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ORIGINAL PAPER

Comparing resource exploitation and allocation of two closely related aphid parasitoids sharing the same host

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Abstract Species belonging to the same guild (i.e. sharing the same resources) can reduce the negative effects of resource competition through niche partitioning. Coexisting species may differ in their resource exploitation and in the associated allocation of nutrients, depending on their resource niche. Trade-offs in nutrient allocation, such as between reproduction and survival, or between early and late reproduction, are moderated by the abundance and distribution of resources. In this study we investigate differences in larval resource exploitation and adult reproductive strategy of two sympatric aphid parasitoids sharing a common host. The habitat specialist *Aphidius rhopalosiphi* and the generalist *Aphidius avenae* occur in cereal crops of Western Europe, where both species attack the major host resource: the grain aphid *Sitobion avenae*. For this purpose, we measured their acquisition of capital lipid resources, their age-specific fecundity and reproductive effort, their life span and their metabolic rate. We found that these species do not differ neither in larval lipid accumulation nor in the number of eggs at emergence and the timing of egg production, but diverge in other adult reproductive strategies. The rate of adult egg production was higher in *A. rhopalosiphi* than *A. avenae*, but at the expense of producing smaller eggs. Throughout adult life, reproductive effort was higher in *A. avenae*, perhaps facilitated by its higher metabolic rate than *A. rhopalosiphi*. The divergence between species in life history syndromes likely reflects their adaptations to their resource niche. A high egg production probably allows the specialist *A. rhopalosiphi* to exploit more *S. avenae* individuals in cereal crops, while the generalist *A. avenae* because of its variety of hosts, maximizes the investment per egg but at the expense of a lower lifespan. Our results suggest that differential resource allocation may be a more common pattern that promotes coexistence of species within a guild.

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Introduction

One of the major challenges in ecology is to explain the coexistence of species that exploit a common resource (i.e. species belonging to the same guild). It is generally assumed that species with shared resources show some sort of niche partitioning to reduce the negative effects of resource competition, for example through resource specialization (MacArthur and Levins 1967; Tilman 1982) or by shifting the temporal and/or spatial pattern of resource exploitation (Chesson 2000; Chase and Leibold 2003). Within a resource niche, the abundance and distribution of resources crucially affect important life history trade-offs, such as between early and late reproduction and between reproduction and survival (van Noordwijk and de Jong 1986; Ellers and van Alphen 1997; Pexton and Mayhew 2002). For this reason, coexisting species may differ substantially in their age-specific fecundity curves and the associated allocation of stored and incoming nutrients to reproduction and survival, depending on their resource niche (Boggs 1997; Ellers and Jervis 2003). Reciprocally, life history trade-offs may also play an important role in shaping the structure of ecological communities (Bonsall et al. 2004).

Parasitoids are excellent model organisms to study questions about exploitation of shared resources. Parasitoids develop in or on other arthropods, which means that larval resource acquisition is limited by the quantity of resources that is contained in a single host. The intimate physiological interaction between host and parasitoid larvae facilitates the evolution of specialized physiological traits to maximally exploit host resources (Price 1972; Vinson and Iwantsch 1980; Godfray 1994; Rivero et al. 2001; Harvey and Strand 2002). Adult parasitoids are free-living and their reproductive opportunities are largely influenced by the number and the distribution of host resources in which they lay eggs (Godfray 1994; Rosenheim 1999; Rosenheim et al. 2000; Richard and Casas 2009). As a result, parasitoids often evolved egg production strategies that closely reflect host availability (Ellers et al. 2000; Ellers and Jervis 2004). For example, if the host species is scarce or widely dispersed, parasitoids tend to emerge with low numbers of eggs and have long life span, whereas parasitoids attacking hosts that are numerous or aggregated usually emerge with nearly their entire complement of mature eggs and generally live for a shorter period of time (Ellers et al. 2000). The syndrome of life history traits associated with the timing of egg production has been described in comparative studies and is reflected in the ovigeny index which is 'the proportion of the initial egg load to the lifetime potential fecundity' (Jervis et al. 2001, 2003; Jervis and Ferns 2004). In addition to this parameter, the reproductive effort (i.e. egg load multiplied by egg volume of females) is also relevant, in particular when examining the allocation trade-off between survival and reproduction (Jervis and Ferns 2004).

A single host species is typically attacked by multiple parasitoid species within and across different life stages (Godfray 1994). Coexistence of parasitoid complexes associated with the same host species is thought to be enabled by niche differentiation, such as different levels of host specialization (Harvey and Witjes 2005; Harvey 2008), or specialization on different host stages (Price 1972; Askew and Shaw 1986). Specialization may give a competitive advantage in two possible ways. First, specialized parasitoids may be better able to adapt their physiology to their hosts, which increases the efficiency with which the

developing larva can manipulate and utilize the host, resulting in increased physiological suitability (Carton et al. 1986; Stilmant et al. 2008) and increased capital resources at emergence (Harvey et al. 2008). Second, specialized parasitoids can closely match their egg production to host availability better than generalists that have to switch between hosts that may have different distribution and availability. This difference may alter resource allocation at emergence and during adult life, affecting the outcome of reproductive trade-offs (Eijs and van Alphen 1999; Harvey 2008; Harvey et al. 2009; Pelosse et al. 2007, 2010). The relative importance of these two ways giving a competitive advantage in specialization has only rarely been considered in a single coexisting species system (Harvey 2008). Both aspects of specialization are especially important to parasitoids, because the majority of parasitoid species are constrained in their resource acquisition and allocation. In parasitoids, lipids are the main and essential energetic resources fuelling competing main functions such as reproduction and maintenance (Ellers 1996; Ellers and van Alphen 1997; Rivero and West 2002). A large number of parasitoid species has been found to be unable to synthesise lipids from carbohydrates food sources as adults (Visser and Ellers 2008; Visser et al. 2010). Therefore, they rely entirely on the quantity of lipids they acquire from their host, and host exploitation for lipids is expected to be under strong selection.

The habitat specialist *Aphidius rhopalosiphi* De Stefani- Perez and the generalist *A. avenae* Haliday (Hymenoptera: Braconidae: Aphidiinae) are two closely related sympatric aphid parasitoids (Khambhampati et al. 2000) which attack a common host: the grain aphid *Sitobion avenae* (Hemiptera: Aphididae) which occurs in cereal crops of Western Europe (Krespi 1990). *Aphidius rhopalosiphi* attacks few aphid species feeding exclusively on cultivated and wild Poaceae and is mainly parasitizing *S. avenae* (Starý 1970). By contrast, *A. avenae* attacks a larger variety of host species feeding on a wide range of families of cultivated and wild plants (e.g. Leguminoseae, Poaceae, Solanaceae, etc.; Starý 1970, 1974). In cereal crops, their reproductive opportunities differ because *A. rhopalosiphi*, the most abundant species, is present year-round and has already parasitized a large proportion of available hosts when *A. avenae* arrives later in the season (Krespi 1990).

In this study we investigate differences in larval efficiency in host exploitation and in adult reproductive strategy in these two coexisting species. Our aims were twofold: (1) To detect differences in host exploitation efficiency between both species by comparing acquisition of capital resources. We expect *A. rhopalosiphi* to be able to obtain a larger quantity of lipid resources because as a habitat specialist it attacks mainly *S. avenae*, whereas the generalist *A. avenae* has a larger host range. (2) To compare adult reproductive strategies between the two species; with emphasis on age-specific fecundity and reproductive effort, life span and metabolic rate. We expect the habitat specialist *A. rhopalosiphi* to have an earlier reproduction (i.e. more eggs matured at emergence), matching better the distribution and abundance of resources in cereal crops, than the generalist *A. avenae* that has to switch between habitats. Moreover, because of the trade-off between reproduction and survival, we expect the species with the higher reproductive effort to have a shorter life span, possibly associated with a higher metabolic rate (Le Lann et al. 2011b).

Materials and methods

Rearing

Aphidius rhopalosiphi and *A. avenae* were collected from *S. avenae* mummies (i.e. stage of nymphose of the parasitoid inside the dead aphid) in cereal crops near Rennes in France

(N48°10, W1°79) in June 2006. Both parasitoid species were reared in the laboratory on a mixed-age culture of the grain aphid *S. avenae*. The aphids originated from a single parthenogenetic female (SA1 clone, INRA-zoology collection) collected in 1990 from a cereal crop of the same location. The aphids were reared on winter wheat, *Triticum aestivum*, "Boston" cultivar, provided by Saaton Union Research (France). Colonies of hosts and parasitoids were kept in Plexiglas cages (33 × 33 × 33 cm) in climate rooms at 20 ± 1°C, 70 ± 10% of relative humidity and a 12:12 h light:dark regime. All the experiments were conducted between October 2008 and March 2009 at the same conditions used for the rearing.

Experimental design

Resource exploitation

To test for differences in host exploitation efficiency between species we compared lipid percentage and dry mass of parasitized and unparasitized aphids at different life stages, and at parasitoid emergence. Since the two *Aphidius* species are koinobionts, aphids continue to move and grow for about 9 days after parasitization, until they turn into immobile mummies that contain nymphal parasitoids. Adult parasitoids emerge about 5 days later and are not able to synthesize lipids (Visser et al. 2010).

We collected 3-days old second instar aphids from the culture. Some of these aphids ($N = 27$) were frozen immediately to analyze the amount of lipids at the time of parasitism. Of the remaining 3-days old second instar hosts, 10 were offered to each of 10 females of each parasitoid species. Second instar hosts were chosen as they are one of the preferred instars of *Aphidius* species (Outreman et al. 2001a, b; Colinet et al. 2005). Females were only allowed to sting a host once. When the aphids were 8 days old, half of them were dissected on a coverslip and the presence or absence of a parasitoid larva was recorded. For *A. avenae* and *A. rhopalosiphi*, 37 hosts and 15 hosts respectively were found to be parasitized; these formed the 8-days old parasitized treatment. The dissected aphids that did not contain a parasitoid larva ($N = 35$) were used as the corresponding 8-days old unparasitized treatment.

The remaining half of hosts stung was allowed to feed on wheat plantlets until the formation of 1 day-old mummies about 9 days after the sting (*A. avenae*: $N = 10$; *A. rhopalosiphi*: $N = 17$) when they were frozen for further analyses. No corresponding unparasitized treatment is possible for the mummies, since they are only formed after parasitism. From another batch of isolated 1-day old mummies, a fifth treatment was formed, which contained freshly emerged parasitoids (*A. avenae*: $N = 62$; *A. rhopalosiphi*: $N = 51$).

Lipid contents of dissected 8-days old unparasitized hosts, 8-days old parasitized hosts and newly emerged female parasitoids (i.e. these females were dissected as they were also used in the resource allocation experiment) were measured using the method of Ellers (1996). The piece of cover slip with the dissected body of the individual was dried for 3 days at 80°C and weighed (Metler-Toledo UMX2, micro-electrobalance, sensitivity: 0.1 μg). We obtained the dry weight of the individual by subtracting the weight of the cover slip. Lipids were extracted by placing the cover slip in a vial containing 4 ml of ether. After 24 h, the cover slip was washed with fresh ether and re-dried for 3 days at 80°C. The dry weight of the individuals was determined and lipid amount was calculated as the difference in dry weight before and after ether extraction. Lipid percentage was then calculated by dividing the lipid amount by the dry mass before extraction. Lipid contents of

non-dissected 3-days old unparasitized hosts, mummies and emerging parasitoid males were measured using the method of Visser et al. (2010). This method is derived from the one of Ellers (1996), except that individuals are freeze-dried 2 days before and after ether extraction. Lipid percentages were calculated as explained above.

Resource allocation

Reproductive traits and lipid percentages In a first experiment we measured allocation of resources to reproductive traits in the absence of hosts. Both species are pro-synovigenic as they have some mature eggs at their emergence as adults but still produce eggs during their adult life (Jervis et al. 2001, 2003). Both species produce hydropic eggs. We measured egg load, egg volume, lipid percentage and dry mass of recently emerged, unfed females, and females fed with honey for 1, 10 and 10 days (see Table 1 and Fig. 3, for numbers of females tested for each measurement). To obtain standardized female parasitoids for experiments, mummies were collected from the culture and placed individually in gelatine capsules. Newly emerged females were used for experimentation. For each age tested, females were frozen and stored in the freezer (−20°C) until further analysis. Egg load and lipid content of each female were determined following the method of Ellers (1996). A female was placed in a drop of Ringer's solution on a piece of cover slip of known weight and dissected under a binocular (×40, Olympus SZX9) to remove the ovaries. Eggs were counted under a microscope (×4, Olympus BH2) and photographed (Olympus Camedia C3040). Length and width of a minimum of 20 eggs for each female were measured using the numeric image analysis software ImageJ to calculate egg volume (taken as two joined cones, volume: $V = 2/3 \prod (L/2 * (w/2)^2)$; L = Length, w = width). The piece of cover slip with the dissected body of the female was dried, weighed and lipids were extracted as explained above. We calculated the reproductive effort of each female by multiplying the number of mature eggs by the mean egg volume.

In a second experiment, we estimated the potential lifetime egg production of females. For this purpose, newly emerged females ($N = 8$ for *A. rhopalosiphi* and $N = 3$ for *A. avenae*) were mated with males of the same age. Singly mated, 1-day old females were then placed into individual Plexiglas boxes ($L = 16.8$ cm, $Ø = 4$ cm) containing wheat plantlets and 100 s instar *S. avenae* aphids. They were kept at 20°C with ad libitum access to a 10% glucose solution and allowed to oviposit for 24 h (day 1). After 24 h, females were removed and placed in new boxes containing 100 fresh hosts (day 2). This procedure was repeated for a total of four sequential days followed by 100 hosts being provided on days 5, 7, and 11; i.e. females could spend multiple days to parasitize. The last day of the experiment was day 14,

Table 1 Mean percentages of fat (±CI 95%) and dry masses (±SE) of *A. avenae* and *A. rhopalosiphi* females aged 0, 1, 5 and 10 days

Females	*A. avenae*		*A. rhopalosiphi*	
Age (days)	Percentage of fat ± CI 95%	Dry mass (μg) ± SE	Percentage of fat ± CI 95%	Dry mass (μg) ± SE
0	4.8 ± 1.8 (15)	148.8 ± 16.7 (15)	6.6 ± 2.3 (14)	180.5 ± 11.1 (14)
1	6.1 ± 2.9 (12)	167.7 ± 19.0 (12)	6.0 ± 2.0 (23)	186.3 ± 12.2 (23)
5	4.5 ± 1.4 (15)	176.9 ± 12.1 (15)	6.8 ± 1.5 (22)	147.2 ± 11.9 (22)
10	7.0 ± 3.2 (11)	163.8 ± 15.5 (11)	7.3 ± 2.4 (18)	161.0 ± 12.1 (18)

Numbers between brackets indicate the number of replicates

which corresponds to the maximum lifespan of females. Realized fecundity was calculated as the total number of mummies produced by a single female during her life.

Survival To measure potential differences in longevities between species, we calculated the percentage of females fed with honey that reached the age of 1, 5, 10 and 15 days in *A. avenae* and *A. rhopalosiphi*. For this purpose, 1-day old (*A. avenae*: $N = 21$, *A. rhopalosiphi*: $N = 44$), 5-days old (*A. avenae*: $N = 17$, *A. rhopalosiphi*: $N = 48$), 10-days old (*A. avenae*: $N = 31$, *A. rhopalosiphi*: $N = 67$) and 15-days old (*A. avenae*: $N = 30$, *A. rhopalosiphi*: $N = 73$) females were tested.

Metabolic rate We used flow-through respirometry to measure the Basal Metabolic Rate (BMR) of female parasitoids at emergence (*A. avenae*: $N = 31$; *A. rhopalosiphi*: $N = 26$), one (*A. avenae*: $N = 37$; *A. rhopalosiphi*: $N = 26$) and five (*A. avenae*: $N = 27$; *A. rhopalosiphi*: $N = 23$) days old. Recordings were taken at regular hours with light (from 10.00 am to 17.00 pm). Females were placed individually in small cylindrical chambers in a climate room regulated at 20°C. Their CO_2 production was measured with a CO_2 analyser (CA-10A Carbon Dioxide Analyzer, Berlin). Temperature was checked with a temperature controller (Pelt-5). A mass flow valve controller (MFC-2) maintained constant flow rates. Ambient air was drawn and CO_2 and water were scrubbed with a Drierite-Ascarite column. Four 85 min cycles of records, with a sample every second, were performed for each individual and were automatically transformed from ppm to µl-CO_2 per hour by a program recorded in Expedia software (Sable Systems, Berlin), taking into account the flow rate, temperature and barometric pressure. We allowed the parasitoids to accustom to their new environment for 90 min before recording their metabolic rate. Previous experiments showed that females remained mostly immobile during the experiment (Le Lann et al. 2011b). We took the average of the last three cycles of records as a measure of the BMR for each individual. As fresh body mass is known to be positively correlated with metabolic rate (Gillooly et al. 2001), individuals were frozen after measuring their BMR and then weighed with a microbalance (Sartorius M4 $\pm$ 0.001 mg; Le Lann et al. 2011b).

Statistical analysis

Resource exploitation

To test whether lipid levels changed with aphid age, host manipulation by parasitoids and parasitoid species exploiting the host, lipid percentages were compared with ANOVAS between 3-days old unparasitized aphids, 8-days old unparasitized aphids, 8-days old aphids parasitized by *A. avenae* or *A. rhopalosiphi* females, mummies of *A. avenae* or *A. rhopalosiphi* and emerging adults of *A. avenae* or *A. rhopalosiphi*. Cube root transformations were applied to lipid percentages as residuals were not normally distributed and the residual variance was not constant over the response variable.

Dry masses were compared using Wilcoxon tests as residuals were not normally distributed, residual variances were not constant and no transformation could be applied. Twelve pairwise comparisons were made between the eight treatments; therefore we applied Bonferroni correction for multiple testing by adjusting α to $0.05/12 = 0.004$.

We did not separate males and females of the emerging adults in the analyses to maintain comparability with the parasitized and mummy treatments, where we could not distinguish the sex of the developing parasitoids.

Resource allocation

We used ANOVA models to compare egg load, egg volume, lipid percentage and dry mass between females of different ages and between species. Parasitoid age and species were considered as factors and the interaction between the two was also analyzed. Dry mass was not correlated with egg load and egg volume ($P > 0.05$). Log transformations (for egg volumes) and cube root transformations (for lipid percentages) were applied when residuals were not normally distributed or when the residual variance was not constant over the response variable. For lipid percentages, we have performed regression analyses of dry weight before ether extraction with dry weight after ether extraction to detect potential outliers in the data. Following Visser et al. (2010), outliers were only removed if they deviated from a 99% confidence interval of the linear regression line. We used ANCOVA models to compare metabolic rate between females of zero, 1 and 5 days old and between species. Fresh body mass was taken as a first variable as it is correlated to the BMR of the insects ($P < 0.001$, $R = 0.62$; Gillooly et al. 2001; Le Lann et al. 2011b). We used model simplification to sequentially remove variables and assess the more parsimonious model, and examined residuals. Mean number of mummies produced per day and total mean realized fecundities were compared between species with Wilcoxon tests. We also compared mean age of mummy production (i.e. the number of mummies times the age of the female, cumulative over all ages, and then divided by the total number of mummies of that female; Ellers and van Alphen 1997) between species but we did not include it in the results as it was also not significant. Survival of females of 1, 5, 10 and 15 days old was compared between species with a global χ^2 test. Tukey *post hoc* comparisons were carried out when variation of variables were non linear between ages. Data analyses have been done with the R free software environment version 2.12.0 (R Development Core Team, 2010).

Results

Resource exploitation

There were significant differences between aphid stages in their lipid percentage ($F_{7,246} = 14.82$, $P < 0.001$). Three-days old unparasitized aphids had lower dry mass ($W = 156.5$, $P < 0.004$) but a significantly higher lipid percentage than 8-days old unparasitized ones (Tukey test, $P < 0.001$). However, there was no difference in dry mass and lipid percentage between 8 days-old unparasitized aphids and 8 day-old parasitized ones by *A. rhopalosiphi* (dry mass: $W = 361$, $P = 0.04$; lipid percentage: Tukey test, $P = 0.99$) or by *A. avenae* (dry mass: $W = 876$, $P = 0.01$; lipid percentage: Tukey test, $P = 0.99$; Figs. 1, 2). During parasitoid development, there were no significant differences in dry mass (8-days old parasitized aphids: $W = 289$, $P = 0.83$; mummies: $W = 140$, $P = 0.005$; adults: $W = 1{,}689$, $P = 0.54$) and lipid percentage between species (Tukey test: 8-days old parasitized aphids: $P = 0.99$; mummies: $P = 0.99$; adults: $P = 0.64$). *Aphidius avenae* emerging adults had lower dry mass and lipid percentage than mummies of *A. avenae* (dry mass: $W = 65$, $P < 0.004$; lipid percentage: Tukey test, $P < 0.05$) and 8-days old aphids parasitized by *A. avenae* (dry mass: $W = 675.5$, $P < 0.004$; lipid percentage: Tukey test, $P < 0.01$; Fig. 1). In *A. avenae*, there was no difference in dry mass ($W = 262$, $P = 0.05$) nor in lipid percentage (Tukey test: $P = 0.95$) between mummies and 8 day old parasitized aphid. In *A. rhopalosiphi*, no difference in dry mass (8-days old

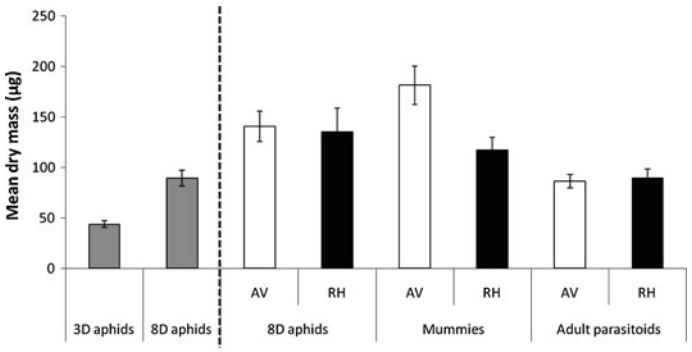

Fig. 1 Mean dry mass (±SE) of 3-days-old (3D; $N = 27$) and 8-days-old (8D; $N = 35$) unparasitized aphids (*grey bars*), 8-days-old (8D) aphids parasitized by *A. avenae* ($N = 37$; AV, *white bar*) or *A. rhopalosiphi* ($N = 15$; RH, *black bar*), mummies of *A. avenae* ($N = 10$; AV, *white bar*) or *A. rhopalosiphi* ($N = 17$; RH, *black bar*) and newly emerged parasitoid adults of *A. avenae* ($N = 62$; AV, *white bar*) or *A. rhopalosiphi* ($N = 51$; RH, *black bar*)

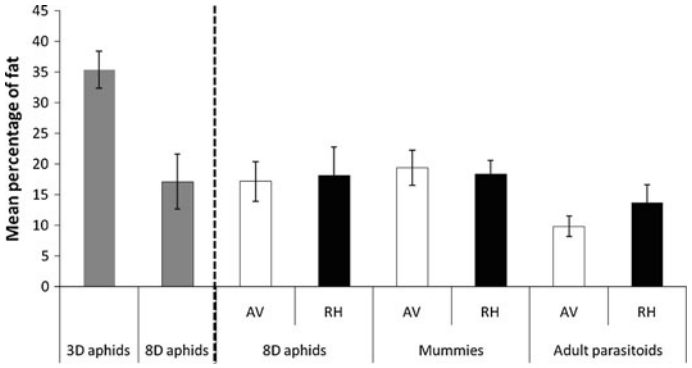

Fig. 2 Mean fat percentage (±CI 95%) of 3-days-old (3D; $N = 27$) and 8-days-old (8D; $N = 35$) unparasitized aphids (*grey bars*), 8 day-old (8D) aphids parasitized by *A. avenae* ($N = 37$; AV, *white bar*) or *A. rhopalosiphi* ($N = 15$; RH, *black bar*), mummies of *A. avenae* ($N = 10$; AV, *white bar*) or *A. rhopalosiphi* ($N = 17$; RH, *black bar*) and newly emerged parasitoid adults of *A. avenae* ($N = 62$; AV, *white bar*) or *A. rhopalosiphi* ($N = 51$; RH, *black bar*)

parasitized aphids-mummies: $W = 106.5$, $P = 0.44$; mummies-adults: $W = 236.5$ $P = 0.005$; 8-days old parasitized aphids-adults: $W = 238$, $P = 0.03$) and lipid percentage (Tukey test: 8-days old parasitized aphids-mummies: $P = 0.99$; mummies-adults: $P = 0.16$; 8-days old parasitized aphids-adults: $P = 0.48$) was found during parasitoid development.

Resource allocation

For all ages, females of *A. avenae* and *A. rhopalosiphi* differed significantly in the number of eggs ($F_{1,229} = 85.73$, $P < 0.001$) and egg volume ($F_{1,166} = 4{,}456.58$,

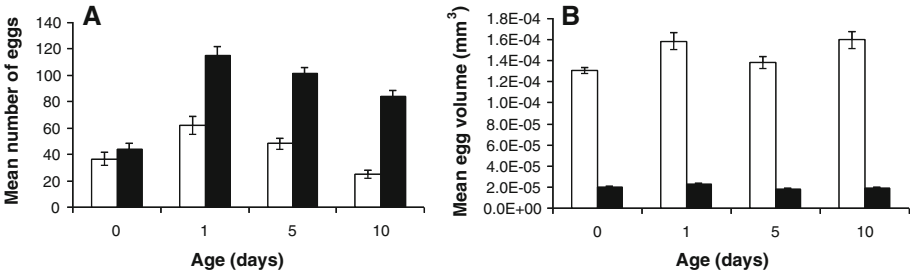

Fig. 3 Mean (±SE) number of eggs (**a**) and egg volume (**b**) of *A. avenae* (*white bars*) and *A. rhopalosiphi* (*black bars*) females aged of zero (*A. avenae*: $N = 20$; *A. rhopalosiphi*: $N = 42$), one (*A. avenae*: $N = 18$; *A. rhopalosiphi*: $N = 41$), five (*A. avenae*: $N = 15$; *A. rhopalosiphi*: $N = 43$) and ten (*A. avenae*: $N = 13$; *A. rhopalosiphi*: $N = 39$) days that were kept without hosts and provided with honey ad libitum

$P < 0.001$). Throughout adult life, *A. rhopalosiphi* had a higher number of mature eggs than *A. avenae*, but *A. rhopalosiphi* eggs were consistently smaller (Fig. 3). There was also a significant effect of age on the number of eggs ($F_{3,227} = 40.82$, $P < 0.001$) and egg volume ($F_{3,164} = 7.90$, $P < 0.001$), as well as a significant interaction between parasitoid age and species (number of eggs: $F_{3,227} = 7.85$; $P < 0.001$; egg volume: $F_{3,164} = 2.60$; $P = 0.05$). The number of eggs increased between emergence and 1-day old for *A. rhopalosiphi* (Tukey test, $P < 0.001$) but not for *A. avenae* (Tukey test, $P = 0.17$). The number of eggs decreased between 1 and 10 days-old females of both species (Tukey test: *A. avenae*: $P < 0.05$; *A. rhopalosiphi*: $P < 0.001$), but this decrease was more pronounced in *A. avenae* females (Fig. 3a). Egg volume, on the other hand, increased between emergence and 1 day-old females of *A. avenae* (Tukey test, $P < 0.05$) but only as a trend for the ones of *A. rhopalosiphi* (Tukey test, $P = 0.07$; Fig. 3b). During the rest of adult life, egg size showed small variations without an apparent pattern (Fig. 3b). As a consequence, the reproductive effort of *A. avenae* females was 6 times higher than that of *A. rhopalosiphi* females at emergence, and 4 (1-day old) to 2.4 (10-days old) times higher during the course of their lives (Fig. 3a and b).

Age-specific fecundity curves differed between species for the first day of progeny production, with *A. rhopalosiphi* females producing more mummies than *A. avenae* ($W = 1$; $P = 0.05$), but there were no significant differences for the other days ($P > 0.05$; Fig. 4). Mean realized fecundities were 159 ± 28 and 92 ± 33 for *A. rhopalosiphi* and *A. avenae*, respectively, but they did not differ significantly ($W = 5.5$; $P = 0.22$).

Lipid percentages and dry masses did not differ between species (lipid percentage: $F_{1,128} = 2.05$, $P = 0.15$; dry mass: $F_{1,128} = 0.09$, $P = 0.77$) nor among ages (lipid percentage: $F_{3,126} = 0.83$, $P = 0.48$; dry mass: $F_{3,126} = 0.96$, $P = 0.41$; Table 1). For both parameters, the interaction between age and species was not significant (lipid percentage: $F_{3,126} = 0.61$, $P = 0.61$; dry mass: $F_{3,126} = 1.93$, $P = 0.13$).

Percentages of survival differed between species ($\chi^2_3 = 8.33$, $P < 0.05$) as *A. avenae* had shorter life-spans than *A. rhopalosiphi* (Fig. 5). For both species, the metabolic rate varied among ages ($F_{2,172} = 4.68$, $P < 0.05$), with an increase between 1 and 5 days old ($P < 0.01$), and was consistently higher in *A. avenae* females than in *A. rhopalosiphi* ones ($F_{1,173} = 26.66$, $P < 0.001$; Fig. 6).

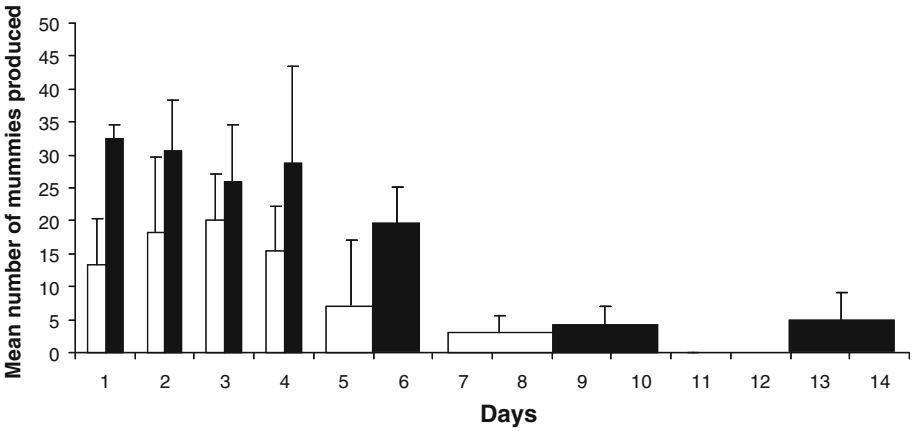

Fig. 4 Age specific fecundity curve: mean numbers of mummies (±SE) produced by *A. avenae* (*white bars*; $N = 3$) or *A. rhopalosiphi* (*black bars*; $N = 8$) females between 1 and 14 days old provided with ad libitum sugar sources. Each day, females were provided with 100 new fresh hosts except females aged of 5, 7 and 11 days old that were allowed to oviposit longer on the hosts (to 5–6, 7–10 and 11–14 days)

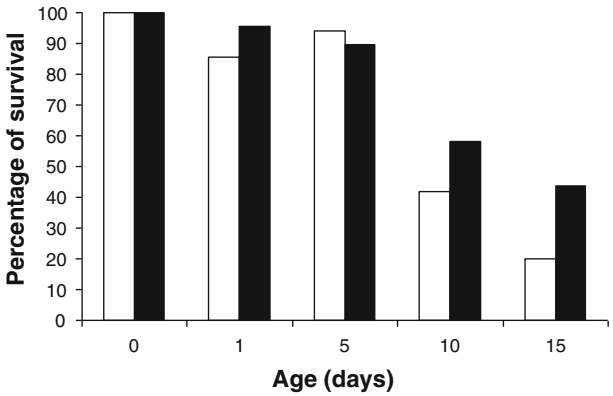

Fig. 5 Percentage of surviving *A. avenae* (*white bars*) and *A. rhopalosiphi* (*black bars*) females at emergence, one (*A. avenae*: $N = 21$, *A. rhopalosiphi*: $N = 44$), five (*A. avenae*: $N = 17$, *A. rhopalosiphi*: $N = 48$), ten (*A. avenae*: $N = 31$, *A. rhopalosiphi*: $N = 67$) and fifteen (*A. avenae*: $N = 30$, *A. rhopalosiphi*: $N = 73$) days old that were kept without hosts and provided with honey ad libitum

Discussion

Similar resource exploitation but contrasting resource allocation in species developing on the same resource

Generally, specialists should better exploit host resources than generalists (Carton et al. 1986; Stilmant et al. 2008; Harvey et al. 2008). Contrary to our predictions, *A. rhopalosiphi* individuals accumulated similar levels of lipid reserves as *A. avenae* during their larval development (i.e. similar lipid percentages at the mummy stage). There was also no apparent host manipulation (i.e. similar lipid percentage and dry mass between

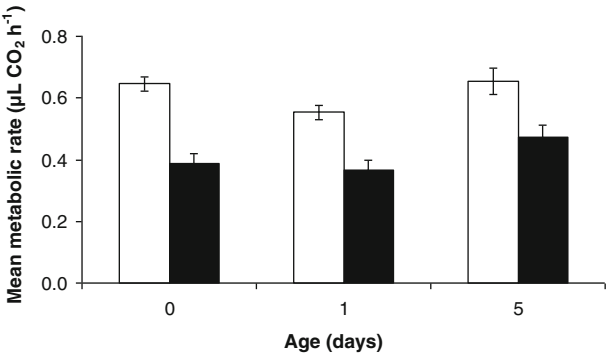

Fig. 6 Mean metabolic rate (µl CO_2 h^{-1}; ±SE) of *A. avenae* (*white bars*) and *A. rhopalosiphi* (*black bars*) females aged of zero (*A. avenae*: $N = 31$; *A. rhopalosiphi*: $N = 26$), one (*A. avenae*: $N = 37$; *A. rhopalosiphi*: $N = 26$) and five (*A. avenae*: $N = 27$; *A. rhopalosiphi*: $N = 23$) days old that were kept without hosts and provided with honey ad libitum

unparasitized and parasitized aphids of the same age) but we observed a decrease of the percentage of lipid reserves between 3 day-old unparasitized aphids just before parasitism and 5-days older aphids parasitized of both species. Despite being a host specialist, host exploitation by *A. rhopalosiphi* is not more efficient than in the generalist *A. avenae*, and capital resources did not differ between the two species at emergence. A convergence in lipid content was also found in idiobiont parasitoid species sharing the same host (Harvey 2008). Idiobionts differ from koinobionts because they use resources that are fixed at parasitism and then gradually decline in quality as the host ages, whereas koinobionts exploit dynamic host resources that continue growing and feeding after parasitism. For idiobionts, the optimal strategy is then always to maximize the acquisition of resources inside the host whereas a variety of optimal strategies can be used in koinobionts depending on the host size at the time of parasitism and the growth rate (Harvey 2008). Here, we did not find any evidence for such flexibility in the accumulation of lipid resources between the two species. Further experiments are needed to investigate whether these species diverge in other aspects of their developmental strategies, for instance by measuring their growth rate.

The stronger decrease in lipid percentage in *A. avenae* shortly before adult emergence may be due to somatic investment in body construction as adults of this species usually have a longer tibia length and a higher dry body mass than *A. rhopalosiphi* (Le Lann et al. 2011a). However, in this study we did not find any differences between species in the dry masses probably because of the large variance between individuals within species. Alternatively, the more pronounced reduction in lipid percentage during pupation in *A. avenae* may be a result of increased allocation of energy in the process of egg production. Both species produced eggs during pupation and emerged with mature eggs, but *A. avenae* females had a higher initial reproductive effort (i.e. similar number of mature eggs at emergence but larger eggs) than *A. rhopalosiphi* females.

In contrast to resource exploitation, adult reproductive strategy differed greatly between the two *Aphidius* species. Age-specific fecundity in *A. rhopalosiphi* exhibited a peak early in life and then declined, whereas the fecundity curve of *A. avenae* was more dampened. *A. rhopalosiphi* females had a higher rate of egg production early in life, but produced significantly smaller eggs than *A. avenae*. Total mean realized fecundities were similar for *A. rhopalosiphi* and *A. avenae*, probably because of the low sample size in *A. avenae*. We

found that *A. avenae* had a higher reproductive effort throughout life than *A. rhopalosiphi*. As predicted by life history theory, higher reproductive effort incurs a longevity cost (Ellers 1996; Ellers and van Alphen 1997; Rivero and West 2002) and *A. avenae* had the shorter lifespan of the two species, probably also as a result of its higher metabolic rate. Our results are not fully matching those of other parasitoid groups, where broad generalists have lower fecundities but live longer than more specialized parasitoids (Harvey 2008; Harvey et al. 2008, 2009) and may be taxa specific. Aphid host resources can be found in a large range of habitats and the generalist *A. avenae* may benefit by being able to attack and develop in many of them, whereas *A. rhopalosiphi* may pay the cost of specializing on few aphid species. The abundance and availability of potential hosts may thus determine the amount of metabolic resources invested in somatic versus reproductive traits. Our study also demonstrates that egg volume has to be considered in addition to egg load to account for real reproductive effort and better understand the trade-off between reproduction and survival.

Reproductive strategies in parasitoids represent an adaptive response to a range of selection pressures, including host abundance and accessibility (Price 1972; Ellers et al. 2000; Pexton and Mayhew 2002). Although both *Aphidius* species have evolved in natural habitats with more complexity and heterogeneity systems than the cropping systems, the two species may have evolved in divergent resource conditions (i.e. contrasting habitats). *Aphidius avenae* is a generalist species that is therefore likely to switch between various hosts from different plant species and habitats depending on their abundance and accessibility (Starý 1970). *Aphidius avenae* has thus been under some selective pressure from different hosts and habitats. In cereal crops, *A. avenae* can still access suitable hosts because: (1) *A. rhopalosiphi* leaves aphid colonies under-exploited (Outreman et al. 2001b), (2) *A. avenae* has a particular oviposition behavior that reduce host defenses (van Baaren et al. 2004) and (3) has the ability to avoid hosts parasitized by *A. rhopalosiphi* (van Baaren et al. 2009). *Aphidius rhopalosiphi*, on the other hand, has evolved a reproductive strategy that is intimately associated with a high proportion of suitable hosts available, as this species is the first to establish in cereal crops in the spring (Krespi 1990). Because of its higher egg rate production, *A. rhopalosiphi* can exploit a higher proportion of hosts in the habitat, but at the cost of producing smaller eggs.

Consistent with the result found in hyperparasitoids sharing the same primary parasitoid host (Harvey 2008), we demonstrated that coexisting species have evolved similar resource use during larval development but strong differences for resource allocation in both maintenance and reproductive traits. These differences between the reproductive strategies of two *Aphidius* species, together with their contrasting oviposition behaviours (van Baaren et al. 2004) and host discrimination strategies (van Baaren et al. 2009) are likely to be adaptations to different resource niches that may allow them to share the same host resource in cereal crops (Krespi 1990). Our results suggest that differential resource allocation in traits may be a more general pattern that allows coexistence of species sharing the same host resource.

Egg size and egg load variation with age: adaptation versus constraint

Several studies have shown that insect females can adjust the investment per egg as a function of age or food availability, a pattern reflecting an adaptive strategy (Begon and Parker 1986; Clutton-Brock and Godfray 1991; Bernardo 1996; Roff 2002). We showed that coexisting species had convergent patterns in the plasticity of egg investment: egg size of *A. avenae* clearly increased in the first days of adult life and a similar pattern existed in

A. rhopalosiphi. In parasitoids, two development modes with two different egg types can be distinguished: koinobiont parasitoids like *A. rhopalosiphi* and *A. avenae* usually produce small, yolk-deficient 'hydropic' eggs (i.e. the egg is swelling as food is absorbed from the host through the chorion) whereas idiobionts produce large, yolk-rich anhydropic eggs (i.e. no food absorption), containing large amounts of lipids and proteins (Chapman 1998; Rivero and Casas 1999; Rivero et al. 2001; Rivero and West 2002). For these parasitoids and many other insects, producing smaller eggs may thus be detrimental via an increased mortality and/or a decreased activity at the adult stage (Fox and Czesak 2000; Giron and Casas 2003; Boivin and Gauvin 2009). In parasitoids, plasticity in egg size or composition has rarely been investigated (Giron and Casas 2003; Bezemer et al. 2005; Le Lann et al. 2011b) and for koinobionts, the link between egg size and fitness of progeny has never been proven (Kraaijeveld and van Alphen 1994; Lalonde 2005). To our knowledge, this work is the first to report a change in egg size with age and/or food ingestion (i.e. 1 day-old females were fed with honey whereas emerging ones were not) in a koinobiont parasitoid with hydropic eggs. As suggested in a previous study (Le Lann et al. 2011b), in such parasitoids, a larger egg volume may be adaptive if it increases the absorption of nutrients by the egg inside the host. Further experiments are now needed to investigate whether an increase in egg size results in an increase of offspring fitness in koinobiont species.

Insect females may also decrease their clutch size investment as a function of age. This pattern of variation in the number of eggs may reflect an adaptive strategy, such as egg resorption, which is the reallocation of reserves from reproduction to maintenance under conditions of limited host resources in parasitoids, or physiological constraints on egg production, such as reduced food availability or ageing (Begon and Parker 1986; Clutton-Brock and Godfray 1991; Rivero et al. 2001; Roff 2002). In addition to the similarity of the egg size variation pattern, we also demonstrated for both species that after the age of 1 day, the number of eggs decreases linearly. Except for the non-host feeder *Opius concolor*, which is able to resorb hydropic eggs (Stavraki-Paulopoulou 1966), egg resorption has been mainly found in idiobiont species producing anhydropic yolk-rich eggs. *Aphidius* species are expected to be unable to reallocate reproductive reserves toward maintenance, as they produced hydropic yolk-deficient eggs. Egg resorption is thus probably not responsible for the decrease in the number of eggs in these species. In both species, we noticed that some 5-days old and older females had eggs at the extremity of the ovipositor (Le Lann, pers. obs.). Egg deposition without hosts was already observed in the koinobiont parasitoid *Venturia canescens* (Roberts and Schmidt 2004) and may occur in *Aphidius* species because of mechanical pressure of additionally matured eggs. Here, females had ad libitum access to food so that both ageing and mechanical pressure of additional matured eggs are potentially the main similar constraints acting on the number of eggs of both species.

Adaptation and coexistence

Ecological processes have been shown to affect evolutionary adaptations but few studies have been conducted on the life history traits syndromes of coexisting species or reproductive modes within species (Pelosse et al. 2007, 2010; Harvey 2008). Here, we demonstrated that two related species sharing the same host resource have convergent resource exploitation, similar pattern of variation in egg size and number of eggs but divergent resource allocation, particularly toward maintenance and reproduction. Future studies on more species of the *Aphidius* guild will hopefully reveal the extent to which the reproductive biology and ecology of these parasitoids are similar or if each species possesses

slightly different adaptations, according to their degree of specialization on the host resource. Evolutionary adaptations of species may also largely influence ecological processes, such as species interactions within a guild (Bonsall et al. 2004). Our results suggest that differential life history syndromes may promote coexistence between species and enable them to exploit the same host resources in cereal crops. Therefore, there is also a need for further work investigating evolutionary adaptations of various species belonging to the same a guild to uncover general patterns promoting coexistence and their influence on shaping these communities. Finally, a better knowledge of the exact resource availability and resource distribution in both agricultural and natural habitats would undoubtedly increase our understanding of resource sharing and evolutionary adaptations of coexisting species.

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