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Variation in Predator Recognition Across Three Species of Jumping Spiders (*Salticidae*)

Janka Plate[1] **and Daniela C. Rößler**[2,3,4,*]

[1]Institute of Cell and Systems Biology of Animals, University of Hamburg, Hamburg, Germany
[2]Zukunftskolleg, University of Konstanz, Konstanz, Germany
[3]Department of Biology, University of Konstanz, Konstanz, Germany
[4]Department of Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany

*Corresponding author (Email: daniela.c.roessler@gmail.com)

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Abstract – The ability to recognize threats and to respond in a timely and appropriate manner carries significant benefits. Depending on the recognition task, this can be cognitively demanding. The zebra jumping spider (*Salticus scenicus*) is capable of visually recognizing static predator stimuli and reacts via a robust "freeze and retreat," a potentially innate response in this species. Here, we extend this finding, asking whether the ability of spiderlings to recognize a static predator and to initiate an escape response is common across juvenile salticids, and if so, whether there is species-specific variation of anti-predator responses. We found that captive-reared spiderlings of three European salticid species from different genera (*Heliophanus* cf. *cupreus, Evarcha arcuata*, *Marpissa muscosa*) were able to robustly recognize and retreat from a stationary predator stimulus. Additionally, we found differences in the reaction times between the species as well as different behavioral repertoires associated with the escape response which may reflect species-specific predator avoidance strategies.

Keywords – Anti-predator behavior, Escape, Recognition, Salticids

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For species with similar life histories, a strong selective pressure to recognize and avoid predators may generate similar behavioral responses that transcend taxonomic boundaries. Early life stages are typically the most vulnerable, due to the small size of the animals, which likely makes them prey for a wide range of predators. This vulnerability could be exacerbated by a lack of experience. Newly emerged jumping spiders frequently fall prey to other jumping spiders (Okuyama, 2007; pers. obs. DCR), thus, it is reasonable to assume that newly emerged spiderlings are already able to recognize threats such as larger salticids without requiring experience or learning. Being precocial, once emerged, jumping spiders are equipped with the visual acuity of adults and readily hunt and navigate through their environment (Goté et al., 2019). While predator recognition is indeed linked to learning in some animals (Griffin et al., 2001; Ferrari et al., 2008; Polo-Cavia & Gomez-Mestre 2014; Mezrai et al., 2020), a recent study has demonstrated that newly emerged spiderlings of the zebra jumping spider (*Salticus scenicus*) readily recognize and flee from static 3D-printed salticid models (Rößler et al., 2022). To test whether this recognition ability in *Salticus scenicus* is also present in other jumping spiders, we experimentally tested static predator recognition in early life stages of three species of European jumping spiders of different genera. Furthermore, since predator recognition and responses likely are the result of species-specific selection pressures, we also tested whether species differed in reaction time or overall predator avoidance response.

Methods

Ethics Statement

This study was conducted on invertebrates and did not require ethics approval. We adhered to the guidelines for the treatment of animals in behavioral research by the Association for the Study of Animal Behaviour (ASAB) (Buchanan et al., 2012).

Study Species

We used a total of 45 captive-reared spiderlings of unknown sex between two and six weeks post-emergence. We tested three different species native to Europe: 15 individuals of *Evarcha arcuata* (hereafter *Evarcha*), 16 individuals of *Heliophanus* cf. *cupreus* (hereafter *Heliophanus*) and 14 individuals of *Marpissa muscosa* (hereafter *Marpissa*). *Evarcha* spiderlings came from three different females collected in Trier, Germany. *Heliophanus* were collected around Konstanz, Germany and spiderlings from four different eggsacs/mothers were used. *Marpissa* originated from two females collected around Hürth and Konstanz, Germany. All spiderlings were lab-raised and had no prior exposure to predatory salticids other than their conspecifics (i.e., mother and siblings). Spiderlings were separated from their mothers upon emergence and kept in enclosures (5.2 × 5.2 × 15.3 cm) with their siblings. Two to three days before the experiment, spiderlings were separated from their siblings and housed singly in plastic vials (5.5 × 5.5 × 8.5 cm). Each spiderling was fed 2-3 *Drosophila* every 3-4 days and provided with water via a small damp cotton ball. Spiderlings were kept on a 12:12 h dark:light cycle and at a mean temperature of 22°C with 60% humidity.

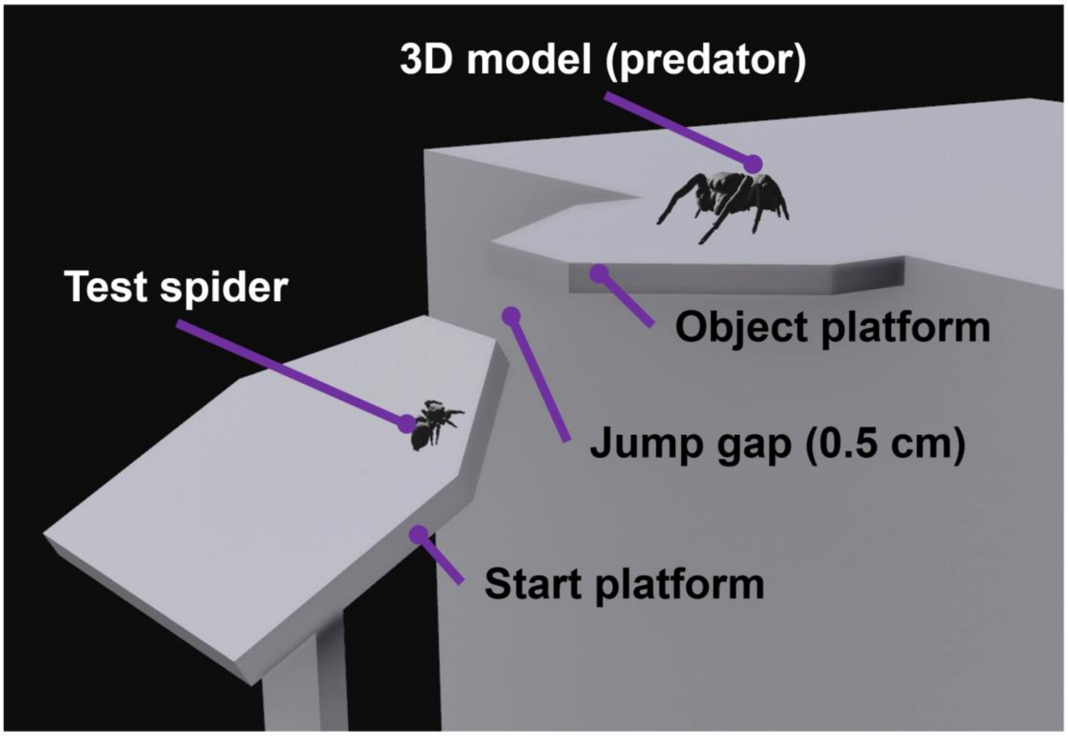
Experimental Setup for and Procedure of Trials

The experimental setup was based on a previous study on *Salticus scenicus* (Rößler et al., 2022) but was adjusted to accommodate the smaller size of the spiderlings as well as to include a jump. This jump served as an integrated test to guarantee visual and physical fitness of spiders and to control for an overall explorative behavioral state. Spiders who failed to successfully jump in any trials were excluded from the experiment (three inidividuals). The setup consisted of a start platform and an object platform (Figure 1). The static model (spider or control model, described below) was placed one centimeter from the edge of the object platform. Spiderlings were gently placed onto the start platform by manually transferring them from a plastic vial (3 × 7 cm). This included either spiders voluntarily jumping out of the vial and onto the lower half of the start platform or the experimenter gently tapping onto the vial and placing the spider in the lower half of the start platform. From the start platform spiderlings could not see the model because the start platform was placed at an angle and below the object platform with a 0.5 cm gap between the platforms (Figure 1). Only once the spiderling jumped across the gap, it could see the model, after which the spiderling had to decide whether to retreat from it or move towards it (i.e., passing the model). Both the start and object platform were covered with filter paper which was replaced after each trial to avoid potential effects of chemical cues via silk trails. Spiders were filmed from above using a Nikon D7200 with a 40mm DX Micro Nikkor lens at 30 fps (Nikon, Tokyo, Japan).

Two models were used in this experiment: A black sphere (length = 6 mm) made from plasticine clay (Noris Club, Staedtler) and a black 3D-printed model based on a micro-CT scan of a *Phidippus audax* specimen (length = 6 mm) (Formlabs, Cambridge, the stl file of the model is publicly available from Zenodo open science repository, see Rößler & Shamble, 2022). The 3D-printed model's frontal eyes (anterior median and anterior lateral eyes) were painted with shiny black enamel paint (Item-Nr. REV-32107, Revell GmbH, Bünde, Germany) to ensure a more realistic reflection or "shininess" of the eyes, since eye features have been shown to be crucial for recognition (Harland and Jackson, 2000, Rößler et al., 2022). *Phidippus audax* is a large salticid, known to prey on other salticids, and is found in North America (Okuyama, 2007), meaning that tested spiderlings were both ontogenetically and evolutionarily naive to the model. Each spiderling completed six trials, three with each model, all in randomized order.

Figure 1

Experimental Setup for a Predator Recognition Trial in Jumping Spider Spiderlings



Video Analysis

Videos were scored manually using the software BORIS (Friard & Gamba, 2016). A trial started as soon as the spiderling was on the start platform. The following behaviors were scored: “jump” (defined as a leap across the gap onto the object platform); “freeze” (defined as when the spiderling came to a noticeable, complete stop while oriented towards the model), “retreat” (defined as a sudden increase in distance to the model after a freeze), and “pass” (defined as when the spiderling walked past the model or climbed on top of it). Any time the frontal eyes were directed at the tested object (approximated by a perpendicular line from the pedicel through the midline of the frontal eyes meeting the object), we scored these phases as “oriented towards the object.” A trial ended after a retreat, a pass, or if the spiderling was oriented towards the object but showed no reaction. Reaction time was calculated from the beginning of the last freeze to the beginning of the retreat. Due to this definition, reaction time was only scored for trials with a retreat reaction and is therefore not available for control trials. Additionally, we scored distinct behaviors that were associated with the retreat such as “backward walking”, “leg waving”, “instant jump/drop”, or “pedipalp spreading”. Multiple behaviors could co-occur during a retreat.

Statistical Analysis

We only used trials in which spiders were oriented towards the object presented to them (see definition above). Statistical analyses were conducted using R version 4.2.2 (R Core Team, 2019). Generalized linear mixed models (GLMMs) were performed using the package *glmmTMB* (Brooks et al., 2017). Subject ID was included as a random factor. We then used an analysis of deviance on the resulting model with the package *car* to test which factors had significant effects on the dependent variable (Fox & Weisberg, 2019). The *emmeans* package was used to carry out post-hoc analyses with Bonferroni-correction (Lenth et al., 2019) and model fit was checked using the *DHARMa* package (Hartig, 2017). Binomial distribution was used to model the probability of a spiderling passing the object in both tested conditions. The *ggplot2* package was used to generate all plots (Wickham, 2016). All data and R scripts for analyses are available in the supplementary information of this article.

Results

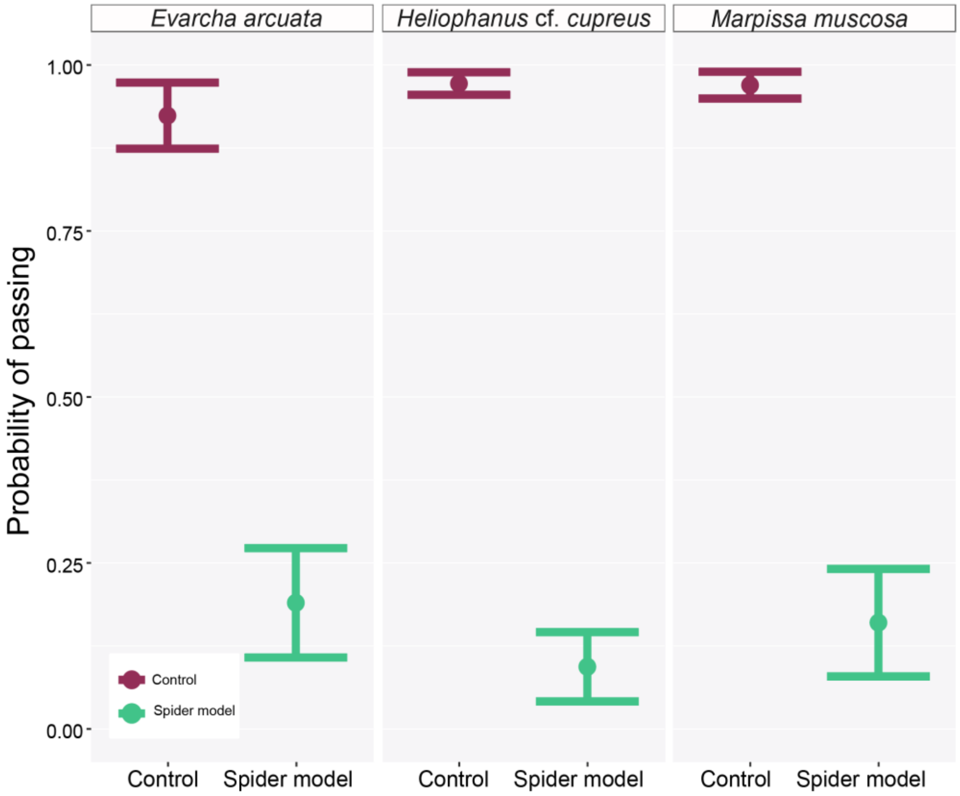
In total, we conducted 265 trials. In 217 trials, spiders oriented towards the presented object. In trials using the 3D-printed spider model, we could observe the same freeze and retreat behavior reported for *Salticus scenicus* (in Rößler et al., 2022) in all three salticid species (Video S1).

The probability of passing the object was significantly higher towards the control than towards the spider model, regardless of species (GLMM analysis of deviance, $\chi^2 = 35.17$, $p < .001$, $n_{obs} = 217$). Post-hoc analysis showed significant differences between all spider model/control pairings ($p < .001$, Figure 2). There was no significant difference of each condition (spider model or control) between the species (all at least $p > .7$). There was no effect of presentation order ($\chi^2 = 0.38$, $p = .54$), test date ($\chi^2 = 3.67$, $p = .72$), age ($\chi^2 = .20$, p = .65) or mother ($\chi 2 = 3.4$, $p = .90$).

A second measure of trial outcome, the probability of retreating from the model, was greater when the object was a 3D-printed spider, compared to the control object (GLMM analysis of deviance, $\chi^2 = 17.26$, $p < .001$, n = 217).

Figure 2

Model-Based Plot for Post Hoc Analyses Showing Probability to Pass the Tested Object

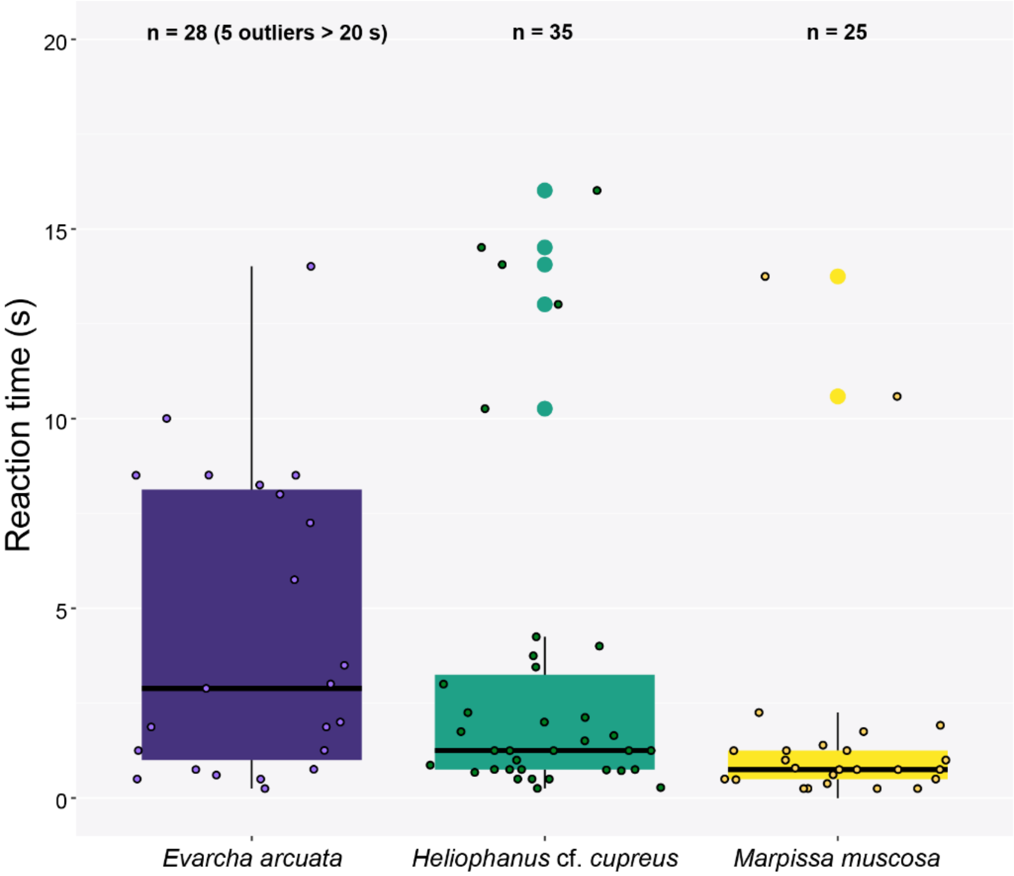


Note. Points show means, error bars indicate SE.

Likely due to the small sample size, no GLMM could be converged to analyze the differences in reaction time towards the spider model. However, *Evarcha* took the longest time to react (median (IQR); 4.63 s (7.63 s); n_{obs} = 28), followed by *Heliophanus* (1.25 s (2.50 s); n_{obs} = 35), while *Marpissa* had the fastest reaction time (0.75 s (0.75 s); n_{obs} = 25) (Figure 3).

Figure 3

Boxplots Showing Reaction Time Towards the Spider Model for Tested Species

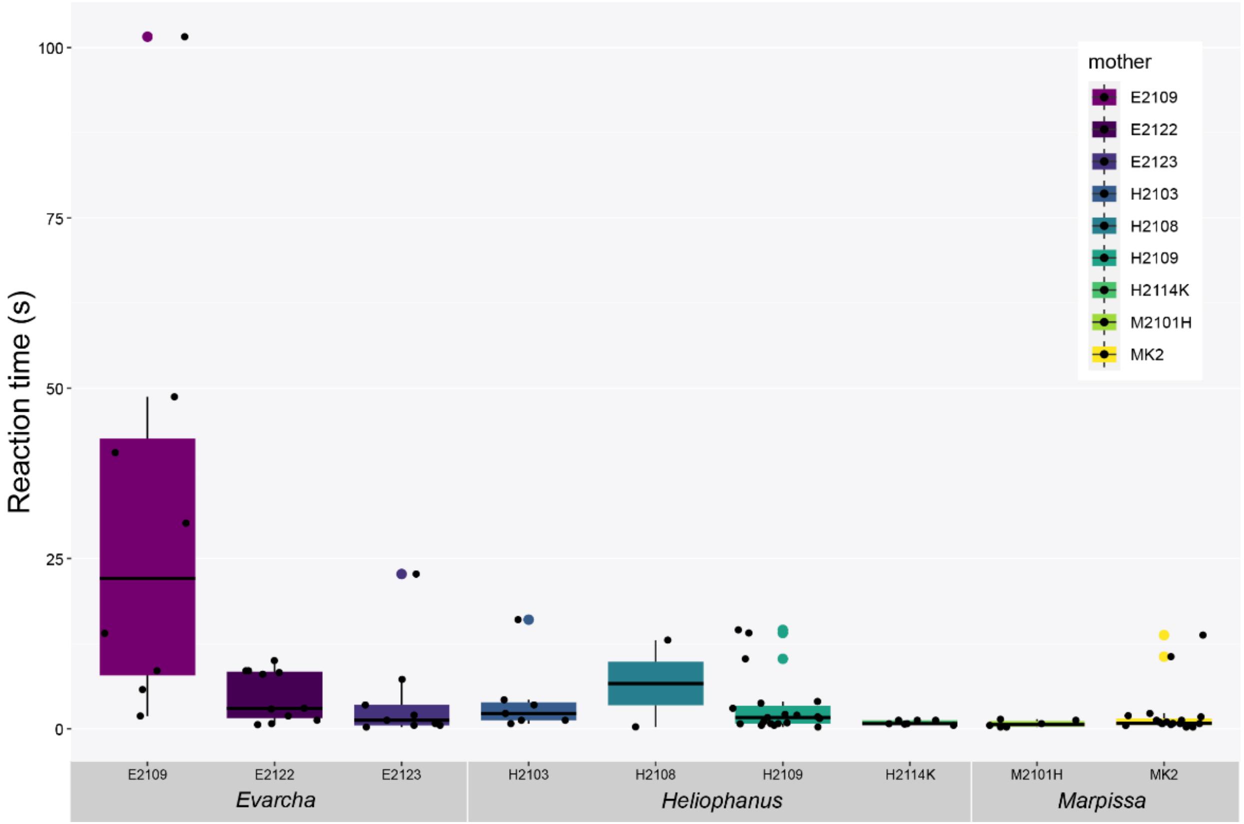


Note. Black horizontal lines represent the medians, lower and upper bound of the boxes show 25th and 75th percentiles with whiskers representing ±1.5 interquartile range. Small circles represent all data points, larger circles represent outliers. For *Evarcha*, 5 outliers above 20 s are not shown in the figure.

Although we detected no overall effect of eggsac/mother, we additionally visualized reaction time per eggsac/mother because of the limited number of eggsacs the spiderlings derived from. Spiderlings with the longest reaction times in *Evarcha* all stemmed from the same mother (Figure 4).

Figure 4

Boxplots Showing Reaction Time of Spiderlings Towards the Spider Model, Grouped by Egg Sac/Mother

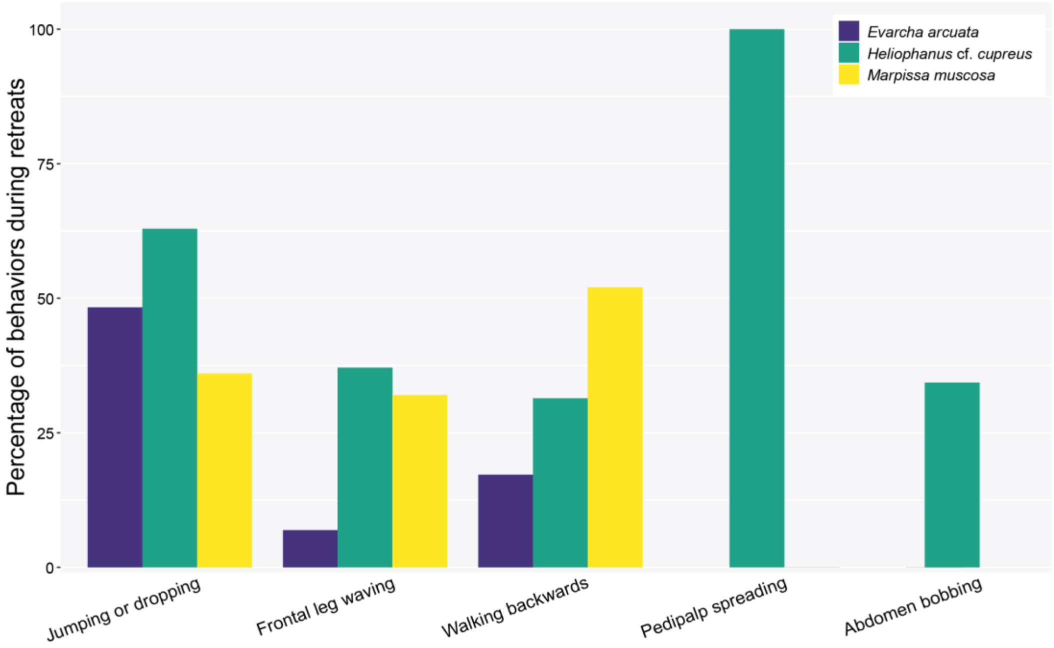


Note. Black horizontal lines represent the medians; lower and upper bound of the boxes show 25th and 75th percentiles with whiskers representing ±1.5 interquartile range. Black dots represent all data points, larger dots represent outliers.

Lastly, we observed differences in retreat-associated behaviors across the three tested species (Figure 5, Video S2). *Heliophanus* showed a broader behavioral repertoire associated with the reaction towards the 3D model than the other two species. It is particularly noteworthy that *Heliophanus* always spread their pedipalps and often bobbed their abdomen when reacting towards the predator model, exhibiting behaviors which were completely absent in the other two species.

Figure 5

Percentage of Retreat-Associated Behaviors Towards the Spider Model Across Three Tested Species with Multiple Behaviors Possible per Retreat



Note. Total number of trials with retreats for each species: *Evarcha*: $n_{obs} = 28$, *Heliophanus*: $n_{obs} = 35$, *Marpissa*: $n_{obs} = 25$.

Discussion

Our study indicates that the recognition of stationary salticid predators is potentially common in European jumping spiders. Testing such abilities across different species holds valuable information about the origin and evolution of cognitive traits and how life history or ecology may play a role in shaping these traits (Aguilar-Arguello & Nelson, 2021).

The robust static visual recognition of potential threats and the subsequent behavioral response carry a selective benefit; therefore, we predicted it to be a common trait across jumping spiders, which are highly visual and apt predators. Given the morphologically conserved features of jumping spiders such as their characteristic large anterior eyes and their unique eye arrangement (Morehouse, 2020), it is not surprising that spiderlings could detect the models and were triggered to retreat, even when the model was based on a spider that spiderlings were naïve to.

We detected variation in the reaction time, raising questions around the underlying factors causing this. We consider several possibilities that warrant follow-up studies and further inquiry. First, there could be an overall difference of cognitive abilities between species (Aguilar-Arguello & Nelson, 2021; Gómez, 2005), which might lead to differences in processing information. For example, jumping spiders in the genus *Portia* are recognized for their high levels of cognitive abilities that include the ability to detour (Cross et al., 2020; Jackson & Cross, 2011; Tarsitano & Andrew, 1999). Other species of jumping spiders have demonstrated associative learning and reversal learning (Liedtke & Schneider, 2014), while others are seemingly lacking associative learning abilities, even for ecologically relevant cues (Vickers et al., 2021). An alternative, but not mutually exclusive explanation, could be species-specific differences in life history and habitat use (Carducci & Jakob, 2000; Steinhoff et al., 2018). While *Heliophanus* and *Evarcha* are mainly found amongst highly structured, three-dimensional vegetation in meadows (Sanders et al., 2015; Scheidler, 1990), *Marpissa* resides predominantly on two-dimensional surfaces such as bark, fences or walls (Steinhoff et al., 2020), offering fewer structural opportunities to hide or retreat from predators during close-range encounters, such as the one simulated in our experiment. Lastly, the response differences could indicate species-specific anti-predator strategies. It is especially noteworthy that spiders sometimes froze for extended periods before initiating an escape response, particularly so in *E. arcuata*. Here, it is particularly noteworthy that the longest freezing times were consistently observed in spiderlings from one specific eggsac/mother, including one freeze that lasted over 100 sec before a reaction was initiated (Figure 4). Due to the overall relatively small sample size, we cannot be certain whether the overall longer freezing can generally be attributed to *Evarcha* or whether we are observing a parental effect, as is known, for example, from damselfish (Atherton & McCormick, 2020). Similarly, in *Heliophanus*, spiderlings from one eggsac/mother have seemingly longer reaction times.

Freezing likely entails scanning and information gathering, but it seems unlikely that extended freezing periods (> 10 sec) would result from ongoing stimulus processing, since predators are likely to strike more rapidly in a natural setting. Freezing most likely already indicates a successful recognition; thus, freezing may be a first line of defense and an anti-predator mechanism in itself. Rather than swiftly investing in a potentially costly escape response, staying motionless could prevent an attack. Freezing is a common response to threats in animals (Eliam, 2005; De Franceschi et al., 2016). This may be particularly effective in close range encounters and when the predator is likely to react to movement by the prey. This explanation could also be connected to differences in habitat. The highly complex structure of dense vegetation would allow species like *Heliophanus* and *Evarcha* to simply drop or jump into a highly structured surrounding when a potential attack is imminent, potentially driving this initial and extensive "freezing" response. To fully investigate the natural differences in anti-predator strategies, an experiment testing the reaction to predator models in more natural settings is crucial. This could also include an experimental setup better reflecting the three-dimensionality of natural habitat as described earlier.

During the trials, we observed differences in retreat-associated behaviors between the tested species (Figure 5, Video S2) that substantiate the presence of species-specific responses and may inspire follow-up studies. We regularly observed what appears to be signaling with the front legs in all species, but it seems to be less common in *Evarcha*. Similar, but mostly unilateral, front leg movements can sometimes be observed in neutral context locomotion in *Marpissa* (pers. obs. DCR). All three species, but more so *Evarcha* and *Heliophanus*, engage in jumping away or dropping as a response towards the 3D model. This is in line with our previous hypothesis that these responses may reflect a beneficial strategy in a more complex habitat setting. Additionally, *Heliophanus* frequently bobs its abdomen when faced with the predator model and always extensively spreads its pedipalps. While abdomen bobbing is generally observed in this species during locomotion stops, the frequency and extent of the behavior is visibly increased during predator encounters (pers. obs. DCR). These behaviors are completely absent in the other two species and warrant a deeper inquiry. *Marpissa* showed the highest proportion of walking away backwards, which may, again, reflect a strategy that is adapted to its less structurally complex habitat. Our study had some limitations that need to be addressed in future studies, such as the range in age and the resulting range in size of the tested spiderlings (from 2 to 5 mm), as well as a generally small sample size. Ideally, spiderlings would also stem from a higher number of different eggsacs/mothers to enable specifically testing parental effects. Explicitly testing the effect of previous parental predator exposure on offspring in jumping spiders could also be an intriguing future avenue.

Additionally, testing ontogenetic changes of the response and reaction time could be important in understanding the impact of experience and development or whether the reaction time and response is hard-wired within a species. Preliminary analyses using the data from Rößler et al. (2022), which used adults and spiderlings of the same species (*Salticus scenicus*), indicate that reaction time might be relatively constant within a species (spiderlings: median reaction time = 4.22 s (IQR = 6.25, $n_{obs} = 62$); adult median reaction time: 3.49 s (IQR = 5.62, $n_{obs} = 131$). Beyond the species level, a deeper inquiry into individual variation and within-individual robustness of anti-predator behavior is equally possible and offers an intriguing opportunity to test questions of animal personality in this group.

The robustness of threat recognition in salticids when faced with a larger salticid (i.e., a potential predator) offers numerous opportunities to explicitly test aspects of anti-predator adaptations, behavioral strategies, and visual stimulus processing that can feasibly be examined across a range, if not all, salticids.

Ultimately, larger comparative studies across the salticid tree of life could yield powerful insights into this intriguingly robust visual-cognitive behavior and its evolution. An extension of the paradigm into spider lineages that are also visually apt (e.g., lynx spiders, Oxyopidae, or wolf spiders, Lycosidae) would confirm if this cognitive ability has evolved several times independently in visual hunters among spiders.

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Conflict of Interest: The authors declare no conflict of interest.

Author Contributions: D.C.R. initiated the idea and designed the experiments. J.P. conducted the experiments and manually scored the behavioral data. J.P. and D.C.R. analyzed the data. D.C.R. and J.P. wrote the manuscript.

Inclusion and Diversity Statement: The authors greatly value equity, diversity and inclusion (EDI) in science. This study was conducted under consideration of EDI best practice. The authors represent different career stages (graduate student and postdoc). One or more of the authors self-identifies as a member of the LGBTQ+ community. We actively worked to promote gender balance (of first author) in our reference list, which, however, we did not fully reach (Rößler et al., 2020; Sweet, 2021).

Data Availability Statement: Experimental data and the R script used for statistical analyses are available from Zenodo open data repository (https://doi.org/10.5281/zenodo.10552655).

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Supplementary Material

Video S1: https://doi.org/10.6084/m9.figshare.25139129.v1

Video S2: https://doi.org/10.6084/m9.figshare.25139132.v1