



# Invasive brown widow spiders avoid parasitism despite high densities

Monica A. Mowery<sup>1</sup> · Valeria Arabesky<sup>1</sup> · Tamir Rozenberg<sup>1</sup> · Yael Lubin<sup>1</sup> · Michal Segoli<sup>1</sup>

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## Abstract

Invasive species are sometimes less susceptible to natural enemies compared to native species, but the mechanism is often unclear. Here we tested two potential mechanisms for lower parasitism of invasive species: density-dependent parasitism and preference for human-dominated habitats. We investigated how variation in host density and habitat type affect egg sac parasitism in two widow spider species (family Theridiidae). We compared parasitism on the egg sac of the brown widow, *Latrodectus geometricus*, an urban invasive species, and the white widow, *Latrodectus pallidus*, a species native to Israel. To investigate variation in host and parasitoid density, we measured nearest-neighbor distance between spider webs and parasitism rates in 16 sites, and in a single site monthly throughout a year. In *L. pallidus*, denser sites were more heavily parasitized (up to 55%) and parasitism rate increased with population density throughout the season. Extremely dense *L. geometricus* populations, however, had very low rates of parasitism (0–5%). We then conducted an egg sac transplant experiment in human-dominated and natural habitats. We found no parasitism of either species in the human-dominated habitat, compared to 30% parasitism of both species in the natural habitat. In addition, we found evidence for higher predation of *L. pallidus* than of *L. geometricus* egg sacs, particularly in the natural habitat. These combined results suggest that the human-dominated habitats inhabited by *L. geometricus* have a lower abundance of predators and parasites. We conclude that lower parasitism and predation in human-dominated habitats could contribute to the invasion success of *L. geometricus*.

**Keywords** Invasive species · *Latrodectus* · Spider · Urbanization · Parasitoid

## Introduction

Ecological interactions of invasive species with competitors, predators, prey, and parasites can facilitate or impede invasion (Heimpel and Mills 2017). In particular, invasive species may escape or be better defended against natural enemies compared to native species (Ceryngier et al. 2018). In some cases, invasive species are less attractive and less suitable hosts for parasites compared to native species (Bertoldi et al. 2019). In addition, invasive species may avoid high rates of mortality by thriving in habitats with fewer parasites and predators, especially at the invasion front (Brown-scombe and Fox 2013; Phillips et al. 2010). Although many invasive species are urban-dwelling and are transported by

humans to urban areas, few studies have considered whether adapting to new, urban habitats facilitates invasion establishment by reducing the burden of predators and parasites.

Highly disturbed human-dominated habitat can differ from natural environments in the abundance and species richness of natural enemies. In particular, urbanization generally decreases arthropod diversity (Burks and Philpott 2017; Corcos et al. 2019; Fenoglio et al. 2021) and diversity of potential predators of arthropods, including birds (Sol et al. 2020). Studies show that parasitoid populations decline in fragmented habitats (Bennett and Gratton 2012; Kruess and Tschardtke 1994, 2000) and in urbanized areas (Korányi et al. 2022). However, urban parks and gardens with floral resources may support high levels of biodiversity of parasitoids (Piekarska-Boniecka et al. 2022) and predators (Aronson et al. 2017; Uchida et al. 2021). Hence, parasitism and predation pressure experienced by an invasive species may depend on the specific conditions in the environment it inhabits. Studying these interactions across habitats may shed light on the ecological impacts of invasive species,

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✉ Monica A. Mowery  
monicaan@post.bgu.ac.il

<sup>1</sup> Mitrani Department of Desert Ecology, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 8499000 Midreshet Ben-Gurion, Israel

displacement of native species, and effects on native food webs (Carlsson et al. 2009; Theodorou 2022).

Differences in parasitism and predation of invasive and native species could be related to their population densities. Invasive species can reach high densities in their new habitat (McDowell and Byers 2019; Zhao et al. 2021), but at the edge of the invasion front they are initially at low densities (Contarini et al. 2009; Tobin et al. 2007). Parasitoid population dynamics is often affected by the density of their host populations (Rohani and Miramontes 1995) through multiple mechanisms (Lessells 1985). For example, oviposition by egg parasitoids may be higher in dense host patches (Heimpel and Casas 2008). Conversely, limited egg loads and time available for oviposition may result in lower parasitism at high host densities (Walde and Murdoch 1988). At a larger spatial scale, high density sites may attract more parasitoids or support faster parasitoid population growth rate (Segoli et al. 2008; Segoli and Rosenheim 2013). Hence, population density can have different and even opposite effects on parasitism rate depending on the spatial scale. At the temporal scale, there may be a time lag between population density increase and parasitism rate (Murdoch et al. 2005). The link between population density, parasitism rate and invasion success is difficult to predict due to interacting causes and requires disentangling the effects of density and habitat characteristics.

Most studies on density-dependent parasitism in arthropods thus far are on insects. Spider-parasitoid population dynamics over time have not been well-studied, however some studies suggest positive density dependence. In *Anelosimus eximius*, egg sacs in larger spider colonies were more likely to be parasitized (Avilés and Tufiño 1998). In four species of spiders, areas with sparse egg sacs had no parasitism, whereas in dense sites, parasitism was up to 66% (Finch 2005). With high rates of mortality caused by parasitism of egg sacs, egg sac parasitoids have the potential to be a significant limiting factor in spider population growth, but have not been widely studied in an experimental ecological context.

Here, we tested the effects of habitat type and of spatial and temporal variation in density on egg sac parasitism in a pair of host species: the highly invasive brown widow spider, *L. geometricus* and the white widow spider, *L. pallidus*, native to Israel, by an egg sac parasitoid wasp, *Philolema latroedecti*, that commonly attacks widow spider egg sacs (Fullaway 1953; Marie and Vetter 2015; Mowery et al. 2022a). *Latroedectus geometricus*, is an invasive species that is distributed widely in warm, dry climates around the world (Taucare-Ríos et al. 2016) and thrives in human-dominated habitats in its invaded range (Sadir & Marske 2021). *Latroedectus pallidus*, the white widow spider, occurs in northern Asia and the Middle East, and

lives in desert scrub habitats, but is rarely found in human-dominated habitats. Egg sacs of the invasive species *L. geometricus* suffer from lower parasitism in the field and were a less preferred host in lab experiments compared to *L. pallidus* egg sacs (Mowery et al. 2022a). In the present study, we examined two potential mechanisms that may explain this difference.

Based on qualitative assessment from previous field collections, we predicted that parasitism would increase with increased host density at both the spatial and temporal scale. In addition, we predicted that parasitism rate would be higher in natural compared to human-dominated habitats, based on observed low dispersal propensity of the parasitoid. Although we focused on egg sac parasitism, one of our experiments also yielded interesting results related to egg sac predation, hence we report these as well. We predicted lower parasitism and predation in human-dominated habitats due to lower abundance of natural enemies. Following the above predictions, it is likely that across a range of densities and habitat types, *L. geometricus* will have lower parasitism rates than *L. pallidus*.

## Methods

### Spatial variation in density and parasitism rate

To assess parasitism rate and population density, we surveyed ten sites with *L. pallidus* populations and six sites with *L. geometricus* populations for nests with adult females and egg sacs. *Latroedectus pallidus* spiders were found on shrubs in natural and semi-natural habitats, while *L. geometricus* spiders were found in human-dominated habitats, such as under garbage bins, in walls, fences, and under structures in gardens and playgrounds. Each site was approximately 100 × 200 m in area, except for two low density *L. pallidus* sites (Midreshet Ben-Gurion and Yeruham) where we needed to search a larger area to collect a minimum of 10 egg sacs. At each site, we counted the total number of nests with adult females and the number of unhatched egg sacs and collected the unhatched egg sacs to assess parasitism rate. We visually searched each site for 2 h using transects of the length of the site approximately 5 m apart. To estimate population density, we measured nearest neighbor distances between spider nests with unhatched egg sacs. We focused on nests with unhatched egg sacs as they represent host population density from the point of view of a foraging parasitoid wasp, *P. latroedecti*. Collected egg sacs were incubated in the laboratory under controlled conditions (25 ± 1 °C, 14:10 L:D) and the emergence of spiderlings or wasps was noted. After two months, we opened any sacs from which wasps

or spiderlings had not emerged and noted the presence of dead wasps or spiderlings. See Supplementary Table 1 for sites, collection dates, and the number of egg sacs collected at each site.

### Seasonal variation in density of *L. pallidus* and parasitism rate

Seasonal variation in density and parasitism was assessed only for *L. pallidus*, because parasitism rate in *L. geometricus* was too low to detect changes. From November 2020 to November 2021, we conducted a monthly field survey in a desert scrub habitat near Ashalim, in the Negev Desert, Israel (30.9608 °N, 34.7146 °E). We surveyed the site as indicated above, counting the number of nests with adult *L. pallidus* females and the number of nests with unhatched egg sacs. To estimate population density, we measured nearest neighbor distances between spider nests with unhatched egg sacs, as indicated above. We collected egg sacs from up to 10 nests in different, adjacent areas. Egg sacs were incubated in the lab and checked for emergence of wasps or spiderlings, as described above. See Supplementary Table 1 for sites, collection dates, and the number of egg sacs collected at each site.

### Habitat transplant experiment

To assess the effects of habitat type on egg sac parasitism and predation, we conducted an egg sac transplant experiment in settled and natural environments. We maintained field-collected, adult *L. geometricus* and *L. pallidus* females in the laboratory (25 ± 2 °C, 14:10 L:D). The spiders were fed weekly with one grasshopper (*Schistocerca gregaria*) nymph. We placed each spider to be released on a wooden platform with a three-dimensional frame for web attachment (see Mowery et al. 2022a for details on the structure). The spiders were maintained for at least one week so that they could build webs. Once the spiders constructed their webs and produced egg sacs (normally less than one week after placement on the structure), we removed the spider and placed the structure with the web and egg sac in areas that would be suitable for *L. geometricus*, under garden furniture, or *L. pallidus* residence, near desert shrubs, for one week. In some cases, after one week, the egg sacs were damaged or completely absent from the nest. Since egg sacs are firmly anchored to the inner wall of the nest and were unlikely to fall out of the nest, we considered such incidents as evidence for predation. We then collected and incubated the egg sacs under controlled conditions (25 ± 1 °C, 14:10 L:D). We recorded whether wasps or spiderlings emerged from the egg sacs, and after two months, we opened all remaining egg sacs to record their contents.

We conducted the habitat transplant experiment twice during peaks of parasitoid abundance: July 2021 and November 2021. The July 2021 experiment was conducted near Hatzetim, representing *L. pallidus* desert scrub habitat ( $n=33$  *L. pallidus* egg sacs;  $n=27$  *L. geometricus* egg sacs), and in private gardens in Midreshet Ben-Gurion, representing *L. geometricus* human associated habitat ( $n=17$  *L. pallidus* egg sacs;  $n=15$  *L. geometricus* egg sacs). In November 2021, we conducted a second experiment near Ashalim, representing *L. pallidus* habitat ( $n=20$  *L. pallidus* egg sacs;  $n=20$  *L. geometricus* egg sacs), and Midreshet Ben-Gurion, representing *L. geometricus* habitat ( $n=20$  *L. pallidus* egg sacs;  $n=20$  *L. geometricus* egg sacs). We chose these sites because wasp presence had been recorded there in earlier collections of *L. pallidus* or *L. geometricus* egg sacs. In the first experiment egg sacs were ~10 m distance to the nearest *L. pallidus* nest with egg sacs, while in the second experiment, we reduced the distance to ~0.3 m to increase opportunities for egg sac parasitism, which did not occur in the first experiment.

### Statistical methods

All analyses were conducted in R (version 4.0.2, R Core Team). In all models, we checked for over- and under-dispersion of the residuals by comparing the residual deviance to the degrees of freedom and did not find any deviations. To test whether the likelihood of parasitism was related to population density at the individual egg sac level in *L. pallidus*, we constructed a generalized linear mixed model with egg sac parasitism as the binary response variable, nearest neighbor distance as a fixed factor and site as a random factor, using a binomial distribution with a logit link function (lme4; R Studio, Inc, Bates et al. 2015). To assess the relationship between mean nearest neighbor distance and parasitism on a site level in *L. pallidus*, we used a general linear model with the percentage of egg sacs parasitized as the response variable and mean nearest neighbor distance within a site as the predictor, weighted by the number of egg sacs collected, using a Gaussian distribution. To test if the number of wasps emerged was affected by the distance of the egg sac from which they emerged to the nearest neighbor, we used a general linear mixed model with log-transformed total number of wasps emerged as the response variable, site as a random factor, and nearest neighbor distance as a fixed factor. To compare parasitism rates between *L. geometricus* and *L. pallidus* egg sacs, we constructed a GLMM with nearest neighbor distance and species as predictors, site as a random factor, and a binomial distribution with a logit link function. Parameters and significance were calculated using Wald F tests for GLMs and Chi-squared tests for GLMMs (*car* package, Fox and Weisberg 2019). To assess the effects of species of egg sac and habitat on parasitism and predation rates in the habitat transplant experiment, we used Fisher's exact tests.

## Results

### Spatial variation in density and parasitism rate

At the level of the individual egg sacs across all sites, the likelihood of an *L. pallidus* egg sac to be parasitized was not significantly related to the nearest neighbor distance (GLMM,  $X^2_1 = 1.209$ ,  $p = 0.271$ ). At the site level, however, a higher percentage of *L. pallidus* spider egg sacs were parasitized in denser sites (Fig. 1, GLM,  $F_{1,8} = 10.829$ ,  $p = 0.011$ ), all by the parasitoid wasp, *P. latroecti*. In contrast, *L. geometricus* egg sacs were rarely parasitized, despite very high web density (Fig. 1, GLMM,  $X^2_1 = 2.479$ ,  $p = 0.013$ ). Only one parasitized *L. geometricus* egg sac collected from Hatzerim was found across all sites, and contained *Necyla sacra* (Neuroptera, Mantispidae), a mantisfly egg predator. The distance to the nearest *L. pallidus* egg sac predicted the number of wasps emerging from an egg sac. More wasps emerged from more isolated egg sacs (GLMM,  $X^2_1 = 23.572$ ,  $p < 0.001$ ). Smaller wasps emerged from *L. pallidus* egg sacs containing more wasps (GLM,  $F_{1,33}$ ,  $p = 0.006$ ).

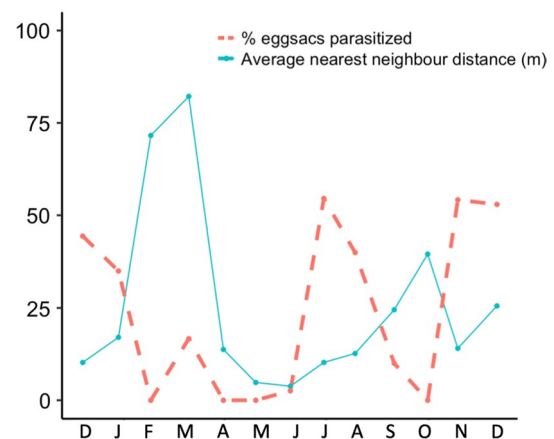
### Seasonal variation in density of *L. pallidus* and parasitism rate

Egg sac parasitism ranged from none to 55% (median: 16.7%) over the 1 year survey. Both the abundance of spider webs with egg sacs and egg sac parasitism showed seasonal variation, with egg sac density peaking (low nearest neighbor values) in May–June and November, and egg sac parasitism rate

peaking slightly later in July–August and November–December (Fig. 2). Photo credits: Alfred Daniel J.

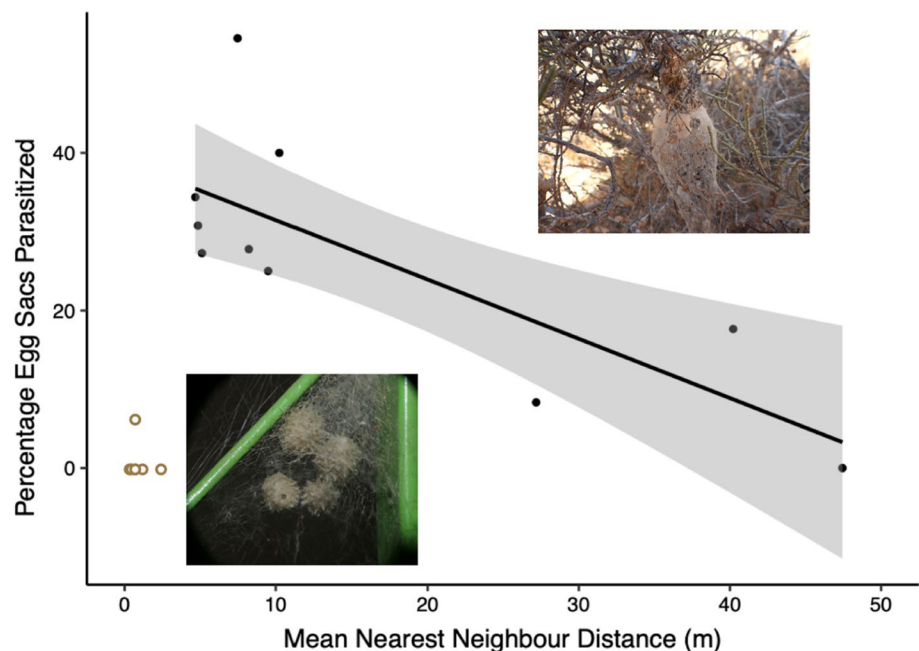
### Habitat transplant experiment

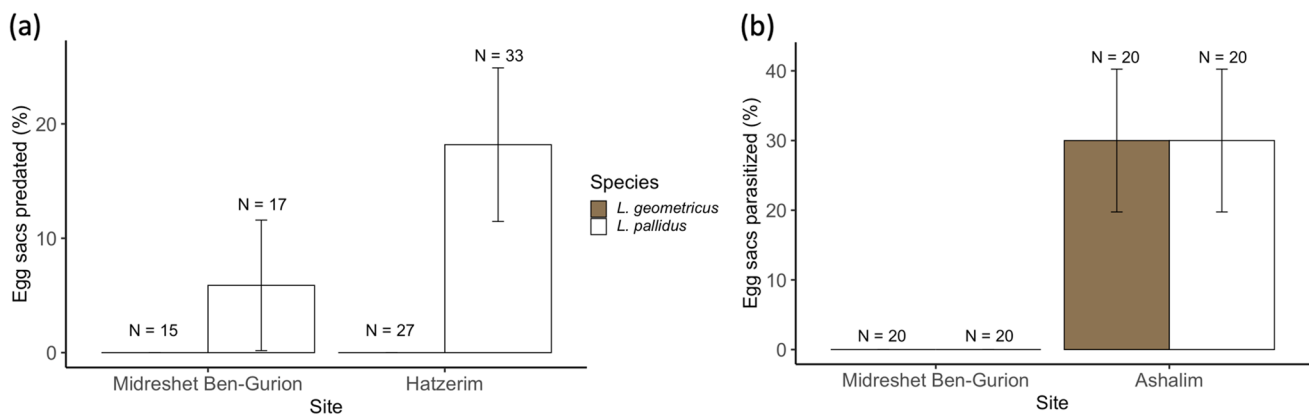
The habitat transplant experiment in July 2021 resulted in no parasitism in either the natural or human associated site. However, the frequency of predation events differed among the species and habitats. Comparing between the host species, *L. pallidus* egg sacs were more likely to be preyed upon (Fig. 3a, Fisher's exact test,  $p = 0.015$ ), compared to no *L. geometricus* egg sacs (zero out of 42) preyed upon during the experiment. 18% of *L. pallidus* egg sacs in the natural



**Fig. 2** Seasonal survey of *L. pallidus* density (measure by mean nearest neighbor distance) and egg sac parasitism rates. The survey was conducted monthly from December 2020 to December 2021

**Fig. 1** The percentage of egg sacs collected that were parasitized for each site in relation to site mean nearest neighbour distance. *L. pallidus* sites are shown as black circles, and *L. geometricus* sites are shown as outlined points in brown





**Fig. 3** **a** Predation and **b** parasitism of *L. geometricus* egg sacs (brown) and *L. pallidus* egg sacs (white) in two habitat transplant experiments: **a** in human-dominated habitat (Midreshet Ben-Gurion)

and natural habitat (Hatzerim) in July 2021; and **b** human-dominated habitat (Midreshet Ben-Gurion) and natural habitat (Ashalim) in November 2021

habitat (six out of 33) were preyed upon, compared to 6% (one out of 17) in the human-dominated habitat (Fisher's exact test statistic = 0.028). In the second field transplant experiment in November 2021, we found that no egg sacs were parasitized in the human-dominated habitat, compared to 30% of both species' egg sacs were parasitized in the natural habitat (Fig. 3b, Fisher's exact test,  $p < 0.001$ ). There were no differences in parasitism rate between the species (Fisher's exact test,  $p = 1$ ), nor between the species within sites. One *L. pallidus* egg sac was preyed upon in the human-dominated site in the second experiment.

## Discussion

In this study, we examined two potential mechanisms for the observed differential parasitism between the invasive *L. geometricus* egg sacs and the native *L. pallidus* egg sacs: host density and habitat type. We found that density-dependent parasitism is not likely to explain the lower susceptibility of *L. geometricus* egg sacs to parasitism. In *L. pallidus*, parasitism rate increased with increasing host density, while *L. geometricus* egg sacs, with extremely dense populations, were rarely parasitized. In contrast, habitat preference may provide an explanation for the observed pattern, as both parasitism and predation of egg sacs were higher in the natural desert habitat typical for *L. pallidus*, compared to the human-dominated habitat typical to *L. geometricus*. No difference in parasitism rate was found between the species in the natural habitat. Hence, association with human-dominated habitats may contribute to the invasion success of *L. geometricus*.

Denser sites of the native species, *L. pallidus*, were more heavily parasitized by the parasitoid *P. latrodecti*, with up to 55% of egg sacs parasitized. This pattern was significant

at the field site level, but not at the individual web level, suggesting that density-dependent parasitism may differ depending on the spatial scale relevant to the parasitoid. For example, in leafhoppers, parasitism rate decreased or was not affected at by host densities at the individual leaf level, but increased with host density at the larger spatial scale of the site (Segoli 2016). Density of *L. pallidus* egg sacs also affected the number and resulting body size of emerging wasps, suggesting effects on parasitoid oviposition behavior. More wasps emerged from more isolated *L. pallidus* egg sacs, either indicating that an egg sac was parasitized by multiple females, or that a female laid more eggs in these more isolated egg sacs. This finding is consistent with foraging theory predicting that to increase overall success, a forager would stay longer in a patch when the distance between patches increase (Pyke 1984). Host density may also affect parasitoid oviposition decisions, and parasitoids are predicted to reduce host handling time and lay fewer eggs in each host if there are many available hosts (Heimpel and Casas 2008; Rosenheim and Hongkham 1996). Accordingly, studies demonstrate that parasitoids are less likely to accept, and oviposit fewer eggs per host, at high host densities, where there are many oviposition opportunities (Bezemer and Mills 2003; Samková et al. 2019).

Habitat characteristics related to human habitation may have led to the lack of parasitism, as well as lower predation rates, in the human-dominated sites. The sites in the habitat transplant experiment were residential gardens vs. desert scrub habitat three to four kilometers from human settlements. The settled sites had ornamental vegetation, water sources, and overall high arthropod abundance, yet egg sacs that were placed in these locations were not parasitized. Moura et al. (2021) found higher parasitism rate of *L. geometricus* egg sacs by *Baeus latrodecti* in an urban park in Brazil compared to both an urban area and a natural



protected area, but no difference among sites in parasitism by a parasitoid wasp (Eulophidae), which suggests that urbanization could affect different parasitoid species differently. Further research is needed to characterize factors contributing to parasitoid abundance in different habitats, such as parasitoid dispersal ability and requirement of nectar sources for adult wasps. Although habitat preference may explain low rates of parasitism in *L. geometricus*, it is not likely to explain the entire difference between species. Under lab conditions where parasitoid exposure was standardized, *L. pallidus* was still more heavily parasitized than *L. geometricus* (Mowery et al. 2022a). Defensive behaviours of female spiders, which were removed from the webs in the current habitat transplant experiment, may be another line of defense against parasitoids.

In addition to higher egg sac parasitism in natural sites, we found more predation of native *L. pallidus* egg sacs in this habitat. Predation of spider egg sacs is likely by birds, spiders (Toft and Lubin 2018), ants (Austin 1985; Fink 1987), or other arthropods. Out of the seven total missing *L. pallidus* egg sacs, two (29%) of the spider nests had holes, suggesting that some, but not all of the predators were birds, and could have been arthropods that did not damage the nests. Personal observations (M. Mowery) indicate that desert birds such as Arabian babblers remove egg sacs from widow spider nests to feed on them. Interestingly, no *L. geometricus* egg sacs were preyed upon during the experiment in either habitat, which suggests that they may not be a good food source, may not be recognized as food by predators, or may be better defended physically. There is some evidence that *Latrodectus* eggs are toxic to vertebrates (Schmidt et al. 2017), but no studies have tested toxicity when eggs were ingested nor compared toxicity between the two focal species. Predator naivete (i.e., predators not recognizing an invasive species as prey) could explain this pattern of predators selecting the native prey (Pereira et al. 2019). The light yellow color and rough, spiky surface of *L. geometricus* egg sacs could additionally camouflage the egg sacs in the nest, resulting in lower detection by predators, also noted in other spider species with multilayered egg sacs (da Ponte et al. 2021; Sethy & Ahi 2022). Higher predation of egg sacs, combined with higher parasitism, could limit the abundance of the native species, *L. pallidus*.

We found no or low levels of parasitism in high-density populations of invasive *L. geometricus* that had been established in Israel for approximately 20 years. Our findings of low parasitism are consistent with studies on newly-invasive populations of American minks and bank voles, which had fewer parasites than longer-established invasive populations (Kołodziej-Sobocińska et al. 2018; Stuart et al. 2020), lower tick abundance in urban invasive cane toad populations (DeVore et al. 2020), and lower parasitism burden in invasive vs. native populations of ladybird beetles (Comont

et al. 2014). Parasite burdens may be relatively low when a species is first introduced, and then increase with increasing establishment time. Previous research has suggested that evading natural enemies in the invasive range may result in increased invasion success and spread. For example, invasive lionfish populations were less likely to be infected with parasites, and individuals from invasive populations were larger, at higher density, and grew faster (Tuttle et al. 2017). Further studies could compare population parasitism across dated invasive populations to evaluate change over time, and measure the fitness consequences of lower parasite burden to better understand the effects of lower parasitism pressure on the invasive populations.

Urbanized environments are disproportionately suitable for generalist, highly dispersive species, such as those already successfully established in a novel environment (Kotze et al. 2011). Urban environments select for traits conducive to further invasive spread, such as thermal tolerance, dispersal ability, novelty-seeking behavior, and increased reproductive investment (Lapwong et al. 2021; Santana Marques et al. 2020). As a result, invasive species often evolve or may have pre-adapted traits enhancing successful establishment in urban areas (Borden & Flory 2021; Padayachee et al. 2017). In addition to thriving in urban areas, invasive *L. geometricus* are good aerial dispersers (Mowery et al. 2022b, c) and have high fecundity (Danielsen et al. 2014). A lower burden of parasitism and predation, despite reaching high densities, could be another advantage of this invasive species. Overall, this study suggests that lack of positive density-dependent parasitism and urban colonization could explain lower susceptibility of an invasive host to parasitoids. These factors likely increase the persistence and spread of this invasive species.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-023-05378-x>.

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**Author contribution statement** MAM, YL, and MS conceived and designed the experiments. MAM, VA, and TR performed the experiments. MAM analyzed the data and wrote the initial draft of the manuscript. All authors provided editorial comments and made contributions to the final manuscript.

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**Data availability** All data associated with this manuscript are available on the Dryad data repository at <https://doi.org/10.5061/dryad.th76hf43>.

## Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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