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Factitious hosts for *Goniozus omanensis* (Hymenoptera: Bethylidae), a parasitoid of the lesser date moth *Batrachedra amydraula* Meyrick (Lepidoptera: Batrachedridae)

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ABSTRACT
The bethylid wasp *Goniozus omanensis* has been identified as a key natural enemy of *Batrachedra amydraula* Meyrick (Lepidoptera: Batrachedridae), an important pest of date palm. Efficient rearing of natural enemies can be an important part of biological pest control programmes but cultures of *G. omanensis* are challenging to maintain on *B. amydraula*. We evaluate two readily available species of Pyralid moths, *Corcyra cephalonica* and *Galleria mellonella*, as potential factitious hosts. We find that *G. omanensis* can develop on the larvae of either species, but the probability of failure is *circa* 75% overall. Both trialled host species were approximately equally suitable, but failures were typically during the early stages of brood production when presented with *C. cephalonica* and during the later stages when presented with *G. mellonella*. This suggests that *C. cephalonica* larvae may be more difficult to suppress and that *G. mellonella* larvae may be of lower nutritional value. The average production of adult parasitoids per host provided was approximately 1 and, given the observed female biased sex ratio, the average number of females was around 0.8. We suggest potential routes to improving the efficiency of rearing *G. omanensis* on these factitious hosts.

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Introduction

Programmes of biological pest control commonly involve the field release of laboratory mass-reared natural enemies to inoculate or inundate the environment of the target pest (Heimpel & Mills, 2017; van Lenteren, 2003; Wajnberg & Hassan, 1994). Populations of target pests are often difficult or expensive to maintain in laboratory settings and mass-rearing units. The successful use of parasitoids as agents of biological control may thus depend on finding alternative, or factitious, host species that are more readily reared than the target pest host and that are sufficiently suitable for parasitoid development

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and post-release performance (Abdi et al., 2021; Ehteshami et al., 2023; Kumar & Murthy, 2000; Latifian, 2017; Lemos et al., 2003; Lupi et al., 2017; Malabusini et al., 2023; Pérez-Lachaud & Hardy, 2001; Pratissoli et al., 2004; Ramalho & Dias, 2003).

Here we evaluate two commonly laboratory-reared lepidopteran species as factitious hosts for *Goniozus omanensis* Polaszek (Hymenoptera: Bethylidae), which is naturally a parasitoid of *Batrachedra amydraula* Meyrick (Lepidoptera: Batrachedridae). *Batrachedra amydraula,* also known as the lesser date moth (LDM) and vernacularly as 'Hummeira', is a pest of economic importance that attacks date palm fruits during the young developmental stage and causes production loss of up to 70-80% when infestation levels are high (Abd-Allah et al., 1998; Abdel-Wahab, 1974; Al Khatri, 2009; Al-Yahyai & Khan, 2015; Argaman, 1992; Eitam, 2001; Michael, 1970; Sadeghi et al., 2012; Shameer et al., 2024). *Goniozus omanensis* is a gregarious larval idiobiont ectoparasitoid that was recently identified, based on morphology and DNA sequence data, as a new species (Polaszek et al., 2019). Field surveys carried out in Oman during 2005–2006 have found it to be the most prevalent natural enemy of LDM (Abbas et al., 2008, 2014; Al-Naabi, 2008). Aspects of its reproductive biology, such as the timing of host attack, offspring developmental period, adult sex ratio and longevity, have been evaluated in the laboratory under a range of temperatures when the parasitoid was supplied with field-collected LDM larvae (Abbas et al., 2014). However, LDM larvae enter diapause at the end of the third generation each year (June) and date fruits are not available year-round for maintaining laboratory cultures of its natural enemies. Furthermore, while it is possible to maintain cultures of LDM in the laboratory, the diet required is relatively complex and time-consuming to prepare (Jatoi et al., 2020; Marouf et al., 2004; Mohammad et al., 2015; Shayesteh et al., 2010). It is therefore desirable to find alternative host species that can be used to maintain efficient cultures of *G. omanensis* throughout the year (Al-Naabi et al., 2023).

Several potential host species have been tested as factitious hosts for rearing *G. omanensis:* the cotton leaf worm, *Spodoptera littoralis* (Lepidoptera: Noctuidae), the Mediterranean flour moth, *Ephestia kuehniella* (Lepidoptera: Pyralidae), the rice moth *Corcyra cephalonica* (Lepidoptera: Pyralidae), and the greater wax moth, *Galleria mellonella* (Lepidoptera: Pyralidae). Initial studies identified only *G. mellonella* as suitable for *G. omanensis* development (Abbas et al., 2008) and, as this species is straightforward to rear, it was considered promising as a suitable factitious host (Abbas, 2012; Abbas et al., 2008; Al-Naabi, 2008; Al-Naabi et al., 2023). After importing *G. omanensis* to our UK laboratory in 2017, we carried out pilot trials using *C. cephalonica* and concluded that it could also be used to rear *G. omanensis* (T.A. pers. obs.). As both *C. cephalonica* and *G. mellonella* are similarly straightforward to maintain in culture, and as both are known to be suitable factitious hosts for some other species of *Goniozus* (e.g. Abdi et al., 2020a; Khidr et al., 2013a; Mohan & Shameer, 2003; Sreenivas & Hardy, 2016), we decided to provide a more detailed evaluation of *G. omanensis* developmental performance on these species, with the ultimate aim of enhancing the capacity to mass-rear this parasitoid efficiently for biocontrol release. We do this by evaluating parasitoid performance at multiple life-history stages, starting with the presentation of the host through to adult offspring production. Further, as host size may influence both parasitoid attack success (e.g. Abdi et al., 2020b; Al-Naabi et al., 2023) and offspring production on suppressed hosts (e.g. Hardy et al., 1992), we present female parasitoids with a range of host sizes of each species. As the provision of honey may influence parasitoid performance (including that of species which are idiobiont ectoparasitoids) and the consequent efficiency of mass-rearing protocols (e.g. Benelli et al., 2017; Harvey et al., 2017; Tunçbilek et al., 2021; Wäckers, 2003), we include evaluation of effects of the presence or absence of honey as food for the adult parasitoid.

Materials and methods

Insects

A culture of *Goniozus omanensis* was imported from Oman to the UK and was maintained in the laboratory at the University of Nottingham from September 2017 until May 2021. During the establishment phase, it was reared on *G. mellonella* or *C. cephalonica*, providing a pilot test of the suitability of the latter species. *Goniozus omanensis* was initially presented with *C. cephalonica* larvae which had been paralyzed, but not oviposited on, by a female of the congeneric species *Goniozus legneri* Gordh. After using this method for several generations of *G. omanensis* rearing, females were presented with unparalysed *C. cephalonica* larvae. In each generation mated adult female wasps were placed individually into glass vials containing one host larva. The vials were then closed with a cotton and nylon gauze plug. The subsequently produced brood was allowed to develop to adulthood whereupon the process was repeated. Both species of hosts were reared on a diet of coarsely ground corn meal (polenta), wheat bran, glycerol, honey, and dried yeast (following Lizé et al., 2012) and kept in ventilated glass jars. Culturing and experimental conditions were a daily light cycle of 16hL: 8hD, a temperature of 26 ± 2°C and a relative humidity of 26 ± 5%.

Host species trials

We used a factorial experimental design to test the influences of host species, host weight and the provision of honey, and their potential interactions, on parasitoid performance. Prior studies of reproductive responses of *Goniozus* females to host size have indicated that common measures of size (weight, length, and head-capsule width) are mutually correlated and that most of the variance is explained when using weight as the size metric (Aspin et al., 2024; Hardy et al., 1992). Head-capsule width can also be used to identify host instar within a species but, for a given instar, *G. mellonella* larvae are larger than *C. cephalonica*. We thus used host weight as the measure of the quantity of resource available to the parasitoid and considered host species as a further aspect of host quality.

In each replicate, a single adult female *G. omanensis* was presented with one (unparalyzed) host in a stoppered glass vial. Half of the vials had a small drop of honey placed on the inner surface to provide food for the wasp. No honey was present in the remaining vials. The host in each vial was either a *G. mellonella* or a *C. cephalonica* larva. Each host was weighed prior to presentation to the wasp (range 1–60 mg) and the range of host sizes provided was the same across honey and host species treatment combinations. There were five replicates of every combination of host size, host species and honey treatment, giving 120 replicates in total.

Table 1. Life-table of *Goniozus omanensis* brood development. The number of broods of each stage of production that failed to develop further were used to obtain *k*-values (*k*1, *k*2, *k*3, *k*4, *k*5), calculated as $k = (\log_{10}$ number before failure – $\log_{10}$ number after failure), which indicate the probability of failure of broods during successive stages of development (for each treatment and also overall). *K* is the sum of contributions of failures at each stage to the overall probability of failure ($K = k1 + k2 + k3 + k4 + k5$). *indicates the stage of failure that contributed the most importantly to the overall failure for each treatment and also overall.

Treatment	Hosts presented	Hosts paralysed	% hosts not paralysed	*K1* (paralysis failure)	Hosts oviposited on	% hosts not oviposited on	*k2* (oviposition failure)	hosts bearing hatched larvae	% of oviposited on hosts bearing no hatched larvae	*k3* (hatching failure)	Hosts with pupae	% of larval broods failing to pupate	*k4* (pupation failure)	Hosts generating adults	% pupal broods failing to generate adults	*k5* (adult emergence failure)	% presented hosts from which no adult parasitoids were produced	*K* (overall reproductive failure)
Corcyra cephalonica with honey	30	17	43.33	0.247*	17	0	0	15	11.76	0.054	15	0	0	10	33.33	0.176	66.66%	0.477
Corcyra cephalonica without honey	30	19	36.66	0.198*	19	0	0	18	5.26	0.023	12	33.33	0.176	11	8.33	0.038	63.33%	0.436
Galleria mellonella with honey	30	26	13.33	0.062	23	11.53	0.053	16	30.43	0.158	9	53.84	0.250	5	44.44	0.255*	83.33%	0.778
Galleria mellonella without honey	30	26	13.33	0.062	26	0	0	20	23.07	0.114	12	40.00	0.222	6	50.00	0.300*	80.00%	0.699
Overall	120	88	26.66	0.135	85	3.41	0.015	69	18.82	0.091	48	30.43	0.158	32	33.33	0.176*	73.33%	0.574

Replicates were examined daily using a binocular dissection microscope to observe and record the following parameters: paralysis of the host, oviposition by the wasp, the size of any clutches of eggs laid, the developmental time of any offspring, the number and sex ratio of any adult offspring and the time of the initial female ('mother') wasp's death. When the initial female died, it was transferred to a separate tube to prevent confusion with any offspring. In cases were the female lived until the brood reached the pupal stage, the female was transferred alive to a separate vial.

Statistical analysis

A life table approach (Jervis et al., 2023, Table 1) was used to identify how failures to progress between successive stages of brood production contributed to the overall probability of failure. Generalized linear models in the statistical software package *GenStat* (19th edition, VSN International, Hemel Hempstead, UK) were used to analyse aspects of parasitoid performance. Log-linear models were used for responses consisting of integer data and logistic models were used for proportional response variables (Aitkin et al., 1989; Hardy & Smith, 2023). These models were factorial analyses of covariance (ANCOVA), with host species and the presence or absence of honey fitted as factors with two levels and host weight fitted as a variate. First and second order interactions between these main effects were included in the initial models and statistical significance was assessed by progressive model simplification (Hardy & Smith, 2023). No second-order interactions were significant and results for these are not reported. Most first-order interactions were non-significant; those of interest are reported.

Influences on the timing of life-history events were explored using Wiebull and exponential models with censoring (Aitkin et al., 1989). The influences of the candidate explanatory variables were explored by their inclusion into the chosen exponential or Weibull model. Data on timings were entered as the number of days since the start of the experiment (e.g. time taken to paralyse a host) or since the previous life-history event (e.g. from eggs being laid to eggs hatching). Replicates that failed to progress were treated as censors, with the censored value being either the time of the end of the experiment or the time of the parasitoid's death. Possible Type I errors due to multiple comparisons in time-to-event analyses were controlled for by using the false discovery rate procedure with the family-wide α-value set stringently to 0.05 (McDonald, 2014).

Results

Probability of reproductive events

Reproductive failure was common overall, with only one quarter of females producing offspring from the provided host (Table 1). Offspring production failed at all stages, from host presentation to adult emergence (Table 1). When the presented host was *C. cephalonica*, the stage of failure that contributed the most to the overall failure was host paralysis, with around 40% of hosts remaining unsuppressed. All suppressed *C. cephalonica* hosts were oviposited on and around half of these clutches developed to become adult offspring (Table 1). When the presented host was *G. mellonella*, most females suppressed, and laid eggs on, the host (Table 1) and the probability of paralysis was higher than when presented with *C. cephalonica* (logistic analysis: $G_1 = 11.30$, $P < 0.001$, %Deviance explained = 8.11). The probability of paralysis also declined as host size increased (logistic analysis: $G_1 = 15.12$, $P < 0.001$, %Dev = 19.86), with a steeper decline when *G. mellonella* was the host species (Host species × Host weight interaction: $G_1 = 6.64$, $P = 0.010$, %Dev = 4.76, Figure 1). The provision of honey did not influence the probability of paralysis significantly ($G_1 = 0.21$, $P = 0.650$, %Dev = 0.15). However, the presence of honey decreased the probability of oviposition on paralysed hosts from 100% to 93% ($G_1 = 4.41$, $P = 0.036$, %Dev = 16.8) but this probability was not significantly affected by host species ($G_1 = 3.16$, $P = 0.075$, %Dev = 12.09) or host size ($G_1 = 0.01$, $P = 0.907$, %Dev = 0.052).

Clutches laid on *G. mellonella* commonly failed at pupation or during pupal development, and overall success was lower than when *C. cephalonica* hosts were presented (Table 1). The proportion of laid eggs that survived was affected by host species and by an interaction between host size and species (logistic analysis: Species: $G_1 = 5.10$, $P = 0.027$, %Dev = 6.14; Size: $G_1 = 2.11$, $P = 0.150$, %Dev = 2.48; Interaction: $G_1 = 4.69$, $P = 0.033$, %Dev = 5.17): when clutches were laid on *G. mellonella*, the survival of eggs to adulthood was highest when developing on larger hosts while on *C. cephalonica* egg survival declined slightly as host size increased (Figure 2). Using an index of resource availability per developing offspring (host weight/clutch size) found that although survival increased as *per capita* resources increased, the effect was not significant ($G_1 = 1.10$, $P = 0.293$, %Dev = 0.33). The provision of honey did not influence offspring survival ($G_1 = 0.09$, $P = 0.760$, %Dev = 0.10), nor did it greatly influence the overall probability of producing offspring (Table 1).

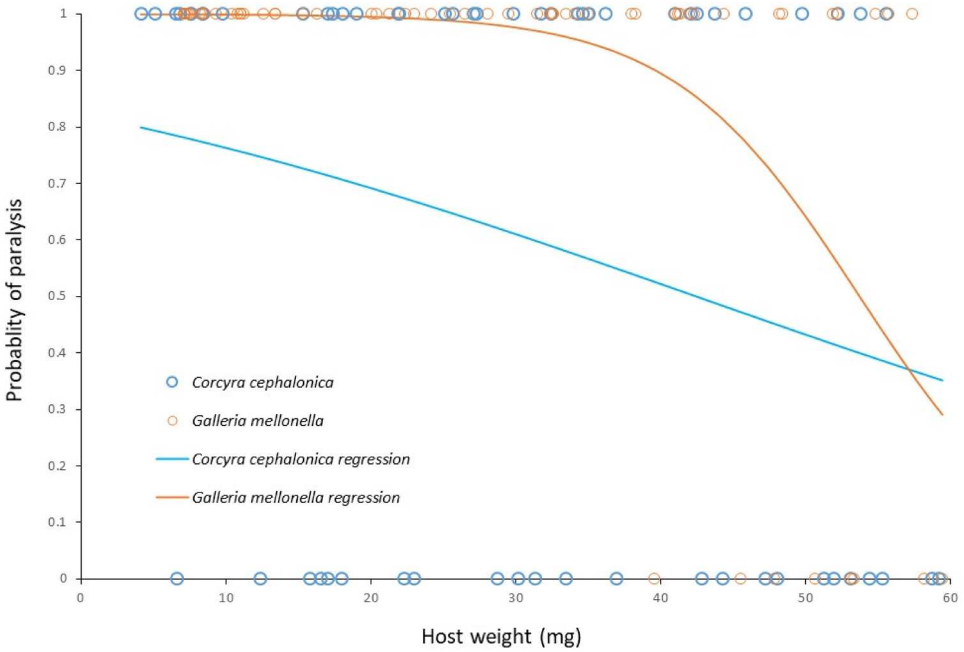

Figure 1. Relationship between the probability of parasitism and host size and species.

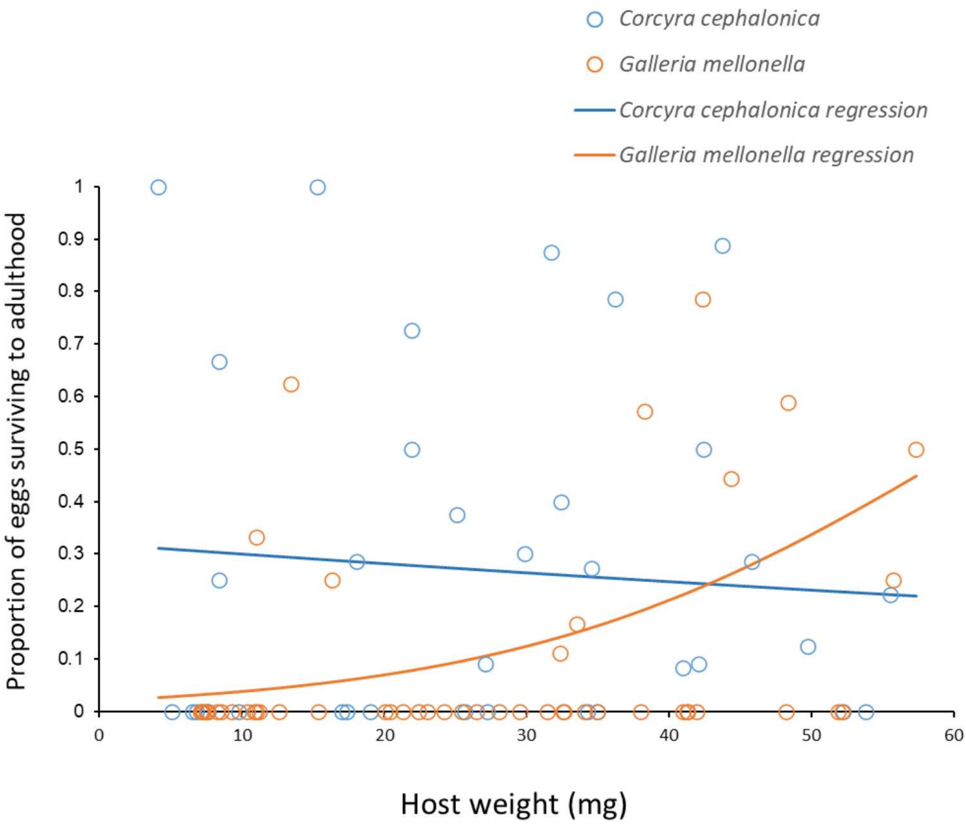

Figure 2. Relationship between the probability of eggs surviving to adulthood and host size and species.

Timing of life-history events

It took up to 17 days after presentation with a host for adult offspring to be produced (Figure 3). The time taken to reach successive developmental stages was affected by host species, host size, and by the provision of honey (Table 2). Provision of honey increased the longevity of females presented with hosts, and also led to them being slower to attack and lay on hosts (Table 2), but honey had no influence on the time taken for offspring to develop nor on offspring longevity (Table 2). Females took longer to paralyse larger hosts, but host species did not affect the time taken for host suppression (Table 2). Once hosts were suppressed, reproduction took longer on *G. mellonella* than on *C. cephalonica* hosts (Table 2), but hatched eggs developed to adulthood more rapidly when hosts were larger (Table 2). There was no significant interaction between these main effects ($G_1 = 3.35$, $P = 0.067$).

Characteristics of produced broods

The number of eggs laid onto hosts (clutch size) increased with host size (log-linear analysis, with replicates in which no eggs were laid excluded: $F_{1,83} = 70.12$, $P < 0.001$, %Dev = 45.70, Figure 4), but was not significantly affected by host species ($F_{1,82} = 0.14$,

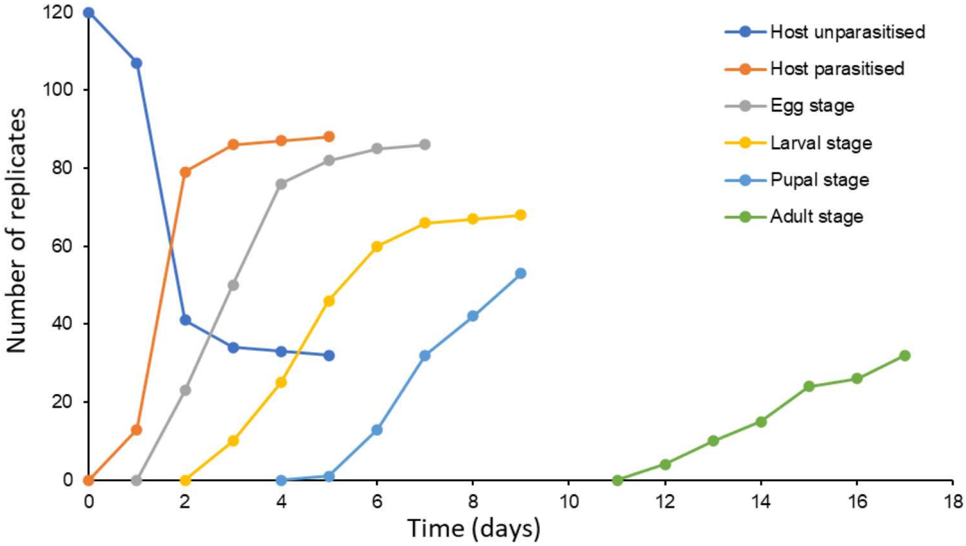

Figure 3. Timing of *G. omanensis* brood production. The lines show the numbers of replicates at each developmental stage at any given time. Not all hosts became paralyzed and the corresponding line thus does not descend to zero. The rising lines are plotted until the end of each development stage.

$P = 0.714$, %Dev = 0.19, Figure 4), or the provision of honey ($F_{1,81} = 0.01$, $P = 0.992$, %Dev = 0.005). There was a marginally non-significant interaction between host weight and host species that explained less than 3% of the variation in clutch size ($F_{1,80} = 3.67$, $P = 0.059$, %Dev = 2.39). Due to developmental mortality of offspring (see above) the numbers of offspring produced from each host were not significantly affected by host characteristics or the provision of honey, whether excluding or including replicates in which no offspring matured (Excluded: Host size: $F_{1,30} = 2.31$, $P = 0.14$, %Dev = 7.3; Host species: $F_{1,29} = 0.44$, $P = 0.513$, %Dev = 1.4; Honey: $F_{1,28} = 0.40$, $P = 0.532$, %Dev =

Table 2. Influences on the timing of *Goniozus omanensis* life-history events.

	Potential influence[1]			
Event	Host species	Host weight	Honey	Interpretation
Time to adult female's death[2]	$G_1 = 5.70$, $P = 0.017$	$G_1 = 2.96$, $P = 0.853$	$G_1 = 5.22$, $P = 0.022$	Females lived longer when presented with *Galleria mellonella* and when provided with honey
Time to host paralysis[2]	$G_1 = 1.69$, $P = 0.193$	$G_1 = 62.04$, $P < 0.001$	$G_1 = 12.69$, $P < 0.001$	Females took longer to paralyse hosts when hosts were larger and when honey was provided
Time to oviposition[2]	$G_1 = 3.90$, $P = 0.048$*	$G_1 = 1.77$, $P = 0.183$	$G_1 = 22.50$, $P < 0.001$	Females took (equivocally*) longer to oviposit on paralysed hosts when the host was *Galleria mellonella* and when honey was provided
Time to hatching[3]	$G_1 = 7.05$, $P = 0.008$	$G_1 = 0.23$, $P = 0.632$	$G_1 = 1.03$, $P = 0.310$	Laid eggs took longer to hatch when the host was *Galleria mellonella*
Time to emergence[2]	$G_1 = 14.38$, $P < 0.001$	$G_1 = 7.43$, $P = 0.006$	$G_1 = 0.00$, $P = 1.000$	Hatched eggs took longer to develop to adulthood when the host was *Galleria mellonella* and less time when their host was larger
Time to first offspring death[3]	$G_1 = 0.12$, $P = 0.729$	$G_1 = 0.05$, $P = 0.823$	$G_1 = 0.01$, $P = 0.920$	Offspring longevity was not affected by host species or size, or whether their mother had been provided with honey.

[1] Each explanatory variable was fitted separately. [2] Analysis based on a Weibull model. [3] Analysis based on an exponential model. *Result not significant after multiple-comparisons correction using a false discovery rate of 0.05.

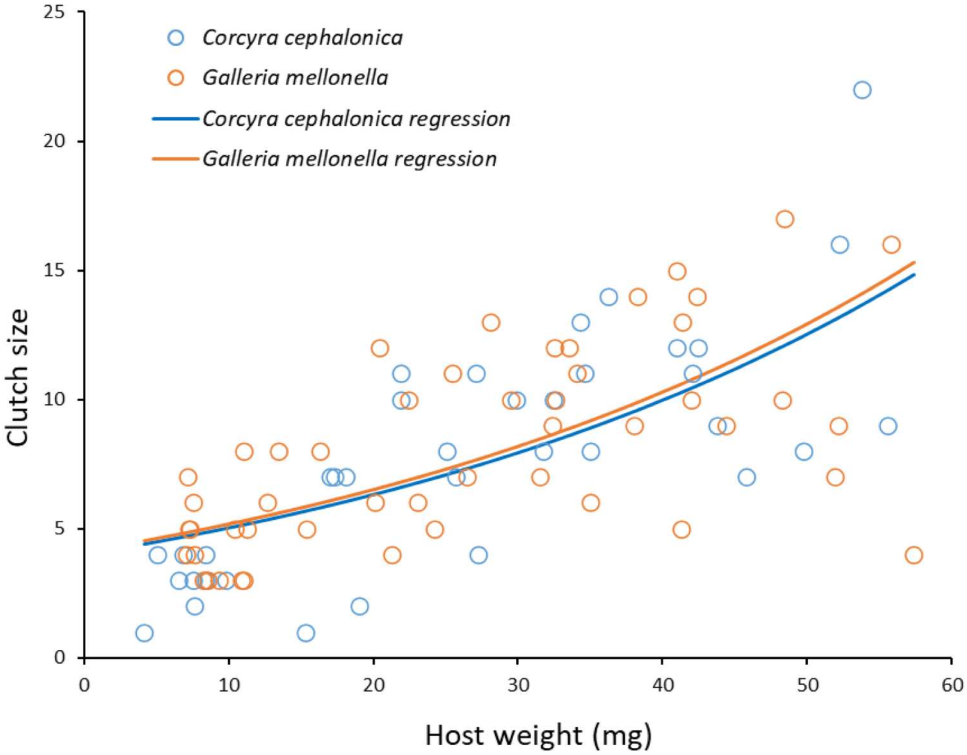

Figure 4. Relationship between clutch size and host size. Regression lines are shown for each species but the difference in their clutch size response was not significant.

1.28; Mean production per host = 3.84, +SE = 0.57, −SE = 0.50; Included: Host size: $F_{1,118} = 3.72$, $P = 0.056$, %Dev = 3.06; Host species; $F_{1,117} = 1.26$, $P = 0.264$, %Dev = 1.03; Honey: $F_{1,16} = 0.56$, $P = 0.455$, %Dev = 0.46; Mean production per host = 1.025, +SE = 0.184, −SE = 0.156), but note the positive marginally-non-significant relationship between production and host size when all replicates were included.

The sex ratios of maturing *G. omanensis* broods were female biased and under-dispersed (mean proportion of offspring that were male = 0.087, +SE = 0.025, −SE = 0.020, Heterogeneity Factor = 0.656; to obtain these estimates broods containing no females were excluded on the basis that the mother was probably unmated and constrained to produce males only, following Hardy & Cook, 1995; Du et al., 2021). Sex ratios were not significantly affected by host characteristics or the provision of honey (logistic analysis; Host species: $F_{1,20} = 1.13$, $P = 0.299$, %Dev = 5.05; Host size: $F_{1,19} = 0.26$, $P = 0.613$, %Dev = 1.17; Honey: $F_{1,18} = 0.01$, $P = 0.930$, %Dev = 0.035). The mean number of females produced per host (including failures) was 0.783 (+SE = 0.153, −SE = 0.128). The number of females per host increased significantly as host size increased (log-linear analysis: $F_{1,118} = 4.10$, $P = 0.045$, %Dev = 3.36, Figure 5) but was not influenced by host species ($F_{1,118} = 0.00$, $P = 1.00$, %Dev = 0.00) or the provision of honey ($F_{1,118} = 0.23$, $P = 0.635$, %Dev = 0.192). The mean number of mated females (maturing in a brood that also contained at least one adult male, assuming a strictly sib-mating population structure) was 0.383 (+SE = 0.093, −SE = 0.075). The number of

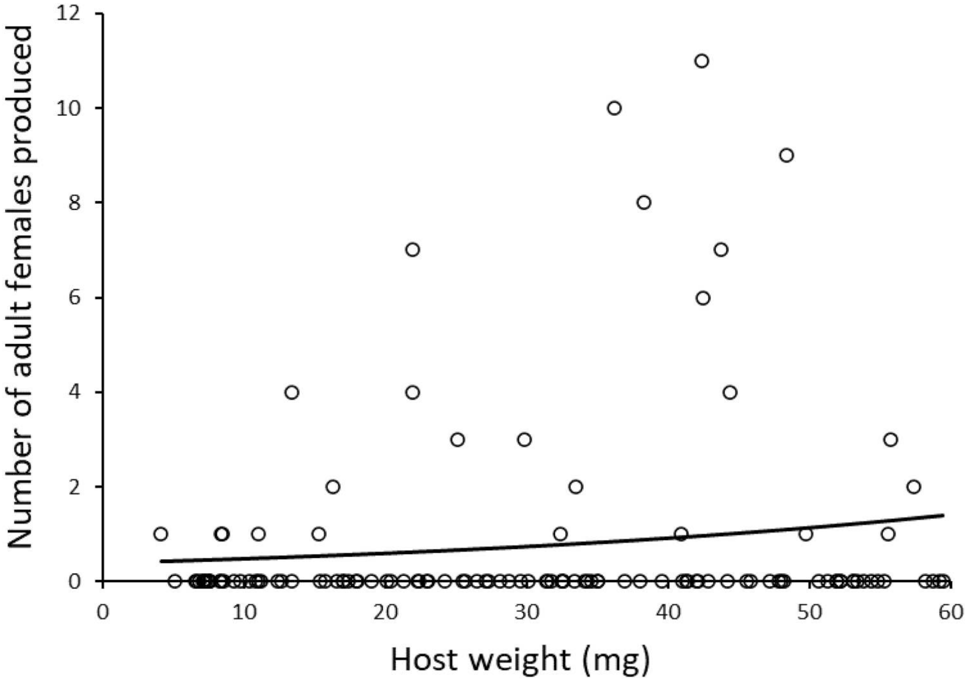

Figure 5. Relationship between the number of female offspring produced per host and host size.

mated females produced per host was uninfluenced by host characteristics or the provision of honey (Host size: $F_{1,118} = 2.31$, $P = 0.1315$, %Dev = 1.92; Host species: $F_{1,118} = 2.02$, $P = 0.158$, %Dev = 1.71; Honey: $F_{1,118} = 2.02$, $P = 0.158$, %Dev = 1.71).

Discussion

Species of *Goniozus*, and many other bethylids, are not typically monophagous but nonetheless have relatively narrow (oligophagous) host ranges (Gordh & Móczár, 1990). We have trialled two species of lepidopterans as alternative hosts for *Goniozus omanensis*, normally a parasitoid of the moth *Batrachedra amydraula* (Superfamily Gelechioidea, family Batrachedridae), using *Corcyra cephalonica* and *Galleria mellonella* (Superfamily Pyraloidea, family Pyralidae). As members of a different lepidopteran superfamily, the trialled hosts were not chosen on the basis of close relatedness to the natural host (Mitter et al., 2017) but on the basis of general availability and practical ease of laboratory rearing (Ehteshami et al., 2023), and also because other members of the genus *Goniozus* can be reared on these hosts (Abdi et al., 2020a; Khidr et al., 2013a; Mohan & Shameer, 2003; Sreenivas & Hardy, 2016). Distantly related hosts, which have had diets different from the native host and may have different biochemical compositions and behaviours, may prove entirely unsuitable for a given species of parasitoid and any ability to develop to maturity on a presented host may thus be regarded as an asset in the search for factitious hosts. In the present case, around one quarter of female *G. omanensis* presented with these potential alternative hosts produced adult offspring and, as such, *Corcyra cephalonica* can join *Galleria mellonella* on the short list of its factious hosts

(Abbas et al., 2008). Nonetheless, successful reproduction was the minority outcome and the numbers of adult offspring produced even when success was achieved was also low. Below we discuss influences on reproductive success and suggest approaches to its potential improvement.

Reproductive success on the two host species trialled was similar overall but differed in detail. Females presented with *C. cephalonica* more frequently failed to paralyze the host, although all of those that did suppress the host then oviposited and the subsequent developmental success of oviposited clutches was relatively high. These results suggest that *C. cephalonica* may be able to resist attack, for instance by violent reactions to attempted parasitism, more successfully than does *G. mellonella.* The lower probability of paralysis when hosts of either species were larger also suggests that the strength of a host's behavioural response to attempted stinging may provide a substantial challenge for *G. omanensis* to overcome (as noted by Al-Naabi et al., 2023, when providing *G. mellonella* as hosts). *Goniozus omanensis* is physically smaller than congeners that are commonly reared on *C. cephalonica* and *G. mellonella* and that rarely fail to suppress provided hosts (e.g. Abdi et al., 2020a; Du et al., 2021; Hardy et al., 1992). Failure to suppress hosts can be common in other bethylids that are small and attack large and powerful hosts (Abdi et al., 2020b; Malabusini et al., 2023). We note that, as small wasp that attacks large and aggressive hosts, *Goniozus omanensis* appears to be a candidate for an evolutionary transition from single-foundress host attack and brooding to multi-foundress reproduction, as discussed by Abdi et al. (2020a).

In contrast to the results for *C. cephalonica* (and in contrast to observations by Al-Naabi et al., 2023), females presented with *G. mellonella* rarely failed to paralyze the host, and typically then oviposited, but their broods tended to fail at the later developmental stages. This suggests that the nutritional resources provided by a *G. mellonella* larvae are less suitable for *G. omanensis* development or less abundant than those of *C. cephalonica* larvae. Also suggestive of a nutritional deficit is the finding that the size of adult *G. omanensis* tends to decline after several generations of culturing on *G. mellonella* (Al-Naabi et al., 2023). As *G. omanensis* is an ectoparasitoid, and encapsulation of immatures by the host is not possible, we consider it unlikely that these differences are due to differing immune responses by the host species.

The clutch size response to increasing host size exhibited by ovipositing *G. omanensis* was similar to those observed in congeners (e.g. Hardy et al., 1992), and was uninfluenced by the species of host presented. Similarly, the numbers of *G. omanensis* offspring that were produced from each host (including data on reproductive failures) increased with host weight and were uninfluenced by host species. Although up to 11 adults were produced per host, there were many instances of complete reproductive failure and the mean value for adult production was close to unity. For the biocontrol practitioner attempting to rear parasitoids for mass-release, the latter quantity is of importance as it reflects the overall efficiency of the culturing methodology. The sex ratios of the offspring produced is an important additional consideration because female, but not male, parasitoids attack hosts and produce recruits for the next parasitoid generation (Ehteshami et al., 2023; Hassell, 2000; Ode & Hardy, 2008). The sex ratios of *G. omanensis* broods are female biased and exhibit less than binomial variance, in common with many congeners (Aspin et al., 2024; Du et al., 2021; Gardner & Hardy, 2020; Hardy et al., 1998; Khidr et al., 2013b). While female biased sex ratios are generally an asset for biocontrol success (Ode & Hardy, 2008), the observed production of on average less than one female per provided host indicates that further improvements to the reproductive success of *G. omanensis* in laboratory cultures would be desirable. It may also be that there are other, more suitable, host species that are, as yet, untrialled.

Finally, our experimental design included the provision or absence of honey as a treatment. Honey increased the longevity of the females that were provided with a host, in accord with findings from a congener and in other parasitoids (Snart et al., 2018), but also reduced the probability of oviposition on paralysed hosts and the speed of offspring production. Honey did not benefit developing or mature offspring or enhance their numerical production. We conclude that providing honey will not be a useful component of any system set up to rear *G. omanensis* for biocontrol release.

Conclusions

Goniozus omanensis may be laboratory reared on factitious hosts. We have shown that it can be reared successfully on *C. cephalonica* as well as the previously established *G. mellonella*, and that the provision of honey is neither necessary nor generally beneficial. However, the number of adults that can be raised per host is low (approximately 1) and the number of females, the sex that attacks hosts, is lower. One route towards improving numerical production of *G. omanensis* would be to use the largest hosts available. While there is no difference in the relationship between production and host size between host species, it is more straightforward to obtain large *G. mellonella* than *C. cephalonica* larvae as the latter tend to pupate at lower weights (Abdi et al., 2020a). However, behavioural defence by large hosts may constrain this approach. Another route to improving success might be to increase the probability of host suppression and parasitism by presenting two female parasitoids with one host larva. However, the numbers of offspring produced would need to double for this to improve the growth of laboratory-reared populations of *G. omanensis.*

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Data availability statement

Raw data will be made available upon article publication and upon reasonable request.

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