Interpopulation Variations in Behavioral Syndromes of a Jumping Spider from Insecticide-Treated and Insecticide-Free Orchards

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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 (3nd and 4th 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 ($\pm$ 0.001 mm) using a WILD MMS 225 digital length measuring set. Body mass was determined ($\pm$ 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 ($\varnothing$ = 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 $1 \times 1 \times 4.5$ 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 ΔDIC < 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 $r_{insecticide-treated}$ - $r_{insecticide-free}$) 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 ΔAIC < 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: $1.49 \pm [1.30; 1.68]$; insecticide-treated: $1.07 \pm [0.85; 1.29]$) (Table 2-2), while individuals from the insecticide-treated orchard tended to be more voracious (number of prey captured) (insecticide-free: $3.01 \pm [2.59; 3.43]$; insecticide-treated: $3.54 \pm [3.03; 4.05]$). There was a significant population $\times$ 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: $0.95 \pm [0.89; 1.01]$; 2011: $0.46 \pm [0.31; 0.62]$).

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 ($\Delta r =$ 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 ($\Delta r = -0.64 ± [-1.07; -0.23]$; 99.7 % of estimates < zero), and correlation differences between climbing activity vs. voracity ($\Delta r = -0.29 ± [-0.72; 0.08]$; 94.0 % of estimates < zero) and aggression vs. voracity ($\Delta r = 0.33 ± [-0.14; 0.73]$; 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.

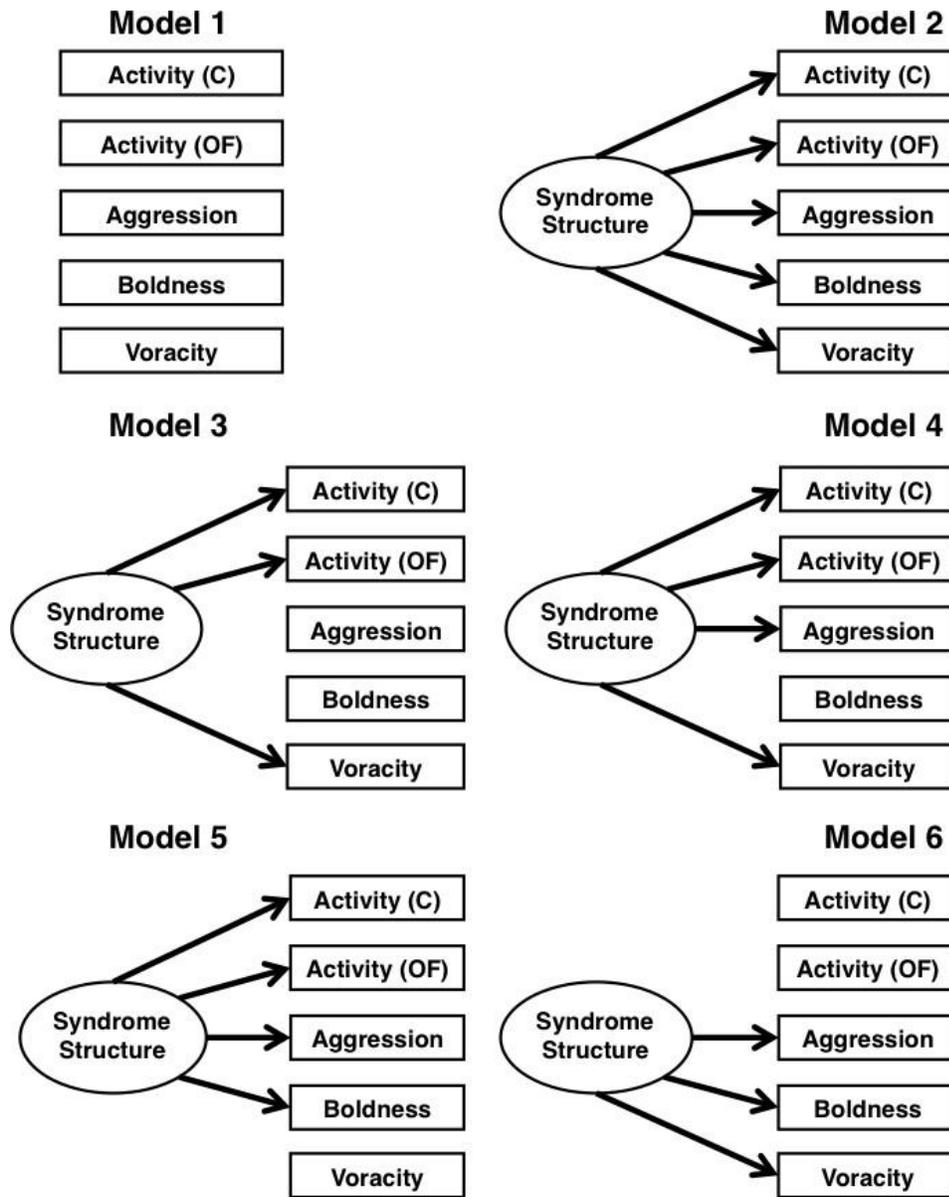| Population	Model	k	AIC	ΔAIC	W	E.R.
Insecticide-Free						
	2	**10**	**1247.8**	**0**	**0.76**	**1.00**
	5	9	1250.9	3.15	0.16	4.83
	6	8	1253.9	6.11	0.03	21.3
	4	9	1254.5	6.74	0.03	29.0
	3	8	1254.6	6.82	0.02	30.2
	1	5	1267.8	19.99	0.00	21785.5
Insecticide-Treated						
	6	**8**	**838.5**	**0**	**0.69**	**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.
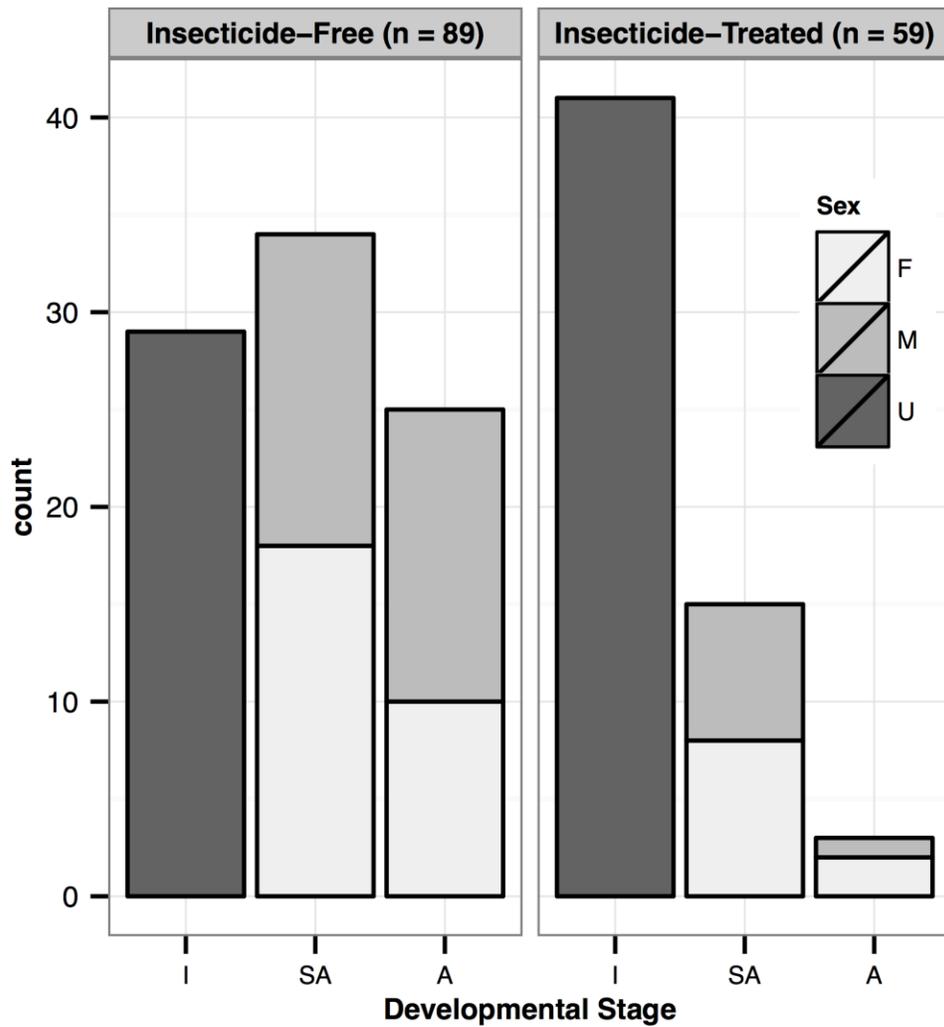
Fig. 2-2: Demographic structure compared between the insecticide-free and insecticide-treated populations. F: females, M: males, U: unknown, I: immatures, SA: sub-adults, A: adults.
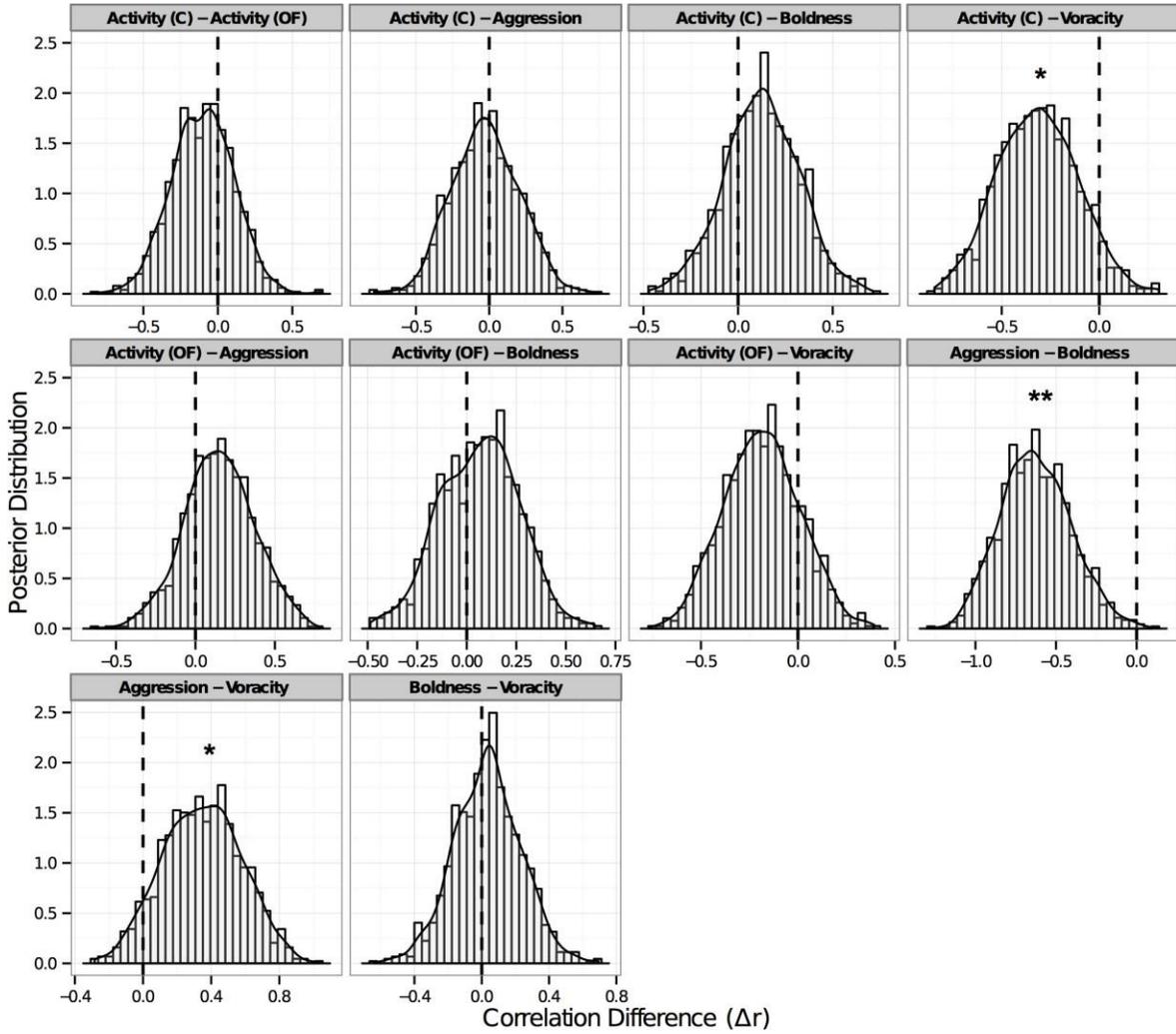
Fig. 2-3: Posterior distribution for the difference in correlation estimates between the insecticide-treated and insecticide-free populations (Δr). * more than 90 % of estimates exclude zero, ** more than 95 % of estimates exclude zero.
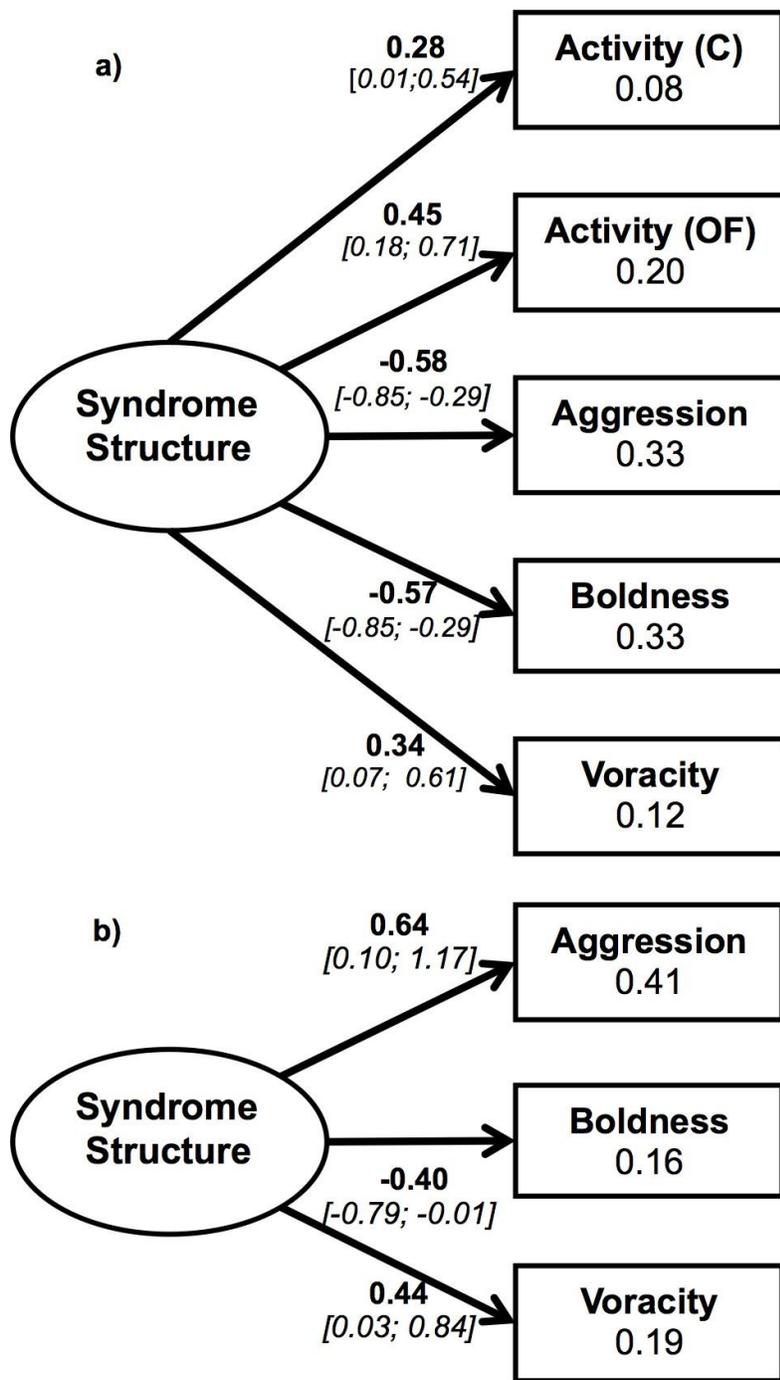
Fig. 2-4: Path coefficients for best models of syndrome structure in the insecticide-free (a) and insecticide-treated (b) orchards. The number associated with arrows represent standardized coefficients. Numbers in brackets represent 95 % confidence intervals for each path coefficients and numbers in boxes correspond to the R^2 for a given behaviour (i.e., the **%** of variance explained by the latent variable for each behaviour).

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Supporting Information

Additional supporting information may be found in the online version of this article: Table S1. Deviance information criterion (DIC) for the selection of significant fixed effects in multiresponse models. Bold indicates significant fixed effects compared with the null model for ΔDIC <2.