The 'Goldilocks Grub': reproductive responses to leafroller host development in *Goniozus jacintae*, a parasitoid of the light brown apple moth

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Abstract

Many parasitoids alter their reproductive behaviour in response to the quality of encountered hosts. They make adaptive decisions concerning whether to parasitise a potential host, the number of eggs laid on an accepted host, and the allocation of sex to their offspring. Here we present evidence that *Goniozus jacintae* Farrugia (Hymenoptera: Bethylidae), a gregarious ectoparasitoid of larval tortricids, adjusts its reproductive response to the size and developmental stage of larvae of the light brown apple moth (LBAM), *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae). *Goniozus jacintae* parasitises instars 3–6 of LBAM, but most readily parasitises the later, larger, instars. Brood sizes were bigger on larger hosts and brood sex ratios were female biased (proportion of males = 0.23) with extremely low variance (never >1 male in a brood at emergence), perhaps the most precise of all studied bethylids. Host size did not influence brood development time, which averaged 19.64 days, or the body size of male offspring. However, the size of females was positively correlated with host size and negatively correlated with brood size. The sizes of individual males and females were positively related to the average amount of host resource available to individuals within each brood, suggesting that adult body size is affected by scramble competition among feeding larvae. Average brood sizes were: 3rd instar host, 1.3 (SE ± 0.075); 4th instar, 2.8 (SE ± 0.18); 5th instar, 4.7 (SE ± 0.23); 6th instar, 5.4 (SE ± 0.28). The largest brood size observed was 8 individuals (7 females, 1 male) on the 6th instar of LBAM. These results suggest that later instars would give the highest yield to optimise mass-rearing of *G. jacintae* if used for augmentative biological pest control.

Introduction

Upon finding a potential host, female hymenopteran parasitoids typically assess the quality of the host for offspring development (Rehman and Powell, 2010; Hajek and Eilenberg, 2018) and make oviposition decisions in response to host condition (Visser *et al.*, 1990; Hardy *et al.*, 1992; Godfray, 1994; Bezemer and Mills, 2003; Ayala *et al.*, 2018; Li *et al.*, 2019). These oviposition decisions include the number of eggs laid (Godfray, 1987, 1994), and the allocation of sex to offspring (West, 2009). Size-dependent selection of hosts is common in parasitoids, since the size of a host is often positively correlated with host quality via the quantity of resources available to offspring (Charnov and Skinner, 1984; Godfray, 1994; Goubault *et al.*, 2004; Rehman and Powell, 2010), which influences how many progeny can be supported per host. In general, females are selected to lay a clutch size that maximises their gain in fitness across all hosts they expect to find during their lifetime (Godfray *et al.*, 1991). In terms of sex allocation, mated haplo-diploid hymenopteran parasitoids are able to control whether their eggs remain unfertilised or become fertilised, developing into males or females, respectively (Godfray, 1994; Quicke, 1997). Understanding the reproductive strategies of parasitoids can be important for the successful implementation of biological pest control programmes, as these directly influence the number of female offspring recruited into each generation, and therefore, the degree to which target pest populations are likely to be suppressed (Hassell, 2000; Ode and Hardy, 2008).

Here we report on the responses of *Goniozus jacintae* Farrugia (Hymenoptera: Bethylidae) to the size and developmental stages of larvae of the light brown apple moth (LBAM), *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) (Danthanarayana, 1980; Aspin *et al.*, 2021). This moth feeds on a wide range of crops and other plants (Suckling and Brockerhoff, 2010), and is the most damaging insect pest of grapevines in Australia (Scholefield and Morison, 2010). Despite the common occurrence of *G. jacintae* (fig. 1a) as a beneficial insect, there is surprisingly little knowledge of its efficacy as a biological control
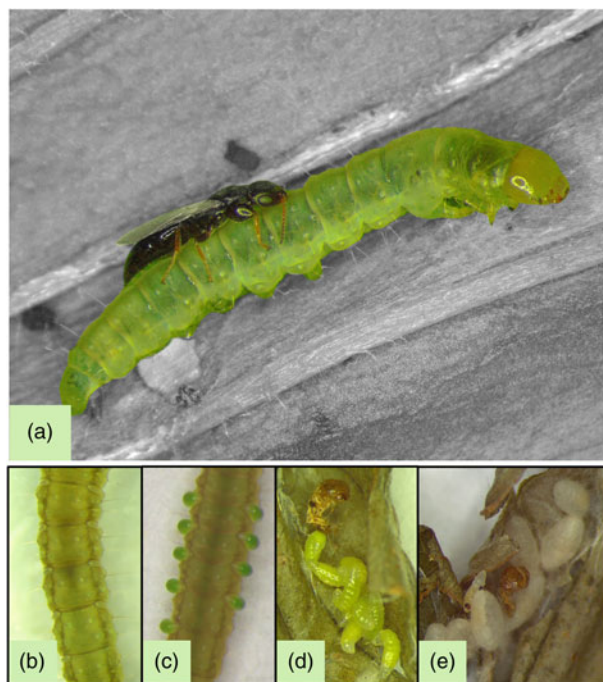
Figure 1. Development of *G. jacintae* on light brown apple moth. Successive stages of development of a brood of *G. jacintae* on *E. postvittana*: (a) Host encounter: female *G. jacintae* on a paralysed 6th instar LBAM larva on a plantain leaf, (b) Day 1: eggs of *G. jacintae* laid on host's integument, (c) Day 6: larvae of *G. jacintae*, (d) Day 8: late instar larvae of *G. jacintae* and the head capsule of the consumed host, (e) Day 10: pupating larvae of *G. jacintae* inside their silken cocoons. Photo (A) has had the background changed to greyscale for clarity; the original leaf colour is green.

agent for LBAM (Danthanarayana, 1980; Paull and Austin, 2006) and limited information on its reproductive biology (Danthanarayana, 1980; Hopper and Mills, 2015). A recent study of *G. jacintae* foraging behaviour found that females have a stronger foraging response to larger hosts, which have a higher rate of feeding and produce more feeding damage (Aspin *et al.*, 2021). This is consistent with reports of other species of *Goniozus*, that have a greater reproductive success when attacking larger hosts (Hardy *et al.*, 1992; Luft, 1993; Abdi *et al.*, 2020).

The Bethylidae is a cosmopolitan family of ectoparasitoid wasps, containing over 2000 described species within around 100 genera (Gordh and Móczár, 1990). Their hosts are predominantly coleopteran or lepidopteran larvae that often live in cryptic locations, such as seed-borers and leafrollers (Evans, 1978; Mayhew and Hardy, 1998). However, some bethylid species are reported to attack hosts in the pupal stage (Pérez-Lachaud *et al.*, 2004) and even hosts from other insect orders (Zhang *et al.*, 1984). Bethylid species have been used in research on the evolution of key life history traits, such as clutch size, sex allocation and sociality (Hardy *et al.*, 1992; Mayhew and Hardy, 1998; Goubault *et al.*, 2007; Khidr *et al.*, 2013; Abdi *et al.*, 2020; Guo *et al.*, 2022, 2023; Malabusini *et al.*, 2022). Further, as many bethylid species utilise hosts that are pests of agriculturally important products, multiple species have been deployed, or considered as, biological control agents across a wide range of agro-ecosystems (Legner and Gordh, 1992; Batchelor *et al.*, 2006; Shameer *et al.*, 2018; Polaszek *et al.*, 2019).

Goniozus jacintae readily parasitizes larval instars 3 to 6 of LBAM (Danthanarayana, 1980; Aspin *et al.*, 2021). We thus investigated whether its reproductive behaviour varies according

to host size and instar, first establishing whether host head capsule size or host weight better represents host size. Our ultimate aim was to provide a broader understanding of bethylid reproduction that could elucidate the potential of *G. jacintae* to control LBAM in the field. Information from this study will further contribute to the growing collection of other agro-ecosystems using species of *Goniozus* and other bethylids as agents of biological pest control (Legner and Gordh, 1992; Baker, 1999; Batchelor *et al.*, 2006; Shameer *et al.*, 2018; Polaszek *et al.*, 2019) and assist the increase in efficacy of mass-rearing bethylid parasitoids in the laboratory.

Materials and methods

Host rearing

The culture of *Epiphyas postvittana* (LBAM) used in this experiment was established at the South Australian Research and Development Institute in 1994 and has since been maintained with annual additions of wild-caught moths. LBAM was reared on an artificial diet at $22 \pm 2°C$ under 12L:12D photoperiod, following methods reported in Yazdani *et al.* (2015).

Parasitoid rearing

A culture of *G. jacintae* was established from individuals reared from parasitized LBAM that were collected in vineyards at McLaren Vale, South Australia in 2017. The wasp culture was reared at $23 \pm 2°C$, 14L:10D in cages on larval LBAM that infested plantain, *Plantago lanceolata* L. (Lamiales: Plantaginaceae). Adult wasps were provided with water and honey *ad libitum*. Wasp cocoons were isolated in 50 mm × 18 mm diam. glass vials containing a drop of honey and fitted with caps that had screens for ventilation. Upon emergence, females were caged serially, 2–5 at a time, with 5 males to allow mating, and then re-isolated and held in vials for at least 1 h before being used in experiments.

Parasitoid reproduction

One hundred and sixty female *G. jacintae* were individually presented with one 4th instar LBAM larva feeding on a plantain leaf in a 50 mm × 18 mm diam. glass vial for 1 h so that they may have obtained oviposition experience prior to the experiment. The 4th instar was chosen as it represented the mean size of LBAM larvae, and according to Danthanarayana (1980), are the most predominantly parasitized instar by *G. jacintae*. Following this, each wasp was presented with a single host of known instar (3rd–6th), head capsule width and weight in a fresh glass vial. Once host attack was observed, the vial was left for 2 h to allow for oviposition behaviour to occur.

After oviposition, the female parasitoid was removed and the host and parasitoid clutch were maintained at at $22 \pm 2°C$ under 12L:12D photoperiod until brood emergence. Upon emergence of the adult parasitoids, the following measurements were recorded: brood size (= number of adult offspring), sex ratio (= proportion of offspring that were males), time from oviposition to adult eclosion (= developmental time) and length of thorax (an indicator of parasitoid body size).

Host size may be measured in several ways, including weight and head capsule width, and both may correlate with host instar. We took both measurements for LBAM larvae of each instar used in this experiment (3rd–6th), including the head capsule measures sizes for the 6th instar which have not been reported
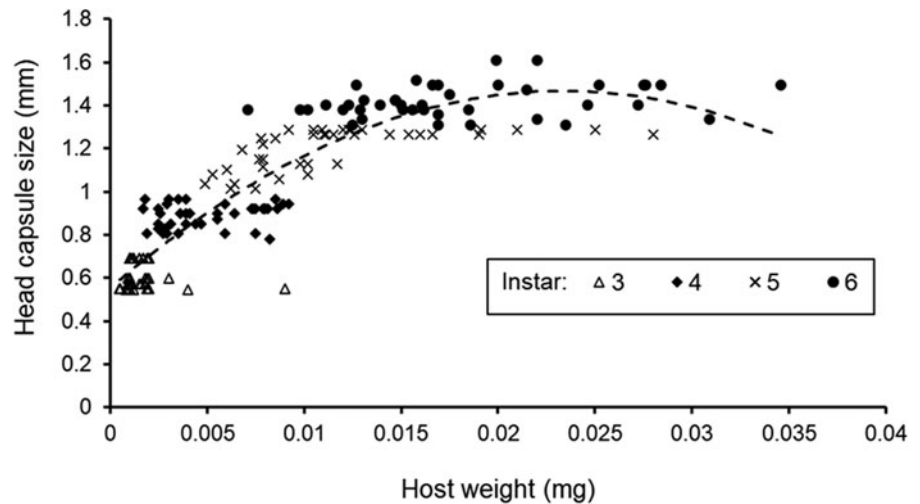
Figure 2. The relationship between head capsule size and weight of *E. postvittana*.

previously (Yazdani *et al.*, 2014). Head capsule width was measured under a dissecting microscope at a magnification of $40 \times$ with a calibrated ocular micrometre (precision ± 0.0125 mm). Host weight was measured using an A&D HR-250AZ analytical balance with a 0.1 mg resolution (A&D Company, Limited, Tokyo, Japan).

Statistical Analysis

We used generalised linear modelling (GLM) and mixed modelling (GLMM) techniques (Dobson, 1983; McCullagh and Nelder, 1983; Aitkin *et al.*, 1989; Hardy and Smith, 2023) which allow for the analysis of data with non-normal error distributions, such as binomial or Poisson, without prior transformation. Log-linear analyses, utilising the log-link function, were used to determine the relationship between host weight and head capsule size as well as host weight and brood size. Parasitoid sex ratios were analysed using logistic regression and adopted a logit-link function. Broods consisting only of males on emergence were excluded from analyses (one brood of 4 individuals and one brood of 6 individuals) as they were most likely produced by virgin mothers (following Hardy and Cook, 1995). Variance in brood sex ratio was summarised using Heterogeneity Factors and the variance ratio, R, and departures from binomial distributions were assessed using the Meelis test (test statistic U) (Krackow *et al.*, 2002). Development time of parasitoid offspring was analysed using the Cox's proportional hazards model. A generalised linear model and a generalised linear mixed model analysis were conducted to determine the influence of host weight on the size of male and female parasitoids, respectively. When categorial variables (factors) with more than two levels were significant, model simplification was carried out via aggregation of factor levels (Hardy and Smith, 2023). GLM and GLMM analyses were conducted using the statistical software GenStat (version 20, VSN International, Hemel Hempstead, UK).

Results

Head capsule width, host weight and host instar

Larval instars are identified by head capsule width (Yazdani *et al.*, 2014). Head capsule width was associated with host weight (log-linear ANCOVA: $F_{(2,157)} = 418.64$, $P < 0.001$; fig. 2) in a

curvilinear relationship (quadratic term: $F_{(1,157)} = 132.77$, $P < 0.001$; fig. 2) that explained 84% of the variance in head capsule width. Head capsule width reached a maximum of approx. 1.4 mm. As larvae with head capsules of this width ranged widely in weight, between approximately 0.01 and 0.035 mg (fig. 2), host weight was used as the measure of host size in subsequent analyses (table 1).

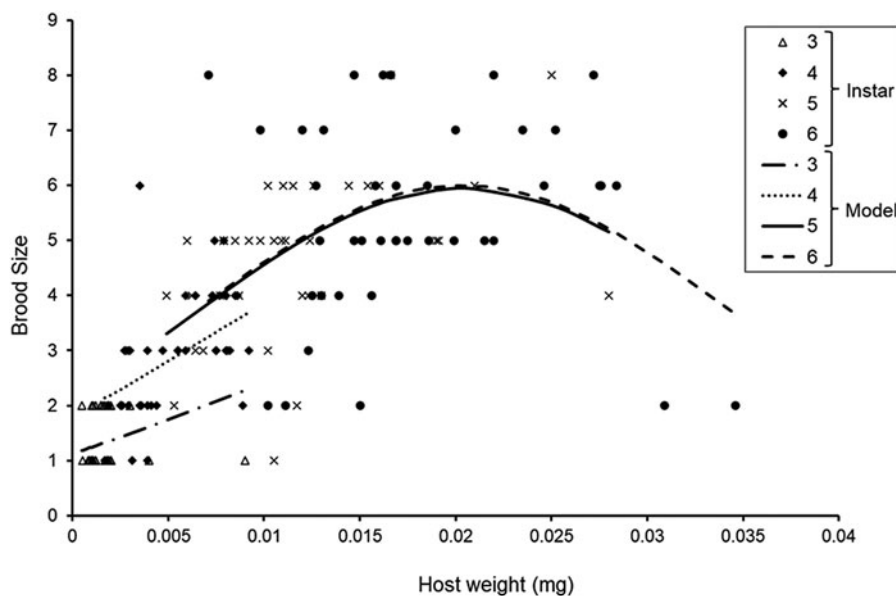### Brood size and host weight/instar

Goniozus jacintae brood size increased with host weight (log-linear ANCOVA: $F_{(5,154)} = 73.18$, $P < 0.001$; fig. 3) in a curvilinear relationship (quadratic term: $F_{(1,154)} = 28.07$, $P < 0.001$; fig. 3). Broods laid on larger instars (5 and 6) did not differ significantly in size (aggregation of factor levels: $F_{(4,155)} = 0.02$, $P = 0.890$). The average brood sizes developing from hosts of different instars were: 3rd instar, 1.3 (SE ± 0.075); 4th instar, 2.8 (SE ± 0.18); 5th instar, 4.7 (SE ± 0.23); 6th instar, 5.4 (SE ± 0.28).

Sex ratio

Goniozus jacintae brood sex ratios were female biased: the mean proportion of offspring that were male was 0.23 (SE ± 0.01). The maximum number of males recorded in any brood was 1 and sex ratio variances were significantly under-dispersed (HF = 0.09; Meelis test: $R = 0.022$, $U = -8.77$, $P < 0.001$; table 2). When the brood size was one adult offspring, the offspring was always a female. There were no all-female broods when multiple offspring developed (brood sizes of 2 or more). Among instars 4, 5 and 6, sex ratios decreased significantly as brood size increased ($F_{(3,156)} = 162.06$, $P < 0.001$; fig. 4) but did not differ between host instars 4, 5 and 6 (aggregation of factor levels:

Table 1. Head capsule widths (mm) of *Epiphyas postvittana* reared at 22°C.

Instar	Mean	Std. dev.	Range	*n*
3	0.610	0.059	0.552–0.690	40
4	0.890	0.055	0.782–0.966	40
5	1.203	0.095	1.012–1.288	39
6	1.420	0.075	1.311–1.610	41

Figure 3. The relationship between brood size and host weight, classified by host instar. Data points for each instar are shown as symbols and the log-linear models fitted for each instar are defined as the following: 3rd instar: long dash and dot line, 4th instar: round dotted line, 5th instar: solid black line, 6th instar: dashed line.

$F_{(3,156)} = 0.85$, $P = 0.495$). Broods produced on 3rd instar hosts consisted of either one or two offspring and their sex ratios were either zero (a single female) or 0.5 (one male and one female), resulting in a positive relationship between sex ratio and brood size over this narrow brood size range (fig. 4). Sex ratios of broods produced on 3rd instar hosts were significantly different to broods produced on all other instars ($F_{(1,156)} = 142.24$, $P < 0.001$).

Developmental time of brood

There was no difference in parasitoid development time on different host instars (Cox PH model, $\chi^2 = 2.78$, d.f. = 3, $P = 0.427$). The mean development time from oviposition to adult eclosion was 19.64 days, SD = 0.88.

Table 2. Sexual composition of realised broods of *Goniozus jacintae*, and a test of sex ratio variance

Brood size	Frequency	Frequency of number of males per brood		R	U
		0	1		
1	32	32	–	–	–
2	32	–	32	0.000	−5.523
3	19	1	18	0.081	−3.370
4	21	1	20	0.066	−3.426
5	25	–	25	0.000	−3.893
6	17	–	17	0.000	−3.134
7	6	–	6	0.000	−1.784
8	8	–	8	0.000	−2.073
Overall totals	160	34	126		
Approx. proportion (%)		21	79		

Values lower than 1 for the variance ratio 'R' indicate sex ratio precision (less than binomial sex ratio variance). 'U' is the test statistic from the Meelis test.
Overall: $R = 0.022$, $U = −8.77$, $P < 0.001$.

Size of emerging parasitoids

Female *G. jacintae* were larger than males; mean thorax lengths for male and female *G. jacintae* were (1.13, S.D. = 0.083) and (1.31, SD = 0.097), respectively. For adult males, there was no significant relationship between thorax length and host weight ($F_{(4,71)} = 0.33$, $P = 0.858$; fig. 5a), nor was male size related to brood size ($F_{(4,71)} = 0.32$, $P = 0.865$). Conversely, the body size of females was influenced by both host weight ($F_{(1,88)} = 4.44$, $P = 0.038$, fig. 5b) and brood size ($F_{(1,84)} = 7.03$, $P = 0.01$). There was also a significant interaction between these main effects ($F_{(1,81)} = 7.46$, $P = 0.008$), with larger females developing from larger hosts, and smaller females developing from larger broods.

The statistical interaction between host weight and brood size indicates that these are not separate influences on adult female size. We calculated a resource index (host weight/brood size) as a proxy for how much food resource, on average, was available to each individual in each brood. The effects of resource index, host larval instar and offspring sex on the size of each individual parasitoid were then explored using a generalised linear mixed model, with brood identity included as a random factor (Bolker et al., 2009). Thorax length was significantly influenced by both resource index ($F_{(1,104)} = 5.83$, $P = 0.017$) and sex of the wasp ($F_{(1,244)} = 445.07$, $P < 0.001$), such that the mean size of a parasitoid increased with increasing resource index, and males were smaller than females (fig. 5c), but thorax length was not influenced by host instar ($F_{(3,84)} = 1.20$, $P = 0.316$).

Discussion

Goniozus jacintae females produce larger broods on larger hosts. This is consistent with prior reports on this species (Danthanarayana, 1980; Hopper and Mills, 2015) and on other *Goniozus* species (Gordh et al., 1983; Hardy et al., 1992; Abdi et al., 2020) having greater reproductive success when attacking larger hosts. It is also consistent with the finding that *G. jacintae* have a stronger foraging response as hosts develop through instars 3 to 6, reflecting their growth in size (Aspin et al., 2021).

The host represents the sole nutritional resource for immature parasitoids. Larger hosts are preferential for the development of
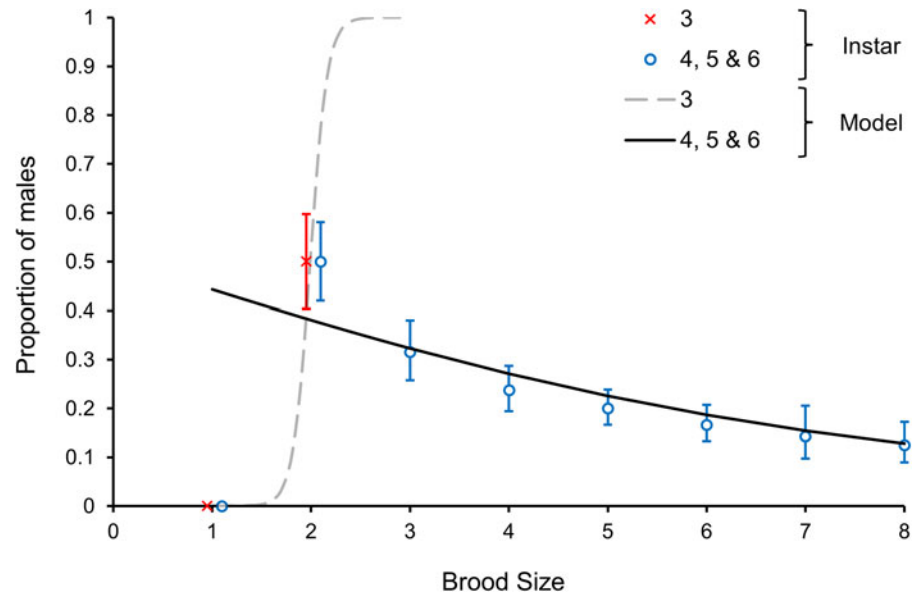
Figure 4. The relationship between brood size and off-spring sex ratio, classified by host instar. For instar 3 (dashed line), the fitted line is extrapolated to illustrate the bounded nature of the relationship: note that broods on 3rd instar hosts never exceeded 2 offspring. Sex ratios of broods developing on host instars 4, 5, and 6 did not differ significantly and were combined across instar classes (solid line). Lines were fitted by logistic ANCOVA. Data are shown as the mean values for each host instar group at each brood size ±1 standard error. Note that standard errors cannot be calculated for means of zero and also that they are asymmetrical around the non-zero means due to back-transformation from logit-scale estimates. Some estimates are slightly horizontally displaced to avoid visual overlap.

parasitoid larvae, since they contain more resources than their smaller counterparts (Godfray, 1994; Mackauer *et al.*, 1997; Farahani *et al.*, 2016; Jervis *et al.*, 2023). Smaller hosts may result in greater mortality and/or the production of smaller parasitoid offspring, with fitness measures such as fecundity and longevity also being lower among smaller adults (Godfray, 1994; Quicke, 1997; Mayhew, 2016; Zhang *et al.*, 2022). Hence, identifying the most suitable host size for a potential biological control agent could enhance the success of mass-rearing parasitoids in the laboratory.

Host size influenced the size of emerging *G. jacintae* offspring, with larger females emerging from larger hosts. Fitness of female parasitoids is typically positively influenced by their body size (Hardy *et al.*, 1992; Kazmer and Luck, 1995; Ellers *et al.*, 1998; Sagarra *et al.*, 2001; Samková *et al.*, 2019). Larger females exhibit higher fertility and longevity compared to smaller ones (Visser, 1994; Harvey *et al.*, 2001; Samková *et al.*, 2019; Wang *et al.*, 2021), as well as greater foraging efficiency when searching for hosts or food resources (Visser, 1994; Kazmer and Luck, 1995; Sarfraz *et al.*, 2012). In addition, larger females have higher success in the outcome of conflicts for host resources against smaller, competing females (Petersen and Hardy, 1996; Hardy *et al.*, 2013). Thus, it can be inferred that when a female *G. jacintae* is accepting a host for oviposition, host size will play a key role in determining not only the size of her brood but the size of the female offspring within that brood.

The size of female offspring was also significantly influenced by brood size; smaller females emerged from larger broods, a trend also reported in the congener *Goniozus nephantidis* (Muesebeck) when clutches were artificially created on hosts of a fixed size (Hardy *et al.*, 1992). However, the opposite pattern was seen in broods that were laid naturally (Hardy *et al.*, 1992). In contrast to solitary parasitoids, where only one offspring per host can survive and develop, gregarious offspring may share a host – the sole nutritional resource – with their siblings and even the offspring of conspecific females (Godfray, 1994). Parasitoid growth and development varies depending on both the quality and quantity of the host resource available (Mackauer *et al.*, 1997; Cusumano *et al.*, 2016; Pekas *et al.*,

2016). Hence, scramble competition may arise between parasitoid larva on the same host, with potential impacts on offspring mortality (Salt, 1961; Brodeur and Boivin, 2004; Fox and Messina, 2018), fitness (Hardy *et al.*, 1992; Bernstein *et al.*, 2002; Pereira *et al.*, 2017), and size (Visser, 1996; Bezemer and Mills, 2003; Malabusini *et al.*, 2022).

Conversely, the size of male *G. jacintae* offspring was not related to either host size or brood size when these were treated as separate explanatory variables. However, it was influenced by these properties when combined into an index of *per capita* resource availability, as was female size. This suggests that, as above, there may be scramble competition between offspring within a brood for food as a resource, with direct consequences on offspring size. This competition may influence male offspring size to a lesser extent than females, since males require fewer resources than females due to their smaller size. As is common in bethylids, adult *G. jacintae* males emerge from their cocoons before females in preparation for mating (Hardy *et al.*, 2000; Amante *et al.*, 2017; E. Aspin, pers. obs.). There may be little advantage for males in acquiring more resources to become larger, as development to a larger size may extend development time and result in the male missing the opportunity to emerge before females and secure mating opportunities (reviewed in Boulton *et al.*, 2015; Wang *et al.*, 2019; Teder *et al.*, 2021). Furthermore, as there is typically no more than 1 male in a *G. jacintae* brood, larger body size will not normally enhance competitive ability with male siblings.

The sex ratio of *G. jacintae* is female biased (mean proportion of males = 0.23), similar to that of most bethylids, most likely due to high levels of sibling mating and the resulting selection from local mate competition (Green *et al.*, 1982; Mayhew and Hardy, 1998; Tang *et al.*, 2014; Abdi *et al.*, 2020). In addition, the sex ratio of *G. jacintae* has extremely low variance (significantly less than binomial); all broods with a size greater than one contained only one male. Notably, the variance ratio for *G. jacintae* ($R = 0.022$) is lower than estimates obtained for several congeners: *G. nephantidis*, $R = 0.743$ (Hardy and Cook, 1995); *G. legneri*, $R = 0.572$, (Khidr *et al.*, 2013); *G. nigrifemur*, $R = 0.37$; *G. emigratus*, $R = 0.42$ (Hardy *et al.*, 1998).
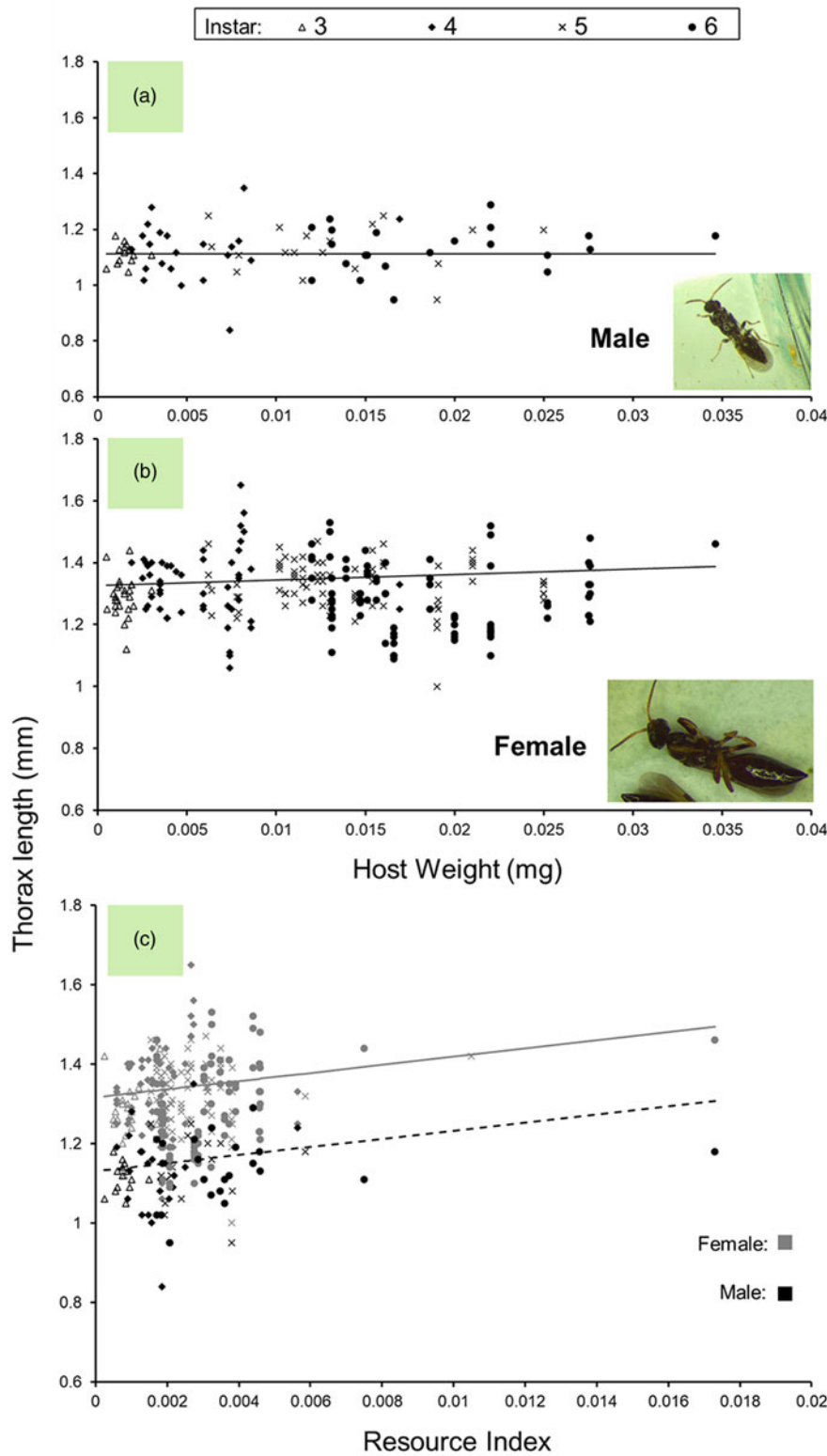
Figure 5. Parasitoid size and resource availability. Relationship between emerging parasitoid size and host weight, classified by host instar, for male (a) and female (b) offspring. Effect of increasing resource index on parasitoid size for male and female offspring (c).

Sex allocation is a behaviour of interest for the application of biological control and the mass rearing of bethylids, as the number of female offspring recruited into each generation positively influences the degree to which target pest populations are likely to be suppressed (Ode and Hardy, 2008). It is well known that parasitoids make adaptive decisions about sex allocation (reviewed in Charnov, 1982; Waage, 1986; West, 2009; Whitehorn et al., 2015; Fellowes et al., 2023), and that selection favours mothers that are able to produce precise sex ratios, as this does not produce any superfluous males and instead promotes the number of dispersing females (Green et al., 1982; Hardy, 1992; West and Herre, 1998; Khidr et al., 2013).

However, there are multiple factors that influence selection for, and the attainment of, precise sex ratios, such as the order in which sexes are produced when clutches are laid and developmental mortality (Green *et al.*, 1982; Nagelkerke and Hardy, 1994; Kapranas *et al.*, 2011). Mortality of parasitoid larva during the developmental stage increases the variance of observed sex ratios at eclosion, introducing the risk that no males survive to maturity, resulting in a brood of virgin females with very limited fitness under single foundress local mate competition (reviewed in Nagelkerke and Hardy, 1994; Hardy *et al.*, 1998; see also Kapranas *et al.*, 2011). The advantage of precise sex ratios can vary considerably depending on the different distributions of mortality within a brood (Nagelkerke and Hardy, 1994). Although this study did not provide a direct assessment of *G. jacintae* mean mortality or its distribution across broods and sexes, the extremely low brood sex ratio variance we recorded (see above) suggests that very few offspring die between oviposition and maturity and further that laying just one male per clutch will represent optimal sex allocation. In addition, parasitoids exhibit different sequence patterns when laying a clutch; some species lay female eggs first whereas others lay male egg(s) first (reviewed in Hardy, 1992). In the current study, all single egg broods produced females, and all 2-egg broods produced one male and one female, suggesting that this bethylid may fit in the group of parasitoids that lay male eggs last, although empirical assessment will be required to confirm this. Therefore, in order to obtain a fuller understanding of how the observed *G. jacintae* brood sex ratios arise, the sequence of sex allocation during the oviposition of a clutch and, especially, developmental mortality, should be assessed.

This study provides new information on the reproductive behaviour of a relatively unstudied potential biocontrol agent as well as complementing findings from existing work on bethylids (Griffiths and Godfray, 1988; Hardy *et al.*, 1992, 2000; Luft, 1993; Hardy and Mayhew, 1998; Polaszek *et al.*, 2019). Although some aspects require further investigation, we have demonstrated that (1) like other bethylids, *G. jacintae* has greater reproductive success on larger hosts and exhibits female biased sex ratios (2) these sex ratios have extremely low variance, seemingly lower than all previously studied bethylids, and finally, (3) female parasitoid offspring size is influenced by brood size and host weight whilst male size is not, but the body size of both sexes is positively determined by the *per capita* availability of resources during development. Such information is key for designing and implementing effective biological control programmes for LBAM, for instance, when considering which larval instar would produce the most (large and mated female) parasitoid offspring per host during mass-rearing procedures.

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