans nos populations (Araújo *et al.,* 2011).

5.3 Conclusion générale

Notre recherche se place dans le cadre d'une écologie évolutive des différences individuelles (Dall *et al.,* 2012; Wilson *et al.,* 1998). L'objectif premier de ce projet était de mettre en évidence la corrélation entre la variation de traits comportementaux et de traits écologiques. Nous avons apporté des preuves empiriques, basées sur un suivi sur plusieurs années et des tests de personnalité répétés, que la variation comportementale constante entre individus affectait la spécialisation individuelle de niche écologique chez le tamia rayé. Plus largement, l'objectif général était de contribuer à améliorer notre compréhension des facteurs qui peuvent générer et maintenir les traits de personnalités dans les populations naturelles. À l'inverse, la variation individuelle est un prérequis à la sélection naturelle, à la divergence intraspécifique et ultimement à la spéciation écologique. Des pistes de recherche futures mériteraient d'étudier le rôle de la personnalité animale dans la divergence des espèces sur un temps évolutif plus long ou à des échelles spatiales plus larges.

À ma connaissance, quelques études récentes se penchent sur la relation entre la variation intraspécifique et les conditions écologiques à large échelle, notamment

dans l'étude des traits fonctionnels chez les plantes (*ex.* Fajardo et Piper, 2011; Siefert *et al.,* 2015) mais aussi des spécialisations du régime alimentaire chez des animaux (Murray et Wolf, 2013; Yurkowski *et al.,* 2016). Pour étendre l'hypothèse de variation de niche à l'écologie comportementale, nous pourrions nous attendre à ce que des populations/espèces généralistes au niveau de leurs conditions écologiques montrent une variance plus grande dans leurs traits comportementaux (Holekamp et Dloniak, 2010). En retour, les traits comportementaux les plus variables ont le plus grand potentiel évolutif dans les zones biogéographiques où la diversité des niches est aussi la plus grande (*ex.* tropique *versus* arctique, Araújo et Costa-Pereira, 2013). À l'instar des *hotspots* de biodiversité où le taux de diversification des espèces est plus élevé (Kozak et Wiens, 2010; Mittelbach *et al.,* 2007), existe-t-il des *hotspots* de biodiversité intrapopulationnelle comportementale ? Est-ce que la sélection diversifiante y agit de manière prédominante ? Est-ce que le rythme d'évolution des traits comportementaux y est plus élevé qu'à d'autres latitudes ?

ANNEXE A

PROCEDURE DETAILS OF INDIVIDUAL BEST LINEAR UNBIAISED PREDICTORS (BLUPS) USE

Open-field tests and the measurement of our different response variables (burrow sampling, chapter II; body accelerations, chapter III; stable isotopes, chapter IV) were done at different times or years. We thus could not use a multivariate mixed-model approach recommended for the study of trait associations (Houslay et Wilson, 2017). Alternatively, we obtained an individual's best linear unbiased predictor (BLUP) as an individual phenotypic value of exploration, once controlling for year, date, hour of the test, waiting time before the test, site and number of trials as fixed effects and chipmunk and experimenter IDs as random effects. We used a method proposed by Dingemanse et al. (2019) comparing two procedures. We simulated 1000 series of individual BLUPs for exploration using the *sim* function of the *arm* library (Gelman et Su 2018).

To test our predictions in the distinct chapters, we tested two procedures:

(1) Using the average individual exploration BLUP values from the 1000 estimates (*ex.* Villegas-Ríos *et al.,* 2018) in the subsequent statistical models.

(2) Running 1000 times each statistical model on our different response variables (*ex.* ODBA, $\delta^{15}N$) involving the exploration score. This method allowed extracting posterior distribution (95% confident intervals) of the estimated coefficient (effect of exploration).

The two methods provided the same results and we used the first procedure in each chapter. Here, as an example, we show posterior distributions of the interaction Exploration*Year tested on $\delta^{15}N$ and $\delta^{13}C$ (chapter IV), from the 1000-times simulated models (see Fig. A).

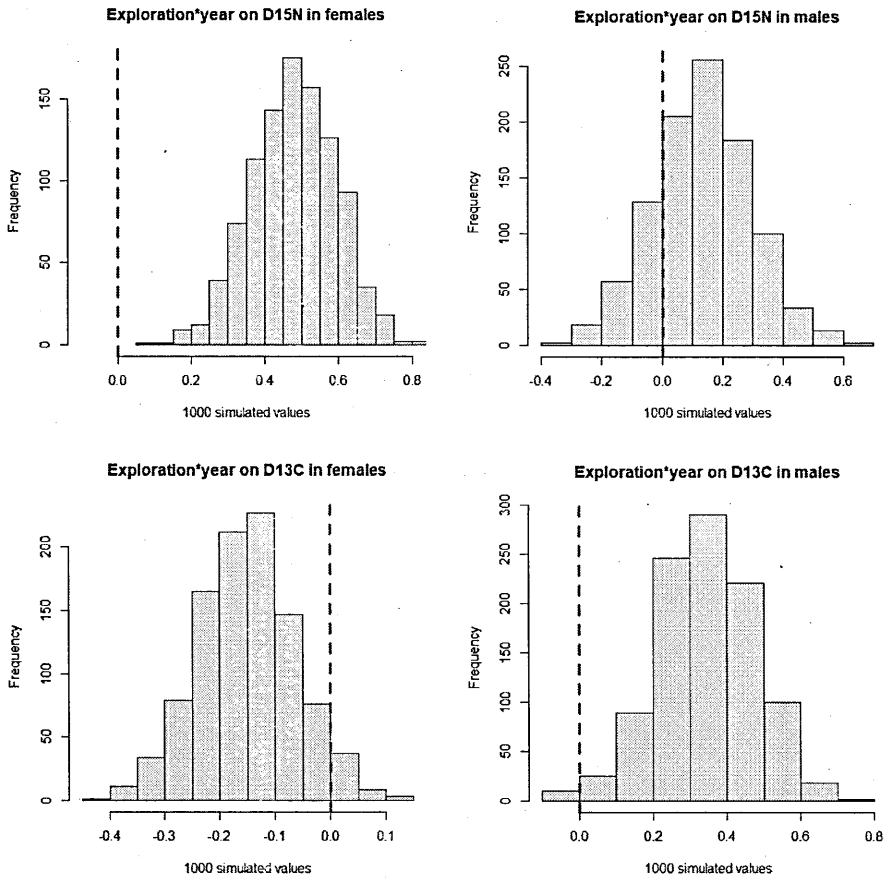

Figure A Posterior distribution of the estimated coefficient of the exploration*year effect on $\delta^{15}N$ and $\delta^{13}C$ in males and females. Distributions are based on 1000-simulations models testing exploration BLUPs (1000 times simulated). From the 1000 estimated coefficients, we calculated the 95% CIs (above distributions) of the effect and considered these effects significant when they did not significantly overlap with zero ($P < 0.05$).

Compared to table 4.2, the two procedures provided the same results concerning Exploration*Year effects on $\delta^{15}N$ and $\delta^{13}C$. Stable nitrogen values varied significantly with exploration, but this effect was year-specific: in mast years $\delta^{15}N$ increased significantly with exploration in females, but not in males (Fig. 4.4). The

stable carbon value ($\delta^{13}C$) decreased significantly with exploration score in males and in mast years particularly (Fig. 4.5).

ANNEXE B

MUTLTIDIMENSIONNALITÉ DE NICHE CHEZ LE TAMIA RAYÉ

Il est recommandé de mesurer la multidimensionnalité de la spécialisation de niche sur plusieurs années (Bolnick *et al.,* 2003) chez les mêmes individus pour prédire d'une meilleure façon ses effets sur la régulation de la compétition intra et interspécifique et à terme sur la divergence adaptative intra et inter populationnel (Ingram *et al.,* 2018).

Comme analyse complémentaire, j'ai utilisé une analyse de partition de variance (*varpart*, librairie *vegan,* R) afin d'évaluer les interrelations entre les variables d'habitat, d'activité, de diète et de comportements (quadridimensionnalité de la niche individuelle, Fig. B1, Ingram *et al.,* 2018).

La variation dans les valeurs d'isotopes stables (δ^{15}N et δ^{13}C, chapitre IV) a été décomposée en fonction des 16 variables de microhabitat (voir table S2.1, chapitre II), des 5 variables d'activité (ODBA du jour, ODBA matinale, ODBA soir, Durée moyenne des séquences d'activité et Nombre des séquences d'activité, chapitre III) et des 3 traits comportementaux (Exploration, témérité et docilité en main). La réunion des différents jeux de données n'a permis la comparaison que pour l'année 2016 uniquement (année de non-mast), pour 22 individus et 21 terriers.

La figure B1 révèle qu'une large partie de la variation de l'utilisation trophique est également expliquée par l'hétérogénéité de l'habitat (56 %) et des patrons d'activité (9 %). Des fractions de variation qui ne peuvent être décomposées représentent aussi la variation conjointe de i) l'activité et de l'habitat (15 %), ii) la variation comportementale et de l'habitat (5 %) et iii) la variation comportementale et de l'activité (5 %) sur la variation de l'azote et du carbone.

Cette analyse descriptive suggère que les spécialisations individuelles de niche sont interreliées et que les utilisations différenciées du microhabitat peuvent en partie expliquer la spécialisation individuelle temporelle et trophique (liens a et c, Fig. B2). Les patrons d'activités et la ségrégation des fenêtres d'activités peuvent aussi être impliqués dans la spécialisation alimentaire (lien b, Fig. B2). Dans l'objectif de mesurer ces interrelations, l'utilisation d'analyses de pistes peut aider à évaluer les relations causales entre variation comportementale et variation dans l'utilisation des ressources au niveau abiotique, spatiale, temporelle et trophique.

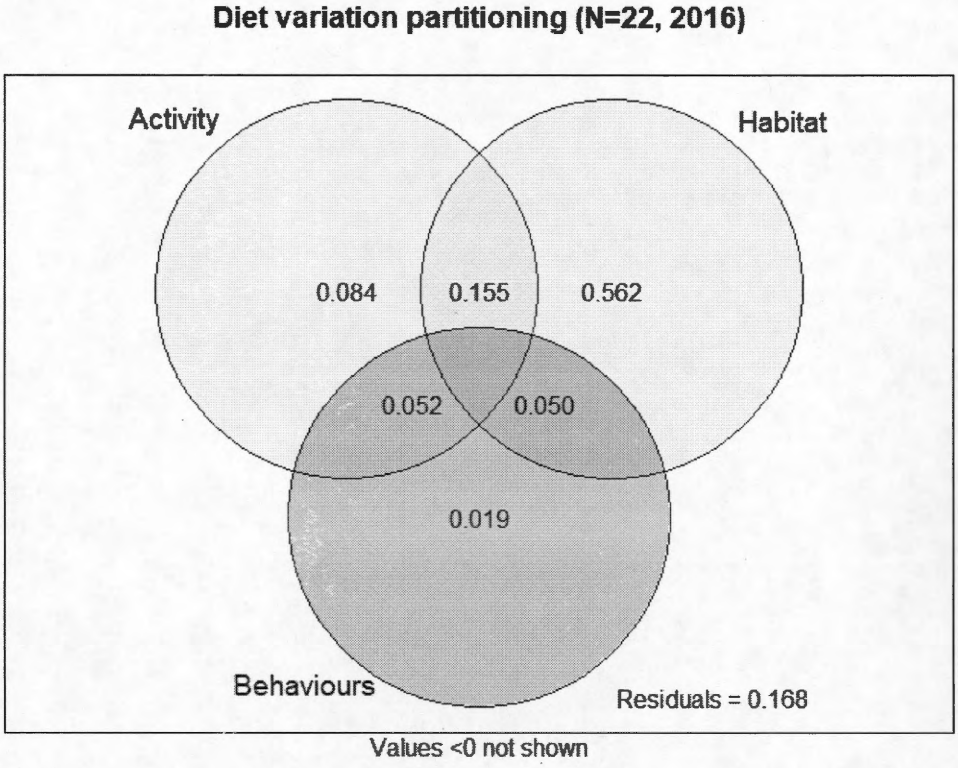

Figure B1 Partition de la variation de l'azote (δ^{15}N) et du carbone (δ^{13}C, chapitre IV) en tenant compte de la variation dans les traits d'activité (chapitre III), les variables d'habitat (chapitre II) et les traits comportementaux (exploration, témérité et docilité en main) chez 22 tamias rayés (*Tamias striatus*), dans le sud du Québec (Canada, 45° 05'N; 72° 25'W) et pour l'année 2016. Les valeurs d'isotopes stables correspondent à la niche trophique utilisée par les individus au cours du printemps (mai-juin) et de l'été (juin-juillet) 2016. Les variables d'activité ont été mesurées au cours du mois de juin 2016.

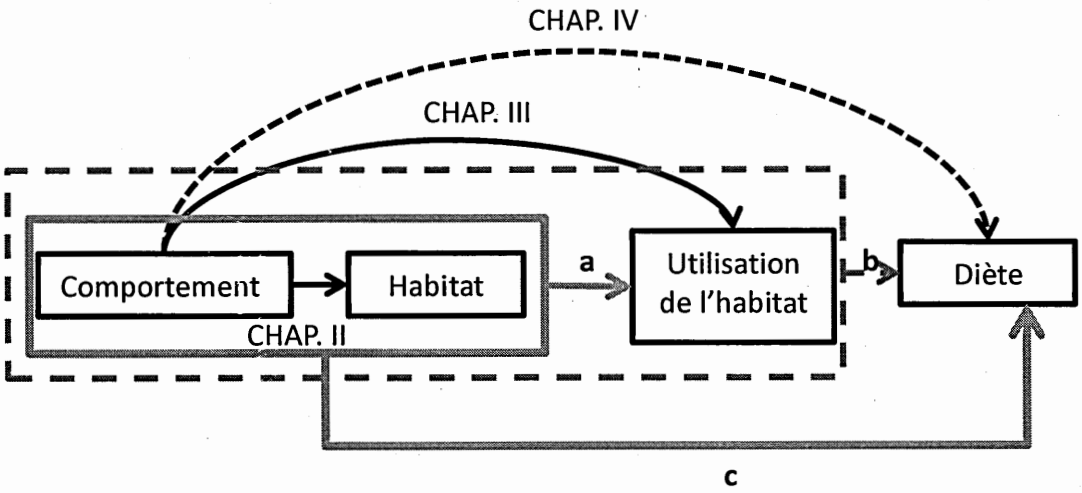

Figure B2 Interrelations entre les dimensions écologiques de la niche écologique étudiées chez le tamia rayé au cours des chapitres II, III et IV. Les liens a, b et c représentent les relations de cause à effet possibles de la spécialisation individuelle au niveau de plusieurs dimensions de la niche écologique et qui n'ont pas été testées dans cette étude.

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