

## Article

# Behavioral predictability in a lynx spider is interactively influenced by mean behavior, prey density, and an insecticide

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## Abstract

Behavioral predictability, i.e., short-term intra-individual variability under relatively constant environmental conditions, has only recently begun to gain attention. It is unknown, however, whether predictability of individuals with distinct mean behavior changes differently as a response to ecological factors such as resource availability. Moreover, the response might be affected by anthropogenic contaminants that are ubiquitous in the environment and that can affect animals' variability in behavior. Here, we investigated the relationship between mean predatory activity and predictability in predatory activity along a prey density gradient in the lynx spider *Oxyopes lineatipes*. We further examined how this relationship is influenced by insecticides, azadirachtin, and a plant extract from *Embelia ribes*. We found that all studied variables affected the predictability. In the control and *Embelia* treatments, that did not differ significantly, the predictability decreased with increasing prey density in a mean behavior-specific way. Individuals with low mean predatory activity were relatively less predictable than were those with high activity from low to moderate prey densities but more predictable at high prey densities. Azadirachtin altered this pattern and the individuals with low predatory activity were less predictable than were those with high predatory activity along the whole gradient of prey density. Our results show that predictability can change along an environmental gradient depending on a mean behavior. The relative predictability of the individuals with distinct mean behavior can depend on the value of the environmental gradient. In addition, this relationship can be affected by anthropogenic contaminants such as pesticides.

**Key words:** azadirachtin, environmental gradient, intra-individual variability, pesticide, resource availability.

Investigating the causes and consequences of behavioral variability is the keystone of behavioral ecology. However, behavioral variability in a population is highly complex and involves several components (Westneat et al. 2015; Stamps 2016). One component is behavioral predictability, which refers to short-term intra-individual variability in behavior under relatively constant conditions (Stamps et al. 2012). In other words, this is the degree to which an individual

behaves differently in identical situations. Predictability has started to gain more attention only recently and therefore its adaptive function and the factors that influence it remain poorly understood (Pruitt et al. 2011; Stamps et al. 2012; Biro and Adriaenssens 2013; Westneat et al. 2015; Okuyama 2015; Stamps 2016).

Predictability can, for example, influence predator–prey interactions (Stamps et al. 2012; Briffa 2013; Chang et al. 2017).

Unpredictable behavior in prey can reduce the probability of being captured, because a predator is unable to learn the prey's activity pattern (Briffa 2013). On the other hand, prey can alter the timing of their own foraging activity to correspond with times they expect a predator's activity to be low and thereby minimize their probability of encountering predators (Tambling et al. 2015). Therefore, unpredictable predators might enjoy higher predation success than do predictable predators, because prey may be unable to learn such predators' activity patterns. However, if we want to know the adaptive function of predictability, we first need to know which factors influence it so that we can generate testable hypotheses about its adaptiveness.

Predictability of a behavior can be influenced by various internal and external factors. The internal factors can be related to the inter-individual differences in mean behavior (Stamps et al. 2012; Chang et al. 2017; He et al. 2017). For example, bolder individuals can be more predictable than shy individuals (Chang et al. 2017). The external factors that have been found to influence the predictability are temperature (Briffa et al. 2013) and pesticides (Royauté et al. 2015). To date, however, no study has investigated how the predictability changes along an ecological gradient in relation to mean behavior.

A common ecological gradient, which the foragers encounter in nature, is the spatio-temporal gradient of food availability (Stephens et al. 2007). Prey of predators has patchy occurrence in nature, and its densities are highly changeable among these patches (Stephens et al. 2007). Predictability in predatory activity may, consequently, change in response to different prey densities (Figure 1A). There is, for instance, a natural fluctuation in predatory activity of spiders that follows the satiation-hunger dynamics (e.g., Michalko and Košulič 2016). The prey density may influence the amplitude of the fluctuations (Figure 1A). At low prey densities, a predator's state of satiation can switch to the state of hunger before it encounters another prey item. Consequently, the predator will be motivated to prey during each encounter with a prey item (Holling 1965). This will result in a relatively constant predatory activity and low intra-individual variability, i.e., high predictability (Figure 1A). At high prey densities, the encounter rate can be so high that it enables feeding *ad libitum* and the foraging bouts to be followed by relatively long periods of predatory inactivity (Figure 1A). This will result in relatively large fluctuations in predatory activity and low predictability in predatory activity (Figure 1A). The predictability may therefore decrease with prey density (Figure 1B).

The individuals with distinct mean behavior may, however, adjust their repeatability as a response to the changing prey density differently (Figure 1). For example, the individuals with different level of predatory activity often differ also in their level of shyness, i.e., willingness to take a risk (Pruitt and Riechert 2012). The shy individuals with low predatory activity invest more into maintaining vigilance against enemies rather than into foraging and they are motivated to prey at lower energy states than the bold individuals with high predatory activity do (Riechert and Hedrick 1993; Pruitt and Riechert 2012). At low prey densities, after consuming one prey item, the state of satiation may switch to that of hunger before encountering another prey item in all individuals, regardless of their mean behavior. The predatory activity may remain constant and consequently the predictability may remain relatively high and will not differ between the individuals with different mean predatory activities (Figure 1). At high prey densities, the encounter rate with prey can be greater than the decrease in energy states to the motivation level for foraging in the shy individuals. Bold individuals, on

the other hand, will still be motivated to prey. Therefore, at high prey density, the predatory activity might fluctuate in the shy individuals but it might remain constantly high in the bold individuals. As a consequence, the differences in the predictability between the individuals with different mean predatory activity might increase with growing prey density because the predictability of shy and bold individuals will decrease rapidly and slowly, respectively (Figure 1B).

The way in which individuals with distinct mean behavior adjust their repeatability according to prey density might be affected by the sub-lethal doses of pesticides, which can have various effects on behavior (Pekár 2012). For example, the sub-lethal doses of pesticides can reduce mean predatory activity of pests' natural enemies (Michalko and Košulič 2016). The research on the sub-lethal effect of pesticides traditionally focused on the mean behavior (Pekár 2012). Recently, some authors (Montiglio and Royauté 2014; Royauté et al. 2015) emphasized that the research on the sub-lethal effects of pesticides should focus also on the variability in behavior. For example, Royauté et al. (2015) found that an insecticide did not affect the population mean in a set of behaviors in a salticid spider. However, the insecticide reduced inter-individual variability and increased intra-individual variability, i.e. reduced predictability (Royauté et al. 2015). As both, the mean and the variability in behavior, influence the predator-prey interactions (Pruitt et al. 2016; Chang et al. 2017; Michalko and Pekár 2017), it is necessary to investigate the effect of pesticides on the behavioral variability if we are to evaluate their toxicity and predict their possible impact on the ecological dynamics.

In the present work, we investigated the relationship between mean predatory activity and predictability in predatory activity along the prey density gradient in the lynx spider *Oxyopes lineatipes* (C.L. Koch, 1847). We further investigated how this relationship is influenced by exposure to two pesticides, namely azadirachtin and a plant extract from *Embelia ribes* (Burm f.) (Primulaceae). *Oxyopes lineatipes* is a cursorial spider that is highly abundant within various agroecosystems in South-East Asia; it also occurs in higher vegetation, on branches, and in canopies (Barrion and Litsinger 1995; Murphy and Murphy 2000). We expected that (1) the predictability will decrease with increasing prey density, but (2) the predictability will decrease more slowly in those individuals with high mean predatory activity than in those individuals with low mean predatory activity, and (3) the pesticides will alter the relationship between mean behavior, predictability, and prey density.

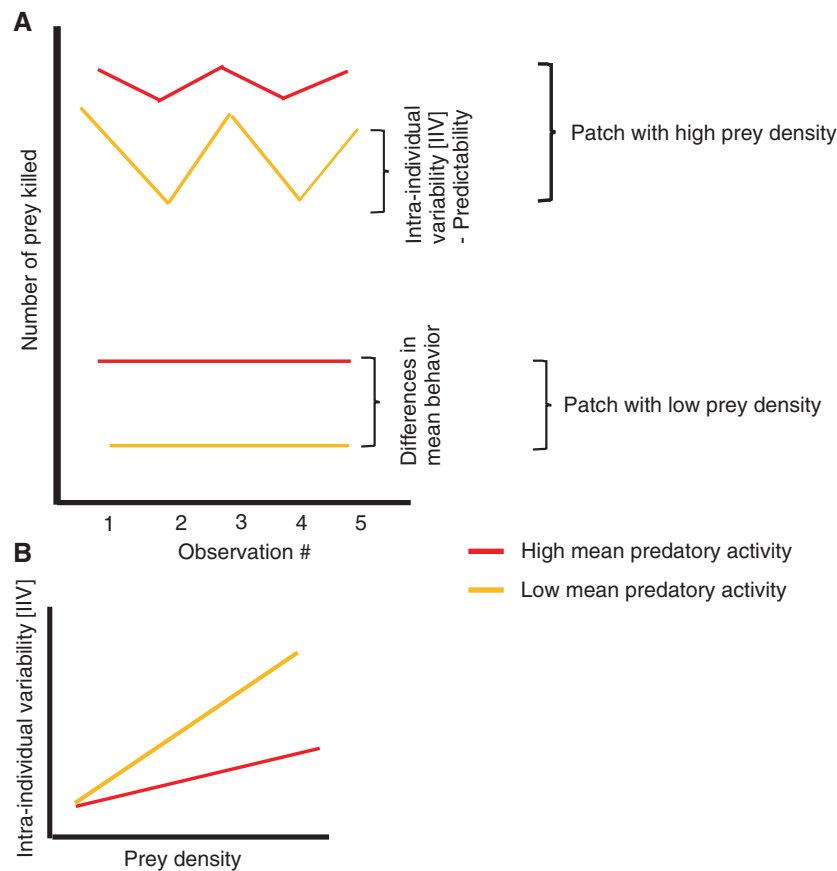
## Materials and Methods

### Spider collection

We collected 75 subadult and adult females of *O. lineatipes* (mean carapace length = 2.2 mm, *SE* = 1.3, range = 0.9–2.7) by sweeping and visually searching herbaceous vegetation from crop fields on the experimental farm of Kamphaeng Saen Campus in Nakhon Pathom (Thailand) at the end of June 2014. The crop fields had not been sprayed with pesticides. Size did not influence any of the studied parameters (see below). After collection, spiders were kept individually in plastic tubes with a half of a facial tissue at the bottom that was periodically moistened.

### Tested chemicals

We evaluated the effect of two agrochemicals: an extract from dried *E. ribes* leaves and azadirachtin. We chose to compare these two insecticides because *Embelia* is a potential new biopesticide while



**Figure 1.** Conceptual figure explaining how IIV, i.e., behavioral predictability, of individuals with different mean predatory activities may change with prey density. The panel (A) shows the temporal courses of predatory activities of individuals with different mean predatory activities throughout five observations in patches with low and high prey density. At low prey density, there may be small fluctuations in predatory activity among observations because the encounter rate is small and the predators are motivated to prey upon encounter with each prey item. At high prey density, the encounter rate can be high, and it enables the foraging bouts to be followed by relatively long periods of resting. This may result in relatively large fluctuations in predatory activity. Individuals with different levels of mean predatory activity often differ in their level of shyness, i.e., willingness to take a risk. At low prey densities, after consuming one prey item, the state of satiation may switch to that of hunger before encountering another prey item in all individuals, regardless of their mean behavior. Consequently, predatory activity may be relatively constant in all individuals. At high prey densities, the encounter rate with prey can be greater than the decrease in energy states to the motivation level for foraging in the shy individuals with low mean predatory activity. Bold individuals with high mean predatory activity, on the other hand can be often motivated to prey. At high prey density, therefore, the predatory activity might fluctuate in the shy individuals, but it might remain constantly high in the bold individuals. As a consequence, the IIV and differences in IIV between the individuals with distinct mean behaviors might increase with growing prey density (B).

the azadirachtin is a commercial pesticide widely used across various agroecosystems (Stark 2013). Ideally, the pesticides used in the agroecosystems with integrated pest management should have no or minimal effect on the non-target organisms.

The plant extract was prepared as follows. Leaf samples of *Embelia ribes* were air-dried at room temperature (28–32 °C) for 24 h and ground to a powder before extraction. The fixed-bed method was employed to extract plant metabolites. Fixed-bed extraction (hot extraction) was done in a Soxhlet extractor, where the samples were sequentially extracted with *n*-hexane for 8 h. The extracts were then vacuum-filtered through Whatman® No. 1 filter paper and the residue was consequently extracted in dichloromethane and methanol by the same procedure. Solvents were removed on a rotary evaporator and the crude extracts were weighed and refrigerated at 10 °C for further experimentation.

The crude extract from dry *E. ribes* leaves (hereinafter *Embelia*) contains a rich array of bioactive chemicals. The main active ingredient, embelin, is considered to have pesticidal and/or repulsive effects against broad mites, spider mites, and common cutworm

(Noosidum et al. 2007; Insung et al. 2008; Noosidum and Chandrapatya 2015).

Azadirachtin, a chemical compound belonging to the limonoid group, is a secondary metabolite and is present in seeds from the neem tree (*Azadirachta indica* A. Juss., 1830). Azadirachtin is an insecticide acting as an antifeedant, repellent, and deterrent to egg-laying. Azadirachtin is highly effective against thrips, hemipterans, and lepidopterans (Sundaram 1996; Kumar and Poehling 2006). It works as a contact and systemic food poison (Stark 2013).

We tested the lower rate of the recommended field dose for azadirachtin ( $1.25 \times 10^{-4}\%$ ), which is much lower than the lethal concentration required to kill 50% of the population, the so-called  $LC_{50}$  for *O. lineatipes* (0.045; authors, submitted). For *Embelia*, we used the recommended dose (0.75%) because the  $LC_{50}$  for predacious beneficial mites is 0.83% for residual effect and 0.67% for direct contact, respectively (Leelawan et al. 2010). It is desirable to determine the most effective combination of the plant extract concentration and activities of possible biocontrol agents. We used distilled water as the solvent for pesticide dilutions and as a control treatment.

## Experimental design

Spiders were acclimated in the laboratory for 1 week. Laboratory conditions were  $22 \pm 1$  °C,  $70 \pm 5\%$  relative humidity, and a natural photoperiod (Light: Dark = 12: 12). Spiders were fed *ad libitum* with laboratory-reared fruit flies *Drosophila melanogaster* (Diptera, Drosophilidae) 1 week before the experiments to standardize their hunger level.

We used only females because the effect of chemicals can be sex-specific (e.g., Royauté et al. 2015). Spiders were first sorted into five size categories. Thereafter, the individuals within the size categories were assigned to the treatment/prey density (see later) randomly without replacement. We sprayed 50 µl of one or the other of the two tested solutions or water as a control directly onto each spider from a distance of 10 cm using a pharmaceutical pump sprayer. Direct exposure is one of the common modes of exposure in agroecosystems. After 10 s, spiders were removed from the plastic container to Petri dishes (diameter 8.5 cm, height 1.5 cm) containing a wet cotton ball to maintain humidity. The spiders were allowed to acclimate for 30 min. Flightless fruit flies, *D. melanogaster*, maintained on agar medium, were used as prey. The flies were untreated to prevent any effect of contaminated prey. Each spider was exposed to one of the following prey densities: 1, 3, 6, 12, or 25 fruit flies. We conducted five replicates per density/treatment ( $N=75$ ). The experiments were run for 3 days. The number of killed flies was checked every 8 h and the killed flies were replaced with living ones to ensure constant prey densities. We thus obtained eight observations per each individual. Spiders that did not accept prey and molted within 24 h ( $N=2$ ) were excluded from further statistical analyses. All animal experimentation met the ABS/ASAB guidelines for ethical treatment of animals.

## Statistical analyses

All analyses were performed within the R environment (R Development Core Team 2017). We conducted three groups of analyses, namely 1) estimation of repeatability to investigate whether there are consistent inter-individual differences in behavior, 2) estimation of intra-individual variability (IIV) as a measure of predictability for each individual, and 3) investigation of how IIV is influenced by mean behavior, prey density, and pesticides.

### Estimation of repeatability

To investigate whether there are consistent interindividual differences in predatory activity, we computed the adjusted repeatability to avoid potential pseudo-repeatability caused by differences in prey density and size differences (Stoffel et al. 2017). Because the response variable was counts, we used generalized linear mixed effects models (GLMM) with Poisson error structure and log link (GLMM-p) (Stoffel et al. 2017). The fixed effects were represented by prey density, size, and the random effects represented the ID. As we investigated whether there is a significant repeatability in each treatment, we estimated the repeatability for each experimental treatment separately. The statistical significance was tested by permutations while the 95% confidence intervals were obtained by parametric bootstrapping, both with 1000 iterations. The analysis of repeatability was performed within the R package 'rptR' (Stoffel et al. 2017).

### Estimation of predictability

As we were interested in the interaction among mean behavior, predictability, and prey density, we needed an individual-level index

of IIV instead of a population-level estimate of IIV (Stamps et al. 2012; Cleasby et al. 2015; Chang et al. 2017). We therefore used the residual individual standard deviation (i.e., riSD index) as a measure of IIV and the method to obtain it proposed by Stamps et al. (2012). First, we fitted GLMM for each pesticide and control treatment. The response variable was the number of killed prey, the fixed effects were represented by prey density and by time, and the random effects were then represented by ID as a random intercept and by time as a random slope. We used GLMM with gamma error structure and inverse link (GLMM-g) and we also inversely transformed the prey density before the analysis to account for the asymptotic relationship between predatory activity and prey density (Juliano 2001; Pekár and Brabec 2016). In addition, as gamma distribution works only with the positive values, the response variable was  $x+1$  transformed. We next extracted residuals for each individual and each time point and then computed the riSD index (Stamps et al. 2012). The higher the value of IIV, the lower the predictability.

### Relationship between prey density and IIV

To investigate the relationship between IIV, prey density, and mean predatory activity, we used generalized linear models (GLM) with gamma error structure and inverse link function (GLM-g). The response variable was IIV, while the explanatory variables were treatment, standardized mean predatory activity (see later), prey density, and all their 2-fold and the 3-fold interactions. We used this full model because we were specifically investigating how BTs influences the change in predictability along the prey density gradient and how this relationship is affected by the two pesticides.

The two explanatory variables, predatory activity and prey density, required transformations before the analysis. First, as predatory activity increases with prey density (Holling 1965), we had to transform the mean predatory activities of individuals from the different prey densities onto the same scale. We range-standardized the mean predatory activities within each prey density between 0 and 1 separately for each treatment. Consequently, those individuals scored with 0 have the lowest predatory activity within the prey density/treatment, while those with 1 have the highest predatory activity. Second, the prey density was inversely transformed because the relationship between predictability and prey density seemed to be asymptotic during the data exploration (Pekár and Brabec 2016).

The post hoc comparisons were made by the treatment contrasts and if the pesticide treatments proved not to differ significantly, we pooled the levels for the parameters estimation (Pekár and Brabec 2016).

## Results

Size did not influence any of the studied parameters, i.e., repeatability or IIV ( $P > 0.205$ , Supplementary Table S1). There was significant repeatability in predatory activity in all treatments (GLMM-p; 1000 permutations; Control: 0.37,  $CI_{95\%} = 0.13-0.52$ ,  $P = 0.001$ ; *Embelia*: 0.47,  $CI_{95\%} = 0.23-0.63$ ,  $P = 0.001$ ; azadirachtin: 0.14,  $CI_{95\%} = 0-0.27$ ,  $P = 0.028$ ).

The IIV changed along the prey density gradient in a mean behavior-specific way and this mean behavior-specific change differed among the treatments because there was significant three-fold interaction among treatment, prey density, and mean predatory activity (GLM-g,  $P = 0.039$ ; Tables 1 and 2; Figure 2). According to our hypothesis, IIV increased with prey density in all treatments (contrasts,  $P < 0.045$ ; Figure 2). With respect to the pesticide

treatment, the *Embelia* treatment did not differ significantly from the control treatment in any parameters (contrasts,  $P > 0.260$ ). In contrast, the azadirachtin treatment differed significantly from both control and *Embelia* treatments and it altered how the individuals with distinct mean predatory activities adjusted their IIV as a response to the prey density (contrasts,  $P < 0.001$ ; Figure 2). In the control and *Embelia* treatments, there was a significant interaction between density and mean predatory activity (contrasts,  $P < 0.003$ , Table 2; Figure 2A). Consequently, the IIV increased asymptotically with prey density in those individuals with low predatory activity but linearly in the individuals with high predatory activity. In addition, IIV was higher in individuals with low predatory activity than in individuals with high predatory activity at low and medium prey densities, but the opposite was true at high prey densities (Figure 2A). In the azadirachtin treatment, the IIV increased with foraging aggressiveness (contrasts,  $P = 0.045$ ) but foraging aggressiveness had only an additive effect on IIV as the interaction was not significant (contrasts,  $P = 0.525$ ). Thus, IIV increased asymptotically with prey density in individuals with low as well as high predatory activity in the azadirachtin treatment (Figure 2B). The temporal dynamics of predatory activity by individuals with the highest and lowest predatory activities at low and high prey densities in the three treatments are shown in Figure 3.

**Table 1.** Results of the GLM-g error structure and inverse link investigating the effect of pesticide treatment, prey density, and mean predatory activity on the IIV in predatory activity in the lynx spider *Oxyopes lineatipes*

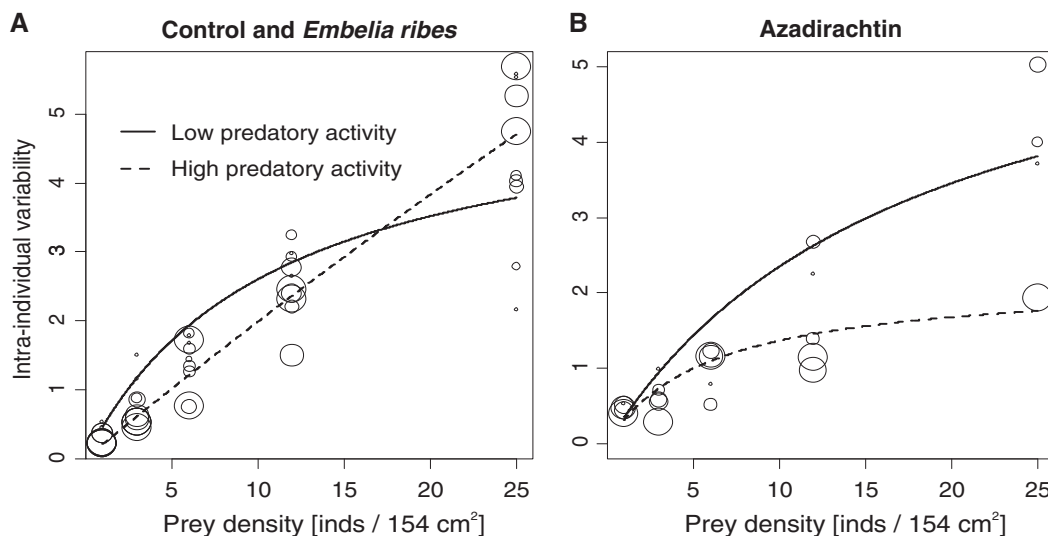
Term	df	F-statistic	P
Treatment	2, 71	7.0	0.002
1/Density	1, 70	473.0	<0.001
Activity	1, 69	3.3	0.074
Treatment: 1/Density	2, 67	1.3	0.274
Treatment: Activity	2, 65	2.8	0.071
1/Density: Activity	1, 64	15.1	<0.001
Treatment: 1/Density: Activity	2, 62	3.4	0.039

**Discussion**

We investigated how mean predatory activity of the lynx spider *O. lineatipes* influences the relationship between predictability in predatory activity and prey density and how this relationship is influenced by two insecticides, azadirachtin and plant extract from *Embelia ribes*. Firstly, in line with our hypothesis, the predictability of predatory activity decreased (IIV increased) with prey density. Secondly, mean behavior influenced the relationship in an unexpected way. In the control and *Embelia* treatments, that did not differ significantly, IIV of individuals with low predatory activity increased asymptotically while IIV of individuals with high activity increased linearly. Consequently, those individuals with low predatory activity were less predictable than were the individuals with high activity from low to moderate prey densities but more predictable at high prey density. There was also a parameter space where the mean behaviors did not differ in their predictability. Thirdly, with respect to the effects of pesticides, only azadirachtin affected the predictability of *Oxyopes*. Where azadirachtin was applied, mean behavior had only an additive effect and the individuals with low predatory activity were less predictable than were individuals with high predatory activity along the whole gradient of prey density.

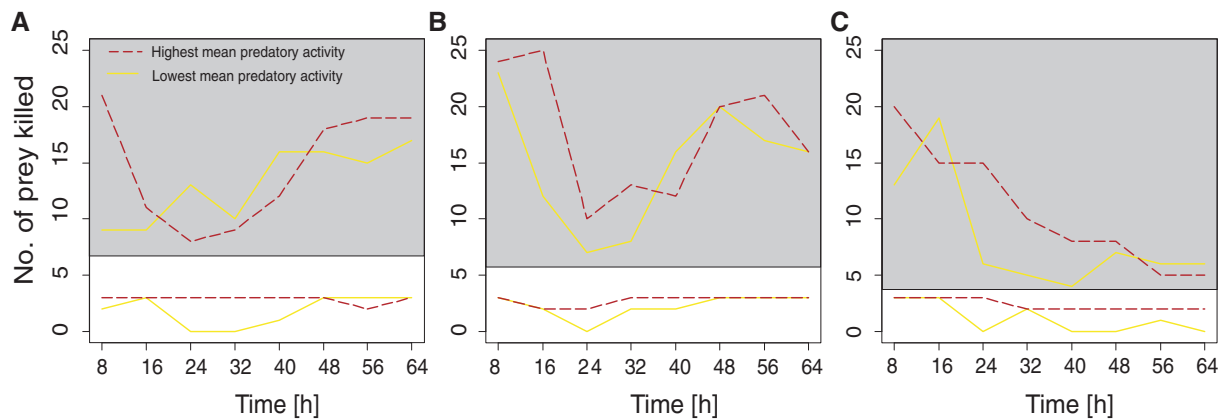
It needs to be noted that we used adult and sub-adult females, which means that the differences in mean predatory activity can be caused by the differences in behavioral types or so-called animal personality as well as by developmental flexibility/plasticity. The different developmental stages can use different behavioral strategies (Westneat and Fox 2010). However, age is highly correlated with size in spiders (Foelix 2011) and we accounted for the size differences in our analyses and therefore also, to a large extent, for the age differences. Nevertheless, we still interpret our results as differences in mean behavior, keeping in mind that they may be caused by the differences in behavioral types as well as developmental flexibility.

Our results have important implication for further studies on behavioral predictability. Studies investigating the relationship between mean behavior and predictability have uncovered various patterns. For example, there has been found a negative, a positive,



**Figure 2.** Relationship among prey density, mean predatory activity (range-standardized within prey density groups), and IIV in the lynx spider *Oxyopes lineatipes* exposed to water control and plant extracts from *Embelia ribes* (A) and the insecticide azadirachtin (B). Higher intra-individual variability indicates lower predictability. Fitted relationships are for those individuals with lowest (0) and highest (1) mean predatory activity. Point sizes correspond with the level of mean predatory activity, with larger points indicating greater predatory activity. The parameter estimates are stated in Table 1.





**Figure 3.** Temporal trend in predatory activity during 64 h by *Oxyopes lineatipes* individuals with the highest and lowest mean predatory activities within treatment/prey density exposed to low prey density (the lower clusters of lines in white fields; 3 flies per 154 cm<sup>2</sup>) or to high prey density (upper clusters of lines in the gray fields; 25 flies per 154 cm<sup>2</sup>) and exposed to water control (A), plant extract from *Embelia ribes* (B), or azadirachtin pesticide (C). Various individuals within the line clusters (prey density and pesticide treatments) are depicted by the different dashing of lines. The individuals differed in their mean predatory activity, which is depicted by different colors.

**Table 2.** Parameter estimates (SE) from the GLM-g error structure and inverse link investigating the effect of pesticide treatment, prey density, and mean predatory activity on the IIV in predatory activity in the lynx spider *Oxyopes lineatipes*. Dash indicates a nonsignificant term. A common estimate for the control and *Embelia* treatments is shown because the two did not differ significantly ( $P > 0.260$ ).

Treatment	Intercept	1/Density	Predatory activity	1/Density: Predatory activity
Control + <i>Embelia</i>	0.184 (0.040)	2.005 (0.346)	−0.166 (0.066)	2.854 (0.599)
Azadirachtin	0.153 (0.074)	2.729 (0.616)	0.307 (0.151)	–

and no relationship between boldness and predictability in boldness (Stamps et al. 2012; Chang et al. 2017; He et al. 2017). Our results show that the distinct pattern might be obtained just because the experiments are conducted at different values of an environmental gradient and because the individuals with distinct mean behavior respond differently to the gradient, which can itself adjust its predictabilities.

Although the exact reason for the observed pattern is unknown, we suggest potential mechanisms that interactively could generate the observed pattern and that can be tested in further experiments. The observed pattern might be caused by 1) the interaction between encounter rate with prey and the hunger-satiation states dynamics, 2) mean predatory activity-specific energy level of motivation to prey and/or differences in metabolism rate, 3) cognitive styles, and 4) the degree of wasteful killing or gluttony.

### Effect of prey density on predictability

The reason for the decrease of predictability with prey density is the only one that is relatively straightforward. In spiders, there is a natural fluctuation in capture rate that follows the satiation–hunger dynamics (Michalko and Košulić 2016). At low prey densities, a spider's state of satiation after a prey capture could switch to a state of hunger before it will encounter another prey item. That would result in a relatively constant capture rate among the time periods. The predictability at high prey density could be lower because the encounter rate of spiders and flies enabled the spiders to feed *ad libitum* during a foraging bout that was followed by a period of digestion and rest. Consequently, the prey capture relatively fluctuated among the time periods.

### Effects of mean behavior on predictability

One possible explanation why the predictability changed in a mean behavior-specific manner might be that those individuals with low predatory activity can be shy while the individuals with high predatory activity can be bold, which relationship often is reported in spiders (Pruitt and Riechert 2012). The shy individuals invest more into enemy vigilance, while bold individuals invest more into foraging. Therefore, unlike the bold individuals, shy individuals are motivated to prey at lower energy states (Pruitt and Riechert 2012). Also, shy individuals might have slower metabolism than do the bold individuals (Shearer and Pruitt 2014). Thus, at low to medium prey density, the encounter rate with flies could be low for the bold individuals and their energy states might reach a level at which they are motivated to prey upon encounter with each prey. In contrast, the encounter rate for the shy individuals could still be sufficiently high and their energy states would not decrease to such level where they would be motivated to prey upon encounter with each prey item. This could be the cause of why that the capture rate in the individuals with high mean predatory activity remained relatively constant, and was accompanied by relatively high predictability, and meanwhile the capture rate fluctuated in the individuals with low predatory activity and predictability was relatively low (Figure 3).

Another possible explanation for the mean predatory activity-specific relationship between predictability and prey density is that individuals with different predatory activity might employ different prey-sampling strategy and/or possess different cognitive styles (Mathot et al. 2012; Sih and Del Giudice 2012). Individuals with low predatory activity can be choosy while the individuals with high predatory activity can be non-choosy (Riechert 1991; Michalko and Pekár 2014, 2017). Various prey represent different quality for generalist spiders, even at intra-specific level, and spiders are able to

recognize that (Toft 1999; Mayntz et al. 2005). In addition, spiders do not know the complete prey offer and need to sample the prey offer first (Stephens et al. 2007). Therefore, the choosy individuals might invest more time to evaluate the prey characteristics and/or overall prey offer at first, then initiate the foraging bout after careful sampling (Mathot et al. 2012; Sih and Del Giudice 2012). The long time spent in prey evaluation followed by the time of foraging bout might have caused the capture rate relatively to fluctuate among the observations. In contrast, the non-choosy individuals decide quickly and attack any prey item that they are able to overcome immediately (Sih and Del Giudice 2012; Michalko and Pekár 2017), and this might cause a relatively constant rate of prey capture. These assumptions might be supported by the fact that some individuals with low predatory activity killed a lower number of prey at first but then their capture rates increased while the individuals with high predatory activity killed high numbers of prey immediately (Figure 3).

The switch in relative predictability of the mean behaviors at high prey density can be explained by the differences in wasteful killing and/or gluttony among the individuals (Samu and Bíró 1993; Maupin and Riechert 2001, Pruitt 2010). The individuals with high predatory activity can be aggressive and perform high wasteful killing and/or consume larger amounts of prey than timid individuals with low predatory activity (Samu and Bíró 1993; Maupin and Riechert 2001; Pruitt 2010; Pruitt and Krauel 2010). The incidence of wasteful killing increases with prey density, as the encounter rate with prey increases and spiders perceive more stimuli from prey (Samu and Bíró 1993). Therefore, the difference in numbers of killed prey between those periods, when the individuals with high predatory activity were in the state of relative satiation with low motivation to prey and periods of relative hunger with high motivation to prey, might increase with prey density. The capture rate of individuals with low predatory activity that engage in low wasteful killing or gluttony might reach the asymptote sooner and the decrease in predictability would therefore also approach the asymptote. Consequently, the capture rate of individuals with high predatory activity might still be in its increasing phase due to wasteful killing and the predictability might continue to decrease linearly below the asymptotic level of the predictability level of the individuals with low predatory activity.

### Effects of pesticides on predictability

Only azadirachtin affected the predictability of the oxyopids while *Embelia* did not have any significant effect. Azadirachtin caused mean behavior to have only an additive effect on the relationship between prey density and predictability in predatory activity, and the individuals with low activity were less predictable than were those individuals with high activity along the whole gradient of prey density. This pattern corresponds with the results of our previous study (authors, submitted manuscript), in which case azadirachtin reduced the capture rate of *O. lineatipes* (which rate decreased continuously through time) while *Embelia* had no significant effect. The reason behind the change in the mean behavior-specific relationship between prey density and predictability due to azadirachtin application is difficult to guess. This is because the pesticides might affect any of those factors that could drive the relationship in the control and *Embelia*, i.e., metabolic rate, appetite, as well as cognitive abilities (Pekár 2012).

Azadirachtin, which is widely used across various agroecosystem, has been traditionally considered harmless for the non-target organisms (Stark 2013). Therefore, our study and results of the recent studies (e.g. Řezáč et al. 2010; authors submitted) show that

azadirachtin can restructure the behavioral architecture in the populations of the pests' natural enemies as it influences mean predatory activity as well as variability in predatory activity. Azadirachtin therefore has a potential to disrupt the biocontrol services provided by the natural enemies.

In conclusion, we show for the first time that behavioral predictability can change along an ecological gradient depending on the differences in mean behavior, which can be the behavioral type, for example. Consequently, the relative predictability of individuals with certain mean behavior can depend on the value of that gradient. In addition, exposure to such anthropogenic contaminants as pesticides can alter that relationship.

### Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>

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