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Association between personality traits and cognitive abilities in jumping spiders

Master thesis

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Annotation:
I measured two personality traits in jumping spiders *Phidippus regius*, boldness and explorativeness, to identify the presence of these traits and their repeatability. Also I analysed the correlation between explorativeness and boldness, and the correlation between these traits and learning abilities of Salticidae spiders.

ACKNOWLEDGEMENTS

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INTRODUCTION

Behavioural types

Recently, in studies of the behaviour of animals, enough attention has been paid to their individual differences in behaviour, called personalities, as well as individual temperaments, behavioural tendencies, behavioural types, or behavioural syndromes (Sih et al., 2004a, 2004b; Reale et al., 2007). Individuals of the same conditions as size, sex and in the same population can consistently differ in their behaviour. For example, some of them can be bolder or more aggressive than others (Bell, 2007). If this behaviour is constant through time and situations and/or across context, it is called personality, or behavioural type (Gosling, 2001).

There is a lot of research focused mainly on humans, primates and domesticated animals personality, but recent studies show that individual differences in personality appear in a wide range of taxa, and there is increasing evidence that these differences are ecologically and evolutionary important (Sih & Giudice, 2012). For example, there are no benefits for an aggressive female to eat male before copulating because she will lay unfertilized eggs and will not reproduce, but it might be explained by an "ecological spillover" of aggressiveness. High level of aggressiveness can help the female survive as a juvenile with poor food sources, however it can cause low fitness in her adulthood. This approach is called 'puzzling behaviour' and it is used when the behaviour of an individual has rewards in one context but costs in another (Bell, 2007). There is often correlation of behavioural tendencies in different contexts. For example, individuals that show more aggressive behaviour in competitive contests also often tend to be bolder in the presence of predators or worse in taking care of their offspring and have higher probability to disperse away from their place of origin (Sih & Giudice, 2012). The purpose of research in this field is to study the causes and consequences of various personality traits. For example, indicators such as activity level and boldness can predict the success of predation, mating, and survival (Lichtenstein et al., 2017).

When investigating behavioural syndromes, two requirements should be met: variation in behaviour should be present, and each individual must be evaluated several times. This can be achieved by running each individual through a series of standardised tests, and evaluating whether differences in individual behaviour are repeatable throughout these tests (Bell, 2007).

Advantages of studying personality in invertebrates

Studying personality in invertebrates has a number of advantages. They have a range of aspects in life histories and behaviour which are rare or absent in vertebrates (metamorphosis, asexual reproduction, eusociality) (Kralj-Fiser & Schuett, 2014), they are easy to maintain in the lab/semi-field conditions, and have fast life cycle and short generation time.

An interesting example of studying peculiarity of invertebrates is described in the research by Schuett et al. (2011). Distinctive behavioural variations in response to predator attacks were observed among individuals of clonal pea aphids, with some of them opting to drop off plants and others choosing to remain. Interestingly, these behavioural tendencies were not consistent at the clonal level. Despite being genetically identical, the clones displayed a range of phenotypes. Moreover, different clones exhibited varying proportions of each phenotype, including dropper, nondropper, and inconsistent responses. The Barth et al. (2010) study on eusocial insects, ant *Platythyrea punctata,* shows that ant workers exhibit behavioural plasticity that depends on the situation rather than displaying consistently aggressive personality traits. Workers who targeted reproductive individuals following an experimental merging of colonies exhibited reduced engagement in nest defence, and conversely. Kralj-Fišer et al. (2013) showed that aggressive males of spider *Larinioides sclopetarius* preferred to mate with aggressive females, and nonaggressive males preferred nonaggressive females, which can cause preservation of aggressivity traits among individuals.

Due to the predaceous nature of spiders, a lot of attention in the published works is given to studying the benefits and costs of aggressive and passive/docile behaviour. There are a lot of behavioural traits that are usually measured in spiders, such as: number of prey killed, size of prey, latency to attack (foraging behaviour); running speed, activity level, exploration (locomotory); boldness, shyness (antipredator); sexual cannibalism, male courtship components, female choice (sexual); tolerance of conspecifics (social); choosiness (habitat selection) (Pruitt & Riechert, 2012).

Thanks to its keen eyesight and noticeable response to the surrounding events, jumping spiders were an object for research for many years. For example, Peckham & Peckham (1890) observed jumping spiders and their behaviour from late 1800. Jumping spiders are also known as animals who can respond to different objects (conspecific, prey, predator) thanks to their good vision (Winsor et al., 2023). The study of Harland et al. (1999) showed

at what distance spiders recognize a reflection in a mirror as a spider. Recently Chang et al. (2017) measured aggressiveness of *Portia labiata* using a test with a mirror. The tests with mirrors help to avoid impact of different size or weight of another spider if boldness or aggressiveness need to be measured in the presence of another spider. Jumping spiders are also capable of using visual cues alone to differentiate between prey and non-prey, as well as among various types of prey (Winsor et al., 2023).

Foraging and mating behaviour of Salticids has been studied for many years, but only recently have new studies begun to emerge about their exploration and learning abilities, not just in mating or foraging context but in absolutely new conditions or reversal learning tests (Aguilar-Arguello & Nelson, 2021).

Cognition

We can describe cognition as the integrating process that uses phylogenetic and individual memory, allows an animal to create an internal model of the world and predict the outcomes of its own actions in a given situation (Menzel et al., 2007). For example, in order to reduce risks and increase the probability of acquiring benefits in the presence of quick and unpredictable changes in the environment, individuals need adaptive abilities that allow them to expect events that are biologically important and adjust their behaviour in accordance with these events (Menzel et al., 2007). Nevertheless, individuals of numerous species throughout the animal kingdom exhibit less behavioural flexibility than anticipated, even in traits that are considered to be plastic. The presence of consistent behavioural variations among individuals, referred to as "personality differences", is puzzling, as flexible behaviour is typically deemed ideal for enabling individuals to respond adaptively to changes in environmental conditions (Liedtke et al., 2015).

Cognition in invertebrates

Despite the fact that much attention in such studies is most often paid to vertebrates, in recent decades scientists have shown that invertebrates are sometimes not inferior even to birds and mammals in solving some tasks (Menzel et al., 2007). For example, Chittka & Skorupski (2011) showed that bumblebees are capable of social learning, that is, the transfer of knowledge from conspecifics, and even that they not only copy each others, but are also able to optimise the strategy which they learned from others for a quick reward. *Drosophila* flies can learn association of odour with aversive stimuli such as electric shock (Menzel et

al., 2007). Learning and memorising abilities were observed in a wide range of insects including ants, crickets, locusts, mosquitos, moths, parasitic and parasitoid wasps (Arican, 2022).

Cognition in spiders

Due to their small brains, spiders were once thought of as primitive "biological machines" driven only by instincts. However, later research is providing growing evidence of their cognitive abilities (Jackson et al., 2011). Tarsitano & Jackson (1997) tested the ability of aranaeophagic jumping spiders *Portia* to plan ahead their path to the prey by constructing special apparatus for detour-planning ability test. Salticidae are capable of solving cognitive tasks, which was previously considered a feature of vertebrates. They can learn association with shape (Dolev & Nelson, 2014), abstract symbols (x/o) (De Agrò et al., 2017; Mannino et al., 2023), colours and other features of preferred/not preferred reward (prey (Skow, C. & Jakob, E., 2006; Taylor et al., 2016), avoiding unpleasant taste (Liedtke & Schneider, 2014)), place-avoidance tasks with aversive stimuli (heat (Nakamura & Yamashita, 2000), vibration (Long et al., 2015), shock (Peckmezian & Taylor, 2015)), maze tasks (Jakob et al., 2007). Salticid aranaeophagic spiders also have an innate predisposition to form search images for preferred prey (spiders) rather than for non preferred prey (insects) (Jackson & Li, 2004). Most jumping spiders are known to be cursorial predators that use their sharp vision in navigating, hunting and communicating. They are able to learn in different contexts, use "trial and error" methods to solve tasks, perform complex navigational detours, and adjust their behaviour in situations that were not experienced before (Pekmezian & Taylor, 2015).

Correlation between behavioural types and cognition

The first description of a connection between cognition and personality of an animal (though formulated in different terms) dates back to Pavlov's work in the beginning of 20th century. Based on these tests, Pavlov introduced four "types" of nervous systems: the "Excitable type" (strong excitatory but weak inhibitory conditioning, low flexibility), the "Inhibited type" (weak excitatory but strong inhibitory conditioning, low flexibility), the "Lively type" (strong excitatory and inhibitory conditioning, high flexibility) and the "Quiet type" (slow but consistent learning, less flexible than the Lively type). These four types of nervous systems, in Pavlov's opinion, determined individual personalities of different dogs (Dougherty & Guillette, 2018). Animals make adaptive decisions during foraging, employing cognitive mechanisms such as sampling prey, forming search images, and

addressing constraints arising from attending to other stimuli that impact fitness. This combination of approaches has enhanced our comprehension of the evolution of behaviour (Skow & Jakob, 2006). Recently, the link between variation in personality and variation in cognition have been made in several publications, and a large number of empirical studies on this topic reveal evidence that variation in personality and variation in learning abilities are related across different species in the absolute scale. This relationship is small but significant (Dougherty & Guillette, 2018).

There is a traditional expectation that bold or exploratory individuals show better results in learning tasks. For example, there is an assumption that bold or explorative animals tend to encounter and navigate their environment more extensively and swiftly. As a result, they come into contact with associations to be learned more readily compared to shy or less explorative individuals (Dougherty & Guillette, 2018). In addition, bold individuals might learn high-activity tasks (e.g. maze-learning) quicker, but be slower in learning low-activity tasks (e.g. avoidance-learning task). For example, quail displaying fearful traits demonstrated faster learning in an avoidance task that demanded reduced activity. However, they exhibited slower performance in a maze-learning task that necessitated higher activity, contrasting with the bolder quail (Miller et al., 2006). Dougherty & Guilette (2018), studying personality and cognition relationship analysis of 25 studies and 19 species, discovered that some of the studies show a positive effect in this relationship (bold, aggressive, explorative, etc. individuals were quicker learners), but some of the studies show negative effect (bold individuals were slower learners and made more mistakes). Sih & Guidice (2012) assume that the relationship between personality and learning abilities may depend on context. They propose the idea that individual variations in the speed-accuracy trade-off define, to some extent, individual differences in cognition, and that these variations are correlated with individual differences on the scale of bold–aggressive–active–exploratory behavioural traits. These authors also argue that in many behaviours the connection between cognitive decision-making styles defined by the speed–accuracy trade-off and several "fast–slow" behaviour traits scales can be provided by the risk–reward trade-off, and that many behavioural traits scales studied by behavioural ecologists are in some way connected with variation along a risk–reward axis. So, we should pay attention to the fact that sometimes exploratory tendency may not have a correlation with ability to learn or solve tasks, because this tendency can affect speed or ability to learn in opposing directions during the process following the appearance of a learning situation (Sih & Guidice, 2012).

While there is increasing number of research on the correlation between personality and decision-making style across various species, the connection between personality and decision-making style across tasks of differing difficulty has not been explored yet (Chittka et al., 2009; Mamuneas et al., 2015; Chang et al., 2018). Most behavioural studies have been conducted on fish, birds and mammals (Gosling, 2001) and only in the last 2 decades have studies on arthropods begun to appear. For example, Udino et al. (2017) showed that the performance in learning tasks was significantly correlated with the exploratory behaviour of individual ants, *Camponotus aethiops*. Those classified as "active-explorers" demonstrated a slower learning pace compared to their "inactive-explorer" counterparts. This study reveals, for the first time, a connection between a personality trait and cognitive performance in eusocial insects, highlighting the potential impact of individual variability on colony performance and overall success. Due to the fact that spiders show great variation in behavioural syndromes, they are also starting to be an interesting group to study (Hernandez et al., 2021).

Aims

In the present study I used jumping spiders *Phidippus regius* (Salticidae) for the experiment. Jumping spiders (Araneae, Salticidae) are a good choice for studying cognition due to their sharp vision and complex vision-guided behaviour (Pekmezian & Taylor, 2015).

The goal of this study was to investigate if spiders *Phidippus regius* have personality traits, such as explorativeness and shyness/boldness. According to Dougherty & Guilette (2018), some personality traits may seem independent when evaluated with different tests, but in fact could form sets of correlated traits. Based on the known data, I wanted to test whether *Phidippus regius* spiders have repeatable explorativeness and shyness/boldness traits, and if there is a correlation between those two traits.

The second goal was to investigate their ability to learn to avoid aversive stimuli, and find out if their ability to learn aversive tasks correlate with tested personality traits.
To address my aims I did a series of laboratory experiments with 15 individuals grown in the lab from egg sacs to test whether they have repeatable personality traits and whether there is a correlation between these traits and learning abilities.

METHODS

We used adult females of *Phidippus regius* for the experiment. All spiders used in the experiments (n = 15) were offspring of two males and one female (2 spiders from one male, and 13 from the other one). It is important to note that I tested the repeatability of behavioural traits only in females, but not in males. Male and female spiders may have different characteristics in behaviour and learning abilities (Liedtke, 2015; Tailor et al., 2016; Kwek et al., 2021; Hernandez et al., 2021; Beydizada & Pekár, 2022), therefore, to exclude the influence of sex on the results of the experiment, I used only females. They live longer and their activity and foraging behaviour are less affected by sexual behaviour. On the other hand, males live shorter periods of time, and after they are sexually mature, their behaviour is more affected by searching for females to mate with them. The mating behaviour was observed even among juvenile males in our lab lately, also there is evidence of aggressiveness-boldness syndrome occurring in the subadult age of other species of spiders, *Agelenopsis lisa* (Bosco et al., 2017). Also *Phidippus regius* females are bigger than males which makes it easier to fit experimental conditions. Also female jumping spiders can respond to lower contrast stimuli than males (Zurek & Nelson, 2012) which was important for our colour avoidance learning test. For these reasons, female spiders are easier to work with.

Breeding and rearing

Spiders were reared in the climatic room (temperature 26±3°C, photoperiod: 14-h day, 10-h night). Humidity for spiderlings and juveniles was maintained within 80–90% to minimise morphological defects often occurring during moulting.

Spiders were reared in plastic containers with wet paper towels inside to keep moisture and strips of expanded polyethylene (EPE foam, sizes: 70 x 10 mm; 90 x 15 mm; 120 x 17 mm) as an artificial structure where the spiders could climb and hide instead of vegetation. Containers were sprayed with water on the inside walls on a daily basis. Paper towels were changed every second day to prevent the appearance of fungi and bacteria in containers.
Spiderlings stayed the first 1–2 weeks inside the cocoon, therefore the mother was kept with them in the same container. As soon as the spiderlings started to leave the cocoon, the mother was moved away. When spiders reached the third instar, they were moved into 50 ml containers (Ømin = 50 mm, Ømax = 60 mm, h = 50 mm). Starting from the 6th instar, the

spiders were kept individually. The spiders were moved into larger containers according to their size; up to 4–5 mm of body size in 200 ml containers (Ømin = 65 mm; Ømax = 80 mm; h = 65 mm), up to 7 mm in 400 ml containers (bottom = 75 x 50 mm; top = 100 x 75 mm; h = 100 mm).

Spiders were fed with various insects appropriate to their size and age. Spiderlings were fed by *Drosophila melanogaster* ad libitum. Juveniles (in a group of three individuals) were fed by 5–6 fruit flies three times a week. To enrich the spiders' diet and lower the mortality, juveniles were also occasionally, at least once during each instar, offered other food, such as cockroaches (*Shelfordella lateralis*), *Lucilia sericata* or *Musca domestica*.

Due to the fact that known personality tests in jumping spiders, such as mirror test (Chang et al., 2018), brush test (Pruitt et al., 2013), exploration test (Walsh & Cummins, 1976; Beydizada & Pekar, 2022), etc., did not fit our goals (measuring personality traits and learning abilities in a short period of time without long intervals between tests), I modified simple tests used to measure exploration and boldness traits (Pruitt et al., 2013) in other species of spiders, into the tests which could fit *Phidippus regius* species. I conducted preliminary tests on males and females of this species to optimise the details of the methods before I started the main experiments.

Behavioural tests

To determine behavioural types of spiders we repeatedly carried out a set of two behavioural tests investigating a level of exploration and boldness. I fed each spider 24 hours before the start of trials with *Lucilia sericata* to assure the same level of satiety for all individuals. Both tests were performed on the same day, with the Boldness test started immediately (in 5–15 seconds) after finishing Exploration latency test at the same arena.

Exploration latency

Each spider was placed in a non-transparent black film canister (Ø = 35 mm; h = 50 mm) with a lid on one side and a small round hole (Ø = 10 mm), through which a spider could come out, on the other side, closed by a small piece of kitchen cleaning sponge. The canister was placed in a vertical position on the experimental arena (L x W x H: 130 x 150 x 100 mm). I left the film canister on the experimental arena for 3 minutes to allow the spider inside to acclimatise to a new environment. After 3 minutes, the sponge was gently removed, and the time until the spider left the canister, i.e. the exploration latency, was recorded. If the

spider did not come out in 15 minutes, the test was terminated and the individual was excluded from the experiment.

Boldness

To evaluate boldness we observed behaviour expressed after meeting a new, potentially dangerous stimulus: the eraser-tip pencil. The red eraser on the end of black and red coloured pencil was placed 3–5 cm in front of the spider and then slowly moved towards the spider. The shyest individuals fled from "danger" immediately, while the boldest tried to bite the eraser.

Spiders' responses were scored on a semi-quantitative scale from the boldest to the least bold. I developed this scale based on spiders' reaction to a "dangerous" object:

- 4: attacking (biting)
- 3: pouncing (pounce to the danger without biting, beat it with front legs)
- 2: warning pose 2 (open chelicerae, raised and outstretched first pair of legs)
- 1: warning pose 1 (open pedipalps showing chelicerae, slightly spaced legs)
- 0: no response
- -1: legs towards body and front legs lowered together with thorax
- -2: moving backwards
- -3: fleeing

Learning abilities

I investigated colour discrimination ability of spiders by heat-avoidance learning in association with different coloured surfaces of the experimental arena. Memory experiment consisted of a pre-training session (control), two training sessions and a test session. On the first day spiders were allowed to walk freely on both coloured areas without heating, followed by two training sessions (with heating) and one test session. On the following two days, two training sessions and one test session were performed each day.

A Petri dish (Ø = 90 mm; h =~5 mm) was used as an experimental arena, the floor and walls of which were covered with blue and yellow paper in such a way that the arena was divided into two coloured semicircles. The height of the arena was sufficient for the spider to move freely inside, but not climb the walls or ceiling. Petri dish was covered by a transparent PMMA sheet. During the control and test sessions, the arena was located on an unheated wooden surface. During training, the blue part of the arena was heated by a heating mat, and

a yellow semicircle was placed on a wooden surface. The temperature of the heated part of the arena was around 40±1°C, and the unheated part was 28°C.

During each session (control, two training and test) at the start of trial (control session) Petri dishes were positioned in the same way for each spider. To avoid spatial learning, the Petri dish was rotated by 90 degrees counterclockwise for each next session. The arena was fenced with cardboard walls so that the spiders could not see surrounding objects, and the light was always right above the Petri dish.

Pre-training

Pre-training (control) session for each spider was performed once at the beginning of the experiment, on the first day, for 5 minutes, without heating the arena.

The arena was located on an unheated wooden surface and positioned according to the "Learning abilities" subsection above. Each spider was placed in the middle of the arena for 5 minutes. I used stopwatches to record the exact time spent on both colours.

Training and test sessions

There were 3 trials (one day = one trial) in a row with both training and test sessions to see how fast the individuals learned.

Training sessions

Each spider was placed in the middle of the heated arena for 5 minutes. After the first training each spider was moved during 30–60 seconds to the second heated arena.

Test session

Test sessions took place at the same area as previous sessions, but without heating. Test session started 30–60 seconds after the last training session. The spider was placed in the middle of the arena for 5 minutes.

After each trial spiders were fed with 3–5 *Drosophila hydei*, which are big enough to prevent spiders from starving during three days of trials, but at the same time are not as big as *Lucilia* or domestic flies, so spiders do not get overfed.

Data analysis

All analyses were conducted in the R software version 4.2.0 (R Core Team, 2022). I tested whether there are consistent among-individual differences in boldness and exploration latency using the analysis of repeatability (Nakagawa & Schielzeth, 2010). I estimated the coefficient of repeatability R by an approach based on linear mixed effects models implemented in the R package rptR (Stoffel at al., 2017). I then tested whether boldness and exploration latency were correlated by calculating the Pearson's correlation coefficient.

To look for evidence of learning, I calculated the choice ratio based on the proportion of time spent on the blue and yellow part of the arena following Nakamura & Yamashita (2000). The choice ratio is (P-N)/(P+N), where P is the proportion of time on the heat-associated blue part of the arena and N is the proportion of time on the yellow part. I used a t-test to compare the choice ratio in the control trials and in the trials after the learning process to see whether there was a difference in the choice of time spent on the blue part of the arena. I also tested whether the choice ratio differed between the first, second, and third trial. I then used a linear model to test whether the difference of the time spent at the blue area compared to the control depended on the behaviour of the individual spiders.

RESULTS

First, I tested whether there are consistent among-individual differences among the spiders in the two behavioural traits, i.e. boldness and exploration latency. Repeatability analysis showed that both traits were repeatable. Boldness was highly repeatable with an estimated value of repeatability $R = 0.557$ (standard error $SE = 0.1481$), 95% confidence interval = (0.2182, 0.7739). Repeatability of boldness was significantly larger than zero with probability value $P = 0.001$ based on a permutation test. Exploration latency (log-transformed) was also strongly repeatable: $R = 0.571$, $SE = 0.1412$, 95% confidence interval = (0.2310, 0.7768), $P = 0.002$. Hence, I detected clear evidence that there are consistent among-individual differences in the behaviour of the spiders.
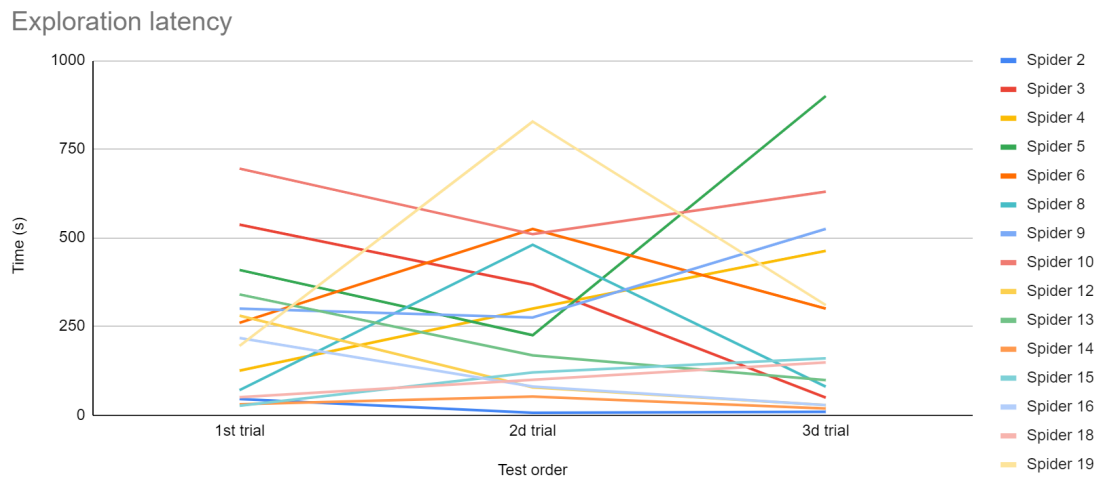
Fig. 1. Exploration latency over trials.
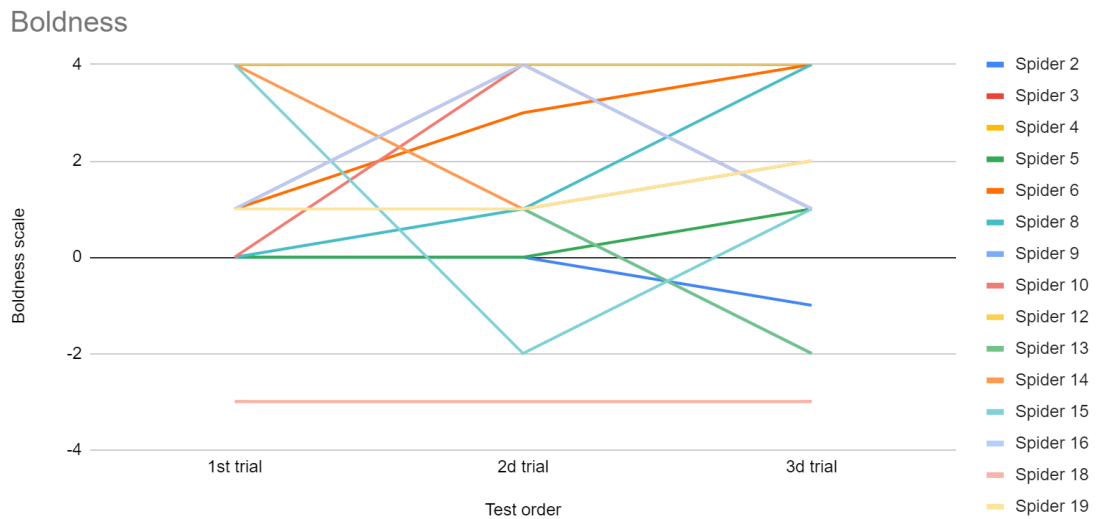
Fig. 2. Boldness over trials. Boldness scale is described in the Methods section.

Boldness and exploration latency were not significantly correlated: Pearson's correlation coefficient = 0.158, t-statistic t = 1.0484, degrees of freedom df = 43, P = 0.3003, 95% confidence interval = (-0.1422494, 0.4314177). Hence, there is no evidence of a behavioural syndrome characterised by correlated boldness and exploration latency.

There was weak, but statistically significant evidence that the spiders learned to avoid the hot area. A t-test showed that the spiders significantly avoided the blue colour (which was hot in the learning trials) even in the following tests when the blue part of the Petri dish was no longer hot (t = -2.0975, df = 44, P = 0.04173), although the effect was very weak. The mean difference of the choice ratio in the tests to the control was -0.0733 with SE = 0.03493, 95% confidence interval = (-0.1436, -0.0029). The spiders spent on average 60.2% of the time on the blue substrate in the control trials and 56.5% in the tests after the learning period. The difference in the choice ratio compared to the control did not differ between three tests performed during three days (F = 0.0425, df = 2,42, P = 0.9584).
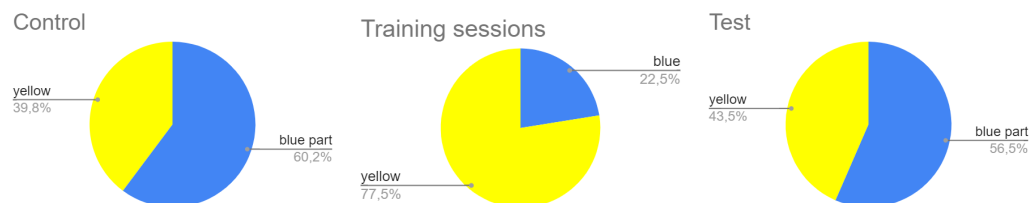
Fig. 3. Pie charts of percentages of total time that the spiders spent on blue and yellow parts of the arena in control, training and test sessions over all three trials.

I found no evidence that the ability of individual spiders to learn to avoid the blue area depends on their personality. A general linear model testing whether the difference of the choice ratio of individual spiders in the tests compared to the control trials depends on the behaviour of the spiders showed no significant effect of boldness: $F = 0.7372$, $df = 1,43$, $P = 0.3953$ and no significant effect of exploration latency: $F = 2.904$, $df = 1,43$, $P = 0.09558$.

DISCUSSION

I found out that the boldness and exploration were repeatable in the spider *Phidippus regius*, but they were not correlated with each other. There was weak but statistically significant learning ability to avoid the blue substrate in the learning test. However, the learning skills of individual spiders were not dependent on their personality traits.

Repeatability of behavioural traits

Both boldness and exploration latency were repeatable, i.e. some individual spiders were consistently bolder or more explorative than other individuals. This is evidence that the jumping spiders *Phidippus regius* have distinct behavioural types. To my knowledge, the repeatability of behavioural traits has not been previously tested in this species. Both traits had relatively high values of repeatability ($R = 0.557$ for boldness and $R = 0.571$ for exploration). My results on trait repeatability are thus consistent with previous studies which show consistent behavioural differences, i.e. personality, across various animal taxa.

There is an increasing amount of evidence from previous studies that different species of spiders and other invertebrates show consistent among-individual differences in their behaviour (Bell et al., 2009; Laskowski et al., 2022). Most studies focused on different measures of boldness, aggressivity, exploration behaviour and activity (Dall et al., 2004, Sih et al., 2004b, Bell et al., 2009). For example, the repeatability of activity traits of jumping spiders *Terralonus californicus* was shown in the study of Lichtenstein et al. (2017). The repeatability of boldness and aggressiveness was previously tested on spiders *Drassodes lapidosus* (Gnaphosidae) by Beydizada and Pekár (2022). Exploration traits were repeatedly tested on jumping spiders *Marpissa muscosa* in the study of Liedtke et al. (2015). Jumping spiders *Portia labiata* (Chang et al., 2018) and *Siler semiglaucus* (Kwek et al., 2021) showed consistent aggressivity traits. My results thus add another example to the growing body of studies which demonstrate that spiders and other invertebrates have distinct individual behavioural types (Bell et al., 2009; Stamps et al., 2012; Mather & Logue, 2013; Kralj-Fišer & Schuett, 2014; Laskowski et al., 2022).

It is important to note that I have tested the repeatability of behavioural traits only in females, but not in males. Many previous studies on activity and boldness have also used only females (e.g. Johnson & Sih, 2007; Liechtenstein et al., 2017). Bell at al. (2009) showed that females have more repeatable behaviour when we do not consider mating

behaviour. However, some studies which tested both sexes revealed differences in the behaviour of male and female spiders (e.g. Kralj-Fišer & Schneider, 2012; Kralj-Fišer et al., 2017), so comparing the mean values and repeatability of boldness and exploration latency between sexes in jumping spiders *Phidippus regius* would be interesting in the future.

Trait correlations and behavioural syndromes

The two behavioural traits I measured, boldness and explorativeness, were not correlated. This means I found no evidence of a behavioural syndrome in *Phidippus regiu*s. Previous studies on arthropods show that several behavioural traits are often correlated in insects, crustaceans, and arachnids, and that they form behavioural syndromes which are similar to those observed in vertebrates (Mather & Logue, 2013; Kralj-Fišer & Schuett, 2014).

Correlation between traits was observed, for example, in Beach-dwelling jumping spiders *Terralonus californicus* by Lichtenstein et al. (2017). They observed how far the spiders move in the open field test and how much prey they kill during trial and how their activity level correlates with body mass. Similar trait correlations were also described previously in other invertebrates and vertebrates, where personalities were studied in more detail, and seem to form pretty common behavioural syndromes (Mather & Logue, 2013; Kralj-Fišer & Schuett, 2014; Liedtke et al., 2015; Lichtenstein et al., 2017; Kwek et al., 2021; Beydizada & Pekár, 2022). However, as my data and some other published studies show, these behavioural syndromes are not universal. More studies in different groups of animals are needed to see how common these behavioural syndromes really are and whether they are more common in certain groups of animals.

Learning and discrimination of colours

I found only a weak effect of the training process, where the blue half of the Petri dish was hot, on the avoidance of the blue colour in subsequent tests, where both yellow and blue halves of the Petri dish had normal room temperature. This contrasts with the study of Nakamura & Yamashita (2000) who showed a very strong effect of the same training procedure on the avoidance of colours in another species of jumping spiders *Hasarius adansoni*. There are several possible explanations for the very weak evidence that *Phidippus regius* learned to avoid the blue colour after it was exposed to high temperature on the blue part of the arena in my experiments.

First, there is uncertainty about the visual system and colour discrimination in spiders. DeVoe (1975) study says that *Phidippus regius* have vision with UV- and green-cells, which could mean that they can not see yellow and blue colours. This could be the reason why the spiders in my experiment did not learn differences between these colours, since distinguishing different colours just based on different degrees of luminance is more difficult. However, the same article also mentions that green, yellow and orange colours have low reflectivity below ~480 nm and will only stimulate green receptors. On the other hand, purple and blue colours with about equal reflectivity in the blue spectrum will stimulate UV and green receptors together. Due to this difference in receptor stimulation, it is likely that the spiders in my experiment were able to distinguish between yellow and blue colours. Also Nakamura & Yamashita (2000) showed that jumping spiders *Hasarius adansoni* can learn blue-green, blue-yellow, blue-red, blue-grey, green-yellow and other combinations of blue, yellow, green, red and grey colours. However, Jakob's lab tried to replicate the Nakamura & Yamashita (2000) study with several species of *Phidippus*, but they did not succeed (Jakob & Long, 2016). Nevertheless, my data from the learning tests might be a confirmation of their results. I also noticed in my experiment that the spiders often stopped for a while at the border between the colours such as black and white, bright blue and yellow, medium blue and yellow, but not light/faded blue and yellow, which means they could at least see a difference in hue between those colours.

The second reason could be highly flexible behaviour. I observed many times during training sessions that the spiders stopped at the border of the hot area and gently touched it with the first pair of legs. I observed the same behaviour during test sessions too. It seems that they probably learned that the blue area was hot during the learning trials, but instead of simply avoiding it in the subsequent test trials, they assessed the temperature of the blue area by touching it carefully with their front legs before crossing the line to the blue area. Jakob & Long (2016) also noticed that their spiders seemingly preferred the heated part of the arena until they increased temperature even more than it was in Nakamura & Yamashita (2000) study. Another evidence of this learning ability is that in my experiment during the first ca. 60 seconds of the test sessions 8 from 15 spiders immediately returned back to the yellow part after they crossed to the blue part, and only after a while started to spend more time on the blue part too.

Another possible reason is that the aversive stimulus (heating) was too predictable. One half of the Petri dish during the training sessions was constantly heated, and then during the test session (without heating) spiders could sense that there is no "danger" anymore and they can

walk freely on both sides. Since the Petri dish was covered with plexiglass during the experiment, the air inside it also heated up accordingly. Whereas during the test sessions, the air in the Petri dish remained at room temperature, which could affect the formation of the association "warm air = hot blue side, regular temperature air = no longer dangerous". This effect can be further investigated by using non-predictable aversive stimuli, such as electric shock (Bednarski, 2012) or vibrating arena (Long et al., 2015; VanderSal & Hebets, 2007). In the study of Bednarski (2012), spiders *Phidippus audax* learned to avoid preferred stimulus (cricket with natural motion) by electric shock aversive stimulus which they got several times in a row during training sessions. Also the same species were trained to avoid favoured stimulus by using vibrating arena aversive stimulus in Long et al. (2015) study. The experimental spiders were fixed on the experimental arena orienting to the favoured stimulus with their tarsi on a vibrating platform, whereas the control spiders in the same conditions were on a platform without vibration. After training sessions experimental spiders preferred the favoured stimulus less than control spiders and also avoided the vibrating platform when they walked freely.

Also, for the experiment I only used laboratory reared spiders, which means that individuals had a poor environment compared to natural conditions. For example, in Carducci & Jakob (2000) study the captured jumping spiders *Phidippus audax* showed better results in Open field, Video-prey and Detour tests than laboratory reared spiders. On the other hand, the article of Liedtke & Schneider (2017) states that physical deprivation did not have as great an impact as social deprivation. Nevertheless, in our case, the spiders were divided into groups of 3–5 spiders in each box until juvenile age and after that they were kept alone, but continued to have contacts with other individuals, because they stayed in transparent plastic boxes placed next to each other tightly enough, so that each spider could see and interact from distance with at least 2–4 other spiders, so in this case the question of the effect of deprivation remains open. My suggestions for further experiments are: use other aversive stimuli (e.g. electric shock or vibrating platform) instead of heating; use more combinations of different colours to see if there will be any difference in learning ability; and also have two groups of spiders, laboratory reared and captured. Also it would be beneficial to have more individuals for experiment, because the tendency in the learning test was: one from ten spiders seemed to learn to avoid the blue area.

The relationship between individual personality and learning ability

I found no evidence that behavioural traits of individual spiders affected their responses in the learning tests. Despite the growing body of research on personality and behaviour in invertebrates, only a handful of studies have focused on the relationship between behaviour traits and learning abilities in spiders. As an example, there is a recent study from Chang et al. (2018) about a correlation between aggressiveness and ability to solve a decision-making task of jumping spider *Portia labiata*. The study shows that spiders with aggressive tendencies demonstrated enhanced accuracy in straightforward tasks, whereas docile individuals exhibited greater precision in challenging tasks. Beydizada & Pekár (2022) found out that personality traits forecast the method of assault in spiders *Drassodes lapidosus*. Individuals of the *Drassodes* species exhibited consistent variations in their hunting behaviours. The use of venom in attacks was linked to heightened aggression when targeting spider prey (considered dangerous) and increased boldness when targeting cricket prey (deemed safe). On the other hand, the deployment of silk in attacks was more common among individuals characterised as shy (when targeting cricket prey) and docile (when targeting spider prey). Interestingly, the quantity of venom employed did not correlate with the chosen attack strategy. Finally, Beydizada et al. (2023) found that personality was not correlated with the rates of habituation/dishabituation in jumping spiders *Menemerus semilimbatus*. The lack of a relationship between boldness, explorativeness, and learning ability in my experiment could be explained in several ways. First, the relationship may truly not exist. Second, I had a rather low sample size (15 spiders), so the power of the statistical analyses was limited and could not reveal a potential weak effect of behaviour on learning ability.

Studies on other animals showed that individuals characterised as proactive, often displaying traits of boldness and increased aggression, are expected to exhibit a slower rate of reversal learning. This pertains to their ability to grasp changes in environmental quality or shifts in the meaning of signals (Sih & Giudice, 2012). Bold individuals may rapidly acquire tasks demanding heightened activity, but they might be slower in learning tasks that necessitate reduced activity. For example, fearful quail demonstrated a quicker learning pace than bold ones in an avoidance-learning task that demanded less activity, while they were slower in a maze-learning task that required increased activity (Miller et al., 2006). Thus, the examples of different studies (Chang et al., 2018; Beydizada & Pekár, 2022; Beydizada et al., 2023; Sih & Giudice, 2012; Miller et al., 2006) show that in different cases the correlation between personality and cognitive abilities can be positive, negative or absent. Hence, exploring the

link between boldness, explorativeness, or other behavioural traits and learning abilities, such as the speed of learning, error rate, and long-term memory of the learned behaviours, will be an interesting avenue for further research on spiders as well as other invertebrates.

CONCLUSIONS

In my experiment, I combined measurements of two behavioural traits, boldness and exploration latency, with measurements of the ability to learn to avoid the blue part of the arena based on the exposure to high temperature during the learning process in a jumping spider *Phidippus regius*. My results show that both boldness and exploration latency were repeatable. Despite growing evidence of behavioural syndromes in invertebrates, boldness and exploration latency were not correlated. I observed only a weak but statistically significant avoidance of the blue area after the heat-avoidance learning trials. Finally, behavioural traits of individual spiders had no effect on their ability to learn to avoid the blue part of the arena.

REFERENCES

Aguilar-Arguello, S. & Nelson, X.J. (2021). Jumping spiders: An exceptional group for comparative cognition studies. *Learning & Behavior,* 49, 276–291. https://doi.org/10.3758/s13420-020-00445-2

Arican, C. (2022). Sensory to motor transformation during innate and adaptive behavior in the cockroach. PhD thesis, Universität zu Köln. https://kups.ub.uni-koeln.de/64251/

Bell, A. (2007). Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences,* 274(1611), 755–761. https://doi.org/10.1098/rspb.2006.0199

Bell, A., Hankison, S. & Laskowski, K. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour* 77(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022.

Balda, R.P., Pepperberg, I.M. & Kamp, A.C. (1998). *Animal Cognition in Nature: The Convergence of Psychology and Biology in Laboratory and Field*. Academic Press.

Barth, M.B., Kellner, K. & Heinze, J. (2010). The police are not the army: context-dependent aggressiveness in a clonal ant. *Biology Letters,* 6, 329–332. https://doi.org/10.1098/rsbl.2009.0849

Bartos, M. & Szczepko, K. (2012). Development of prey-specific predatory behavior in a jumping spider (Araneae: Salticidae). *The Journal of Arachnology*, 40, 228–233. https://www.jstor.org/stable/41758964

Bednarski, J., Taylor, P. & Jakob, E. (2012). Optical cues used in predation by jumping spiders, Phidippus audax (Araneae, Salticidae). *Animal Behaviour*, 84, 1221–1227. https://doi.org/10.1016/j.anbehav.2012.08.032

Bell, A.M., Hankison S., Laskowski K.L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour,* 77(4), 771–83. https://doi.org/10.1016/j.anbehav.2008.12.022

Beydizada, N., Cannone, F., Pekar, S., Baracchi, D. & De Agro, M. (2023). Habituation to visual stimuli is personality-independent in a jumping spider. *Preprint*. https://doi.org/10.1101/2023.05.09.539210

Beydizada, N. & Pekar, S. (2022). Personality predicts mode of attack in a generalist ground spider predator. *Behavioral Ecology*, 34, 42–49. http://dx.doi.org/10.1093/beheco/arac095

Bosco, J., Riechert, S. & O'Meara, B. (2017). The ontogeny of personality traits in the desert funnel-web spider, Agelenopsis lisa (Araneae: Agelenidae). *Ethology*, 123, 648–658. https://doi.org/10.1111/eth.12639

Carazo, P., Noble D.W.A., Chandrasoma D. & Whiting M.J. (2014). Sex and boldness explain individual differences in spatial learning in a lizard. *Proceedings of the Royal Society B: Biological Sciences,* 281(1782). https://doi.org/10.1098/rspb.2013.3275

Carduccu, J., Jakob, E. (2000). Rearing environment affects behaviour of jumping spiders. Animal Behaviour, 59, 39–46. http://dx.doi.org/10.1006/anbe.1999.1282

Cerveira, A., Nelson, X. & Jackson, R. (2021). Spatial acuity-sensitivity trade-off in the principal eyes of a jumping spider: possible adaptations to a 'blended' lifestyle. *Journal of Comparative Physiology A*, 207, 1–12. https://link.springer.com/article/10.1007/s00359-021-01486-2

Chang, C., Lim, Z., Klomp, D., Norma-Rashid, Y. & Li, D. (2018). Aggressive spiders make the wrong decision in a difficult task. *Behavioral Ecology*, 29, 848–854. https://doi.org/10.1093/beheco/ary066

Chang, C., Ng, P. & Li, D. (2016). Aggressive jumping spiders make quicker decisions for preferred prey but not at the cost of accuracy. *Behavioral Ecology*, 28, 479–484. http://dx.doi.org/10.1093/beheco/arw174

Chang, C., Teo, H., Norma-Rashid, Y & Li, D. (2017). Predator personality and prey behavioural predictability jointly determine foraging performance. *Scientific Reports*, 7, 40734. http://dx.doi.org/10.1038/srep40734

Chittka, L. & Skorupski, P. (2011). Information processing in miniature brains. *Proceedings: Biological Sciences,* 278(1707), 885–888. http://www.jstor.org/stable/41148704

Chittka, L., Skorupski, P., Raine, N. (2009). Speed–accuracy tradeoffs in animal decision-making. *Trends in ecology & evolution*, 24, 400–407. https://doi.org/10.1016/j.tree.2009.02.010

Dall, S.R.X., Houston, A.I. & McNamara J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters,* 7, 734–739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

Davies, N.B., Krebs, J.R. & West, S.A. (2012). *An Introduction to Behavioural Ecology* (4th ed.). John Wiley & Sons.

De Agro, M. (2020). SPiDbox: design and validation of an open-source "Skinner-box" system for the study of jumping spiders. *Journal of neuroscience methods*, 346, e108925. https://doi.org/10.1016/j.jneumeth.2020.108925

De Agro, M., Regolin, L., & Moretto, E. (2017). Visual discrimination learning in the jumping spider Phidippus regius. *Animal Behavior and Cognition,* 4(4), 413–424. http://doi.org/10.26451/abc/.04.04.02.2017

De Agro, M., Robler, D., Kim, K. & Shamble, P. (2021). Perception of biological motion by jumping spiders. *PLoS Biology*, 19(7): e3001172. https://doi.org/10.1371/journal.pbio.3001172

De Voe, R.D. (1975). Ultraviolet and green receptors in principal eyes of jumping spiders. *Journal of General Physiology,* 66 (2), 193–207. https://doi.org/10.1085/jgp.66.2.193

Dolev, Y. & Nelson, X.J. (2014). Innate Pattern Recognition and Categorization in a Jumping Spider. *PLoS ONE,* 9(6), e97819. https://doi.org/10.1371/journal.pone.0097819

Dougherty, L.R. & Guillette, L.M. (2018). Linking personality and cognition: a meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373(1756). http://doi.org/10.1098/rstb.2017.0282

Edwards, G. (2004). Revision of the Jumping Spiders of the Genus Phidippus (Araneae: Salticidae). *Occasional Papers of the Florida State Collection of Arthropods*, 11, 1–156.

Edwards, G. & Jackson, R. (1994). The role of experience in the development of predatory behaviour in Phidippus regius, a jumping spider (Araneae, Salticidae) from Florida. *New Zealand Journal of Zoology*, 21, 269–277. https://doi.org/10.1080/03014223.1994.9517994

Edwards, G. & Jackson, R. (1993). Use of prey‑specific predatory behaviour by North American jumping spiders (Araneae, Salticidae) of the genus Phidippus. *Journal of Zoology*, 229, 709–716. http://dx.doi.org/10.1111/j.1469-7998.1993.tb02666.x

Gardner, B. (1965). Observations on three species of Phidippus jumping spiders (Araneae: Salticidae). *Psyche: A Journal of Entomology*, 72, 133–147.

Gosling, S. (2001). From mice to men: What can we learn about personality from animal research? *Psychological bulletin,* 127, 45–86. https://doi.org/10.1037/0033-2909.127.1.45

Guenther, A., Brust, V., Dersen, M. & Trillmich, F. (2014). Learning and Personality Types Are Related in Cavies (Cavia aperea). *Journal of comparative psychology,* 128(1), 74–81. http://doi.org/10.1037/a0033678

Harland, D., Jackson, R. & Macnab, A. (1999). Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals. *Journal of Zoology*, 247, 357–364. https://doi.org/10.1111/j.1469-7998.1999.tb00998.x

Herborn, K., Heidinger, B., Alexander, L., & Arnold, K. (2014). Personality predicts behavioral flexibility in a fluctuating, natural environment. *Behavioral Ecology*, 25, 1374–1379. https://doi.org/10.1093/beheco/aru131

Herborn, K., Macleod, R., Miles, W.T.S., Schofield, A.N.B., Alexander, L. & Arnold, K.E. (2010). Personality in captivity reflects personality in the wild. *Animal Behaviour*, 79(4), 835–843. https://doi.org/10.1016/j.anbehav.2009.12.026

Hernandez D.L., Wilson, D., Briffa, M. & Rymer, T. (2021). Beyond spider personality: The relationships between behavioral, physiological, and environmental factors. *Ecology and Evolution*, 11, 2974–2989. http://dx.doi.org/10.1002/ece3.7243

Hill, D.E. Orientation by jumping spiders of the genus Phidippus (Araneae: Salticidae) during the pursuit of prey. (1979). Behavioural Ecology and Sociobiology, 5, 301–322 (1979). https://doi.org/10.1007/BF00293678

Jackson, R.R. & Cross, F.R. (2011). Spider Cognition. *Advances in Insect Physiology,* 41, 115–174. https://doi.org/10.1016/B978-0-12-415919-8.00003-3

Jackson, R.R. & Li, D. (2004). One-encounter search-image formation by araneophagic spiders. *Animal cognition*, 7, 247–254. http://dx.doi.org/10.1007/s10071-004-0219-x

Jakob, E.M. & Long, S.M. (2016). How (not) to train your spider: successful and unsuccessful methods for studying learning. *New Zealand Journal of Zoology,* 43(1), 112–126. https://doi.org/10.1080/03014223.2015.1127263

Jakob, E.M., Skow, C.D., Haberman, M.P. & Plourde, A. (2007). Jumping Spiders Associate Food With Color Cues In A T-Maze. *The Journal of Arachnology,* 35(3), 487–492. https://doi.org/10.1636/JOA-ST06-61.1

Japyassu, F.H. & Laland, K. (2017). Extended spider cognition. *Animal Cognition*, 20, 375–395. https://link.springer.com/article/10.1007/s10071-017-1069-7

Johnson, J.C. & Sih, A. (2007). Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, Dolomedes triton. *Animal Behaviour,* 74(5), 1131–1138. https://doi.org/10.1016/j.anbehav.2007.02.006

Kralj-Fišer, S., Hebets, E. A. & Kuntner, M. (2017). Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization. *Behavioral Ecology and Sociobiology,* 71(8), 1–15. https://doi.org/10.1007/s00265-017-2353-x

Kralj-Fišer, S., Mostajo, G., Preik, O., Pekár, S. & Schneider, J. (2013) Assortative mating by aggressiveness type in orb weaving spiders. *Behavioral Ecology*, 24(4), 824–831. https://doi.org/10.1093/beheco/art030

Kralj-Fišer, S. & Schneider, J.M. (2012). Individual behavioural consistency and plasticity in an urban spider. *Animal Behaviour,* 84(1), 197–204. https://doi.org/10.1016/j.anbehav.2012.04.032

Kralj-Fišer, S. & Schuett, W. (2014). Studying personality variation in invertebrates: why bother? *Animal Behaviour,* 91, 41–52. https://doi.org/10.1016/j.anbehav.2014.02.016

Kwek, B., Tan, M., Yu, L., Zhou, W., Chang, C., & Li, D. (2021). Aggressive males are more attractive to females and more likely to win contests in jumping spiders. *Animal Behaviour*, 179, 51–63. http://dx.doi.org/10.1016/j.anbehav.2021.06.030

Laskowski, K.L., Chang, C.C., Sheehy, K. & Aguiñaga, J. (2022). Consistent Individual Behavioral Variation: What Do We Know and Where Are We Going? *Annual Review of Ecology, Evolution, and Systematics,* 53. https://doi.org/10.1146/annurev-ecolsys-102220-011451

Lichtenstein, J.L.L., Chism, G.T., Kamath, A. & Pruitt, J.N. (2017). Intraindividual Behavioral Variability Predicts Foraging Outcome in a Beach-dwelling Jumping Spider. *Scientific Reports,* 7. https://doi.org/10.1038/s41598-017-18359-x

Liedtke, J. (2015). Effects of early environmental conditions on the development of behaviour in a jumping spider. *Doctoral dissertation*, University of Hamburg.

Liedtke, J., Redekop, D., Schneider, J. M. & Schuett, W. (2015). Early Environmental Conditions Shape Personality Types in a Jumping Spider. *Frontiers in Ecology and Evolution,* 3. https://doi.org/10.3389/fevo.2015.00134

Liedtke, J. & Schneider, J. (2014). Association and reversal learning abilities in a jumping spider. *Behavioural processes*, 103, 192–198. http://dx.doi.org/10.1016/j.beproc.2013.12.015

Liedtke, J. & Schneider, J. (2017). Social makes smart: rearing conditions affect learning and social behaviour in jumping spiders. *Animal Cognition*, 20, 1093–1106. https://link.springer.com/article/10.1007/s10071-017-1125-3

Long, S., Leonard, A., Carey, A. & Jakob, E. (2015). Vibration as an effective stimulus for aversive conditioning in jumping spiders. *Journal of Arachnology*, 43, 111–114. https://doi.org/10.1636/S14-49

Loukola, O., Perry, C., Coscos, L. & Chittka, L. (2017). Bumblebees show cognitive flexibility by improving on an observed complex behavior. *Science,* 355, 833–836. https://doi.org/10.1126/science.aag2360

Mamuneas, D., Spence, A., Manica, A. & King, A. (2015). Bolder stickleback fish make faster decisions, but they are not less accurate. *Behavioral Ecology*, 26, 91–96. https://doi.org/10.1093/beheco/aru160

Mannino, E., Regolin, L., Moretto, E. & De Agro, M. Study Replication: Shape Discrimination in a Conditioning Procedure on the Jumping Spider Phidippus regius. *Animals*, 2023, 13, 2326. https://doi.org/10.3390/ani13142326

Mather, J.A., & Logue, D.M. (2013). The bold and the spineless: invertebrate personalities. *Animal personalities. Behavior, physiology, and evolution*, 13–35. https://doi.org/10.7208/chicago/9780226922065.003.0001

Menzel, R., Brembs, B. & Giurfa, M. (2007). Cognition in Invertebrates. *Evolution of Nervous Systems, Academic Press,* 403–442. https://doi.org/10.1016/B0-12-370878-8/00183-X

Miller, K.A., Garner, J.P. & Mench, J.A. (2006). Is fearfulness a trait that can be measured with behavioural tests? A validation of four fear tests for Japanese quail. *Animal Behaviour*, 71, 1323–1334. https://doi.org/10.1016/j.anbehav.2005.08.018

Millroth, P., Juslin P., Winman A., Nilsson H. & Lindskog M. (2020). Preference or ability: Exploring the relations between risk preference, personality, and cognitive abilities. *Journal of Behavioral Decision Making,* 33(4), 477–491. http://doi.org/10.1002/bdm.2171

Nakagawa, S. & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews,* 85(4), 935–956 https://doi.org/10.1111/j.1469-185X.2010.00141.x

Nakamura, T. & Yamashita, S. Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). (2000). *Journal of Comparative Physiology A,* 186(9), 897–901. https://doi.org/10.1007/s003590000143

Parthasarathy, B., Muller, M., Bilde, T. & Schneider, J. (2022). Hunger state and not personality determines task participation in a spider society. *Animal Behaviour*, 190, 143–152. https://doi.org/10.1016/j.anbehav.2022.06.002

Peckham, G.W. & Peckham E.G. (1890). Additional observations on sexual selection in spiders of the family Attidae, with some remarks on Mr. Wallace's theory of sexual ornamentation. *Occasional Papers of the Natural History Society of Wisconsin*, 1(3), 117–151.

Peckmezian, T., Taylor, P. (2015). Electric shock for aversion training of jumping spiders: Towards an arachnid model of avoidance learning. *Behavioural processes,* 113, 99–104. https://doi.org/10.1016/j.beproc.2015.01.015

Peckmezian, T., Taylor, P.W. (2017). Place avoidance learning and memory in a jumping spider. *Animal Cognition,* 20, 275–284. https://doi.org/10.1007/s10071-016-1048-4

Perry, J.N., Arpaia, S., Bartsch, D., Birch, A.N.E., Devos, Y., Gathmann, A., Gennaro, A., Kiss, J., Messean, A., Mestdagh, S., Nuti, M., Sweet, J.S. & Tebbe, C.C. (2013). No evidence requiring change in the risk assessment of Inachis io larvae. *Ecological Modelling,* 268, 103–122. https://doi.org/10.1016/j.ecolmodel.2013.08.004

Pruitt, J., Grinsted, L. & Settepani, V. (2013). Linking levels of personality: personalities of the average and most extreme group members predict colony-level personality. *Animal Behaviour*, 86, 391–399. https://doi.org/10.1016/j.anbehav.2013.05.030

Pruitt, J. & Riechert, S. (2012). The ecological consequences of temperament in spiders. *Current Zoology*, 58(4), 589–596. https://doi.org/10.1093/czoolo/58.4.589

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/

Rayor, L. (2012). Spider Behaviour: Flexibility and Versatility. *Animal Behaviour*, 84(1), 289–290. https://doi.org/10.1016/j.anbehav.2012.04.004.

Reale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 365(1560), 4051–63. https://doi.org/10.1098/rstb.2010.0208

Riechert, S. & Hedrick, A. (1993). A test for correlation among fitness-linked behavioural traits in the spider Agelenopsis aperta (Araneae, Agelenidae). *Animal Behaviour*, 46, 669–675. https://doi.org/10.1006/anbe.1993.1243

Robler, D., De Agro, M., Kim, K. & Shamble, P. (2021). Static visual predator recognition in jumping spiders. *Functional Ecology*, 36, 561–571. https://doi.org/10.1111/1365-2435.13953

Robler, D., Kim, K., De Agro, M., Jordan, A., Galizia, C.G., & Shamble, P.S. (2022). Regularly occurring bouts of retinal movements suggest an REM sleep-like state in jumping spiders. *Proceedings of the National Academy of Sciences of the USA*, 119(33), e2204754119. https://doi.org/10.1073/pnas.2204754119

Schuett, W., Dall, S.R., Baeumer, J., Kloesener, M.H., Nakagawa, S., Beinlich, F. & Eggers T. (2011). Personality variation in a clonal insect: the pea aphid, Acyrthosiphon pisum. *Developmental Psychobiology*, 53(6), 631–640. https://doi.org/10.1002/dev.20538

Sih, A., Bell, A. & Johnson, J.C. (2004a). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution,* 19(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., Bell, A., Johnson, J. & Ziemba, R. (2004b). Behavioral Syndromes: An Integrative Overview. *Quarterly Review of Biology,* 79, 241–277. https://doi.org/10.1086/422893

Sih, A. & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 367(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Sih, A., Mathot, K.J., Moiron, M., Montiglio, P.O. Wolf., M & Dingemanse, N.J. (2015). Animal personality and state-behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology and Evolution,* 30(1), 50–60. https://doi.org/10.1016/j.tree.2014.11.004

Skow, C. & Jakob, E. (2006). Jumping spiders attend to context during learned avoidance of aposematic prey. *Behavioral Ecology*, 17, 34–40. https://doi.org/10.1093/beheco/ari094

Stamps, J., Briffa, M. & Biro, P. (2012). Unpredictable animals: Individual differences in intraindividual variability (IIV). *Animal Behaviour*, 83, 1325–1334. https://doi.org/10.1016/j.anbehav.2012.02.017

Stoffel, M., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed‑effects models. *Methods in Ecology and Evolution*, 8(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Tarsitano, M. & Jackson, R. (1997). Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. *Animal Behaviour*, 53, 257–266. https://doi.org/10.1006/anbe.1996.0372

Taylor, L., Zarreen, A., Maier., E., Byrne, K. & Morehouse, N. (2016). Flexible color learning in an invertebrate predator: Habronattus jumping spiders can learn to prefer or avoid red during foraging. *Behavioral Ecology,* 27(2), 520–529. https://doi.org/10.1093/beheco/arv182

Taylor, L. & Mcgraw, K. (2013). Male ornamental coloration improves courtship success in a jumping spider, but only in the sun. *Behavioral Ecology,* 24, 955–967. http://doi.org/10.1093/beheco/art011

Titulaer, M., Kees van Oers & Naguib, M. (2012). Personality affects learning performance in difficult tasks in a sex-dependent way. *Animal Behaviour,* 83(3), 723–730. https://doi.org/10.1016/j.anbehav.2011.12.020

Udino, E., Perez, M., Carere, C. & D'Ettorre, P. (2017) Active explorers show low learning performance in a social insect. *Current Zoology*, 63, 555–560. https://doi.org/10.1093/cz/zow101

VanderSal, N. & Hebets, E. (2007). Cross-modal effects on learning: A seismic stimulus improves color discrimination learning in a jumping spider. *The Journal of experimental biology*, 210, 3689–3695. https://doi.org/10.1242/jeb.009126

Walsh, R.N., Cummins, R.A. (1976). The open-field test – a critical review. *Psychological Bulletin*, 83, 482–504. https://doi.org/10.1037/0033-2909.83.3.482

Westneat, D. & Fox, C. (2010). *Evolutionary Behavioral Ecology*. Oxford University Press. https://doi.org/10.1086/656864

Wiggins, W.D., Bounds, S. & Wilder, S.M. (2018). Laboratory-reared and field-collected predators respond differently to same experimental treatments. *Behavioral Ecology and Sociobiology*, 72(19). https://doi.org/10.1007/s00265-017-2437-7

Winsor, A.M., Morehouse, N.I., Jakob, E.M. (2023). Distributed Vision in Spiders. In: Buschbeck, E., Bok, M. (eds) Distributed Vision. Springer Series in Vision Research. Springer, Cham. https://doi.org/10.1007/978-3-031-23216-9_10

Zurek, D., Nelson, X. (2012). Hyperacute motion detection by the lateral eyes of jumping spiders. *Vision research* 66, 26–30. https://doi.org/10.1016/j.visres.2012.06.011

N	2	3	4	5	6	8	9	10	12	13	14	15	16	18	19
T1	45	537	125	409	260	70	300	695	280	340	30	26	217	50	195
T2	6	368	300	225	525	480	275	510	78	168	52	120	80	99	828
T3	9	49	463	900	300	80	525	630	28	98	18	160	28	148	310

N	2	3	4	5	6	8	9	10	12	13	14	15	16	18	19
T1	0	1	4	0	1	0	1	0	-3	1	4	4	1	-3	1
T2	0	4	4	0	3	1	1	4	-3	1	1	-2	4	-3	1
T3	-1	1	4	1	4	4	-2	1	-3	-2	2	1	1	-3	2

Table S1. Time in sec. spent by spider N to get out of the film canister during trials T1, T2, T3.

Table S2. Boldness of spider N estimated during trials T1, T2, T3 according to Methods section

N	Control			Test 1			Test 2			Test 3		
	BP, s	M, s	YP, s	BP, s	M, s	YP, s	BP, s	M, s	YP, s	BP, s	M, s	YP, s
2	156	32	112	134	47	119	142	40	118	156	35	109
3	143	34	123	133	35	132	189	13	98	108	22	170
4	109	35	156	108	33	159	165	15	120	108	42	150
5	148	92	60	181	21	98	103	36	161	148	18	134
6	117	40	143	97	20	183	160	38	102	85	32	183
8	157	35	108	149	31	120	158	40	102	158	28	114
9	147	32	121	148	44	108	125	18	157	166	17	117
10	248	20	32	188	29	83	180	31	89	140	51	109
12	174	54	72	181	53	66	180	35	85	182	57	61
13	104	69	127	88	14	198	97	29	174	151	21	128
14	154	24	122	180	20	100	159	16	125	207	22	71
15	179	27	94	102	29	169	209	21	70	112	26	162
16	187	16	97	200	41	59	152	43	105	201	47	52
18	159	38	103	169	33	98	146	35	119	207	15	78
19	238	26	36	208	40	52	180	35	85	189	27	84

Table S3. Time in seconds spent by tested spider N on blue (BP), middle (M) and yellow (YP) parts of arena during learning trials (control and test sessions). Total time spent on arena for each session was always 300 s.

N	1st trial						2nd trial						3rd trial					
	training 1			training 2			training 1			training 2			training 1			training 2		
	BP, s	M, s	YP, s	BP, s	M, s	YP, s	BP, s	M, s	YP, s	BP, s	M, s	YP, s	BP, s	M, s	YP, s	BP, s	M, s	YP, s
2	65	29	206	50	25	225	72	27	201	68	36	196	54	43	203	82	25	193
3	28	30	242	47	25	228	32	24	244	47	18	235	10	36	254	25	24	251
4	42	30	228	20	16	264	24	26	250	37	16	247	28	29	243	33	45	222
5	51	48	201	42	26	232	45	52	203	34	48	218	57	65	178	65	23	212
6	34	23	243	16	20	264	27	24	249	13	18	269	20	40	240	39	26	235
8	39	37	224	40	26	234	40	31	229	53	21	226	50	42	208	31	20	249
9	76	38	186	75	23	202	56	55	189	59	24	217	47	35	218	75	23	202
10	23	70	207	43	21	236	47	23	230	53	20	227	29	22	249	36	20	244
12	59	44	197	62	24	214	69	45	186	71	21	208	58	39	203	51	21	228
13	36	23	241	61	22	217	66	28	206	40	36	224	42	29	229	52	34	214
14	73	36	191	79	92	129	78	29	193	54	36	210	82	28	190	73	23	204
15	103	38	159	59	37	204	71	33	196	94	38	168	79	79	142	23	13	264
16	41	35	224	106	23	171	54	34	212	65	24	211	42	39	219	63	25	212
18	74	36	190	50	35	215	50	34	216	57	32	211	30	47	223	48	39	213
19	60	37	203	68	26	206	73	34	193	54	21	225	75	38	187	56	25	219

Table S4. Time in seconds spent by tested spider N on blue (BP), middle (M) and yellow (YP) parts of arena during learning trials (training sessions). Total time spent on arena for each session was always 300 s.