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# Parasitoid development and superparasitism in invasive versus native widow spider host egg sacs

**J. Alfred Daniel · Valeria Arabesky · Tamir Rozenberg · Yael Lubin · Michal Segoli · Monica A. Mowery**

**Abstract** The brown widow spider, *Latrodectus geometricus*, is a hazardous and highly invasive species globally. One of the suggested mechanisms enhancing this spider's invasiveness is lower susceptibility to natural enemies compared to other widow species. The parasitoid wasp, *Philolema latrodecti*, is known to attack egg sacs of *L. geometricus*, as well as those of other species of *Latrodectus*. Despite its potential importance as a natural enemy of *L. geometricus*, little is known about the development of this wasp and factors mediating its parasitism success. We investigated the development of this parasitoid in two widow spider host species, one native to Israel, the white widow, *L. pallidus*, and the invasive brown widow, *L. geometricus*. We compared wasp developmental success in egg sacs exposed to increasing wasp densities. We found increased wasp emergence and brood size, and smaller emerging wasp body size with increasing wasp density. Across all wasp densities, more and larger parasitoids developed in the egg sacs of the native host species, *L. pallidus*, compared to the invasive host species, *L. geometricus*. Parasitoid sex ratio was highly female-biased and the proportion of males increased with wasp density, suggesting local mate competition. Overall, our results suggest that *L. pallidus* is a better host for the egg sac parasitoid *P. latrodecti*, which could give a competitive advantage to the less-affected invasive brown widow spider.

**Keywords** Spider · *Latrodectus* · Parasitoid · Superparasitism · Development · Density

## Introduction

Globalization and international trade increase transport and establishment of alien species to new environments (Holden et al. 2022; Hulme 2009; Parepa et al. 2013). Ecological and evolutionary hypotheses focused on invasive species traits have been proposed to explain invasion success, including high fecundity, high dispersal rate and high competitiveness of the invasive species (Abhilasha and Joshi 2009; Callaway and Ridenour 2004; Moravcová et al. 2015; Rehage and Sih 2004). In addition, interactions with natural enemies such as predators, parasites, and parasitoids may play a crucial role in the determining ability of a species to invade (Elton 1958; Heimpel and Mills 2017; Newsome and Noble 1986; Ricklefs and Cox 1978; White and Perkins 2012). Invasive species may have traits that lower their susceptibility to parasitism

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throughout their distribution. For example, the invasive harlequin ladybird beetle has chemical defenses that make the species unpalatable to predators and defend against infection (Ceryngier et al. 2018). Regardless of the mechanisms involved, lower susceptibility to parasites may give an invasive species a relative advantage over native species. Hence, comparing parasitism success on invasive versus native species can contribute to understanding the mechanisms of successful invasive establishment.

Studies of invasive species are biased towards relatively few taxonomic groups, which can affect our understanding of invasion mechanisms and success. Over 60% of studies focus on insects and plants (Pysek et al. 2008), while other groups are understudied. Studies related to invasive spiders have only recently started to attract scientific attention (Campbell et al. 2020; Mowery et al. 2021; Narimanov et al. 2021; Nentwig 2015), despite high prevalence both in agricultural (Hogg and Daane 2010) and natural habitats (Pétillon et al. 2020) and their essential role as generalist predators (Birkhofer et al. 2017; Michalko et al. 2019). Parasitoids are common and important predators of spiders at all life stages, including the egg sacs (Fei et al. 2023). Egg sac parasitoids may find hosts using species-specific spider silk cues, such as in a parasitoid of linyphiid spider egg sacs (van Baarlen et al. 1996). Spider egg sacs may differ in their quality for the parasitoid. For example, larger spider host egg sac mass was found to increase resulting parasitoid offspring body size (Morse 1994). Yet, we lack direct comparisons of predation and parasitism in congeneric invasive and native spider hosts (Snyder and Evans 2006).

The brown widow spider, *L. geometricus*, is an invasive species worldwide, in some cases outcompeting native species and threatening human health, as its bite can cause a serious reaction requiring hospitalization (Goddard et al. 2008; Marie and Vetter 2015; Muller 1993). One of the main natural enemies of widow spiders, including the brown widow, is the gregarious parasitoid wasp *P. latrodecti* (Eurytomidae, Hymenoptera). A single wasp will lay a clutch of eggs inside the spider's egg sac, and multiple wasps emerge after consuming all the spider eggs, thereby completing their development inside the egg sac. It has been suggested that the brown widow spider is less susceptible to egg sac parasitism due to the occurrence of silk spike-like structures produced by the female spider on the surface of its egg sac (Vetter et al. 2012). Consistent with this idea, previous studies found lower parasitism rates on egg sacs of the invasive brown widow compared to native widow spider species in both field and lab settings (Mowery et al. 2022; Triana et al. 2012; Vetter et al. 2012). However, despite its potential ecological importance, very little is known about the development of this parasitoid inside the spider egg sac and on factors mediating its success.

The suitability and quality of hosts to parasitoids are often tested under unrealistic conditions, where a single host is exposed to a single parasitoid. In nature, when parasitoid density is high, several females may compete for a host, with more than one female parasitizing the same host individual (termed super-parasitism), thus reducing resource availability for the developing offspring (Godfray 1994; Van Alphen and Visser 1990). The outcome of super-parasitism may depend on the host species and quality, as well as on the relative timing of multiple ovipositions and the rate of depletion of resources inside of the host egg sac. Measuring successful development and rates of developmental failure may provide insight into the effects of superparasitism on parasitoid development (Keasar et al. 2006). However, to our knowledge, no studies have considered the effects of intraspecific competition and super-parasitism in invasive versus native hosts.

In this study, we first describe the development of *P. latrodecti* in widow spider egg sacs. This is one of few descriptions of the development of an egg sac parasitoid in general. We compared parasitism success in egg sacs of two widow spider host species, one native to Israel, the white widow, *L. pallidus* (Levy and Amitai 1983), and the invasive brown widow, *L. geometricus*, following exposure to an increasing number of parasitoid wasps (from one to four female wasps) under controlled conditions. We also measured parasitoid fecundity before and after feeding on honey to assess the potential for egg depletion, which could affect the number of eggs laid in the host. We predicted that parasitism success and brood size would increase with the number of parasitizing wasps up to a threshold, after which it could level off or even decrease. This may occur if female wasps interfere with one another preventing oviposition, or if the larvae compete for resources inside the host, preventing some of the parasitoids from completing

their development (Hassell and Waage 1984; Van Alphen and Visser 1990). In addition, we predicted lower development success of the parasitoid on the egg sacs of the invasive *L. geometricus*. This prediction was based on the presumably better egg sac defences of *L. geometricus*, as well as on the smaller size of their egg sacs, which contain fewer spider eggs on average than *L. pallidus* egg sacs (Danielsen et al. 2014; Levy and Amitai 1983; Mowery et al. 2022). Female parasitoids adjust their offspring sex ratios based on host quality (Charnov 1982; Godfray 1994; King 1987) and conditions of superparasitism (Shuker et al. 2005). Evidence of varying sex ratios may also shed light on the wasp mating system (Werren 1983). We have compared the sex ratio of wasps emerging out of egg sacs of the two host species and at increasing parasitoid densities, and predicted proportionately more males in lower-quality *L. geometricus* and superparasitized hosts,

## Methods

### Spider and wasp rearing

We kept field-collected adult female *L. geometricus* and *L. pallidus* in laboratory conditions (25 ± 1 °C, 14:10 L:D). Females were fed weekly with one grasshopper nymph (*Schistocerca gregaria*). Spider egg sacs used in all experiments were less than seven days old. Wasps for the experiments emerged from *L. pallidus* spider egg sacs collected in the field (Hatzerim and Beer Sheva area, Israel). We fed wasps with honey immediately after emergence.

### Development of *P. latrodecti* in *L. geometricus* egg sacs

We exposed egg sacs (n = 12) of *L. geometricus* each to a single *P. latrodecti* parasitoid female in a plastic vial. We then incubated the egg sacs under controlled conditions (25 ± 1 °C, 14:10 L:D). On days one, three, five, 10, 15, and 20 post-parasitism, we dissected two parasitized egg sacs each day and photographed and recorded parasitoid development using a Nikon stereomicroscope (SMZ-18) with a Nikon digital camera (DS-FI2).

### Wasp density

We observed the effect of the presence of multiple parasitoid wasps on the outcome of parasitism in *L. geometricus* and *L. pallidus* egg sacs by exposing the egg sacs to one (*L.g.:* N = 69, *L.p.:* N = 26), two (*L.g.:* N = 33, *L.p.:* N = 30), three (*L.g.:* N = 37, *Lp:* N = 17), or four (*L.g.:* N = 35, *Lp:* N = 17) parasitoid females simultaneously. The sample size for each treatment was determined by the availability of fresh egg sacs (less than one week old) and wasps. Female wasps normally survived for few days under these conditions. After two months, we recorded the contents of each egg sac as: adult wasps that emerged; adult wasps that developed but did not successfully emerge; underdeveloped wasps; unhatched spider eggs; or emerged spiderlings. In egg sacs from which wasps emerged, we counted the total number of emerging wasps. Using a Nikon stereomicroscope and digital camera (see above), we photographed and measured the body length of a sample of 10 females and up to 10 males (depending on availability) per egg sac. We measured wasp body length from the anterior of the prosoma to the posterior of the metasoma using NIS-Elements D software. We recorded the sex ratio of wasps emerging from each egg sac, differentiating between males and females according to their metasomal size and shape, their funicular pubescence and presence or absence of an ovipositor (Burks 1971). Sex ratio was calculated as the number of adult males divided by the total number of adult offspring in the egg sac.

### *P. latrodecti* fecundity

We dissected newly emerged, unfed adult female *P. latrodecti* wasps (n = 25) under a Nikon stereomicroscope on the day of their emergence and counted the number of eggs in their ovaries. We noted the size distribution of eggs of each female to assess the occurrence of immature eggs. To determine whether females mature more eggs following emergence, we fed wasps with honey solution and after three days, dissected them (n = 20) and counted their eggs.

### Statistical methods

All analyses were conducted in R (version 4.0.2, R Core Team 2023). To compare measures of parasitism

development, we first compared rates of failed para-
sitoid development in the two species' egg sacs using
Fisher's exact test. We then compared parasitism emer-
gence success from *L. geometricus* and *L. pallidus* egg
sacs exposed to 1–4 wasps using a Generalized Linear
Model (GLM) with successful parasitoid emergence as
the binary response variable (yes or no), and species
and wasp density as well as the interaction between
them as predictors, with a binomial distribution and
a logit link function in R (lme4; R Studio, Inc, Bates
et al. 2015). We compared the total number of wasps
emerging from the egg sacs of each spider species and
at each wasp density using a generalized linear model
with the number of wasps emerging as the response
variable, modelled with a quasi-Poisson error distri-
bution due to overdispersion, and wasp density, spider
species, and the interaction between wasp density and
spider species as predictors. In cases where data were
found to be overdispersed based on a dispersion param-
eter greater than one, quasi-models were used.

To compare body size of emerging wasps we con-
structed a generalized linear mixed model (GLMM)
with wasp density treatment and spider species as
fixed factors, the body size of female wasps (up to ten
per egg sac) as response variables, egg sac ID as a ran-
dom factor, and a Gamma error distribution with a log
link function. For comparing sex ratio (males/total off-
spring) among wasp density treatments and host spe-
cies, we used a GLMM with sex ratio as a binomial
outcome, with egg sac ID as a random factor. To assess
the effect of brood size on emerging female wasp body
length, we used a GLMM with wasp body size as the
response variable with a Gamma distribution and log
link function, species and brood size as the predictors,
with egg sac ID as a random factor. Parameters and sig-
nificance were calculated using Wald F tests for GLMs
and Chi-squared testes for GLMMs (*car* package, Fox
and Weisberg 2019), and multiple comparisons were
conducted using Tukey HSD post-hoc tests using the
*multcomp* package (Hothorn et al. 2022) in R. To com-
pare female egg load before and after feeding, we used
a two-tailed t-test.

## Results

### Development of *P. latrodecti* in *L. geometricus*

The different developmental stages of *P. latrodecti* are
presented in Fig. 1. After one day, *P. latrodecti* eggs
were found next to the spider eggs, close to the inner
surface of the egg sac. *P. latrodecti* eggs hatched after
two to three days inside of the egg sac. The larvae fed
on the content of *L. geometricus* spider eggs, leaving
empty spider egg shells, pupated by 15 days after ovi-
position, and emerged after 20 days of development
inside of the spider egg sac after depleting all spider
eggs.

### Wasp density and host species

Increasing wasp density resulted in an increasing pro-
portion of egg sacs in which parasitoids successfully
emerged (Fig. 2a, GLM, $F_{1,324} = 13.138$, $P < 0.001$),
with no significant effects of host species egg sac
($F_{1,324} = 0.0005$, $P = 0.982$) or the interaction between
wasp density and host species ($F_{1,324} = 1.181$,
$P = 0.278$). In particular, wasps were more likely
to emerge from egg sacs exposed to three and four
wasps compared to those exposed to a single wasp
(Tukey HSD, three wasps: $z = 2.874$, $P = 0.024$; four
wasps: $z = 2.985$, $P = 0.017$). In most cases where
wasps did not emerge, spiderlings emerged out of the
egg sac, suggesting that no parasitism occurred. How-
ever, in a few cases, we found evidence that the wasps
failed to complete their development or to emerge
out of the egg sac. This occurred in 7 out of 107 *L.
geometricus* egg sacs and in one out of 65 *L. palli-
dus* egg sacs (Fisher's exact test $P = 0.261$) and only
occurred in cases where the egg sac was exposed to
more than one wasp. However, the number of cases in
which parasitoids were undeveloped may have been
too low to detect differences among species. In a few
cases, we observed behavioral interactions between
wasps such as jumping off the egg sac following
contact with another wasp that may have resulted in
interference in oviposition.

More wasps emerged with increasing wasp den-
sity (Fig. 2b, GLM, $F_{1,133} = 20.825$, $P < 0.001$) and
from *L. pallidus* egg sacs compared to *L. geomet-
ricus* egg sacs ($F_{1,133} = 11.023$, $P = 0.001$), with
no significant interaction between wasp density
and host species ($F_{1,133} = 0.280$, $P = 0.597$). More

**Fig. 1** Development of *Philolema latrodecti* in egg sacs of *Latrodectus geometricus* observed on days one (**a**, egg), three (**b**, larva), five (**c**, larva), 10 (**d**, larva), 15 (**e**, pupa), and 20 (**f**, adult wasp) after *P. latrodecti* female oviposition
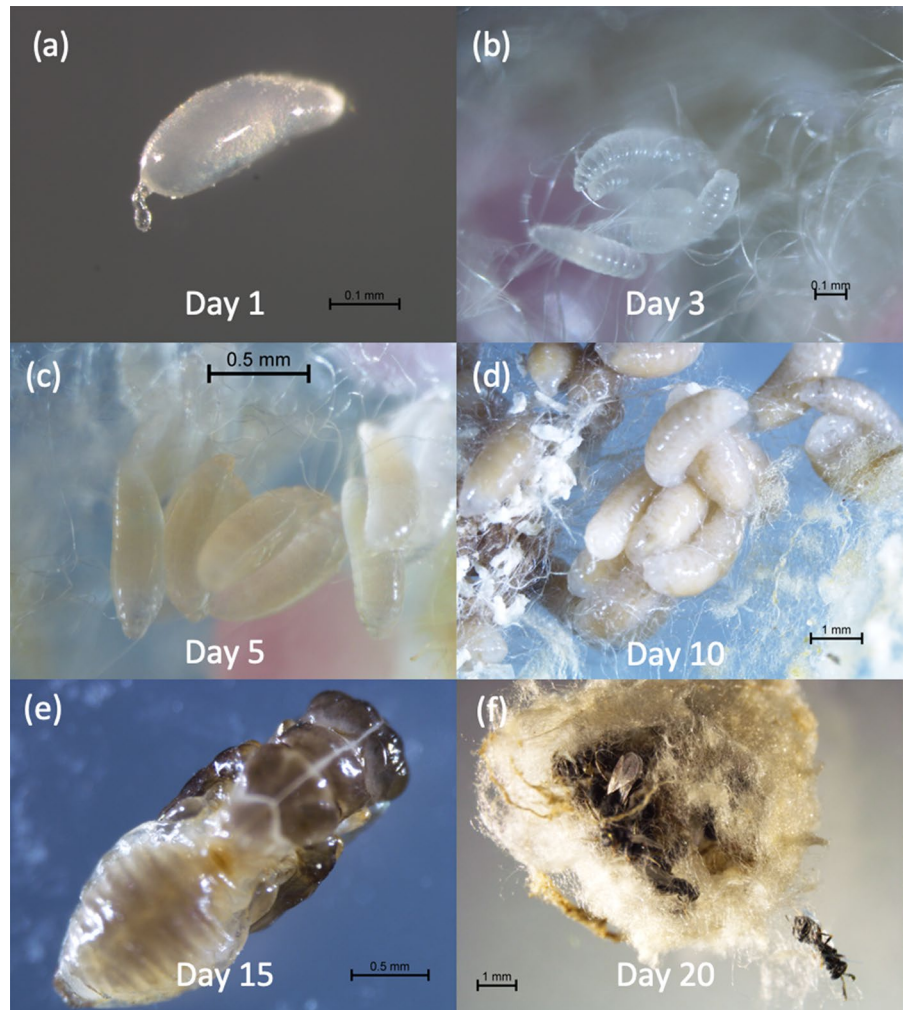


wasps emerged from egg sacs exposed to more than one wasp than from the the single wasp exposure (Tukey HSD, one-two wasps: $z = 3.970$, $P < 0.001$; one-three wasps, $z = 2.568$, $P = 0.059$; one-four wasps: $z = 5.189$, $P < 0.001$). Larger female wasps emerged from *L. pallidus* egg sacs (Fig. 3a, GLMM, $X^2_1 = 19.520$, $P < 0.001$) and from egg sacs exposed to lower wasp densities ($X^2_1 = 13.654$, $P < 0.001$), with no interaction between host species and wasp density ($X^2_1 = 0.009$, $P = 0.925$). We found a negative relationship between emerging wasp brood size and body size (Fig. 3b). Mean female wasp body size decreased with increasing brood size in both host species (GLMM, $X^2_1 = 69.101$, $P < 0.001$), and wasps were consistently larger when developing in *L. pallidus* egg sacs ($X^2_1 = 41.423$, $P < 0.001$), with

no significant interaction between brood size and host species ($X^2_1 = 2.526$, $P = 0.112$).

Wasp density also affected the resulting sex ratio of the wasps emerging. Sex ratio was generally female biased. The proportion of males increased with increasing wasp density (Fig. 4, quasi-binomial GLM, $F_{1,126} = 76.728$, $P < 0.001$), but was not affected by the host species ($F_{1,126} = 0.911$, $P = 0.342$), nor was there an interaction between wasp density and host species ($F_{1,126} = 0.070$, $P = 0.791$).

### *P. latrodecti* fecundity

All eggs from dissected *P. latrodecti* females were similarly shaped and sized, suggesting that they were already mature upon wasp emergence. The
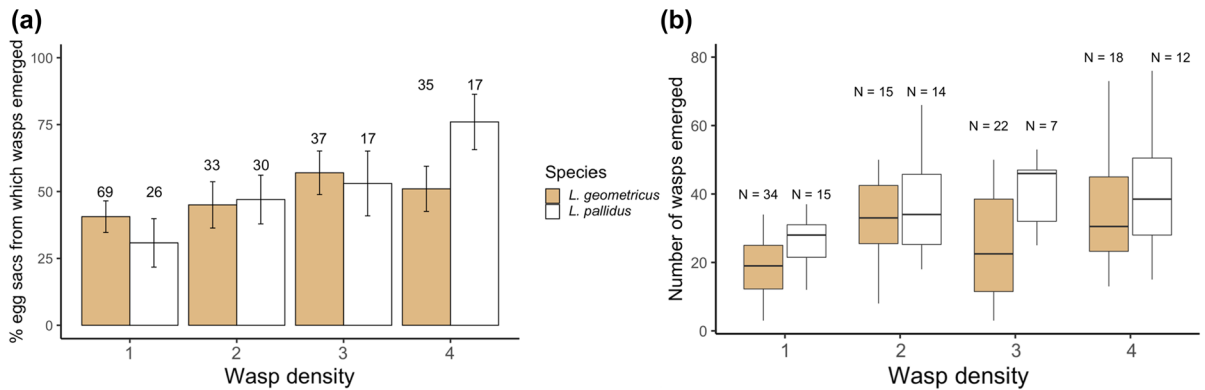
**(a)**



**(b)**



**Fig. 2** **a** Parasitoid wasp (*P. latrodecti*) emergence success from *L. geometricus* egg sacs (brown bars) and *L. pallidus* (white bars) exposed to one, two, three, and four parasitoid wasps. Error bars are standard errors calculated for the proportions. **b** Number of parasitoid wasps emerged after exposure of *L. pallidus* egg sacs (white) and *L. geometricus* egg sacs (brown) to one, two, three, and four *P. latrodecti* females. Samples sizes indicate total number of egg sacs in each treatment. Boxplots show median and 25th and 75th percentiles. The whiskers on the plots indicate values within 1.5 times the interquartile range, and the outliers are indicated with black points
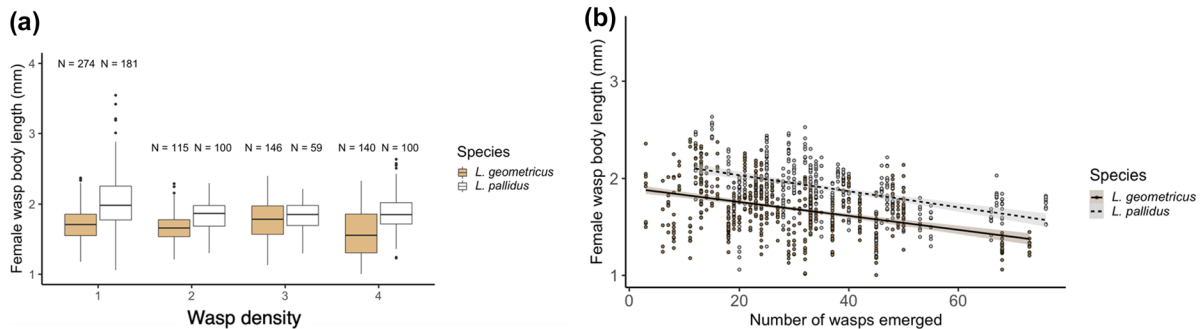
**(a)**



**(b)**



**Fig. 3** **a** Female parasitoid wasp body size in *L. geometricus* (brown) and *L. pallidus* egg sacs (white) after parasitism by one to four *P. latrodecti* females. Boxplots show median and 25th and 75th percentiles. The whiskers on the plots indicate values within 1.5 times the interquartile range, and the outliers are indicated with black points. **b** Parasitoid *P. latrodecti* brood size and female parasitoid body size in parasitoids that developed in *L. geometricus* (brown) and *L. pallidus* (white) egg sacs

mean number of *P. latrodecti* eggs before feeding was $39 \pm 1.6$ eggs (mean $\pm$ SE; n = 25), and was not significantly different from the number of eggs in females dissected three days after feeding ($40 \pm 2.2$, mean $\pm$ SE; n = 20 fed females, t = 0.518, P = 0.608).

## Discussion

We compared measures of parasitism success of the egg sac parasitoid wasp *P. latrodecti* at increasing parasitoid densities between two host species: the globally invasive brown widow spider *L. geometricus*, and the white widow spider *L. pallidus*, native to Israel. We found evidence for increased parasitism success (wasp emergence) with increasing wasp density, and some evidence that the invasive species is an inferior host, as more and larger wasps emerged from native *L. pallidus* compared to *L. geometricus* egg sacs. These, combined with previous results (Mowery et al. 2022), suggest the lower susceptibility and suitability of *L. geometricus* to parasitism, potentially contributing to the invasion success of this species.

**Fig. 4** Parasitoid wasp sex ratio (proportion of males out of all emerging offspring) in *L. geometricus* (brown) and *L. pallidus* host egg sacs (white) after parasitism by one to four *P. latrodecti* adult female wasps. Boxplots show median and 25th and 75th percentiles. The whiskers on the plots indicate values within 1.5 times the interquartile range, and the outliers are indicated with black points
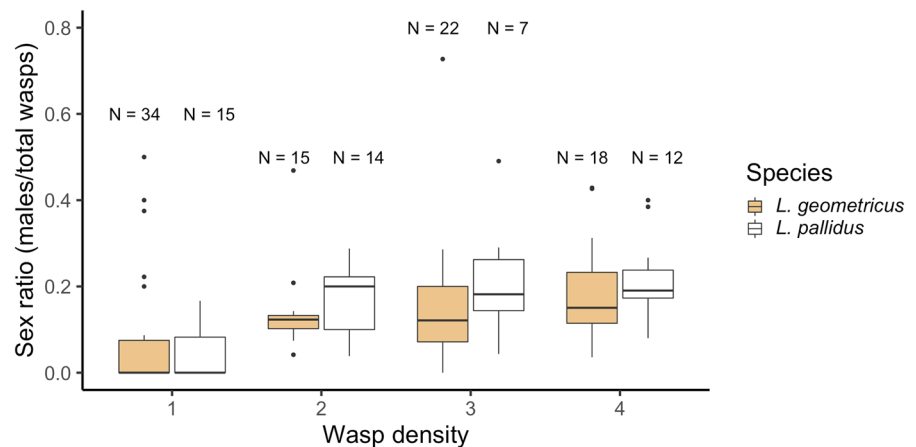


Greater parasitism success with greater wasp density was observed in previous studies (Gu and Dorn 2003; Khafagi and Hegazi 2008; Silva-Torres et al. 2009). In our study, however, succesful parasitism rate did not increase proportionally with wasp density, and differed mainly between the single versus multiple wasp treatments. A possible reason could be interference competition between wasps at higher densities that prevented females from laying their eggs. Direct interference between ovipositing females was observed in many parasitoid species (including our observations of *P. latrodecti*, current study) that could reduce parasitism success (Boivin and Martel 2012; Grenier et al. 2001; Huang et al. 2017). Failed parasitism could also result from intense resource competition of larvae within the host, causing parasitoid brood death. Indeed, in some cases we found dead immature wasps, or wasps that failed to emerge, inside the egg sacs. These cases of failed emergence occurred only when the egg sac was exposed to multiple wasps, and mostly in the smaller *L. geometricus* egg sacs, and could be related to extreme resource shortage within the host (Harvey et al. 2013; Wajnberg et al. 1990).

We found an increasing number of offspring emerging from egg sacs that were exposed to several wasps, compared to a single wasp, which suggests the occurrence of multiple parasitism events inside a single host (*i.e.*, super-parasitism, (Dorn and Beckage 2007; Roitberg et al. 1992; Van Alphen and Visser 1990). However, similarly to parasitism success, brood size did not increase proportionally with wasp density. In addition, parasitoid brood size in *L. geometricus* egg sacs was smaller than in *L. pallidus*

egg sacs. These observed patterns were probably at least partially due to fewer eggs laid per female wasp at higher wasp densities (Harvey 2000; Le Masurier 1991; West et al. 2001; Zaviezo and Mills 2000), and on the inferior host (Barrett and Schmidt 1991), but could also be due to lower survival of the developing wasps within the host due to resource shortage (Godfray 1994; Harvey 2005; Mackauer et al. 1997; Vinson and Iwantsch 1980). In the current experiment, we could not distinguish between these two options, since it is impossible to count wasp eggs laid inside the host without interfering with their development.

Results on wasp body size further supported the occurrence of resource shortage within the host. The body size of emerging females was smaller when developing in egg sacs exposed to multiple wasps, and in those developing on the inferior host *L. geometricus* compared to *L. pallidus*. This is in accordance with many studies suggesting that host quality affects parasitoids' adult size (Farahani and Goldansaz 2013; Godfray 1994). Moreover, wasp body size was negatively affected by brood size in both species, suggesting a trade-off between the number and size of offspring, as observed in other parasitoids (Gu and Dorn 2003; Hardy 1992; Takagi 1987).

Despite the lack of alternatives hosts in our experiment, females did not seem to lay all of their eggs in a single host, even in the absence of competition. This is inferred by the smaller number of wasps emerging from host exposed to a single female (20–30), compared to the mean egg load of females (~ 40). In addition, in another experiment, we dissected females soon after they oviposited in the host, and found that usually eggs were still available in their reproductive

tract (A. D. Johnson, unpublished data). The wasps may be adapted to spread their eggs among several hosts as a bet-hedging strategy (Cronin and Strong 1993; Hopper 1999), or to optimize their lifetime reproductive success (Bezemer and Mills 2003; Sevenster et al. 1998). Future studies should characterize clutch size decisions of these parasitoids when foraging freely in nature and while searching for native or invasive hosts.

Parasitoid sex ratio was highly female-biased in both host species. Although little is known about the mating behavior of these wasps, a skewed sex ratio suggests that mating in this species occurs locally inducing local mate competition between related males (Hamilton 1967; Werren 1980). Personal observations of *P. latrodecti* matings soon after emergence are consistent with this interpretation, although it should be considered that in our experimental set-up, dispersing away from the natal host was not possible. The observed increase in sex ratio with the increasing number of competing females is also consistent with the predictions of local mate competition theory, as well as with empirical evidence for increased sex ratio when the number of female founders in a patch increases (Hardy 1994; Herre 1987). However, even at a high wasp density sex ratio remained highly female-biased (~20% males), suggesting the potential occurrence of additional mechanisms that might favor a biased sex ratio, such as high relatedness between ovipositing females (Herre 1985).

We provide one of the first descriptions of wasp development inside a spider egg sac. Other studies reported the occurrence of egg sac parasitism in different spider species (Austin 1985; Bowden and Buddle 2012; Cobb and Cobb 2004; Finch 2005) including *L. geometricus* (Marie and Vetter 2015; Moura et al. 2021; Vetter et al. 2012), but none observed the developmental sequence from egg, throughout the different larval stages, to the pupal and adult stage. Our observations suggest that the eggs are laid close to the egg sac surface, and that the larvae hatch soon after egg laying and grow while consuming the contents of the spider eggs, almost always depleting the eggs (in very few cases we observed the emergence of both spiderlings and wasps). As the number of wasps emerging from an egg sac (3–76 wasps in our study) is lower than the number of spider eggs in a egg sacs of either species (100–300 eggs, Levy and Amitai 1983), each wasp must feed on multiple eggs during

its development. Egg sac parasitoids are sometimes considered predators rather than parasitoids as they feed on several prey items during their lifetime (Eggleton and Belshaw 1992; Eggleton and Gaston 1990; Strand and Obrycki 1996). However, given the phylogenetic background, and the life cycle of this wasp, we think it is more reasonable to consider it a parasitoid (Cobb and Cobb 2004; Fei et al. 2023), with the whole egg sac, rather than a single egg, as a host.

To our knowledge, rarely have parasitism and predation been compared in native versus invasive spiders. One example involves a North American dwarf spider, *Mermessus trilobatus*, that has undergone a range expansion in Europe, spreading by more than 1000 km in less than 50 years (Hirna 2017; Schmidt et al. 2008). This invasion success was once thought to be attributed to reduced susceptibility to native predators of *M. trilobatus* in Europe. However, when Narimanov et al. (2021) compared the susceptibility of the invasive *M. trilobatus* and a native *Erigone dentipalpis* (Araneae: Linyphiidae) to a shared native predator, they found that the invasive species was consumed almost three times as often as the native species. In contrast, in stink bugs, invasive hosts were accepted equally by parasitoids compared to a native species, but there was no successful development in the invasive host (Abram et al. 2014). Parasitism can result in significant declines in native host populations (Abram et al. 2020), and thus could increase successful establishment of an invasive species that is not highly parasitized. Our study supports the notion of lower suitability and susceptibility of the invasive *L. geometricus* to parasitism under varying environmental conditions, either due to their smaller size, better defenses, or other aspects that were not measured here, which may potentially promote this species' invasion success. Such knowledge enhances our understanding of biological invasions and may help better manage species invasions.

**Data availability** All data associated with this manuscript are available on the Dryad data repository at https://doi.org/10.5061/dryad.tb2rbp053

## Declarations

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

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