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

Raphaël Royauté†, Christopher M. Buddle* & Charles Vincent†

* Department of Natural Resource Sciences, McGill University, Ste-Anne-de-Bellevue, QC, Canada
† Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, Saint-Jean-sur-Richelieu, QC, Canada

Abstract

Variations in environmental conditions can influence behavioral syndromes (correlated tendencies in behaviors), and understanding the factors that shape trait covariation is particularly relevant when species are challenged by environmental changes. We investigated how behavioral 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. Behavioral syndrome structure was compared between the two populations using Bayesian multiresponse 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 behavioral types vs. aggressive and bold types while the insecticide-treated population showed a negative correlation between aggression-boldness and voracity. This research is a first step in investigating the impact of anthropogenic disturbances on behavioral syndromes and demonstrates that behavioral syndromes may vary with respect to insecticidal applications.

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 behavioral shifts (Sol et al. 2013). Behavioral variation plays a central role in the context of species’ response to HIREC. Species that express a wide range of behavioral phenotypes or that adjust their behaviors to current environmental conditions may cope better with HIREC (Sih et al. 2010).

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

A key research avenue for behavioral ecology is to link changes in behavioral variation to the intensity and frequency of HIREC. One interesting feature of behavioral 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 interspecific competition (Dochttermann et al. 2012) are known to affect the direction and strength of behavioral 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 behavioral 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 & Szinétár 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 & Szinétár 2002). Finally, frequent exposure to pesticides can cause a variety of direct or indirect behavioral shifts. At sublethal doses, pesticidal exposure can disrupt behavioral expression (Desneux et al. 2007) and may affect the strength or direction of behavioral syndromes. In addition, pesticidal application causes dramatic shifts in arthropod communities (Letourneau & 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 & Rypstra 1995; Riechert & Lawrence 1997). Their performance as biocontrol agents depends on suites of behavioral characteristics such as intraguild predation (Balfour et al. 2003), cannibalism (Buddle 2002), prey preference (Toft 2005; Harmon & Andow 2007), and dispersal capacities in agricultural habitats (Sackett et al. 2009; Royauté & Buddle 2012). Various studies have shown correlations between such behavioral characteristics, notably aggression, boldness, and voracity (Riechert & Hedrick 1993; Johnson & Sih 2005, 2007). In this 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 behavioral ecology (Jackson & Pollard 1996; Jakob et al. 2011; Nelson & Jackson 2011a,b; Uhl & Elias 2011). However, few studies have documented individual variations in their behavioral traits (but see Sweeney et al. 2013a), notably concerning anthropogenic disturbance.

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

Methods

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 2 yrs (Dondale 1961). Individuals reproduce in mid-June and spiderlings emerge around the end of July. Individuals overwinter as juveniles and become subadults (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 Québec, 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 in 1988 and was treated with other fungicides (mean number of treatments over 5 yrs ± 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 behavioral 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 & Jakob 2000) and a small plastic straw retreat (L = 2.5 cm, φ = 1.2 cm). Water was provided ad libitum 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 (3rd and 4th instars Acheta domestica) depending on the developmental stage of the spider. Immature spiders were fed five D. melanogaster per week, while subadult spiders were fed three D. hydei per week. Adult spiders were offered four D. hydei and one A. domestica per week.

**Behavioral 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 behavioral 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 behavioral 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 48 h.

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 min 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 behavioral data were recorded using video playback with The Observer XT.

**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-cm³ plastic syringe taped vertically at the base of a 50 cm length apple tree log (φ = 15 cm) and were left at rest for 2 min. They were individually released at the base of the log and given a maximum of 15 min 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.

**Activity: open-field test**

Open-field arenas are commonly used to assess variations in activity and exploratory behaviors in animal personality studies (Montiglio et al. 2010). As Carducci & Jakob (2000), we used a 30 × 30 cm wooden arena divided into 36 5 × 5 cm quadrats. The spiders were put in a 5-cm³ plastic syringe for 2 min 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 min in 2010, and the duration of the test was reduced to 5 min in 2011. Duration of the test had no effect on activity (t = −1.02, df = 130, p = 0.31). Activity was strongly correlated with the total explored surface (i.e., number of unique quadrats visited, r = 0.74, n = 98, p < 0.001).

**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 & Jackson 2009). Aggressive contests in Eris militaris are very similar to that of other jumping spider species, and male-to-male contests proceed 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 zigzag 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 $25 \times 7$ cm plastic arena with opaque walls. A $7 \times 7$ cm mirror was taped on a vertical side (i.e., 7 cm) of the arena. Petroleum jelly was applied to the three other vertical sides (i.e., $2 \times 25$ cm and 7 cm) of the arena to prevent the spider from escaping. Spiders were left to acclimate for 2 min in a $2.5 \times 7$ cm section at the side opposite to the mirror using a $7 \times 7$ 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 min 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 zigzag) from the first orientation toward the mirror to retreat or until the 20 min limit was reached. Spiders with higher time spent reacting to their mirrored image were considered as most aggressive. Approximately 30% of the spiders did not show any sign of response to their mirrored image and were not given any value for aggression.

**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 $50 \times 7$ cm plastic arena with opaque walls and petroleum jelly applied on two vertical sides (i.e., $2 \times 50$ 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 $5 \times 7$ 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 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.

**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 min, and the total number of prey captured was recorded. Preliminary tests showed that if prey items were presented to the spider every 15 min until the spider stopped feeding, the number of captures in the first 60 min of the test was strongly correlated with the total number of prey captured ($r = 0.87$, $n = 85$, $p < 0.001$).

**Statistical Analyses**

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

**Mean population differences in behavior and morphology**

We compared mean behavioral and morphological values (i.e., body size and mean body condition) between orchard populations using one-way ANOVAs. Similarly, all behaviors 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).

**Behavioral correlation estimations per population**

We used Bayesian multiresponse mixed modeling in package MCMCglmm (Hadfield 2010) to estimate behavioral correlations per population and correct for fixed effects (Dingemanse & Dochtermann 2013). This approach has the advantage of removing the need for adjustment of error rates (e.g., Bonferroni correction). Moreover, because behavioral correlations are often <0.2, statistical significance based solely on p-values is overconservative (Garamszegi et al. 2013). Instead,
we estimated the magnitude of the correlation based on a continuous scale (|r| ~ 0.1: weak effect, |r| ~ 0.3: medium effect, |r| ~ 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 behavioral 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 with 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 S1).

To compare behavioral correlations across populations, we split the data into two sets, each containing the behavioral values for a given population. We fitted a multireponse 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 & Rubin 1992). We compared the strength and precision of behavioral 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.

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 behavior 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. 1). Model 1 represents the null model where all behaviors vary independently of each other. Model 2 is a domain-general model where all behaviors 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 behaviors 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 & Sih 2005, 2007). Model 5 represents a situation where behaviors 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 Akaike information criterion (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 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 & Anderson 2002).

Results

Behavioral and Morphological Differences Between Populations

The two populations were different in terms of spider abundance, proportion of developmental stages, morphology, and average behaviors. All sexes and life stages were represented in the insecticide-free population (Fig. 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 1) and had higher climbing activity (cm/s) (X ± [lower Confidence Interval; upper CI], insecticide-free: 1.49 ± [1.30; 1.68]; insecticide-treated: 1.07 ± [0.85; 1.29]) (Table 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, behaviors were consistent between years except for boldness, which had a lower average in 2011 (\( \bar{x} \pm [\text{lower CI}; \text{upper CI}], 2010: 0.95 \pm [0.89; 1.01]; 2011: 0.46 \pm [0.31; 0.62] \)).

Syndrome Structure Compared Across Populations
When correcting for effects of body size, developmental stage, and sex with multiregression models, we observed significant differences in behavioral correlations between populations. There was no overall difference in correlation strength between populations (\( \Delta r = 0.03 \pm [-0.78; 0.55] \)) and behavioral correlations were highly variable depending on the pair of behavior considered (\( r = -0.12 \pm [-0.40; 0.45] \) (Table 3). In the insecticide-free population, we found significant positive correlations between climbing and open-field activity (posterior mode \( r = 0.29 \pm [0.003; 0.48] \)), activity and voracity (climbing activity vs. voracity: \( r = 0.33 \pm [0.06; 0.51] \); open-field activity vs. voracity: \( r = 0.18 \pm [0.01; 0.44] \)), and between aggression and boldness (\( r = 0.42 \pm [0.05; 0.57] \)). This population also showed negative correlations between open-field activity, aggression and boldness (open-field activity vs. aggression: \( r = -0.25 \pm [-0.43; 0.07] \); open-field activity vs. boldness: \( r = -0.19 \pm [-0.44; 0.05] \)) and between boldness and voracity (\( r = -0.16 \pm [-0.44; 0.03] \)). 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: \( r = -0.26 \pm [-0.60; -0.001] \); aggression vs. voracity: \( r = 0.28 \pm [-0.17; 0.55] \); boldness vs. voracity: \( r = -0.18 \pm [-0.45; 0.15] \)). In addition, the posterior distribution of difference in correlation strength significantly excluded zero for the aggression-boldness correlation (\( \Delta r = -0.64 \pm [-1.07; -0.23] \); 99.7% of estimates < zero), and correlation differences between climbing activity vs. voracity (\( \Delta r = -0.29 \pm [-0.72; 0.08] \); 94.0% of estimates < zero) and aggression vs. voracity (\( \Delta r = 0.33 \pm [-0.14; 0.73] \); 92.9% of estimates < zero) had >90% of the posterior distribution excluding zero (Fig. 3).

SEM analysis confirmed that the syndrome structure differed in the two populations (Table 4). We found strong evidence for the presence of a behavioral syndrome in the insecticide-free population as the null model (Model 1) was ranked last (\( \Delta \text{AIC} \approx 20 \)). The domain-general model (Model 2) was selected as the best model, followed by the risk model (Model 5) (\( \Delta \text{AIC} = 3.15 \)) and the risk-voracity model (Model 6) (\( \Delta \text{AIC} = 6.11 \)). In the insecticide-treated population, the risk-voracity model (Model 6) ranked first, and the null model was also rejected (\( \Delta \text{AIC} = 3.62 \)).

Interpretation of path coefficients for Model 2 showed an opposition between active-voracious and bold-aggressive behavioral types in the insecticide-free population. This indicated that active and
Table 3: Behavioral 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).

<table>
<thead>
<tr>
<th></th>
<th>Climbing activity</th>
<th>Open-field activity</th>
<th>Aggression</th>
<th>Boldness</th>
<th>Voracity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climbing activity</td>
<td>–</td>
<td>0.15 (54)</td>
<td>–0.06 (35)</td>
<td>0.03 (53)</td>
<td>–0.11 (55)</td>
</tr>
<tr>
<td>Open-field activity</td>
<td>0.29 (72)</td>
<td>–0.18; 0.43</td>
<td>−0.39; 0.30</td>
<td>−0.21; 0.37</td>
<td>−0.32; 0.30</td>
</tr>
<tr>
<td>Aggression</td>
<td>−0.02 (48)</td>
<td>0.25 (63)</td>
<td>–</td>
<td>0.26 (36)</td>
<td>0.28 (39)</td>
</tr>
<tr>
<td>Boldness</td>
<td>−0.08 (61)</td>
<td>0.19 (73)</td>
<td>0.42 (50)</td>
<td>−0.60; −0.001</td>
<td>−0.17; 0.55</td>
</tr>
<tr>
<td>Voracity</td>
<td>0.33 (73)</td>
<td>0.18 (88)</td>
<td>−0.13 (64)</td>
<td>−0.16 (74)</td>
<td>–</td>
</tr>
</tbody>
</table>

Bold values indicate significant correlations based on overlap of 95% CI with zero. Numbers in parentheses indicate the number of pairwise observations for a given correlation coefficient estimate.

Fig. 3: Posterior distribution for the difference in correlation estimates between the insecticide-treated and insecticide-free populations (∆r). * more than 90% of estimates exclude zero, ** more than 95% of estimates exclude zero.
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. 4a–b).

Discussion

We found evidence for interpopulation variation in behavioral 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 behavioral traits along a continuum between active and voracious behavioral types vs. bold and aggressive types. In the insecticide-treated population, climbing and open-field activity did not correlate with any other behavior, and we found a negative correlation between boldness and aggression-voracity.

Our results contrast with those of previous studies investigating interpopulation variations of behavioral syndrome in spiders. The presence of a general aggression-boldness syndrome is a well-established fact in the spider literature (reviewed by Pruitt & Riechert 2012), though variation exists between species. Studies that have documented syndrome variation across two or more populations in spiders showed little interpopulation variations. Riechert & 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 behavior were observed across populations. Pruitt et al. (2010) showed that the social spider Anelosimus studiosus shared within-population behavioral correlations even when populations were strongly geographically separated. Our study provides evidence that interpopulation 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 behavioral syndromes has been the subject of few publications. Scales et al. (2011) compared populations of song sparrows (Melospiza melodia)

| Table 4: AIC comparisons for all a priori models of syndrome structure across populations |
|---------------------------------|-------|---------|---------|-------|------------------|
| 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 |

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.

Fig. 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 behavior (i.e., the % of variance explained by the latent variable for each behavior).
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 behavioral 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 behavioral syndromes in the two spider populations, caution is warranted when relating results directly to insecticidal disturbance because 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 behavioral 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 behavioral types from the insecticide-treated population. Interpopulation variation in syndrome structure can be indicative of adaptation to local environmental conditions. For example, populations of three-spined sticklebacks show strong evidence of behavioral 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 using mark–recapture method to witness the survival of individuals of known behavioral type (Bell & Sih 2007; Sweeney et al. 2013b).

Second, the two populations possibly shared the same behavioral syndrome but behavioral 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 behavioral and physiological shifts (Desneux et al. 2007; Pekar 2012). For example, exposure to organophosphate can cause shifts in circadian activity and affect mating behavior in certain spider species (Tietjen 2006; Tietjen & Cady 2007). In addition to causing shifts in average behavior, insecticides could also affect behavioral variation and uncouple previously correlated behaviors. However, sublethal intoxication can be limited in duration (Desneux et al. 2004), 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 to monitor the resulting effects on behavioral 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 & Goldstein 2001; Whitehouse et al. 2005), affecting in turn the behavioral response of individuals. Although 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 intraspecific competition at early stages in the insecticide-treated population. It can also explain the presence of aggressive and voracious behavioral 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 behavioral syndrome. If adults and juvenile stages differ in their behavioral 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 behavioral syndrome were recently demonstrated in the spider Agelenopsis aperta 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 behavioral syndrome over ontogeny will enable to test this possibility.

Our research is a first step in investigating the consequences of anthropogenic changes on behavioral variation in agroecosystems. We demonstrated that behavioral 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
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orchards, behavioral 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 behavioral syndromes. The next step would be to investigate each of these processes and determine which have the most influence on the generation of behavioral syndromes in a context of increasing anthropogenic change.

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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 ∆DIC <2.