Host range in solitary versus gregarious parasitoids: a laboratory experiment

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Abstract

Behavioural interactions among relatives may have consequences for many other traits. We tested the hypothesis that solitary parasitoids (displaying siblicidal behaviour in their larvae) have narrower host ranges than gregarious parasitoids (with tolerant larvae). In laboratory experiments, we compared parasitization success in two sister species of braconid wasp [*Aphaereta genevensis* (Fischer), solitary, and *Aphaereta pallipes* (Say), gregarious (Hymenoptera: Braconidae: Alysiini)] on eight *Drosophila* species or strains. Host species or strain was the most important factor affecting parasitization success, and some of this variation was accountable to host physiological defences. Although two hosts were more suitable for the solitary species, and one more suitable for the gregarious species, these differences were small, and there was no consistent difference across all hosts. Wasp body size was positively correlated with parasitization success in both wasp species. This may be because body size increases oviposition success, or the motivation to oviposit. In *A. pallipes* parasitization success peaked after 3–4 days, but later in *A. genevensis*. This is likely due to low life expectancy and high egg loads increasing oviposition tendency in young *A. pallipes*, and egg limitation decreasing oviposition tendency in old *A. pallipes*. These data suggest that interactions among wasp larvae do not greatly affect the size of the fundamental niche examined here. However, they show the potential for life history traits, which differ between the species as a likely consequence of larval interactions, to affect the extent of the realized niche.

Introduction

The evolution of the ecological niche is a long-standing problem in evolutionary ecology. One useful distinction is between the 'fundamental niche', which is the range of environments in which an organism can maintain a positive population growth rate, and the 'realized niche', which is the actual niche occupied in nature (see Futuyma, 2001). Selection pressures and constraints on the fundamental niche include the presence of trade-offs in fitness in different environments, interspecific interactions such as competition, as well as intraspecific competition (see Futuyma & Moreno, 1988; Jaenike, 1990; Futuyma, 2001; Schluter, 2001). The realized niche is a subset of the fundamental niche modified through limits on dispersal or individual decision-making (see Jaenike, 1990; Mayhew, 1997). In this paper we investigate the evolution of the ecological niche in relation to interactions between relatives, a relatively neglected selection pressure in this context.

It is increasingly apparent that interactions between related individuals can affect many aspects of a species evolution (see Hamilton, 1996; Frank, 1997; Svensson & Sheldon, 1998; Stockley & Parker, 2002; Gardner & West, 2004). In parasitoid wasps, which develop to maturity on the bodies of other arthropod species, recent work has suggested that the interactions between offspring on a host can radically affect life histories and adult behaviour. In solitary wasps, only a single individual completes development on each host, and the parasitoid larvae display contest competition. In gregarious species, several offspring can successfully develop on each host, and the larvae display scramble competition. Previous work has suggested that gregarious species tend to be smaller (Mayhew, 1998; Mayhew & van Alphen, 1999; Traynor & Mayhew, 2005), lay larger clutches of eggs (Mayhew & van Alphen, 1999; Mayhew & Glaizot, 2001), respond differently to conspecific females (Pexton & Mayhew, 2005), and may also be shorter-lived and more fecund (Pexton & Mayhew, 2002) than

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solitary species, differences that are likely to be a consequence of the different types of larval interaction.

In parasitoid wasps, a major component of the ecological niche is the range of host species parasitized (see Askew & Shaw, 1986; Godfray, 1994; Shaw, 1994; Müller et al., 1999). Previous anecdotal observations suggest that gregarious species might have broader host ranges than closely related solitary species. For example, Wharton (1984) and Shaw & Huddleston (1991) both note that some of the endoparasitic gregarious alysiine braconids (Hymenoptera: Braconidae: Alysiinae) have been reared from a relatively large number of host species. In the braconid subfamily Microgasterinae, the solitary *Cotesia rubecula* (Marshall) is a specialist on *Pieris rapae* (L.), while the gregarious *C. glomerata* (L.) is a generalist on several *Pieris* species (Brodeur et al., 1996, 1998). In addition, observations on bruchid beetles, with a parasitoid-like biology, show that species with tolerant larvae have decreased oviposition specificity, implying a larger host range (Smith, 1991). However, there is a need to improve on anecdotal observations, and to test the generality of these trends across parasitoids as a whole.

In this study, we compared host use in two closely related species of parasitoids: *Aphaereta genevensis* (Fischer) (solitary) and *Aphaereta pallipes* (Say) (gregarious) (Hymenoptera: Braconidae: Alysiinae). *Aphaereta genevensis* normally lays one egg per host (Mayhew & van Alphen, 1999), but can lay more than one egg in the presence of conspecific females (Pexton & Mayhew, 2005). Only one offspring normally completes development successfully. *Aphaereta pallipes* lays normally between one and five eggs per host, with a mean of about two, and several offspring can successfully complete development (Mayhew & van Alphen, 1999). Using a pair of closely related species allowed us to eliminate, as far as possible, potentially confounding biological differences that were not a result of solitary/gregarious development. We exposed both wasps to a range of potential hosts under controlled conditions, monitoring the consequences for parasitization success. We tested the hypothesis that the proportion of hosts that were successfully parasitized (i.e., from which an adult wasp successfully developed) was greater in the gregarious compared to the solitary species, as must generally be the case if gregarious species have larger host ranges. We hoped therefore to further establish whether interactions between relatives can modify the fundamental ecological niche in this group of organisms, using solitary or gregarious development as markers.

Materials and methods

Cultures

Aphaereta genevensis, recorded only from New York State, USA, and *A. pallipes*, occurring throughout the New World, are almost indistinguishable morphologically (Wharton, 1977). Details of the wasp culture history and establishment are given in Mayhew & van Alphen (1999).

A number of *Drosophila* species were used in the experiments. An advantage of using only *Drosophila* is that they display a variety of biological traits that might potentially affect host range, and yet many species can be cultured under identical conditions. We chose hosts to maximize taxonomic spread, because host taxonomy is a likely constraint on the fundamental niche (Shaw, 1994). Therefore, each host species came from a different species group. We also selected some hosts on the basis of the strength of their defences to parasitoids.

Drosophila virilis (subgenus *Drosophila*, virilis group, virilis subgroup) is the normal culturing host for the wasps in the laboratory. It was obtained from Dr Peter Chabora, Queens College, New York and in 1997. *Drosophila melanogaster* (Meigen) (Silwood strain) (subgenus *Sophophora*, melanogaster group, melanogaster subgroup) came from a culture in Silwood Park, UK, which was originally collected in Italy 2001. This strain has been selected for high encapsulation ability against a closely related alysiine wasp, *Asobara tabida* (Nees) (Kraaijeveld & Godfray, 1997). *Drosophila melanogaster* (York strain) came from a culture established over 20 years ago at York University (originally obtained from the Bloomington Fly Stock Centre, Indiana University) which has not been exposed to parasitoids since that time. Lack of selection pressure is known to reduce encapsulation ability over time because that ability is costly (Kraaijeveld & Godfray, 1997). *Drosophila subobscura* (Collin) (subgenus *Sophophora*, obscura group, obscura subgroup) was obtained from a culture at Silwood Park (originally collected from two sites in the Netherlands; the flies from the two sites were pooled together in 1984 to form a lab strain), which has been cultured for almost 20 years. This species is known to be unable to encapsulate parasitoids (Kraaijeveld & van Alphen, 1993). *Drosophila funebris* (Fabricius) (subgenus *Drosophila*, funebris group, funebris subgroup) came from a culture collected in 2000 from Leeds, UK. The following three fly species were obtained from the Tucson *Drosophila* Species Stock Centre, Arizona, USA. *Drosophila busckii* (Coquillet) (subgenus *Dorsilopha*) was originally collected from Costa Rica (stock number 13000–0081.0, genotype Dbus\wild-type). *Drosophila willistoni* (Sturtevant) (subgenus *Sophophora*, willistoni group, willistoni subgroup) was originally collected from Florida, USA (stock number 14030–0811.2, genotype Dwil\wild-type). *Drosophila immigrans* (Sturtevant) (subgenus *Drosophila*, immigrans group, immigrans subgroup) was originally collected from Colombia (stock number 155111–1731.0, genotype Dimm\wild-type).

Glass jars (5 cm in diameter) with foam stoppers were used to culture the parasitoids. The base of these jars

contained a 2-cm layer of set nutrient agar, on top of which was a dab of viscous yeast medium. Several 5–8-day-old *D. virilis* larvae were added to each jar, as were 2–5 mated parasitoid females (with no prior host experience). The jars were placed in secure plastic boxes to ensure that both parasitoid species were kept separate within a single culturing room. All *Drosophila* species were kept in this culture room and were reared separately in glass bottles with foam stoppers, containing standard medium. The medium comprised sucrose, nutrient agar, maize meal, water, and dried yeast in the following weight ratios: 65:11:75:612:10. The culture room was kept at 20 °C, constant light and ambient humidity (experiments were carried out under these conditions).

Host range experiments

To standardize the host stage, only third instar host larvae were used for the experiments; this stage is known from previous work to be relatively suitable for parasitoid oviposition and also has the advantage of reduced host mortality prior to pupation relative to earlier host stages. Each replicate (20 per fly and wasp species) was run for a total of 6 days because preliminary work showed that experience is required before peak oviposition activity occurs. This also enabled us to observe age-dependent effects on parasitoid reproductive success. Glass rearing tubes (2 cm in diameter), containing 2 cm of agar with a dab of viscous yeast medium and a plastic stopper with air holes, were used. Each tube contained one female parasitoid wasp (which had emerged and mated up to 24 h previously) and 20 third instar larvae of a given *Drosophila* species. For each replicate, on days 3 and 5, the female wasp was placed into a new rearing tube containing fresh medium and *Drosophila* larvae (as described previously). Each individual female wasp was treated as an independent replicate.

After the 6-day period, the female wasp was placed into a labelled tube and killed by freezing at −20 °C. Rearing tubes were checked every day over the course of 50 days for emerged flies/wasps. Emerged individuals were placed in labelled tubes and killed by freezing (as mentioned previously). Hind tibia length (mm) was recorded for all wasps, and thorax length (mm) was recorded for all flies. For all fly and wasp species, 20 male and 20 female individuals were dried at 70 °C for 4 days, and weighed. These data were used to convert fly thorax length into fly dry mass, and wasp hind tibia length into wasp dry mass. For conversion equations, we used regressions of hind tibia length (wasps) or thorax length (flies), against dry weight. If tibia length or thorax length were not significant predictors of individual dry weight, all individuals were assumed to have the mean mass of those weighed. If sex was significant, either on its own or as part of an interaction with hind tibia length or thorax length, then analyses were conducted separately for the two sexes. All equations (or means if appropriate) are given in Table 1.

The number of flies and wasps emerging per tube was recorded, as was the total number of pupae per rearing tube. After the 50-day period, all puparia were removed and examined for emergence holes, those with no emergence

Table 1 Equations used to estimate *Aphaereta* and *Drosophila* mass from hind tibia length and thorax length, respectively. If lengths were not significant predictors, mean (SE) dry weights are given. Equations are given separately for males and females if sex was significant in an ANCOVA, otherwise they are given together

Species (sex)	Regression equation	r^2	P
D. busckii (m + f)	Dry weight (mg) = 0.063 + [0.266 × thorax length (mm)]	0.315	<0.0005
D. funebris (m)	Dry weight (mg) = 0.007 + [0.310 × thorax length (mm)]	0.337	= 0.007
D. funebris (f)	Dry weight (mg) = 0.206 + [0.175 × thorax length (mm)] (Mean = 0.381 mg, SE = 0.0172)	0.039	0.403
D. immigrans (m)	Dry weight (mg) = 0.285 + [0.194 × thorax length (mm)]	0.307	0.011
D. immigrans (f)	Dry weight (mg) = 0.267 + [0.059 × thorax length (mm)]	0.385	0.047
D. melanogaster (Silwood) (m + f)	Dry weight = 0.092 + [0.243 × thorax length (mm)]	0.204	0.003
D. melanogaster (York)(m + f)	Dry weight (mg) = 0.091 + [0.150 × thorax length (mm)]	0.231	0.002
D. subobscura (m + f)	Dry weight (mg) = 0.127 + [0.178 × thorax length (mm)]	0.109	0.038
D. virilis (m)	Dry weight (mg) = 0.115 + [0.223 × thorax length (mm)]	0.225	0.035
D. virilis (f)	Dry weight (mg) = 0.519 – [0.144 × thorax length (mm)] (Mean = 0.369 mg, SE = 0.0095)	0.097	0.182
D. willistoni (m + f)	Dry weight (mg) = 0.136 + [0.100 × thorax length (mm)]	0.169	0.008
A. genevensis (m)	Dry weight (mg) = −0.124 + [0.410 × hind tibia length (mm)]	0.325	0.011
A. genevensis (f)	Dry weight (mg) = −0.098 + [0.412 × hind tibia length (mm)]	0.472	0.002
A. pallipes (m + f)	Dry weight (mg) = −0.094 + [0.402 × hind tibia length (mm)]	0.462	<0.0005

holes were dissected to see if there was a failed fly/wasp inside. This allowed us to record the actual number of fly pupae that gave rise to adult wasps.

Statistical analysis

Except where stated, data analysis was carried out using general linear modelling in GLIM (Numerical Algorithm Group, Oxford). Binomial error variance was assumed for proportion data and Poisson error variance was assumed for count data. Statistical models were constructed by stepwise subtraction from a full model, which included all potential explanatory variables for which we had data, starting with the least significant terms. Significance was assessed by the change in deviance under both binomial errors and Poisson errors by a χ^2 test. Only significant terms remained in the model, which was then termed 'the minimal adequate model'. The appropriateness of binomial and Poisson errors was assessed by a heterogeneity factor. This factor is equal to the residual deviance divided by the residual degrees of freedom. If the heterogeneity factor was greater than 1.3, this indicates overdispersion, and the model was rescaled using the value of Pearson's χ^2/d.f. (Crawley, 1993).

One potential pitfall of our data is that the same individual wasp was used to gather three successive data points, as each wasp aged over the first 6 days of its life. These are potential pseudoreplicates and should not be treated as independent in any analysis. To avoid pseudoreplication we only analysed data from one of the time periods in any one analysis, or pooled all the data from each wasp individual into a single number representing its total behaviour over the 6-day period. To investigate the effect of wasp age, we used the non-parametric within-subject Friedmann test, which controls for relatedness amongst observations. Where necessary, we applied sequential Bonferroni correction (Rice, 1989) to the significance values to control for multiple comparisons (Table 1). To test whether host phylogenetic relatedness was a significant factor affecting wasp species success, we constructed a cladogram by clustering species groups according to Grimaldi (1990) and subgenera according to Tatarenkov et al. (1999). The mean proportion of pupae successfully parasitized for each wasp species (Table 2) was 'hung' on the cladogram. We used a likelihood ratio test to compare the log-likelihood of a null model (where λ was set to zero) to that of the alternative model (where λ was set to its maximum likelihood value). The parameter λ, when set to zero, indicates that species are independent (1 indicates species values are maximally dependent on phylogeny). Significance was assessed by a χ^2 test. The analysis was performed in the CONTINUOUS software package (Pagel, 1997, 1999).

Results

Proportion of pupae from which wasps emerged

Across all fly species, the proportion (mean ± SE) of pupae successfully parasitized across all 6 days was similar for both wasp species (0.076 ± 0.037 and 0.038 ± 0.017 for *A. genevensis* and *A. pallipes*, respectively). Fly species or strain on its own was highly significant ($\chi^2 = 367.40$, d.f. = 7, $P<0.001$) but wasp species was not ($\chi^2 < 0.001$, d.f. = 1, $P>0.1$). The best hosts overall were *D. virilis* and *D. funebris* (Table 2). *Drosophila immigrans* was the least suitable host, failing to produce a single wasp. Female dry mass was included in the minimum adequate model ($\chi^2 = 5.03$, d.f. = 1, $P<0.05$): the proportion of pupae successfully parasitized was positively correlated with female dry mass (Figure 1). There was also a significant interaction between fly and wasp species ($\chi^2 = 23.810$, d.f. = 7, $P<0.05$). *Aphaereta genevensis* parasitized more *D. melanogaster* (York) and more *D. subobscura* than *A. pallipes*. However, *A. pallipes* parasitized more *D. busckii* than *A. genevensis* (Table 2). Fly species was a significant factor ($\chi^2 = 45.70$, d.f. = 2, $P<0.001$) explaining the differences in parasitization success across the three fly cultures specifically selected for their varying encapsulating abilities (*D. melanogaster* Silwood and York strains and *D. subobscura*).

Host body size was not a significant predictor of the parasitization success in either *A. genevensis* (Spearman's $r < 0.01$, $P = 1.0$; $n = 8$) or *A. pallipes* (Spearman's $r < 0.01$, $P = 1.00$; $n = 8$) (Figure 2). There was no significant affect of host phylogeny on the parasitization success of either

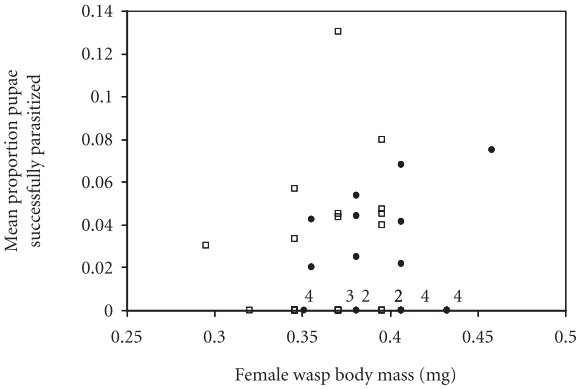

Figure 1 Female *Aphaereta* body mass (mg) plotted against proportion of pupae successfully parasitized for *Drosophila melanogaster* (York). There is a positive effect of wasp body size on parasitization success, and for a given body size, *Aphaereta genevensis* (open squares) is more successful on this host than *Aphaereta pallipes* (closed circles) (see also Table 1). Numbers above and to the right of symbols represent the number of superimposed datapoints.

Table 2 Mean ± SE proportion *Drosophila* pupae parasitized successfully, and the general linear model of this data, sample size of 20 fly pupae per replicate tube, and 20 replicate *Aphaereta* wasps per host and wasp species combination. All d.f. = 1. (*P<0.05; **P<0.001). Brackets indicate P-values that are still significant after sequential Bonferroni correction over the entire table, rejecting the null hypothesis that there are no significant results in the table. By chance, 4.2 significant results are expected, but 19 are found

			Explanatory variables		
Fly species	*A. genevensis*	*A. pallipes*	Wasp species	Female mass (mg)	Interaction
D. busckii					
Days 1–2	0.032 ± 0.012	0.157 ± 0.025	($\chi^2 = 22.750^{**}$)	$\chi^2 = 2.713$	($\chi^2 = 19.590^{**}$)
Days 3–4	0.062 ± 0.019	0.169 ± 0.033	$\chi^2 = 7.556^{*}$	$\chi^2 = 0.006$	$\chi^2 = 7.980^{*}$
Days 5–6	0.109 ± 0.032	0.028 ± 0.011	$\chi^2 = 4.432^{*}$	$\chi^2 = 4.954^{*}$	$\chi^2 = 2.191$
Overall	0.056 ± 0.014	0.123 ± 0.013	($\chi^2 = 11.820^{**}$)	$\chi^2 = 0.001$	($\chi^2 = 13.220^{**}$)
D. funebris					
Days 1–2	0.178 ± 0.039	0.193 ± 0.059	$\chi^2 = 0.290$	$\chi^2 = 8.571^{*}$	$\chi^2 = 0.144$
Days 3–4	0.290 ± 0.048	0.330 ± 0.059	$\chi^2 = 0.676$	$\chi^2 = 0.037$	$\chi^2 = 0.788$
Days 5–6	0.332 ± 0.055	0.222 ± 0.041	$\chi^2 = 1.032$	$\chi^2 = 1.738$	$\chi^2 = 1.852$
Overall	0.256 ± 0.039	0.243 ± 0.042	$\chi^2 = 0.005$	$\chi^2 < 0.001$	$\chi^2 = 0.005$
D. melanogaster (York)					
Days 1–2	0.112 ± 0.042	0.072 ± 0.018	$\chi^2 = 2.136$	$\chi^2 = 3.201$	$\chi^2 = 2.159$
Days 3–4	0.224 ± 0.049	0.199 ± 0.052	$\chi^2 = 2.032$	$\chi^2 = 0.043$	$\chi^2 = 2.372$
Days 5–6	0.218 ± 0.048	0.132 ± 0.038	$\chi^2 = 4.654^{*}$	$\chi^2 = 2.409$	$\chi^2 = 4.095^{*}$
Overall	0.184 ± 0.037	0.104 ± 0.018	$\chi^2 = 6.399^{*}$	$\chi^2 = 2.741$	$\chi^2 = 6.305^{*}$
D. melanogaster (Silwood)					
Days 1–2	0.003 ± 0.012	0.004 ± 0.013	$\chi^2 = 0.481$	$\chi^2 = 1.044$	$\chi^2 = 7.423$
Days 3–4	0.019 ± 0.014	0.005 ± 0.005	$\chi^2 = 1.466$	$\chi^2 = 8.611^{*}$	$\chi^2 = 0.242$
Days 5–6	0.006 ± 0.004	0.063 ± 0.063	$\chi^2 = 2.994$	$\chi^2 = 2.505$	$\chi^2 = 1.042$
Overall	0.020 ± 0.006	0.028 ± 0.008	$\chi^2 = 0.983$	$\chi^2 = 0.056$	$\chi^2 = 1.178$
D. subobscura					
Days 1–2	0.058 ± 0.021	0.045 ± 0.026	$\chi^2 = 1.256$	$\chi^2 = 0.698$	$\chi^2 = 2.459$
Days 3–4	0.117 ± 0.044	0.092 ± 0.022	$\chi^2 = 0.805$	$\chi^2 = 2.373$	$\chi^2 = 0.802$
Days 5–6	0.253 ± 0.056	0.101 ± 0.029	$\chi^2 = 10.990^{**}$	$\chi^2 = 3.353$	$\chi^2 = 8.762^{*}$
Overall	0.178 ± 0.033	0.074 ± 0.013	$\chi^2 = 11.280^{**}$	$\chi^2 = 2.718$	$\chi^2 = 9.227^{*}$
D. virilis					
Days 1–2	0.160 ± 0.050	0.280 ± 0.059	$\chi^2 = 2.122$	$\chi^2 = 0.270$	$\chi^2 = 3.181$
Days 3–4	0.338 ± 0.058	0.307 ± 0.057	$\chi^2 = 0.190$	$\chi^2 = 0.207$	$\chi^2 = 0.093$
Days 5–6	0.301 ± 0.048	0.241 ± 0.046	$\chi^2 = 0.591$	$\chi^2 = 1.691$	$\chi^2 = 0.156$
Overall	0.270 ± 0.038	0.277 ± 0.045	$\chi^2 = 0.040$	$\chi^2 = 0.878$	$\chi^2 = 0.719$
D. willistoni					
Days 1–2	0.023 ± 0.012	0.012 ± 0.007	$\chi^2 = 1.337$	$\chi^2 = 4.755^{*}$	$\chi^2 = 0.306$
Days 3–4	0.040 ± 0.014	0.059 ± 0.015	$\chi^2 = 0.262$	$\chi^2 = 1.800$	$\chi^2 = 2.164$
Days 5–6	0.007 ± 0.005	0.031 ± 0.011	$\chi^2 = 2.932$	$\chi^2 = 0.931$	$\chi^2 = 2.180$
Overall	0.024 ± 0.007	0.032 ± 0.007	$\chi^2 = 0.551$	$\chi^2 = 1.417$	$\chi^2 = 1.724$

wasp species. For *A. genevensis* the maximum likelihood estimate of $\lambda = 0.117$, $\chi^2 = 0.06$, d.f. = 1, P = 0.82. For *A. pallipes* the maximum likelihood estimate of $\lambda = 0$, $\chi^2 = 0$, d.f. = 1, P = 1.00.

Age-dependent effects were significant for both wasp species (Table 3). *Aphaereta genevensis* successfully parasitized the greatest number of pupae on days 5–6 and was the least successful on days 1–2. *Aphaereta pallipes* successfully parasitized the greatest number of pupae on days 3–4 and was the least successful on days 1–2. Wasp species was a significant factor ($\chi^2 = 4.81$, d.f. = 1, P<0.05) on days 5–6, explaining the differences in parasitization success between the two wasp species. However, there was no significant effect of wasp species on days 1–2 ($\chi^2 = 2.88$, d.f. = 1, P>0.01) or on days 3–4 ($\chi^2 = 0.27$, d.f. = 1, P>0.01).

Number of parasitoid offspring produced

For total offspring produced per individual wasp, over all hosts, the minimum adequate model contained female dry mass ($\chi^2 = 5.44$, d.f. = 1, P<0.05), fly species ($\chi^2 = 273.70$,

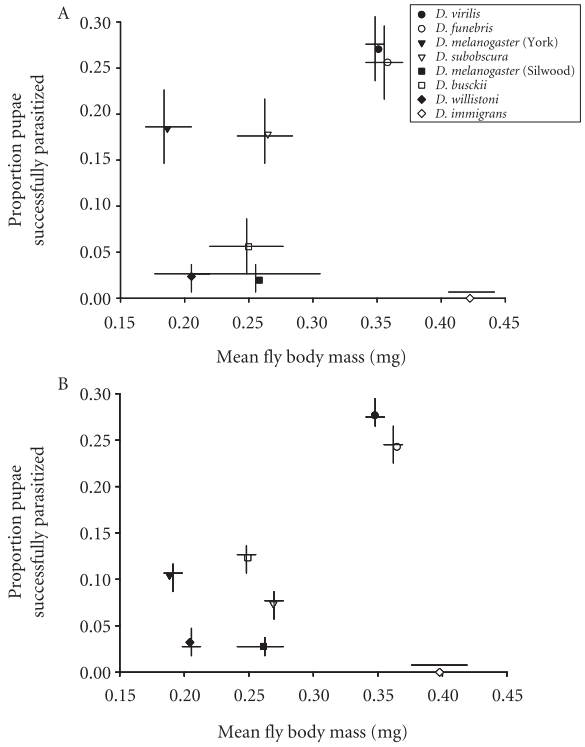

Figure 2 Mean (± SE) proportion of *Drosophila* pupae that successfully gave rise to (A) *Aphaereta genevensis* offspring and (B) *Aphaereta pallipes* offspring, across different fly species or strains.

d.f. = 7, P<0.001), and wasp species ($\chi^2 = 12.01$, d.f. = 1, P<0.001), but no interaction terms. *Aphaereta pallipes* produced a greater number of offspring than *A. genevensis* (Table 4), there was a positive relationship between number of offspring produced and female dry mass, and again *D. virilis* and *D. funebris* were the best hosts in terms of number of wasp offspring produced (Table 4). For brood size, over all hosts, wasp species was the only significant factor ($\chi^2 = 14.730$, d.f. = 1, P<0.001), with *A. pallipes* producing larger broods than *A. genevensis*.

Discussion

The main finding of this study is that host species affects parasitization success similarly, over a range of potential

Table 4 Mean ± SE number of offspring per female *Aphaereta* wasp over all 60 hosts

Fly species	*A. genevensis*	*A. pallipes*
Fly species combined	5.713 ± 2.05	7.556 ± 2.95
D. busckii	2.950 ± 0.63	6.450 ± 0.71
D. funebris	12.050 ± 1.67	18.650 ± 4.59
D. melanogaster (York)	7.700 ± 1.60	6.200 ± 1.04
D. melanogaster (Silwood)	0.900 ± 0.26	0.600 ± 0.18
D. subobscura	5.050 ± 0.38	3.550 ± 0.52
D. virilis	16.000 ± 2.32	21.850 ± 3.10
D. willistoni	1.050 ± 0.30	2.650 ± 0.67

Drosophila hosts, in two sister species of parasitoids that differ in larval behaviour. Although two hosts are more suitable for the solitary species, and one more suitable for the gregarious species, these differences are small. In addition, wasp size and age are important explanatory variables explaining wasp success, suggesting they may make important contributions to the realized niche. Below we put these results in the context of previous work, before discussing how they can be furthered.

Theoretically, a broader host range might be the consequence of increasing the range of suitable hosts available, in other words increasing the fundamental host niche. Some of the hosts parasitized by endoparasitic gregarious alysiines are large relative to the size of the wasp (see Vet et al., 1993). Because they pupate internally, the host must be completely consumed prior to parasitoid pupation and this can only be achieved in a big host by increasing the number of offspring sharing the host. Therefore, larger-bodied hosts may be more easily exploited by gregarious species. In addition, laying several eggs may increase host suitability by helping to overwhelm the host's immune response (see Ode & Rosenheim, 1988). Gregarious parasitoids may also have larger realized niches due to individual decision making. Being generally smaller bodied, gregarious species should have shorter lifespans than related solitary species. State-dependent decision-making models suggest that expected future lifespan should negatively correlate with oviposition tendency (see Mangel, 1987; Roitberg et al., 1993). In addition, if they allocate

Table 3 Age-dependent effects on the success of *Aphaereta* parasitization (Friedmann test). Rank values are in italics; mean proportion parasitized successfully (± SE) is given

Wasp species	Days 1–2		Days 3–4		Days 5–6		d.f.	P
A. genevensis	*1.77*	0.09 ± 0.01	*2.08*	0.16 ± 0.02	*2.15*	0.18 ± 0.02	2	<0.001
A. pallipes	*1.86*	0.12 ± 0.015	*2.24*	0.17 ± 0.017	*1.90*	0.12 ± 0.015	2	<0.001

resources preferentially to eggs rather than survival, the resulting higher egg loads should also increase oviposition tendency (Pexton & Mayhew, 2002).

The most suitable host species for both wasps in our experiments were *D. virilis* and *D. funebris*. The least suitable host was *D. immigrans* and the other host species were of intermediate suitability. Host body size cannot explain this, as large hosts could be either highly suitable or completely unsuitable, and the two traits were not significantly correlated overall. Host taxonomic affiliation is also unable to explain host suitability for the wasps. Encapsulation ability does seem to explain some of the variation in success. A strain of *D. melanogaster* that has been selected for high encapsulation ability was of low suitability for both wasps. However, both wasps were more successful on a control strain of *D. melanogaster*, as well as on the closely related *D. subobscura*, which is known to be unable to encapsulate parasitoids. Therefore, physiological features of the host, such as host defence capability, can account for some of the variation in fundamental host niche. What exactly affects host suitability in the other species examined is unknown, but possible factors include other host defence responses and physiological traits, as well as a species' apparency to searching female parasitoids.

The effect of wasp size on wasp performance was positive. A likely reason is that larger-bodied wasps contain more eggs in both species (Pexton & Mayhew, 2002). State-dependent models of behaviour show that higher egg loads should increase oviposition tendency and several studies have confirmed this (Godfray, 1994). An additional reason for the trend may be that larger wasps are better able to reach, subdue, or oviposit into hosts. For example, Rotheray & Barbosa (1984) noted that host handling time increased with host size in *Brachymeria intermedia*. The percentage host parasitism was greater in small hosts that were also less aggressive towards the parasitoids. Kouamé & Mackauer (1991) found that aphids attacked by *Ephedrus californicus* kicked to prevent parasitism and that larger aphids were more successful at preventing parasitism. It is possible that such defence reactions are also size-related in our hosts and that larger wasps are better able to overcome them.

The effects of wasp body size on performance may have implications for the host ranges of solitary and gregarious species. Gregarious species are generally smaller bodied than solitary relatives (e.g., Mayhew, 1998; Mayhew & Hardy, 1998; Mayhew & van Alphen, 1999; Traynor & Mayhew, 2005). Our data suggest that small body size has the effect of decreasing realized host range by virtue of generally lower performance. However, it is possible that other factors counterbalance this. Gregarious species may have larger egg loads and lower life expectancies than solitary species of the same size, which could increase oviposition motivation and overall performance in gregarious species. The effects of age on performance may reflect this: *A. pallipes* reached peak performance earlier in life than *A. genevensis* and this may indicate a generally higher motivation to oviposit. Overall, in our experiments there is no indication that the wasp species differed in overall performance. However, these factors might have different quantitative effects in the field compared to the laboratory.

The drop in parasitization success in 5–6-day-old *A. pallipes* may reflect egg limitation; ageing insects are predicted to reduce oviposition activity in response to reduction in egg load in a number of theoretical models (Mayhew, 1997). In contrast, there is no indication of such a drop in *A. genevensis*. Previous data on resource allocation in these two species (Pexton & Mayhew, 2002) have also suggested that *A. pallipes* is more egg limited than *A. genevensis*. Models of the dynamics of parasitoid populations that assume such a difference make specific predictions, such as a higher likelihood that the solitary species will coexist with its host population, and that the gregarious species will suppress its host's population to a greater extent (Heimpel, 2000). These predictions would merit testing on this system.

Clearly, we have not provided here a definitive comparison of the host ranges of the two wasp species, but merely shown that they do not differ extensively over certain taxa and under certain conditions. Clearly, this similarity will largely be due to shared characteristics of the wasps that are a result of common ancestry. The differences in larval behaviour that have evolved since these wasps shared a common ancestor have not greatly changed their performance on these particular hosts. If there is a large difference in the total extent of the host ranges of the species, it is likely to be a result of some hosts not considered here, from which solitary species are excluded, rather than a greater performance of gregarious species more generally. There is room to extend the comparisons to other taxa, particularly large-bodied taxa to which we might expect that solitary species would be less suited.

Finally, as discussed by Harvey & Pagel (1991), our study represents a single independent contrast between the two wasp species being studied and, therefore, cannot be used alone to confirm or reject the hypothesis that gregarious parasitoid species as a whole have broader host ranges than solitary species. Nonetheless, other similar comparisons have already been carried out (e.g., Smith, 1991; Brodeur et al., 1996, 1998), or could be done for pairs of species in other groups (e.g., Boivin & van Baaren, 2000). A collective understanding of the niche differences between solitary and gregarious species should emerge from several such studies, of which ours is one example.

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