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Static visual predator recognition in jumping spiders

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Abstract

1. Visually detecting, recognizing and responding appropriately to predators increases survival. Failure to detect a predator or long decision time carries high and potentially fatal costs. Consequently, many animals show general anti-predatory responses towards threatening stimuli, for example, looming objects. However, in the context of lurking or stalking predators, visual recognition is based on static visual cues, making this task computationally demanding.

2. Jumping spiders (Salticidae) have superb vision and are excellent predators but they can equally fall prey to other jumping spiders. In a hierarchical decision-making setup, we tested whether the common zebra jumping spider *Salticus scenicus* can visually recognize stationary predators. We measured the spiders' behavioural responses towards predator (naturally co-occurring, non-co-occurring and artificial) and non-predator objects as well as towards objects with modified features.

3. Our experiments show that salticids demonstrate a robust, fast and repeatable 'freeze and retreat' behaviour when presented with stationary predators, but not similarly sized non-predator objects. Anti-predator responses were triggered by co-occurring and non-co-occurring salticid predators, as well as by 3D-printed salticid models (based on micro-CT scans), suggesting a generalized predator detection/classification. Using modified 3D-printed models, we found evidence that eyes act as an important cue. However, eyes alone did not explain the responses, suggesting that underlying processes rely on multiple rather than single features.

4. To address the role of learning and memory, we tested newly emerged spiderlings and found the same behavioural responses towards predator objects suggesting an innate response. The ability of jumping spiders to innately recognize a non-moving threat is surprising in terms of underlying cognitive processes and the evolution thereof.

5. Escaping from a predator before an attack has been launched likely carries sufficient selective benefits. From a cognitive perspective, the overlap of static visual characteristics between salticid predators, prey and conspecifics invites further questions considering the mechanisms of such nuanced visual discrimination and categorization in animals with complex vision but relatively small nervous systems.

1 | INTRODUCTION

When animals interact with their surroundings, many detect, recognize and potentially classify objects, for example, into landmarks, foraging sites, prey, conspecifics, mates or predators and modify their behaviour accordingly. The task of recognizing predators, however, is unique in that the stimulus is not paired with a concrete reward, making it fundamentally different from most recognition processes. Moreover, different recognition tasks underlie different selective forces. While arguably errors in recognition are often costly across contexts, costs are particularly high, and even fatal, when it comes to recognizing—or failing to recognize—predators. This stronger selection on the species that has more to lose in such interactions was described by Dawkins & Krebs (1979) as 'the life-dinner principle'. Thus, the ability to appropriately modify behaviour in response to predators provides a major selective advantage across a wide range of organisms (Eilam, 2005). For example, potential prey often avoid chemical cues associated with a predator (Caldwell & Lamp, 1981; Ferrari et al., 2008; Persons et al., 2001), or reduce activity in the presence of such cues thereby lowering the chances of detection and/or capture (Cooper & Blumstein, 2015; Coss, 2010; Fischer & Frommen, 2019; Lima & Dill, 1990).

When relying on visual information, would-be prey typically demonstrates freezing, escape behaviours or threat displays in response to moving stimuli representing real or model predators (Edmunds, 1974; Hemmi, 2005; Sherman, 1985) and many species respond to simple looming stimuli (De Franceschi et al., 2016; Evans et al., 2019; Stankowich, 2009). However, entire classes of predators ambush or stalk prey from stationary or near-stationary positions (Zoroa et al., 2011), minimizing the amount of motion-derived information available to the visually reliant receiver. In such cases, visual predator recognition must be based on static visual features. This makes the task of mitigating predator-related risk more difficult from a cognitive perspective, as research in visual neuroscience and computer vision has shown that object detection and recognition in static visual scenes is complex and computationally demanding (DiCarlo et al., 2012; Kubilius et al., 2019). This task is made particularly challenging because variation in the natural scene (e.g. light levels, background, etc.; Leavell & Bernal, 2019) as well as among predators and predator communities generates a broad range of dissimilar cues present during each predator–prey encounter. Detection must be followed by accurate recognition to avoid costly false alarms (Card & Dickinson, 2008; Green et al., 2020; Lagos et al., 2014) and a swift behavioural response as time for recognition is negatively correlated with survival in this context (Herberholz & Marquart, 2012). Static visual predator recognition, thus, poses a fundamental visual-cognitive problem, the solution of which yields strong selective advantages.

Predator recognition might be driven by innate or learned processes—or a combination of the two. Learning arguably involves predator encounters, posing a significant risk for the prey. Yet it is known that visual predator recognition in vertebrates including mammals and birds (Griffin et al., 2001; McLean et al., 1999) as well as chemical predator recognition in amphibians or fish (Chivers et al., 2021; Polo-Cavia & Gomez-Mestre, 2014) is often dependent on experience—a feature exploited in captive breeding programs where prior to release, animals are trained to recognize predators (Griffin et al., 2001; McLean et al., 1999). Whether visual recognition of relevant predators is learned or innate in invertebrates is less well understood.

To investigate this sensory ecological problem, we asked how jumping spiders (Salticidae) respond to stationary predator-like objects. These animals have acute visual systems, with a resolution that exceeds even the best insect eyes (Foelix, 2010; Harland et al., 2012). They are also capable of a wide range of visually complex behaviours including navigating 3D mazes and elaborate conspecific displays (Cross et al., 2020; Foelix, 2010; Jackson & Cross, 2011).

Salticids are active predators, who stalk and slowly pursue their prey, commonly initiating attacks from a motionless position (Drees, 1952) and intraguild predation is widespread across the group with jumping spiders regularly preying on other jumping spiders (Figure 1a,b, Okuyama, 2007). The overall aim of our study was to test the anti-predatory response of jumping spiders to larger, stationary jumping spiders. We first asked how the jumping spider *Salticus scenicus* responds to stationary predator-like objects, including co-occurring predatory jumping spiders, non-co-occurring predatory jumping spiders, size-matched non-predator objects and 3D-printed models (based on micro-CT scans) of a predatory jumping spider. As all predator-like objects were avoided, we then specifically tested whether spiders were using single or multiple features to classify targets by manipulating the presence/absence of eyes on the 3D-printed model. Finally, to directly address the impact of experience and learning, we presented 3D-printed objects to 1- to 3-day-old spiderlings.

2 | MATERIALS AND METHODS

2.1 | Subject details

The study was conducted using the common zebra jumping spider *S. scenicus*, a relatively small jumping spider (body length = 6 mm) with a wide native distribution across Europe (World Spider Catalog, 2021). For this study, a total of 45 individuals were collected around Trier, Germany, between March and April 2020. Spiders comprised 15 adult males, 15 penultimate females (i.e. one moult away from the adult stage) and 15 adult females. While other species of *Salticus* occur in the area, *S. scenicus* can clearly be distinguished by their

FIGURE 1 Hierarchical decision-making setup to test predator recognition in salticids. (a) Large European salticid *Marpissa muscosa* preying on the common zebra jumping spider *Salticus scenicus* (red arrow). © Daniela C. Rößler (b) Large North American salticid (*Phidippus* sp.) preying on *S. scenicus* (red arrow) in the field in North America. © Sean McCann (c) Sketch of the experimental setup showing start, object and main platform (with shelter structures). A camera is mounted above the setup and there are two light sources. (d) Example picture showing a tested spider *S. scenicus* after having jumped the gap between start and object platform towards a 3D-printed salticid model without eyes
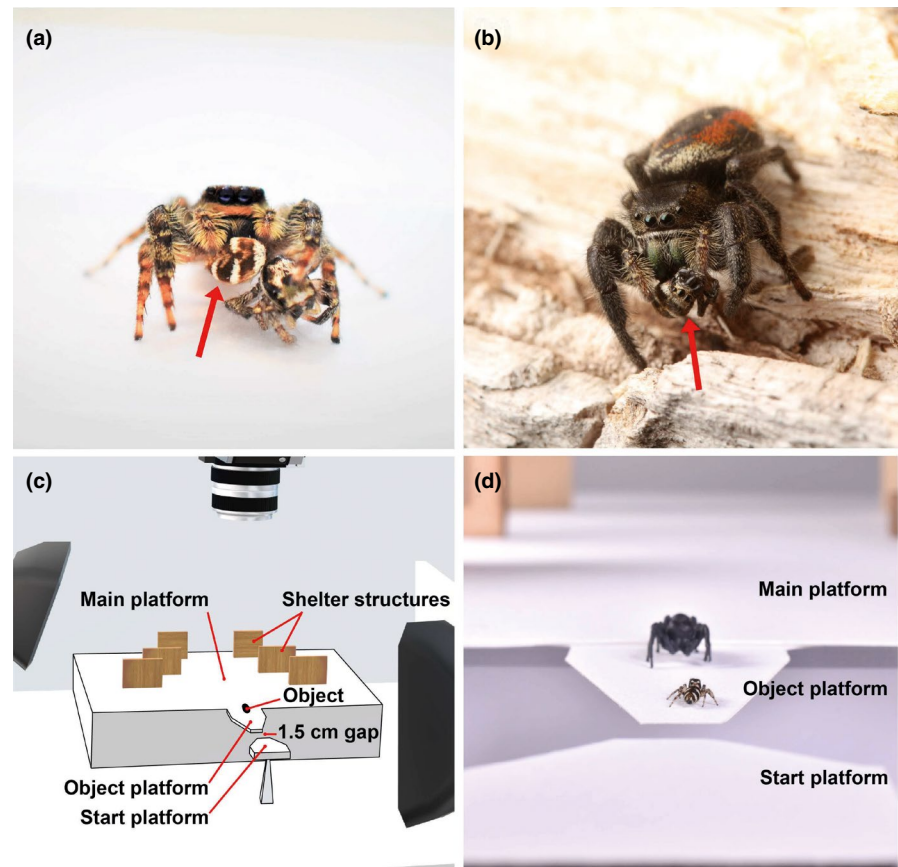
larger size, as well as species-specific colour markings present across all life stages—most notably a pair of light markings on the cephalothorax and three dark bands on the abdomen. Spiders were kept individually in plastic containers (6 × 6 × 16 cm), with enrichment structure (plywood) and water-filled Eppendorf tubes stoppered with a cotton ball for water supply. Spiders were kept for at least 1 week before any experiments were conducted. Animals were fed twice a week (Tuesday and Friday) with two or three *Drosophila*. No experiments were conducted on Wednesdays to control for an overall balanced satiation state of the spiders during experiments. The mean temperature and humidity during housing was 22°C and 70%. The day–night light regime was 12:12.

The focal species of this study is not under protection. No permission or ethical approval was required for this study.

2.2 | Procedure of the experimental trials

Every spider entered the setup by climbing out of a vial onto the start platform (Figure 1c). The trial start was defined as the time a spider oriented towards the object placed across the gap. The setup included two light sources (Genaray SpectroLED Essential 365 Daylight and SP-E-365D). All trials were recorded from directly above (resolution = 1920 × 1,080; 60 frames per second) using a Nikon D7200 with a 40-mm DX Micro Nikkor lens (Camera setting = ISO 400 F20, 1/125). The gap between start and object platform was 1.5 cm, an easily manageable jump for *S. scenicus*. The trial

ended once the spider jumped across the gap and passed the object, after the spider retreated from the object (before or after jumping) or if the spider chose not to jump after orienting towards the object while on the start platform. The main platform was enriched with wooden shelter structures to increase motivation for spiders to jump across the gap, thereby encouraging them to look at the object (see Figure 1c). Start and object platforms were topped with filter paper, which was changed after every spider to avoid silk traces and chemical cues that might interfere with trials.
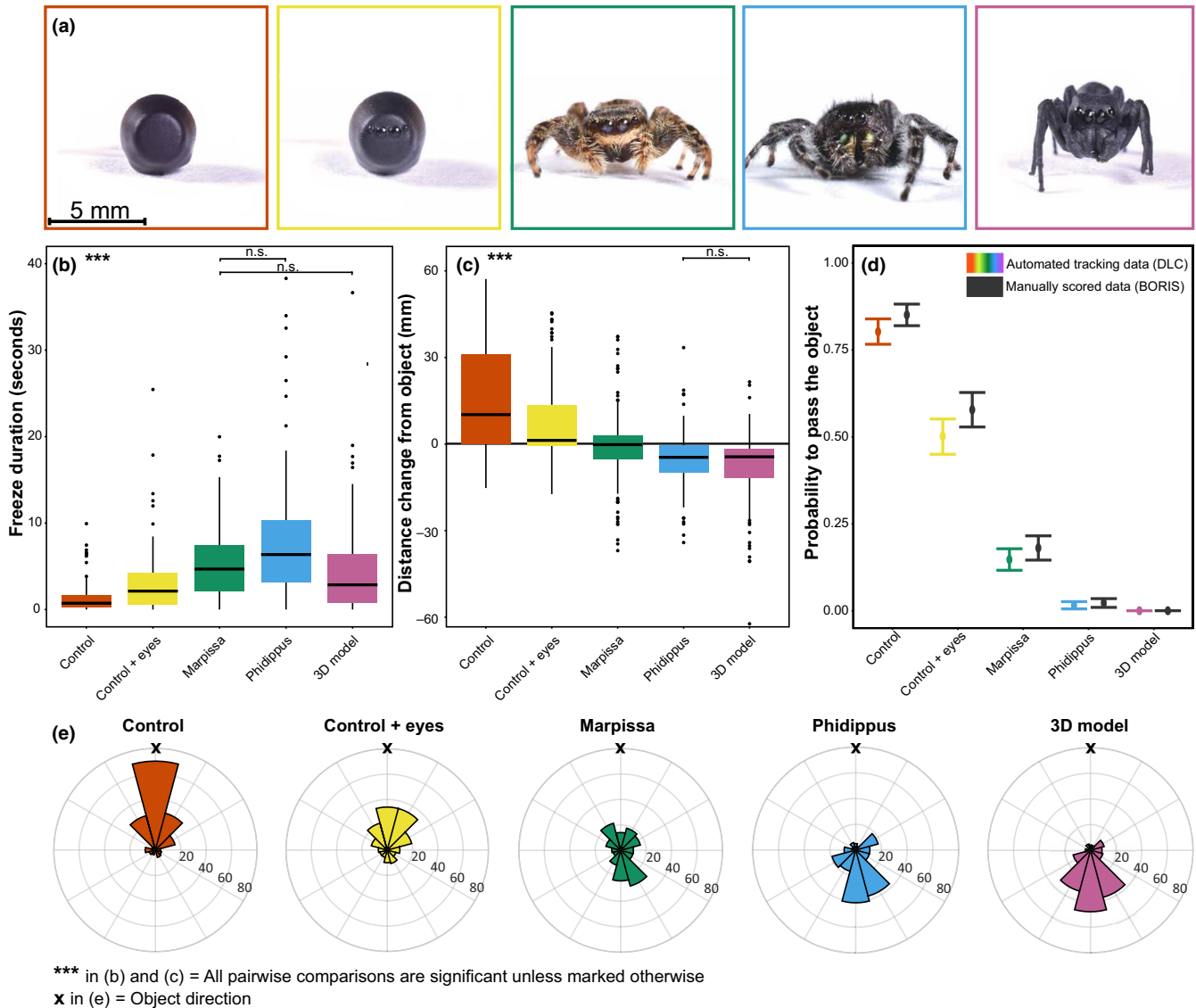
2.3 | Experiments

2.3.1 | Predator versus non-predator objects

To test whether jumping spiders can recognize stationary predators, we used 15 adult males and 15 penultimate females to control for any effects of sex. Penultimate females were chosen to decrease potentially distracting chemical cues that could interfere with males during trials. Test subject and trial order were completely randomized. Each spider was tested on two different days with 8–10 days between test days. On each test day, spiders were presented with each condition three times in random order (i.e. a total of 15 trials per spider per day) resulting in a total of 900 trials. There was a minimum break of 30 s between trials. Spiders were presented with five objects (Figure 2a): (a) a 3D-printed spheroid with a flattened anterior region as a control, (b) a control with

salticid-like forward-facing anterior median and anterior lateral eyes, (c) a dead specimen of larger predatory salticid *Marpissa muscosa* which co-occurs with the collected *S. scenicus* throughout its native European range, (d) a dead specimen of *Phidippus audax*, another larger predatory salticid, but a non-co-occurring genus native to the Americas and (e) a 3D-printed model based on a micro-CT

scan of *P. audax*. Dead specimen objects are referred to as 'Marpissa' and 'Phidippus' to avoid confusion. Objects used in the experiment had similar dimensions: flattened spheroid (control, object length = 12 mm), control with salticid frontal eyes (control + eyes; object length = 12 mm), dead specimen of *M. muscosa* (Marpissa; object length = 9 mm), dead specimen of *P. audax* (Phidippus; object

FIGURE 2 Static visual recognition of predator and non-predator objects. (a) Objects used in the first experiment. (Left to right) Control, 3D-printed spheroid with flattened front (red); control + eyes: salticid-like frontal eyes (anterior median and anterior lateral) placed on the control (yellow); Marpissa: dead specimen of *M. muscosa*, a large European salticid (green); Phidippus: dead specimen of *P. audax*, a large North American salticid (blue); 3D-printed predator: 3D model based on a micro-CT scan of *P. audax* (purple). Scale is identical across images, scale bar shown at left. (b) Boxplots showing freeze duration depending on condition based on the longest freeze detected in each trial (n_{trials} = 900, 180 trials/condition). Black horizontal lines represent the median, lower and upper bound of the boxes show 25th and 75th percentiles with whiskers representing ±1.5 interquartile range. Black dots show outliers (one outlier for Marpissa at 60 s is not shown). All pairwise comparisons of the post hoc test are significant with $p < 0.01$. Pairwise comparisons noted as 'n.s.' are not significantly different ($p > 0.05$). Colours as in (a). (c) Boxplots showing distance change from the object during 2 s post-freeze for each trial, grouped by condition. Positive values represent movement towards the object, negative values represent movement away from the object. Differences for all pairwise comparisons are significant ($p < 0.01$) unless noted 'n.s.' ($p > 0.05$). Boxplot parameters and colours as in (b). (d) Model-based plot of post hoc analyses showing probability to pass the object depending on condition. Points show means, error bars ±*SE*. Coloured graphs (left in each condition) represent data based on automated video tracking using DeepLabCut, grey graphs show manually scored data using BORIS. (e) Polar histograms showing direction of post-freezing trajectories

length = 12 mm) and 3D-printed model based on a micro-CT scan of *P. audax* (3D model; object length = 12 mm). 3D-printed objects were printed with a layer height of 25 μm using a Formlabs 2 resin printer (Formlabs, Cambridge). To increase the realness of the eyes on the control + eyes and on the 3D-printed spider model, eyes were additionally painted with black acrylic paint (Talens art creation, colour 701; Royal Talens) to achieve a reflective glossy effect (shininess). Dead specimens were separately fixed in 70% ethanol. *Phidippus audax* was obtained from the private collection of a breeder and *M. muscosa* was collected at the same field site as *S. scenicus*. Being the largest salticid species in Germany, *M. muscosa* can easily be identified by its size, coloration, elongated shape and a conspicuous light stripe beneath the frontal eyes (in females). At the beginning of each experiment day, specimens were taken out of the ethanol, rinsed with water, and left to dry and to evaporate the remaining ethanol at least 30 min before the start of experiments.
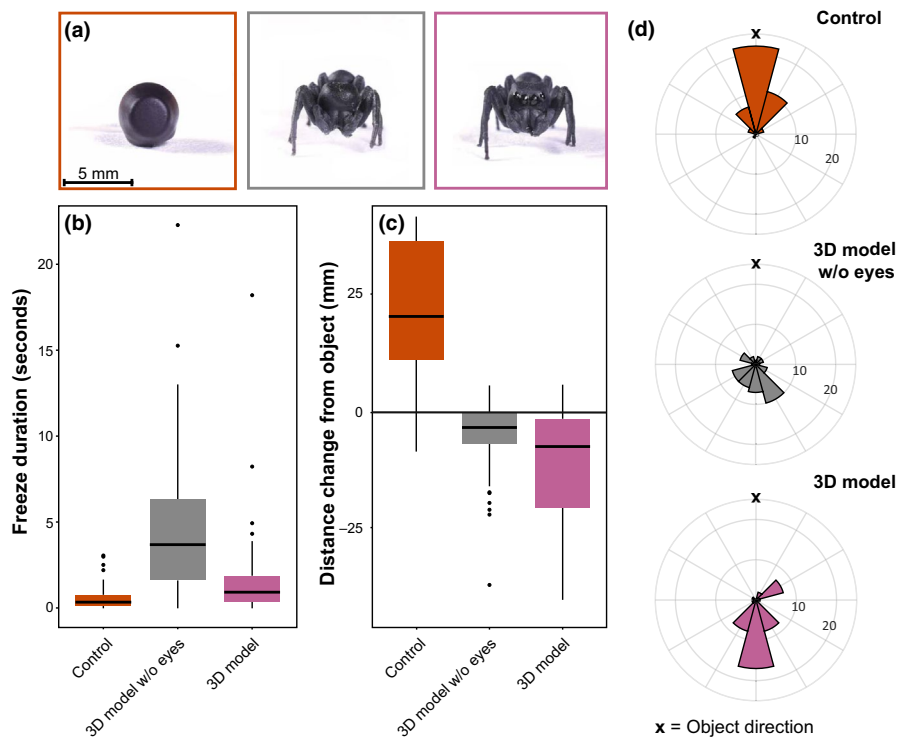
2.3.2 | Modified features

To test the importance of eyes as cues in predator recognition, we used 15 adult females (after confirming that there was no effect of sex on any of the variables in the first experiment, see Appendix S1, Section 1.1) and only one test day (after confirming there was no effect of test day, see Appendix S1, Section 1.2). We tested three objects in the same manner as in the first experiment in a random order (control, 3D model without eyes, 3D model; all objects with length = 12mm; Figure 3a) totalling nine trials per spider (total number of trials = 135).

2.3.3 | Newly emerged spiderlings

To test the role of learning and memory in predator recognition, we tested the behavioural responses of newly emerged spiderlings (1–3 days post-egg sac emergence; $n = 32$; body length = ~2 mm; see Appendix S1, Section 1.3). Spiderlings emerged from three separate egg sacs laid in captivity. Mothers were separated from egg sacs at least 1 week prior to spiderling emergence and spiderlings were separated immediately after they left the egg sac; spiderlings therefore had no experience with any large salticids of any kind. Spiderlings are known to possess an ontogenetically constant number of photoreceptors and are thus believed to have comparable visual acuity to adults (Goté et al., 2019). The experimental setup was altered to

FIGURE 3 Testing static visual predator recognition with modified features. (a) Objects used in the second experiment. (Left to right) Control (red); 3D-printed model without eyes (grey); 3D-printed model (purple). Scale is identical across images, scale bar shown at left. (b) Boxplots showing freeze duration depending on condition based on the longest freeze detected in each trial ($n_{\text{total trials}} = 135$, $n_{\text{trials per condition}} = 45$). Black lines represent the median, lower and upper bound of the boxes show 25th and 75th percentiles with whiskers representing ±1.5 interquartile range. Black dots show outliers. All pairwise comparisons of the post hoc test are significant with $p < 0.001$. (c) Boxplots showing distance change from the object 2 s post-freezing for the tested conditions based on the longest freeze detected for each trial. Black horizontal lines represent the median, lower and upper bound of the boxes show 25th and 75th percentiles with whiskers representing ±1.5 interquartile range. Black dots show outliers. Positive values represent movement towards the object, negative values represent movement away from the object. (d) Polar histograms showing direction of post-freezing trajectories
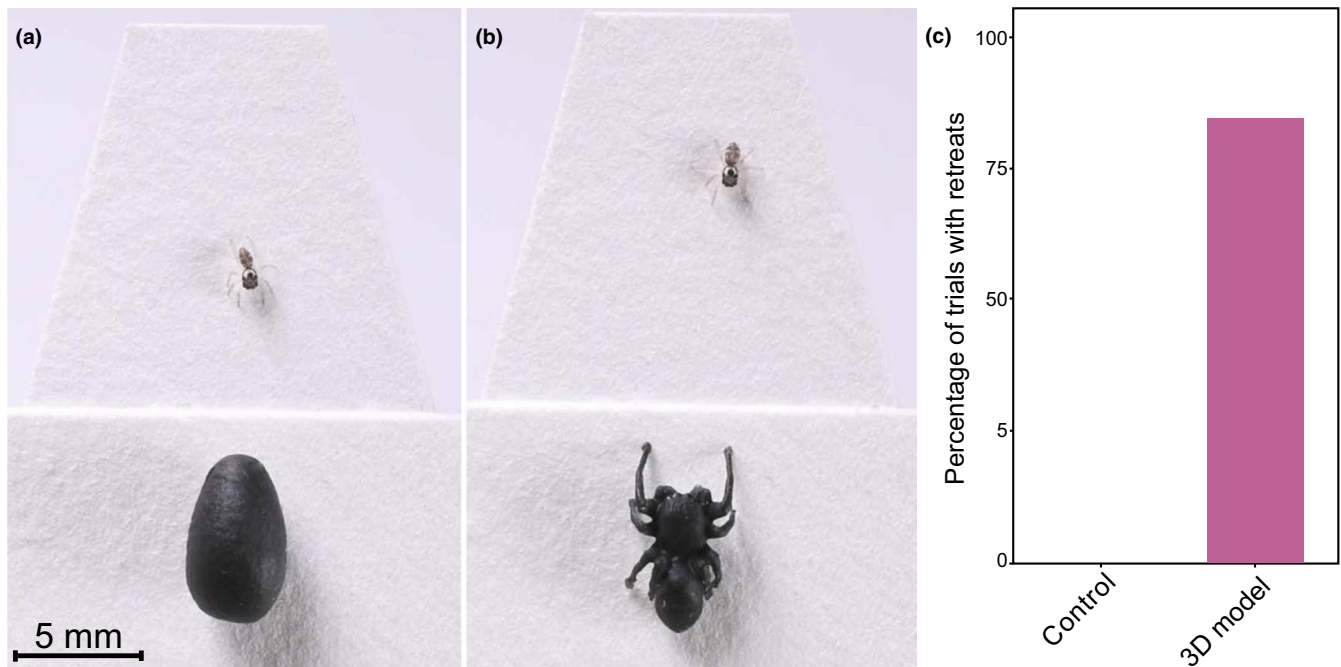
FIGURE 4 Predator recognition in newly emerged spiderlings. (a) A spiderling facing a 6 mm spheroid. (b) A spiderling facing a 6 mm version of the 3D model. (c) Bar plot showing the percentage of trials with retreats for all trials in which the spider looked at the presented object

account for the smaller size of these animals, with no gap between platforms and stimulus objects of smaller size (6 mm control and a 6 mm 3D model; Figure 4a,b). The smaller size of the predator object (and respectively of the control) was chosen to best match the size of an ecologically relevant predator. Each object was randomly presented to each spiderling three times (total number of trials = 192). Videos were manually scored for the presence of retreat behaviour and to check whether spiderlings looked at the object. The control object in this experiment was made from plasticine clay (Noris Club®, Staedtler), as 3D printing was not accessible during this phase of the 2020 pandemic.

2.4 | Manual and automated video analysis

Videos were handled twofold (except for experiments using spiderlings). First, each video was hand-scored for different behaviours using the software BORIS (Friard & Gamba, 2016). Main scores and definitions were as follows: Start of trial = time that a spider on top of the start platform orients towards the object across the gap; jump = spider jumps across the gap (independent whether the object has been seen or not); pass = passing the target and reaching the main platform (including: walking past the object, climbing on top of the object, climbing underneath the object platform, jumping to the main platform from the object platform); freezing = a sudden and complete stop of rotational and directional movement while oriented towards the object (proxy for object perception/visual inspection); approaching = decreasing the distance to the object after freezing (i.e. first assessment); looking

at the object = all states in which the spider's frontal eyes are directed straight towards the object; retreat = a sudden increase in the distance to the object after freezing; and end of trial = either after retreating or passing the object or after the spider visually encountered the object but shows no response roaming the start platform.

In addition to this manual scoring, we used DeepLabCut, an automated, neural network-based video tracking software (Mathis et al., 2018), to track nine spots on the dorsal side of the spiders' body in each frame of the video: three locations on the head, the pedicel, four locations on the abdomen and the spinnerets (Figure S3). Tracked body spots were subsequently used to determine spider position, velocity and field of view to track when the spider was looking at the object. The field of view was calculated as ±10 degrees horizontal angular offset from the midline of the head (and thus the main frontal eyes), with this angular range accounting for the retinal movements of the main eyes (cf. Land, 1969, for details on calculations, see Appendix S2; Figure S3). We defined object detection as occurring when the spider came to a complete halt (directional and rotational) with the head oriented towards the object (max angular offset of 10 degrees), presumably scanning the object with the main frontal eyes during this 'freeze' (Land, 1969). Values based on pixels were converted into millimetres using scales in videos as standards. All times were converted from frames to seconds. From position, velocity and viewing angle, we then defined behaviours that had also been scored manually (e.g. freezing = zero velocity, while looking at the object) to quantify these behaviours more precisely and to cross-check the reliability of the datasets, enabling a completely automated and standardized workflow in future studies.

For a more detailed description of the automated video tracking pipeline including neural network training and post-tracking calculations, see Appendix S2.

2.5 | Quantification and statistical analysis

Statistical analyses were carried out in R 3.6.2 (R Core Team, 2019). We used GLMMs using the package GLMMTMB (Brooks et al., 2017). For the first experiment, we first checked for potential effects of sex and test day. To test which factors had significant effects on the dependent variables, we then applied an analysis of deviance to the resulting models using the package CAR (Fox & Weisberg, 2019). Subject ID was always included as a random effect. Post hoc analyses with Bonferroni correction were conducted with the packages EMMEANS and LSMEANS (Lenth et al., 2019). Model fit was confirmed using the package DHARMa (Hartig, 2017). The probability of a spider to pass the object in each tested condition was modelled using a binomial distribution. All plots were generated using the package GGPLOT2 (Wickham, 2016). The analyses of both datasets support the same results (Figure 2d). As video tracking data are more reproducible, precise and include multiple additional variables (distance, velocity, ability to calculate viewing angle), results presented are based on the automated tracking data unless stated otherwise. All python code, R scripts for analyses of manually scored and automated tracking data along with experimental data are available from the Zenodo open science repository (Rößler et al., 2021).

3 | RESULTS

3.1 | Predator versus non-predator objects

Freeze duration differed significantly for the five tested conditions (Figure 2b, GLMM analysis of deviance, $\chi^2 = 317.93, p < 0.001, n = 30$). We recorded short freezes in control trials (mean ± SE; 1.24 ± 0.12 s), freezes that were twice as long for the control + eyes (2.98 ± 0.25 s) and still longer freezes in Phidippus trials (7.45 ± 0.47 s).

Post-freezing behaviour was quantified by measuring the distance change with respect to the tested object during the 2 s after the end of the freeze. We found a significant difference between conditions (Figure 2c, analysis of deviance, $\chi^2 = 423.32, p < 0.001$). Post hoc analysis revealed a significant difference in all pairwise comparisons ($p < 0.01$) except for Phidippus and the 3D model (post hoc, estimate = −2.45, SE = 1.29, t-value = −1.89, p = 0.58). It is worth noting that the average distance from the object increased for all predator-like objects (Marpissa, Phidippus, 3D model) but decreased for non-predator objects (control + eyes, control). The flight response was robust across all predator objects, usually characterized by a fast backward retreat (see Video S1). The visualization of post-freezing trajectories demonstrates the directionality of behavioural responses (Figure 2e; Figure S2), showing that spiders typically moved towards the object when faced with the control, and away from it when faced with the 3D model.

When considering trial outcome, condition had a significant effect on the probability of the spider to pass the object (Figure 2d, $\chi^2 = 151.26, p < 0.001$) showing that Marpissa, Phidippus and the 3D model were not approached and passed, even to gain access to shelter. There was no effect of presentation order ($\chi^2 = 2.74, p = 0.09$) and behavioural response showed no fall-off with trial number, underlining the robustness and repeatability of these responses. It is noteworthy, however, that for the control + eyes condition, the probability to pass the target appears to increase with presentation order (Figure S1). There was no effect of sex on any of the tested variables (see Appendix S1, Section 1.1).

3.2 | Modified features

Condition (control, 3D model without eyes, 3D model) had a significant effect on the probability of spiders to pass the tested object (analysis of deviance, $\chi^2 = 10.18, p = 0.0062, n = 15$). Almost all spiders passed the control (43/45, 95.56%), while only a few passed the 3D model without eyes (6/45, 13.33%) and no spider passed the 3D model (0/45, 0%). Due to this data separation, no model could be calculated to assess the significance of pairwise comparisons.

However, there was a significant difference between the three conditions in freeze duration (Figure 3b, $\chi^2 = 91.96, p < 0.001$), with post hoc analysis showing significantly longer freezes in response to the 3D model without eyes compared to the 3D model (ratio = 2.869, SE = 0.65, p < 0.001).

Regarding post-freezing behaviour, we found significant differences between the three conditions (Figure 3c, $\chi^2 = 203.41, p < 0.001$). Post hoc analysis showed that spiders moved significantly further away from the 3D model compared to the 3D model without eyes (post hoc, estimate = −7.15, SE = 2.6, t-value = −2.747, p = 0.0206). There is also a clear difference in the path choice of post-freezing behaviour, with most spiders choosing direct away paths from the 3D model, direct towards paths towards the control and less direct paths away in response to the 3D model without eyes.

3.3 | Newly emerged spiderlings

In total, the presented objects were visually encountered in 140 of 192 trials. Spiderlings never showed retreat behaviour in control-object trials (0/67, 0%), but showed clear retreat behaviours in predator-like 3D-printed model trials (62/73, 84.93%), often jumping rapidly away from the test object (Figure 4c, see Video S1).

4 | DISCUSSION

We found that jumping spiders are capable of visually recognizing static predator-like objects whether they are real co-occurring or

non-co-occurring spiders or 3D-printed models. The anti-predatory behaviours that we observed consisted of a series of robust responses in which spiders oriented towards objects while multiple body lengths away, remained stationary for a short period, then retreated from the static predator-like object. We also found evidence that spiders likely use multiple static visual features when making predator/non-predator decisions and that eyes are one of the cues used to identify predators. Finally, exposing newly emerged spiders to predator objects resulted in the same behavioural responses, suggesting that this cognitive ability and anti-predatory behaviour is likely innate in these animals.

Freeze durations and post-freezing behaviour differed, with a robust retreat from all predator-like objects. We should note that freeze duration does not necessarily indicate slower recognition— recognition might take place quickly, but latency to respond may depend on further factors (cf. Evans et al., 2019). For example, depending on the size of the predator, remaining motionless for some period may be beneficial to avoid attracting attention, a known defence strategy from vertebrate prey species (Eilam, 2005). Further, *M. muscosa* shows coloration that is cryptic and potentially disruptive, including a dark facial stripe across the eyes (Figure 1a) which may reduce recognition of important features. Finally, longer freezes may be required to plan the escape trajectory. Given that salticids possess eight eyes with a combined near 360-degree field of view (Land, 1969), such planning may require additional visual processing, but may not require additional visual scanning.

The addition of salticid frontal eyes to the control increased freeze duration and decreased movement of the spider towards the object compared to the control. Yet, responses towards the control + eyes object were still significantly different from responses to the predator-like objects. Interestingly, the control + eyes was the only condition where the response was not robust across presentations (Figure S1). Instead, the probability of spiders to pass the control + eyes increased with presentation order, suggesting only an initially aversive response. This experience-dependent change in response is particularly noteworthy given that none of the conditions in our experiment were paired with explicit positive or negative reinforcement (e.g. food, heat or electric shock). It will be interesting in future work to more directly explore this result.

Reactions towards the control + eyes and the eyeless 3D-printed model suggest that eyes are important, but that they are not the only cue used in recognition. Eyes have repeatedly been demonstrated to be used as visual cues in predator recognition in vertebrate species (e.g. in birds or bonnet macaques), with forward-facing eyes (i.e. direct gaze) of a predator triggering behavioural responses (Curio, 1993; Ramakrishnan & Coss, 2000). The presence of anterior median eyes on targets is also used as key visual cues by an araneophagic salticid when identifying its salticid prey (Harland & Jackson, 2000, 2002). However, many species, including a salticid that specializes on mosquitos, have been found to use specific isolated visual features (i.e. local cues) in recognizing prey (Dolev & Nelson, 2014). This local cue strategy relies more on the presence/absence of key features rather than on more complex whole-object trait combinations or multi-trait

spatial relationships. While this local strategy is a viable solution for simplifying the computational challenge of recognizing objects, it appears that predator recognition in *S. scenicus* may proceed through a more global, multi-trait strategy. That is, while the presence/absence of eyes on models impacted the response, this single feature did not overwhelmingly drive the response, suggesting that other traits are also required. Indeed, this more holistic approach might reflect the visual-cognitive challenges faced by these animals in the field, as salticid predators, prey and mates overlap strongly in terms of their visual features but necessitate starkly different behavioural responses each with strong selective effects.

Our results provide three lines of evidence suggesting that experience does not play a strong role in predator recognition. First, we found a lower probability of retreat behaviour for Marpissa, which was unexpected, because tested spiders were likely familiar with this spider, as these species co-occur in the field, and we might have expected a heightened response from prey spiders. It is noteworthy, however, that Marpissa was smaller compared to the two other predator objects and we cannot exclude that size affects visual assessment or categorization of predators. It is possible that the behavioural response is linked to the size of the predator. Particularly in intraspecific male–male competition, absolute size of the opponent, but also relative opponent size is known to play a role in visual assessment (McGinley & Taylor, 2016; Tedore & Johnsen, 2015). Whether similar processes apply in the assessment of a potential predator requires further testing. Second, the most robust anti-predator response was observed for the 3D-printed model followed by Phidippus. Both these objects were novel to the tested spiders, strongly suggesting that experience does not play a strong role in recognition—either at the individual level or over longer evolutionary time-scales. Rather, jumping spiders' recognition of salticid-like predators appears sufficiently general that it allows recognition despite variation across a range of features (colour, texture, posture, etc.), and even when predators are stationary. It is also noteworthy that positions where freezes (detection and recognition) occurred were evenly distributed across the start platform, demonstrating robust recognition from a range of spatial perspectives and evidence for some degree of angular invariance (angles: −15 to 15 degrees, distance from object at freeze in trials where spiders retreated (mean $\pm$ *SD*): 61.1 $\pm$ 16.9 mm, Figure S2). Viewing angles in our setup were limited, all allowing a largely head-on view of the object, thus, future experiments should increase the potential perspectives on the tested object to gain more insight on which features are used in the recognition process and how different perspectives influence the behavioural response. Besides looking into angular invariance of predator recognition, future experiments should also target the invariance of ambient light as well as background to further test how robust recognition is in complex natural settings with variations in light and background in the visual scene.

Finally, robust anti-predator responses of newly emerged spiderlings provide the strongest evidence that predator recognition and anti-predatory behaviour are likely innate in these animals.

To comprehensively test innateness of the behaviour, however, separation of spiderlings must take place before hatching. That anti-predatory responses of 1- to 3-day old spiderlings were elicited by 3D-printed models that lack the fine detail of natural predators (hair, colour patterns, etc.) suggests that the cues used to characterize predators are indeed broad rather than species-specific. It is noteworthy that responses were object-specific—that is, size-matched control objects did not elicit anti-predatory responses. Thus, while the categorization of predator-like targets is sufficiently general as to include 3D-printed models, it is not simply a response towards objects of a given size and colour. Such well-defined categories seem likely to be highly adaptive in these animals. Many spider species use ballooning as a form of dispersal (Foelix, 2010), which allows spiders to move long distances, but also increases exposure to novel habitats and novel predator communities. By relying on well-defined but broad categories, these animals might be able to respond to species-level variation among predators while maintaining some degree of specificity—for example avoidance of large predatory salticids while still ignoring non-threating objects. That *S. scenicus* collected in Germany showed anti-predatory responses towards stimuli of *P. audax*, a representative of a genus not found in Europe, provides further evidence for this adaptive hypothesis. However, we should note that much remains unknown about how this visual recognition process is implemented at the cognitive level. For example, observed behavioural differences might be based on discrete categorical differentiation, or on states in a more continuous cognitive space. Future work will be required to better understand how these are carried out.

For several vertebrate species, it was shown that predator recognition can be learned (Ferrari et al., 2008; Steindler et al., 2020) and predator-naïve animals often lack the ability to respond appropriately to novel predators. That animals such as jumping spiders, with far less complex brains, are capable of innately recognizing predator-like objects is surprising, supporting the many findings of the last decades demonstrating the cognitive and behavioural complexity of invertebrate animals (Avarguès-Weber et al., 2011; Chittka & Niven, 2009; Giurfa, 2013; Schnell & Clayton, 2019).

The robustness of these behaviours, and the ability to use 3D-printed models to standardize and manipulate stimulus features and presentation, sets the stage for a range of future experiments in both the laboratory and the field. For example, the neural and cognitive processes that underlie these behaviours could be explored through neural recordings (cf. Menda et al., 2014; Shamble et al., 2016) and eye-tracking systems to monitor gaze and visual attention (Winsor et al., 2021). In the field, 3D models could be used to stage interaction with manipulated stimuli, similar to approaches used with clay lures or mounts (Rößler et al., 2018; Steindler et al., 2020) but enabling these questions to be asked with much smaller animals.

Anti-predator adaptations are often initially thought of as morphological or behavioural. However, the sensory and cognitive ability to perceive/detect and recognize a predator equally falls under the high selective pressure imposed by 'the life-dinner principle' (Dawkins & Krebs, 1979). The recognition of static predator stimuli in animals that otherwise heavily rely on motion cues (Bednarski et al., 2012) demonstrates just how strong the selection on anti-predator adaptations is.

CONFLICT OF INTEREST

The authors declare they have no competing interests.

AUTHORS' CONTRIBUTIONS

D.C.R. initiated the idea; D.C.R. and P.S.S. designed the experiments; D.C.R. conducted the experiments and manually scored the behavioural data; K.K. ran automated video tracking analyses and subsequent calculations with help from P.S.S. and M.D.A.; D.C.R., M.D.A. and P.S.S. analysed the data; D.C.R. wrote the manuscript with feedback from P.S.S., M.D.A. and K.K.

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 come from three different countries (Germany, Italy and USA) and range from undergraduate to post-doctoral career stages. One or more of the authors self-identifies as a member of the LGBTQ+community (Rößler et al., 2020; Sweet, 2021).

DATA AVAILABILITY STATEMENT

The data are available from the Zenodo open science repository https://doi.org/10.5281/zenodo.5547744 (Rößler et al., 2021).

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