Contests between beneficial natural enemies: brood-guarding parasitoids vs. foraging predators

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Abstract

Beneficial insects, such as natural enemies, are important to agro-ecosystem functioning and thus agricultural production. Parasitoids and predators can provide sustainable long-term solutions to pest problems (biological control), reducing the need for expensive and sometimes polluting pesticide applications. When several species of beneficial insects are present, their pest control actions may be additive, synergistic, or disruptive. One form of disruptive interaction between parasitoids and predators is direct interspecific contest for access to individual pests (the resource to be exploited). This study evaluated behavioural interactions between brood-guarding wasps, Goniozus nephantidis (Muesebeck) (Hymenoptera: Bethylidae), which are known to engage in intra-specific contests, and a predatory bug, Cardiastethus exiguus (Poppius) (Hemiptera: Anthocoridae), which attack the same pest species, Opisina arenosella (Walker) (Lepidoptera: Oecophoridae), a major pest in coconut production systems. Dyadic parasitoid–predator and predator–predator contests were staged to determine the factors that influence the behaviours within, and outcomes of, such interactions. Parasitoids were aggressive towards predators, sometimes killing them, but predators were not aggressive towards parasitoids. Biting and stinging only occurred when there was a host larva present. In the absence of the parasitoid that had oviposited onto a host, predators often consumed the parasitoid's eggs. Egg consumption sometimes occurred when the parasitoid was present. Intra-specific competition between pairs of predators was also evaluated: adults were aggressive towards each other, but interactions were not fatal. Biting was more common when there was no prey larva present. When a larva was present, predators were observed feeding simultaneously. We conclude that direct parasitoid–predator interactions are likely to influence pest population dynamics, possibly reducing the overall suppression of O. arenosella by its natural enemies.

Introduction

The black headed caterpillar, Opisina arenosella (Walker) (Lepidoptera: Oecophoridae), is an important pest that feeds on the leaves of coconut palm, Cocos nucifera (L.) (Arecaceae), making galleries of silk and frass on the leaf under-surface and causing severe yield loss. The most important infestations occur in November to May each year (Sreekanth & Muralimohan, 2013; Shameer et al., 2018). Attempts to control O. arenosella have been made by applying chemical pesticides, via stem injection or via spraying, but this has had adverse non-target effects. Biological control, using natural enemies, has provided an effective alternative and can deliver long-term sustainable pest management (Sujatha & Singh, 1999) and avoids detrimental side effects of pesticides on the environment (Roince et al., 2012).

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One of the principal parasitoids of *O. arenosella* is *Goniozus nephantidis* (Muesebeck) (Hymenoptera: Bethylidae) (Cock & Perera, 1987; Sujatha & Singh, 1999; Sreenivas & Hardy, 2016; Shameer et al., 2018). Adult females enter the galleries constructed by feeding *O. arenosella* larvae and paralyze them by stinging. Around 1 day later, they lay a clutch of 5–18 eggs onto the host's outer surface. The eggs hatch the following day and the larvae feed on the host via punctures in its integument. Unusually for parasitoids, the mother wasps remain with their broods for around 5 days after laying eggs, guarding the brood against other foraging *G. nephantidis* females (intruders), which they attempt to drive away via agonistic contest behaviour (Hardy & Blackburn, 1991; Petersen & Hardy, 1996; Stokkebo & Hardy, 2000; Sreenivas & Hardy, 2016, see also Abdi et al., 2020). Such behaviour successfully decreases, but does not always prevent, infanticide and super-parasitism by 'intruder' females (Hardy & Blackburn, 1991; Venkatesan, 2009). Due to the large amount of time invested in brood defence, it is unlikely that females survive for long enough to produce more than one or two broods in their lifetimes (Cock & Perera, 1987) and thus the attack rate of hosts is relatively low. Nonetheless, augmentative field releases of mass reared *G. nephantidis* are found to effect successful biological control. Other species of *Goniozus* with similar brood-guarding behaviour have also been successfully deployed as, or considered as, agents of biological pest control in further agro-ecosystems worldwide (e.g., almonds in southwestern USA – Legner & Gordh, 1992, Gianessi, 2009; vines in Australia – Paull & Austin, 2006, Aspin et al., 2021; date palm in Oman – Polaszek et al., 2019).

One of the most important predators of *O. arenosella* larvae are hemipteran bugs in the genus *Cardiastethus* (Anthocoridae). This cosmopolitan genus includes important biocontrol agents of agricultural pests (Yamada et al., 2008). Individual *Cardiastethus* have been found preying on *O. arenosella*, within their silken galleries (Nasser & Abdurahiman, 1990, 1998; Kumar, 2002) and are efficient at reducing populations of *O. arenosella* (Lyla et al., 2006; Venkatesan et al., 2008).

Given that *G. nephantidis* and *C. exiguus* are both beneficial natural enemies of *O. arenosella*, the net effect of both being present may be to enhance control (specifically, a reduction in pest population density and the consequent reduction in economic damage). However, population dynamic theory and analyses of biocontrol case histories both indicate that the presence of multiple natural enemies in agro-ecosystems can be disruptive under some circumstances and that the best long-term suppression of hosts may be achieved by just one species of biocontrol agent (Denoth et al., 2002; Pérez-Lachaud et al., 2004; Batchelor

et al., 2006; Murphy et al., 2018). Overall, it is seldom possible to predict with confidence the optimal combination of biocontrol agents to deploy in a particular agro-ecosystem without empirical assessment of the competitive interactions between the various species of agents available.

Contest interactions between *Goniozus* females and other *Goniozus* females have been studied extensively, exploring the effect of variation in contestant weight, age, host value, and intruder or owner roles (e.g., Humphries et al., 2006; Bentley et al., 2009; Venkatesan et al., 2009; Hardy et al., 2013), but little is known about behavioural and ecological interactions between *Goniozus* and predators. *Cardiastethus* species and *G. nephantidis* are present in coconut crops throughout the year and higher parasitism rates are normally observed between February and March (Sujatha & Singh, 1999; Kumar, 2002). Venkatesan et al. (2008) showed that *G. nephantidis* and *C. exiguus* may be combined or used alone against *O. arenosella* and can provide pest control in all cases, but the relative advantages of the various combinations of natural enemies are unknown.

Goniozus nephantidis females may be able to drive foraging *C. exiguus* away from the vicinity of their host, via biting and stinging and possibly also via the release of volatile chemicals (Goubault et al., 2008), but it may be that *C. exiguus* is able to resist, and even overcome, guarding females and subsequently consume both the *O. arenosella* larvae and the developing *G. nephantidis* brood [as observed in the congener *Cardiastethus affinis* (Fieber); Srinivasa, 1996; Cock & Perera, 1987]. The outcomes of direct behavioural interactions between guarding *G. nephantidis* females and foraging *C. exiguus* are thus likely to influence resource use by individuals and the population dynamics of these species, which will in turn have consequences for biological control. Here we examine direct contest competition between these parasitoid and predator species and consider how their interspecific interactions might affect crop pest control.

Materials and methods

Insects
Hosts were the larvae of the rice moth, *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae), a suitable factitious host for laboratory studies (Petersen & Hardy, 1996), reared on a diet of semolina (following Shameer et al., 2002). Parasitoids were female *G. nephantidis* using a culture, established in the laboratory of NM at the University of Calicut, of a strain obtained from ICAR-NBAIR (Indian Council of Agricultural Research, National Bureau of Agricultural Insect Resources, Bangalore, India). Females used in experiments were of known size (measured under

a Luxeo 4Z binocular stereo-microscope; Labomed, Los Angeles, CA, USA) and had been kept with males since emergence and were thus assumed to be mated. They were fed using a small piece of card soaked with 50% honey solution, which was changed every 3 days. When females were 5 days old, they were used in experiments and had had no prior oviposition experience; however, 5-day-old females typically have matured a compliment of eggs (Sreekanth & Muralimohan, 2013).

As predator we used mated adult female *Cardiastethus exiguus* (Poppius) (Hemiptera: Anthocoridae), following Ballal et al.'s (2012) guide to identify adult females. Females were of known size and aged 1–4 weeks. *Cardiastethus exiguus* can lay eggs for up to 11 weeks and can live for 48–100 days (Nasser & Abdurahiman, 1990; Ballal et al., 2012). We also used fourth and fifth stage nymphs, these actively forage for prey and can encounter brood-guarding wasps. Predators were maintained in ventilated glass beakers with cotton strands to allow oviposition and avoid cannibalism; they were fed ad libitum on *C. cephalonica* eggs obtained from ICAR-NBAIR.

All rearing and experiments were carried out under laboratory conditions at 33 ± 4 °C, 65–70% r.h., and L12: D12 photoperiod. In all experiments, individual insects were used only once to avoid pseudo-replication.

Contest experiments

Inter-specific contests. We used small arenas to observe parasitoid–predator contest behaviour. These were glass Petri dishes (9 cm diameter, 1.5 cm high) into which we put an individual fourth or fifth instar host larva. We then allowed an individual female parasitoid to attack and paralyze the larvae, and lay eggs on them, leaving them undisturbed for 24 h: this is the normal time-frame for *G. nephantidis* host attack and oviposition (Shameer et al., 2018) and females remain with their hosts for several days after egg laying (Petersen & Hardy, 1996; Takasu & Overholt, 1998; Goubault et al., 2007). After 24 h, a predator was introduced into the arena and behavioural interactions were observed for 3 h (following Petersen & Hardy, 1996) or until the contest was clearly resolved, e.g., one contestant was killed. Some behavioural interactions were recorded from above using digital Sony video cameras. Before and after each observation we counted the parasitoid eggs laid onto each host; differences indicated the numbers of eggs that were consumed by the predators. From each replicate, we recorded the numbers of touches, stings, bites, chases, or other physical interactions during the contest (Pérez-Lachaud et al., 2002; Goubault et al., 2008) and whether winners kill their opponent (Velasco-Hernández et al., 2013). We also recorded whether the contest was resolved and, if so, which individual won and

the time taken for resolution. Following Humphries et al. (2006), we considered a winner to be the individual in possession of the host at the end of the initial series of encounters (although we note that losers that are not killed may subsequently return to attempt to exploit the host resource).

Replicates were set up to observe (1) parasitoid–predator contests in the presence of a host (n = 20 for adult predators, n = 20 for nymphal predators), (2) a parasitoid and an adult predator without a host larva present (n = 11), (3) a parasitoid and a nymphal predator without a host larva present (n = 12), (4) an adult predator provided with a host larva that had parasitoid eggs laid onto it but with the parasitoid removed (n = 20), (5) a nymphal predator presented with a host larva with parasitoid eggs laid with the parasitoid removed (n = 20), and (6) an undisturbed parasitoid with a host larva (n = 20). The latter three sets of replicates allowed us to evaluate predation on parasitoid eggs in the absence of a guarding wasp and the probability of a *G. nephantidis* ceasing to brood-guard if undisturbed.

Intra-specific contests. Predator–predator contests were set up between pairs of mated adult female *C. exiguus*. Pairs of predators were confined in Petri dishes (as above) and provided with either early (first or second) instar *C. cephalonica* larvae (n = 20 replicates) or no prey (control, n = 20). We repeated the experiment using late (fourth or fifth) instar *C. cephalonica* larvae (n = 20) as prey or no prey (control, n = 20). When late instars were used, we first allowed them to be paralyzed by a *G. nephantidis* female (and then removed the wasp). We recorded behaviours exhibited by the predators, e.g., whether or not they fought and, if so, the numbers of fights, bites (a predator's mouthparts were extended towards and contacting the other predator), and touches (contacts using the antennae) during the contest and whether one predator consumed the other.

Statistical analysis

Data analysis was carried out in the GenStat statistical software package (19th edn, VSN International, Hemel Hempstead, UK). MANOVAs were used to evaluate whether the behavioural profiles observed differed across treatments. As MANOVA assumes normally distributed errors and homoscedasticity, we transformed data prior to analysis. For inter-specific contests, we $\log_{10}(x + 1)$-transformed data on touches and $\ln(x)$-transformed data on bites. For intraspecific contests, data on bites and fights were $\sqrt{x}$-transformed. After carrying out MANOVAs, effects of treatments on the frequencies of individual behaviours were analysed using

log-linear modes, and effects on the proportion of eggs surviving with logistic models.

Results

Inter-specific contests

Parasitoids with a host never left the vicinity of the host. In all cases with hosts present, parasitoids initially won contests for the host by attacking the predators. In one replicate, the parasitoid killed the predator by repeatedly stinging it until it ceased to move. Although parasitoids were aggressive towards adult predators, adult predators were never aggressive towards parasitoids. Predators typically appeared to attempt to escape from the parasitoid by moving away rapidly but sometimes remained very still, apparently to avoid detection. Although parasitoids won the initial direct contests, predators always returned to the vicinity of the host to feed on it or, apparently, to hide from the parasitoid near it. As parasitoids and predators were typically active through the observation periods, the time until resolution was indeterminate and not analysed.

The profile of behavioural interactions between parasitoids and adult predators was greatly affected by the presence of a host (MANOVA: Wilks' $\lambda = 0.5581$, $F_{4,26} = 5.15$, $P = 0.003$; Figure 1A). The number of touches was not affected by the presence or absence of the host (log-linear ANOVA: $F_{1,30}<0.01$, $P>0.95$). The number of bites was higher when a larva was present ($F_{1,30} = 34.70$, $P<0.001$). Similarly, the number of stings and chases were higher in the presence of a larva (stings: $F_{1,30} = 29.76$; chases: $F_{1,30} = 32.64$, both $P<0.001$) and, in

fact, these behaviours were not displayed at all when larvae were not present (Figure 1A).

The presence of a host larva also affected the profile of behavioural interactions when parasitoids were paired with nymphal predators (MANOVA: Wilks' $\lambda = 0.6392$, $F_{4,27} = 3.81$, $P = 0.014$; Figure 1B). There were more touches when larvae were present than when larvae were absent ($F_{1,31} = 8.71$, $P = 0.006$) and bites, stings, and chases occurred only in the presence of larvae (bites: $F_{1,31} = 15.09$, $P<0.001$; stings: $F_{1,31} = 7.51$, $P = 0.010$; chases: $F_{1,31} = 28.02$, $P<0.001$). Despite the aggression exhibited by the parasitoids, nymphal predators were often able to hide motionless underneath the larvae and thus avoid parasitoid attack and were, consequently, also able to feed on the larvae.

The proportion of initially present parasitoid eggs consumed by the predator at the end of the observation period was negatively affected by the presence of the parasitoid (two-way logistic ANOVA: $F_{1,78} = 29.5$, $P<0.001$; Figure 2), but was not affected by the developmental stage of the predator ($F_{1,77} = 0.39$, $P = 0.54$) or by an interaction between predator stage and parasitoid presence ($F_{1,76} = 2.7, P = 0.11$).

Intra-specific contests

Although no instances of mortality were observed, pairs of adult predators often interacted aggressively. One individual often appeared to avoid attack by the other by moving away but also sometimes an apparently weaker competitor remained motionless, as observed in encounters with *G. nephantidis*.
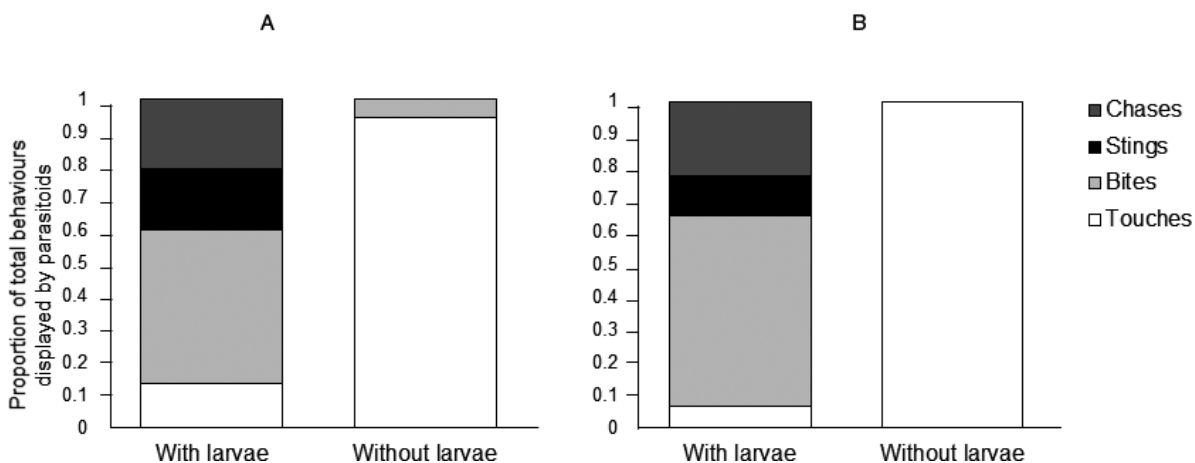

Figure 1 Behavioural profiles of parasitoids in parasitoid–predator interactions with and without host larvae present: (A) adult predators, (B) nymphal predators. All behaviours were displayed by the parasitoid and directed towards the predator. 'Touches' were when parasitoids contacted the predator with their antennae without displaying aggression.
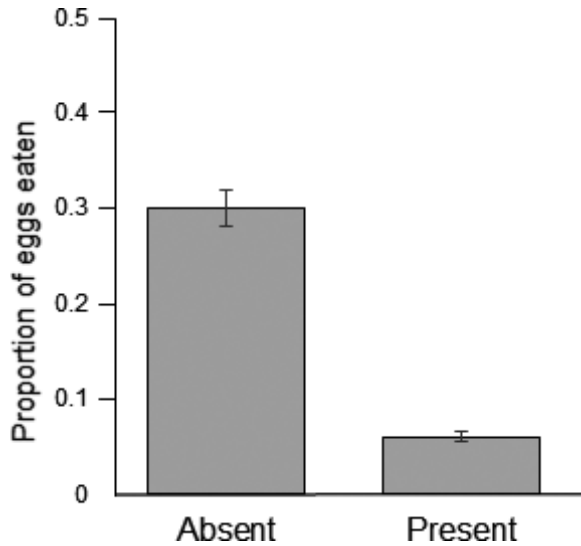
Figure 2 Mean ($\pm$ SE) proportion of parasitoid eggs eaten by predators when parasitoids were absent or present.

The presence or absence of an early instar did not affect the overall profile of behaviours (MANOVA: Wilks' $\lambda = 0.8735$, $F_{3,36} = 1.74$, P>0.05; Figure 3) and there were no differences in the numbers of each of the behaviours expressed (touches: $F_{1,39} = 0.14$, P = 0.71; bites: $F_{1,39} = 0.10$, P = 0.75; fights: $F_{1,39} = 2.66$, P = 0.11). For late instars, the numbers of touches or fights were not affected (touches: $F_{1,39} = 1.17$, P = 0.29; fights: $F_{1,39} = 0.77$, P = 0.39) but bites were more common when larvae were absent ($F_{1,39} = 13.49$, P<0.001) and the

overall profile of behaviours was different (MANOVA: Wilks' $\lambda = 0.8013$, $F_{3,36} = 2.98$, P<0.05; Figure 3).

In most replicates with a *C. cephalonica* larva provided, both predators fed upon it simultaneously. When the *C. cephalonica* larva was unparalysed (early instar replicates) it often moved actively away from encounters with the predators.

Discussion

Individual natural enemies can encounter each other whilst foraging for limited resources and, as pests in agri-field conditions are often attacked by an array of natural enemies, both intra- and inter-specific competitive interactions may result (Batchelor et al., 2005; Venkatesan, 2009; Boivin et al., 2012; Benelli, 2015). Most prior studies of contests during inter-specific interactions have focused on parasitoid–parasitoid encounters (Hardy & Blackburn, 1991; Bográn et al., 2002; Pérez-Lachaud et al., 2002; Batchelor et al., 2005; Venkatesan et al., 2009; Mohamad et al., 2011, 2015; Vankosky & Hoddle, 2017; Yang et al., 2018) with fewer considering direct resource competition between parasitoids and predators (Sloggett et al., 1998; Sloggett & Majerus, 2003; Venkatesan, 2008). This study explored inter-specific encounters between *G. nephantidis*, a parasitoid species well known to engage in intra-specific contests for host larvae (Humphries et al., 2006; Goubault et al., 2007; Hardy et al., 2013) and *C. exiguus*, a generalist predator present in the same agro-ecosystem (Nasser & Abdurahiman, 1990, 1993; Venkatesan, 2008), and also documented intra-specific competitive interactions
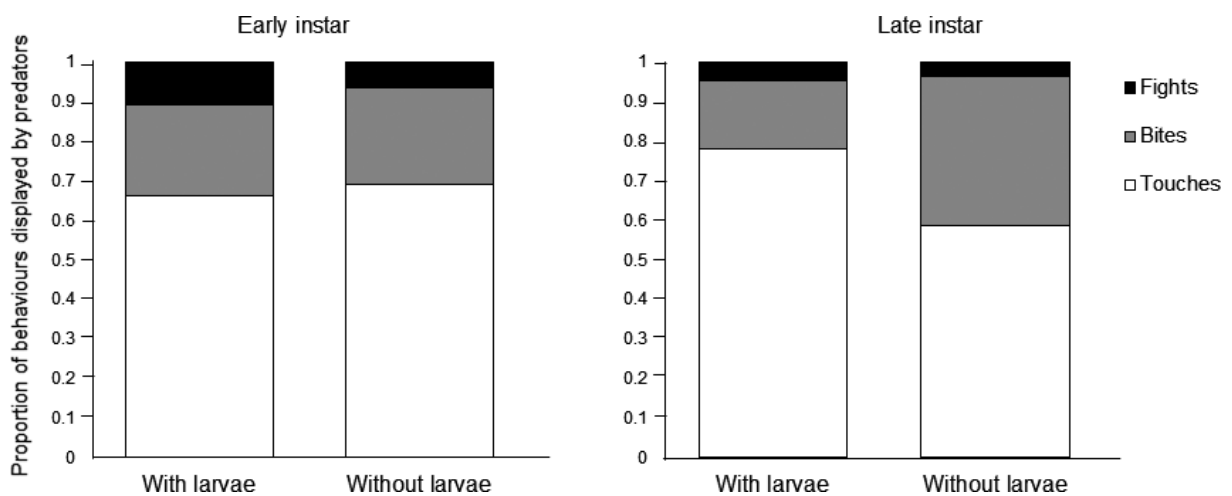

Figure 3 Behavioural profiles of predators in interactions between pairs of adult predators with and without early instar larvae (left panel) or (paralyzed) late instar larvae (right panel) present. 'Bites' were when a predator's mouthparts were extended towards and contacting the other predator, 'touches' were contacts using the antennae.

between *C. exiguus* individuals. Behavioural interactions between these species have not previously been evaluated; however, Nasser & Abdurahiman (1998) found that populations of both species are present with *O. arenosella* in coconut plantations.

Inter-specific contests

During parasitoid–predator encounters, parasitoids were active, searching for intruders and driving them away but rarely leaving the vicinity of the host for prolonged periods. The behaviours exhibited were essentially similar to those observed when *G. nephantidis* attempt to protect their hosts and broods against conspecific females (Stokkebo & Hardy, 2000; Goubault et al., 2007; Hardy et al., 2013). Touches occurred as commonly when hosts were absent as when they were present but escalation to aggression (chasing, stinging, and biting) was very rare when hosts were absent. *Goniozus nephantidis* probably uses touches as a means to establish the identity of an encountered individual via assessment of the chemical composition of its integument and then responds according to this information and to the value of any resource present (Humphries et al., 2006; Lizé et al., 2012; Khidr et al., 2013; Stockermans & Hardy, 2013). Similarly, in crickets antennal fencing provides a means to assess the identity and the state of an opponent and to decide whether or not to escalate to fighting (Hofmann & Schildeberger, 2001). When there was no resource present, the costs of escalated contests could not be offset by benefits accruing from utilizing the resource, and thus aggression by *G. nephantidis* towards *C. exiguus* is only likely to be selectively favoured when hosts are present (Arnott & Elwood, 2008; Stockermans & Hardy, 2013). Both adult and nymphal stage predators responded to the parasitoid aggression by trying to actively escape from or to avoid the parasitoid but sometimes instead remained motionless; these behaviours represent different means of reducing further attack (Sih, 1982; Barnard, 1983; Miyatake, 2001; Mohamad et al., 2012; Stevenson & Rillich, 2019). For instance, motionless behaviour in the predatory ladybirds *Coccinella magnifica* Redtenbacher (adults and larvae) and *Coccinella septempunctata* L. has been found to reduce attack by *Formica rufa* L. ants (Sloggett et al., 1998; Sloggett & Majerus, 2003).

Whereas we found that *G. nephantidis* was behaviourally dominant over *C. exiguus*, other studies of interactions between predators and parasitoids of a common host (prey) have reported parasitoids being killed by the predator (Traugott et al., 2012; Velasco-Hernández et al., 2013) and parasitoids have been found to avoid areas where predators are present (Meisner et al., 2011). Although the outcomes of such interactions may require separate evaluation for each combination of species considered, we suggest that, in general, dominance will be influenced by the interplay of several selective factors. First, the relative physical challenges faced by the predator and by the parasitoid in suppressing prey or hosts, as these may have selected for morphological and behavioural adaptations that can also play a role during intra-guild interactions. Second, the relative importance of intra-specific competition, which can also select for contest ability. Third, the relative importance of the contested host as an essential resource: to generalist predators and parasitoids, that attack a range of prey/host species and encounter a possibly wide array of competing natural enemies, selection for the ability to compete for any particular one of them against any particular opponent species may be weaker than among predators and parasitoids with narrow diet ranges. In the inter-guild interactions studied here, *G. nephantidis* may be dominant over *C. exiguus* because it has a narrower diet range and may more commonly experience intra-specific contest competition. Irrespective of the selective factors that led to the current environment, two asymmetries were present that favoured *G. nephantidis*: adult female *G. nephantidis* (mean length = 4.9 mm) are larger than *C. exiguus* nymphs (2.1 mm) and adults (2.9 mm), with larger size often being advantageous in animal contests, including those involving *G. nephantidis* (Petersen & Hardy, 1996; Humphries et al., 2006; Hardy & Briffa, 2013; Rosa et al., 2018; Guerra-Grenier et al., 2020), and *G. nephantidis* females had established ownership of the host prior to the introduction of the predator; again, prior owners tend to be advantaged (Maynard Smith & Parker, 1976; Petersen & Hardy, 1996; Hardy et al., 2013; Kokko, 2013).

Despite *C. exiguus* being dominated in encounters with *G. nephantidis*, some parasitoid eggs on ostensibly defended hosts were consumed by the predators (with a lack of difference between nymphs and adults indicating a lack of age-dependent prey specialization; Jaworski et al., 2013), as observed in the congener *C. affinis* (Cock & Perera, 1987; Srinivasa, 1996) and other systems where parasitoids and predators attack the same herbivore (e.g., Colfer & Rosenheim, 2001). Similarly, observations of inter-specific interactions between *G. nephantidis* and the competing parasitoid *Bracon hebetor* Say showed that brood-guarding was only partially successful (Hardy & Blackburn, 1991). In both cases, the physically inferior competitor of *G. nephantidis* obtained resources by persistence beyond the initial encounter. Similar patterns of short-term and longer-term competitive outcomes have been found in other studies of interspecific contests between parasitoids (Mohamad et al., 2012).

As *C. exiguus* consumed parasitoid eggs, this feeding interaction constitutes a form of intra-guild predation (IGP) (Rosenheim et al., 1995; Lucas et al., 1998; Pérez-Lachaud et al., 2004). IGP is generally considered detrimental to biological control because the beneficial actions of natural enemies are interfered with by negative interactions (Kester & Jackson, 1996; Pérez-Lachaud et al., 2004; Meyling et al., 2004; Batchelor et al., 2005, 2006; Naranjo, 2007; Sohrabi et al., 2013) decreasing at least one of the competitor populations and leading to an increase in the pest population. However, according to Venkatesan et al. (2008), *C. exiguus* released together with *G. nephantidis* can control the pest *O. arenosella* populations, suggesting that disruptive competitive parasitoid–predator interactions may not actually be very frequent in the field.

Intra-specific competition

Pairs of adult *C. exiguus* predators were aggressive towards each other, with fights and bites observed in all experimental combinations. As in interactions with *G. nephantidis*, the apparently less competitive *C. exiguus* individual either actively moved away from the other or remained motionless. Intra-specific aggression did not, however, result in any fatalities (consistent with results from studies on other predatory hemipterans; Tommasini et al., 2003). Individuals may compete for access to a food item but interactions may also represent attempts at cannibalism – previously reported in *C. exiguus* (Nasser & Abdurahiman, 1993) and in many other predator species (Polis, 1981; Hironori & Katsuhiro, 1997) – and the observed highest frequency of biting when no larva was provided fits the notion that scarcity of other food sources can increase cannibalism (Arvaniti et al., 2019). As the individuals had not been starved prior to the experiment their motivation to engage in costly interactions may have been relatively weak (Taylor & Schmidt, 1996) and when a *C. cephalonica* larva was provided it was large enough for both predators to feed simultaneously, rather than being an indivisible resource. Similarly, short term aggression between *G. nephantidis* females rarely leads to fatalities (Humphries et al., 2006) and over longer time-scales larger hosts are more likely to be shared with lower fatality rates (Abdi et al., 2020). In contrast, in the predatory mite *Phytoseiulus persimilis* Athias-Henriot, intraspecific competition has been found to lead to a decline in numbers even when prey is abundant (Schausberger & Walzer, 2001).

Conclusion

Behavioural interactions between the parasitoid *G. nephantidis* and the predator *C. exiguus*, which both attack the coconut pest *O. arenosella*, showed that parasitoids were aggressive towards the predators, sometimes killing them, but not vice versa (although predators were non-fatally aggressive towards each other). However, predators were sometimes able to feed on immature parasitoids, despite the presence of a guarding mother. These parasitoid–predator interactions are likely to interfere with the biological control of *O. arenosella*.

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