Factors influencing behavioural variation in apple orchard populations of the jumping spider “Eris militaris” (Araneae: Salticidae)

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Abstract

Behavioural differences between individuals are often consistent over time (personality traits) and correlated across multiple behavioural contexts (behavioural syndromes). These individual differences are ubiquitous across taxa and have far-reaching implications for ecology and evolution: determining the mechanisms maintaining them is central to behavioural ecology. These individual differences vary along ecological gradients and can be affected by human-induced environmental changes.

Agroecosystems vary considerably in their intensity and frequency of human disturbances and are suitable systems to study alteration and modification of behavioural responses by individuals. Many beneficial arthropods, such as spiders, can be negatively affected by different management practices, notably the use of insecticides. In this thesis, I explore the determinants of individual behavioural variation in the context of agroecosystems, using the jumping spider *Eris militaris* (Araneae: Salticidae) as a model organism. My focus on spiders is motivated by their importance in agroecosystems as generalist predators. In addition, spider personality traits and behavioural syndromes are well described in the literature. I tested whether behavioural syndromes varied between populations with different histories of insecticidal exposure, how consistent behavioural correlations were through ontogeny and how sublethal exposure to insecticides disrupted behavioural consistency and correlations.

I found evidence for differing behavioural syndromes between spider populations from insecticide-free and insecticide-treated apple orchards. Individuals with highest activity and voracity had low aggression and boldness in the insecticide-free population while aggressive and voracious individuals behaved less boldly in the insecticide-treated population. These two populations had differing age-structure as more juvenile stages were collected in the insecticide-treated population leading to investigate further the role of development in the generation of behavioural syndromes and consistent behavioural tendencies.

When taking development into account, I found that behavioural tendencies were not strongly maintained over the course of ontogeny and only activity showed evidence of heritability and repeatability. I found strong evidence for ontogenic shifts in behavioural

syndrome during the transition from subadult to adult stages, mediated by rearing environment and sex. Behavioural correlations were mostly underpinned by within-individual variation indicating high behavioural plasticity through ontogeny. These results confirm that the differences in syndrome structure found between the two apple orchard populations may in part be generated by ontogenic shifts and lower abundance of adult stages in the insecticide-treated population.

I performed direct insecticidal exposure tests to determine the effects of sublethal disruption on the consistency and correlation of behavioural traits. Exposure to the organophosphate phosmet at a sublethal dose had a stronger effect on the repeatability of activity than on its average value, indicating that individuals react differently to insecticide exposure. I found strong alterations on the correlations between activity and prey capture that were more pronounced in females.

This research provides an opportunity to bridge the gaps between animal personality, agroecology and ecotoxicology by focusing on suites of related traits that affect spider performance in agroecosystems.

Résumé

Les différences comportementales entre individus sont souvent stables au cours du temps (traits de personnalité) et en de multiples contextes (syndromes comportementaux). Ces différences individuelles sont communes à de nombreux taxons et ont de profondes implications pour l'écologie et l'évolution. Déterminer les mécanismes maintenant ces variations est ainsi un aspect central de l'écologie comportementale. Ces différences individuelles varient également le long de gradients écologiques et elles peuvent être affectées par les changements anthropiques.

Les agroécosystèmes varient considérablement dans leur intensité et fréquence de perturbations humaines. Ils sont ainsi des systèmes adéquats pour l'étude des altérations et des modifications de la réponse comportementale des individus. De nombreux arthropodes, tels les araignées, sont affectés par les pratiques culturales, notamment par l'utilisation d'insecticides. Au cours de cette thèse, j'examine les facteurs déterminant la réponse comportementale des individus dans le contexte des agroécosystèmes en se focalisant sur l'araignée sauteuse *Eris militaris* (Araneae : Salticidae) en tant qu'organisme modèle. Mon intérêt pour les araignées en tant que système d'étude est motivé par leur importance en tant que prédateur généraliste en agroécosytèmes. De plus, les traits de personnalité et les syndromes comportementaux des araignées sont bien décrits dans la littérature scientifique. J'ai testé la présence de variations de syndromes comportementaux entre des populations ayant différents niveaux d'exposition aux insecticides, la stabilité de ces corrélations au cours du développement ainsi que les effets d'une exposition sublétale sur la stabilité des traits comportementaux et la robustesse de leurs corrélations.

J'ai mis en évidence la présence de syndromes comportementaux différents chez des populations non exposées et exposées aux insecticides en vergers de pommiers. Les individus les plus actifs et voraces ont fait preuve d'une agressivité et témérité réduite chez la population non-exposée tandis que les individus agressifs étaient également voraces dans le verger exposé mais avec une témérité diminuée. Ces deux populations ont également montré des différences marquées dans leur structure démographique puisque seuls des stades juvéniles ont été collectés dans le verger exposé aux insecticides. Ceci m'a conduit à étendre mon investigation au rôle joué

par le développement dans la génération des syndromes comportementaux et de tendances comportementales stables dans le temps.

En prenant en compte le développement, j'ai montré que les tendances comportementales étaient faiblement maintenues et seule l'activité a montré des preuves d'héritabilité et de répétabilité. J'ai également découvert la présence de changement ontogénique de syndromes comportementaux, variant selon l'environnement d'élevage et le sexe lors de la transition du stade subadulte à adulte. Les corrélations comportementales ont été majoritairement influencées par les variations intra-individuelles, suggérant une forte plasticité comportementale au cours du développement. Ces résultats confirment le fait que les différences de structure des syndromes comportementaux entre populations en vergers de pommiers sont en parties dues aux transitions ontogéniques et à une abondance réduite des stades adultes dans la population exposée aux insecticides.

J'ai ensuite réalisé une expérience d'exposition directe aux insecticides afin de déterminer les effets d'une perturbation subléthale sur la stabilité des traits comportementaux et leurs corrélations. L'exposition à l'organophosphate phosmet a eu un plus grand effet sur la répétabilité de l'activité que sur sa moyenne, indiquant des réponses variables à l'exposition insecticide d'individus à individus. J'ai également observé une altération plus prononcée des corrélations comportementales entre traits relatifs à l'activité et la capture de proies chez les femelles.

Ces recherches permettent de combiner les expertises relatives aux domaines de la personnalité animale, de l'agroécologie et de l'écotoxicologie en se focalisant sur des traits comportementaux affectant la performance des araignées dans les agroécosystèmes.

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Thesis format, contribution of co-authors and contributions to knowledge

Thesis format and contribution of co-authors

This thesis is a collection of published manuscripts and chapters in manuscript style with the exception of the Introduction (Chapter 1) and Conclusion (Chapter 6). These chapters introduce the thesis and its objectives, provide a review of the literature, summarize the main finding of my research and provide recommendations and guidelines for future research. Chapters 2 and 5 have been accepted for publication in peer-reviewed journals. Chapter 3 and 4 will be submitted shortly. No chapter appears in another thesis.

My co-supervisors, Dr. Christopher M. Buddle (McGill University) and Dr. Charles Vincent (Agriculture and Agri-Food Canada) are co-authors on manuscripts for Chapters 2 to 4 and participated actively in the conceptualization of experiments and editing of manuscripts. Chapter 5 is a review paper written in collaboration with Dr. Pierre-Olivier Montiglio (UQAM, now a Post-Doctoral Fellow at UC Davis). Both authors contributed equally at every step of Chapter 5 and share first authorship on the resulting publication.

Contributions to Knowledge

Chapter 2:

This study provides the first comparison of spider behavioural syndromes across populations inhabiting agroecosystems and is the first test for across-context correlations (i.e. correlations between functionally different behaviours) in the family Salticidae. Syndrome structure differs significantly between populations. In the insecticide-free population, active and voracious individuals had lower conspecific aggression and lower boldness in response to predator presence. In contrast, aggressive and voracious individuals from the insecticide-treated

population had lower boldness. This study provides the first line of evidence that insecticidal applications can affect the strength and shape of behavioural syndromes.

Chapter 3:

This experiment investigates further the developmental factors affecting the consistency of behavioural traits and their correlations. It provides the first report for a heritable basis of behavioural traits in Salticidae and is the first study to report how phenotypic correlations are organized into between (i.e., repeatable) and within-individual (i.e., plastic) components over the course of development. This chapter provide a strong case for increasing the research effort devoted to the estimation of correlation at between and within-individual levels rather than focusing solely on estimates of phenotypic correlations. Heritability and repeatability of behavioural traits is moderate for activity but weak for all other behaviours. Within-individual variation during development has the most important effect on behavioural correlations at the phenotypic level. The only consistent correlation is a negative correlation between activity and boldness, although variations between rearing environment and sex are also reported. These results highlight the influence of environmental variation and sexual differences on the ontogeny of behavioural syndromes and the consistency of personality traits.

Chapter 4:

This is the first evidence that exposure to a sublethal dose of insecticide alters not only average behaviour of jumping spiders, but also reduces the consistency of personality traits and the strength of their correlations. There is a sharp decline in the repeatability of activity following insecticidal exposure and a weaker effect on repeatability of attack rates on prey. I also report a collapse of the activity-prey capture syndromes in the insecticide-treated group. Repeatability does not differ between sexes but females are much more sensitive to alterations of behavioural correlations. Only two previous studies report similar effect either on repeatability or behavioural correlations on different classes of contaminants. My results indicate that insecticide exposure may lead to suboptimal behaviours in population of natural enemies important for biocontrol. They also highlight the importance of considering effects on phenotypic variance in ecotoxicological studies and bioassay procedures.

Chapter 5:

This chapter is the first to review the contribution of insecticides and other anthropogenic contaminants to behavioural variation. These contaminants are widespread in the environment but their influence is rarely taken into account in behavioural studies and ecotoxicological studies often ignore potential effects on phenotypic variance. This review provides a comprehensive framework integrating the relationships linking individual differences in behaviour, exposure to and accumulation of anthropogenic contaminants, and resource acquisition/allocation patterns.

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Thanks to Dr. Murray Humphries who served as the third member of my academic committee and whose excellent guidance and thoughtful feedback challenged me to constantly broaden my horizons and look at the bigger picture. Your suggestions were particularly influential during the early stages of the project and your spot-on comments helped raise the scientific quality of my work.

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Chapter 1: Introduction, literature review, and objectives

1.1. Introduction

There is tremendous variation in the way individuals react to a given situation. This simple observation has often frustrated scientists and resulted in the formulation of the famous Harvard Law of Animal Behaviour: "under carefully controlled experimental circumstances, an animal will behave as it damned well pleases". While behavioural variation among individuals has long been seen as annoying "noise" around an adaptive population mean (Wilson 1998), research conducted by behavioural ecologists in the last 10 years suggests otherwise. There is now overwhelming evidence that individuals from a given species or population display consistent behavioural tendencies over time, a phenomenon referred to as "animal personalities" or "temperament" (Dingemanse and Réale 2005, Réale et al. 2007). These individual tendencies can also be correlated across a number of behavioural contexts and form behavioural syndromes (Sih et al. 2004a, b). For example, in great tits (*Parus major*), some individuals are consistently more explorative than others. These individuals also have greater dispersal tendencies, higher aggression levels and lower object neophobia (Dingemanse et al. 2003).

Consistent behavioural differences among individuals has now been demonstrated in many taxa and ecosystems (invertebrates: Riechert and Hedrick 1993, Hedrick 2000, Johnson and Sih 2005, 2007, Sinn et al. 2008; fish: Huntingford 1976, Bell 2005, Dingemanse et al. 2007, Wilson and Godin 2009; birds: Dingemanse et al. 2003,. 2004; mammals: Réale and Festa-Bianchet 2003, Dochtermann and Jenkins 2007, Montiglio et al. 2012), including humans (Gosling 2001), and is now regarded as a major biological phenomenon with broad consequences for ecology and evolution (Sih et al. 2012, Wolf and Weissing 2012). An important implication of behavioural variation is that it provides a framework to study how individuals cope with anthropogenic pressures. Human activities are ubiquitous and challenge species to respond adaptively to the novel conditions they create. Indeed, some combinations of personality type may perform better in human-disturbed environment (Madden and Whiteside 2013), and the overall architecture of behavioural syndromes may differ between populations depending on the degree of anthropogenic pressures they face (Scales et al. 2011, Miranda et al. 2013).

Despite growing interest in the role played by behavioural variation in the way species cope with increasing human disturbances, the insights of animal personalities and behavioural syndromes have yet to be applied to agricultural environments. This is a significant gap in our knowledge as many of the processes that contribute to the establishment of pest species in agricultural habitats or that affect the success of pest suppression by biocontrol agents are regulated by a suite of behavioural traits (e.g., dispersal capacities: Pintor et al. 2008, Pintor et al. 2009; prey consumption: Riechert and Hedrick 1993, Maupin and Riechert 2001; intra-guild predation and cannibalism: Buddle 2002, Balfour et al. 2003). The biocontrol benefits provided by parasitoids and generalist arthropod predators are also influenced by agricultural practices and may have limited efficiency in fragmented landscapes or in crop productions schemes that rely heavily on chemical control. Studying the influence of agricultural practices on behavioural variation within agroecosystems is an important step forward in order to devise new management techniques allowing high productivity while reducing their toll on biodiversity.

It is this interplay between applied and fundamental aspects of animal behaviour that motivated my choice of studying behavioural variation in an agroecological context. The overall objective of my thesis is to understand the determinants of behavioural variation in the context of agroecosystems, using the jumping spider *Eris militaris* (Araneae: Slaticidae) as a model organism. My focus on spiders is motivated by their importance in agroecosystems, as spiders are major generalist predators and efficient biocontrol agents (Riechert and Bishop 1990, Carter and Rypstra 1995). In this thesis, I wanted to extend applied knowledge on the effects of human-driven environmental changes on personality differences, with particular attention given to insecticide use, as well as address fundamental questions relevant to how personality differences are maintained over time.

The chapters are presented in an order reflecting the threads of evidence followed during the progression of the research. In Chapter 2, I tested how behavioural syndromes varied for populations of jumping spiders exposed to different frequencies of insecticidal applications. In Chapter 3, I tested how consistent behavioural differences remained over ontogeny, and examined subsequent variation between sex and rearing environments. Chapter 4 tested the effects of sublethal exposure to an insecticide on personality expression. Chapter 5 presents a framework by which the interactions between behavioural variation and various classes of anthropogenic contaminants (including insecticides) can be investigated.

This thesis provides an opportunity to bridge the gaps between animal personality, agroecology and ecotoxicology by focusing on suites of related traits that affect spider performance in agroecosystems.

1.2. Literature review

1.2.1. Importance of behavioural variation in ecology and evolution

Animal behaviour is an important driver of ecological and evolutionary processes (Dall et al. 2012, Sih et al. 2012, Wolf and Weissing 2012). Behavioural decisions have consequences within an individual's lifespan (e.g., at the ecological timescale) that are tied to an individual's survival and fitness (Krebs and Davies 2009) such as the capacity to avoid predators, to find suitable habitats for growth, reproduction or food sources. Behavioural interactions between different species have far-reaching consequences and in turn shape population and community processes. For example, antagonistic interactions among arthropod predators in bromeliad systems have cascading effects that alter CO_2 release (Atwood et al. 2013), and territorial behaviour in ants deters key decomposer species and reduces plant biomass in alpine meadows (Zhao et al. 2013). Behaviour also operates at an evolutionary timescale. Behavioural adaptations are shaped by past selective pressures (Westneat and Fox 2010), which in turn constrain future evolution (Sih et al. 2012). Behaviours often have a genetic and heritable basis, meaning that selective pressures can erode or sustain phenotypic variation over the course of multiple generations (Shaw and Wiley 2010).

An important implication of behavioural variation between individuals (hereafter behavioural variation) is that populations should not be reduced to their mean while overlooking the frequency distribution for a given trait. Populations are composed of a multitude of individuals with different genetic backgrounds, physiological characteristics and developmental histories. As a consequence, each individual may not necessarily contribute equally to population processes (e.g., reproductive output, niche expansion). Behavioural interactions between conspecific and heterospecific individuals may therefore scale up and affect population and community dynamics and is part of an increasing effort to account for phenotypic variations in ecological studies (Nakagawa and Schielzeth 2012, Violle et al. 2012a, b, Turnbull et al. 2014). These so-called behavioural type × behavioural type interactions have been demonstrated in

multiple systems and their effects include non-assortative mating as a mechanism maintaining behavioural variation (Pruitt and Riechert 2009a, Pruitt et al. 2011), different capture rates depending on the joint phenotype of predators and prey (Pruitt et al. 2012, DiRienzo et al. 2013, Sweeney et al. 2013a) and different social functions within populations depending on aggressive phenotypes (Pruitt and Riechert 2011a, b).

An important body of literature has developed in order to understand the wide-ranging consequences of behavioural variation. However, many questions remain as to why such a disparate range of behavioural phenotypes is observed in the first place and the mechanisms enabling the maintenance of behavioural variation are still subject to debate.

1.2.2. Mechanisms affecting behavioural variation

Much research is currently devoted to identifying the mechanisms allowing for consistent behavioural differences to be maintained over evolutionary time. In this section I review the main mechanisms that drive individual differences in behavioural traits and shape their correlations into syndromes.

1.2.2.1. Genetic and physiological constraints

Genetic and physiological pathways are proximal factors involved in the expression of a multitude of behavioural traits (Tinbergen 1963, Ketterson and Nolan 1999). Because these pathways are costly to build and act on multiple behaviours simultaneously (e.g., pleiotropic genes, hormonal mechanisms affecting the expression of several behaviours), they may therefore be resilient to selective pressures and constrain the extent of behavioural variation expressed by individuals (i.e., constraint hypothesis, Bell 2005).

Many insights on the underlying causes of personality differences have derived from studies on the proactive-reactive axis – a behavioural syndrome involving exploratory behaviour, aggression, boldness, dispersal and response to environmental change (Koolhaas et al. 1999, Dingemanse et al. 2003). Reactive individuals are shy, slow explorers and seem to do better in changing environments whereas proactive individuals are more aggressive, have higher dispersal capacities and are dominant when environmental conditions are more predictable. In laboratory mice (*Mus musculus domesticus*), these behavioural differences are related to levels of serotonin, with reactive individuals having higher levels than proactive ones (Koolhaas et al. 1999). Similar

influences of physiological traits on personality differences have been uncovered in wild populations as well (Careau et al. 2008). For example, individual differences in stress reactivity in Eastern chipmunks (*Tamias striatus*), measured by cortisol production, are linked to exploratory patterns (slow vs. fast explorers), with fast explorers having higher consistency in cortisol levels over the long term (Montiglio et al. 2012).

Personality traits also have a genetic basis with heritability estimates ranging around ~ 30 % (reviewed in Stirling et al. 2002), meaning that a significant portion of parental phenotypic variance is passed on to offspring. Repeatability, a measure of extent of personality differences, typically sets the higher bound for heritability (Dohm 2002) and ranges from 30 to 50 % (reviewed in Bell et al. 2009). Tools derived from quantitative genetic approaches allow the estimation of the degree of genetic constraints involved in the expression of personality traits (Dochtermann and Roff 2010) and are a powerful way to investigate how behavioural syndromes respond to selective pressures. However, the identity and function of genes underlying personality traits remains poorly understood apart for a few well-studied laboratory species (Bell and Aubin-Horth 2010). In zebrafish (*Danio rerio*), mutation on a gene encoding for a growth receptor jointly affects aggressive, bold, and exploratory behaviours (Norton et al. 2011). However, this study was not coupled with observation of wild population, and the degree of constraint due to this genetic factor remains to be explored.

If neuroendocrine, physiological and genetic factors do indeed constrain the expression of an individual's behaviours, this implies that behavioural syndromes should be resilient to selective forces and would constrain the independent evolution of behavioural traits. A recent meta-analysis of genetic covariance among behavioural traits (so-called G matrices) shows that behavioural syndromes can indeed constrain the evolution of behavioural characters up to 30 %, an estimate higher than those found for morphological or physiological traits (~ 15 %) (Dochtermann and Dingemanse 2013). Behavioural syndromes should therefore be maintained even across populations with drastically different environments. This hypothesis has however generated mixed results in wild populations. Some taxa show surprisingly similar correlations independently of environment type (e.g., spiders: Riechert and Hedrick 1993, Pruitt et al. 2010), while other show strong interpopulation variation (threespined sticklebacks: Bell 2005, Dingemanse et al. 2007). Despite strong evidence for physiological and genetic constraints, correlations between behavioural traits are not always found (Snekser et al. 2009), or correlations

may remain context-specific (Nelson et al. 2008, Sinn et al. 2008, Snekser et al. 2009). Although the genetic basis of behavioural variation may constrain the evolution of behavioural characters, this genetic basis can also respond to selective pressures from the environment. In the next section I describe how personality traits and behavioural syndromes can be shaped by natural selection and represent adaptations to local environmental conditions (i.e., adaptive hypothesis, Bell 2005).

1.2.2.2. Adaptive personality differences

The fact that personality traits tend to be heritable implies that these traits respond to natural selection (Dingemanse and Réale 2005). Within populations, different types of selective pressure may act to sustain or erode behavioural variation, resulting in different fitness consequences depending on personality type.

In Eastern chipmunks, disruptive selection favours extremes of exploratory personality types while individuals with medium exploration score have higher mortality (Bergeron et al. 2013). Selective forces may also be variable in time and these yearly fluctuations can result in differing fitness outcomes depending on personality type. One of the most comprehensive investigations of the fitness consequences of personality types in wild populations comes from studies conducted on great tits (*Parus major*) (Dingemanse et al. 2002, 2003, 2004, Dingemanse and de Goede 2004). Individuals of this species show differences along a continuum of slow vs. fast explorers. Years of scarce resource abundance favoured slow male explorers and fast-exploring females, while the reverse was found in years of beech masting. These differential fitness outcomes were also conditional on the combined personality type of mating pairs. Mating pairs of same personality types produced higher quality offspring but their fitness was reduced in years of food scarcity (Both et al. 2005).

The fact that personality traits have a multidimensional component and organize into syndromes involving multiple behavioural contexts suggests that certain combinations of personality types work well in association, resulting in higher fitness under the right environmental conditions (i.e., adaptive hypothesis for behavioural syndromes, Wilson et al. 1998, Bell 2005). For example, long calls in male crickets (*Gryllus integer*) attract both mates

and predators. Long-calling males were found to be generally shyer than short-calling males and this could represent an adaptation to compensate for this risky behaviour (Hedrick 2000).

Since selective forces can be widely variable between environments, one should expect strong interpopulation differences in behavioural syndromes. One of the first reports of a behavioural syndrome was made by Huntingford (1976) who demonstrated a positive correlation between boldness toward predators and aggressiveness toward male rivals in threespined sticklebacks (*Gasterosteus aculeatus*). Further investigation of this syndrome showed that strong behavioural correlations between activity, aggression and boldness were only expressed in populations regularly exposed to predators (Bell 2005, Dingemanse et al. 2007). Manipulative experiments confirmed that predation exposure acted as a correlated selective pressure directly shaping the association between these functionally different behavioural traits (Bell and Sih 2007).

Personality differences and behavioural syndromes may therefore represent adaptations to local environmental conditions and, under certain conditions, selective forces may maintain high phenotypic variance. An important step forward in the understanding of personality differences is to investigate how these tendencies influence life-history trajectories.

1.2.2.3. Life history trade-offs

Personality traits are frequently correlated with life-history traits (e.g., reproductive output, growth, lifespan) (Boon et al. 2007, Biro and Stamps 2008, Réale et al. 2009) and variations in life-history strategies may also give rise to personality differences. For example, Stamps (2007) has suggested that differences in growth rates can target individuals in different personality trajectories and these two components could be understood within the same integrative framework. The pace-of-life syndrome hypothesis (POLS, Réale et al. 2010) posits that a suite of metabolic, hormonal and immune traits coevolved jointly with life-history trade-offs between "slow" and "fast" lifestyles, thus giving rise to consistent behavioural differences. Individuals on the "fast pace-of-life tracks" would therefore have shorter lifespans, grow more rapidly and reproduce earlier than "slow" individuals, predicted to exhibit more cautions in their behavioural and life-history strategies. Fast individuals are predicted to have higher dispersal rates, behave more boldly and have lower sociability coupled with higher metabolism rates and lower immune response.

Empirical tests of the predictions generated by the POLS hypothesis has generated positive support in laboratory conditions (Biro and Stamps 2008, Smith and Blumstein 2008), but empirical evidence remain scarce in wild populations (Niemelä et al. 2012b, McGhee et al. 2013, Montiglio et al. 2014). In addition, this approach tends to neglect developmental shifts happening over the lifespan of individuals (Stamps and Groothuis 2010a, b, Groothuis and Trillmich 2011). Behavioural carryovers from early developmental stages to adulthood can be sustained in some cases (Johnson and Sih 2005, 2007, Brodin 2009, Wilson and Krause 2012). However, this does not seem to be a generality and many other studies suggest that certain behavioural syndromes are unstable over ontogeny. Certain correlations are more strongly expressed at a given life-stage (Bell and Stamps 2004, Sinn et al. 2008, Sweeney et al. 2013b) or vary due to spatiotemporal fluctuations in environmental conditions (Sinn et al. 2010).

1.2.2.4. State-dependent feedbacks

While proximal characteristics are an important basis for personality differences, behavioural traits are also much more plastic and reversible than life-history or physiological traits. Mechanisms that sustain personality differences may not all have a genetic component. State-dependent models are particularly interesting because they suggest that behavioural differences may arise through dynamic feedbacks between characteristics that affect the payoff of behavioural decision (i.e., states: age, size, energy balance, residual reproductive value, morphological defenses) and behaviour (Houston and McNamara 1999, Dingemanse and Wolf 2010).

For example, in a positive feedback scenario, individuals that behave boldly may gain assets, which are in turn converted into increased state (e.g., larger size, increased vigour). Increased state leads to a higher payoff per unit of behaviour thus leading to the maintenance of bold behaviour through time (Luttbeg and Sih 2010). State-dependent feedbacks may also be negative and erode behavioural differences over time. Individuals that increase state over time have more to lose and are less likely to engage in risky behaviour (asset protection principle: (Mangel and Clark 1988, Clark 1994). Another example of negative state-dependent feedback is the trade-off between early and delayed reproduction. Individuals investing more of their energy into immediate reproduction than in long term survival may also be bolder while foraging (Wolf et al. 2007).

To date, state-dependent feedbacks have been mostly proposed as theoretical explanations for personality differences. Manipulation of states such as expected fitness in great tits - through brood size manipulations - has shown that individuals with reduced fitness expectations increase risk taking (Nicolaus et al. 2012) However, manipulations of perceived risk of exposure to predators showed more evidence for negative frequency-dependent effects of predation exposure (i.e., group vigilance decreases as predation exposure increases) than state-dependency (Mathot et al. 2011). More empirical studies are therefore required in order to gather reliable information on the influence of state-dependent dynamics on personality differences and behavioural syndromes.

An important research effort has been devoted to understanding the mechanisms underlying behavioural variation. In addition, behavioural variation have important implications for ecological and evolutionary dynamics, this means that such variations are crucial to consider when studying how species cope with increasing environmental pressures generated by human activities. In the next section I describe the recent studies that have investigated the role of behavioural variation in the context of environment subject to high levels of anthropogenic disturbances.

1.2.3. Behavioural variation and anthropogenic disturbances

Human activities have greatly increased their impact on ecosystems since the Industrial Revolution. These activities are large-scale and have caused changes in community composition and population size of wildlife (Vitousek et al. 1997). As a result, human activities threaten species persistence in their environment and pauses new challenges to which individuals must adapt. Individual behavioural variations are predominant independently of taxa or type of ecosystem (Sih and Bell 2008). As reviewed above, a genetic underpinning is common for many personality traits (Dingemanse and Réale 2005) or behavioural syndromes (Dochtermann 2011, Taylor et al. 2012, Dochtermann and Dingemanse 2013), and the maintenance of personality differences and correlated behavioural tendencies can itself be shaped by natural selection (Dingemanse et al. 2004, Bell and Sih 2007, Bergeron et al. 2013). The new selective pressures generated by so-called Human Induced Rapid Environmental Changes (HIREC, *sensu* Sih et al. 2010) may therefore act on behavioural variations and shape new associations between traits, or favour different personality types than those encountered in the wild. These HIREC include

environmental alterations such as habitat loss and fragmentation and novel biotic (e.g., introduced species, changes in density of predator, prey and/or conspecifics) or abiotic conditions (exposure to chemicals: pollutants and pesticides, changes in light or noise pollution, climate change).

HIREC may shift and alter the evolution of behavioural traits through a series of direct and indirect effects. Certain behavioural types may have lower success and be selected against in environments heavily altered by human presence. For example, docile and explorative Eastern chipmunks (*Tamia striatus*) are more likely to establish themselves in humanly frequented areas (Martin and Réale 2008a), pheasants with bold personality types are more likely to be harvested during hunting season (Madden and Whiteside 2013), and bird populations inhabiting urban areas tend to exhibit higher aggression and lower object neophobia across many species (reviewed in Miranda et al. 2013). At the community level, invasive species respond positively to human-driven environmental changes and may out-compete native populations because of stronger associations between dispersal capacities, boldness, aggression and voracity, as shown with the invasive signal crayfish *Pacifastacus leniusculus* and its native competitor *P. fortis* (Pintor et al. 2008, Pintor and Sih 2009).

To date, only a handful of HIREC have been the subject of investigation for their effects on behavioural traits, but the conclusions of these studies support the importance of integrating behavioural variation in order to better understand species' response to environmental changes (reviewed in Sih et al. 2013 and Sol et al. 2013). One limitation of the current studies of HIREC effects on behavioural traits is that they often rely on correlational approaches but have not identified the causal mechanisms underlying these changes. For example, studies on effects of urbanization typically compare differences in average personality types or in syndrome structure between populations living in differently urbanized habitats (Scales et al. 2011, Bokony et al. 2012) but how much these interpopulation differences are due to pollution, tolerance to human presence and urban noise or varying degrees of resources or competition is hard to pin down. In the following section, I argue that agroecosystems are much more amenable to manipulative studies and can help untangle the relative contribution of different classes of HIREC (e.g., habitat fragmentation, frequency of mechanical disturbance and of pesticide spraying) on behavioural variation.

1.2.4. Agroecosystems as models for studying anthropogenic disturbance

1.2.4.1. Agroecological gradients

Agroecosystems are suitable systems to study behavioural variation because they provide strong gradients of disturbances affecting both abiotic (e.g., habitat type, different frequency and intensity of exposure to pesticides) and biotic conditions (e.g., food resources, predation pressure). By definition, agroecosystems are modified environments heavily impacted by human activities. The intensity and frequency of anthropogenic disturbance varies greatly depending on the type of crops being cultivated (perennial or annual crops), management methods (presence/absence of pesticides or tilling) or the proportion of surrounding landscape which can serve as alternative or refuge habitats. All of these factors are known to impact biodiversity (Vitousek et al. 1997, Purvis and Hector 2000), community structure (Schmidt et al. 2008) and population size in agricultural fields (Winfree et al. 2009). Yet, little is known as to how these factors influence behavioural variation.

An interesting feature of agroecosystems is that there are amenable to field manipulations, much more so than urban environments. The degree and frequency of mechanical operations (e.g., tilling, seeding, harvesting, pesticides spraying) or habitat manipulations (intercropping or flowering strips to enhance natural enemy abundance) can directly be adjusted and provide much more opportunities for controlling confounding sources of behavioural variation. In addition, the importance of arthropods, often overlooked in current studies of HIREC and behavioural variation, is highly documented in agroecosystems as most pest species and their natural enemies are arthropods (Vincent et al. 2007).

Studying behavioural variation in the context of agroecosystems can be mutually beneficial for the fields of agroecology and behavioural ecology. By taking advantage of the possibilities of habitat manipulation and adjustment of frequency of agricultural disturbance, behavioural ecologists can better understand how different classes and frequency of HIREC may disrupt or shape the correlated evolution of behavioural traits and study their consequences for population and community dynamics under highly controlled conditions. Similarly, agroecologists may benefit from understanding how prevalent personality differences and behavioural syndromes are in agroecosystems, particularly for understanding the behavioural characteristics that make for successful biocontrol agent (e.g., high voracity, wasteful killing

Maupin and Riechert 2001) or that favour pest species to cause important damage to crops (e.g., high dispersal capacities).

1.2.4.2. Pesticides and their effects on behaviour

One of the major disturbances occurring in agroecosystems is the spraying of pesticides to manage pest species. These compounds are often wide-spectrum and may affect many non-target organisms, especially arthropods. Although some pesticides may degrade rapidly, most arthropod fauna get exposed to pesticidal residues, which cause shifts in physiology and behaviour rather than direct mortality (reviewed in Desneux et al. 2007). Neurotoxic insecticides in particular have been reported to disrupt several categories of behaviours on non-target arthropods, including navigation and orientation (Henry et al. 2012), host recognition (Desneux et al. 2004a), circadian activity (Tietjen and Cady 2007) and mating behaviour (Tietjen 2006).

Despite increasing knowledge of the extent of sublethal disruption on behaviour of non-targeted arthropod, individual differences are poorly accounted for in ecotoxicological assays. Most studies focus on unique traits rather than using the multidimensional approach favoured by behavioural syndrome studies. Current studies of pesticide effects on behaviours tend to report shifts in average behaviour values post-exposure rather than understanding the sensitivity of individuals through pre and post-exposure phases. Stated another way, current ecotoxicological studies ignore potential effects that may be due to personality differences (but see Kolok et al. 1998, Brodin et al. 2013). It is important to understand if consistent tendencies in aggressive, bold or explorative behaviours remain consistent when individuals are exposed to pesticide stress. We need to study how repeatability and correlation of behavioural traits vary under exposure to pesticides. Such studies would be particularly relevant for species that have a high importance for biocontrol. Certain behavioural phenotypes may participate more actively to biocontrol (e.g., active and voracious individuals) and a decoupling of these tendencies through insecticidal exposure may limit their contribution to pest control.

1.2.5. Spiders in agroecosystems

Generalist arthropod predators are important in agroecosystems as they prey on pests and can buffer their outbreaks (Young and Edwards 1990, Symondson et al. 2002). Spiders are

among the most abundant generalist predators found in agroecosystems and prey on numerous pest insects (e.g., lepidopteran eggs in cornfields, Pfannenstiel 2008). As generalist predators, they are unlikely to regulate pests in a density-dependent fashion. However, when considering spider assemblages (i.e., multiple species), research has shown that predation pressure applied by spiders can result in top-down effects, thus limiting pest damages and increasing yields in some crops (Riechert and Bishop 1990, Carter and Rypstra 1995). Maximizing spiders' impact on pests thus relies more on providing optimal conditions for successive recolonization of agroecosystems. Recent research has shown that habitat manipulation such as intercropping or mulching can increase spider diversity and abundance, (Halaj et al. 2000, Landis et al. 2000, Lemke and Poehling 2002, Prasifka et al. 2006). There is also evidence that non-crop habitats can provide suitable overwintering sites or shelters when human disturbance occurs (e.g., tilling, seeding, chemical spraying) and participate in spiders' success in pest regulation (Sackett et al. 2008, 2009, Schmidt et al. 2008).

In the past 10 years, spiders have become a model taxon for studying personality traits and behavioural syndromes (Riechert and Hedrick 1993, Johnson and Sih 2005, 2007, Pruitt et al. 2008, Kralj-Fišer and Schneider 2012). To date more than seven families have been tested for the presence individual differences in behaviour and an aggression-boldness syndrome seems to be common across most species (reviewed by Pruitt and Riechert 2012). The first evidence for such a syndrome comes from Riechert and Hedrick (1993) who found positive correlations between boldness, aggression and voracity in the funnel web spider *Agelenopsis aperta* (Araneae: Agelenidae) consistent across populations. In the fishing spider *Dolomedes triton* (Araneae: Pisauridae), voracity in young females is linked with aggression toward potential mates, which can explain precopulatory cannibalism (Johnson and Sih 2005, 2007). Populations of the social spiders *Anelosimus studiosus* (Araneae: Theridiidae) share within-population correlations between traits related to sociality, boldness and voracity even when populations are strongly geographically separated (Pruitt et al. 2010). Despite increasing documentation of spider behavioural syndromes and the factors underlying their variations, there is little knowledge of how these consistent behavioural tendencies apply to successful pest control.

Although much is known about the ecology of agricultural spiders, factors that influence different rates of predation, aggressive interactions and predatory behaviours remain understudied. The recent findings on the ecological importance of personality traits and

behavioural syndromes strongly suggest that the consistency of these traits may be affected by different intensity and frequency of agricultural disturbances. Using spiders as models, further investigation of personality differences and behavioural syndromes in agricultural contexts could help gain useful knowledge on the impact of human activities (especially pesticide exposure) on the fauna at a behavioural level. Ultimately, such knowledge can be used to better predict the efficiency of natural enemies and design farming techniques maximizing their impact on pests.

1.2.6. *Eris militaris* (Araneae: Salticidae)

Jumping spiders are well-studied models in behavioural ecology (Jackson and Pollard 1996, Herberstein 2011). Their well developed eyesight make them ideal models to study their response to a variety of visual cues including response to prey (Hill 1979), reaction to conspecifics in courtship (Jackson 1977, Clark and Uetz 1990, 1992, Elias et al. 2003) or to the presence of conspecifics (Faber and Baylis 1993, Taylor et al. 2001, Elias et al. 2008, Elias et al. 2010) and predators (Stankowich 2009). Despite well-documented behaviours, jumping spiders have not been used to document the presence of personality traits and behavioural syndromes in spiders. To date, only one publication exists documenting individual differences in foraging activity in this group with the species *Phidippus clarus* (Sweeney et al. 2013a) and across context correlations of multiple behavioural traits have yet to be investigated.

Eris militaris is a medium-sized jumping spider (males: 4.7-6.7 mm, females: 6.0-8.0 mm in length, Paquin and Dupérré 2003) common in hedgerows (Hill 1996). *Eris militaris* spiders have a two-year life cycle in north-temperate regions (Dondale 1961). Individuals reproduce in mid-June and spiderlings emerge around the end of July. Individuals overwinter as juveniles and become sub-adults (i.e., the stage before sexual maturity) at the end of September. They reach adulthood by early June in the next year. It is one of the dominant agrobiont spider found in apple orchards (Sackett et al. 2009) although its density is highly reduced in presence of pesticides (Bostanian et al. 1984, Sackett et al. 2007). Previous work also demonstrated that this species is an important predator of the tortricid moth *Choristoneura rosaceana* (Lepidoptera: Tortricidae) (Sackett 2007), a major pest in apple orchards (Reissig 1978, Smirle et al. 2002). This spider was easy to collect in apple orchard and could be effectively reared under laboratory conditions, an attribute allowing to test a wide range of behavioural traits for repeatability and correlations and their response to agricultural disturbances.

1.3. Thesis objectives and scientific approach

The overarching goal of this thesis is to understand the factors influencing behavioural variation in an agroecological context with a jumping spider common to apple orchards. To reach this goal, I set four specific objectives that were answered by a series of experiments and a literature review.

1) My first objective was to test whether variations in insecticidal exposure could drive interpopulation variation in behavioural syndrome structure in *Eris militaris* caught in apple orchards. This objective was investigated using a common garden experiment where spiders caught in insecticide-free and insecticide-treated populations were tested for a wide array of behavioural traits under laboratory conditions.
2) My second objective was to understand the consistency of behavioural syndromes over multiple life-stages by comparing patterns of phenotypic covariance between field-collected and F1 laboratory-reared populations and sexes.
3) My third objective was to investigate the effects of sublethal exposure to insecticides on the consistency of personality traits and their behavioural syndromes. This objective was met by comparing the repeatability and differences in behavioural correlations for control and insecticide-treated group under standardized conditions.
4) My final objective was to provide a review and synthesis of the effects of anthropogenic contaminants on behavioural variation and to generate a framework by which behavioural variation can be included in ecotoxicological studies.

In order to meet these objectives, I tested the following hypotheses:

Hypothesis 1: Insecticidal applications alter the correlation between behavioural traits either by acting as a selective force shaping trait correlation (a) or by disrupting pre-existing behavioural correlations at sublethal doses (b), leading to interpopulation differences in syndrome structure (Chapter 2). If insecticides act as selective forces, different behavioural correlations should be expressed between populations. If insecticides disrupt behavioural correlations, we should observe weaker or no syndromes expressed in the insecticide-treated correlation.

Hypothesis 2: Behavioural consistency is influenced by rearing environment and sex in the jumping spider *Eris militaris* (Chapter 3). If this hypothesis is true, we should expect behavioural traits to be heritable and their repeatability to vary between field-collected and F1 laboratory-reared individuals and sexes.

Hypothesis 3: Behavioural correlations are conserved over ontogeny (Chapter 3). If this is true, correlation strength may vary between groups (rearing environment or sex) but will remain consistent over multiple life-stages within groups.

Hypothesis 4: Insecticidal exposure at sublethal dose provokes shifts in personality trait expression (Chapter 4). This hypothesis is met if either one of the following condition is verified:

(a) The average personality trait differs between insecticide-treated and control groups.
(b) The repeatability of behavioural traits differs between insecticide-treated and control groups.
(c) The strength of behavioural correlation between personality traits differs between insecticide-treated and control groups.

Chapter 5 presents a short review of anthropogenic contaminants (e.g., heavy metals, pesticides, endocrine disrupters) that affect behavioural traits and may therefore act as a source of behavioural variation.

1.4. Connecting Statement

The first Chapter was a literature review, and presented an outline of my thesis objectives. The next Chapter presents the first test of interpopulation variation in behavioural syndromes set in agroecosystems. I compared the behavioural syndromes between activity, aggression, boldness and voracity in populations of the jumping spider *Eris militaris* (Araneae: Salticidae) from apple orchards with different intensity of exposure to insecticides.

Chapter 2: Inter-population variation in behavioural syndromes in a jumping spider from insecticide-treated and insecticide-free apple orchards

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2.1. Abstract

Variations in environmental conditions can influence behavioural syndromes (correlated tendencies in behaviours), and understanding the factors that shape trait covariation is particularly relevant when species are challenged by environmental changes. We investigated how behavioural syndromes varied at extremes of a gradient of anthropogenic disturbance, using apple orchards with different histories of insecticidal applications as a model system. *Eris militaris* (Araneae: Salticidae) jumping spiders were sampled from an insecticide-free orchard and an insecticide-treated orchard from Southern Québec. Spiders were tested for activity, aggression, boldness and voracity under standardized conditions. Behavioural syndrome structure was compared between the two populations using Bayesian multi-response models and structural equation modeling. Syndrome structure differed significantly between the two populations. The insecticide-free population showed evidence of a syndrome involving all measured traits, while only aggression, boldness and voracity were correlated in the insecticide-treated population. The insecticide-free population showed negative correlations between active and voracious behavioural types vs. aggressive and bold types while the insecticide-treated population showed a negative correlation between aggression-voracity and boldness. This research is a first step in investigating the impact of anthropogenic disturbances on behavioural syndromes and demonstrates that behavioural syndromes may vary with respect to insecticidal applications.

2.2. Introduction

Human Induced Rapid Environmental Changes (HIREC) (Sih et al. 2010) are powerful and rapidly moving selective forces that challenge species' ability to respond adaptively to their environment. These environmental changes can result in a variety of morphological (Evans et al. 2009), physiological (Partecke et al. 2006, Wingfield 2013) and behavioural shifts (Sol et al. 2013). Behavioural variation plays a central role in the context of species' response to HIREC. Species that express a wide range of behavioural phenotypes or that adjust their behaviours to current environmental conditions may cope better with HIREC (Sih et al. 2010).

The recent literature on animal personality (behavioural consistency over time, Réale et al. 2007) and behavioural syndromes (correlated tendencies in behaviour, Sih et al. 2004a, b) provides a conceptual framework to study the impact of HIREC on behavioural variation (Sih 2013). First, the selective pressures generated by HIREC may favor different behavioural types than those encountered in the wild (Evans et al. 2010, Scales et al. 2011). Second, HIREC may alter correlations between behavioural traits (i.e., behavioural syndromes). This can happen through correlational selection (Bell and Sih 2007) or when certain classes of HIREC (e.g., pesticides, pollutants) directly disrupt behavioural expression (Zala and Penn 2004, Desneux et al. 2007).

A key research avenue for behavioural ecology is to link changes in behavioural variation to the intensity and frequency of HIREC. One interesting feature of behavioural syndromes is that they can vary along ecological gradients. For example, variations in predation pressure (Bell 2005, Dingemanse et al. 2007) or in intra and inter-specific competition (Dochtermann et al. 2012) are known to affect the direction and strength of behavioural syndromes. However, few studies have examined syndrome variation in the context of gradients of anthropogenic disturbance (Scales et al. 2011, Bokony et al. 2012) and data on most taxa or trophic levels are lacking.

Agroecosystems are ideal for the study of behavioural responses to HIREC. They offer a range of disturbance gradients, especially with respect to the intensity and frequency of farming operations (e.g., harvesting, pesticidal applications, tilling, seeding; Thrall et al. 2011). Arthropod species with high affinity for crop systems (e.g., agrobiont species; Luczak 1979, Samu and Szinetár 2002) are particularly sensitive to these disturbances and show specialized adaptations to agriculture. For example, some species have adapted their dispersal rates (Margolies 1995) or life cycles with habitat changes and disturbances within agroecosystems

(Samu and Szinetár 2002). Finally, frequent exposure to pesticides can cause a variety of direct or indirect behavioural shifts. At sublethal doses, pesticidal exposure can disrupt behavioural expression (Desneux et al. 2007), and may affect the strength or direction of behavioural syndromes. In addition, pesticidal application causes dramatic shifts in arthropod communities (Letourneau and Goldstein 2001, Whitehouse et al. 2005) and could result in altered conspecific densities or prey abundances.

Spiders (Araneae) are important generalist predators in agroecosystems (Carter and Rypstra 1995, Riechert and Lawrence 1997). Their performance as biocontrol agents depends on suites of behavioural characteristics such as intra-guild predation (Balfour et al. 2003), cannibalism (Buddle 2002), prey preference (Toft 2005, Harmon and Andow 2007), and dispersal capacities in agricultural habitats (Sackett et al. 2009, Royauté and Buddle 2012). Various studies have shown correlations between such behavioural characteristics, notably aggression, boldness and voracity (Riechert and Hedrick 1993, Johnson and Sih 2005, 2007). In the present study, we used the jumping spider *Eris militaris* (Araneae: Salticidae) as a model organism. This spider is common in apple orchards (Sackett et al. 2008, 2009) and hedgerows (Hill 1996), and can be effectively reared under laboratory conditions. Jumping spiders are well-studied models in behavioural ecology (Jackson and Pollard 1996, Jakob et al. 2011, Nelson and Jackson 2011a, b, Uhl and Elias 2011). However, few studies have documented individual variations in their behavioural traits (but see Sweeney et al. 2013a), notably concerning anthropogenic disturbance.

Our objective was to investigate the effects of insecticidal applications on behavioural syndromes. We compared the behavioural correlations between activity, aggression, boldness and voracity in populations of *E. militaris* collected from two apple orchards with different histories of insecticidal applications.

2.3. Methods

2.3.1. Spider collection and rearing

Eris militaris is a medium-sized spider (males: 4.7-6.7 mm, females: 6.0-8.0 mm in length, Paquin et al. 2003) that completes its life cycle within two years (Dondale 1961). Individuals reproduce in mid-June and spiderlings emerge around the end of July. Individuals

overwinter as juveniles and become sub-adults (i.e., the stage before sexual maturity) at the end of September. They reach adulthood by early June in the next year (Dondale 1961).

Individuals of all active stages and sexes were collected in an insecticide-free and an insecticide-treated apple orchard in Quebec, Canada. The insecticide-free orchard was located at Agriculture and Agri-Food Canada's experimental farm in Frelighsburg (W 45.0462, N -72.8565). This orchard has received no insecticide treatments since its creation in 1988, and was treated with other fungicides (mean number of treatments over 5 years ± SE: 12.6 ± 2.8) and herbicides (1.2 ± 0.4). The insecticide-treated orchard was located 5 km away in Dunham (W 45.0885, N -72.8496) and was a commercial orchard treated with pesticides according to the Guide to Foliar Treatments of Apple Trees (CRAAQ 2012) since at least 15 years (insecticides and acaricides: 5.2 ± 1.8; fungicides: 13 ± 2.5; herbicides: 2 ± 0).

Both orchards were surrounded by a deciduous forest border dominated by *Acer saccharum* and *Fagus grandifolia*. We collected *E. militaris* individuals by beating the foliage of apple trees and adjacent forest borders. Spiders were brought to the laboratory for behavioural testing and maintained under a 16 L: 8 O photoperiod at 24 °C and 40 % humidity. The spiders were housed individually in 11.5 × 8 cm cylindrical containers that included a plastic plant to lessen effects of captivity (Carducci and Jakob 2000) and a small plastic straw retreat (L = 2.5 cm, ⌀ = 1.2 cm). Water was provided *ad lib.* using dental wadding inserted in an Eppendorf tube. The spiders were fed weekly with a mixed diet of adult fruit flies (*Drosophila melanogaster* and *Drosophila hydei*) and juvenile domestic crickets (3^{nd} and 4^{th} instars *Acheta domestica*) depending on the developmental stage of the spider. Immature spiders were fed five *D. melanogaster* per week, while sub-adult spiders were fed three *D. hydei* per week. Adult spiders were offered four *D. hydei* and one *A. domestica* per week.

2.3.2.Behavioural tests

We tested 148 individuals, collected between May 2010 and September 2011 in the insecticide-free orchard (n = 89) and the insecticide-treated orchard (n = 59). The individuals were subjected to a series of four or five behavioural tests: 1) climbing activity on an apple trunk (climbing), 2) activity in an open-field arena (open-field activity), 3) aggression with Mirror Image Stimulation (aggression), 4) boldness in front of a moving predator mimic (boldness), and 5) voracity in prey capture (voracity). All behavioural tests were performed on individuals

collected during the 2010 field season. The climbing activity test was dropped in 2011 in order to reduce the duration of the testing procedure to 48h.

Spiders were randomly assembled in blocks of 10 - 12 individuals (hereafter: experimental batches) and were offered one *D. melanogaster* 12 h prior to the tests. Two tests were performed per day over a 60 h period (48 h in 2011) between 08:00 and 17:00. The climbing, open-field activity, aggression and boldness tests were performed in a randomized sequence to avoid bias due to winner and loser effects (Dochtermann 2010). Voracity was performed last to standardize for satiety.

Cephalothorax width, used as a proxy for body size (Jakob et al. 1996), was measured (± 0.001 mm) using a WILD MMS 225 digital length measuring set. Body mass was determined (± 0.1 mg) on the first and last day of tests using a Sartorius TE214S scale. To remove traces of conspecific cues, test arenas were cleaned with 70% ethanol and air-dried for 2 minutes between individuals. The parameters related to climbing activity were directly recorded using The Observer XT (Noldus Information Technology, Wageningen, The Netherlands). All other tests were videotaped using a Canon Vixia HF200 camera and behavioural data were recorded using video playback with The Observer XT.

2.3.2.1. Activity: climbing test

Activity refers to distance travelled in a given amount of time. *Eris militaris* is a foliage-dwelling spider and has a tendency to climb up vertical surfaces when exploring novel environments, as many other jumping spider species do (Hoefler 2007). This particularity allows for easy assessment of individual differences in locomotory performance with jumping spiders (Sweeney et al. 2013a). Spiders were set in a 5 cc plastic syringe taped vertically at the base of a 50 cm length apple tree log (⌀ = 15 cm) and were left at rest for 2 minutes. They were individually released at the base of the log and given a maximum of 15 minutes to reach the top of the log. Climbing speed (cm/s) was calculated as the amount of time spent climbing (s) divided by the total distance travelled (cm). Spiders with higher climbing speed were considered the most active.

2.3.2.2. Activity: open-field test

Open-field arenas are commonly used to assess variations in activity and exploratory behaviours in animal personality studies (Montiglio et al. 2010). As Carducci and Jakob (2000), we used a 30 × 30 cm wooden arena divided into 36 5 × 5 cm quadrats. The spiders were put in a 5 cm^3 plastic syringe for 2 minutes before being released at the center of the arena. A thin layer of Petroleum Jelly was applied on the vertical sides of the arena to prevent the spiders from escaping during the test. We used the speed of arena exploration (total number of quadrats visited per minute) as a measure of activity. Activity was recorded for 15 minutes in 2010 and the duration of the test was reduced to 5 minutes in 2011. Duration of the test had no effect on activity ($t = -1.02$, $df = 130$, $p = 0.31$). Speed of exploration was strongly correlated to the total explored surface (i.e., number of unique quadrats visited, $r = 0.74$, $n = 98$, $p < 0.001$).

2.3.2.3. Aggression: Mirror Image Stimulation test

Jumping spiders often engage in complex escalating contests against conspecifics (Elias et al. 2008). Simulating these contests using Mirror Image Stimulation (MIS) minimizes biases associated with asymmetries in contestant size or mass (Cross et al. 2007, Cross and Jackson 2009). Aggressive contests in *Eris militaris* are very similar to that of other jumping spider species and male-to-male contests proceeds through four successive stages. First, upon encountering an opponent at a distance, males extend their forelegs in a threatening posture. Second, they approach their opponent in a zig-zag pattern. If none of the males have retreated, opponents try to grapple one another by interlocking their chelicerae. After this stage, males engage in violent fights often resulting in injuries or death of one of the opponent. Ritualized displays are rare in females, but their contests are more likely to result in injuries or death. Females also spend more time immobile before retreating or attacking their opponent (Elias et al. 2010). The spiders were introduced into a 25 × 7 cm plastic arena with opaque walls. A 7 × 7 cm mirror was taped on a vertical side (i.e., 7cm) of the arena. Petroleum Jelly was applied to the three other vertical sides (i.e., 2 × 25 cm and 7 cm) of the arena to prevent the spider from escaping. Spiders were left to acclimate for 2 minutes in a 2.5 × 7 cm section at the side opposite to the mirror using a 7 × 7 cm vertical cardboard wall that visually isolated the spider from the mirror. At the beginning of the test, the cardboard was removed and individuals were allowed a maximum of 20 minutes to interact with their image in the mirror. We measured the time spent

in aggressive posture against the mirror (spider tilting its abdomen to the side, extending its forelegs or moving sideways in a zig-zag) from the first orientation toward the mirror to retreat or until the 20 minute limit was reached. Spiders with higher time spent reacting to their mirrored image were considered as most aggressive. About 30 % of the spiders did not show any sign of response to their mirrored image and were not given any value for aggression.

2.3.2.4. Boldness: predator mimic test

Boldness refers to the tendency for an individual not to respond to potentially dangerous situations (e.g., disturbance) or to react only when the stimulus proves to be an actual threat (Sirot 2007). Following Stankowich (2009), we build a 1 × 1 × 4.5 cm arthropod predator mimic made of brown clay. The mimic was composed of three body parts with yellow painted front eyes and three toothpicks inserted on each side as legs. We used a 50 × 7 cm plastic arena with opaque walls and Petroleum Jelly applied on two vertical sides (i.e., 2 × 50 cm). The predator mimic was attached to a 60 cm wooden stick and concealed at one end of the arena. The spider was introduced into a 5 × 7 cm resting area in the middle of the arena and visually isolated from the mimic by vertical cardboard walls. At the beginning of the test, the cardboard walls were simultaneously removed and the predator mimic was pushed in the direction of the spider at a speed of 1 cm/s in order to simulate the approach of a fast moving arthropod predator. The assessment time (i.e., the time spent observing the predator before fleeing or letting the predator pass) was used as a response variable and was standardized per the speed of the predator mimic. Spiders that spent the most time visually assessing the predator before fleeing were considered the boldest. Spiders that did not show any sign of visual orientation toward the predator mimic (< 15% of individuals) were not assigned any value for boldness.

2.3.2.5. Voracity: prey capture test

Voracity is defined as the propensity of predators to feed on multiple prey items (Mills 1982, Lucas et al. 1997). Each individual was introduced into a 9 cm Petri dish containing 10 *D. melanogaster* for 60 minutes, and the total number of prey captured was recorded. Preliminary tests showed that if prey items were presented to the spider every 15 minutes until the spider stopped feeding, the number of captures in the first 60 minutes of the test was strongly correlated with the total number of prey captured ($r = 0.87$, $n = 85$, $p < 0.001$).

2.3.3. Statistical analyses

All analyses were performed with the R software, version 3.0.0 for Macintosh (R Core Team 2013).

2.3.3.1. Mean population differences in behaviour and morphology

We compared mean behavioural and morphological values (i.e., body size and mean body condition) between orchard populations using one-way ANOVAs. Similarly, all behaviours were compared across populations. These comparisons included body size, mean body condition, year and their interactions with populations as covariates. Mean body condition was estimated using a residual index by fitting a linear mixed model in the package lme4 (Bates et al. 2012), with $\log_{10}$(body mass) as a dependent variable (two measurements per individual), $\log_{10}$(body size) as a predictor variable and individual as random effects. This residual index provides a measure of fat reserves independent from the size of the spider (Jakob et al. 1996).

2.3.3.2. Behavioural correlation estimations per population

We used Bayesian multi-response mixed modeling in package MCMCglmm (Hadfield 2010) in order to estimate behavioural correlations per population and correct for fixed effects (Dingemanse and Dochtermann 2013). This approach has the advantage of removing the need for adjustment of error rates (e.g., Bonferonni correction). Moreover, since behavioural correlations are often < 0.2, assigning biological significance based solely on p-values is over-conservative (Garamszegi et al. 2012). Instead, we estimated the magnitude of the correlation based on a continuous scale ($|r| \sim 0.1$: weak effect, $|r| \sim 0.3$: medium effect, $|r| \sim 0.5$: strong effect) and used the 95 % credible intervals (CI) to assess the precision of the estimates.

We first performed model selection to remove non-significant fixed effects independently of population. Body size, developmental stage, mean body condition, population, sex, trial order and year were used as fixed effects and experimental batches as random effects. All behavioural data were $\log_{10}(x+1)$ transformed and expressed as standard deviation units. We used a non-informative inverse gamma prior with 2.5×10^8 iterations, 500 000 iteration burn-in and a thinning interval of 2000. This yielded Monte Carlo Markov Chains (MCMC) with a sample size of 1000 and low autocorrelation. The deviance of each fixed effects was compared to that of the null model using the Deviance Information Criterion (DIC). Fixed effects with $\Delta DIC < 2$ were

removed and the final model included the effects of body-size, developmental stage and sex (Table A1-1).

To compare behavioural correlations across populations, we split the data into two sets, each containing the behavioural values for a given population. We fitted a multi-response model on each dataset separately with the same parameters as mentioned above, to examine the posterior distribution of the correlation coefficients between populations. We tested the convergence of our models with Gelman and Rubin's test, using five separate chains with overdispersed starting values (Gelman and Rubin 1992). We compared the strength and precision of behavioural correlations across populations based on their posterior modes and 95 % CIs. To further investigate differences in correlation strength between populations, we calculated the posterior distribution for the difference in correlation estimates: Δr (defined as $r_{insecticide\text{-}treated} - r_{insecticide\text{-}free}$) and based inference on overlap of the 95 % CIs with zero and percentage of estimates excluding zero.

2.3.3.3. Testing hypotheses of syndrome structure between populations

Structural Equation Modeling (SEM) allows testing for different a priori models of syndrome structure by comparing the loadings of each behaviour on a latent variable. Following Dingemanse et al. (2010), we formulated six a priori models of syndrome structure that were compared between populations using the package lavaan (Rosseel 2012) (Fig. 2-1). Model 1 represents the null model where all behaviours vary independently of each other. Model 2 is a domain-general model where all behaviours are correlated. Models 3 to 6 represent domain-specific syndrome structure depending on the response to foraging (models 3-4) or to risky situations (models 5-6). Model 3 represents a situation where behaviours linked to foraging are correlated (climbing and open-field activity, voracity). Model 4 is a similar model but includes a voracity-aggression spillover as found in some spider species (Johnson and Sih 2005, 2007). Model 5 represents a situation where behaviours linked to risk-taking are correlated (climbing and open-field activity, aggression and boldness), and model 6 includes a spillover between risk-taking (aggression and boldness) and voracity while excluding activity.

For each population, we extracted the posterior mode of the correlation matrix generated from the MCMC procedure. We then fitted each SEM model to both correlation matrices. Model ranking was performed using the Aikake Information Criterion corrected for small sample sizes

(AIC) computed by maximum likelihood. Small AIC values indicate better support for a given model and $\Delta AIC < 2$ indicates low support for a model with respect to the best model. We also reported model weights and evidence ratios in order to facilitate model selection. Model weights indicate the probability of a given model being the best model while evidence ratios, calculated as the ratios of the model weights, indicate how likely a given model is relative to another (Burnham and Anderson 2002).

2.4. Results

2.4.1. Behavioural and morphological differences between populations

The two populations were different in terms of spider abundance, proportion of developmental stages, morphology and average behaviours. All sexes and life stages were represented in the insecticide-free population (Fig. 2-2) and 83 % of the individuals were found inside the orchard. Few adults were collected in the insecticide-treated orchard and 94 % of the individuals were collected in the adjacent forest border. Spiders from the insecticide-free population were bigger (Table 2-1) and had higher climbing activity (cm/s) (mean ± [lower Confidence Interval; upper CI], insecticide-free: 1.49 ± [1.30; 1.68]; insecticide-treated: 1.07 ± [0.85; 1.29]) (Table 2-2), while individuals from the insecticide-treated orchard tended to be more voracious (number of prey captured) (insecticide-free: 3.01 ± [2.59; 3.43]; insecticide-treated: 3.54 ± [3.03; 4.05]). There was a significant population × body size interaction for climbing activity, indicating that climbing activity increased with body size for the insecticide-free population (insecticide-free: $r = 0.38$, $p < 0.001$; insecticide-treated: $r = -0.06$, $p = 0.67$). We also observed a significant increase in open-field activity and voracity with body size (open-field activity vs. body size: $r = 0.46$, $p < 0.0001$; voracity vs. body size: $r = 0.26$, $p < 0.005$) and a decrease in boldness with mean body condition ($r = -0.21$, $p < 0.05$). In addition, behaviours were consistent between years except for boldness, which had a lower average in 2011 (mean ± [lower Confidence Interval; upper CI], 2010: 0.95 ± [0.89; 1.01]; 2011: 0.46 ± [0.31; 0.62]).

2.4.2. Syndrome structure compared across populations

When correcting for effects of body size, developmental stage and sex with multi-response models, we observed significant differences in behavioural correlations between

populations. There was no overall difference in correlation strength between populations (Δr = 0.03 ± [-0.78 0.55]) and behavioural correlations were highly variable depending on the pair of behaviour considered (r = -0.12 ± [-0.40; 0.45]) (Table 2-3). In the insecticide-free population, we found significant positive correlations between climbing and open-field activity (posterior mode ± [CI], r = 0.30 ± [0.003; 0.48]), activity and voracity (climbing activity vs**.** voracity: r = 0.33 ± [0.06; 0.51]; open-field activity vs**.** voracity: r = 0.18 ± [0.01; 0.44]), and between aggression and boldness (r = 0.42 ± [0.05; 0.57]). This population also showed negative correlations between open-field activity, aggression and boldness (open-field activity vs**.** aggression: r = -0.25 ± [-0.43; 0.07]; open-field activity vs**.** boldness: r = -0.19 ± [-0.44; 0.05]) and between boldness and voracity (r = -0.16 ± [-0.44; 0.03]). The insecticide-treated orchard showed evidence for weak to moderate correlations between aggression, boldness and voracity but only the aggression-boldness correlation was significant (aggression vs**.** boldness: r = -0.26 ± [-0.60; -0.001]; aggression vs**.** voracity: r = 0.28 ± [-0.17; 0.55]; boldness vs**.** voracity: r = -0.18 ± [-0.45; 0.15]). In addition, the posterior distribution of difference in correlation strength significantly excluded zero for the aggression-boldness correlation (Δr = -0.64 ± [-1.07; -0.23]; 99.7 % of estimates < zero), and correlation differences between climbing activity vs. voracity (Δr = -0.29 ± [-0.72; 0.08]; 94.0 % of estimates < zero) and aggression vs. voracity (Δr = 0.33 ± [-0.14; 0.73]; 92.9 % of estimates > zero) had > 90 % of the posterior distribution excluding zero (Fig. 2-3).

SEM analysis confirmed that the syndrome structure differed in the two populations (Table 2-4). We found strong evidence for the presence of a behavioural syndrome in the insecticide-free population as the null model (model 1) was ranked last (ΔAIC ~ 20). The domain-general model (model 2) was selected as the best model, followed by the risk model (model 5) (ΔAIC = 3.15) and the risk-voracity model (model 6) (ΔAIC = 6.11). In the insecticide-treated population, the risk-voracity model (model 6) ranked first and the null model was also rejected (ΔAIC = 3.62). Interpretation of path coefficients for model 2 showed an opposition between active-voracious and bold-aggressive behavioural types in the insecticide-free population. This indicated that active and voracious individuals showed less conspecific aggression and boldness toward predators. In the insecticide-treated orchard, the path coefficients of model 6 indicated that aggressive and voracious individuals were less bold (Fig. 2-4).

2.5. Discussion

We found evidence for inter-population variation in behavioural syndromes depending on the presence/absence of insecticidal treatment in apple orchards. The insecticide-free population showed a mixture of positive and negative correlations between all behavioural traits along a continuum between active and voracious behavioural types vs. bold and aggressive types. In the insecticide-treated population, climbing and open-field activity did not correlate with any other behaviour, and we found a negative correlation between boldness and aggression-voracity.

Our results contrast with those of previous studies investigating inter-population variations of behavioural syndrome in spiders. The presence of a general aggression-boldness syndrome is a well-established fact in the spider literature (reviewed by Pruitt and Riechert 2012), though variation exists between species. Studies that have documented syndrome variation across two or more populations in spiders showed little inter-population variations. Riechert and Hedrick (1993) showed that desert and riparian populations of the funnel-web spider *Agelenopsis aperta* shared a common aggression-boldness-voracity syndrome, even though strong differences in mean behaviour were observed across populations. Pruitt et al. (2010) showed that the social spider *Anelosimus studiosus* shared within-population behavioural correlations even when populations were strongly geographically separated. Our study provides evidence that inter-population variation in syndrome structure can occur with spiders inhabiting agricultural environments, and that these differences are potentially tied to the intensity of HIRECs in these environments.

To date, the role of HIREC in shaping the strength and direction of behavioural syndromes has been the subject of few publications. Scales et al. (2011) compared populations of song sparrows (*Melospiza melodia*) along an urbanization gradient and found no correlations between boldness and aggression in urban populations, while a strong correlation was present in rural populations. In a similar study, Bokony et al. (2012) found evidence for behavioural syndromes in house sparrows (*Passer domesticus*), but only risk taking and activity covaried in the urban populations, while object neophobia was also part of the syndrome in rural populations. Although we detected differences in behavioural syndromes in the two spider populations, caution is warranted when relating results directly to insecticidal disturbance since we did not have the opportunity to compare multiple populations. However, as apple orchards

are not commercially manageable without insecticides, we were limited in selecting pesticide-free sites.

We suggest four processes that could explain our results. First, insecticidal applications could directly select against certain behavioural types. For example, spiders that are more active and consume more prey items may have decreased survival as a result of higher accumulation of insecticides. This would explain the absence of active and voracious behavioural types from the insecticide-treated population. Inter-population variation in syndrome structure can be indicative of adaptation to local environmental conditions. For example, populations of three-spined sticklebacks show strong evidence of behavioural syndrome only when exposed to predators (Bell 2005, Dingemanse et al. 2007). However, this is not a sufficient condition for concluding the syndrome is adaptive and confirmation requires an evaluation of selection gradients, for example by using mark-recapture method to witness the survival of individuals of known behavioural type (Bell and Sih 2007, Sweeney et al. 2013b).

Second, the two populations possibly shared the same behavioural syndrome but behavioural expression was frequently disrupted by exposure to sublethal concentrations of insecticides. Exposure to sublethal concentrations of insecticides is common for non-targeted arthropod species in agroecosystems and results in a wide variety of behavioural and physiological shifts (Desneux et al. 2007, Pekar 2012). For example, exposure to organophosphate can cause shifts in circadian activity and affect mating behaviour in certain spider species (Tietjen 2006, Tietjen and Cady 2007). In addition to causing shifts in average behaviour, insecticides could also affect behavioural variation and uncouple previously correlated behaviours. However, sublethal intoxication can be limited in duration (Desneux et al. 2004b), and many insecticides have short persistence in the environment (Leahey 1985). Because we captured spiders at least 7 days after any pesticidal application, sublethal disruption is unlikely to have been involved in our dataset. Laboratory experiments that control the intensity and duration of sublethal exposure in order to monitor the resulting effects on behavioural syndromes would be a next step in order to investigate this effect.

Third, insecticidal applications can generate indirect changes in biotic conditions and alter arthropod community composition and the density of prey and conspecifics (Ripper 1956, Letourneau and Goldstein 2001, Whitehouse et al. 2005), affecting in turn the behavioural response of individuals. Though prey densities were not formally compared between orchards,

we observed higher arthropod densities in the insecticide-free orchard. In contrast, the insecticide-treated population was mostly composed of immature and subadult individuals from the forest border. In the insecticide-treated orchard, we often found immature *E. militaris* in patches of high density (R. Royauté, personal observation). This indicates the potential for high intra-specific competition at early stages in the insecticide-treated population. It can also explain the presence of aggressive and voracious behavioural types, as spiders often resort to cannibalism in the absence of sufficient prey abundance (Buddle 2002, Balfour et al. 2003).

Last, *E. militaris* may express ontogenic shifts in behavioural syndrome. If adults and juvenile stages differ in their behavioural syndromes, the quasi-absence of adults sampled in the insecticide-treated population could have caused to select different models of syndrome structure between populations. Such ontogenic shifts in behavioural syndrome were recently demonstrated in the spider *Agelenopsis pennsylvanica* by Sweeney et al. (2013b), who showed that the development of a boldness-aggression syndrome was considerably influenced by the rearing environment. We suggest the activity-voracity correlation may be expressed mostly by adults**,** which would explain the absence of such a correlation in the insecticide-treated orchard. Tracking the changes in behavioural syndrome over ontogeny will enable to test this possibility.

Our research is a first step in investigating the consequences of anthropogenic changes on behavioural variation in agroecosystems. We demonstrated that behavioural syndromes of jumping spider populations varied in two orchards with presence/absence of insecticidal applications, supporting the hypothesis that anthropogenic disturbances affect syndrome structure. We discussed four processes that can explain the observed changes in syndrome structure: variation in selective pressures between the two orchards, behavioural disruption due to sublethal insecticidal exposure, indirect effects of insecticides on prey and conspecific densities and populational differences in life-stage composition along with ontogenic shifts in behavioural syndromes. The next step would be to investigate each of these processes and determine which have the most influence on the generation of behavioural syndromes in a context of increasing anthropogenic change.

Table 2-1: Comparison of morphological attributes between spider populations. All F statistics were based on df = 1.

Population	Body Size			Mean Body Condition (MBC)		
	Mean ± CI	F	p	Mean ± CI	F	p
Insecticide-Free	1.35 [1.31; 1.40]	11.85	< 0.001	0.001 [0.003; 0.005]	0.295	0.59
Insecticide-Treated	1.22 [1.17; 1.28]			-0.001 [-0.006; 0.004]		

Table 2-2: Effect of body size, mean body condition (MBC), year and their respective interactions with population on behavioural traits. All F statistics were based on df = 1. Bold values indicate significant p-values at $\alpha = 0.05$.

	Climbing Activity		Open-Field Activity		Aggression		Boldness		Voracity	
	F	p	F	p	F	p	F	p	F	p
Body Size	7.12	**<0.01**	49.45	**<0.0001**	1.56	0.22	0.23	0.63	7.78	**<0.01**
MBC	0.43	0.51	8.03	**<0.01**	0.13	0.72	7.26	**<0.01**	0.46	0.50
Population	4.25	**<0.05**	0.00	0.96	0.40	0.53	0.71	0.40	5.32	**<0.05**
Year	-	-	1.24	0.27	0.14	0.71	28.35	**<0.0001**	0.00	0.95
Body Size × Population	6.94	**<0.01**	0.41	0.52	1.79	0.18	0.06	0.80	0.01	0.92
Body Size × Year	-	-	3.13	0.08	2.62	0.11	0.06	0.80	2.25	0.14
MBC × Population	0.05	0.82	1.18	0.28	0.29	0.59	3.08	0.08	1.39	0.24
MBC × Year	-	-	0.19	0.66	0.21	0.65	0.68	0.41	1.19	0.28
Year × Population	-	-	0.08	0.77	2.00	0.16	0.43	0.52	1.99	0.16

Table 2-3: Behavioural correlations between climbing activity, open-field activity, aggression, boldness and voracity in the insecticide-free (lower diagonal) and insecticide-treated orchard (upper diagonal) posterior mode ± [95 % credible intervals (CI)]. Bold values indicate significant correlations based on overlap of 95 % CI with zero. Numbers in parentheses indicate the number of pair-wise observations for a given correlation coefficient estimate.

	Climbing Activity	Open-Field Activity	Aggression	Boldness	Voracity
Climbing Activity	-	0.15 (54) [-0.18; 0.43]	-0.06 (35) [-0.39; 0.30]	0.03 (53) [-0.21; 0.37]	-0.11 (55) [-0.32; 0.30]
Open-Field Activity	**0.29** (72) [0.032; 0.48]	-	-0.006 (38) [-0.37; 0.32]	-0.17 (55) [-0.41; 0.14]	0.03 (58) [-0.25; 0.36]
Aggression	-0.02 (48) [-0.29; 0.26]	-0.25 (63) [-0.43;0.06]	-	**-0.26** (36) [-0.60; -0.001]	0.28 (39) [-0.17; 0.55]
Boldness	-0.08 (61) [-0.31; 0.21]	-0.19 (73) [-0.44; 0.05]	**0.42** (50) [0.05; 0.57]	-	-0.18 (56) [-0.45; 0.15]
Voracity	**0.33** (73) [0.06; 0.51]	**0.18** (88) [0. 01; 0.44]	-0.13 (64) [-0.38; 0.09]	-0.16 (74) [-0.44; 0.03]	-

Table 2-4. AIC comparisons for all a priori models of syndrome structure across populations. Best models (indicated in bold) correspond to the model with lowest AIC values for each population. k: number of free parameters for a given model; W: weight associated with a given model; E.R.: evidence ratio.

Population	Model	k	AIC	ΔAIC	W	E.R.
Insecticide-Free						
	2	**10**	**1247.8**	**0**	**0.76**	**1.00**
	5	9	1250.9	3.15	0.16	4.83
	6	8	1253.9	6.11	0.03	21.3
	4	9	1254.5	6.74	0.03	29.0
	3	8	1254.6	6.82	0.02	30.2
	1	5	1267.8	19.99	0.00	21785.5
Insecticide-Treated						
	6	**8**	**838.5**	**0**	**0.69**	**1.00**
	2	10	841.8	3.32	0.13	5.27
	1	5	842.1	3.62	0.11	6.12
	4	9	844.5	6.03	0.03	20.4
	3	8	845.9	7.41	0.02	40.6
	5	9	846.7	8.24	0.01	61.5

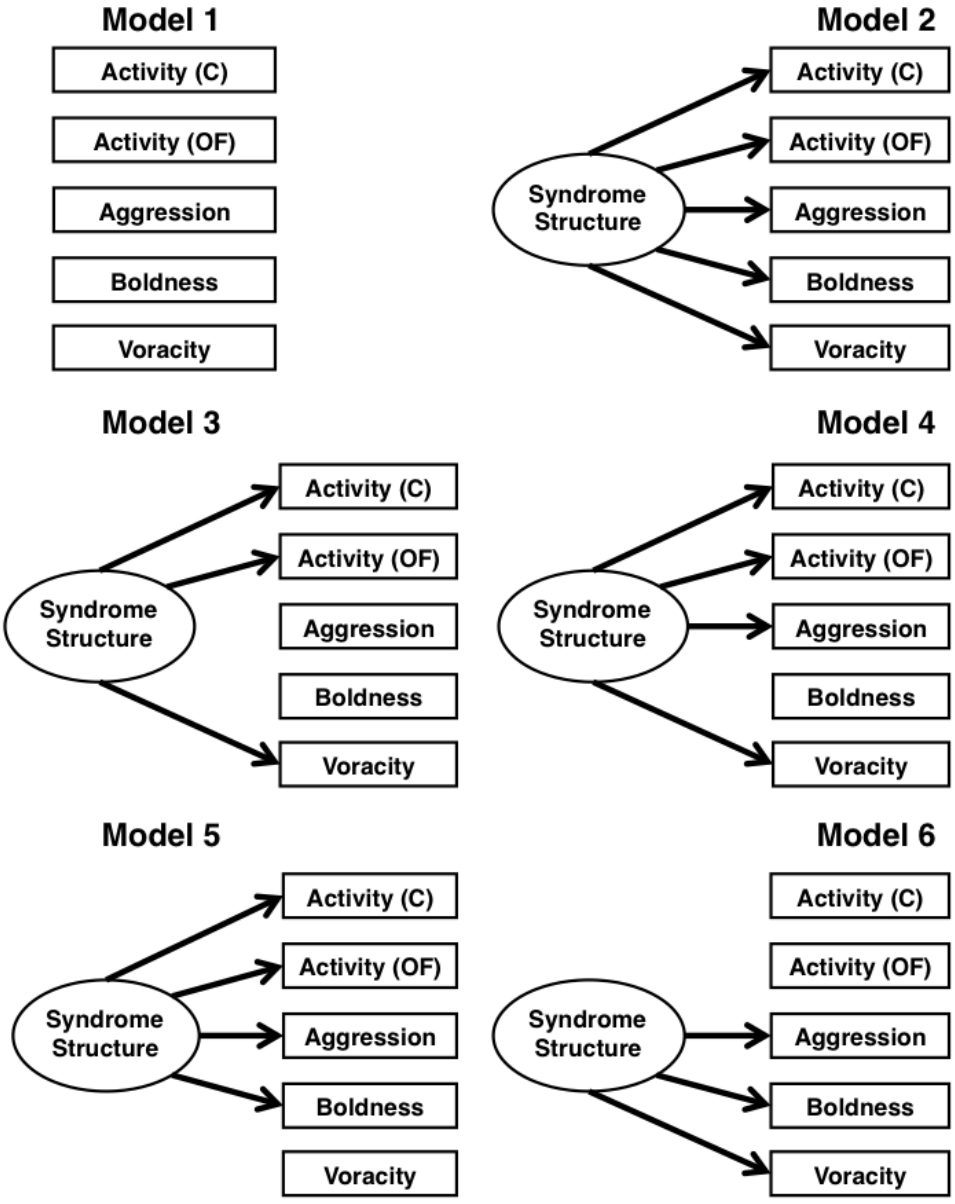

Fig. 2-1: Six a priori hypothesis of syndrome structure and their corresponding structural equation models. Model 1 represents the null model where all behaviours are independent, model 2 is a domain general model with all behaviours covarying and model 3 to 6 represent domain specific hypotheses of syndrome structure.

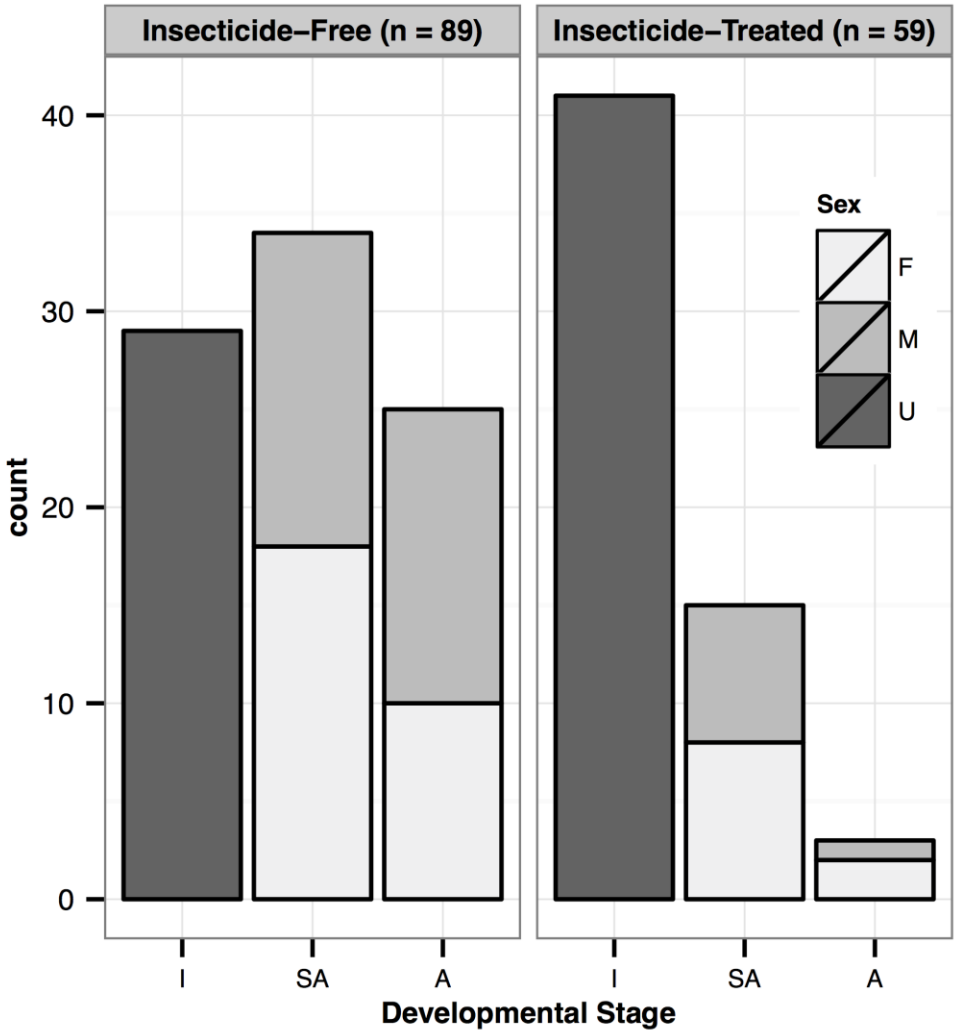

Fig. 2-2: Demographic structure compared between the insecticide-free and insecticide-treated populations. F: females, M: males, U: unknown, I: immatures, SA: sub-adults, A: adults.

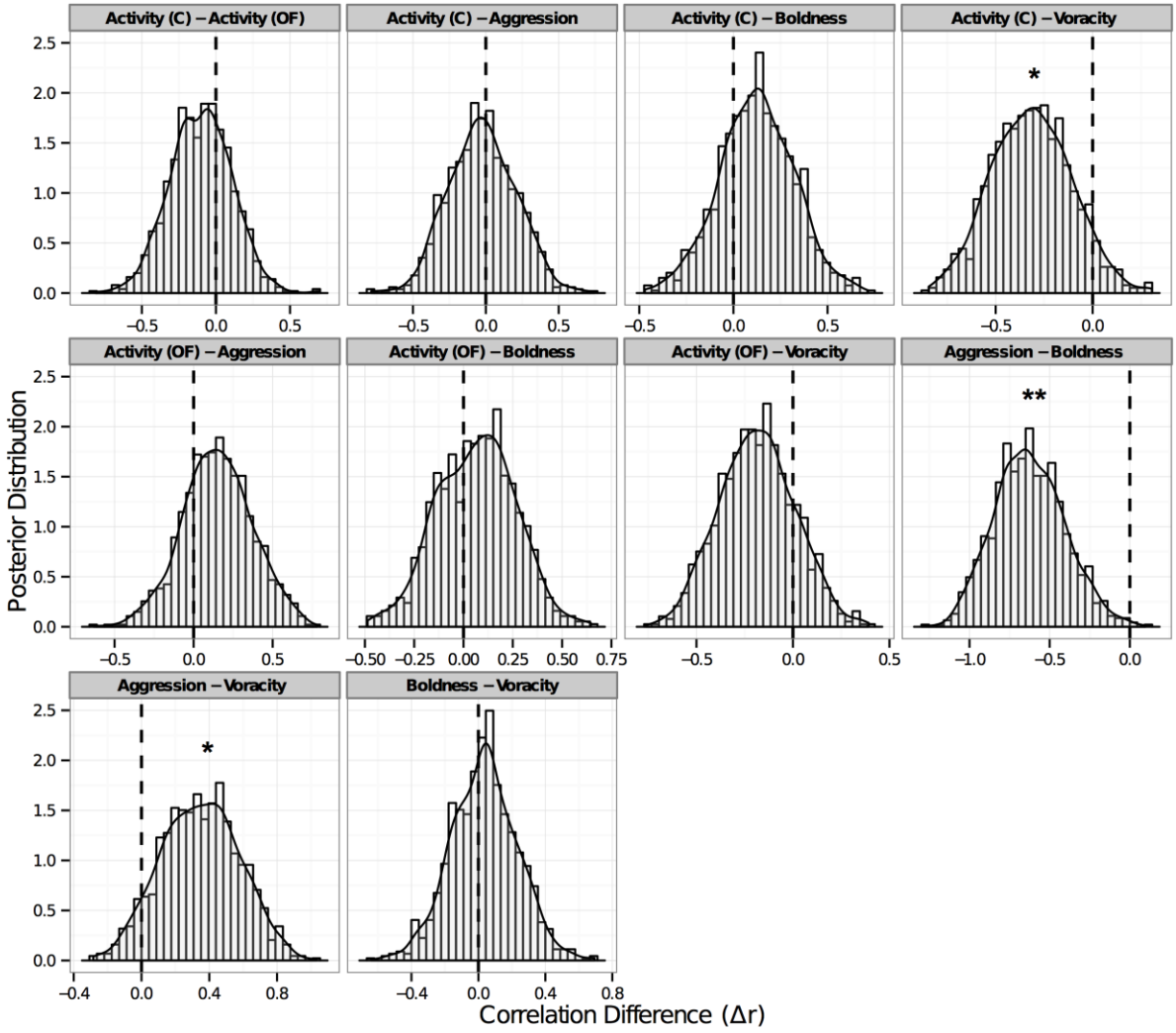

Fig. 2-3: Posterior distribution for the difference in correlation estimates between the insecticide-treated and insecticide-free populations (Δr). * more than 90 % of estimates exclude zero, ** more than 95 % of estimates exclude zero.

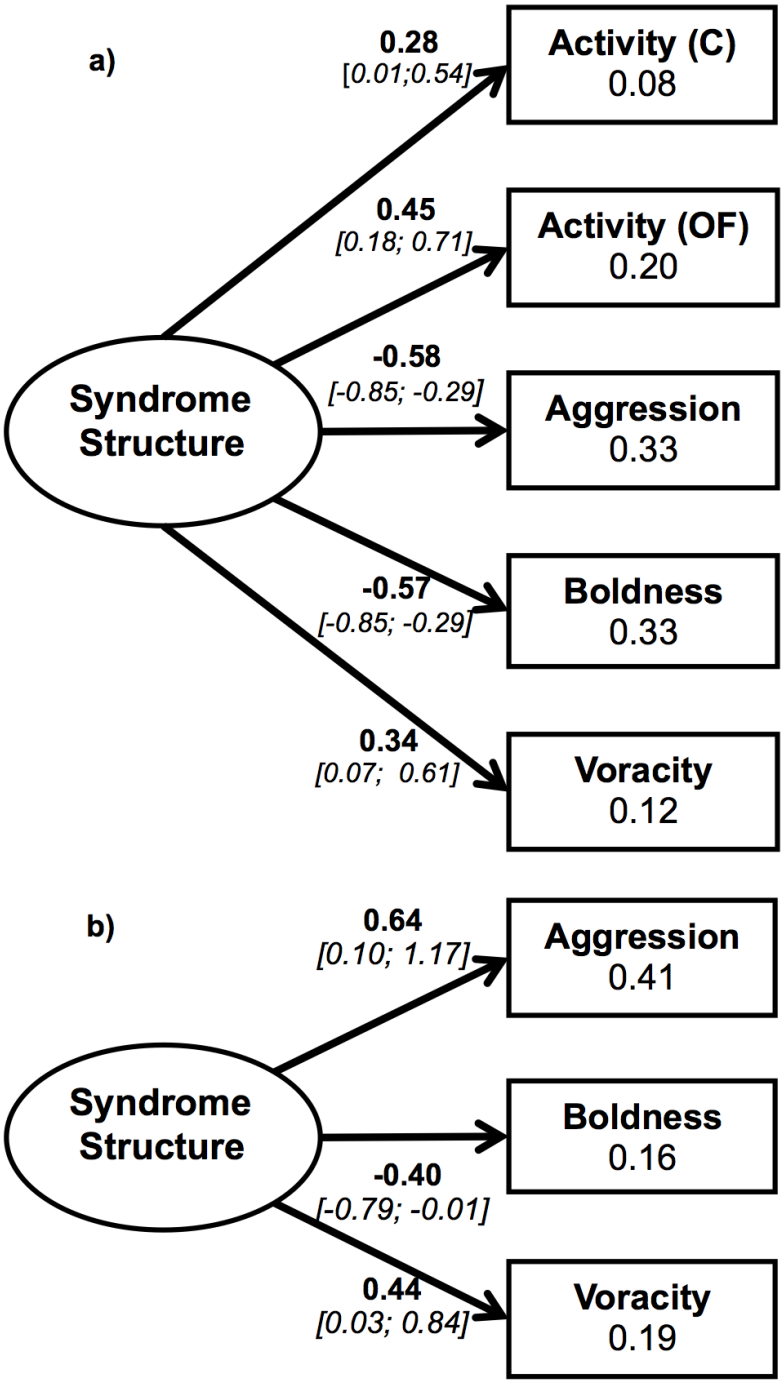

Fig. 2-4: Path coefficients for best models of syndrome structure in the insecticide-free (a) and insecticide-treated (b) orchards. The number associated with arrows represent standardized coefficients. Numbers in brackets represent 95 % confidence intervals for each path coefficients and numbers in boxes correspond to the R^2 for a given behaviour (i.e., the **%** of variance explained by the latent variable for each behaviour).

2.6. Connecting Statement

The results from Chapter 2 revealed high variations in syndrome structure between the two spider populations as well as in their age structure. This led me to question whether the differences in syndrome structure could be an artefact due to the lack of adult stages in the insecticide-treated population. In Chapter 3, I aimed to understand the roles of developmental environment, sex and life-stages in the generation of behavioural correlations by focusing on the transition from subadult to adult life-stages.

Chapter 3: Ontogenic shifts in a behavioural syndromes of a jumping spider

Raphaël Royauté, Christopher M. Buddle & Charles Vincent

3.1. Abstract

Investigating behavioural syndrome variation across ontogeny helps understanding whether certain behavioural correlations are stage-specific or stay consistent through development. We used the jumping spider *Eris militaris* (Araneae: Salticidae) sampled from two Québec apple orchards and an F1 laboratory-reared population to test ontogenic effects on behavioural correlations. Spiders were reared into adulthood under laboratory conditions and were tested for activity (using climbing and open-field tests), aggression, boldness and voracity under standardized conditions at subadult and adult stages. We used Bayesian mixed models to estimate the heritability of behavioural traits and compare inter-stage repeatability between sex and rearing environment (field-collected and laboratory-reared). We tested for the presence of stage-specific behavioural correlations and compared these correlations between rearing environment and sex. We estimated the relative contribution of between and within-individual components to the total phenotypic correlation between behaviours. Heritability and inter-stage repeatability of behavioural traits ranged from low to moderate ($0.06 < h^2 < 0.21$; $0.10 < R < 0.36$) with open-field activity showing highest heritability and repeatability. In addition, inter-stage repeatability of activity traits was lower with laboratory-reared individuals. Ontogenic shifts in behavioural syndrome were detected during the transition from subadult to adult stages. Activity behaviours were significantly correlated at both stages ($0.24 < r < 0.32$). However, subadults showed negative correlations between activity and aggression and activity and boldness ($r \sim -0.15$), which shifted to positive activity-voracity and aggression - boldness correlations ($0.16 < r < 0.20$) as adults. In addition, behavioural correlations differed between rearing environments and sexes. Correlations at phenotypic level were mostly underpinned by within-individual components, indicating high behavioural plasticity through ontogeny. The only significant between-individual correlation was a negative correlation between activity and boldness ($r = -0.42$) and this correlation was more strongly expressed with field-collected ($r = -$

0.54) and male individuals (r = -0.37). Our results showed evidence for stage-specific correlations differing between sexes and rearing environment and indicates developmental plasticity and sex play an important role in the generation of behavioural syndromes in jumping spiders.

3.2. Introduction

The study of animal personality has involved a considerable research effort and focuses on understanding consistent individual variations in behaviour over time (personality traits) and across contexts (behavioural syndromes) (Sih et al. 2004a, b, Réale et al. 2007). Personality traits imply the existence of repeatable and heritable behavioural variation that can respond to natural selection (Dingemanse and Réale 2005). Behavioural correlations at the phenotypic level can be underpinned by genetic correlations, which in turn may constrain behavioural evolution (Dochtermann 2011, Dochtermann and Dingemanse 2013). However, behavioural syndromes are highly influenced by ecological gradients and factors such as predation pressure (Bell 2005, Dingemanse et al. 2007), competition (Dochtermann et al. 2012) or yearly fluctuations in resource availability (Dingemanse et al. 2004) may affect the direction and strength of behavioural correlations.

While our understanding of personality variation along ecological gradients has improved, a developmental perspective is lacking. Ontogeny is an important source of behavioural variation as many species display ontogenic shifts through the course of their development. Some behaviours may be more expressed at certain life-stages and selective pressures may vary between life-stages (Stamps and Groothuis 2010a, b). Conceptual advances have called for greater research effort in understanding variations in personality differences over ontogeny (e.g., pace of life syndrome, *sensu* Réale et al. 2010, see also Stamps and Groothuis 2010a, b, Groothuis and Trillmich 2011). However, while such approaches are increasingly included in personality studies (Niemelä et al. 2012b), data on consistency of behavioural syndromes over ontogeny are much more limited (but see Bell and Stamps 2004, Niemelä et al. 2012a, Sweeney et al. 2013b). Until recently, behavioural syndrome studies have often relied on "snapshot" approaches where several behavioural traits are measured, focusing on a unique life-stage or sex rather than tracking individuals' behaviours over multiple life-stages. Studies that

have included a developmental perspective on behavioural syndrome show mixed evidence for high consistency of behavioural syndromes over ontogeny. Taxa that undergo metamorphosis do display high consistency in personality traits and behavioural syndromes despite ontogenic niche shifts (e.g., damselflies: Brodin 2009, salamanders: Wilson and Krause 2012). However, behavioural correlations are sometimes more expressed at a specific life-stage (Bell and Stamps 2004) and can vary between sexes (Dingemanse et al. 2004) or developmental environments (Kralj-Fišer and Schneider 2012, Hedrick and Bunting 2013, Sweeney et al. 2013b).

Advances in statistical approaches can be used to shed light on syndrome consistency through ontogeny. In certain cases, correlations among traits may persist even though individual ranks are reshuffled over multiple measures (Bell and Stamps 2004, Bell and Sih 2007). Using variance-partitioning approaches derived from quantitative genetic and mixed modeling, one can split trait covariance into between and within-individual components (Dochtermann and Roff 2010, Dingemanse and Dochtermann 2013). The between-individual component gives information on how consistent behavioural correlations are over multiple behavioural measures and is underpinned by genetic variation. The within-individual component indicates correlated changes in behaviours over multiple measures due to behavioural plasticity. This approach has the advantage to estimate the relative contribution of consistent tendencies with trait plasticity on correlations at the phenotypic level within a single framework. This is particularly important since patterns of phenotypic correlations among behavioural traits often have weak effects ($r \sim 0.19$, reviewed in Garamszegi et al. 2012) and this may be due to between and within-individual correlations having opposite signs and therefore masking patterns of correlation at the phenotypic level (Dingemanse and Dochtermann 2013).

We used the jumping spider *Eris militaris* (Araneae: Salticidae) to investigate how personality varied across subadults and adult stages depending on rearing environment (field-collected or laboratory-reared) and sex. Previous work on this model showed variation in behavioural syndromes between two populations from insecticide-treated and insecticide-free orchards (Royauté et al. 2014). However, the two populations had strong differences in age structure, leading to question whether the differences in syndrome structure were due to ontogenic shifts. We ask the following questions: 1) Are behavioural traits of the jumping spider *E. militaris* heritable? 2) Does inter-stage repeatability of behavioural traits vary between rearing environment and sex? 3) Are there ontogenic shifts in behavioural syndromes? 4) What is the

relative contribution of correlations at the between-individual and within-individual levels to phenotypic correlations depending on rearing environment and sex?

3.3. Methods

3.3.1. Spider collection and rearing

Eris militaris spiders of all stages and sex were collected in two apple orchards from South-Eastern Québec (Agriculture and Agri-Food Canada's experimental farm in Frelighsburg: W45.0462, N-72.8565 and a commercial orchard in Dunham: W45.0885, N-72.8496, respectively, the insecticide-free and insecticide-treated orchards from Chapter 2). Spiders were collected by beating the foliage of apple trees and adjacent forest borders and brought back to the laboratory. Spiders were maintained in 11.5 × 8 cm cylindrical containers that included a plastic plant to lessen the effect of captivity (Carducci and Jakob 2000) and a small plastic straw retreat (L = 2.5 cm, ⌀ =1.2 cm). Water was provided ad lib using dental wadding inserted in an Eppendorf tube and spiders were fed weekly with a mixed diet of cabbage looper larvae (*Trichoplusia ni*), fruit flies (*Drosophila melanogaster and Drosophila hydei*) and domestic crickets (*Acheta domestica*). Field-collected adults (n = 28) were tested for behavioural correlation within 15 days of capture. Juvenile (n = 57) and sub-adult (n = 49) field-collected stages were reared to adulthood in the laboratory and tested for behavioural correlations at subadult and adult stages. We also established an F1 laboratory-reared population of 65 individuals in fall 2010 and tested these individuals at sub-adult and adult stages. This population was established by randomly pairing 24 males and females from each apple orchard population (insecticide-free population: 9 pairs, insecticide-treated population: 15 pairs).

3.3.2. Behavioural tests

We tested a total of 199 individuals for behavioural correlations between summer of 2010 and January 2012 and obtained repeated measures of behaviour at sub-adult and adult stages for 130 individuals. At any given stage, each individual was subjected to a series of four to five behavioural tests following the procedure outlined in Chapter 2: 1) climbing activity on a tree trunk, 2) activity in an open-field arena, 3) aggression with Mirror Image Stimulation (MIS), 4) boldness in front of a moving predator mimic and 5) voracity in prey capture. The climbing

activity test was removed in summer 2011 in order to reduce the testing period to 48h. Spiders were randomly assembled in groups of 10 to 12 individuals and were offered an adult fruit fly (*Drosophila melanogaster*) 12 h prior to the tests. Two tests were performed per day between 08:00 and 17:00. Three to four behavioural tests (i.e., open-field, MIS and predator mimic tests) were performed in a randomized sequence to avoid any bias due to winner and loser effects (Dochtermann 2010). In order to standardize satiety, the prey capture test was consistently performed last.

3.3.3. Statistical analyses

All analyses were conducted with R version 3.0.0 for Macintosh (R Development Core Team 2012). Behavioural data were $\log_{10}(x+1)$ transformed prior to analyses to comply with the assumption of normality and were expressed as standard deviation units.

3.3.3.1. Ontogenic shifts in behaviour and morphological atributes

We used linear mixed models in order to test for interactions between life-stage, rearing environment and sex with the package lme4 (Bates et al. 2012). Life-stages, population, rearing environments sex and their interactions as fixed effects. Morphological attributes (i.e., body-condition and body-size) were included as covariates and individuals were included as random effects. We tested the significance of each variable using likelihood ratio tests (Zuur 2009). Body condition was estimated using a residual index (Carducci and Jakob 2000) by fitting a linear mixed model with $\log_{10}$(body mass) as the dependant variable, $\log_{10}$(body size) as the predictor variable and individuals as the random effect with package lme4. This index gives a measure of fat reserves independently from the size of the spider. We used the same approach to compare morphological attributes between life-stages, population, rearing environment, sex and their interactions

3.3.3.2. Heritability of behavioural traits

We fitted animal models on each behavioural trait except for climbing activity, which was not recorded for F1 laboratory-reared individuals, in order to estimate heritability. We used Bayesian mixed models in the package MCMCglmm (Hadfield 2010, Wilson et al. 2010). This approach partitions the phenotypic variance (V_P) into additive genetic (V_A, derived from

pedigree information), between-individual (V_{BI}) and error variance (V_R). Heritability of behaviour can therefore be calculated as $h = V_A / V_P$, with $V_P = V_A + V_{BI} + V_R$. We specified Markov Chains Monte Carlo (MCMC) with 2.5×10^8 iterations, 500 000 iteration burn-in and a thinning interval of 1000. This yielded chains with a sample size of 2000 and low autocorrelation (<0.1). We included all significant fixed effects for each trait and added individuals and pedigree relationships as random effects. Models were fitted using a weakly informative prior where the phenotypic variance (scaled to standard deviation units) was split equally into additive genetic, between-individual and residual variance components (V = 1/3, n= 1), where V represents the variance and n the degree of belief (Hadfield 2010). We report the posterior mode and 95 % credible intervals (CI) for heritability and each variance component.

3.3.3.3. Inter-stage repeatability compared across rearing environments and sex

Repeatability is a measure of the extent of individual differences in behaviour, and can be calculated by partitioning the phenotypic variance into between and within-individual components. Behavioural data were expressed as standard-deviation units. For each behaviour we fitted a model including all significant terms in order to avoid over-confident estimates of repeatability (Nakagawa and Schielzeth 2010), and individuals as random effects. Models were fitted using a weakly informative prior where the phenotypic variance was split equally between the between-individual (V_{BI}) and residual (i.e., within-individual, V_{WI}) variance components (V = 1/2, n= 1). Inter-stage repeatability was estimated across groups (i.e., rearing environments and sexes) by comparing the Deviance Information Criterion (DIC) of a model where the random variance components were equal across groups and a model where individual and residual variances differed across groups (Dingemanse and Dochtermann 2013). Lower DIC indicates support for one model over another. We used the following criteria to judge significance: ΔDIC<0: no support for differences in repeatability between groups, ΔDIC< 2: no to low support, ΔDIC>2: moderate support, ΔDIC > 4: strong support (Teplitsky et al. 2011). To ease the estimation of individual variance components, we directly specified heterogeneous random variances per group rather than using the multivariate approach described in Dingemanse and Dochtermann (2013). Repeatability was calculated as the posterior mode of $R = V_{BI} / (V_{BI} + V_{WI})$ along with 95% CI.

3.3.3.4. Behavioural correlations over ontogeny compared across rearing environments and sex

We first tested whether behavioural correlations at the phenotypic level varied between groups over ontogeny. We created 8 datasets by subdividing our data per group at each life-stage (i.e., correlations per life-stage and rearing environment, per life-stage and sex) and estimated the phenotypic correlation for each dataset. We fitted a Bayesian multi-response model on each dataset that included all behavioural traits as response variables and all significant fixed effects as dependent variable to estimate the phenotypic correlation based on residual correlations. All models were fitted using the same specification as above and using a non-informative inverse gamma prior (V = diag(5); n= 4.002). Climbing activity was not recorded for laboratory-reared individuals and had lower sample size. We therefore removed this behaviour for correlation comparisons between rearing environments (the prior was then adjusted to V = diag(4); n= 3.002). We report the posterior mode and 95 % CI for each behavioural correlation in order to judge the direction (i.e., sign), strength (i.e., value) and precision (i.e., width of the CI) of each correlation.

When repeated measures are taken on multiple traits, the phenotypic covariance may be split into between and within-individual (or error) components. A strong between-individual covariance indicates correlations between the repeatable components of behaviour and is indicative of a consistent correlation over time. Within-individual covariance represents correlated changes in behaviour attributable to phenotypic plasticity or error correlation. To estimate between and within-individual covariance across group, we used the Bayesian approach outline above and added individuals as random effects (Dingemanse and Dochtermann 2013). For each pair of behaviour, we tested three models: a full model where both between and within-individual covariances were estimated, a model where between-individual covariance was constrained to be null and a model where within-individual covariance was constrained to be null (Ferrari et al. 2013). All models were fitted using the bivariate form for the inverse gamma prior (V = diag(2); n= 1.002). We compared the DICs between models and used the same guideline as above in order to judge the significance of each covariance component. We report the posterior mode and 95 % CI for between (r_{BI}), within-individual (r_{WI}) and total phenotypic (r_P) correlations. The phenotypic correlation was calculated using the following formula (described in Dingemanse and Dochtermann 2013):

$$r_{Px,Py} = r_{BIx,y} \times \sqrt{R_x \times R_y} + r_{WIx,y} \times \sqrt{(1 - R_x) \times (1 - R_y)}$$

where $r_{Px,Py}$ represents the phenotypic correlation between behavioural traits x and y, $r_{BIx,y}$ and $r_{WIx,y}$ represent their between and within-individual correlations respectively, and R_x, R_y represents the repeatability for trait x and y.

3.4. Results

3.4.1. Ontogenic shifts in average behaviour

All behaviours, with the exception of climbing activity, showed substantial increase over ontogeny (Fig. 3-1, Table 3-1). A significant influence of rearing environment was also found for open-field activity and voracity. Open-field activity had a significant rearing environment × sex interaction ($p < 0.05$), with females showing a steeper decline in activity when reared in the laboratory than males (average quadrats/min ± [CI]; females: field-collected = 5.42 ± [4.95; 5.88], laboratory-reared = 3.99 ± [3.32; 4.66]; males: field-collected = 5.30 ± [4.70; 5.90], laboratory-reared = 4.62 ± [3.80; 5.43]). Field-collected individuals increased their voracity when adults (average prey captured ± [CI]; subadults = 3.11 ± [2.76; 3.47]; adults: = 4.57 ± [4.28; 4.96]), while no such effect was noticed for laboratory-reared individuals (subadults: = 2.30 ± [1.84; 2.76]; adults: 2.33 = ± [1.76; 2.90]) (rearing × life-stage interaction $p < 0.01$). We also noticed a significant interaction between population and rearing environment with voracity ($p < 0.01$). Laboratory-reared individuals had a steeper decline in voracity in the insecticide-treated population compared to the insecticide-free population (insecticide-free: field-collected = 3.36 ± [3.02; 3.07], laboratory-reared = 2.48 ± [1.88; 3.08]; insecticide-treated: field-collected = 4.11 ± [3.71; 4.51], laboratory-reared = 2.15 ± [1.72; 2.58]). Body-condition showed no difference over ontogeny for the insecticide-free orchard but increased in the insecticide-treated population (population × site interaction $p < 0.05$) (Table A2-1). As expected, body-size increased over ontogeny and growth did not vary between population, rearing environment or sex (all interaction terms with life-stage $p > 0.05$). However, the insecticide-treated population had smaller body-size on average ($p < 0.05$). Laboratory-reared males were smaller compared to

field-collected males while females showed no variation between rearing environments (rearing × sex interaction $p < 0.05$).

3.4.2. Heritability and repeatability of behavioural traits

Heritability was low for all behaviours ($h^2 < 0.25$) with open-field activity traits showing highest estimate ($h^2 = 0.21$) (Table 3-2). Inter-stage repeatability of behaviour was moderate to low, and ranged between 10 up to 36 % (Fig. 3-2). We found strong support for significant differences in repeatability of open-field activity between field-collected and laboratory-reared individuals (field-collected: $R = 0.36 \pm [0.21; 0.57]$; laboratory-reared: $R = 0.19 \pm [0.06; 0.43]$, $\Delta DIC > 21$). Moderate differences in repeatability were detected for boldness between sexes (females: $R = 0.10 \pm [0.05; 0.25]$; males: $R = 0.13 \pm [0.04; 0.38]$, $\Delta DIC > 3$) (Table A2-2).

3.4.3. Ontogenic shifts in behavioural correlations

We found evidence for shifts in behavioural syndromes over ontogeny as demonstrated by changes in phenotypic correlations from subadult to adult stages (Table 3-3). The correlation between activity traits was the only one to remain stable between life-stages (sub-adults: $r_P = 0.32 \pm [0.04; 0.51]$, adults: $r_P = 0.24 \pm [-0.06; 0.46]$). The open-field activity - boldness correlation was only expressed with subadults (subadults: $r_P = -0.17 \pm [-0.36; -0.03]$, adults: $r_P = -0.05 \pm [-0.23; 0.14]$). Correlations between activity and voracity were stronger in adult stages (climbing activity - voracity, sub-adults: $r_P = 0.11 \pm [-0.14; -0.26]$, adults: $r_P = 0.21 \pm [-0.02; 0.43]$; open-field activity - voracity, subadults: $r_P = 0.04 \pm [-0.11; 0.20]$, adults: $r_P = 0.15 \pm [-0.05; 0.32]$). We also found evidence for strong group × life-stage interactions with respect to correlation strength (Fig. 3-3). The correlation between activity traits was stronger in females (females: $r_P > 0.35$; males: $0.02 < r_P < 0.20$) and correlations between activity and voracity were stronger with males (females: $-0.10 < r_P < 0.10$; males: $0.20 < r_P < 0.34$). The open-field activity - boldness correlation was more strongly expressed for field-collected individuals independently of the life-stage (subadults: $r_P = -0.41 \pm [-0.57; -0.13]$; adults: $r_P = -0.22 \pm [-0.40; 0.00]$). Finally, the negative correlation between boldness and voracity found for subadults did not vary between sexes, but was mostly expressed by field-collected individuals (field-collected: $r_P = -0.38 \pm [-0.56; -0.22]$; laboratory-reared: $r_P = 0.11 \pm [-0.18; 0.38]$).

3.4.4. Patterns of correlation at between and within-individual levels

We found a stronger influence of the within-individual correlations when comparing the relative contribution of between and within-individual components to the phenotypic covariance. This indicates behavioural correlations were poorly conserved across ontogeny as confirmed by low overall phenotypic correlations ($r_P < 0.2$) (Table 3-4). Only correlations between climbing and open-field activity ($r_{BI} = -0.23 \pm [-0.57; 0.39]$, $\Delta DIC > 2$) and open-field activity - boldness ($r_{BI} = -0.42 \pm [-0.72; -0.01]$, $\Delta DIC > 8$) showed substantial consistency over ontogeny, as indicated by the strength of their between-individual correlation. At the within-individual level, we found positive correlations between activity and voracity behaviours (climbing activity - open-field activity: $r_{WI} = 0.27 \pm [0.07; 0.52]$, $\Delta DIC > 21$; climbing activity - voracity: $r_{WI} = 0.27 \pm [0.03; 0.43]$, $\Delta DIC > 12$) and a negative correlation between open-field activity and aggression ($r_{WI} = -0.11 \pm [-0.31; 0.11]$, $\Delta DIC > 2$). This indicates that individuals who increased their activity levels over development also increased in voracity, and individuals with higher activity as adults tended to decrease their aggression.

We also found evidence for high variability in correlation strength when breaking down these patterns per rearing environment and sex (Table A2-3). Laboratory rearing seemed to erode behavioural correlations as phenotypic correlations were only detected for field-collected individuals ($r_P \pm$ [CI]; open-field activity - boldness, field-collected: $-0.23 \pm [-0.47; 0.15]$, laboratory-reared: $0.00 \pm [-0.22; 0.21]$; open-field activity - voracity, field-collected: $0.17 \pm [0.03; 0.31]$, laboratory-reared: $0.02 \pm [-0.21; 0.18]$; boldness - voracity, field-collected: $-0.19 \pm [-0.35; 0.06]$, laboratory-reared: $-0.01 \pm [-0.22; 0.20]$). Similarly, the open-field activity - boldness correlation at the between-individual level was absent for laboratory-reared individuals (field-collected: $r_{BI} = -0.54 \pm [-0.76; -0.01]$, $\Delta DIC > 9$; laboratory-reared: $r_{BI} = -0.13 \pm [-0.69; 0.42]$, $\Delta DIC = -0.15$) and more behavioural traits showed significant within-individual correlations in the laboratory environment ($r_{WI} \pm$ [CI]; open-field activity - aggression, field-collected: $-0.19 \pm [-0.36; 0.01]$, $\Delta DIC > 5$; laboratory-reared: $-0.04 \pm [-0.36; 0.39]$, $\Delta DIC > 5$; aggression - boldness, field-collected: $0.02 \pm [-0.15; 0.26]$, $\Delta DIC < 1$; laboratory-reared: $-0.20 \pm [-0.47; 0.15]$, $\Delta DIC > 3$; aggression- voracity, field-collected: $0.01 \pm [-0.19; 0.20]$, $\Delta DIC < 1$, laboratory-reared:$-0.21 \pm [-0.51; 0.18]$, $\Delta DIC > 7$).

Males and females showed differences in behavioural correlations as well. Phenotypic correlations were complex in males with a mixture of positive (climbing activity - voracity: $r_P =$

0.23 ± [0.02; 0.47]; open-field activity - voracity: r_P = 0.23 ± [0.02; 0.37]) and negative (open-field activity - boldness: r_P = -0.16 ± [-0.38; -0.02]; boldness - voracity: r_P = -0.18 ± [-0.36; -0.01]) associations between behavioural traits. In contrast, only a positive correlation involving climbing and open-field activity was detected for females (r_P = 0.34 ± [0.10; 0.51]), while all other correlations remained <0.10. Males also showed stronger inter-stage consistency in their correlation between open-field activity and boldness at the between-individual level (females: r_{BI} = -0.17 ± [-0.64; 0.31], ΔDIC < 1; males: r_{BI} = -0.37 ± [-0.79; 0.15], ΔDIC > 3). At the within-individual level, strong correlations were detected between activity, aggression and voracity in females (climbing activity - open-field activity: r_{WI} = 0.39 ± [0.18; 0.65], ΔDIC > 23; aggression - voracity: r_{WI} = -0.20 ± [-0.47; 0.15), ΔDIC > 3) and between climbing activity, aggression, boldness and voracity in males (climbing activity - boldness: r_{WI} = 0.27 ± [-0.31; 0.56], ΔDIC > 6; climbing activity - voracity: r_{WI} = 0.34 ± [0.04; 0.60], ΔDIC > 9; aggression - boldness: r_{WI} = -0.28 ± [-0.46; 0.10], ΔDIC > 5).

3.5. Discussion

Our objective was to determine the consistency of behavioural traits and their correlations over development and examine subsequent influence of rearing environment and sex. Most behavioural traits showed substantial shifts between subadult and adult life-stages, which corresponded to strong shifts in behavioural correlation between life stages and low heritability and repeatability of behavioural traits. Behavioural repeatability and correlations showed substantial differences between groups. Within-individual correlations provided the strongest contribution to phenotypic correlations, indicating developmental plasticity plays a strong role in shaping behavioural syndromes with *E. militaris*. These results highlight the importance of adopting a developmental perspective when studying behavioural syndromes and indicate that some correlations are stage specific and vary depending on rearing environment and sex.

With the exception of climbing activity, all tested behaviours showed an increase in average value from subadult to adult stages. Adult spiders were quicker to explore new environments, had higher aggressive and bold tendencies and captured more prey. In the case of voracity we also found a strong influence of the rearing environment, as no inter-stage differences in voracity was found for laboratory-reared individuals. Developmental shifts in

behaviour are common in nature and can be the result of stage-specific selective pressures or cognition and learning (reviewed in Stamps and Groothuis 2010a, b). A similar study with the funnel-web spider *Agelenopsis pennsylvanica* reported a decrease in aggressive and bold tendencies with more mature (e.g., subadult) life-stages (Sweeney et al. 2013b), indicating potential asset protection as individuals build-up energy reserves through their development (Mangel and Clark 1988, Clark 1994, Luttbeg and Sih 2010). We found the opposite trend in our study and this may be due to high payoff for aggressive and bold behaviour as sexual maturity occurs. An alternative explanation could be that our behavioural assays for aggression and boldness rely on high visual accuracy and these capacities may be more limited at subadult stages.

Heritability and repeatability of behavioural traits was relatively low compared to other spider studies ($0.2 < h^2 < 0.4$; (Pruitt and Riechert 2009b, Kralj-Fišer and Schneider 2012, Sweeney et al. 2013b) and repeatability set the upper bound to heritability of behavioural traits (Hoffmann 2000, Dohm 2002, Bell et al. 2009). Low heritability can be due to erosion of additive genetic variance (stabilizing or directional selection) or to strong environmental variances (Barton and Turelli 1989, Roff 1997). Open-field activity was the most consistent trait over ontogeny - with heritability and repeatability estimates > 0.2 - indicating potential for response to selective pressures (Dochtermann 2011, Dochtermann and Dingemanse 2013). The repeatability of this trait was also higher for field-collected individuals, a finding largely consistent with other personality studies (see meta-analysis by Bell et al. 2009). There was however poor evidence of differences in repeatability between sexes. This finding contrasts with other arthropod studies showing stronger inter-stage repeatability of boldness in female field crickets (*Gryllus integer*) (Hedrick and Kortet 2012). The fact that activity traits had highest repeatability and heritability contrasts with previous work on behavioural syndromes and personality traits of spiders. A behavioural syndrome between aggression and boldness is common in many spider species (*Anelosimus studiosus*: Pruitt et al. 2008, *Agelenopsis aperta*: Riechert and Hedrick 1993, *Agelenopsis pennsylvanica*: Sweeney et al. 2013b, *Dolomedes triton*: Johnson and Sih 2005, 2007, *Larinoides sclopetarius*: Kralj-Fišer et al. 2012, reviewed in Pruitt and Riechert 2012) and a heritable basis for these traits have been demonstrated for at least four of these species (*A. aperta, A. pennsylvanica, A. studiosus*, *L. sclopetarius*). However, these species are sit-and-wait predators that rely on webs or ambush strategies while activity plays a

major role in the foraging strategies of jumping spiders since most species stalk their prey (Jackson and Pollard 1996). In addition, low heritability of behavioural traits does not necessarily imply low genetic covariance. For example, Taylor et al. (2012) demonstrated strong genetic correlations between activity, aggression and docility in red squirrels despite heritability estimates < 0.15. Such approaches require large sample sizes however and the pedigree information obtained in our study prevents a reliable estimation of genetic correlations, although patterns of correlation at the between and within-individual level remained possible.

Our study is one of the first to provide information on how phenotypic correlations are organized at between and within-individual levels for behavioural traits commonly correlated in spiders while using a developmental approach. The few studies that have investigated the consistency of behavioural syndromes over multiple life-stages report no strong consensus and developmental consistency of behavioural syndrome varies widely between taxa. For example, damselflies and salamanders showed consistent correlations across larval and adult stages for behaviours related to activity and boldness (Brodin 2009, Wilson and Krause 2012). In contrast, studies conducted on threespined stickelbacks (Bell and Stamps 2004) or spiders (Sweeney et al. 2013b) showed evidence for stage-specific correlations and/or high individual plasticity involved in the generation of behavioural correlations. Yet these studies focus almost exclusively on patterns of correlations at the phenotypic level for each life-stage and do not describe whether these correlations are sustained through correlations between repeatable components of behaviour (i.e., their between individual correlations) or through a reshuffling of ranks due to developmental plasticity (i.e., their within-individual correlations). We suggest that the decomposition of behavioural correlations into between and within-individual components can be a valuable tool in order to better understand how behavioural syndromes are sustained over the course of ontogeny.

In the present study, behavioural correlations in the species *E. militaris* were mostly sustained through high developmental plasticity as the within-individual correlations contributed the most to patterns of phenotypic correlations among behavioural traits and since in many instances, behavioural correlations were found to be stage-specific. These results are corroborated through several lines of evidence. First, climbing and open-field activity were the only traits with significant correlations at both stages. Subadults showed negative correlations between open-field activity, boldness and voracity while positive correlations between activity

and voracity were detected in adults. Second, the total phenotypic correlation was systematically of the same sign as the within-individual component, indicating a stronger influence of the within-individual component relative to the between-individual component. The only strong between-individual correlation was a negative correlation between open-field activity and boldness, indicating more active individuals took less risk in front of predation threats independently of life-stage. Moderate heritability in open-field activity suggests potential influence of selective pressures or trade-offs between foraging activity and predator safety (Luttbeg and Sih 2010). If this correlation is underpinned by strong genetic covariance, this could constrain the capacity of these two traits to evolve independently (Dochtermann and Roff 2010, Dochtermann and Dingemanse 2013). Third, the patterns of correlations showed strong differences depending on rearing environments and sex. The open-field activity-boldness correlation was stronger in field-collected individuals than the F1 laboratory-reared population and was more important in males. At the phenotypic level, the correlations found for field-collected individuals were eroded for F1 laboratory-reared individuals, a finding consistent with studies conducted on other spider species (Sweeney et al. 2013b), and crickets (Hedrick and Bunting 2013). Similarly, females only displayed a positive correlation between the two activity traits while a more complex syndrome structure was found for males.

Our results provide information on the forces generating behavioural syndromes in a jumping spider, a group that have been poorly studied up to now (Sweeney et al. 2013b, Royauté et al. 2014). We showed that the population differences between the insecticide-free and insecticide-treated orchards from Royauté et al. (2014) may, in part, be due to ontogenic shifts and sexual differences in syndrome structure coupled with unbalanced age structure in the insecticide-treated orchard rather than selection or alteration of certain behavioural types through insecticidal applications. This previous study showed differences in the distribution of life-stages between populations from an insecticide-treated population, composed mostly of juvenile individuals, and an insecticide-free population, where all life-stages were found. We reported stronger correlation in the insecticide-free population involving activity and voracity ($r \sim 0.30$) and aggression and boldness ($r \sim 0.40$), while the aggression– boldness correlation was reversed in the insecticide-treated population ($r \sim -0.25$). In the present study, the aggression-boldness correlation was only expressed in laboratory-reared subadults ($r \sim -0.40$). This confirms in part that a negative aggression-boldness syndrome may be a property of early developmental stages,

as reported with individuals captured in the insecticide-treated orchard in Royauté et al. (2014). However, we did not found any evidence that this correlation shifts into a positive correlation in adult stages, and we cannot rule out that other environmental factors may explain part of the differences in syndrome structure between populations (e.g., alteration of conspecific or prey densities, higher mortality in the insecticide-treated environment). Investigating how correlations at the phenotypic level were sustained by between and within-individual correlations revealed patterns of correlations that were not observable when focusing solely on correlations at the phenotypic level, as was done in the previous chapter. The correlation between activity and boldness was poorly expressed at the phenotypic level in both populations ($r_P \sim -0.15$; Royauté et al. 2014). Here, we found a significant activity-boldness correlation at the between-individual level, indicating this correlation was sustained across the transition from subadult to adult life-stages ($r_{BI} \sim -0.40$) while a low within-individual component ($r_{WI} \sim -0.10$) accounts for the low size effect of the correlation at the phenotypic level ($r_P \sim -0.10$).

We demonstrated that behavioural correlations in a jumping spider were stage-specific, differed between rearing environment and sex. Activity showed substantial inter-stage repeatability and moderate heritability, indicating consistent between-individual differences over ontogeny for this trait. Using novel tools derived from quantitative genetic studies, we showed that behavioural correlations were highly plastic and were influenced both by rearing environment and sex as indicated by the strong within-individual component of the covariance between most traits. This research indicates that moderately repeatable and heritable traits – such as activity - can be associated with more developmentally plastic traits (e.g., aggression, boldness and voracity) and, in certain cases these correlations are maintained over ontogeny for field-collected individuals. We also stress the influence of variation in developmental environment as a potent factor for shaping the correlation between behavioural traits over the course of ontogeny for a spider species evolving in highly disturbed ecosystems.

Table 3-1: Results of linear mixed model analyses on behavioural traits. Bold values indicate significance at $\alpha = 0.05$ based on likelihood ratio tests (LRT).

Trait	Term	Coefficient ± SE	LRT	p
Climbing Activity	Intercept	-0.90 ± 0.67		
	Body-Condition	0.68 ± 0.47	2.06	0.15
	Body-Size	-0.40 ± 1.44	0.08	0.78
	Life-Stage (adults)	0.24 ±0.26	1.45	0.23
	Population (insecticide-treated)	**-0.36 ± 0.24**	**5.34**	**<0.05**
	Sex (males)	0.36 ± 0.30	0.06	0.81
	Life-Stage × Population	-0.02 ± 0.29	0.00	0.95
	Life-Stage × Sex	-0.65 ± 0.32	3.50	0.06
	Population × Sex	-0.06 ± 0.36	0.03	0.87
Open-Field Activity	Intercept	-1.26 ± 0.50		
	Body-Condition	**0.91 ± 0.36**	**6.76**	**<0.01**
	Body-Size	0.19 ± 0.85	0.05	0.82
	Life-Stage (adults)	**0.52 ± 0.19**	**12.72**	**<0.0005**
	Population (insecticide-treated)	-0.09 ± 0.18	0.51	0.47
	Rearing-Environment (laboratory-reared)	**-0.58 ± 0.23**	**15.82**	**<0.0001**
	Sex (males)	0.07 ± 0.20	0.85	0.36
	Life-Stage × Population	0.14 ± 0.20	0.52	0.47
	Life-Stage × Rearing	-0.34 ± 0.20	2.92	0.09
	Life-Stage × Sex	-0.12 ± 0.20	0.37	0.54
	Population × Rearing-Environment	0.04 ± 0.25	0.03	0.85
	Population × Sex	-0.20 ± 0.25	0.68	0.41
	Rearing-Environment × Sex	**0.54 ± 0.26**	**4.47**	**<0.05**
Aggression	Intercept	-0.92 ± 0.66		
	Body-Condition	0.59 ± 0.46	1.71	0.19
	Body-Size	**2.02 ± 1.02**	**3.96**	**<0.05**
	Life-Stage (adults)	**0.43 ± 0.24**	**10.61**	**<0.005**
	Population (insecticide-treated)	0.19 ± 0.23	0.24	0.62
	Rearing-Environment (laboratory-reared)	0.08 ± 0.30	0.79	0.37
	Sex (males)	**-0.26 ± 0.25**	**4.20**	**<0.05**
	Life-Stage × Population	-0.25 ± 0.26	0.98	0.32
	Life-Stage × Rearing	-0.28 ± 0.28	1.03	0.31
	Life-Stage × Sex	0.17 ± 0.27	0.45	0.50
	Population × Rearing-Environment	0.04 ±0.31	0.02	0.88
	Population × Sex	0.05 ± 0.31	0.03	0.87
	Rearing-Environment × Sex	-0.18 ± 0.32	0.33	0.57
Boldness	Intercept	-0.71 ± 0.56		
	Body-Condition	0.28 ± 0.41	0.51	0.48

Trait	Term	Coefficient ± SE	LRT	p
Boldness	Body-Size	-1.69 ± 1.13	2.31	0.13
	Life-Stage (adults)	**0.41 ± 0.24**	**10.84**	**<0.001**
	Population (insecticide-treated)	0.12 ± 0.21	0.10	0.75
	Rearing-Environment (laboratory-reared)	0.06 ± 0.27	0.08	0.78
	Sex (males)	0.13 ± 0.23	1.01	0.32
	Life-Stage × Population	-0.30 ± 0.26	1.45	0.23
	Life-Stage × Rearing	0.21 ± 0.27	0.65	0.42
	Life-Stage × Sex	0.12 ± 0.25	0.23	0.63
	Population × Rearing-Environment	0.03 ± 0.27	0.02	0.90
	Population × Sex	-0.47 ± 0.28	2.88	0.09
	Rearing-Environment × Sex	0.28 ± 0.27	1.16	0.28
Voracity	Intercept	-0.94 ± 0.49		
	Body-Condition	0.57 ± 0.35	2.78	0.10
	Body-Size	-1.20 ± 0.93	1.72	0.19
	Life-Stage (adults)	**0.75 ± 0.21**	**13.80**	**<0.0005**
	Population (insecticide-treated)	0.28 ± 0.18	1.48	0.22
	Rearing-Environment (laboratory-reared)	**-0.08 ± 0.22**	**28.75**	**<0.0001**
	Sex (males)	-0.11 ± 0.20	1.73	0.19
	Life-Stage × Population	-0.14 ± 0.22	0.41	0.52
	Life-Stage × Rearing	**-0.62 ± 0.23**	**7.60**	**<0.01**
	Life-Stage × Sex	-0.38 ± 0.22	3.01	0.08
	Population × Rearing-Environment	**-0.62 ± 0.23**	**7.49**	**<0.01**
	Population × Sex	0.27 ± 0.23	1.41	0.24
	Rearing-Environment × Sex	0.21 ± 0.24	0.83	0.36

Table 3-2: Heritability (h^2) and variance components of behavioural traits (posterior mode ± credible intervals (CI)). V_A: additive genetic variance, V_{BI}: between individual variance, V_R: residual variance.

Trait	h^2	Lower CI	Upper CI	V_A	Lower CI	Upper CI	V_{BI}	Lower CI	Upper CI	V_R	Lower CI	Upper CI
Open-Field Activity	0.21	0.07	0.35	0.15	0.05	0.29	0.07	0.03	0.22	0.53	0.42	0.67
Aggression	0.06	0.02	0.20	0.06	0.02	0.20	0.08	0.03	0.27	0.73	0.57	0.93
Boldness	0.08	0.03	0.18	0.07	0.03	0.20	0.08	0.02	0.19	0.82	0.66	0.99
Voracity	0.07	0.03	0.19	0.07	0.02	0.17	0.06	0.02	0.16	0.68	0.55	0.83

Table 3-3: Phenotypic correlation between climbing activity, open-field activity, aggression, boldness and voracity compared across subadult (lower diagonal) and adult (upper diagonal) stages, posterior mode ± [95 % credible intervals (CI)]. Bold values indicate significant correlations based on overlap of 95 % CI with zero, bold italics indicate correlations with > of 90 of posterior estimates excluding zero. Numbers in parentheses indicate the number of pair-wise observations for a given correlation coefficient estimate.

	Climbing Activity	Open-Field Activity	Aggression	Boldness	Voracity
Climbing Activity	-	***0.24*** (75)	-0.01 (66)	***0.18*** (69)	-0.11 (75)
		[-0.06; 0.46]	[-0.22; 0.27]	[-0.07; 0.43]	[-0.32; 0.30]
Open-Field Activity	**0.32** (84)	-	0.06 (104)	-0.05 (119)	***0.15*** (129)
	[0.04; 0.51]		[-0.15; 0.28]	[-0.23; 0.14]	[-0.05; 0.32]
Aggression	-0.16 (62)	-0.16 (125)	-	0.09 (96)	-0.18 (103)
	[-0.37; 0.07]	[-0.43;0.06]		[-0.10; 0.33]	[-0.34; 0.08]
Boldness	-0.15 (79)	**-0.17** (147)	0.06 (108)	-	-0.06 (130)
	[-0.34; 0.13]	[-0.36; -0.03]	[-0.25; 0.13]		[-0.22; 0.14]
Voracity	0.11 (85)	0.04 (169)	0.03 (126)	**-0.25** (148)	-
	[-0.14; 0.26]	[-0.11; 0.20]	[-0.13; 0.21]	[-0.41; -0.09]	

Table 3-4: Between (r_{BI}), within-individual (r_{WI}) and phenotypic (r_P) correlations between climbing activity, open-field activity, aggression, boldness and voracity. Between and within-individual correlations: Bold indicates support for a model accounting for correlation between traits (model 2) compared to the null model (model 1) with ΔDIC > 4. Bold italics indicates support for model 2 with ΔDIC > 2. Phenotypic correlations: bold values indicate significant correlations based on overlap of 95 % CI with zero, bold italics indicate correlations with > of 90 of posterior estimates excluding zero.

Trait 1	Trait 2	r_{BI}	Lower CI	Upper CI	DIC	ΔDIC	r_{WI}	Lower CI	Upper CI	ΔDIC	r_P	Lower CI	Upper CI
Climbing Activity	Open-field Activity	***-0.23***	***-0.57***	***0.39***	***1166.06***	***2.45***	**0.27**	**0.05**	**0.52**	**21.69**	**0.13**	**0.00**	**0.33**
Climbing Activity	Aggression	0.00	-0.50	0.51	1084.53	-0.37	***-0.08***	***-0.26***	***0.16***	***3.36***	0.00	-0.21	0.12
Climbing Activity	Boldness	0.03	-0.48	0.50	1198.06	0.61	**0.02**	**-0.18**	**0.29**	**5.41**	0.02	-0.11	0.24
Climbing Activity	Voracity	-0.04	-0.58	0.38	1226.78	1.35	**0.27**	**0.03**	**0.43**	**12.81**	**0.18**	**0.00**	**0.31**
Open-field Activity	Aggression	-0.21	-0.56	0.29	1372.45	0.16	***-0.11***	***-0.31***	***0.11***	***2.52***	***-0.14***	***-0.25***	***0.04***
Open-field Activity	Boldness	**-0.42**	**-0.72**	**0.01**	**1486.78**	**8.15**	-0.05	-0.18	0.16	-1.01	***-0.11***	***-0.24***	***0.01***
Open-field Activity	Voracity	0.05	-0.36	0.49	1533.91	-0.65	0.09	-0.06	0.26	0.56	***0.13***	***-0.01***	***0.22***
Aggression	Boldness	-0.01	-0.49	0.43	1387.67	-0.48	-0.01	-0.19	0.16	1.25	0.00	-0.17	0.12
Aggression	Voracity	0.12	-0.46	0.45	1437.00	-0.28	-0.03	-0.19	0.15	1.45	-0.02	-0.16	0.10
Boldness	Voracity	-0.23	-0.59	0.30	1555.46	0.71	-0.16	-0.28	0.03	-0.27	**-0.13**	**-0.26**	**-0.02**

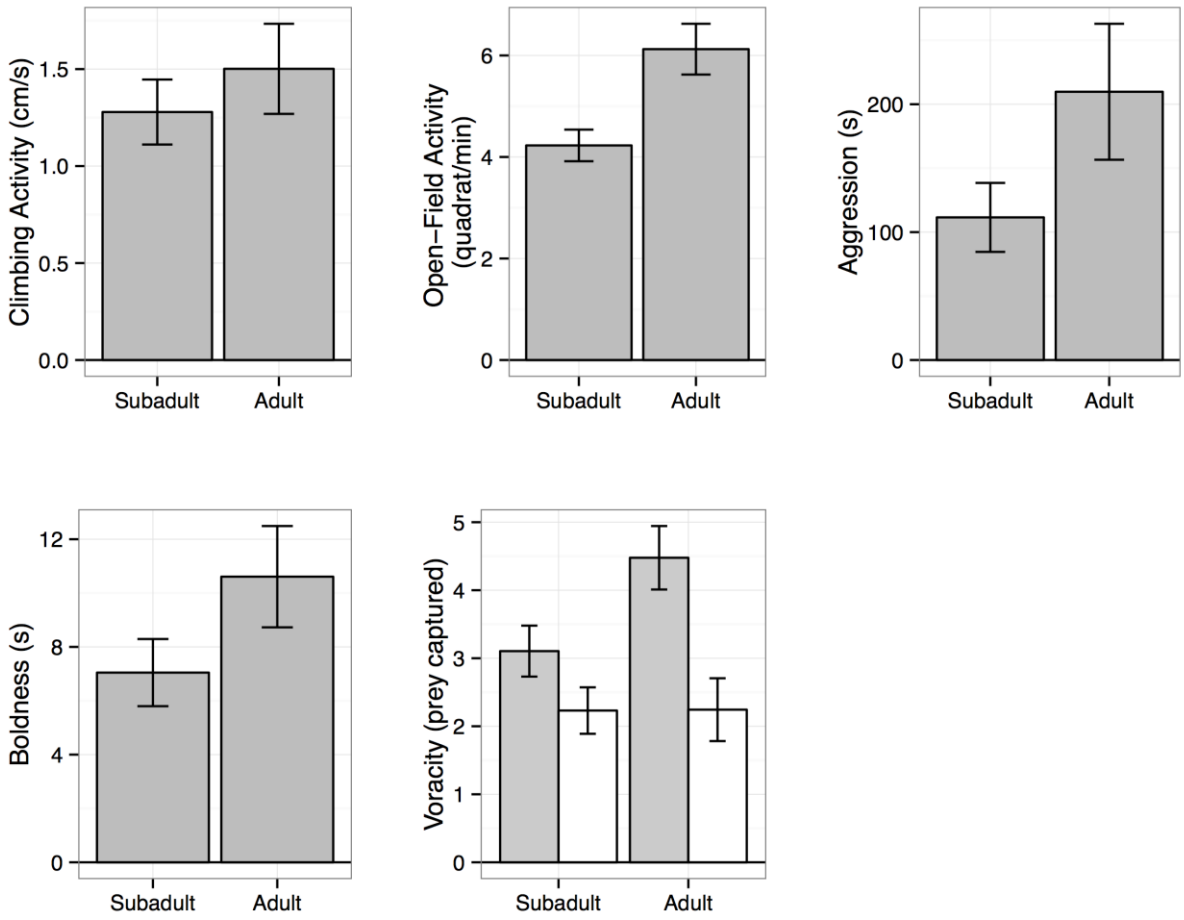

Fig. 3-1: Changes in average behaviour ± 95% CIs between subadult and adult life-stages. Inference is based on overlap of confidence intervals. Voracity: grey bars represent average values for field-collected individuals, white bars represent values for laboratory-reared individuals

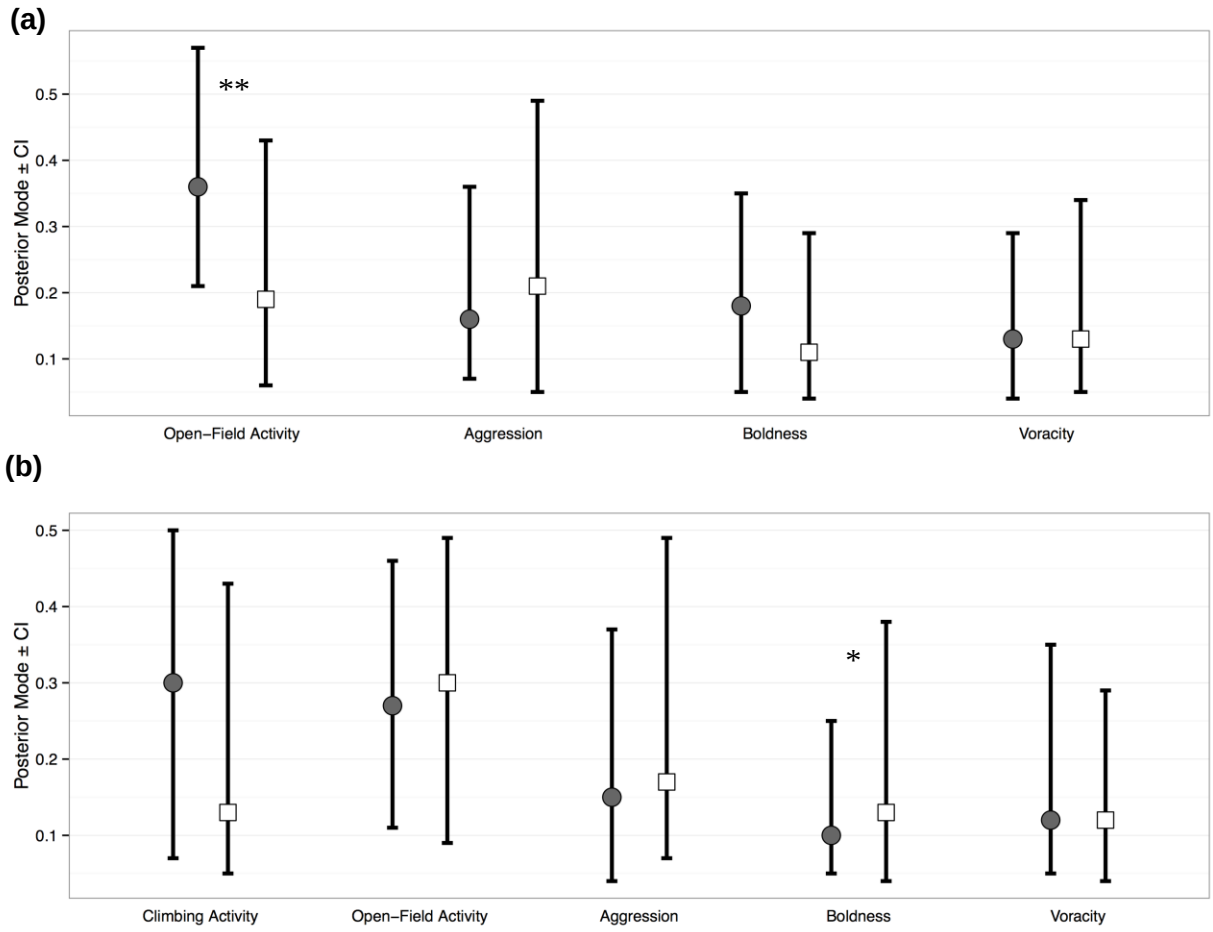

Fig. 3-2: Repeatability of behavioural traits (posterior modes ± credible interval) compared between rearing environments (field-collected: dark circles; laboratory-reared: white squares) (a) and sexes (females: white circles; males: dark squares) (b). Asterisks indicate support for differences in repeatability based on DIC comparison of a model where repeatability varies between groups and a model were repeatability is constrained to equality across groups. *ΔDIC > 2, ** ΔDIC > 4.

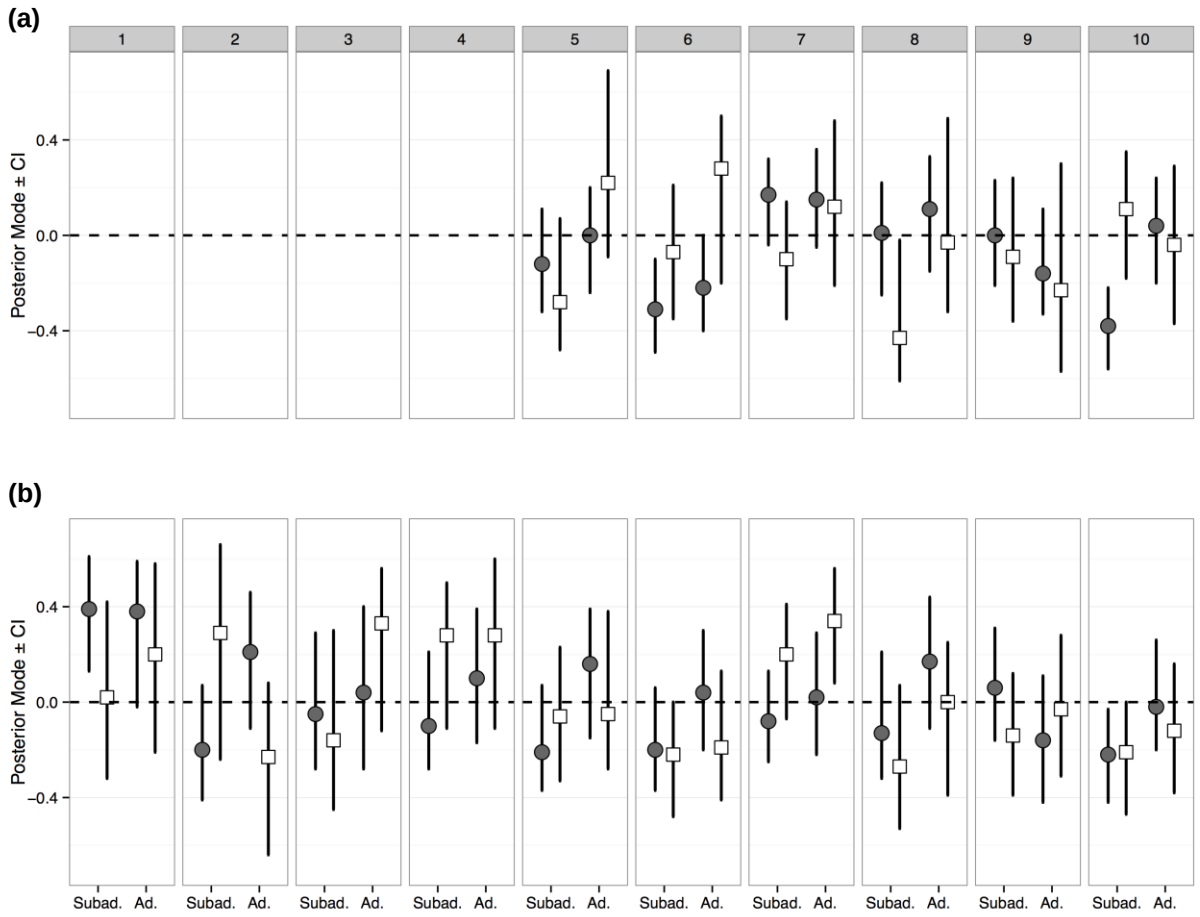

Fig. 3-3: Phenotypic correlations between climbing activity, open-field activity, aggression, boldness and voracity for subadult and adult stages compared across rearing environments (dark circles: field-collected, white squares: laboratory-reared) (a) and sexes (dark circles: females, white squares: males) (b).
1: Climbing Activity × Open-Field Activity, 2: Climbing Activity × Aggression,
3: Climbing Activity × Boldness, 4: Climbing Activity × Voracity,
5: Open-Field Activity × Aggression, 6: Open-Field Activity × Boldness,
7: Open-Field Activity × Voracity, 8: Aggression × Boldness, 9: Aggression × Voracity,
10: Boldness × Voracity.

3.6. Connecting Statement

The results from Chapter 3 indicated that developmental environment and sex had strong influence on the generation of behavioural correlations in *Eris militaris*. These results further confirm the hypothesis that the interpopulation variations in behavioural syndrome documented in Chapter 2 were more likely due to age structure difference between populations and developmental shifts in behavioural correlations than to differences in selective pressures or sublethal disruption of behavioural variation through insecticidal applications. Nonetheless, sublethal effects may be limited in duration. The time scale at which behavioural observations were conducted in Chapter 2 and 3 only allowed for partial characterization of sublethal disruption. A more direct approach through manipulation of insecticidal exposure was therefore required in order to test for effects of insecticidal exposure at sublethal doses on behavioural variation. In Chapter 4, I compared insecticide-treated with control groups at pre and post-exposure phases in order to determine the effects of sublethal exposure on the expression of personality traits linked to activity and foraging.

Chapter 4: Sublethal insecticidal exposure affects personality expression in a jumping spider

Raphaël Royauté, Christopher M. Buddle & Charles Vincent

4.1. Abstract

Many organisms are exposed to residues of insecticides, causing substantial modifications in their behaviour at sublethal doses, and threatening their persistence in agroecosystems. However, there are few studies about how behavioural variation at the individual level is affected by neurotoxic insecticides. Our objective was to determine whether sublethal exposure to an organophosphate insecticide affects the consistency of individual behaviour and disrupt behavioural correlations, in a jumping spider occurring in apple-orchards (*Eris militaris,* Araneae: Salticidae). We tested the effects exposure to a sublethal dose of phosmet (Imidan) on personality expression, using two standard personality assays: an open-field and a prey-capture test. Spiders were tested at pre and post-exposure phases. Half of the individuals received no exposure to the insecticide (control group). Average shifts in behaviour were detected for open-field activity but not for prey capture. Repeatability of distance travelled and attack number on prey decreased significantly in the insecticide-treated group, and females showed higher changes in behavioural correlations after insecticidal exposure. Our study calls for an increasing focus on individual behavioural variation when testing the effects of pesticides on non-targeted fauna.

4.2. Introduction

Agricultural systems are under pressure to increase food production while maintaining biodiversity, and the extensive use of pesticides represents a major threat for many organisms living in agroecosystems. Pesticide use has been linked to decline in birds (Krebs et al. 1999, Donald et al. 2001), pollinators (Brittain et al. 2010) and natural enemy populations (Geiger et al. 2010). In addition to direct mortality of non-targeted organisms, pesticidal effects may persist

well below lethal thresholds, provoking physiological and behavioural shifts (Desneux et al. 2007). For example, exposure to sublethal concentrations of neonicotinoids impairs navigation capacities in honey-bees, in turn affecting colony fitness (Henry et al. 2012). Exposure to the pyrethroid lambda-cyhalothrin can temporarily reduce orientation toward host-plant odour in the parasitoid *Aphidius ervi* (Hymenoptera: Braconidae) (Desneux et al. 2004a, b). In spiders, exposure to organophosphates is known to reduce courtship (Tietjen 2006) and caused shifts in circadian activity (Tietjen and Cady 2007). These studies, however, tend to focus on a single trait, and a broader behavioural assessment that encompasses a suite of traits is required to evaluate the full extent of sublethal disruption. Since behaviours are not equally affected by sublethal disruption (Desneux et al. 2007), using a multi-trait approach allows for a more robust estimation of the toxicity of insecticidal compounds and to better understand the consequences of insecticidal exposure for non-targeted fauna.

Advances in animal behaviour stresses the importance of considering individual behavioural variation in behavioural studies. Within a given species or population, individuals often show consistent behavioural tendencies, often referred to as "animal personalities" or "temperaments" (Réale et al. 2007). These tendencies are sometimes correlated across different behavioural contexts, and form behavioural syndromes (Sih et al. 2004a, b). For example, some individuals are more exploratory than others (Dingemanse et al. 2002) and take more risks in presence of predators (Wilson et al. 1994). Many non-mutually exclusive factors may act on the extent of individual behavioural differences, including predation pressure (Bell 2005, Dingemanse et al. 2007), population density (Dochtermann et al. 2012), parasitic load (Coats et al. 2010) or physiological mechanisms (Montiglio et al. 2012). These differences have fitness consequences (Boon et al. 2007) and can therefore affect the way species cope with anthropogenic disturbances (Sih et al. 2010). For example, behavioural syndromes are known to vary along urbanization gradients (Evans et al. 2010, Scales et al. 2011, Bokony et al. 2012) and personality types can be favoured differently in environments impacted by human activities compared to wild environments (Martin and Réale 2008a). Despite their importance in ecological (Sih et al. 2012) and evolutionary processes (Wolf and Weissing 2012), personality traits and behavioural syndromes are not widely used in applied ecology and ecotoxicology. By focusing on shifts in average behaviour rather than effects on behavioural (co)variance, current ecotoxicological studies risk overlooking potential effects of insecticides on personality traits

and behavioural syndromes. Such effects may be particularly important since alterations of personality traits can feedback into population and community dynamics. In an agroecological context, this may imply reduced efficiency for the ecological services provided by biocontrol agents and pollinators.

Our objective was to test whether sublethal exposure to an organophosphate insecticide can disrupt personality expression, either by affecting the consistency of behavioural traits or by affecting the strength of correlation between traits. We used the jumping spider *Eris militaris* (Araneae: Salticidae) as a model taxon. This species is commonly found in apple orchards (Sackett et al. 2009) and is easily reared under laboratory conditions. We focused on correlations related to activity and prey capture behaviours using standard personality assays. These traits show strong consistency across a range of taxa (Réale et al. 2007). They are frequently correlated in several spider species (reviewed in Pruitt and Riechert 2012) and are important for individuals' survival and fitness (Pruitt et al. 2008, Pruitt and Krauel 2010, Sweeney et al. 2013a).

4.3. Methods

4.3.1. Spider collection and rearing

Juvenile *E. militaris* were collected from "insecticide-naïve populations (i.e., populations not regularly treated and exposed to insecticides) in three sites located in Southern Quebec, Canada. The first site was an apple orchard managed without insecticidal applications since its creation 20 years ago (Agriculture and Agri-Food Canada experimental farm in Frelighsburg W 45.0462, N -72.8565). The other sites were shrubby areas located near the McGill University's Morgan Arboretum (Ste-Anne-de-Bellevue W 45.440185, N -73.946893) and the Pin Rigide Ecological Reserve (Saint-Chrysostome W 45.111657, N -73.876557). Spiders were collected haphazardly by beating the foliage of trees and brought to the laboratory. We also included laboratory-reared specimens (F1) collected in the apple orchard site. Spiders were reared to maturity in cylindrical containers (760 mL Plastipak®) that included a plastic plant to lessen the effect of captivity (Carducci and Jakob 2000) and a small plastic straw retreat (L = 2.5 cm, ⌀ =1.2 cm). They were kept at 24 °C and 40 % humidity, under a 16L:8D photoperiod. Water was provided ad lib using dental wadding inserted in an Eppendorf tube. Spiders were fed weekly

with a mixed diet of cabbage looper larvae (*Trichoplusia ni*), two species of adult fruit flies of different sizes (*Drosophila melanogaster* and *Drosophila hydei*) and juvenile domestic crickets (*Acheta domestica*).

4.3.2.Behavioral tests

We tested 177 adult individuals for behavioural correlations (males: n = 77; females: n = 100; Arboretum population: n = 22; apple orchard population: n = 94; laboratory-reared population: 47; Pin Rigide population: n = 14). Spiders were randomly assembled in groups of 8 to 16 individuals. In order to standardize satiety, spiders were offered one adult fruit fly (*D. hydei*) during the week preceding the tests and one adult *D. melanogaster* 12 h prior to the tests. Spiders were then subjected to open-field and prey capture tests before and after exposure to the insecticide (hereafter referred to as pre and post-exposure phases). Behavioural tests were consistently conducted in the same order, with the open-field conducted from 8:30 to 11:00, and prey capture from 14:00 to 16:00. At the end of the first day of testing, spiders were introduced in 14.5 × 1.4 cm glass test tubes. Half of the test tubes were coated with a 279 μL solution of phosmet (Imidan® 50-WP Instapak®, Gowan Company LLC, Yuma, Arizona) at 0.01% of the maximum recommended field dose (3.75 kg/ha, diluted in 400 L, United Agri Products Canada Inc. 2012; CRAAQ 2012) diluted in acetone. The remaining test tubes were coated with acetone only, to provide a control group (control group: n = 82, insecticide-treated group: n = 95). Test tubes were left to dry for 3h on a hotdog warmer at ambient temperature (20°C). The rotation of the tubes by the hotdog warmer (with the heating device switched off) ensured that all the inner surface of the tubes were homogeneously coated with dry insecticide residues. The spiders were placed in test tubes for 24 h to limit individual variation in activity, which could affect the dose received by each individual (Tietjen 2006, Tietjen and Cady 2007). After 24 h exposure, spiders were reintroduced in their cages, offered one *D. melanogaster* and behavioural tests were repeated on the following day. In the insecticide-treated group, two individuals (out of 95) died, while in the control group, one individual (out of 82) died.

Mass and body-size measurements were taken for 151 individuals. Spiders were massed immediately after the prey capture test at pre and post-exposure phases. Body mass (± 0.1 mg) was determined using a Sartorius TE214S scale. Cephalothorax width (± 0.001 mm) was used as a proxy for body size and measured using a WILD MMS 225 digital length measuring set. All

tests were videotaped using a Canon Vixia HF200 camera. To remove traces of conspecific cues, test arenas were cleaned with 70% ethanol and air-dried for 120 s between trials. Using video playback, the parameters related to activity and prey capture were analysed with the software The Observer XT (Noldus Information Technology, Wageningen, The Netherlands).

4.3.2.1. Open-field test

We used a wooden open-field arena of 30 × 30 cm divided in 5 × 5 cm quadrats for the open-field test (Carducci and Jakob 2000, Royauté et al. 2014). The arena was subdivided in three zones: a central zone (4 quadrats), an intermediate zone (12 quadrats) and an edge zone (20 quadrats). The spiders were set in a 5 cc syringe for 120 s before being released at the center of the arena. Recording was started as soon as the spiders entered one of the four central quadrats. During 300 s, we recorded the latency to exit the first quadrat (s), the total number of quadrats visited, the number of unique quadrat visited and the number of quadrats visited in each zone of the arena.

4.3.2.2. Prey capture test

Spiders were introduced in a 9 cm Petri dish and left to rest for 120 s. At the end of the resting period, an adult *D. hydei* was inserted with a buccal aspirator in the Petri dish through a hole on its side. For a subset of 42 individuals, prey capture tests used the smaller prey species *D. melanogaster*. As none of the observed behaviours differed significantly depending on fly species ($p > 0.3$), this variable was removed from subsequent analyses. Spiders were given a duration of 600 s to capture the prey. We recorded the latencies to detect (defined as the first orientation toward the prey) and capture the prey (s), as well as the average time performing visual and active tracking of the prey, and the total time being non responsive to the prey (s). The test was stopped as soon as the spider captured the prey or when the 600 s duration was reached. The fly was removed from the spider by probing it with the tip of a small brush in order to keep satiety consistent between tests. Spiders that failed to capture the prey were given a duration of 600 s for capture latency. Proportion of capture success did not differ between treatments (Fisher exact test, $P= 0.25$).

4.3.3. Statistical analyses

Analyses were conducted with R version 3.0.0 for Macintosh (R Core Team 2013).

4.3.3.1. Principal Component Analysis

We performed Principal Component Analysis (PCA) on variables of each behavioural test separately to reduce dimensionality and identify variables summarizing most of the behavioural variation. Count data were square-root transformed (i.e., number quadrats travelled, number of attacks on the prey) and continuous data (i.e., first move, detection and capture latencies, duration of visual and active tracking) were $\log_{10}(x)$-transformed prior to entering the PCA. For open-field tests, we also included the slope and intercept of quadrats visited over time. Slope and intercept were calculated for each test phase using random regression over intervals of 60 s (Montiglio et al. 2010) in the package lme4 (Bates et al. 2012). The intercept represents the number of quadrats travelled when time interval equals zero (hereafter initial activity) and was positively correlated with activity within the first minute of test (Pearson's $r = 0.75$, $p < 0.0001$). The slope represents variation in the rate of quadrats travelled over time. Individuals with slopes approaching zero have constant number of quadrats visited over time, and individuals with positive/negative slopes increase/decrease the number of quadrats visited over time (hereafter activity rate). We extracted significant principal components (PC) based on the Kaiser-Guttman criterion (Kaiser 1991) and used the behavioural variable with highest loading on each PC for subsequent analyses (hereafter defined as behavioural traits). For each trait, we compared post-exposure values between treatments using t-tests. Pre-exposure values did not show significant variations between treatments ($p > 0.3$) and we found no evidence for sex × treatment interactions at each test phase ($p > 0.2$).

4.3.3.2. Effect of insecticidal exposure on behavioural repeatability

Repeatability is commonly used as a measure of extent of individual differences in behaviour, and is calculated by partitioning phenotypic variance into between and within-individual components. We used a Bayesian mixed model approach with the package MCMCglmm to compare behavioural repeatability between treatments (Hadfield 2010). For each behavioural trait, we first determined the appropriate fixed effect structure to avoid over confident estimates of repeatability (Nakagawa and Schielzeth 2010). We used an inverse

gamma prior with 1.3×10^8 iterations, 300 000 iteration burn-in and a thinning interval of 1000. This yielded a Markov Chain Monte Carlo (MCMC) with a sample size of 1000 and allowed for low autocorrelation. Fixed effects considered included: body-size and body-condition (expressed as standard deviation units), sex, test phase and population (n = 4). Individuals were included as random effects. Body-condition was estimated as a residual index following Jakob et al. (1996). Fixed effects with 95 % credible intervals (CI) overlapping with zero were removed until each model contained only significant fixed effects (Table A3-1). In order to test for differences in repeatability between treatments, we compared a model where between and within-individual variance components were constrained to be equal between treatments, with a model where these components were estimated independently for each treatment (Dingemanse and Dochtermann 2013). The Deviance Information Criterion (DIC) was used to compare these models and ΔDIC > 4 indicated significant differences in repeatability between treatments. We then estimated the posterior mode and 95 % credible intervals (CI) of traits between groups. We also calculated the posterior distribution for the difference in repeatability estimates ΔR (calculated as $R_{insecticide\text{-}treated}$ - $R_{control}$) in order to test for an overall effect of treatment on behavioural repeatability. We used the same procedure in order to test for any differences in repeatability between sexes.

4.3.3.3. Effect of insecticidal exposure on behavioural correlations

Evaluating consistency in behavioural correlations is a critical step in establishing the presence of a behavioural syndrome. When repeated measures are taken on multiple traits, the phenotypic covariance may be split into between and within-individual (or error) components. A strong between-individual covariance indicates consistent correlations between traits over time and is evidence for a behavioural syndrome. Within-individual covariance represents correlated changes in behaviour attributable to phenotypic plasticity or error correlation. Graphical investigation of correlation patterns between behaviours showed substantial differences between sexes. To compare between and within-individual covariance across treatments, we performed Bayesian bivariate mixed models on each treatment group and sex separately. We included all significant fixed effects for each trait in the models and added individuals as random effects (Dingemanse and Dochtermann 2013, Ferrari et al. 2013). For each correlation between activity and prey capture traits, we tested three models: a full model where both between and within-individual covariances were estimated, a model where between-individual covariance was

constrained to be null and a model where within-individual covariance was constrained to be null. We compared these models using DIC tests in order to judge the significance of each covariance component. Lower DIC values for the full model indicate support for the importance of covariance components and we fixed our significance threshold at $\Delta DIC > 4$. In cases where the covariance components were found significant in one or both treatment group for a given sex, we tested whether covariance strength differed significantly across treatments by comparing a model where covariance did not differ between treatments and a model where the covariance in control and insecticide-treated where estimated separately. We reported the posterior modes and 95 % CI for between (r_{BI}) and within-individual (r_{WI}) correlations for each sex and treatment groups.

4.4. Results

Principal component analysis on open-field and prey capture variables showed the presence of five significant principal components (Table 4-1). For open-field tests the three first principal components explained > 80 % of variation with number of total quadrats visited (loadings > 0.5), activity rate (loading > 0.7) and number of central quadrat visited (loading > 0.6) having highest loading for each PCs. For prey capture, the first two principal components explained ~ 60 % of variation, with capture latency (loading > 0.5) and attack numbers (loading > 0.7) as most influential variables.

Spiders from the insecticide-treated group showed a significant reduction in total and central quadrats travelled (total quadrats: $t = 3.08$, $df = 164$, $p < 0.01$; central quadrats: $t = 2.87$, $df = 167$, p-value < 0.01) indicating that spiders travelled less distance after insecticidal exposure. Other traits showed no significant differences in their average values across treatments ($p > 0.07$) (Fig. 4-1).

Repeatability values ranged from low/moderate (activity variation, central quadrats, attacks) to high (total quadrats, capture speed) (Fig. 4-2). There was no overall decrease in repeatability among all traits ($\Delta R = -0.03 \pm [-0.41; 0.21]$), nor were any differences in repeatability between sexes found (Table A3-2). However, the repeatability of total quadrats and numbers of attacks decreased significantly in the insecticide-treated group (Table 4-2) (total quadrats, control group: $R = 0.51 \pm [0.33; 0.65]$ - insecticide-treated group: $R = 0.17 \pm [0.08;$

0.31]; ΔDIC > 17.00; attacks, control group: R = 0.34 ± [0.20; 0.54] - insecticide-treated group: R = 0.25 ± [0.11; 0.39]; ΔDIC > 4.00).

The strength of between-individual correlations varied depending on sex and treatment group, while within-individual correlations remained ≤ |0.2| (Table 4-3). In the control group, males with higher capture latency consistently travelled more distance in the central zone of the open-field arena (control: r_{BI} = 0.59 ± [0.09; 0.82], ΔDIC > 5.00; insecticide-treated r = 0.34 ± [-0.29; 0.73], ΔDIC = 0.48), and activity rate was negatively correlated with capture latency at the within-individual level in the control group (control: r_{WI} = -021 ± [-0.51; 0.03], ΔDIC > 6.00; insecticide-treated: r_{WI} = 0.03 ± [-0.32; 0.33], ΔDIC = -0.55). However, only the activity rate - capture latency correlation differed significantly across treatments (central quadrats vs. capture latency: ΔDIC = 0.82; activity rate - capture latency: ΔDIC > 10). Females with higher total quadrats visited and higher activity rates had higher capture latencies in the control group (total quadrats vs. capture latency: control, r_{BI} = 0.57 ± [-0.01; 0.81]; ΔDIC = 4.00, insecticide-treated, r_{BI} = -0.04 ± [-0.49; 0.49], ΔDIC = -1.42; activity rate vs. capture latency: control, r_{BI} = 0.61 ± [-0.04; 0.82], ΔDIC > 4.00, insecticide-treated, r_{BI} = 0.06 ± [-0.42; 0.51], ΔDIC = -1.64). However, only the total quadrats - capture latency correlation showed significant changes in behavioural correlation across treatments (total quadrats vs. capture latency: ΔDIC > 7.50; activity rate vs. capture latency: ΔDIC = 0.78).

4.5. Discussion

Our objective was to test sublethal insecticidal exposure as a potential disrupter of personality expression in the jumping spider *E. militaris*. Our results showed strong evidence of sublethal disruption going well beyond shifts in average behaviour.

Behaviours related to open-field activity showed the strongest decrease on average after sublethal exposure, and prey capture behaviours were not affected. Effects of organophosphate effects on arthropod locomotion and mobility have been well documented in past studies. Organophosphates are inhibitors of acetylcholinesterase (Mineau 1991), an enzyme involved in synaptic transmission (Kreissl and Bicker 1989). These compounds can therefore affect many behaviours across a range of non-targeted organisms (Desneux et al. 2007). For example, exposure to malathion can either increase or decrease activity depending on the spider species

(Tietjen and Cady 2007, Hanna and Hanna 2013). In a few cases, acetylcholinesterase inhibition can be irreversible (Alix et al. 2001, Desneux et al. 2004b). In wolf spiders, effects have been noticed up to eight days after exposure (Van Erp et al. 2002). However, these studies focused primarily on shifts in average behaviour or physiological response and may have overlooked effects at the individual level.

Indeed, while insecticide-treated individuals decreased their activity levels, the effect size was moderate (Cohen's d = 0.43) and activity speed was reduced by about one quadrat per minute in the insecticide-treated group. The effect of the insecticide treatment was in fact more pronounced in terms of how it affected behavioural consistency. Repeatability of distance travelled decreased by ~ 30 %, and, while the number of attacks did not differ on average between treatments, its repeatability decreased by 10 %. A decrease in behavioural repeatability may be due either to a decrease in between-individual variance (i.e., individuals become more similar after exposure to the insecticide) or through an increase in their within-individual variance as individuals may show different sensitivity to the exposure (Kolok et al. 1998). In the present study, both between and within-individual variance components differed significantly among treatments for activity (Table 4-2) and further tests are required to understand the precise mechanisms by which insecticides can alter behavioural consistency.

Consistent individual variations in activity and exploratory tendencies have been demonstrated in many taxa (R ~ 30 - 50 %, reviewed in Bell et al. 2009). These tendencies are related to individual differences in physiology (Koolhas et al. 1999, Montiglio et al. 2012), have an underlying genetic basis in many species (Drent et al. 2003, Norton et al. 2011), and have important consequences for individuals' fitness (Dingemanse et al. 2003, Dingemanse and de Goede 2004, Bergeron et al. 2013) or life history strategies (e.g., pace-of-life syndrome Réale et al. 2010, Niemelä et al. 2012b). Effects of insecticidal exposure on behavioural consistency are therefore particularly important as they can alter a population's evolutionary trajectory. Even non-permanent disruption of behavioural traits can have drastic effects if they happen during a critical window (e.g., early development, mating season). For example, the observed decrease in activity repeatability could reduce an individual's encounters with potential mates or prey.

In addition to changes in behavioural consistency, we detected changes in the way traits were correlated after sublethal exposure (i.e., in their behavioural syndrome). Males were more resilient to alterations of correlation strength after insecticidal exposure, as the strength of

correlation between central quadrats and capture latency did not differ between treatments. Females, on the other hand, showed a strong decrease in correlations between distance travelled and capture latency in the insecticide-treated group. In spiders, short capture latencies are related to aggressive tendencies against conspecific (Johnson and Sih 2005, 2007), bolder reactions to predatory threats (Riechert and Hedrick 1993, Pruitt et al. 2008) and, under certain conditions, higher activity levels (Pruitt and Husak 2010, Kralj-Fišer and Schneider 2012). With *E. militaris*, however, the most active females seemed to take more precautions and had longer latencies to capture prey. This could in part be mediated by prey behaviour, as shown in the jumping spider *Phidippus clarus* (Sweeney et al. 2013a). This study demonstrated that the number of prey captured depended on the interaction between prey and predator activity levels, with more active predators being more efficient when presented with more sedentary prey and vice versa. Nonetheless, alterations of the association between activity and prey capture tendencies may result in reduced efficiency when foraging for prey. In agricultural landscapes frequently exposed to pesticides, disruption of individual behavioural variations could have drastic consequences on ecosystem services. In particular, sublethal disruption of personality tendencies may limit the efficiency of pest control by generalist predators.

Few ecotoxicological studies have focused on individual behavioural variations as a currency to study extent of sublethal disruption. Evolutionary studies of toxic exposure traditionally report effects on cohorts or over multiple generations (Massarin et al. 2010, Massarin et al. 2011, Biron et al. 2012) but not on individual variation. To our knowledge, our study is the first to report a sublethal insecticidal exposure affecting individual behavioural variation. Disruption of individual behavioural variations has been previously demonstrated in aquatic systems exposed to other types of contaminants such as heavy metals or psychoactive drugs, with results similar to what we report. For example, fathead minnows (*Pimephales promelas*) had decreased in swimming speed repeatability after standardized exposure to heavy-metal contaminated sediments, indicating individuals differed in their sensitivity to contaminant exposure (Kolok et al. 1998). Individual perches (*Perca fluviatilis*) exposed to anxiolytics drugs expressed increased activity and boldness but a reduced sociality (Brodin et al. 2013). In addition, anxiolytic exposure generated new correlations between previously uncorrelated personality traits. Disruption of behavioural variation is therefore likely to occur with a wide range of chemicals, including insecticides.

The evolutionary and ecological consequences of sublethal effects on behavioural variation are yet unclear and calls for further studies. In our study, we took precautions to ensure each individual had standardized exposure to the insecticide. This assumption may not hold under field conditions, and insecticidal exposure may also show between-individual variations, possibly mediated by each individual's behavioural type. For example, spiders with higher activity may explore larger areas and be more frequently in contact with insecticide residues. Under such a scenario, feedback loops may exist between an individual's personality type and its likelihood to enter in contact with insecticide residues (Luttbeg and Sih 2010). Depending on the sign of the feedback between accumulated dose and personality expression, behavioural consistency may be reduced (negative feedback) or increased (positive feedback).

Our research calls attention on a poorly studied source of behavioural variation: the presence of neurotoxic chemicals in the environment. We demonstrated that exposure to phosmet significantly affected personality expression in a jumping spider by reducing consistency in traits related to activity and prey capture and by altering their correlations. Our results open several new avenues of research, both from fundamental and applied perspectives. First, an individual's sensitivity to insecticidal exposure (or to other types of contaminants) should be more frequently used as an indicator of extent of sublethal disruption. This implies using a repeated measure framework where insecticide dose and behavioural shifts are monitored over time, at the individual level, in order to generate predictions for population persistence. Second, behavioural syndromes have been proposed as generating evolutionary constraints: because of strong association between traits at the genetic level, not all combinations of traits may be possible, despite selective pressures (Dochtermann and Dingemanse 2013). Knowledge of chemicals that can temporarily alter these correlations can be used to better understand under which conditions traits become coupled or uncoupled. Last, our results can be applied in bioassay procedures by incorporating behavioural variations in dose-response ecotoxicological studies.

Table 4-1: PCA analysis for variables measured in the open-field (a) and prey capture tests (b). Bold indicates the behavioural variable that best represents each principal component and italics indicates behavioural variables that contribute significantly to a given principal component (loading > 0.4, based on Martin and Réale 2008b).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
(a) Open-Field Test								
Total Quadrats	**-0.50**	0.12	-0.10	0.10	-0.01	0.28	-0.01	-0.80
Unique Quadrats	*-0.45*	0.13	0.01	-0.04	-0.03	-0.87	-0.10	-0.00
Central Quadrats	-0.23	0.02	**0.69**	0.21	0.63	0.08	0.11	0.11
Intermediate Quadrats	-0.33	-0.06	*0.49*	-0.18	-0.70	0.16	0.25	0.17
Edge Quadrats	*-0.42*	0.15	*-0.49*	0.13	0.15	0.15	0.58	0.41
First Move Latency	0.21	*0.44*	0.09	0.81	-0.29	-0.07	0.01	0.01
Initial Activity	-0.38	*-0.45*	-0.14	0.36	-0.06	0.19	-0.60	0.31
Activity Rate	-0.14	**0.73**	0.01	-0.33	0.04	0.24	-0.46	0.24
Standard Deviation	**1.92**	**1.24**	**1.069**	0.85	0.76	0.52	0.22	0.11
% of Variance	**46.22**	**19.11**	**14.27**	9.02	7.17	3.43	0.61	0.18
Cum. % of Variance	**46.22**	**65.33**	**79.60**	88.62	95.78	99.21	99.82	100.00
(b) Prey Capture Test								
Attack numbers	0.05	**-0.70**	-0.48	0.50	0.14	-0.01		
Detection Latency	-0.40	0.04	-0.68	-0.45	-0.40	0.06		
Capture Latency	**-0.56**	0.09	0.08	0.18	0.33	0.72		
Active Tracking	-0.18	*-0.65*	0.35	-0.61	0.21	-0.04		
Visual Tracking	*-0.44*	-0.19	0.41	0.35	-0.69	-0.13		
No Reaction	*-0.54*	0.19	-0.07	0.12	0.44	-0.67		
Standard Deviation	**1.68**	**1.16**	0.86	0.77	0.68	0.15		
% of Variance	**47.27**	**22.30**	12.43	10.01	7.61	0.38		
Cum. % of Variance	**47.27**	**69.56**	82.00	92.01	99.61	100.00		

Table 4-2: Comparison of between (V_{BI}) and within-individual (V_{WI}) variance components across treatments for all behavioural traits (posterior mode ± credible intervals (CI)). Model 1 corresponds to a univariate model where V_{BI} and V_{WI} are equal across treatments. Model 2 corresponds to a bivariate model where V_{BI} and V_{WI} are estimated independently for each treatment following Dingemanse & Dochtermann (2013). Bold indicates support for model 2 with ΔDIC > 4.

				Control Group						Insecticide-Treated Group					
Trait	Model	DIC	ΔDIC	V_{BI}	Lower CI	Upper CI	V_{WI}	Lower CI	Upper CI	V_{BI}	Lower CI	Upper CI	V_{WI}	Lower CI	Upper CI
Total Quadrats	1	923.56	-	0.26	0.08	0.37	0.67	0.56	0.86	0.26	0.08	0.37	0.67	0.56	0.86
	2	**905.98**	**17.58**	**0.51**	**0.27**	**0.77**	**0.51**	**0.35**	**0.64**	**0.18**	**0.08**	**0.32**	**0.76**	**0.64**	**1.01**
Activity Rate	1	911.52	-	0.21	0.08	0.43	0.69	0.58	0.91	0.21	0.08	0.43	0.69	0.58	0.91
	2	912.93	-1.40	0.25	0.12	0.49	0.67	0.55	0.99	0.30	0.12	0.50	0.69	0.52	0.90
Central Quadrats	1	782.49	-	0.20	0.04	0.38	0.74	0.63	0.98	0.20	0.04	0.38	0.74	0.63	0.98
	2	788.18	0.48	0.31	0.14	0.56	0.66	0.51	0.91	0.23	0.10	0.43	0.74	0.61	1.01
Capture Latency	1	782.49	-	0.46	0.35	0.65	0.38	0.32	0.49	0.46	0.35	0.65	0.38	0.32	0.49
	2	788.18	-5.69	0.43	0.28	0.73	0.42	0.29	0.56	0.50	0.32	0.76	0.36	0.29	0.51
Attack numbers	1	949.55	-	0.22	0.04	0.40	0.74	0.60	0.95	0.22	0.04	0.40	0.74	0.60	0.95
	2	**944.87**	**4.68**	**0.39**	**0.16**	**0.61**	**0.66**	**0.48**	**0.89**	**0.27**	**0.10**	**0.42**	**0.79**	**0.59**	**0.99**

Table 4-3. Between and within-individual correlations of behavioural traits compared across treatment groups for males (a) and females (b). Bold indicates significant correlation based on DIC comparison with a null model with ΔDIC > 4.

Trait 1	Trait 2	Control Group					Insecticide-Treated Group				
(a) Males		r	Lower CI	Upper CI	DIC	ΔDIC	r	Lower CI	Upper CI	DIC	ΔDIC
Between-Individual											
Total Quadrats	Capture Latency	-0.03	-0.38	0.50	388.86	-1.86	-0.11	-0.58	0.52	338.36	-1.06
Total Quadrats	Attack number	-0.23	-0.71	0.17	417.89	0.84	-0.33	-0.77	0.24	376.01	2.59
Activity Rate	Capture Latency	0.18	-0.22	0.74	404.21	0.31	-0.01	-0.57	0.55	319.11	-1.48
Activity Rate	Attack number	-0.03	-0.57	0.56	441.02	-1.53	-0.17	-0.61	0.55	364.15	-0.93
Central Quadrats	Capture Latency	**0.59**	**0.09**	**0.82**	**412.78**	**5.44**	0.34	-0.29	0.73	337.11	-0.48
Central Quadrats	Attack numbers	-0.33	-0.70	0.31	446.57	-0.16	-0.37	-0.76	0.40	376.88	0.69
Within-Individual											
Total Quadrats	Capture Latency	-0.12	-0.44	0.17	388.86	-0.33	-0.04	-0.34	0.29	338.36	-0.68
Total Quadrats	Attack number	0.09	-0.17	0.43	417.89	2.48	0.08	-0.25	0.31	376.01	0.04
Activity Rate	Capture Latency	**-0.21**	**-0.51**	**0.03**	**404.21**	**6.31**	0.03	-0.32	0.33	319.11	-0.55
Activity Rate	Attack number	-0.12	-0.41	0.17	441.02	0.55	-0.08	-0.37	0.28	364.15	-0.28
Central Quadrats	Capture Latency	-0.04	-0.34	0.22	412.78	0.91	0.15	-0.24	0.36	337.11	-0.88
Central Quadrats	Attack numbers	0.06	-0.24	0.32	446.57	0.08	0.13	-0.17	0.42	376.88	1.87
(b) Females											
Between-Individual											
Total Quadrats	Capture Latency	**0.57**	**-0.01**	**0.81**	**385.83**	**4.73**	-0.04	-0.49	0.49	630.24	-1.42
Total Quadrats	Attack number	0.28	-0.39	0.65	417.24	-0.24	-0.20	-0.58	0.42	681.13	-0.77
Activity Rate	Capture Latency	**0.61**	**-0.04**	**0.82**	**394.331**	**4.01**	0.06	-0.42	0.51	601.34	-1.64
Activity Rate	Attack number	0.24	-0.44	0.67	428.28	-0.48	-0.07	-0.56	0.46	658.77	-0.99
Central Quadrats	Capture Latency	0.11	-0.50	0.56	403.77	-1.34	-0.06	-0.56	0.39	605.73	-1.67
Central Quadrats	Attack numbers	-0.27	-0.64	0.46	428.62	-0.80	0.10	-0.54	0.50	668.97	-1.00
Within-Individual											
Total Quadrats	Capture Latency	-0.02	-0.37	0.20	385.83	0.86	-0.04	-0.29	0.17	630.24	-0.17
Total Quadrats	Attack number	-0.16	-0.43	0.14	417.24	2.30	-0.12	-0.36	0.06	681.13	0.95
Activity Rate	Capture Latency	-0.03	-0.29	0.30	394.331	-0.75	-0.08	-0.25	0.23	601.34	-0.44
Activity Rate	Attack number	-0.11	-0.38	0.17	428.28	0.54	-0.13	-0.38	0.06	658.77	1.80
Central Quadrats	Capture Latency	0.03	-0.17	0.38	403.77	-0.27	-0.20	-0.44	0.04	605.73	2.35
Central Quadrats	Attack numbers	-0.15	-0.37	0.18	428.62	-0.34	-0.10	-0.35	0.09	668.97	0.50

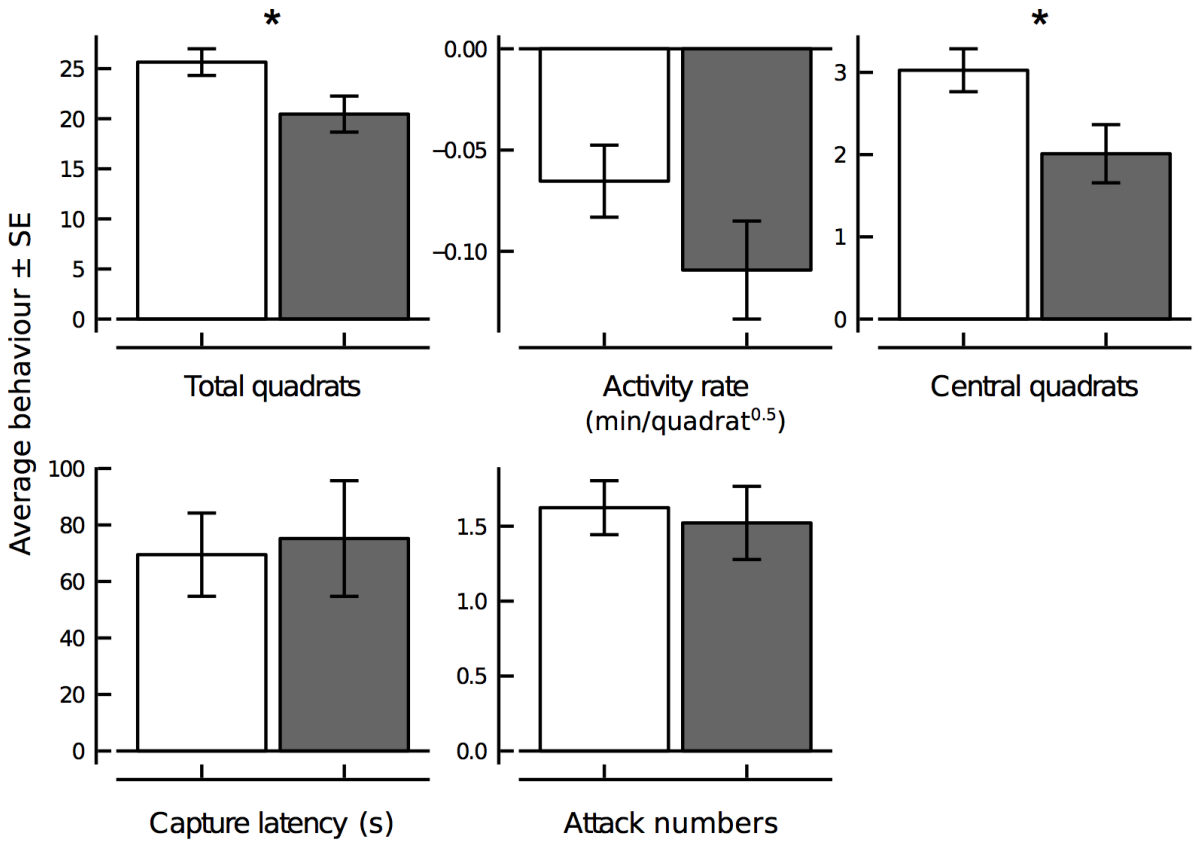

Fig. 4-1: Behavioural traits (average ± SE) compared between control (white bars) and insecticide-treated groups (dark bars) at the post-exposure phase. Asterisk indicates significant difference between treatments (t-test, $\alpha = 0.05$).

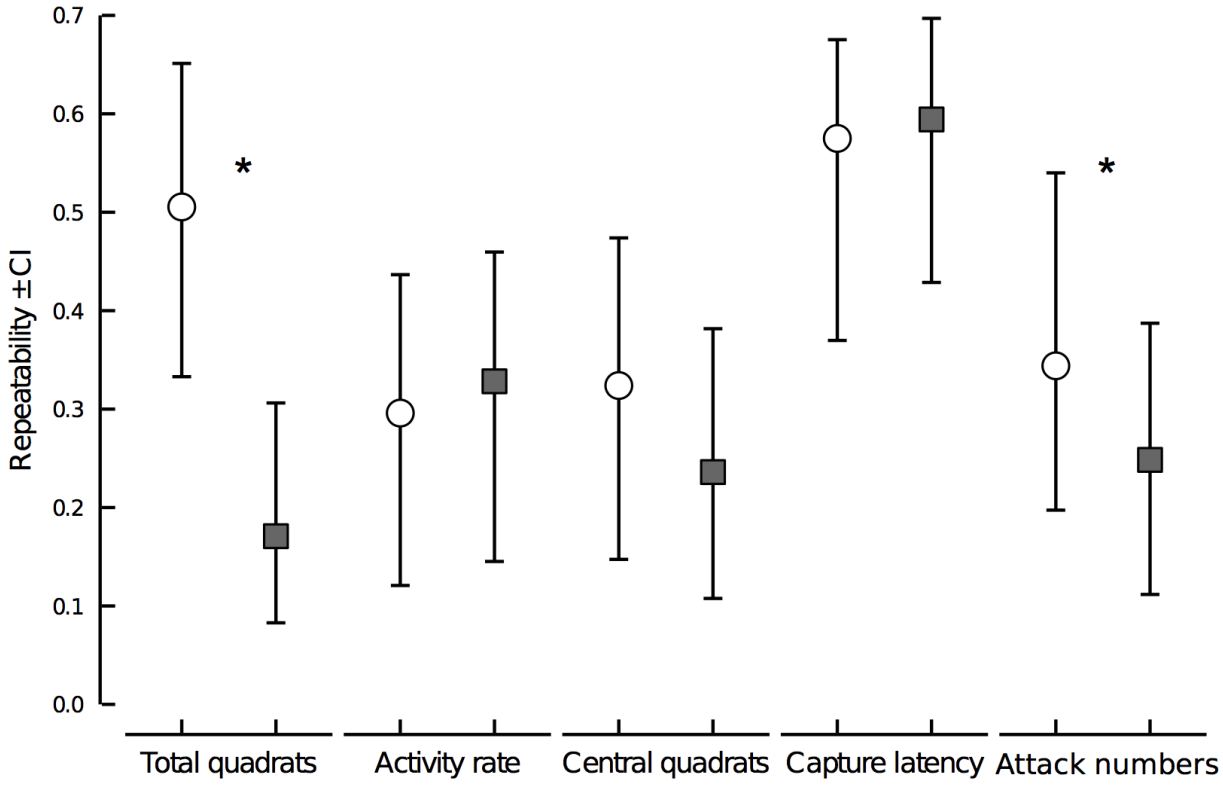

Fig. 4-2: Repeatability of behavioural traits (posterior modes ± credible interval) compared between control (white circles) and insecticide-treated groups (dark squares). Asterisks indicate significant differences in repeatability based on DIC comparison of a model where repeatability varies between treatments and a model were repeatability is constrained to equality across treatments.

4.6. Connecting Statement

Chapter 4 demonstrated that insecticides had the potential to affect the consistency of personality traits and their correlations at sublethal doses and revealed that individuals may be more or less sensitive to insecticidal exposure. Insecticides are only one of the many toxic by-products of human activities that may alter behaviour at sublethal doses. Such anthropogenic contaminants are ubiquitous in the environment and have complex interactions with behaviour, especially if certain personality types are more at risk of encountering and accumulating certain classes of contaminants. In Chapter 5, I propose a framework that details the various interactions occurring between anthropogenic contaminants and behavioural variation. This framework was written in collaboration with P-O Montiglio and is now accepted for publication.

Chapter 5: Contaminants as a neglected source of behavioural variation

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5.1. Abstract

Consistent behavioural differences between individuals have far-reaching implications for ecology and evolution. Determining the mechanisms maintaining them is a central focus of behavioural ecology. Anthropogenic contaminants are rarely considered for their contribution to such behavioural differences. Yet, anthropogenic contaminants and behaviour interact through their respective effects on resource acquisition and the pattern of resource allocation to growth, reproduction and survival. Such interactions between behaviour and anthropogenic contaminants could either increase and maintain or erode consistent behavioural variation in animal populations. We propose a general framework integrating the relationships linking individual differences in behaviour, exposure to and accumulation of anthropogenic contaminants, and resource acquisition/allocation patterns. We discuss the type of approach required, the type of data missing in the current literature, and two study systems where insights could be gained by investigating the relationships between individual behavioural variation and anthropogenic contaminants. We hope to stimulate cross-fertilization between behavioural ecology and ecotoxicology and show how a mechanistic approach based on repeated measurements can contribute to this area of research.

5.2. Introduction

Animal behaviour has broad ecological and evolutionary implications. Among other things, it drives social group and population dynamics, affects inter-specific interactions, and influences how animals cope with environmental changes (Sih et al. 2012). In addition to the average behaviour of a given species or population, behavioural variation among individuals within populations (i.e., so called animal personality, Sih et al. 2004a, Réale et al. 2007) has important implications for ecological and evolutionary processes relevant for multiple fields of

research like community ecology, and conservation (Sih et al. 2004a, McDougall et al. 2006, Réale et al. 2007).

A large amount of effort is currently devoted to identifying the mechanisms responsible for the maintenance of consistent behavioural variation (Dall et al. 2004, Wolf et al. 2007, Wolf et al. 2008, Réale et al. 2010). A main hypothesis is that consistent behavioural variation can be maintained when the fitness benefits of expressing a certain behaviour differ consistently among individuals as a function of their state, such as their energy balance or energy allocation strategy (Houston and McNamara 1999). For example, individuals with a negative energy balance may be consistently bolder than those with a positive energy balance (Rands et al. 2008). Individuals investing more of their energy into immediate reproduction than in long term survival may also be bolder while foraging (Wolf et al. 2007). The behaviour expressed by individuals may further affect their state, leading to a feedback between behaviour and state (Dingemanse and Wolf 2010). For example, individuals with positive energy balance may be better at dealing with predation risk and thus forage more, thereby maintaining a consistently positive energy balance (Luttbeg and Sih 2010). Depending on the type of relationship between behaviour and state, feedback loops may either amplify or erode behavioural variation over time (see Fig. 5-1; Bergmüller and Taborsky 2010, Luttbeg and Sih 2010). Determining the state variables associated with consistent individual differences in behaviour, and investigating their potential feedback with behaviour is now a major area of research. There is an urgent need for more empirical work, particularly on how different state variables (e.g., age, size, energy level, residual reproductive value) interact with each other to affect individual behaviour (recently reviewed in Dingemanse and Wolf 2010).

Anthropogenic contaminants (AC), defined as products typically not found in nature and generated by human activity (e.g., heavy metals, fertilizers, pesticides, residual birth pill compounds [British Geological Society 2013]) could be a particularly potent factor contributing to consistent behavioural variation within populations (see Bell 2001, 2004). AC are ubiquitous in most environments (e.g., Kolpin et al. 2002), and may directly alter the behaviour expressed by individuals (i.e., the level of exposure or contamination would act as a state, hereafter referred to as 'AC state'; Zala and Penn 2004). Examples of AC effects on behaviour include residual psychiatric drugs present in the water increasing the boldness of fishes (Brodin et al. 2013), brominated flame retardants altering male parental nest guarding (Verboven et al. 2009), sublethal doses of pesticides altering navigation and orientation behaviours (Bortolotti et al.

2003, Colin et al. 2004), heavy metal accumulation, decreasing anti-predator behaviour or foraging activity (Cheung et al. 2002), and exposition to pyrene affecting the probability of winning staged contests in males (Dissanayake et al. 2009).

AC state could also interact with other state variables. Hence, the behavioural shifts resulting from AC state could differ among individuals as a function of their life history strategy or energy balance (just as natural hormones do, Lancaster et al. 2008). More importantly, an individual's AC state and behaviour may feedback into each other if behaviour both determines and is affected by AC exposure and accumulation. This is likely to apply in a first scenario, where AC exposure and accumulation occurs through feeding, and affects the behaviours driving food acquisition. For example, individuals with a higher activity level may also incur higher encounter rates with AC in their environment, which may further affect their activity level. Likewise, individuals with a higher voracity would be likely to consume more (potentially contaminated) prey items, which could affect further their voracity. A vast array of behaviours shown to be affected by AC exposure are associated with resource acquisition by animals (Clotfelter et al. 2004), and so this first scenario is likely to be ubiquitous among animal study systems. In a second scenario, AC could feedback on behaviour by affecting how much resource individuals allocate to various fitness functions such as growth, reproduction and body maintenance (i.e., AC affect the resource allocation pattern of animals). For example, AC state could decrease the survival of animals or increase their reproductive effort (Massarin et al. 2011), which could lead them to express a more risk-prone behaviour (i.e., individuals would become bolder, Réale et al. 2010), leading to a further increase in AC state (e.g., Brodin et al. 2013). Interestingly, most behaviours currently investigated for their consistent variation among individuals within populations (i.e., so called personality traits, Réale et al. 2007), are tightly associated with the life history strategy of individuals, regulating how resources are allocated to growth, reproduction and maintenance (Réale et al. 2010). Determining the interactions between behaviour and AC state is thus paramount to understanding how consistent variation in behaviour within animal populations is maintained, and why the extent of such variation differs among study systems (Sih et al. 2004a, Wolf and Dingemanse 2010).

Since behaviour and AC may interact through multiple paths of effects, we believe that investigating the relationship between behaviour and AC state requires a mechanistic approach, analysing the interactions among behaviour, AC state, resource acquisition and resource allocation patterns. Note that to be considered mechanistic, such a model need not to directly

analyse the proximate aspects of AC-behaviour interactions. Our objective is to provide such a conceptual framework that accounts for the interactions between AC and consistent behavioural variation. We first discuss how AC can act as a state variable and affect behaviour. Second, we outline how individual behaviour may mediate differences in exposure to and accumulation of AC. Third, we suggest an experimental and mechanistic approach to study the feedbacks between AC and behavioural variation. Finally, we present two case studies and show how the interaction between AC and behavioural variation may be studied in these systems.

5.3. Anthropogenic contaminants contribute to state-dependent behavioural variation

Behavioural expression is sensitive to contaminants, and exposure to contaminants is increasingly regarded as a source of behavioural variation that must be taken into account (reviewed in Clotfelter et al. 2004, see also Dissanayake et al. 2009, (Egea-Serrano et al. 2011), Henry et al. 2012). AC exposure or accumulation rates often act as state variables, affecting the expression of behaviour. For example, ethinyl oestradiol (derived from birth control pills and post-menopausal hormone replacement therapies) occurs in most freshwater streams and decreases aggressiveness of individuals (Bell 2001). Other endocrine-disrupting chemicals also affect boldness under various risky situations (Schantz and Widholm 2001, Eroschenko et al. 2002). Nitrogenous compounds originating from farming and fossil fuel combustion decrease activity in many amphibians both during larval and adult stages (Egea-Serrano et al. 2011, Miaud et al. 2011). By modifying particular behaviours, AC may thus alter existing correlations between behavioural traits, or generate new ones (Brodin et al. 2013). Hence, exposure to contaminants may explain the occurrence of particular behavioural associations in the same way as exposure to predation (Bell 2005) or parasitism does (Barber and Dingemanse 2010).

Mechanistic models of the effects of AC on organisms suggest that exposure to contaminants may affect behaviour through their effects on state variables associated with energy acquisition. Such modifications may in turn alter the cost and benefits of behavioural expression (Dingemanse and Wolf 2010). For example, exposure to heavy metals may result in heightened metabolic costs and negative energy balance (Massarin et al. 2010, Massarin et al. 2011), leading to increased expression of behaviours associated with resource acquisition. In the lizard *Sceloporus occidentalis*, individuals coped with higher maintenance costs associated with AC by decreasing their activity while increasing their feeding rate (Durant et al. 2007). Alternatively,

AC may also alter how the energy is allocated to competing functions such as growth, reproduction or survival. For example, organochlorines (used as pesticides) also cause shifts in energy allocation patterns and life histories tactics (e.g., Congdon et al. 2001), which may eventually affect consistent behavioural variation (Dingemanse and Wolf 2010, Réale et al. 2010).

Variation in AC exposure could also affect behavioural variation if it affects individuals differently. For example, the repeatability (a measure of how much individuals differ consistently from each other) of critical swimming speed in sub-adult male fathead minnows (*Pimephales promelas*) decreased after a standardized exposure to heavy-metal-contaminated sediments (Kolok et al. 1998). Exposure to heavy metals did not affect the average swimming speed of the population, but it impacted the relative rank of individual swimming speed. Thus, some individuals were affected differently by exposure to a given level of AC. To our knowledge, no other studies have yet applied an individual approach to assess the effects of contaminants on behaviour. We believe much insight could be gained by using this approach on available datasets (e.g., Brodin et al. 2013).

5.4. Individual behaviour mediates anthropogenic contaminants exposure and accumulation

Exposure and accumulation of AC can occur by contact (Ragland et al. 2011) or direct ingestion of contaminated food items (Esselink et al. 1995), while animals move in the habitat to forage or find other resources. Several of the behaviours associated with resource acquisition, such as activity, exploration, or voracity, display important variation within populations. For example, individual great tits (*Parus major*) differ in their dispersal tendencies (Quinn et al. 2009), and individual spiders (*Agelenopsis aperta*) differ in their willingness to kill and ingest prey (Riechert and Hedrick 1993). To date, most empirical evidence for behavioural mediation of contaminant exposure comes from studies comparing discrete categories of foraging behaviour (e.g., resident vs. migrants) or diet preferences (Table 5-1). Ragland et al. (2011) showed that migratory male loggerhead sea turtles (*Caretta caretta*) were more prone to accumulate persistent organic pollutants compared to resident males. Resident American dippers (*Cinclus mexicanus*) accumulated more organochlorines than temporary migrants (Morrissey et

al. 2004). Esselink et al. (1995) showed that populations feeding at different trophic levels displayed different rates of heavy metal accumulation in the barn owl (*Tyto alba guttata*).

In contrast to such studies focusing on discrete behavioural categories, there are no empirical studies that investigate the links between continuous behavioural variation and the probability of being exposed to or accumulating AC. Schlink et al. (2010), however, did provide a theoretical approach. They tested different algorithms of human movement patterns on exposure to air contaminants passively absorbed by breathing, and showed that differences in exposure can arise from individual differences in movement patterns. Such theoretical findings await confirmation from empirical investigations. We believe that investigating how AC affect consistent behavioural variation calls for a more mechanistic approach than what is usually employed in current toxicological-behavioural assays (Clotfelter et al. 2004).

5.5. How to study the interaction between behavioural variation and anthropogenic contaminants

5.5.1. A mechanistic approach

Dynamic interactions between individual behaviour, physiology and AC states may be approached through 'process-based' or mechanistic models, derived from Dynamic Energy Budget (DEB) theory (Kooijman 1993). Such models explicitly consider resource acquisition and allocation to various functions such as structural maintenance and growth (see Fig. 5-2, gray flowchart) and thus offer an avenue to incorporate interactions between factors affecting both acquisition and allocation of resources. Extensions of this theory already incorporate the toxic effects of some contaminants on energy allocation (DEBtox, Jager et al. 2006) and provide a framework for modelling various physiological alterations caused by AC exposure. We suggest behaviour can be integrated within such a model, as a determinant of resource acquisition. Resource acquisition can then be associated with AC exposure and accumulation. Indeed, behaviour mediates how individuals acquire resources (black circle), and consequently how much they are exposed to AC, or how much AC they accumulate (white circle). For example, the foraging behaviour of an individual could determine the type and abundance of potentially contaminated food items ingested (see relationship 1 in Fig. 5-2), and how much AC it is likely to assimilate in the body (relationship 2 in Fig. 5-2). Note that individual behaviour could lead to differences in AC accumulation or exposure even when the contaminant is diluted in the

environment and passively absorbed (e.g., Schlink et al. 2010, Brodin et al. 2013). Moreover, individual differences in metabolism or physiology, often linked to individual behavioural differences, may mediate such variation in AC state in homogeneously contaminated environments. In turn, AC state may have a direct impact on behaviour (depicted as relationship 3 in Fig. 5-2, reviewed in Zala and Penn 2004). AC state may also alter how an animal allocates its energy to structural maintenance as opposed to reproduction. For example, *Daphnia* exposed to uranium toxicity display increased allocation of energy to maintenance, probably as a result of the toxic effects of the AC on the digestive tract (relationship 4, Massarin et al. 2011). The energy balance and allocation patterns are known to affect an individuals' behaviour, and to drive consistent differences in behaviour within populations (reviewed in Dingemanse and Wolf 2010). For example, animals with heightened metabolism may need to forage more, or to forage on different prey (relationship 5; Oliveira et al. 2008, Réale et al. 2010).

Investigating the interactions between behaviour and AC may take multiple pathways, potentially leading to feedback interactions. Hence, mechanistic models, explicitly analysing the direction (negative or positive), temporal dynamic and relative importance of such pathways are necessary to understand the links between behaviour and contaminants. As we suggested above, models derived from the DEBtox would provide valuabe tools for this challenge. The framework we outline here also enables us to investigate how AC may maintain or erode consistent behavioural variation within populations by generating knowledge on the potential interactions and feedbacks between the pathways we described. For example, exposure to AC may maintain variation in behaviour if AC increases the expression of a given behaviour and this behaviour increases AC exposure or accumulation. In this way, individuals expressing a behaviour with a higher intensity experience a larger increase in AC state, which consequently increases behaviour expression (Fig. 5-1, upper panel). Conversely, if a behaviour is inhibited by an increase in AC exposure we expect AC to erode or attenuate individual variation in that behaviour over time (Fig. 5-1, lower panel). This is expected because individuals expressing a behaviour with a high intensity will experience larger doses of AC, thus decreasing behaviour expression to a larger extent (Fig. 5-1, lower panel). This may be the case in systems where individual activity level increases AC state (Schlink et al. 2010), and AC decrease the activity level of individuals (e.g., Nyman et al. 2013). The toxic effects of AC would lead us to consider negative feedback loops eroding behavioural variation as more frequent among animal

populations. However, we also emphasize scenarios where AC could increase consistent behavioural variation among individuals (see the two case studies we describe below).

5.5.2. Longitudinal data

A first step in determining the effects of AC on individual behavioural variation is to establish how AC affect behaviours associated with resource acquisition or behaviours that are associated with resource allocation patterns. This can be done using repeated observations conducted at the individual level over time, with special attention paid to the temporal dynamics of individual variation in AC state (Fig. 5-3a). For this approach to be truly mechanistic, one needs to first assess the relationship between a given behaviour and resource acquisition or allocation strategy and then how resource acquisition/allocation affects AC state. This can be achieved by manipulating behaviour and resource acquisition/allocation. Data on how behaviour affects AC state could then be coupled with repeated assessments of each individual's behaviour for different levels of AC state to investigate how each individual responds to AC (see Fig. 5-3b). Note that individuals may react differently to an increase in AC state (i.e., they may show a different relationship between behaviour and AC state). This approach would be complementary to the more conventional one, which compares the average behavioural shift among groups of individuals exposed to different levels of AC (Fig. 5-3c).

The consistency of individual behavioural and AC state variation can be estimated using repeated measure designs, and mixed modelling approaches, partitioning the behavioural and AC state variation into different components such as between and within individual variance (Dingemanse et al. 2010, Nakagawa and Schielzeth 2010). This approach is now widely used in behavioural studies, to quantify the extent of consistent behavioural variation among individuals in a population (reviewed in Bell et al. 2009). Surprisingly, data on AC state effects on individual behavioural variation is extremely rare. In fact, we only found two studies reporting AC effects on individual variation (Kolok et al. 1998, Brodin et al. 2013, Table 5-1). Implementing such an approach would be very valuable for many reasons. First, it would provide a stronger predictive framework to forecast the effects of contaminants exposure on wild animal populations that are hard to study in laboratory settings. Consistent behavioural variation and allocation patterns are likely to affect many population processes like space use as well as interspecific interactions through its effects on diet (Brodin et al. 2013, see also Sih et al. 2012 for a review of this topic). Second, additional knowledge of the multiple paths of effects we

describe here would also increase considerably our ability to assess the consequence of AC by focusing on their effects at doses below thresholds at which they cause death or major health issues in animals. Since AC are found in most ecosystems, our framework would also be an additional step toward understanding consistent behavioural variation in animals. Of course the relative importance of the paths of effects we described and in particular the importance of their interactions remains to be assessed.

5.5.3. Candidate study systems

AC state and behavioural variation may be easier to study in systems where a limited number of contaminants are at play. Indeed, different AC often operate in synergy (i.e., "cocktail effect", Kortenkamp 2007). Implementing longitudinal studies where AC and behavioural variation are monitored at the individual level could also be more feasible with bigger and longer-lived organisms such as birds, mammals, and reptiles. Long-lived organisms may accumulate AC such as brominated flame retardants or organochlorines in fatty tissues that are often amendable for repeated sampling without killing the individuals (Rowe 2008). In contrast, AC accumulation is hard to establish for short-lived organisms such as arthropods. They are however easier to maintain under laboratory conditions and can be used for standardized experimental work where AC state and resources can be manipulated. Despite such limitations, we outline briefly two case studies where the dynamics between AC state and behavioural variation is amenable to empirical investigation.

Psychiatric drugs in fish populations: Psychiatric drugs, such as anxiolytics, are found in urban waste water (Kolpin et al. 2002, Verlicchi et al. 2012). Such drugs are usually found in highly diluted concentrations in rivers, but may be accumulated by aquatic organisms (Meredith-Williams et al. 2012). Individual perch (*Perca fluviatilis*) with a higher burden of accumulated anxiolytics in their body expressed increased activity and boldness but reduced sociality (Brodin et al. 2013). Individuals exposed to higher doses of anxiolytics were also shown to increase their foraging on zooplankton, a prey item that is typically found in the water column, and potentially carrying a higher dose of accumulated anxiolytics. Other studies previously showed that individuals with higher boldness and reduced sociality use the water column more frequently (Magnhagen and Staffan 2005). It is currently unknown whether this change in diet affects individual AC state. However, we suggest that a chain of effect may link individual differences

in foraging behaviour to the level of AC exposure and accumulation. If bolder individuals feed at a higher trophic level than shy ones (i.e., on zooplankton), and if feeding at higher trophic levels leads to increased AC exposure, this chain of effect would become a positive feedback loop, resulting in increased differences in boldness among individuals over time. Unfortunately, the study by Brodin et al. (2013), while using a longitudinal approach, focuses on the average effect of AC on personality traits. A similar experimental design, assessing the repeatability of behavioural traits through time during an extended AC exposure event would provide much insight on the feedback loop we describe, hence building a better knowledge of the interactions of AC with consistent behavioural variation. Such knowledge should increase our ability to predict the effect of contaminants in other perch populations, and related study systems. For example, populations of perch with a different mix of behavioural types could be vulnerable to a different extent to the effects of psychiatric drugs. Considering that AC are found in all environments assayed to this date, we suggest they may be seen as an integral part of the consistent behavioural variation we observe in animal populations.

Neurotoxic insecticides and honey bees: Honey bee (*Apis mellifera*) workers feed on nectar and pollen sources contaminated with neurotoxic insecticides over a wide foraging range (Rortais et al. 2005). Returning foragers also expose other bees and larvae of the colony to contaminated food sources (Krupke et al. 2012). Depending on their social role within the hive, individuals may be exposed to different doses of insecticides (relationship 1 in Fig. 5-2). Neurotoxic insecticides disrupt synaptic transmission and have been shown to impair foraging activity, navigation skills, olfactory memory and learning skills (Bortolotti et al. 2003, Decourtye et al. 2003, Colin et al. 2004, Decourtye et al. 2004). For example, exposure to thiamethoxam was shown to increase the proportion of foragers failing to return to the colony up to 30% per day (Henry et al. 2012). Thus, a potential feedback loop may exist between the social role of individuals and their AC state. Even within a particular social role consistent individual differences have been demonstrated for honey bees. Despite this knowledge, individual behavioural differences have not been incorporated when studying insecticidal effects. It is known, however, that foragers differ consistently along a continuum of speed vs. accuracy of flower exploration (Burns and Dyer 2008). Accurate explorers return more resources (i.e., pollen, nectar) when flower quality is low while fast explorers are more efficient at high flower quality. One could posit that accurate explorers are less likely to get disoriented but may

contribute more to the AC state of the colony by returning more contaminated food sources. Finally, colonies express different average behavioural types (Pinter-Wollman 2012). Wray et al. (2011) showed that defensive response, foraging activity, and undertaking (i.e., the removal of dead workers) are correlated and consistent at the colony level. Colonies with higher foraging activity and defensive response could be more exposed to AC than colonies with lower foraging activity. This could translate into higher AC accumulation for colonies in areas with extensive insecticide use.

5.6. Conclusion

Behaviour and AC are likely to share dynamic links and potentially feedback into each other. We presented two scenarios in which such interactions could occur either through the process of resource acquisition, or through modifications of their resource allocation patterns. While reviews are already available on the effect of AC exposure and accumulation on the average behaviour of a population, literature investigating how individual behavioural differences interact with differences in exposure and accumulation of AC is still scarce. Furthermore, studies investigating the relationships between an individual's behaviour and AC state are completely lacking. We encourage an increased use of mechanistic models that integrate longitudinal studies (repeated observations) on individual behaviour and AC state. This new research area is an outstanding opportunity to build bridges between behavioural ecology and ecotoxicology, and to integrate behavioural ecological knowledge to the investigation of how animal populations respond to human-induced alterations of their environment.

Table 5-1. Studies currently available on the relationships between anthropogenic contaminants and behavioural individual variation. Studies in bold used a modeling approach.

Contaminant	Contaminant class	Organism	Class/Order	Exposure type	Behaviour(s) affected	Behaviour affects AC state	Individual variation in AC state	Individual variation in behaviour	Repeated behavioural measures	Source
Ethinyl oestradiol	Endocrine disrupter	Threespined stickelback	Fish	Passive absorption	Aggression & courtship				X	(1)
Benzodiazepines	Anxiolitic drug	European perch	Fish	Passive absorption	Activity, boldness, feeding rate & sociality			X	X	(2)
Fipronil & imidacloprid	Neurotoxic insecticide	Honey bee	Insects	Ingestion	Foraging				X	(3)
Carbaryl	Neurotoxic insecticide	Fence lizard	Reptiles	Ingestion	Feeding				X	(4)
Nitrogeneous compounds	Fertilizer	Iberian waterfrog	Amphibians	Passive absorption	Activity				X	(5)
Methoxychlor	Endocrine disrupter	Salamander	Amphibians	Passive absorption	Startle response				X	(6)
Cd, Cu, Pb, Mn, & Fe	Heavy metals	Barn owl	Birds	Ingestion	Diet type	X	X	X		(7)
Thiamethoxam	Neurotoxic insecticide	Honey bee	Insects	Ingestion	Foraging				X	(8)
Heavy metals	Heavy metal	Fathead minnow	Fish	Contact with contaminated sediments	Activity			X	X	(9)
Uranium	Heavy metal	Daphnia	Crustaceans	Passive absorption	Foraging				X	(10)
Uranium	Heavy metal	Daphnia	Crustaceans	Passive absorption	Growth & reproduction				X	**(11)**
Organochlorines	Endocrine disrupter	American dipper	Birds	Ingestion	Diet type	X	X	X		(12)
Imidacloprid	Neurotoxic insecticide	Gammarus	Amphipods	Passive absorption	Foraging				X	(13)

Contaminant	Contaminant class	Organism	Class/Order	Exposure type	Behaviour(s) affected	Behaviour affects AC state	Individual variation in AC state	Individual variation in behaviour	Repeated behavioural measures	Source
Persistant organic pollutant	Endocrine disrupter	Loggerhead sea turttle	Reptiles	Ingestion	Diet type or migration?	X	X	X		(14)
Hydrocarbons	Air pollutant	Human	Mammals	Passive absorption	Activity and space use	X	X	X		**(15)**
Persistant organic pollutants	Endocrine disrupter	Glaucus gull	Birds	Ingestion	Parental behavior			X	X	(16)

Sources: (1) Bell (2001); (2) Brodin et al. (2013); (3) Colin et al. (2004); (4) Durant et al. (2007); (5) Egea-Serrano et al. (2011); (6) Eroschenko et al. (2002); (7) Esselink et al. (1995); (8) Henry et al. (2012); (9) Kolok et al. (1998); (10) Massarin et al. (2010); (**11) Massarin et al. (2011)**; (12) Morissey et al. (2004); (13) Nyman et al. (2013); (14) Ragland et al. (2011); **(15) Schlink et al. (2010)**; (16) Verboven et al. (2009).

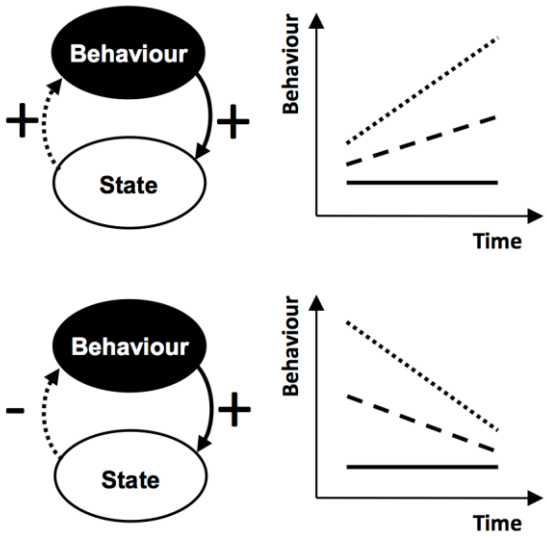

Fig. 5-1: Examples of feedback loops between personality and AC state (left hand diagrams) and their implication for consistent individual behavioural variation (right hand graphs). The right hand graphs present the behaviour of three individuals (solid, dashed and dotted lines) as a function of the time exposed to AC. Note that this axis may be continuous, or discrete (i.e., the behaviour of individuals before and after AC exposure). Upper panel: the behavioural trait value expressed by individuals may increase AC state, which may in turn increase the behavioural trait value of the individual. Such a positive feedback loop may act to exacerbate individual differences in behaviour, thereby increasing repeatability. Lower panel: the behaviour may increase the AC state of individuals, but an increased AC state may decrease the behavioural trait value expressed (e.g., through its toxicity). In such a case, the negative feedback loop will erode or eliminate individual differences in behaviour. Thus, we would expect the repeatability of this behaviour to decrease.

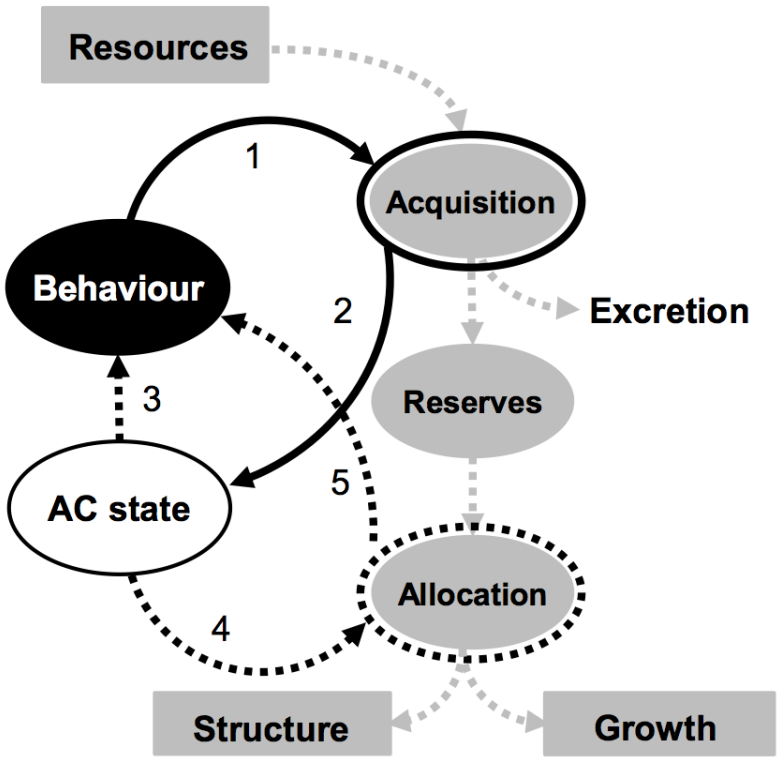

Fig. 5-2: A mechanistic model inspired by the dynamic energy budget (gray boxes and dashed arrows) including the interactions between individual behaviour (black circle, solid arrows) and AC exposure or accumulation levels (white circle, dashed arrows). Individuals acquire resources from their environment. Some of these resources are excreted, and the remaining part is considered to accumulate in a 'reserve' compartment. Reserves may then be allocated to functions such as growth (which includes reproduction in DEB models) or structural maintenance, depending on the animal's allocation pattern or strategy. The behaviour of an individual, for example activity level or aggressiveness, is often associated with resources acquisition, such as food (1). Individuals may be exposed to AC by moving around in their environment or consuming contaminated preys (2). Behaviour, through resource acquisition, would affect the extent to which an individual is exposed to AC state, or how much AC it accumulates over time. AC state may affect behaviours associated with resource acquisition and consequently AC levels (3). Alternatively, AC may modify the individual's allocation pattern (4). For example, it may alter metabolism or life history traits such as growth. The physiological state and life history trajectory of an individual may then modify its behaviour (5).

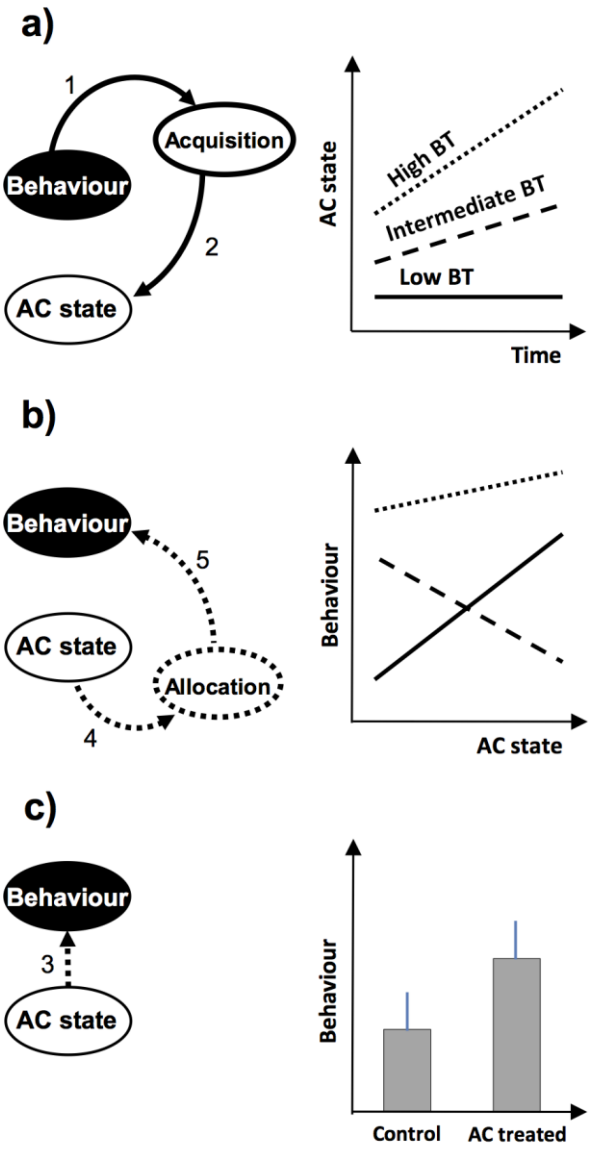

Fig. 5-3: Steps for an empirical investigation of the feedbacks between AC and behaviour. a) A first step is to collect repeated measurements of the AC state of individuals with known behavioural differences (each individual's behavioural type is measured prior to the experiment). The effects of these behavioural differences on resource acquisition and AC state also need to be assessed. b) A second step is to detail how each individual's behaviour changes as a function of a change in AC state. Such relationships require repeated behavioural measurements on individuals subjected to controlled doses or exposure levels of AC. Differences in these relationships among individuals will likely be the result of a change in resource allocation. c) Steps a and b, involving repeated measurements of individuals' AC states and behaviours would greatly complement the more widely used approach, testing the average effect of AC on behaviour through standardized bioassays.

Chapter 6: Research summary and future prospects

6.1. Introduction

Behavioural variations are central to behavioural ecology. They occur at different levels of organization (within, between-individuals and populations, between species), are important drivers of eco-evolutionary dynamics, and may shed light on how organisms cope with human-driven environmental changes (Sih et al. 2010, Sih et al. 2012, Wolf and Weissing 2012). Despite increasing research effort targeted at the interaction between behavioural variation and anthropogenic changes (Pintor et al. 2008, Pintor et al. 2009, Evans et al. 2010, Scales et al. 2011, Bokony et al. 2012, Miranda et al. 2013), these principles have seldom been studied in an agricultural setting. Agroecosystems are heavily affected by human intervention and are ideal systems to study a wide range of disturbances and their effects on the behaviours of pests and their natural enemies. In this thesis, I focused on *Eris militaris*, a jumping spider common in apple orchards, and tested how insecticidal applications, a major agricultural disturbance, affected the consistency and correlation strength in behavioural traits related to their performance in biocontrol. Finally, I provide a framework enabling to test the effects of insecticides and other anthropogenic contaminants on behavioural variation.

6.2. Research summary

6.2.1. Influence of insecticidal application on behavioural syndrome of *Eris militaris* in apple orchards

In Chapter 2, I tested the influence of frequency of insecticidal applications of interpopulation variation in behavioural syndromes for a dominant jumping spider (Araneae: Salticidae) in apple orchards: *Eris militaris*. I sampled two populations from orchards varying in their intensity of insecticidal applications and compared the correlations among suites of behaviours commonly forming behavioural syndromes in many spider species (i.e., activity, aggression, boldness and voracity, reviewed in Pruitt & Riechert 2012). I hypothesized that insecticidal applications would affect behavioural syndrome either by acting as selective

pressures (Hypothesis 1a, Introduction), or by disrupting behavioural expression at sublethal doses (Hypothesis 1b).

I found strong evidence for diverging behavioural syndromes between the two populations, along with an unbalanced age-structure in the insecticide-treated population. The insecticide-free population had equal proportion of life-stages and sexes and presented a complex arrangement of behavioural correlations organized in two negatively correlated axes: an activity-voracity axis and a boldness-aggression axis (Fig. 2-4a). The insecticide-treated population had less active but more voracious individuals than the insecticide-treated population, even though the majority of individuals collected in this orchard were juveniles and subadults. In addition, the activity-voracity axis was absent from the syndrome structure in this population. I found instead an aggression-voracity axis negatively correlated with boldness (Fig. 2-4b).

The insecticide-treated population had lower numbers of significantly correlated behaviours, suggesting sublethal disruption as the main mechanism at play (Hypothesis 1b). However, this hypothesis required a more thorough validation by directly manipulating the insecticide dose received by individuals, as was done in Chapter 4. In addition, the presence of an unbalanced age-structure in the insecticide-treated population lead me to formulate other plausible explanations for the difference in behavioural syndrome expressed by the two populations. First, many studies showed that behavioural correlations may be stage-specific and vary depending on developmental conditions, including in spiders (Bell and Stamps 2004, Kralj-Fišer and Schneider 2012, Sweeney et al. 2013b). Repeated measures of behaviours were not taken, a condition important to understand how consistent behavioural correlations remain. Differences between sexes were statistically controlled for, but patterns of covariance between sexes were not investigated further. These limitations led me to the experiment in Chapter 3, and to focus on the contribution of between and within-individual components to the phenotypic covariance and compare these patterns between rearing environments and sexes. Finally, we cannot exclude the possibility of indirect effects of insecticidal applications on behavioural syndromes through alterations of prey and conspecific densities. Behavioural syndromes tend to vary along ecological gradients and variation in resource availability and inter or intra-specific competition can indeed be a driver of syndrome differences between populations (Dochtermann et al. 2012). I observed lower arthropod densities in the insecticide-treated orchard coupled with patches of high densities of juvenile *E. militaris* during the summer season (R. Royauté, personal observation). This suggests that intra-specific competition for food resources is high in juvenile

stages of *E. militaris* and is a plausible explanation for the aggression-voracity syndrome being present only in the insecticide-treated population. Ultimately, these factors are likely to be non-mutually exclusive and may each play a part in shaping the differences between the insecticide-free and insecticide-treated populations.

6.2.2. Ontogenic shifts in behavioural syndromes and the influence of sex and rearing environment

In Chapter 3, I focused on untangling the effects of ontogeny on behavioural syndrome across rearing environments and sex. Repeated measures for individual spiders were taken at subadult and adult stages for behavioural traits investigated in Chapter 2. I compared the repeatability of behavioural traits between field-collected individuals sampled in the two apple orchards mentioned above and an F1 laboratory-reared population and between sexes. Since parental and F1 phenotypes were known, this allowed me to test for a heritable basis for behavioural traits. I used multivariate mixed modeling approaches to estimate the contribution of between-individual (i.e., correlation between repeatable component of behaviour) and within-individual correlations (i.e., correlation between plastic component of behaviour, or error correlation) to the total phenotypic correlation. I tested the hypothesis that behavioural consistency is influenced by rearing environments and sex (Hypothesis 2), and that correlations are highly consistent within groups (i.e., rearing environment and sex) but may vary between groups (Hypothesis 3).

All behaviour showed a marked increase in average over development but heritability was low. Open-field activity was the only behaviour for which heritability was > 0.2 and had highest repeatability as well ($0.2 < R < 0.3$) (Table 3-2, Fig. 3-2). The repeatability of open-field activity also decreased for laboratory-reared individuals (Hypothesis 2 confirmed) but showed no differences between sex and all other behaviours showed no differences in repeatability across groups. Behavioural correlations showed strong shifts over ontogeny that varied between groups, but there was poor evidence of within-group consistency (Hypothesis 3 rejected) (Fig. 3-3). Decomposing phenotypic correlations into between and within-individual components is a "data hungry" procedure and care must be taken in the interpretation of the results as comparisons between groups (i.e., rearing environment and sex) had low sample sizes often resulting in large confidence intervals. However, describing these patterns of correlation proved to be a much more informative approach than focusing solely on phenotypic correlations estimated at each

stages, as most studies of development of behavioural syndrome have done previously (Bell and Stamps 2004, Sweeney et al. 2013b). The only significant between-individual correlation was a negative correlation between open-field activity and boldness (Table 3-4), meaning individuals that were highly active tended to reduce risk taking in front of predatory threats. This correlation was strongly eroded in the laboratory-reared environment and was poorly expressed in females (Table A2-3). Interestingly, within-individual correlations had the highest contribution to the phenotypic correlation and were more pronounced in laboratory-reared individuals and males. The heritability and repeatability estimates were weaker than those typically reported in studies of personality traits (~ 0.3, Bell et al. 2009, Stirling et al. 2002), which resulted in strong developmental plasticity of behavioural correlations. The open-field activity-boldness correlation was significant at the between-individual level, indicating a possible genetic underpinning for this correlation (Dochtermann and Roff 2010, Dochtermann 2011). This correlation may be sustained by a trade-off between foraging and predator safety, which would explain why it did not develop in a laboratory environment without selective pressures.

These results provided partial confirmation of the findings from Chapter 2. Juvenile individuals from the insecticide-treated population had a negative aggression-boldness correlation and I describe a similar pattern in Chapter 3 with laboratory-reared subadults. However, this correlation was expressed as a positive correlation in the insecticide-free population and I failed to detect a similar pattern with adult stages, even when comparing patterns between sexes or rearing environments, which suggest that other environmental factors may be at play in shaping interpopulation differences in syndrome structure in this system. The activity-boldness correlation provided an interesting case as I reported a weak phenotypic correlation between these traits in both chapters ($r_P \sim -0.15$). The inclusion of a repeated-measure design in Chapter 3 revealed that this correlation was in fact strongly expressed at the between-individual level ($r_{BI} \sim -0.40$) while the weaker size effect of the within-individual component ($r_{WI} < -0.10$) may have masked patterns of variation at the phenotypic level.

This chapter indicated that the factors sustaining the emergence of behavioural syndromes in *Eris militaris* are complex and involve a combination of genetic effects, selective pressures, sexual differences and developmental plasticity.

6.2.3. Sublethal effects of phosmet on personality traits

In Chapter 4, I investigated further the effects of insecticides on the consistency of personality traits and their syndrome. I focused on behaviours involved in activity and prey-capture as the correlation between these traits was absent in the insecticide-treated population from Chapter 2. I compared the average behaviour, behavioural repeatability and between and within-individual correlations across control and insecticide-treated groups exposed to a sublethal dose of a widely used organophosphate: phosmet. I focused on adult spiders captured in insecticide-naive populations: the insecticide-free orchard mentioned above, two natural populations from the Southern Québec and a laboratory-reared population. I randomly assigned spiders to control and insecticide-treated groups and behavioural measures were taken before and after a 24h exposure phase. My hypothesis was that a sublethal dose of phosmet would cause shifts in personality expression and alter the strength of their correlations (Hypothesis 4).

Personality traits only showed small or no shifts in their average when exposed to phosmet (Fig. 4-1). There were however a drastic decrease in the repeatability of distance travelled (~ 30 % decrease), and a smaller but significant decrease in the attack rates directed at the prey (~ 10 % decrease) (Table 4-2, Fig. 4-2). Between-individual correlations also decreased significantly in the insecticide-treated group although males were more resilient to this effect (Table 4-3). Females with higher distance travelled and activity rates took more time to capture prey in the control group (r_{BI} = 0.57) and these correlations were not expressed in the insecticide-treated group (r_{BI} = 0.00). Males with a higher centrality score took more time to capture the prey (r_{BI} = 0.59), and while the posterior mode of the correlation estimate was lower in the insecticide treated group, the reduction in correlation strength itself was not significant.

Positive correlations between activity and voracity were already documented in Chapter 2 and 3. Yet, contrary to what was expected, more active individuals took more time to capture prey items. These differences may be due to variations in experimental procedures for measuring prey capture behaviours. In Chapter 2 and 3, I measured voracity as the rate of capture under high prey density, while Chapter 4 estimated latency to capture a unique prey item. Several possibilities may explain these differences, including individual difference in response to prey densities or mediation of prey capture through the phenotype of the prey items (Sweeney et al. 2013a), and I provide a deeper examination of these factors in section 6.3.

This study confirmed Hypothesis 4 and showed that insecticidal exposure at sublethal dose was likely to involve subtle effects on the consistency of personality traits and their

correlations in addition to the widely reported shift in average behaviour (Desneux et al. 2007). The decrease in repeatability observed in the insecticide-treated group suggests that individuals vary widely in their reaction to a same dose of phosmet. By altering correlations between behaviours linked to foraging and energy intake, insecticidal applications could lead to suboptimal behaviours for spiders inhabiting agroecosystems and to lower biocontrol efficiency. These effects have been poorly studied to date and only two similar reports were found in the literature, none of them involving insecticides or arthropods (Kolok et al. 1998, Brodin et al. 2013). In field conditions, the dose received by each individual may also be mediated by an individual's personality tendencies (e.g., more active individuals are more likely to get in contact with insecticide residues), a possibility that I explore in Chapter 5.

6.2.4. A framework to understand the interactions between behavioural variation and anthropogenic contaminants

Chapter 5 provides a review of the studies that showed effects of anthropogenic contaminants (including pesticides) on behavioural variation and develops a framework to expand our knowledge on how anthropogenic contaminants act on personality differences.

Anthropogenic contaminants are ubiquitous in the environment and can therefore contribute to behavioural variation. In addition, an individual's behavioural type may also mediate contaminant exposure and accumulation. An individual's behaviour may therefore share dynamic interactions that can be understood by considering contaminant load as a state variable (i.e., AC state) affecting the payoff of behavioural decisions (Luttbeg and Sih 2010). I suggest that behavioural differences can be incorporated in existing mechanistic models derived from the Dynamic Energy Budget theory (Kooijman 1993, Jager et al. 2006) and suggest two important paths of effects worth investigating. First, behavioural differences and anthropogenic contaminant state (AC state) may interact through behaviours related to resource acquisition. As an individual increases its activity or feeds on contaminated prey items, its AC state increases. Depending on the type of contaminant this will lead to positive or negative feedback loops, with different results for phenotypic variance. Second, AC state may alter patterns of resource allocation. Individuals that are more exposed may have increased energetic cost due to detoxification. This may ultimately alter how an individual's energy budget gets allocated to structural maintenance vs. growth and affect the life-history trajectories of individuals with high AC states.

Integrating these different paths of effects enables more precise predictions in order to understand how wild populations respond to anthropogenic contaminants and assess the consequences of phenotypic shifts on population dynamics.

6.3. Synthesis and future prospects

Insecticidal applications affected the strength of behavioural syndrome in the jumping spider *Eris militaris*. This result was confirmed both by monitoring of interpopulation differences at extremes of a gradient of insecticidal exposure and a manipulative experiment that tested behavioural response to a sublethal dose of organophosphate. Developmental environment and sexual differences had a profound influence on the consistency of behavioural traits and their syndromes, suggesting plasticity may play a bigger role than genetic constraints in shaping the correlation between behavioural traits in *E. militaris*. I found strong evidence of disruption of behavioural consistency in traits related to activity and prey capture accompanied by a collapse of their syndrome. These types of effects on phenotypic (co)variance of behavioural traits may also apply to the larger class of anthropogenic contaminants (e.g., heavy metals, endocrine disruptors, pesticides). The interaction between phenotypic variation and anthropogenic contaminants can be accounted for by blending approaches derived from evolutionary and behavioural ecology, animal personality, state-dependent feedback and dynamic modeling with ecotoxicology. Such an approach allows a more integrative view of the different components that affect animal populations evolving in environments with a high burden in anthropogenic contaminants.

My investigations of interpopulation differences in apple orchard populations suggested a strong influence of insecticidal application as a potential disrupter of behavioural syndromes. While such effects were confirmed in a separate study using direct exposure to insecticides, caution must be taken when relating these results. The major differences in behavioural correlations between populations were relative to the strength of the activity-voracity and aggression-boldness correlations. The activity-voracity correlation was positive for individuals captured in the insecticide-free population, but not in the insecticide-treated one. This correlation was not maintained over the course of ontogeny however, as we failed to detect a significant between-individual component. In contrast, the within-individual component was significant for males. This implies that males with highest increase in activity through development became

males with highest voracity. Another important caveat is that the correlation between activity and prey capture ability may also be highly context-dependent. When investigating interpopulation differences, I measured voracity as the number of prey captured over a 1h period. This assay was simplified during my assessment of insecticide effects and I focused on the latency to attack and capture a single prey item, a test common for testing individual differences in voracity in previous spider studies (Riechert and Hedrick 1993, Pruitt et al. 2008). Surprisingly, individuals that were the quickest to capture prey (i.e., the most voracious) were those with lowest activity levels, and this correlation decreased significantly in the insecticide-treated group.

Although both of the aforementioned studies reported a decrease in the correlation between activity and prey capture behaviours for insecticide-exposed individuals, the sign of correlation in our control environment was reversed in these two studies. I suggested that this correlation may in part be mediated by prey behaviour as demonstrated recently in a closely related jumping spider (Sweeney et al. 2013a). Activity correlated negatively with boldness in previous tests, meaning that the most active spiders reduced risk taking when confronted with predators. Active and "cautious" spiders may in turn have higher assessment time of prey resulting in high capture latencies. Finally, it is possible that spiders with different activity levels adjust differently their predation rate to food density; in this case the behavioural response to a unique prey item may differ from exposure to 10 prey items. *Eris miltaris* is known to exhibit a type II response to food density when preying on the pest species *Choristoneura rosaceana* (Sackett 2007), however, to my knowledge the way individual phenotypes respond to increases in prey density has yet to be investigated with any arthropod predator. It is not known for example if all individuals display the same type of functional response or whether interindividual differences in slopes of functional response may be noticed. If such effects were proven, this would have a high impact on our understanding of the contribution of behavioural phenotypes to predator-prey dynamics and have important implications for pest control.

Another important finding during my thesis was that developmental environment had a high influence on the expression of behavioural traits and their correlations. Behavioural repeatability over the course of ontogeny had weak estimates ($R \sim 0.15$) apart for activity ($0.2 < R < 0.3$). It is interesting to note that the repeatability of behavioural traits, estimated over a shorter time interval (~ 72h) in our insecticide tests had much higher estimates for all measured traits ($0.25 < R < 0.60$). This suggests that while behavioural differences are poorly maintained over ontogeny, strong within-stage repeatability may still occur. This weak inter-stage

consistency was also reflected in behavioural correlations. Behavioural correlations were found to be stage-specific and variable between rearing environment and sex. The only significant correlation at the between-individual level was a negative correlation between activity and boldness, which was stronger in field-collected individuals and in males. Since activity had moderate heritability, a genetic underpinning may be involved. Correlations at the phenotypic level were strongly sustained by their within-individual components, indicating that the relative ranks in the behaviour of individuals were reshuffled over the course of ontogeny. Since developmental environment showed strong effects on behavioural correlations, it would be interesting to investigate further the relative consequences of various state variables and life-history traits in order to test for the presence of a pace-of-life syndrome (Réale et al. 2010). I often noticed for example that some males had unusually fast development rates when reared under laboratory conditions, although such expeditive growth was often at the cost of a larger size (Royauté, personal observation). Relating growth rates, behavioural correlations and effects of food abundance/scarcity would reveal if part of the interpopulation differences witnessed in apple orchards systems are related to indirect effects of insecticides on prey densities, as suggested earlier.

Finally, my investigation concerning sublethal effects of insecticide suggests that effects on behavioural (co)variance must be more frequently included in ecotoxicological studies. Sublethal disruption may not only proceed by altering brain chemistry and causing shifts in average behaviour, it may also make individuals behave less in accordance with their "normal" personality tendencies. In other terms an active and cautious spider becoming "under the influence" of insecticides may no longer behave as active and cautious. Even if sublethal effects are short lived (Van Erp et al. 2002), this may result in lower fitness due to missed opportunities to capture prey or explore new habitat for example. This research only reveals a glimpse of the potential effects of insecticides on phenotypic (co)variance since only one dose of a very specific compound was tested. In field conditions, sublethal effects may be even more severe since (a) individuals may differ in their exposure level to insecticides and (b) individuals are often exposed to "cocktails" of chemicals rather than a unique chemical compound, since different pesticides are used to control different types of pests. Such cocktails often act in synergy and have drastically different effects than exposure to each compound separately (Kortenkamp 2007). An important way forward is to consider that personality differences may affect insecticide exposure and accumulation, and the received insecticide dose may in turn affect

personality expression in a feedback loop. These types of interaction can be extended to include various classes of anthropogenic contaminants and to model different paths of effects, allowing to better predict the consequences of contaminant exposure.

We live in a world with an increasing influence of our own activities on biodiversity and are only starting to understand the profound changes occurring at multiple levels of organization, be it individuals, populations and communities. The research presented in this thesis provided an opportunity to better understand the consequences of a major class of human disturbance: the spraying of insecticides in agriculture, on the behaviours a spider species of agroecological importance. Further research conducted on spiders in agroecosystems will enable to better understand the roles of behavioural variation on processes linked to important ecological services, such as pest control, and to devise agricultural practices reducing their impact on such variations.

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Appendix 1: Supplementary table for Chapter 2

Table A1-1. Deviance Information Criterion (DIC) for the selection of significant fixed effects in multi-response models. Bold indicates significant fixed effects compared to the null model for ΔDIC > 2.

Fixed effect	DIC	ΔDIC
Null Model	1773.6	0
Body Size	1739.5	**34.1**
Developmental Stage	1739.4	**34.1**
MBC	1780.0	-6.39
Population	1776.7	-3.12
Sex	1763.6	**10.0**
Trial Order	1813.7	-40.2
Year	1772.9	0.69

Appendix 2: Supplementary tables for Chapter 3

Table A2-1: Results of linear mixed model analyses on morphological attributes. Bold values indicate significance at $\alpha = 0.05$ based on likelihood ratio tests (LRT).

Trait	Term	Coefficient ± SE	LRT	p
Body-Condition	Intercept	-0.09 ± 0.15		
	Life-Stage (adults)	-0.35 ± 0.20	0.03	0.86
	Population (insecticide-treated)	-0.06 ± 0.20	0.84	0.36
	Rearing-Environment (laboratory-reared)	0.31 ± 0.24	3.83	0.05
	Sex (males)	0.17 ± 0.21	0.30	0.58
	Life-Stage × Population	**0.56 ± 0.24**	**5.50**	**<0.05**
	Life-Stage × Rearing	-0.19 ± 0.25	0.62	0.43
	Life-Stage × Sex	0.37 ± 0.24	2.44	0.12
	Population × Rearing-Environment	0.20 ± 0.25	0.67	0.41
	Population × Sex	-0.43 ± 0.25	2.94	0.09
	Rearing-Environment× Sex	-0.18 ± 0.26	0.50	0.48
Body-Size	Intercept	0.06 ± 0.12		
	Life-Stage (adults)	**1.02 ± 0.12**	**127.23**	**<0.0001**
	Population (insecticide-treated)	**-0.34 ± 0.16**	**4.57**	**<0.05**
	Rearing-Environment (laboratory-reared)	**-0.29 ± 0.20**	**22.89**	**<0.0001**
	Sex (males)	**-0.49 ± 0.17**	**20.88**	**<0.0001**
	Life-Stage × Population	-0.03 ± 0.14	0.063	0.80
	Life-Stage × Rearing	-0.27 ± 0.14	3.81	0.05
	Life-Stage × Sex	-0.01 ± 0.14	0.01	0.93
	Population × Rearing-Environment	0.24 ± 0.23	1.11	0.29
	Population × Sex	0.14 ± 0.22	0.42	0.52
	Rearing-Environment× Sex	**-0.51 ± 0.23**	**4.89**	**<0.05**

Table A2-2: Comparison of between (V_{BI}) and within-individual (V_{WI}) variance components across rearing environments and sexes for all behavioural traits (posterior mode ± credible intervals (CI)). Model 1 corresponds to a univariate model where V_{BI} and V_{WI} are equal across groups. Model 2 corresponds to a univariate model where V_{BI} and V_{WI} are estimated independently for each group. Bold indicates support for model 2 with ΔDIC > 4. Bold italics indicates support for model 2 with ΔDIC > 2.

Trait	Model	DIC	ΔDIC	V_{BI}	Lower CI	Upper CI	V_{WI}	Lower CI	Upper CI	V_{BI}	Lower CI	Upper CI	V_{WI}	Lower CI	Upper CI
				Rearing Environment											
				Field-Collected						Laboratory-Reared					
Open-Field Activity	1	737.68	-	0.23	0.09	0.36	0.56	0.44	0.71	0.23	0.09	0.36	0.56	0.44	0.71
	2	**716.41**	**21.27**	**0.24**	**0.12**	**0.41**	**0.38**	**0.27**	**0.52**	**0.19**	**0.06**	**0.51**	**0.80**	**0.58**	**1.21**
Aggression	1	635.25	-	0.14	0.05	0.35	0.77	0.59	0.97	0.14	0.05	0.35	0.77	0.59	0.97
	2	634.69	0.56	0.13	0.05	0.34	0.67	0.54	0.95	0.29	0.06	0.65	0.75	0.48	1.28
Boldness	1	753.26	-	0.12	0.03	0.24	0.85	0.70	1.04	0.12	0.03	0.24	0.85	0.70	1.04
	2	752.25	1.00	0.14	0.04	0.34	0.75	0.56	0.98	0.12	0.03	0.35	0.94	0.69	1.34
Voracity	1	798.36	-	0.09	0.04	0.22	0.73	0.59	0.89	0.09	0.04	0.22	0.73	0.59	0.89
	2	798.89	-0.54	0.12	0.04	0.28	0.78	0.59	0.97	0.11	0.05	0.29	0.60	0.05	0.29
				Sex											
				Females						Males					
Climbing Activity	1	447.52	-	0.16	0.05	0.40	0.79	0.57	1.05	0.16	0.05	0.40	0.79	0.57	1.05
	2	445.99	1.53	0.19	0.06	0.53	0.60	0.45	0.98	0.16	0.04	0.55	0.94	0.56	1.43
Open-Field Activity	1	737.68	-	0.23	0.09	0.36	0.56	0.44	0.71	0.23	0.09	0.36	0.56	0.44	0.71
	2	739.80	-2.12	0.22	0.07	0.40	0.54	0.41	0.75	0.20	0.07	0.44	0.51	0.37	0.80
Aggression	1	635.25	-	0.14	0.05	0.35	0.77	0.59	0.97	0.14	0.05	0.35	0.77	0.59	0.97
	2	634.13	1.12	0.14	0.04	0.41	0.86	0.61	1.12	0.17	0.07	0.45	0.61	0.37	0.86
Boldness	1	753.26	-	0.12	0.03	0.24	0.85	0.70	1.04	0.12	0.03	0.24	0.85	0.70	1.04
	2	***750.12***	***3.13***	***0.12***	***0.04***	***0.22***	***0.73***	***0.56***	***0.92***	***0.13***	***0.04***	***0.52***	***0.95***	***0.69***	***1.41***
Voracity	1	798.36	-	0.09	0.04	0.22	0.73	0.59	0.89	0.09	0.04	0.22	0.73	0.59	0.89
	2	797.92	0.43	0.22	0.07	0.40	0.54	0.41	0.75	0.20	0.07	0.44	0.51	0.37	0.80

Table A2-3: Between (a), within-individual (b) and phenotypic (c) correlations between climbing activity, open-field activity, aggression, boldness and voracity compared across rearing environments and sexes. Between and within-individual correlations: Bold indicates support for model 2 with ΔDIC > 4. Bold italics indicates support for model 2 with ΔDIC > 2. Phenotypic correlations: bold values indicate significant correlations based on overlap of 95 % CI with zero, bold italics indicate correlations with > of 90 of posterior estimates excluding zero.

Trait 1	Trait 2	r	Lower CI	Upper CI	DIC	ΔDIC	r	Lower CI	Upper CI	DIC	ΔDIC
(a) Between-Individual (r_{BI})											
Rearing-Environmnent		Field-collected					Laboratory-Reared				
Open-field Activity	Aggression	0.14	-0.33	0.58	950.92	-0.10	-0.02	-0.48	0.63	470.99	-0.42
Open-field Activity	Boldness	**-0.54**	**-0.76**	**-0.01**	**991.73**	**9.43**	-0.13	-0.69	0.42	544.31	-0.15
Open-field Activity	Voracity	0.18	-0.31	0.58	1031.18	-0.08	-0.18	-0.62	0.42	588.37	-0.20
Aggression	Boldness	-0.01	-0.46	0.53	945.57	-0.62	-0.20	-0.63	0.46	448.49	-0.55
Aggression	Voracity	-0.14	-0.60	0.38	972.22	0.02	0.21	-0.37	0.70	497.65	1.21
Boldness	Voracity	-0.21	-0.73	0.22	1022.38	1.86	0.06	-0.54	0.52	566.86	-0.62
Sex		Females					Males				
Climbing Activity	Open-field Activity	0.22	-0.42	0.61	706.08	-1.43	-0.11	-0.65	0.53	462.40	1.05
Climbing Activity	Aggression	0.06	-0.51	0.61	691.15	-0.92	-0.11	-0.72	0.53	384.33	0.42
Climbing Activity	Boldness	0.03	-0.48	0.61	734.86	0.32	0.01	-0.63	0.56	452.56	0.99
Climbing Activity	Voracity	-0.19	-0.62	0.44	753.85	0.83	0.09	-0.55	0.57	478.37	-0.17
Open-field Activity	Aggression	0.30	-0.29	0.60	853.91	0.93	0.33	-0.51	0.56	555.54	-0.20
Open-field Activity	Boldness	-0.17	-0.64	0.31	904.98	0.68	***-0.37***	***-0.79***	***0.15***	***619.04***	***3.61***
Open-field Activity	Voracity	-0.20	-0.58	0.29	921.70	0.95	0.23	-0.26	0.73	651.73	1.53
Aggression	Boldness	-0.07	-0.55	0.42	854.76	-0.28	0.24	-0.51	0.60	540.98	0.12
Aggression	Voracity	-0.20	-0.63	0.46	870.48	0.20	-0.01	-0.46	0.53	569.71	0.52
Boldness	Voracity	-0.22	-0.58	0.41	932.22	0.08	-0.25	-0.67	0.33	642.51	0.62
(b) Within-Individual (r_{WI})											
Rearing-Environmnent		Field-collected					Laboratory-Reared				
Open-field Activity	Aggression	**-0.19**	**-0.36**	**0.01**	**950.92**	**5.90**	**-0.04**	**-0.36**	**0.39**	**470.99**	**5.19**
Open-field Activity	Boldness	-0.12	-0.36	0.03	991.73	-5.81	0.06	-0.21	0.32	544.31	1.02

Trait 1	Trait 2	r	Lower CI	Upper CI	DIC	ΔDIC	r	Lower CI	Upper CI	DIC	ΔDIC
(b) Within-Individual (r_{WI})											
Rearing-Environmnent		Field-collected					Laboratory-Reared				
Open-field Activity	Voracity	0.19	-0.02	0.35	1031.18	0.17	0.06	-0.18	0.32	588.37	1.01
Aggression	Boldness	0.02	-0.15	0.26	945.57	0.81	***-0.20***	***-0.47***	***0.15***	***448.49***	***3.86***
Aggression	Voracity	0.01	-0.19	0.20	972.22	0.71	**-0.21**	**-0.51**	**0.18**	**497.65**	**7.89**
Boldness	Voracity	-0.18	-0.38	0.00	1022.38	-2.23	-0.04	-0.26	0.23	566.86	-0.37
Sex		Females					Males				
Climbing Activity	Open-field Activity	**0.39**	**0.18**	**0.65**	**706.08**	**23.35**	**-0.06**	**-0.39**	**0.47**	**462.40**	**10.96**
Climbing Activity	Aggression	***-0.11***	***-0.29***	***0.21***	***691.15***	***2.27***	**-0.11**	**-0.49**	**0.35**	**384.33**	**8.25**
Climbing Activity	Boldness	**-0.01**	**-0.31**	**0.32**	**734.86**	**5.00**	**0.27**	**-0.31**	**0.56**	**452.56**	**9.64**
Climbing Activity	Voracity	**0.18**	**-0.11**	**0.42**	**753.85**	**7.62**	**0.34**	**0.04**	**0.60**	**478.37**	**9.72**
Open-field Activity	Aggression	**-0.14**	**-0.38**	**0.08**	**853.91**	**5.67**	***-0.14***	***-0.39***	***0.20***	***555.54***	***3.58***
Open-field Activity	Boldness	-0.03	-0.24	0.16	904.98	-0.10	-0.19	-0.38	0.12	619.04	-2.52
Open-field Activity	Voracity	0.06	-0.15	0.26	921.70	1.87	0.23	-0.04	0.41	651.73	-1.35
Aggression	Boldness	0.03	-0.14	0.31	854.76	1.45	**-0.28**	**-0.46**	**0.10**	**540.98**	**5.67**
Aggression	Voracity	***-0.20***	***-0.47***	***0.15***	***870.48***	***3.76***	**0.02**	**-0.15**	**0.26**	**569.71**	**4.86**
Boldness	Voracity	-0.05	-0.27	0.11	932.22	0.06	-0.11	-0.40	0.05	642.51	-0.70
(c) Phenotypic (r_P)											
Rearing-Environmnent		Field-collected					Laboratory-Reared				
Open-field Activity	Aggression	***-0.07***	***-0.26***	***0.04***			0.06	-0.19	0.30		
Open-field Activity	Boldness	**-0.23**	**-0.37**	**-0.09**			0.00	-0.22	0.21		
Open-field Activity	Voracity	**0.17**	**0.03**	**0.31**			0.02	-0.21	0.18		
Aggression	Boldness	0.02	-0.13	0.21			-0.12	-0.43	0.08		
Aggression	Voracity	-0.01	-0.17	0.15			-0.12	-0.36	0.15		
Boldness	Voracity	**-0.19**	**-0.35**	**-0.06**			-0.01	-0.22	0.20		
Sex		Females					Males				
Climbing Activity	Open-field Activity	**0.34**	**0.10**	**0.51**			0.01	-0.27	0.34		
Climbing Activity	Aggression	0.01	-0.24	0.15			-0.08	-0.41	0.21		
Climbing Activity	Boldness	0.05	-0.18	0.27			0.13	-0.20	0.39		

Trait 1	Trait 2	r	Lower CI	Upper CI	DIC	ΔDIC	r	Lower CI	Upper CI	DIC	ΔDIC
(c) Phenotypic (r_P)											
Sex		Females					Males				
Climbing Activity	Voracity	0.10	-0.12	0.27			**0.23**	**0.02**	**0.47**		
Open-field Activity	Aggression	-0.08	-0.22	0.12			-0.06	-0.27	0.15		
Open-field Activity	Boldness	-0.04	-0.22	0.09			**-0.16**	**-0.38**	**-0.02**		
Open-field Activity	Voracity	0.00	-0.14	0.15			**0.23**	**0.02**	**0.37**		
Aggression	Boldness	0.02	-0.13	0.23			-0.12	-0.34	0.11		
Aggression	Voracity	0.03	-0.13	0.23			-0.11	-0.29	0.10		
Boldness	Voracity	-0.08	-0.25	0.07			**-0.18**	**-0.36**	**-0.01**		

Appendix 3: Supplementary tables for Chapter 4

Table A3-1. Fixed effects selection based on overlap of 95 % credibility intervals (CI) with zero (indicated in bold). * Indicates fixed effect for which CI overlapped with zero once refitted and subsequently removed from the final models.

Trait	Fixed Effect	Estimate	Lower CI	Upper CI
Total Quadrats	Intercept	-0.46	-0.80	-0.05
	Body-Size	0.05	-0.14	0.26
	Body-Condition	0.05	-0.06	0.15
	Population (apple orchard)	0.29	-0.12	0.68
	Population (laboratory)	0.24	-0.19	0.76
	Population (Pin Rigide)	0.01	-0.51	0.61
	Sex (males)	**0.55**	**0.18**	**0.92**
	Test Phase (post-exposure)	0.04	-0.18	0.26
Activity Rate	Intercept	-0.42	-0.81	-0.06
	Body-Size	0.13	-0.06	0.31
	Body-Condition	0.03	-0.09	0.14
	Population (apple orchard)	0.20	-0.21	0.58
	Population (laboratory)	**0.51**	**0.07**	**1.01**
	Population (Pin Rigide)	0.06	-0.52	0.62
	Sex (males)	0.32	-0.06	0.72
	Test Phase (post-exposure)	0.15	-0.06	0.36
Central Quadrats	Intercept	-0.16	-0.49	0.22
	Body-Size	-0.06	-0.24	0.13
	Body-Condition	0.07	-0.04	0.17
	Population (apple orchard)	0.17	-0.24	0.61
	Population (laboratory)	-0.34	-0.86	0.14
	Population (Pin Rigide)	-0.28	-0.87	0.29
	Sex (males)	0.34	-0.04	0.72
	Test Phase (post-exposure)	0.02	-0.20	0.22
Capture Latency	Intercept	-0.21	-0.54	0.12
	Body-Size	-0.17	-0.36	0.00
	Body-Condition	0.07	-0.03	0.16
	Population (apple orchard)	0.43	0.04	0.80
	Population (laboratory)	**1.32**	**0.84**	**1.73**
	Population (Pin Rigide)	**0.30**	**-0.24**	**0.84**
	Sex (males) *	**-0.44**	**-0.79**	**-0.06**
	Test Phase (post-exposure)	-0.15	-0.33	0.06
Attacks	Intercept	-0.11	-0.46	0.28
	Body-Size	0.01	-0.18	0.22
	Body-Condition	-0.09	-0.20	0.01
	Population (apple orchard)	0.11	-0.28	0.52
	Population (laboratory) *	**0.49**	**0.00**	**0.97**
	Population (Pin Rigide)	-0.31	-0.87	0.28
	Sex (males)	0.24	-0.17	0.64
	Test Phase (post-exposure)	**-0.22**	**-0.42**	**-0.01**

Table A3-2. Between (V_{BI}) and within-individual (V_{WI}) variance components compared across treatments. Model 1 corresponds to a univariate model where V_{BI} and V_{WI} are equal across treatments. Model 2 corresponds to a bivariate model where V_{BI} and V_{WI} are estimated independently for each sex.

				Males						Females					
Trait	Model	DIC	ΔDIC	V_{BI}	Lower CI	Upper CI	V_{WI}	Lower CI	Upper CI	V_{BI}	Lower CI	Upper CI	V_{WI}	Lower CI	Upper CI
Total Quadrats	1	932.88	-	0.30	0.12	0.47	0.68	0.55	0.85	0.30	0.12	0.47	0.68	0.55	0.85
	2	948.19	-15.30	0.38	0.14	0.60	0.68	0.48	0.86	0.21	0.10	0.44	0.75	0.60	1.00
Activity Rate	1	911.57	-	0.25	0.07	0.42	0.69	0.58	0.93	0.25	0.07	0.42	0.69	0.58	0.93
	2	914.54	-2.97	0.33	0.13	0.61	0.72	0.51	0.97	0.20	0.12	0.47	0.72	0.55	0.93
Central Quadrats	1	953.29	-	0.20	0.04	0.38	0.71	0.62	0.97	0.20	0.04	0.38	0.71	0.62	0.97
	2	958.94	-5.66	0.26	0.11	0.47	0.78	0.59	1.05	0.20	0.11	0.47	0.71	0.56	0.95
Capture Latency	1	782.46	-	0.48	0.33	0.64	0.38	0.32	0.49	0.48	0.33	0.64	0.38	0.32	0.49
	2	788.92	-6.46	0.57	0.34	0.83	0.35	0.25	0.48	0.45	0.24	0.65	0.42	0.34	0.59
Attacks	1	949.39	-	0.21	0.06	0.40	0.74	0.60	0.94	0.21	0.06	0.40	0.74	0.60	0.94
	2	952.39	-3.00	0.42	0.19	0.62	0.64	0.48	0.88	0.20	0.08	0.36	0.82	0.64	1.04