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RESEARCH ARTICLE

Dim-light vision in jumping spiders (Araneae, Salticidae): identification of prey and rivals

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ABSTRACT

Jumping spiders (family Salticidae) are known for their intricate vision-based behavior during encounters with prey and conspecific individuals. This is achieved using eyes specialized for discerning fine detail, but there has been minimal research on the capacity that salticids might have for visual performance under low ambient light levels. Here, we investigated the capacity of two salticid species, *Cyrba algerina* from Portugal and *Cyrba ocellata* from Kenya, to perform two specific visual tasks under low ambient light levels. We used lures made from spiders and midges in prey-identification experiments and mirror images (virtual conspecifics) in rival-identification experiments. These experiments were implemented under a range of ambient light levels (234, 1.35, 0.54, 0.24 cd m^{-2}). In most instances, *C. algerina* and *C. ocellata* were proficient at performing both of these visual tasks when ambient light was 234 and 1.35 cd m^{-2}, and a minority performed these tasks at 0.54 cd m^{-2}, but none succeeded when the light level was 0.24 cd m^{-2}. *Cyrba algerina* and *C. ocellata* showed vision-based discrimination under low ambient light levels previously associated with nocturnal species.

KEY WORDS: Camera eyes, Spatial acuity, Visual sensitivity, Intraspecific-display behavior, Prey-choice behavior, Spartaeinae

INTRODUCTION

Most animals have eyes, but there is considerable variation in their structure, functioning and size, and these variations may reflect the different functions required of them (Land and Nilsson, 2012). To see well under low-light levels, an animal needs especially good sensitivity; yet, to be proficient at discerning the visual detail of objects, an animal needs especially good spatial acuity. However, a well-known trade-off that applies to eyes in general is that features that increase sensitivity tend to reduce spatial acuity and vice versa (Land and Nilsson, 2012). Spatial acuity depends on the quality of the image delivered to the retina and on how fine grained the retinal mosaic is, but sensitivity depends on the reliability with which photoreceptors can capture photons. The trade-off comes about because, for a given light intensity, the number of photons that arrive during the photoreceptor's integration time is a stochastic phenomenon and, as light gets dimmer, the level of uncertainty in photon capture inevitably increases (Barlow, 1956; Warrant, 1999). Sensitivity can be improved by incorporating larger photoreceptors into the retina; however, owing to the retinal mosaic becoming coarser, this improvement in sensitivity is achieved at the cost of spatial acuity.

The sensitivity–acuity trade-off becomes especially serious for animals that rely on seeing considerable spatial detail under dim light, and this can be particularly problematic for small animals. When an eye is small, having large photoreceptors, which can improve sensitivity through increased area for photon capture (spatial summation), may work against achieving a fine-grain retinal mosaic that would improve spatial acuity; yet, some of the best examples of high-performance spatial vision under low light come from insects and spiders (e.g. Kelber et al., 2006; Fenk and Schmid, 2010; Warrant and Dacke, 2011; Honkanen et al., 2014). Instead of camera-type eyes like those of spiders, most arthropods rely on compound eyes made up of multiple smaller light-gathering lenses (facets). Although details vary considerably, structural adaptations by which animals compensate for the trade-off between sensitivity and spatial acuity include preserving a fine-grain retinal mosaic through having long rhabdoms that are proficient at capturing photons while also being narrow. Other compensation mechanisms are neural, such as spatial and temporal summation, which sum photons in space and time, respectively (Warrant, 1999; Warrant et al., 2004; Frederiksen et al., 2008).

When discussing visual systems, jumping spiders (Salticidae) are of particular interest because it is among salticids that we find both some of the most intricate vision-based predatory strategies (Nelson and Jackson, 2011) and intraspecific display behavior (Crane, 1949; Jackson and Pollard, 1997; Girard and Endler, 2014). Salticids have a visual system consisting of a pair of large camera-type forward-facing (antero-medial) eyes, called the 'principal eyes', and three pairs of smaller camera-type eyes, collectively called the 'secondary eyes', positioned to the side or behind the principal eyes (Homann, 1928). Although the secondary eyes have multiple functions (Land, 1972; Zurek et al., 2010; Harland et al., 2012; Zurek and Nelson, 2012; Jakob et al., 2018), they are best known for their role in motion-detection proficiency (i.e. tasks requiring good temporal acuity) and for mediating the orientation behavior by which the salticid brings the corneal lenses of the principal eye into alignment with salient objects in the environment (Land, 1971, 1972; Jakob et al., 2018). Based on observations of hunting behavior (e.g. Forster, 1982) and eye structure (Land, 1969), it is widely assumed that salticids are diurnal (e.g. Foelix, 2011). Commensurate with a diurnal lifestyle, salticids rely primarily on the exceptional spatial acuity of their principal eyes to discern fine detail (Land, 1969; Blest et al., 1990). In fact, the best spatial acuity known for a salticid's principal eyes surpasses that known for any other animal of comparable body size (Williams and McIntyre, 1980; Land and Nilsson, 2012; Harland et al., 2012). However, the assumption that salticids are diurnal has largely deflected interest away from the investigation of dim-light vision in this family. This is despite electrophysiological evidence that sensitivity in the photoreceptors

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of the secondary eyes is remarkably high for the size of the corneal lens – attributed to having a camera-type eye capable of collecting photons more efficiently than the individual facets of compound eyes (Hardie and Duelli, 1978). Additionally, many salticids frequent the leaf-litter zone in the understory of dense-forest habitats and, for some of these species, morphological evidence suggests a sensitivity–acuity trade-off, whereby the principal eyes have improved sensitivity at a cost to spatial acuity (Blest, 1983, 1985).

Most of our knowledge about low-light vision in spiders comes from research on nocturnal species from other families (e.g. Laughlin et al., 1980; Nørgaard et al., 2007, 2008; Pirhofer-Walzl et al., 2007; Fenk et al., 2010a,b; Fenk and Schmid, 2011; Campione and Schmid, 2014). To begin to redress this gap in our understanding, we tested the capacity to implement dim-light vision-based behavior in two salticid species. We chose species from the salticid genus *Cyrba* [*C. algerina* (Lucas 1846) from Portugal and *C. ocellata* (Kroneberg 1875) from Kenya]. Spartaeinae, the salticid subfamily to which these species belong, is known for species with unusual predatory behavior. Although most salticids may prey primarily on insects (Richman and Jackson, 1992), many spartaeines, including species from the genus *Cyrba*, are known from laboratory experiments to express an active preference for spiders as prey (Jackson, 1990, 2000; Jackson and Li, 1998; Guseinov et al., 2004).

While carrying out preliminary experiments we discovered that, unlike other salticids which readily respond in a well-lit laboratory, *C. algerina* and *C. ocellata* become more responsive to prey and mates at low ambient light levels (Cerveira and Jackson, 2011, 2013) and yet *C. algerina* and *C. ocellata* frequent scrubland and desert (Wanless, 1984; Guseinov et al., 2004), habitats that would normally be characterized as well lit. However, the typical microhabitats of *C. algerina* and *C. ocellata* are the dimly lit spaces on the underside of stones (Jackson, 1990; Jackson and Li, 1998; Guseinov et al., 2004), where they often capture prey and interact with conspecific individuals (Guseinov et al., 2004).

We used two well-established methods by which salticids have been tested for their capacity to make decisions while restricted to using vision alone: mirror tests to determine responsiveness when seeing a conspecific rival and lure tests to determine responsiveness when seeing prey. Mirror tests rely on the salticid's predisposition to respond to its mirror image by initiating the threat displays normally directed at same-sex conspecific rivals (e.g. Harland et al., 1999; Lim and Li, 2006). Lure tests rely on salticids often adopting distinctive prey-choice behavior during encounters with living prey and expressing comparable prey-choice decisions when tested with lures made from dead prey (e.g. Nelson and Jackson, 2012). As a step towards investigating dim-light visual capacity among the Salticidae, here we used mirror and prey-choice testing in order to evaluate the capacity of *C. algerina* and *C. ocellata* for visual identification of rivals and prey under progressively lower light levels.

MATERIALS AND METHODS

Maintenance and general testing methods

All spiders were 2nd and 3rd generation unmated adults (body length 6.0–7.0 mm) from laboratory cultures, *C. algerina* originating from Tavira in Portugal and *C. ocellata* originating from Mbita Point in Kenya. For details concerning the field sites, laboratory maintenance methods, rearing-cage design, terminology and basic experimental methods, see Cerveira and Jackson (2011). Each test spider matured 2–3 weeks before being used in an experiment and, to standardize hunger level, spiders were subjected to a 5 day pre-trial fast. Body lengths of all test spiders and lures were accurate to the nearest 0.5 mm. No individual spider and no individual lure was used more than once. International, national and institutional guidelines for the care and use of animals were followed.

Experiments were conducted in a lightproof room illuminated by a 20 W halogen lamp (Mickson-Model MF6356, AppN19584, 230 V, 50 Hz). To reduce the light level, we fastened neutral density filters (Marumi ND4 and ND8) directly below the lamp, leaving no spaces for light to enter the room except through the filters. We used specific combinations of filters (e.g. ND20=1 ND4+2 ND8) to achieve four light levels: (1) 233.89 cd m^{-2} (no filters); (2) 1.35 cd m^{-2} (ND20); (3) 0.54 cd m^{-2} (ND24); (4) 0.24 cd m^{-2} (ND28). Using an International Light radiometer (1L1400) in integrated mode (wavelength range between 450 and 700 nm), we determined light levels by recording reflected light (calibrated on Spectralon reference standard) over an extended time period to average out noise that would interfere with obtaining accurate short-term recordings under low ambient light. For a perspective on natural lighting conditions corresponding to the light levels used in our experiments, note that dim daylight corresponds to about 100 cd m^{-2} (Balkenius et al., 2006), mid- to late dusk is normally about 1–0.01 cd m^{-2}, while full moon is about 0.1 cd m^{-2} and starlight is about 0.001 cd m^{-2} (Warrant, 2004).

Before each trial, the spider was placed inside a glass tube (length 20 mm, diameter 8 mm, rubber stopper in each end) and kept for a 60 min acclimation period at the light level under which it would be tested. After acclimation, we transferred the spider to a testing arena (see details below). We achieved this by opening one end of the tube and then positioning the open-end flush with an introduction hole in the arena. In most instances, the spider promptly walked out of the tube and into the arena; in the rare instances of a spider failing to walk out within 10 min, we opened the other end of the tube and gently prodded the spider with a paintbrush, after which it always walked into the arena. Each trial began when the spider entered the arena.

We recorded behavior using an infrared-sensitive video camera (Sony DCR-TRV18E). With our goal being to investigate the spider's performance when presented with tasks requiring good spatial acuity, we designed the apparatus so that the distance between the introduction hole and the mirror in mirror-response tests, or the lures in prey-choice tests, was considerably farther than the maximum display distances previously determined (Harland et al., 1999) for *C. algerina* (120 mm) and *C. ocellata* (90 mm) and also farther than casual observations suggest is normal when *C. algerina* and *C. ocellata* begin stalking prey. On this basis, we considered it unlikely that test spiders identified the visual stimuli before moving fully into the testing arena. Once in the arena, the spider always walked about, with frequent pauses and changes in orientation. However, before choosing a lure or displaying at the mirror, spiders always first fixated their gaze on a lure or on the mirror (where 'fixate' is defined as remaining stationary for a minimum of 5 s with the corneal lenses of the principal eyes aligned with a lure or the mirror). In successful mirror tests, the spider fixated on the mirror and either displayed from the same location or approached the mirror without turning away and then displayed when closer. In successful prey-choice tests, the spider fixated at least once on each lure and then, having made a choice, moved directly toward that lure and into the choice area (defined below) of the arena without turning away before doing so.

We recorded gaze fixation distance and duration, both of which refer to the instance of fixation that immediately preceded displaying at the mirror or choosing a lure. For mirror tests, we also recorded display distance, which could differ from the fixation

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distance. Fixation distance in prey-choice tests was the distance between the test spider and the lure it chose. In mirror tests, display and fixation distances were defined as twice the distance between the spider and the mirror (i.e. it was the virtual distance between the test spider and its image in the mirror). We measured all distances to the nearest 5 mm from the anterior margin of the spider's carapace, achieving this by placing a sheet of paper with a 5 mm grid under the respective transparent glass or plastic testing arena.

A trial ended when the spider chose one of the lures or began displaying at the mirror, or when 15 min elapsed without the spider displaying or choosing a lure. Using the software package Prism, distance and duration data were analyzed using one-way analyses of variance (see Table S1 for ANOVA) or, if data were not normal, Kruskal–Wallis tests. Prey-choice data were analyzed using binomial tests (null hypothesis, spider equally likely to choose either prey), with chi-square tests of goodness of fit or, when sample sizes were too low, Fisher exact tests to compare between species.

After each trial, the test arena was wiped with 80% ethanol followed by distilled water. Knowing that in many salticid species (Jackson and Pollard, 1997), including *C. algerina* and *C. ocellata* (Jackson, 1990), females are more responsive to prey and males are more aggressive in intraspecific same-sex encounters, we used females in prey-choice testing and males in mirror-response testing.

The mirror-test arena was a transparent plastic Petri dish (diameter 140 mm, height 15 mm), inside which a mirror (length 85 mm, height 15 mm) was positioned upright and facing into the wider space within the dish (center of the mirror 8 mm from the nearest rim of the dish). As the height of the mirror was equal to the inside height of the dish (15 mm), spiders could not move around, over or under the mirror. The introduction hole (diameter 8 mm) was situated in the rim of the dish on the side of the arena opposite to the mirror (i.e. it was 132 mm from the mirror).

Prey-choice tests

For prey-choice testing, we presented spiders with two lures. The prey used for making the lures were collected from the field (Mbita Point, Kenya) as needed. In each trial, one lure was made from a lycosid spider (*Pardosa messingerae*) and the other was made from a chironomid midge (*Nilodorum brevibucca*). For each trial, lure body length matched test-spider body length.

To make a lure, we first used carbon dioxide to immobilize the prey individual and then immersed it in 80% ethanol for 60 min, after which we mounted the prey individual in a lifelike posture on the center of a cork disc (diameter 15 mm). An aerosol plastic-adhesive spray was used to secure the prey to the disc and for preservation (for details pertaining to making lures, see Jackson et al., 2005).

The prey-choice test arena was a rectangular glass box (depth 20 mm, inner dimensions 140 mm long×115 mm wide; other dimensions are given in Fig. S1) as used in previous work (Nelson and Jackson, 2012). Equidistant from the two longer sides of the arena, there was an introduction hole (center of hole 14 mm from the nearest side of the arena). In the base of the arena at the opposite end, there was a 'left lure hole' and a 'right lure hole' (each 8 mm in diameter), the center of each being 14 mm from the nearest sides of the arena, opposite the introduction hole. Lures placed on top of the lure holes faced each other, with left versus right positioning of the insect and spider lures being determined at random for each trial.

The arena sat on a 150 mm high Plexiglas™ plastic stand, with the free end of a camera cable-release cord being accessible from beneath the stand. By pressing on the cable release, the two prongs on a metal fork, which was attached to the cork disc bases of the lures, lifted the two lures in unison 5 mm above the floor of the arena. From the time at which the spider entered the arena until tests ended, the cable release was pressed every 30 s, causing the lures to move simultaneously up and then down once each time.

Two circles made from thin copper wire were placed under the arena, but on top of the paper grid. One lure hole was at the center of one circle and the other lure hole was at the center of the other circle. Part of each copper circle went under the testing area, thereby demarcating a choice area corresponding to that particular lure (Fig. S1). Seeing a spider fixate its gaze on a lure and then enter the choice area corresponding to that lure was our criterion for recording its choice of prey. On the rare occasions when the 15 min test period elapsed with the spider's gaze still fixated on a lure, but with the spider still outside the choice area, we extended the test period until it either made its choice or turned away (i.e. broke off fixation of gaze on the lure).

RESULTS

No spiders made prey choices or displayed at the mirror when the light level was 0.24 cd m^{-2}. Above this, for each light level, there were no significant differences between *C. algerina* and *C. ocellata* with respect to how many spiders responded by choosing prey versus not making a choice (234 cd m^{-2}, χ^2_1=0.370, P=0.542; 1.35 cd m^{-2}, χ^2_1=1.154, P=0.283; 0.54 cd m^{-2}, χ^2_1=0.033, P=0.855; Fig. 1A) or between how many chose one lure instead of the other

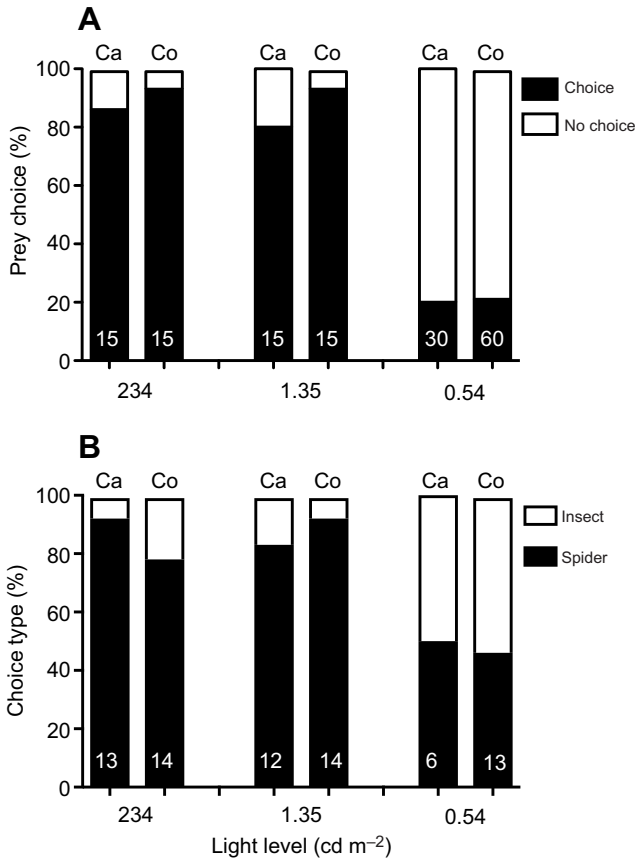

Fig. 1. Prey choices of test spiders. (A) Percentage of test spiders that responded during prey-choice tests at each light level. (B) Prey choices made by test spiders that responded. *N* values are shown within each bar in A and B; data for B are based on the black area in A. Ca: *Cyrba algerina*. Co: *Cyrba ocellata*.

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(234 cd m^{-2}, χ^2_1=1.008, P=0.15; 1.35 cd m^{-2}, χ^2_1=0.574, P=0.449; 0.54 cd m^{-2}, P=1.00, Fisher exact test; Fig. 1B). There were also no differences between species with respect to how many spiders displayed at the image in the mirror (234 cd m^{-2}, χ^2_1=0.7, P=0.403; 1.35 cd m^{-2}, χ^2_1=1.020, P=0.313; 0.54 cd m^{-2}, χ^2_2=0.019, P=0.889; Fig. 2). However, the number of spiders that responded by making a choice of prey (*C. algerina*, χ^2_2=24.2, P<0.001; *C. ocellata* χ^2_2=41.4, P<0.001) or displaying toward their reflection (*C. algerina*, χ^2_2=13.5, P=0.001; *C. ocellata* χ^2_2=24.8, P<0.001) declined sharply at 0.54 cd m^{-2} relative to the two higher light levels (Figs 1A and 2).

In prey identification tests, more spiders of both species chose the spider instead of the midge (Fig. 1B) when the light level was 234 cd m^{-2} (binomial test, P=0.003 for *C. algerina*, P=0.057 for *C. ocellata*) and when it was 1.35 cd m^{-2} (P=0.039 for *C. algerina*, P=0.018 for *C. ocellata*), but not when the light level was 0.54 cd m^{-2} (P=1.000 for *C. algerina* and *C. ocellata*). For those spiders that made a prey choice, we looked for effects of light level on distance from the prey when the spider first fixated its gaze on the prey (Fig. 3A) and on the duration of pre-choice gazing (i.e. how long spiders kept their gaze fixated on the prey before making a choice) (Fig. 3B). For both species, there were significant treatment effects for distance, with fixation distance being lower at the lowest light level (*C. algerina*, H_2=8.173, P=0.017; *C. ocellata*, H_2=13.64, P=0.001), and also for the duration of gaze fixation, with shorter gaze times at the highest light level (*C. algerina*, U_2=11.10, P=0.004; *C. ocellata*, U_2=14.92, P<0.001).

In rival-identification tests, the distances from which spiders first displayed at their mirror images (see description below) under the three higher light levels (Fig. 4A) did not differ significantly for either species (*C. algerina*, $F_{2,19}$=1.236, P=0.313; *C. ocellata*, $F_{2,32}$=2.568, P=0.092). For those spiders that displayed during mirror tests, we looked for effects of light level on how long the spider kept its gaze fixated on the mirror continuously before displaying (Fig. 4B), and at what distance gaze fixation on the mirror occurred (Fig. 4C). Generally speaking, spiders first fixated on their reflection from closer to the mirror under the lowest light condition (Fig. 4C). However, while the distances at which spiders first fixated their gaze at their mirror images under the three light levels differed significantly in *C. ocellata* ($F_{2,32}$=4.427, P=0.020), revealed in *post hoc* tests to be driven primarily by differences between the highest and lowest light levels, this was not the case

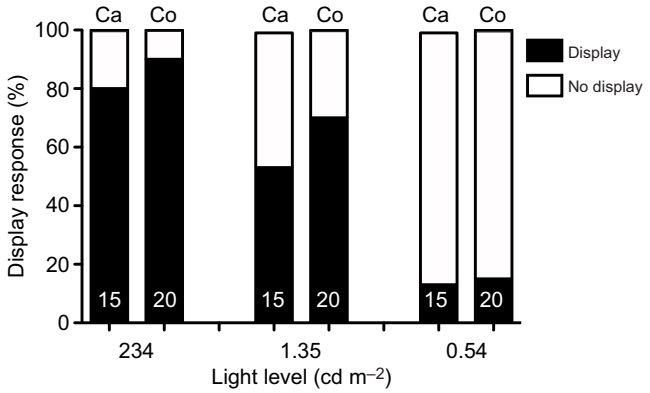

Fig. 2. Percentage of test spiders that responded during mirror rival-identification tests at each light level. A response was recorded when a spider adopted a threat display while its gaze was fixated on the mirror. Ca: *Cyrba algerina*. Co: *Cyrba ocellata*. *N* is shown within each bar.

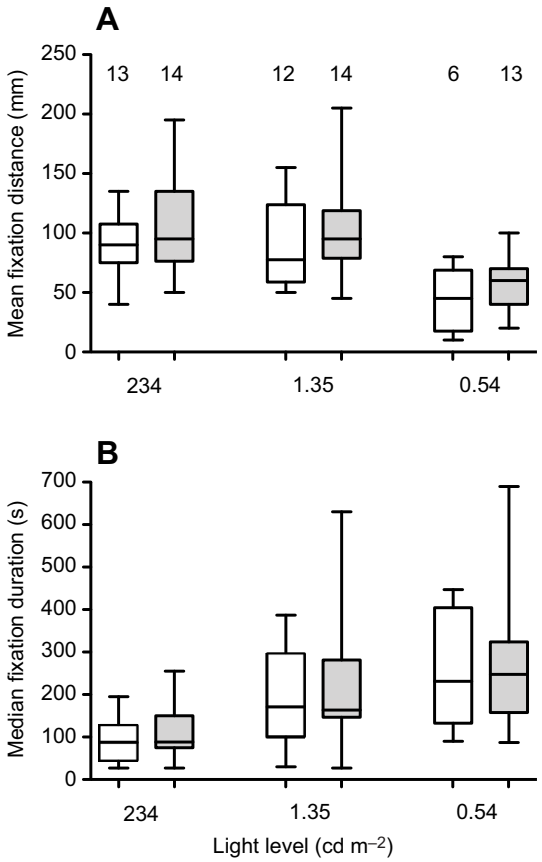

Fig. 3. Pre-prey-choice fixation of gaze on lures by spiders at different light levels. Data for *C. algerina* (white) and *C. ocellata* (gray) are medians, with 25th and 75th percentiles; whiskers indicate minimum and maximum. (A) Distance at which test spiders fixated their gaze on the lures and then, without breaking fixation, chose a lure. (B) Time elapsed between fixating their gaze on the lures and, without breaking fixation, choosing a lure. *N* is shown in A.

for *C. algerina* ($F_{2,19}$=2.560, P=0.104). Nevertheless, light had a significant effect on pre-display fixation duration for both species, with this being markedly lower at the highest light level (*C. algerina*, $F_{2,19}$=6.153, P=0.009; *C. ocellata*, $F_{2,32}$=6.660, P=0.004; Fig. 4B), suggesting a quick transition between perception of the viewed image and recognition or identification of a rival.

When spiders displayed in mirror tests, they typically moved towards the mirror, eventually stopping, with their gaze fixated on the image in the mirror. Then, while facing the mirror, spiders adopted distinctive displays in which they kept their legs on the substrate while swaying their bodies from side to side, sometimes punctuated by making truncated leaps (i.e. covering only 1–2 mm) toward the mirror. Swaying and truncated leaping are typical male–male displays adopted in these species, and not the displays they use when interacting with conspecific females. Spiders never adopted quivering waving of forelegs, dancing or stepping from side to side, these being types of display behavior males typically perform only when interacting with conspecific females (for details, see Jackson, 1990).

DISCUSSION

We presented the salticid spiders *C. algerina* and *C. ocellata* with tasks requiring visual attention to fine detail in two contexts: predation (i.e. detecting and identifying preferred prey) and social encounters (i.e. detecting and identifying conspecific rivals). Most

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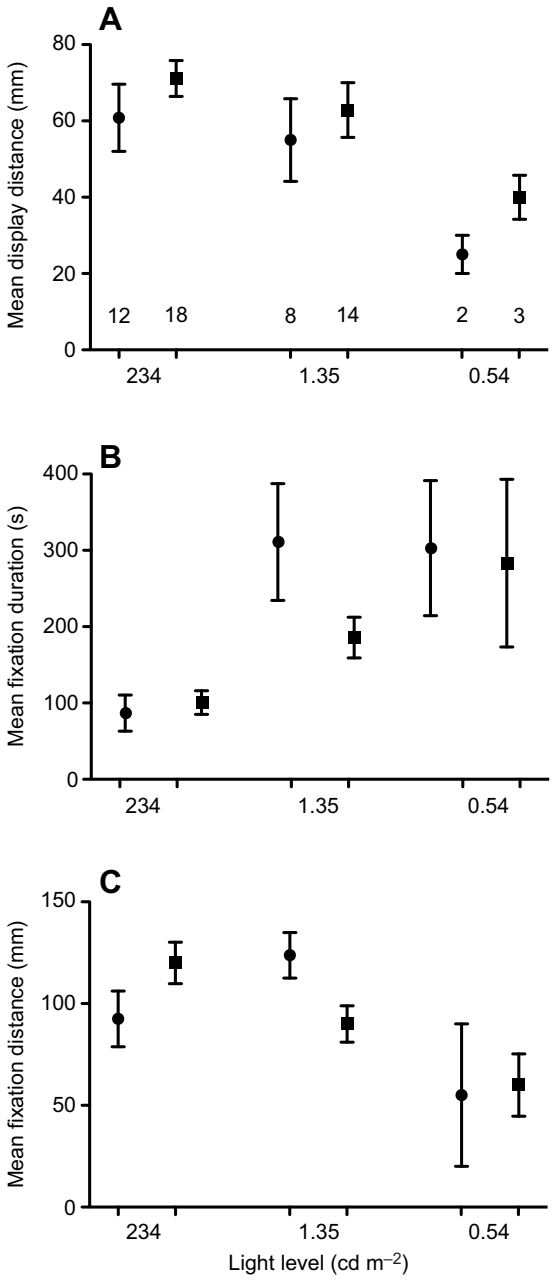

Fig. 4. Responses of spiders to a mirror image at different light levels. Data are means±s.e.m. for *C. algerina* (circles) and *C. ocellata* (squares). (A) Virtual distance from the mirror image at which spiders first displayed. (B) Time elapsed between the test spider fixating its gaze on its mirror image and then, without breaking fixation, initiating display. (C) Virtual distance (2× distance) at which the test spider first fixated its gaze on its mirror image and then, without breaking fixation, performed a threat display. *N* is shown above the *x*-axis in A.

spiders were successful in the performance of both tasks even when the light level was as low as 1.35 cd m^{-2}, which is well below the light level typical of dawn and early dusk (ca. 10 cd m^{-2}). In contrast to their good performance at light levels of 1.35 cd m^{-2}, only a few spiders met our criteria for successful performance at 0.54 cd m^{-2} (i.e. mid- to late dusk, 1 cd m^{-2}) and none succeeded at 0.24 cd m^{-2}, the light levels typical of twilight (0.3 cd m^{-2}).

That cues in any modality other than vision might account for the spiders' responses in our experiments seems unlikely. In mirror tests, spiders responded by performing the display behavior that is specific to conspecific males interacting with each other (Jackson, 1990); yet here, the rival was the spider's odorless, silent, mirror image. Lures instead of living prey were used in the prey-choice experiment, and these lures were outside the arena occupied by the test spider. There were two kinds of lure: one made from a spider (i.e. more preferred prey) and the other from a midge (i.e. less preferred prey). Significantly more test spiders chose the lure made from a spider instead of that from a midge when the light level was 1.35 cd m^{-2} or brighter, but most spiders failed to approach either lure when the light level was 0.54 cd m^{-2} and there was no trend toward choosing the spider lure under this low light level. Moreover, the findings for shorter fixation distance and longer gaze duration among salticids that chose a lure in dim light suggest that identifying prey and rivals was more difficult, or provided more uncertainty, when the ambient light level was lower.

As no test spiders responded when the light level was 0.24 cd m^{-2}, twilight (0.3 cd m^{-2}) and full moon (ca. 0.1 cd m^{-2}) seem not to be bright enough for these species to undertake vision-based identification of specific prey and rivals. However, good performance under a light level of 1.35 cd m^{-2} and marginal performance at 0.54 cd m^{-2} is remarkable considering that salticids are usually considered to be predators that rely on exceptional vision in well-lit habitats (Foelix, 2011). This is comparable to, or better than, findings for the nocturnal spider *Cupiennius salei*, which has the ability to perceive minimal differences when background luminance is above 16 cd m^{-2} (Campione and Schmid, 2014). These results therefore suggest that *C. algerina* and *C. ocellata* may have adaptations that enable them to see well under dim light.

Adaptations that compensate for size constraints have been extensively investigated in insects that specialize at seeing under dim light. For example, Kelber et al. (2006) showed that, compared with diurnal and even crepuscular bees, nocturnal bees have larger ocelli, and larger compound eyes composed of larger ommatidia; all of these characteristics probably function to improve sensitivity by enhancing the photon-capture capacity of the nocturnal bee's eyes. However, when discussing how salticids might improve photon-capture reliability, there are some unusual characteristics of the boomerang-shaped retinae of their principal eyes to consider.

Instead of lying in a single plane, photoreceptors in a salticid's principal-eye retinae, which lie at the end of long, slender eye tubes (Land, 1969; Williams and McIntyre, 1980), are stacked in four distinct tiers (Land, 1969) and, within the tier most distal to the cornea (layer 1), there is a staircase arrangement of receptor tips (Blest et al., 1990). Consistent with this being the layer with the best capacity for high spatial-acuity vision, layer 1 is also where photoreceptors are most densely packed and have the smallest diameter (Williams and McIntyre, 1980).

A variety of functions have been suggested for the four-tier arrangement of the salticid retina (Blest et al., 1981; Nagata et al., 2012; Zurek et al., 2015), including a role in increasing sensitivity by allowing more opportunities for photon capture as light passes through the successive layers (Land, 1969). This mechanism would be akin to how summation is achieved by insects (Warrant, 1999; Frederiksen et al., 2008). How other salticid species perform under dim light is currently unknown, but previous work on *Trite planiceps*, a species that we might consider to be representative of more conventional salticids, being diurnal and a member of the subfamily Salticoida, to which the majority of salticids (but not spartaeines like *Cyrba*) belong, suggests that *Cyrba* really is better at seeing detail under dim light. In the laboratory, *T. planiceps* required light intensities of at least 50 lx (similar to ND16) for normal visual

hunting behavior to occur (Forster, 1982). We currently cannot disambiguate whether dim light vision is a specialized characteristic of *Cyrba* which is enabled by specialized retinal ultrastructure (Blest et al., 1990), or whether dim light vision is widely expressed among salticids because of their four-tier retinal arrangement. Research in this area is needed and, given the variety of visual adaptations adopted by salticids, is likely to yield interesting results.

Spartaeinae, the subfamily to which *Cyrba* belongs, has the widest range in retinal ultrastructure known for salticids (Su et al., 2007). At one extreme, the spartaeine *Portia fimbriata* has rhabdoms in layer 1 packed in a hexagonal retinal mosaic, with the separation of individual rhabdoms minimizing the potential for crosstalk between neighboring rhabdoms and with inter-receptor spacing (1.4 µm) approaching the limit set by the wavelength of visible light. Owing to these characteristics, *P. fimbriata*'s principal eyes support extremely good spatial acuity (Williams and McIntyre, 1980; Blest and Price, 1984). *Yaginumanis sexdentatus* is at the other extreme, as this species' layer 1 receptive segments consist of essentially two contiguous rhabdomeres, each from a rhabdom in a different cell (Blest and Sigmund, 1984). As a consequence of this arrangement, there is optical crosstalk between neighboring receptors which increases photon-capture proficiency in this species' eyes, at the expense of spatial acuity.

Cyrba's retinal arrangement, seemingly intermediate between that of *Yaginumanis* and *Portia*, may allow for sensitivity superior to *Portia*'s but inferior to *Yaginumanis*'s, and spatial acuity superior to *Yaginumanis*'s but inferior to *Portia*'s. Each receptive segment in the central region of *C. algerina*'s principal eye layer 1 is wider than those of *Portia* and bears two rhabdomeres (in contrast to *Portia*'s single rhabdomere); however, when progressing toward the lateral outer edge of the retina, one rhabdomere in each pair becomes gradually shorter, meaning that distally, at the end closest to the corneal lens, receptors 1–3 (out of 13, along a horizontal line) consist of two rhabdomeres, but proximally, deeper into the cephalothorax, only a single rhabdomere exists (see fig. 1 in Blest et al., 1990; see also Blest and Price, 1984; Blest and Sigmund, 1985). In practice, this means that only the long rhabdomeres will absorb light in the foveal region (i.e. no optical pooling occurs), supporting better spatial acuity, while the inner side of the retina, bearing two rhabdomeres per receptor, contributes more strongly to sensitivity through optical pooling.

Our results are a step toward linking *Cyrba*'s retinal ultrastructure to its capacity for specific vision-based discrimination under low ambient light levels. While it is convenient to characterize salticids in general as predators that rely on eyes designed for good spatial acuity in brightly lit environments, this suggests that we know more than is the case. There are more than 5800 described species in the family Salticidae (Maddison, 2015) and it is for only a tiny fraction of these species that we have an understanding inclusive of natural history, behavior and the functioning of the eyes. Instead of making sweeping generalizations, we should be encouraging research aimed at gaining a fuller understanding of salticid diversity. Recent work showing previously unknown mechanisms of salticid vision, such as red-light vision enabled through the use of retinal filters in some species (Zurek et al., 2015), and the role of the secondary eyes in guiding the movement of the retinae of the principal eyes (Jakob et al., 2018), reminds us of how far we are from a full understanding of the salticid's visual system in its various forms.

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