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BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Host specialisation and competition asymmetry in coleopteran parasitoids

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Abstract When specialists and generalists compete for a limited resource, specialists are more constrained because they are less likely to find an alternative resource. In parasitoids with overlapping host ranges, asymmetric competition should therefore exist where specialists are more likely to win the host in a contest. Competition between parasitoids has been studied mostly in hymenopterans. In hymenopteran parasitoid wasps, females must reach the host to lay their eggs and can thus strongly influence the outcome of competition between future offspring by killing eggs or larvae of competitors. We studied competition between the free-ranging larvae of two sympatric coleopteran parasitoid rove beetles (one specialist, *Aleochara bilineata* and a generalist, *Aleochara bipustulata*) with overlapping host ranges competing in agricultural fields for pupae of the cabbage root fly. In these species, females lay their eggs in the soil, then first instars find the host where they will develop as solitary parasitoids and deal with potential competitors. Because adult longevity and fecundity favour the generalist, we postulated that first instars of the specialist would be superior larval competitors. Accordingly, we studied the outcome of encounters between first instars of the two species provided with a single host. Irrespective of its release prior to or simultaneously with its generalist competitor, the larva of the specialist most often won. Moreover, specialist larvae still won half of the encounters when generalist larvae were given a 24-h advantage. This might explain the coexistence of the two species in the field.

Keywords Interspecific competition · Larval competition · Species coexistence · Niche partitioning · Resource limitation

Introduction

Interspecific competition is a strong evolutionary force driving the composition of ecological communities (Schoener 1983). Defined as the exploitation of the same limited resources by different species, it can lead to the disappearance or displacement of weaker competitors if resources are not shared or if they are limited in space and/or time (Gause 1934; Sorribas et al. 2010). Nevertheless, many competing species coexist successfully and previous studies have revealed several mechanisms allowing them to share limited resources, such as spatio-temporal resource partitioning, ecological character displacement or change in the resource spectrum (MacArthur 1972; Brown and Wilson 1956; reviewed in Dayan and Simberloff 2005). More recently, Hubbell (2005) showed by modelling that numerous equivalent species competing for the same resource can both evolve and then coexist in a community if they are both dispersal and recruitment limited. When a limited resource cannot be shared between two individuals, the choice of behavioural responses is to escape or fight (Yamauchi et al. 2005). The investment of species in competitive abilities is strongly influenced by their capacity (1) to find resources in other environments (i.e. their dispersal ability), and (2) to find

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alternative resources in the same environments (i.e. their degree of specialization) (Tilman 2000). Specialist species (exploiting a narrow range of resources and environments) have less alternative options than generalist species (which can use a larger range). If dispersion is limited, or if no alternative resources are available, fighting is the best way to overcome competition. Accordingly, specialists bear a stronger selective pressure to fight instead of avoiding competition. Theory thus predicts that specialist species will invest more in competition and produce better competitors than generalist species which, on the other hand, are expected to be better dispersers than specialists because they are more likely to find alternative resources elsewhere (MacArthur 1972; Force 1972, 1974; Strickler 1979; Hassell and May 1986).

Parasitoids are insects that complete their larval development to the detriment of a single arthropod host, which they kill in the process (Eggleton and Gaston 1990). Studies on parasitoid guilds have shown that many parasitoid species can share the same host species through differences in life history traits and behaviours that mitigate the competitive exclusion between species (Elzinga et al. 2007; Amarasekare 2000; Pérez-Lachaud et al. 2002; Ives 1988). In agreement with the above specialist/generalist theory of competition, specialist parasitoids bear a stronger selective pressure than generalists to become strong competitors because in competition for a limited resource they have fewer or no alternative hosts. Therefore competition may generate strong selective pressure on parasitoid populations and shape host-exploitation strategies in these organisms. Competitive asymmetry where host specialists will dominate generalists in the case of direct competition in or on a host could evolve.

Due to their high species diversity, hymenopteran parasitoids have been the subject of most parasitoid competition studies (reviewed in Harvey et al. 2013; Hardy et al. 2013); far less information is available on dipteran or coleopteran parasitoids, which have a different biology (Reader and Jones 1990; Schmid-Hempel and Schmid-Hempel 1996; Iwao and Ohsaki 1996; Brodeur and Boivin 2004). In particular, these two latter orders are very different from hymenopterans with respect to the developmental stage when contacting the host because, in some cases, it is the mobile first instars (and not the adult females) that search for, evaluate and penetrate the host where they will develop (Godfray 1994; Feener and Brown 1997). Compared to adults, these larvae have poor dispersion abilities, meaning that any host found is a very valuable resource unless hosts are found in large groups (as happen in necrophagous or coprophagous flies). Accordingly, the selective pressure due to competition among specialists and generalists should be even stronger in these parasitoid larvae, making them particularly appropriate models to test the relation between ecological specialisation and competition asymmetry.

Competition between larvae for the same host will take place during superparasitism when the host is parasitised by larvae of the same species (van Alphen and Visser 1990) or during multiparasitism when competitors are of different species (Fisher 1961). The durable coexistence of larvae in a single host is only found in gregarious parasitoid species, where each larva will remain confined to a small part of the host body, without agonistic interactions (Boivin and van Baaren 2000) and few studies even reported host-sharing by two solitary larvae (Goubault et al. 2003; Harvey and Strand 2003). However, most parasitoid species are strictly solitary, meaning that the host allows the development of a unique immature parasitoid and most cases of multiple parasitism lead to the elimination of supernumerary larvae through chemical or physical competition within the host (Fisher 1961; Shi et al. 2004; Tian et al. 2008).

The two rove beetles *Aleochara bilineata* and *Aleochara bipustulata* (Gravenhorst) (Coleoptera; Staphylinidae) are ground-dwelling parasitoids of dipteran pupae. *A. bilineata* is a specialist parasitoid of cyclorrhaphous flies of the genus *Delia* including the cabbage root fly *Delia radicum* L. (Diptera: Anthomyiidae) which is a pest of brassicaceous crops (Maus et al. 1998). *D. radicum* pupae are never very abundant, even in the roots of a large cultivated plant, with typically a few pupae per infested plant and most plants being uninfested. So on a given plant this resource can be considered as severely limited. The close species *A. bipustulata* is more of a generalist as it can parasitise *Delia* sp. in cultivated brassica fields but, unlike *A. bilineata,* it can also use as hosts other phytophagous, saprophagous, coprophagous or necrophagous flies, belonging to various families, such as *Piophila casei*, *Musca domestica*, *Lucilia sericata* and *Ravinia pernix* (Maus et al. 1998). Among these alternative hosts, necrophagous and coprophagous ones typically occur in large groups on temporary but rich patches of decaying organic matter. Adults of both parasitoid species are predators of host eggs and larvae (Fuldner 1960). In Brittany, both *Aleochara* species are found at the same time in the same crop fields (where most available hosts will be *D. radicum* pupae) and competition between these two species can occur (Josso 2012). In agreement with the relationship between specialisation and competition asymmetry (MacArthur 1972), we postulate that the specialist *A. bilineata* is a stronger larval competitor than its generalist competitor. Indeed, since *A. bilineata* has a lower fecundity and longevity, it does not benefit from alternative hosts and is often less abundant in the field (Fournet et al. 2000; Maus et al. 1998; Josso 2012); being a superior larval competitor could compensate for its handicaps in adult traits. Such larval superiority would explain why, despite its abundance, *A. bipustulata* does not exclude *A. bilineata* from these agricultural habitats. An argument in favour of our hypothesis is that *A. bilineata* more often penetrates hosts already parasitised by *A. bipustulata* than the reverse (Fournet et al. 1999).

The aim of the present study is to evaluate the outcome of larval competition between two species with overlapping ecological niches and different degree of specialization, to test the prediction that the specialist will be the better competitor. Our results may also help to explain the coexistence between these two species. To establish experimentally which species is the best larval competitor, we determined the final outcome of competition between one *A. bilineata* larva and one *A. bipustulata* larva competing for a single healthy host. The two conditions tested were: simultaneous release of both larvae in the setup; and a 24-h delay between each release because being first to penetrate the host gives an advantage, and the superior competitor might be able to neutralise such an advantage in the weaker competitor.

Materials and methods

Parasitoid biology

Unlike nearly all hymenopteran parasitoids, coleopteran females do not have a piercing ovipositor. Accordingly, they lay their eggs in locations harbouring hosts. The first instars actively search for and parasitise the host (Fournet et al. 1999). The larva enters the hardened puparium of the fly host by cutting a hole with its sharp mandibles. Then, it settles in the vicinity of its entrance hole and starts feeding. Finally, it excretes a viscous substance through the anus and uses it as a plug to seal the hole (Fuldner 1960; Royer et al. 1998). The plugging process is variable and lasts 18–48 h; it prevents easy entry for pathogens and competitors (Colhoun 1953; Fuldner 1960). Larvae of one species are able to discriminate pupae parasitised by the other from healthy pupae and when given the choice, time and enough physiological reserves, they will avoid such previously parasitised pupae (Royer et al. 1999).

Insect rearing

Host strain

The *D. radicum* population was established in 2011 from pupae collected in broccoli fields at Le Rheu, Brittany, France (48°07′16″N, 1°47′41″O). It was refreshed yearly with wild individuals from the same location. The strain was maintained on swede roots (*Brassica napus*) following a method derived from van Keymeulen et al. (1981).

Parasitoid strain

A. bilineata and *A. bipustulata* strains were established in 2009 from parasitised *D. radicum* pupae collected in broccoli fields at Paramé, Brittany (48°39′28, 12″N, 1°58′55, 65″O). Adults of each species were kept in separate plastic boxes (16 × 9.5 × 8 cm) filled with moistened vermiculite containing *D. radicum* pupae, minced beef ad libitum as the food source and covered with a wet paper towel. Once a week, adults were collected from the rearing box and placed in another one with fresh pupae. Parasitised pupae were recovered and stored separately until parasitoid emergence. Emerging adults were either used for maintaining the rearings or for the experiments.

Immature parasitoid production

For each species, ten to 20 females were placed with males in boxes (diameter 10 cm, height 9.5 cm) filled with moistened vermiculite with wet cotton and minced beef ad libitum as water and food source, respectively. Two to three times a week, vermiculite was sifted (diameter 0.8 mm) and the finest fraction containing the eggs was examined under the binocular. Eggs were collected with a brush and placed individually in a Bleem capsule (Agar Scientific, Essex, England; diameter 0.7 mm, length 1.4 mm). Twenty to 30 capsules were placed together in a Solo Cup (Urbana, IL; diameter 4.2 cm, height 3.2 cm), humidified with a water spray and stored for 10 days in controlled conditions (20 ± 1 °C, 60 ± 10 % relative humidity and a 16-h:8-h light:dark photoperiod). The capsules were monitored daily for hatched larvae and the Solo Cup was humidified.

Preparation and monitoring of experiments

Two larvae aged less than 24 h, one of each *Aleochara* species, were placed with a small moist brush on the surface of the vermiculite, either simultaneously or at an interval of 24 h with 193–256 replicates per treatment. On any given day of the experiment, the same number of replicates with *A. bilineata* first and *A. bipustulata* first were carried out. Pupae were observed under the binocular microscope after 5 days and the number of larvae visible though the translucent puparium were counted. Then, pupae were replaced in the Solo Cup and were stored again in a climatic chamber as above until emergence of parasitoids (30–45 days). The variables measured were: (1) percentage of unparasitised hosts, (2) percentage of hosts parasitised by one larva, (3) percentage of hosts parasitised by both larvae, (4) intra-host mortality (i.e. percentage of parasitised host failing to yield a parasitoid), (5) percentage of each species emerging from parasitised hosts (in the case of multiparasitism, only one parasitoid can develop per host).

Statistical analysis

Total proportions of parasitism and proportions of hosts with one or two larvae inside were compared between experimental treatments by using a generalised linear model assuming a binomial error (quasibinomial error in the case of overdispersed data) and a logit link function. Using the same statistical modeling, proportional mortality and proportion of emerging *A. bilineata* were compared between hosts with one or two larvae inside and treatments and the interaction term between these two factors. To assess the significance of a model term, we used a likelihood ratio test, and when a term was significant, pairwise comparisons between levels were performed with the function esticon in the doBy package (contrast method; author, Søren Højsgaard).

The proportion of *A. bilineata* emerging from host puparia that produce parasitoid adults was analysed using exact binomial tests for each treatment and were compared to our null hypothesis ($P = 0.5$). Statistical tests were employed at a critical level of $\alpha = 0.05$ and performed using R version 3.10 (R Core Team 2014).

Results

Nearly all hosts were parasitised by at least one larva [95 % confidence interval (CI) 94–97 %] (Fig. 1). In the 5 % of remaining cases, both larvae must have died of starvation or combat before penetrating the host and this proportion did not differ significantly between treatments ($\chi^2 = 0.46$, $df = 2$, $P = 0.79$). In half of the parasitised hosts, two larvae were visible inside the host (CI 44–52 %) and this proportion varied between treatments overall ($\chi^2 = 6.4$, $df = 2$, $P = 0.042$). In pairwise comparisons, this proportion was significantly lower when the two larvae were released simultaneously compared to when *A. bilineata* larvae had a 24-h head start (38 vs. 49 % when *A. bipustulata* larvae were released first; Fig. 1).

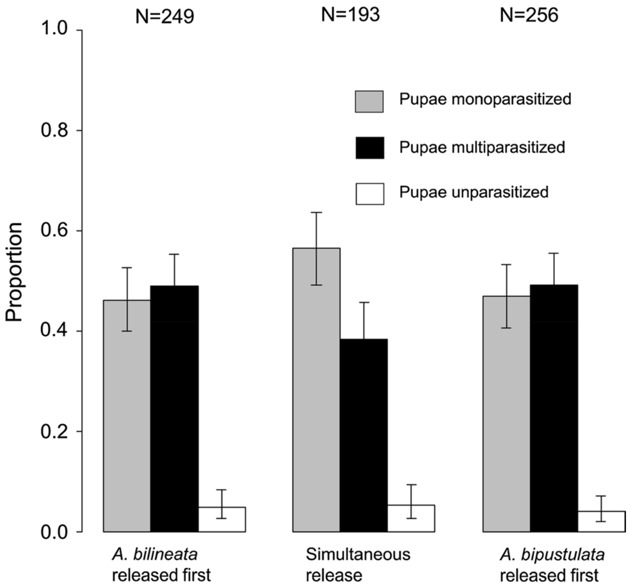

Fig. 1 Proportion of pupae parasitised by both larvae (*black*), one larva (*grey*) or unparasitised (*white*). *Left panel Aleochara bilineata* larva released 24 h before its *Aleochara bipustulata* competitor. *Middle panel* Two larvae released simultaneously. *Right panel A. bipustulata* larva released 24 h before its *A. bilineata* competitor. *Vertical bar* 95 % confidence interval (CI)

Emergence of each species differed according to the order in which larvae of each species was released into the experimental devices ($\chi^2 = 33$, $df = 2$, $P < 0.001$). When *A. bilineata* larvae were released 24 h before their *A. bipustulata* competitors, *A. bilineata* represented over 80 % of emerging parasitoids, irrespective of whether one or two larva were visible inside the host (CI 72–89 % and 71–89 %, respectively). When the two competitors were released simultaneously, most of the recovered adults were again *A. bilineata,* representing 74 % (CI 64–83 %) of adults emerging from monoparasitised pupae and 66 % (CI 51–79 %) of adults emerging from multiparasitised pupae (Fig. 2). Only when *A. bipustulata* larvae were given a 24-h head start did the two species emerge in similar proportions, both from hosts with one or two larvae apparent (Fig. 2). The emergence of each species was not different between multiparasitised hosts and monoparasitised hosts ($\chi^2 = 0.62$, $df = 1$, $P = 0.43$) (Fig. 2). The effect of the order in which larvae of each species were released on the emergence of each species did not depend on the number of larvae inside the host (interaction term, $\chi^2 = 0.14$, $df = 2$, $P = 0.93$).

Intra-host mortality (i.e. the failure to produce any adult) was higher in multiparasitised than in monoparasitised hosts (37 vs. 23 %, $\chi^2 = 16$, $df = 1$, $P < 0.001$) and was not significantly different with respect to the order in which larvae of each species were released into experimental devices ($\chi^2 = 4.5$, $df = 2$, $P = 0.11$). There was also no interaction between the order in which larvae of each species were released and the number of larvae seen inside the host ($\chi^2 = 1.0$, $df = 2$, $P = 0.60$).

Discussion

Outcome of competition

Aleochara spp. provide an example of parasitoids with a particular larval biology that follows the theory predicting that specialists have higher exploitative (i.e. competitive) abilities than their generalist competitors, which have better colonization abilities (fecundity and host range) allowing

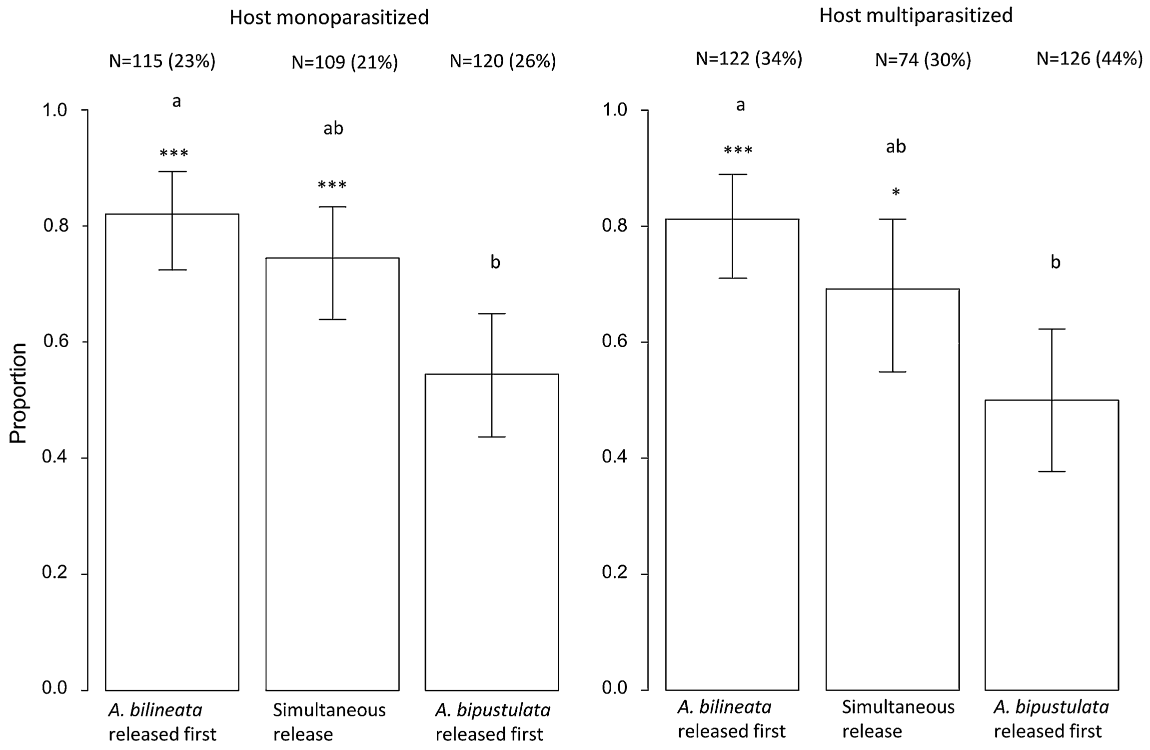

Fig. 2 Proportion of *A. bilineata* among parasitoid adults produced by competition between an *A. bilineata* and an *A. bipustulata* larva competing for a single host. *Left panel* pupae parasitised by a single larva. *Right panel* pupae parasitised by both larvae. The larvae were released in the experimental setup either 24 h apart or simultaneously. The percentage of intra-host mortality (parasitised pupae yielding no adult) is indicated *in parentheses*. *Vertical bar* 95 % CI. Exact binomial test of emergence of each species with null hypothesis: $^{*}P < 0.05$, $^{***}P < 0.001$. *Different letters* indicate significant differences between proportions

the coexistence of both species (MacArthur 1972; Force 1972, 1974; Hassell and May 1986; Carton et al. 1986).

The two parasitoid species with an overlapping host range studied here exploit ephemeral patchily distributed resources and display very similar development strategies to those of solitary pupal ectoparasitoids of dipteran hosts. However, generalist *A. bipustulata* females produce more larvae, which might help them to exploit the numerous pupae of Caliphoridae or Piophilidae flies developing on faeces or carrion (Maus et al. 1998; Fournet 2000). In such abundant patches, *A. bipustulata* larvae likely find more than one possible host which might explain why this species lays more eggs and also why its larvae do not compete as efficiently as *A. bilineata* larvae. *A. bipustulata* females are frequently more abundant than specialist *A. bilineata* females even in brassicaceous crops (Fournet et al. 2000; Josso 2012). There is great potential for coevolution between competitive species in this situation (Vázquez et al. 2007) because it creates strong pressure on the specialist species to either find hosts, exploit them or compete for them more efficiently than the abundant generalist competitor. Here we found that the larvae of the specialist were indeed stronger competitors when the larvae could interact directly.

Several factors affecting parasitoid larval competition have been identified in the past, and feeding strategies (idiobiont vs. koinobiont, endoparasitoids vs. ectoparasitoids, or solitary vs. gregarious) or host-stage preference have been the focus of several studies (reviewed in Harvey et al. 2013). However, few authors have compared a specialist and a generalist species sharing the same feeding strategies (Laing and Corrigan 1987; Iwao and Ohsaki 1996; De Moraes et al. 1999, 2005; Stilmant et al. 2008). Hymenopteran parasitoids provided ambiguous results regarding the theories on the relation between larval fighting abilities and host specialization. On the one hand, the specialist *Cotesia rubecula* is a stronger larval competitor than its more generalist competitor *Cotesia glomerata* on their common host *Pieris rapae* (Laing and Corrigan 1987) while, on the other hand, the generalist *Aphidius ervi* is the strongest larval competitor on *Sitobion avenae* when competing with the specialist *Aphidius rhopalosiphi* and the generalist *Praon volucre* (Stilmant et al. 2008). In dipteran parasitoids, larvae of the highly generalist *Compsilura concinnata* escape competition with those of the specialist *Epicampocera succincta* and are thus able to emerge from multiparasitised *Pieris* hosts (Iwao and Ohsaki 1996). Competition outcome is often difficult to predict because other life stages can compensate disadvantages in larval fighting abilities. For example adult females of the specialist hymenopteran *Cardiochiles nigriceps* find hosts more efficiently than females of the generalist *Microplitis croceipes,* thus compensating for lower larval fighting abilities (De Moraes et al. 1999).

A key factor influencing larval competition is the order in which oviposition occurs: it is usually profitable to be the first species exploiting the host because larvae can start ingesting resources before encountering competitors, and established larvae may prevent other larvae from developing within the same host by destroying supernumerary eggs or larvae (Chow and Mackauer 1984; Mackauer 1990; Harvey et al. 2012). Accordingly, the delay between ovipositions increases the probability that the first larva will win the competition (Mackauer 1990; Tillman and Powell 1992; Goubault et al. 2003). In our study (where larvae are used), the important factor is not oviposition but which larva gets inside the host first, because it will feed first and benefit from a favourable fighting position against an intruder trying to squeeze its way into the host though a narrow hole. One of our key results is therefore that *A. bilineata* represents half of the survivors although its *A. bipustulata* competitor has benefited from a 24-h head start to parasitise the host, while in the reverse situation the survival rate of *A. bipustulata* versus that of an already entrenched *A. bilineata* larva is only 18 %. This result explains previous work (Fournet et al. 1999) where *A. bilineata* penetrated hosts which had already been parasitised by *A. bipustulata* more often than vice versa, and where both species emerged in the same proportions when *A. bilineata* larvae penetrated the host 96 h after *A. bipustulata* larvae. The previous results associated with the outcome of competition presented here suggest that the larvae of both species adjust their host-exploitation decision according to the level of competition risk.

The mechanisms allowing the specialist larva to dominate its generalist competitor have not been identified here. Less suitability of *D. radicum* for *A. bipustulata* development can be excluded since Fournet (2000) showed in a comparative study that both species use *D. radicum* pupae with the same level of success except when using the smallest or largest pupae, the largest ones being more suitable for *A. bilineata* and the smallest ones more suitable for *A. bipustulata*. The key factors are likely to be the life history traits of specialist larvae because they bear a stronger selective pressure to outcompete generalists, while the latter can rely on alternative hosts that specialists cannot use, and which can be very abundant on a patch (e.g. when *A. bipustulata* exploits hosts feeding on dung/carrion). In larval competition, fast development and rapid growth are determinant factors (De Moraes et al. 1999; Goubault et al. 2003; Harvey et al. 2009). The total development time of *A. bilineata* is shorter than that of *A. bipustulata* (and in particular its eggs hatch faster) but the specific difference between first and second instars is unknown (Fournet et al. 2000). *A. bilineata* larvae are also slightly larger (Fuldner 1960), which is usually an advantage in physical interactions (Petersen and Hardy 1996), but not necessarily when the fight takes place in a very confined space. Because *Aleochara* larvae must search for and evaluate the host, traits usually associated with adult parasitoids might play a key role, such as mobility, host-detection capabilities or aggressive behaviours (De Moraes et al. 1999; Jaloux et al. 2004). Mobility and host-detection capability were probably not relevant in our very small experimental setup, but both larvae had ample opportunities to meet and fight their competitor. It is unfortunately not possible to observe directly the possible interaction between competing larvae outside of the host because upon hatching *Aleochara* larvae immediately move below ground and will not attack exposed pupae at the surface. Therefore, observing the outcome of competition between the two species' larvae was the only proxy we could use.

Multiparasitism rate

The multiparasitism rate was 50 % overall and was coherent with previous studies which showed multiparasitism rising to 50 % in interspecific no-choice experiments (Fournet et al. 1999). Intra-host mortality was overall significantly higher in multiparasitised hosts. This result is consistent with other studies: multiparasitism usually decreases parasitism success because fights either lead to the death of both competitors or at least cost the winner energy (Harvey et al. 1993; Tunca and Kilinçer 2009).

Conclusion

Our results report on the outcome of larval competition and might in part explain the coexistence of two competing species which show a double competitive asymmetry (adult traits seem to favour the generalist while larval traits show the reverse). One limitation to our work is that we studied the larvae of only two coleopteran parasitoid species differing in their host range, so we cannot rule out that selective pressures or traits unrelated to the generalist/specialist continuum might play a role in the superior fighting ability of *A. bilineata* larvae. Also, environmental conditions such as temperature are known to influence the balance of competition between parasitoids sharing the same host (DeBach and Sisojević 1960), so studying the competition between *A. bilineata* and *A. bipustulata* in a different climate could yield different results. To have a better view of the relationship between these two species, the competition between adult females should also be studied in terms of interference and exploitation competition. These two particular rove beetles might represent particularly good models to tease apart the components of competition between a specialist and a generalist, but parasitoids in general represent a substantial fraction of biodiversity, and this work shows the value of examining larval behaviours to understand their competitive interactions.

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Author contribution statement M. B., D. P. and A. M. C. conceived and designed the experiments. M. B. performed the experiments. M. B. and Y. O. analyzed the data. M. B. wrote the manuscript. D. P., A. M. C. and Y. O. provided editorial advice.

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