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Maternal care thwarts parasitoids in the invasive brown widow spider (*Latrodectus geometricus*)

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Maternal care can maximize offspring survival and may contribute to the establishment success of invasive species. The brown widow spider, Latrodectus geometricus, is a successful invader worldwide. Here, we investigated the role of maternal care in enhancing its success. We compared the defence mechanisms of the invasive L. geometricus with those of another widow spider native to the Negev desert, Latrodectus pallidus, against an egg sac parasitoid wasp. Both spider species exhibited guarding behaviours following exposure to wasps; however, only L. geometricus efficiently evaded and successfully killed the parasitoid. Accordingly, its egg sacs were parasitized less frequently than those of L. pallidus. Next, we evaluated the defensive role of the silk spike-like structures on L. geometricus egg sacs. When spikes were removed from half of the egg sac surface, the wasps laid more eggs on the spike-free side. In an additional experiment, L. geometricus females increased spike density on subsequent egg sacs after exposure to the parasitoid. We showed that L. geometricus employs both behavioural defences and modifications to the egg sac structure to protect against the parasitoid. These defences may provide L. geometricus with an advantage over native species in its invasive range, potentially contributing to its invasion success.

1. Introduction

Invasive species expand their distribution beyond their natural range and may become a threat to native ecosystems, human health and the economy [1,2]. Several traits associated with successful invasiveness include exploitative competition, as seen in the Italian wall lizard [3]; boldness and high dispersal ability, notably in *Gambusia* fish [4]; large size, e.g. in *Solidago gigantea* plants [5]; and even larger brain size as been documented in several invasive amphibian and reptile species [6]. Additionally, high reproductive output (high fecundity or frequent reproduction) can promote population growth [7] and thus serve as a key element in invasive species establishment, as has been shown in mammals [8], plants [9] and freshwater fish [10]. To effectively manage the negative impacts of invasive species, it is crucial to deepen our understanding of the traits that contribute to their success, particularly those that confer advantages to successful reproduction.

Parental care, defined as parent–offspring-related behaviours that increase offspring fitness [11], may contribute to the establishment success of invasive species by ensuring higher offspring survival and quality. This, combined with high reproductive output, can result in a highly effective invasion tactic. Indeed, enhanced parental care is found in widely invasive birds like the common myna, *Acridotheres tristis*, which demonstrated greater nest attendance than native species [12]. Similarly, invasive fish species exhibit parental care predominantly in the form of guarding behaviours such as brooding, attacking invaders or carrying the offspring [13–15]. While investigated in several marine invertebrates (e.g. brooding behaviour [16]), the role of parental care in invasive terrestrial arthropods is less well understood.

Although spiders are not considered to provide extensive parental care to their offspring, many species do exhibit parental care behaviours exhibited by the female spider, which can reduce the risk of egg sac parasitism or predation. These include guarding the egg sac or carrying it throughout the incubation period [17–19], and even feeding the offspring following the emergence from the egg sac [20]. Indirect mechanisms include constructing a morphologically or chemically defended egg sac, as demonstrated in the spider *Deinopis* cf. *cylindracea* [21].

The invasive brown widow spider, *Latrodectus geometricus* C.L. Koch, 1841 (Theridiidae), is a synanthropic and cosmopolitan species with a potentially dangerous bite [22,23] that has invaded large parts of the world, mostly through human transport [24–26]. *Latrodectus geometricus* has high fecundity and dispersal ability, potentially giving it an advantage over native widow spiders in the invaded range [26,27]. In addition, *L. geometricus* constructs unique spike-like silk structures on the surface of its egg sacs, in contrast to the smooth surface of egg sacs of nearly all other widow spider species [24,28,29]. These structures have been suggested to provide protection against egg sac parasitism [30,31], potentially enhancing its success in invading new regions.

The egg sacs of widow spiders are prone to attack by several species of parasitoid wasps and flies [31]. *Philolema latrodecti* Fullaway, 1953 (Eurytomidae) is a parasitoid wasp that was first detected emerging from *L. geometricus* egg sacs [32] but is also known to attack the egg sacs of other widow spider species around the world [33]. The female wasp inserts her ovipositor through the silk layers of the egg sac, laying up to 40 eggs inside it. The wasp eggs hatch within 3 days, earlier than the spider eggs, and the wasp larvae consume the spider eggs, complete their development inside the egg sac and emerge as adults after around three weeks [34].

Previously, we examined factors contributing to the invasiveness of the brown widow spider in the Negev desert of Israel and found that this spider is less susceptible to egg sac parasitism by *P. latrodecti* than the native white widow spider, *Latrodectus pallidus* O. Pickard-Cambridge, 1872 (Theridiidae), both in nature and under laboratory conditions [30]. Here, we investigated the mechanisms underlying the observed differences in parasitism rate between the two widow spider species, focusing on maternal care mechanisms and defences against the parasitoid wasp. We hypothesized that the invasive *L. geometricus* provides better maternal care to its egg sacs, through both direct (active defence) and indirect (egg sac morphology) mechanisms, compared to *L. pallidus*, thus potentially giving it an advantage in its invasion range.

We addressed this hypothesis in the following three ways: (i) exposing female *L. geometricus* and *L. pallidus* spiders to wasp parasitoids and recording their defensive behaviours; (ii) exposing manipulated *L. geometricus* egg sacs, with silk spikes removed from one-half of their surface, to the parasitoid and recording wasps' egg-laying behaviour; and (iii) examining egg sac spike construction in *L. geometricus* before and following exposure to parasitoids. We predicted that *L. geometricus* would show increased behavioural defences and construct better-defended egg sacs following exposure to wasps. Additionally, we predicted that wasps would first approach and lay more eggs on the smooth, spike-removed side of the egg sacs compared to the unmanipulated spiky side.

2. Methods

(a) Study species

The brown widow spider, *L. geometricus*, has a global distribution [25] and resides mostly in urban habitats like gardens and playgrounds. *L. geometricus* spiders construct their nests concealed within or under man-made structures such as flowerpots, garden furniture, fences and garbage bins [26,35] (V.A., personal observations). The nest is a loose silk structure and is relatively transparent (figure 1a) [36]. The capture web extends from the nest opening, with support threads and gum-footed capture threads attached to surrounding supports. Egg sacs of *L. geometricus* are hung within the nest and are covered by spike-like, silk protuberances (figures 1a and 2).

The white widow spider, *L. pallidus*, can be found on low shrubs in semi-arid habitats in the Middle East [37,38], central Asia [39], the Caucasus [40] and South Africa [41] and may overlap with *L. geometricus* populations, especially in the outskirts of human habitation. Adult females construct a bell-shaped nest with a narrow opening connecting to a capture web [42]. The nest walls are composed of dense silk (figure 1b) and are sometimes covered with dry plant material and the exoskeletons of consumed prey items. The egg sacs of *L. pallidus* are opaque and have a smooth surface (figure 2a).

The parasitoid wasp *P. latrodecti* (figure 3) is known to attack widow spider species' egg sacs in different parts of the world, including North America and Australia [33], French Polynesia and the Cook Islands [43] and Israel [30]. In Israel it was first detected in 2018, emerging from egg sacs of both *L. geometricus* and *L. pallidus* collected in the Negev desert (M.A.M., unpublished results). *Philolema latrodecti* has also been found in the egg sacs of two other native widow spiders, *Latrodectus tredecinguttatus* and *Latrodectus revivensis*, in Israel (V.A., personal observations), but parasitism rates on the egg sacs of these species are yet to be explored.



Figure 1. Webs of *L. geometricus* (a) and *L. pallidus* (b) each with an adult female and egg sac, constructed on experimental platforms. Photos: V.A.



Figure 2. (a) Smooth egg sacs of *L. pallidus* (left) and spiky egg sacs of *L. geometricus* (right). (b) Spiky outer layer on *L. geometricus* egg sac, under a dissecting microscope. Photos: V.A.

(b) Establishing widow spider and wasp laboratory cultures

We collected adult female *L. geometricus* (n = 15) and *L. pallidus* (n = 15) from several locations in Ramat Negev, Israel (Beer-Sheva (31.266 N, 34.821 E), Hatzerim (31.260 N, 34.700 E), Ashalim (30.960 N, 34.714 E) and Midreshet Ben-Gurion (30.880 N, 34.778 E)). We found *L. geometricus* nests mostly underneath garbage bins and garden furniture and *L. pallidus* nests mostly on desert shrubs. Spiders were kept in the laboratory in Midreshet Ben-Gurion ($25 \pm 1^{\circ}$ C, $70 \pm 10\%$ relative humidity, and a light schedule of 14 : 10 L : D). Each spider was placed in a glass terrarium ($10 \times 20 \times 36 \text{ cm}^3$) with a few wooden sticks on which to construct its web. The spiders were fed twice a week with one desert grasshopper nymph (2–3 cm long, *Schistocerca gregaria*). We recorded the date of each egg sac produced and removed the egg sacs from the nests, placing them into individual containers (25 ml vials), maintained in the same room.

In addition, we collected egg sacs of both spider species (n = 103) and kept them in individual containers (25 ml vials) inside an incubator (24°C, 12 : 12 L : D) until the emergence of spiderlings or wasps. When wasps emerged from these egg sacs, we fed them by adding a small drop of honey to the vial twice a week. We used the female wasps to parasitize new spider egg sacs produced in the laboratory by placing one parasitoid female wasp inside a 25 ml vial with an egg sac for 24 h. We then moved the egg sacs into the incubator (24°C, 12 : 12 L : D) for 40–50 days until adult wasps' emergence in successful parasitism or spiderlings in an unsuccessful one. The wasps used for all experiments were up to one week old and were from egg sacs parasitized in the laboratory.

All the experiments were conducted in 2021–2022, in the Blaustein Institutes for Desert Research, Ben-Gurion University, Midreshet Ben-Gurion, Israel.



Figure 3. Female parasitoid wasp, P. latrodecti, under a dissecting microscope. Photo: V.A.

(c) Widow spider behaviour with exposure to parasitoid wasps

We recorded and compared the egg sac-guarding behaviours of the invasive and native widow spiders. We placed platforms each with a single *L. pallidus* (n = 14) or *L. geometricus* (n = 16) adult female, together with its web and a single egg sac into individual glass terraria ($10 \times 20 \times 36$ cm³). The egg sacs were produced less than 1 week before the beginning of the experiment. Ten female parasitoid wasps were then released inside each terrarium. We placed a surveillance video camera (Dahua IR Eyeball Network Camera) adjacent to each terrarium, viewing the whole widow spider nest and egg sac in the frame and recorded spider and wasp position and behaviour for 2 days. As a control, we recorded spider behaviour with their egg sacs but without the wasps (*L. pallidus*, n = 11 and *L. geometricus*, n = 16). The experimental system included eight cameras connected to a recording device (Dahua Eight-channel Network Video Recorder), and the room was kept at 27 ± 1°C and 50 ± 10% relative humidity, 12 : 12 L : D.

For every recorded hour, we observed and documented the occurrence of several typical widow spider behaviours and identified potentially defensive behaviours (see table 1 for a list of potentially defensive behaviours with further explanation on the scoring method and electronic supplementary material, table S1, for additional behaviours described). In 12 cases, the camera stopped recording mid-experiment, which resulted in the loss of parts of the recordings. We included the partial recordings in the analysis and corrected them for a shorter trial duration (see data analysis). Depending on their frequency, behaviours were quantified by the number of female spiders that exhibited them, the number of 1 h segments in which the behaviour occurred and/or the total number of times the behaviour was exhibited (table 1). The frequency of each potentially defensive behaviour was compared between the wasp exposure treatment and the no-wasp control (to determine which behaviours were associated with the presence of the wasps) and between the two spider species.

Occasionally, wasps dropped off the web thread they were standing on to the bottom of the terrarium or onto a lower web thread. This mostly followed spider movements such as walking around the web, tapping the egg sac or shaking the web. We have quantified these occurrences by counting the number of 1 h segments in which wasp-dropping behaviour occurred.

After each trial, we placed the egg sac individually in a vial (25 ml) in an incubator (24°C, 12 : 12 L : D). We checked weekly to see if the egg sacs were parasitized (wasps emerged from the egg sac) or not (spiderlings emerged).

(d) Egg sac spike-removal experiment

To test the possible role of the spike-like structures on *L. geometricus* egg sacs as a physical defence against the parasitoid wasp, we provided the wasps with manipulated egg sacs. We used *L. geometricus* egg sacs that were produced in the laboratory and removed the silk spikes from half (one hemisphere) of the surface of the egg sac (figure 5) using small scissors (Castroviejo Spring Scissors, 10 mm cutting edge). Then, we exposed each egg sac (n = 18) to a single female parasitoid wasp in a Petri dish for 2 h under a table lamp with a 40 W bulb. We released the parasitoid wasp approximately 1 cm away from the egg

Table 1. Potentially defensive spider behaviours observed during the experiment.

widow spider behaviour	description	scoring method
tapping the egg sac	rapidly touching the egg sac with the first and second pair of legs	number of 1 h video segments in which the behaviour was observed and the total number of occurrences per spider
circling the egg sac	walking around the egg sac while touching it with the pedipalps and/or adding silk threads	number of 1 h video segments in which the behaviour was observed
body shaking	rapidly moving the abdomen up and down, creating vibrations in the nest	number of 1 h video segments in which the behaviour was observed and the total number of occurrences per spider
wrapping wasp in silk	capturing a wasp, covering it with silk threads using the fourth pair of legs and biting it with the chelicerae	number of spiders performing this behaviour (yes/no per spider)

sac, facing the midline between the spike-removal and the spiky (non-manipulated) hemispheres, and observed its behaviour on each hemisphere of the egg. Specifically, we recorded the time until approaching the egg sac, which hemisphere the wasp approached first, and the total time spent on each hemisphere. After the trial ended, we removed the wasp to a separate vial (25 ml) and carefully dissected the spider egg sac with small scissors to count the wasp eggs oviposited within each side (spiky and spike-removal side). The wasp eggs were laid in clusters and were easily distinguished from the spider eggs by their small size and elongated shape [34].

(e) Egg sac morphology in response to exposure to wasps

To determine if L. geometricus females modify their egg sac morphology in response to parasitism risk, we compared egg sac spike density and length before and following exposure to parasitoid wasps. L. geometricus females (n = 23) were reared to adulthood from egg sacs or juveniles collected in the field (Midreshet Ben-Gurion area). Female spiders (n = 11) were mated in the laboratory and fed until they each constructed a web on a frame and produced a single egg sac. This first egg sac was removed, and its spike length and density were quantified. We measured spike length by photographing each egg sac and measuring the length of ten randomly chosen spikes per egg sac. For the analysis, we calculated the mean spike length for each egg sac. We measured egg sac spike density by photographing the egg sac under the dissecting microscope and counting the number of spikes in the visible area under the ×4 magnification of the microscope (an area of approx. 0.2 cm²). After the production of a second egg sac (within a period of up to 3 days), we placed the female spiders, each with its web and egg sac, individually in a glass terraria ($10 \times 20 \times 36$ cm³) and added 10 female parasitoid wasps. This was to enable spider-wasp interactions and an actual risk for the egg sacs, as well as for the possibility that the female spider would add silk while the wasps were present. Following 2 days of exposure, we removed the wasps and quantified the spike length and density of the second egg sac produced by each female. When a third egg sac was produced, spike length and density were compared between the first (pre-exposure), second (immediate pre-exposure) and third (post-exposure) egg sacs. The same was measured for a control group of 12 female spiders that were not exposed to parasitoids but were otherwise treated similarly. One spider female from the treatment group and three from the control group did not produce their second and third egg sac and thus were excluded from the analysis, reducing the sample size to 10 for the treatment group and 9 for the control group.

(f) Statistical analysis

For the statistical tests, we used *jamovi* v. 2.5.5.0 and packages *ggplot2*, *ggpubr* and *cowplot* [44–46] for R v. 4.4.2 [47,48]. For all of the datasets, we tested for deviations from normal distribution using the Shapiro–Wilk test and for homogeneity of variances using the Levene test.

In the spider behavioural assays, since the data were not normally distributed, we used a generalized linear model (GLM) with a negative binomial distribution and log link function. For each spider behaviour, we included in the analysis the spider species (*L. geometricus* or *L. pallidus*) and the treatment (exposure to wasps or a no-wasp control) as factors with interaction and the duration of the recording as a covariate (to control for the variation in trial duration, ~species + treatment + recording duration (covariate)). We used Fisher's exact test to compare the parasitism rate (yes/no) of the spider egg sacs under exposure to wasps between the two spider species.

In the spike-removal experiment, we used a binomial distribution to test whether the number of times the wasp first approached either the spiky or non-spiky hemisphere deviated from 1 : 1. Data on parasitoid wasp behaviours and the number of eggs they laid in each hemisphere of the spider egg sac were non-normally distributed; therefore, we used GLMs with a negative binomial distribution and log link function. These were used to compare the time it took the wasp to first approach each side of the egg sac, the total time the parasitoid wasps spent on each hemisphere and the number of parasitoid wasp eggs oviposited inside each hemisphere.

To assess the effect of wasp exposure on *L. geometricus* egg sac spike length and density, we used a generalized linear mixed model (GLMM) with gamma distribution and log link function, for non-normal distributed data. We compared wasp treatment and egg sac order (first, second and third) as factors with interaction, with spider ID as a random factor. In addition, we ran a *post hoc* comparison for the differences between egg sacs in each treatment.

See the electronic supplementary material for full model outputs.

3. Results

(a) Widow spider defensive behaviour with exposure to parasitoid wasps

Females of both spider species were more active during exposure to wasps than during the no-wasp control (GLM, wasp treatment: $\chi^2 = 11.736$, p < 0.001; species: $\chi^2 = 2.048$, p = 0.152; figure 4a). Similarly, both spider species circled the egg sac more in the presence of the wasps. However, L. pallidus spiders tended to circle the egg sac more than L. geometricus, both in the presence of wasps and in the no-wasp control (GLM, wasp treatment: $\chi^2 = 8.988$, p = 0.003; species: $\chi^2 = 3.735$, p = 0.053; figure 4b). Tapping the egg sac occurred more in the presence of wasps than in the no-wasp control for both spider species (GLM, wasp treatment: $\chi^2 = 10.869$, p < 0.001; species: $\chi^2 = 2.829$, p = 0.093; figure 4c). In addition, L. geometricus performed this behaviour more frequently than *L. pallidus* (GLM, wasp treatment: $\chi^2 = 17.41$, p < 0.001; species: $\chi^2 = 6.574$, p = 0.01). In contrast, body shaking behaviour occurred more in *L. pallidus* than in *L. geometricus* (GLM, wasp treatment: χ^2 = 6.287, *p* = 0.012; species: χ^2 = 13.064, p < 0.001; species × treatment interaction: χ^2 = 0.584, p = 0.445; figure 4d). A similar pattern was observed for the frequency of the body shaking behaviour (GLM, wasp treatment: $\chi^2 = 6.315$, p = 0.012; species: $\chi^2 = 13.522$, p < 0.001; species × treatment interaction: $\chi^2 = 0.469$, p = 0.493). Interestingly, only L. geometricus captured wasps and wrapped them in silk (5/18, 27% of L. geometricus compared to 0/17 of L. pallidus, Fisher's exact test, p = 0.045). Altogether 12 wasps were captured: three of the L. geometricus females that captured wasps disposed of the wasps wrapped in silk without feeding on them, while the remaining two spiders fed on the wasps. The number of 1 h segments in which wasps were observed to drop off the spider threads was higher in *L. geometricus* than in *L. pallidus* (GLM, χ^2 = 3.93, *p* = 0.047). Finally, in trials with exposure to parasitoid wasps, L. pallidus egg sacs were more often parasitized than those of L. geometricus (9/14, 64% and 3/16, 19%, respectively, Fisher's exact test, p = 0.023).

(b) Egg sac spike-removal experiment

The wasps tended to first approach the spike-removal side more often than the spiky side (13/18, 72% and 5/18, 28%, respectively, binomial test, z = 1.67, p = 0.096), but spent a similar duration of time on the spiked and spike-removal side of the egg sac (GLM, $\chi^2 = 0.844$, p = 0.358). Nevertheless, parasitoid wasps oviposited more eggs into the spike-removal side of the egg sac than the spiky side within the 2 h observation period (median = 17, interquartile range (IQR) = 4–23 and median = 0, IQR = 0–3.5 eggs, respectively, GLM, $\chi^2 = 6.188$, p = 0.013; figure 5).

(c) Egg sac morphology in response to exposure to wasps

L. geometricus spiders constructed egg sacs with denser spikes in the third egg sac following exposure to parasitoid wasps compared to those of the control females that were not exposed to the parasitoid wasps (GLMM, $\chi^2 = 4.81$, p = 0.09; *post hoc* comparison of third egg sacs z = 2.786, p = 0.005; figure 6). Spike length did not differ between the control and parasitoid wasp treatments (GLMM, $\chi^2 = 1.42$, p = 0.492; *post hoc* comparison of third egg sacs z = 0.715, p = 0.474).

4. Discussion

In this study, we provide evidence for the role of maternal care in evading parasitism. Our results show that the more active behaviour of egg sac defence by *L. geometricus* and the unique spiky structure of its egg sacs contributed to less frequent attacks by an egg sac parasitoid wasp. This novel evidence underscores the adaptive strategies employed by *L. geometricus* to mitigate the risk of parasitism, potentially enhancing its invasion success.

The invasive brown widow spider *L. geometricus* and the native white widow spider *L. pallidus* while differing in their appearance, habitat and distribution [28] share several behaviours related to egg sac guarding. Following exposure to the parasitoid wasps, females of both spider species increased their activity levels and spent more time tapping and circling the egg sac. Such inspection behaviours may serve to ensure that parasitoids are not present on or near the egg sac and can cause the parasitoid wasps to drop down, temporarily removing them from the immediate vicinity of the egg sac. Similar defensive behaviours have been observed in colonial and communal orb-weaving spiders in response to parasitoid threats [49,50]. Another spider behaviour that sometimes caused the parasitoid wasps to drop was body shaking. This is a common female spider behaviour to deter unwanted males, predators and parasitoids, observed, for example, in the orb-weaving spiders *Uloborus glomosus* (Uloboridae) and *Cyrtophora moluccensis* (Araneidae) as well as several *Latrodectus* species [50–53].

In response to spider activities, *P. latrodecti* wasps exhibited dropping behaviour. Dropping is a well-known escape mechanism in herbivorous insects like caterpillars and aphids, allowing them to evade predators and parasitoids [54–57]. However, it has rarely been documented as a defensive behaviour of a parasitoid wasp against its spider host. In another example, the crab spider *Misumena vatia* (Thomisidae) was observed chasing the parasitoids and causing them to drop off the egg sac [58]. The dropping behaviour of *P. latrodecti*, which occurred more often in response to *L. geometricus* than *L. pallidus* behaviours, similarly removes the wasps from the vicinity of the egg sac. In our experiment, releasing 10 wasps in a confined space probably facilitated the occurrence of such interactions. However, in nature, the number of wasps approaching the web simultaneously may be lower, and wasps may escape altogether following aggressive behaviour by the spider. Even more effective than causing the wasps to drop, five of the *L. geometricus* females managed to capture and kill the wasps, indicating that the spider poses a threat to *P. latrodecti* (see video in the electronic supplementary material). *Philolema latrodecti* is much smaller than the typical



Figure 4. Number of hours (out of the total trial period) in which specific spider behaviours were observed during no-wasp control and exposure to wasps trials. The brown boxes represent *L. geometricus* (n = 16), and the beige boxes represent *L. pallidus* (n = 14). The horizontal lines represent the median, the boxes are the IQR and the whiskers are standard deviation (s.d.).

prey of *Latrodectus* spiders, which may include large beetles, scorpions, lizards and even small mammals [52,59,60]; hence, killing the wasps is more likely to be a defensive, rather than predatory behaviour. Indeed, three of the five *L. geometricus* females that wrapped wasps in silk did not feed on them. This behaviour aligns with previous observations of overall high aggressiveness and activity levels of *L. geometricus* [27,61]. In accordance, *L. geometricus* was more difficult to capture during field collection and was aggressive towards *L. pallidus* when kept in the same space (V.A., personal observations). Overall, the high efficiency of *L. geometricus* egg sac guarding is evidenced in the lower parasitism rate on *L. geometricus* egg sacs than on *L. pallidus* egg sacs at the end of the experiment, which is consistent with the results of previous studies [30,34]. Furthermore, in a field experiment conducted by Moura *et al.* [62], the presence of an *L. geometricus* female in the nest tended to reduce parasitism by threefold.

Philolema latrodecti wasps that did manage to pass this first line of defence and approach the egg sac faced another challenge—the outer silk layer of the egg sac. All spider species use silk to cover their eggs [63], and most widow spiders construct egg sacs with relatively thick walls, which may serve as a barrier against parasitoids and egg predators [64]. *L. geometricus* females construct an additional layer on the surface of their egg sac in the form of spiky silk structures, as opposed to the smooth egg sacs in most other (>30) widow spider species [28,52]. These structures were suggested to serve as an extra protective layer against parasitoid wasps [30,31], a hypothesis first tested here.

When exposing manipulated *L. geometricus* egg sacs to parasitoid wasps, we observed a trend of wasps first approaching the spike-removal side, suggesting the possibility of the wasp relying on visual cues to identify and choose a more suitable oviposition location. Parasitoid wasps are known to use visual cues to detect both moving and stationary hosts [57,65–67]. Visual cues may also play a part in choosing the exact oviposition site from a short distance. In addition, despite spending a similar amount of time on both hemispheres of the egg sac, the parasitoid wasp chose (or managed) to lay more eggs on the spike-removal hemisphere. This suggests that in situations with limited time available for egg laying (e.g. under risk of attack by the spider), the wasps will be able to lay more eggs in a smooth-surfaced egg sac. The outer spiky layer on the *L. geometricus* egg sacs appears to pose a challenge for the parasitoid wasp by creating a larger physical barrier than smooth-surfaced egg sacs. The visible silk spikes are interconnected with silk threads (figure 2b), creating a tangled external layer that can make it more difficult for the wasp to approach close to the surface of the egg sac and insert its ovipositor. A similar protective mechanism was observed in *Mecynogea lemniscata* and *Argiope aurantia* (Araneidae), which produce egg sacs with a flocculent (wool-like) outer layer that serves as an effective barrier against egg sac parasitoids such as ichneumonid wasps [68]. Additionally, *L. geometricus* sometimes adds droplets of glue to the outer silk threads of the egg sac, which can further impede the wasp's mobility (figure 2b) [69] (R. Foelix, personal communication). Nonetheless, due to the irregularity of the egg sac outer silk layer structure, we cannot rule out the possibility that our overall interference with the outer layer affected the wasp choice



Figure 5. Number of eggs each parasitoid wasp laid on the spike-removal side (on the right) and/or on the spiky side (on the left). Each black line represents a single wasp (n = 18; 17 lines are visible since two of the lines overlap). The horizontal lines represent the median, the boxes are the IQR and the whiskers are s.d. Inset at top: a manipulated *L. geometricus* egg sac with spikes removed from half of it. Photo: V.A.



Figure 6. Number of spikes counted in a 0.2 cm² area on first, second and third *L. geometricus* egg sacs, in wasp treatment (n = 10) and control (n = 9) trials. The horizontal lines represent the median, the boxes are the IQR, the whiskers are s.d., and the point is a maximum outlier.

behaviour. Therefore, a deeper exploration of the spiky silk layer structure and its exact effect on the wasp's behaviour is needed.

While all *L. geometricus* females create spiky egg sacs, we found that they adjust the density of the spikes in response to the presence of parasitoid wasps. This finding further supports the hypothesis that the spikes serve as a defence mechanism

against parasitoids. The only other known widow spider with spike-like structures (though less pronounced) on its egg sacs is *L. corallinus* from Argentina [24,70,71]. However, the ecology and interaction of this spider with its egg sac parasitoids remain unexplored. The density and length of egg sac spikes were observed to vary in nature, both within and among females of *L. geometricus* (M.A.M., unpublished results), suggesting that egg sac morphology in this species is a plastic trait and may represent an induced response to the presence of enemies. Such predator-induced structure alterations are poorly studied. Among the few examples are sand gobies, which modify their nest shape in the presence of predators [72], and redback widow spiders, which alter their nest structure following egg sac production [73]. Both the behavioural response to the parasitoid and egg sac alteration in *L. geometricus* may represent a strategic allocation of energy and resources with the potential to conserve resources in the absence of parasitoids. The energetic costs and time investment associated with induced egg sac-guarding behaviour and spike production in *L. geometricus* egg sacs are yet to be quantified.

The parasitoid-induced behavioural response of the invasive *L. geometricus*, combined with changes in egg sac morphology, creates a dual defence strategy that enhances offspring survival more effectively than in the native *L. pallidus*. This may also explain patterns observed in other places in the world, with egg sacs of *L. geometricus* being attacked less often than the native western black widow, *L. hesperus*, in California, and less often than other theridiid spider species in Costa Rica [31,69]. Moreover, the higher parasitism rate in the egg sacs of the native white widow, *L. pallidus* [30], may negatively affect its population growth thus reducing competition with *L. geometricus* for food and habitat resources in areas where the two spider species overlap. While the origin of the wasp *P. latrodecti* is unknown, it was first described from *L. geometricus* egg sac [32] and possibly co-invaded with the invasive spider. Cases of negative parasite spillover affecting native species have been demonstrated in invasive oysters in northern Europe and invasive tree frogs in Florida and their respective co-invaded copepod and nematode parasites [74,75]. Future work will examine whether *P. latrodecti* co-invaded with *L. geometricus*, and if this is indeed the case, the invasion of *L. geometricus* can be even more harmful to the native species than previously acknowledged. This work can help us better understand the role of maternal care in the invasion success of *L. geometricus* specifically and invasive species in general providing them with an advantage over native species, in the presence of natural enemies.

Ethics. The experiments in this research involve the use of spiders and wasps, and all experiments comply with the ABS/ASAB ethical guidelines for animal treatment.

Data accessibility. Data collected in the experiments described in this work are available on Dryad [76].

Supplementary material is available online [77].

Declaration of Al use. We have used AI-assisted technologies in creating this article.

Authors' contributions. V.A.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft; A.D.J.: data curation, investigation, methodology; T.R.: data curation, investigation, methodology; Y.L.: conceptualization, data curation, resources, supervision, writing—review and editing; M.S.: conceptualization, data curation, resources, supervision, writing—review and editing; M.A.M.: conceptualization, data curation, formal analysis, investigation, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interests. We declare we have no competing interests.

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