How two different host species influence the performance of a gregarious parasitoid: host size is not equal to host quality

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Summary

1. *Hyssopus pallidus* Askew (Hymenoptera, Eulophidae) is a gregarious ectoparasitoid of the two tortricid moths species *Cydia molesta* Busck and *C. pomonella* L. (Lepidoptera, Tortricidae). It paralyses and parasitizes different larval instars of both species inside the apple fruit, which leads to the death of the caterpillar.

2. We assessed the influence of host species characteristics and host food on the performance of the parasitoid female in terms of clutch size decisions and fitness of the F_1 generation.

3. A comparison of clutch size revealed that female parasitoids deposited similar numbers of eggs on the comparatively smaller *C. molesta* hosts as on the larger *C. pomonella* hosts. The number of parasitoid offspring produced per weight unit of host larva was significantly higher in *C. molesta* than in *C. pomonella*, which is contrary to the general prediction that smaller hosts yield less parasitoid offspring. However, the sex ratio was not influenced by host species that differed considerably in size.

4. Despite the fact that less host resources were available per parasitoid larva feeding on *C. molesta* caterpillars, the mean weight of emerging female wasps was higher in the parasitoids reared on *C. molesta*. Furthermore, longevity of these female wasps was neither influenced by host species nor by the food their host had consumed. In addition we did not find a positive relationship between adult female weight and longevity.

5. Parasitoid females proved to be able to assess accurately the nutritional quality of an encountered host and adjust clutch size accordingly. These findings indicate that host size is not equal to host quality. Thus host size is not the only parameter to explain the nutritional quality of a given host and to predict fitness gain in the subsequent generation.

Key-words: clutch size, fitness, host quality, host size, *Hyssopus pallidus*, parasitoid.

Introduction

One of the major decisions gregarious parasitoids have to make is how many eggs, if any, to oviposit on an encountered host (Waage 1986; Godfray 1994). The concept of optimal clutch size (Lack 1947) suggests that females should lay the number of eggs that maximizes their gain in fitness. This model has been extended to parasitoids, proposing that females lay a precise amount of eggs onto a host of given size and quality

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(Charnov & Skinner 1984), thus resulting in maximum fitness return (Lack 1947). Host size is often considered to be a key factor influencing parasitoid fitness (Godfray 1994; Vet *et al*. 1994). Models have been developed to describe the evolution of clutch size and to predict variation in this life history parameter caused by limited nutritional resources available or limitation in time or in egg supply (Charnov & Skinner 1984; Waage & Godfray 1985; Rosenheim 1999). In gregarious species, fitness is affected not only by host size but also by the number of parasitoids developing on a single host (Waage & Godfray 1985; Harvey *et al*. 1998). In a large clutch the units of resources available for each wasp larva are reduced and can have a significant influence on the ultimate fitness of the subsequent wasp generation (Bezemer & Mills 2003). Oviposition decisions by the

female parent are therefore crucial for competition between siblings (Waage 1986), and the ultimate fitness gain will be determined by the number of viable offspring, offspring size (Godfray 1994) and whether the host has been parasitized previously (Zaviezo & Mills 2001). Thus, to optimize their fitness, female wasps are expected to adjust the allocation of eggs to a host depending on the host's quality.

Offspring sex allocation theory predicts that more fertilized eggs (yielding female offspring) are deposited onto hosts of superior quality, and unfertilized eggs (yielding males) are laid onto lower-quality hosts (Godfray 1994). This prediction presumes that females gain relatively more in fitness from increased body size than males (Charnov 1982; Godfray 1994), because increased female body size results in higher egg loads and enhanced longevity. Parasitoid wasps are therefore assumed to be genetically and ecologically predisposed to display female-biased sex ratios to gain maximum fitness. Especially in gregarious parasitoids, host quality is often reflected by the sex ratio within a clutch (Bertschy et al. 2000; Harvey 2000).

The majority of studies on host quality in parasitoids observed that clutch size increased with host size and therefore concluded that host size was a reliable factor to predict nutritional quality of a host larva (Lemasurier 1987; Hardy, Griffiths & Godfray 1992; Zaviezo & Mills 2000; Bell et al. 2005). Large hosts are expected to be more advantageous in terms of offspring fitness than small hosts because they contain a greater quantity of resources (Harvey et al. 2004). In gregarious parasitoids, not only individual offspring size but also clutch size is correlated positively with host size (Hardy et al. 1992; Zaviezo & Mills 2000; Bell et al. 2005), hence to estimate host quality from only host size may be misleading. Harvey et al. (2004) demonstrated that age-specific differences in host quality affected the growth and development of *Microplitis demolitor* Wilkinson (Hymenoptera: Braconidae), a parasitoid of the soybean looper. Other studies showed that the nutritional and endocrinological status could also impose constraints on the parasitoids' development (Vet et al. 1994; Harvey 2000; Harvey et al. 2004; Colinet et al. 2005).

In this study we examined developmental interactions between the gregarious ectoparasitoid *Hyssopus pallidus* Askew (Hymenoptera: Eulophidae) and two of its potential host species, the comparatively small *Cydia molesta* Busck (Lepidoptera: Tortricidae) and the larger *C. pomonella* L. (Lepidoptera: Tortricidae). *C. pomonella*, in particular, is a notorious pest of apple trees (Dorn et al. 1999) but *C. molesta* is also becoming an increasing problem in apple cultivation (Hughes, Hern & Dorn 2004). It attacks different larval instars (Zaviezo & Mills 1999) inside the apple, always leaving behind a carcass, which is often large enough to allow host species identification even after emergence of the parasitoid's progeny (Tschudi-Rein et al. 2004; J. Häckermann personal observation). *H. pallidus* is

known to adjust clutch size according to host size (Zaviezo & Mills 2000). For an effective clutch size adjustment parasitism experience is not necessary, but how often a female encounters hosts substantially influences its clutch size, resulting in an increased clutch size as the encounter rate declines (Zaviezo & Mills 2000). The sex ratio of *H. pallidus* is heavily female-biased, varying from zero to two males per clutch (Zaviezo & Mills 1999). In addition, lifetime fecundity increases substantially with female size (Zaviezo & Mills 2000). *H. pallidus* is a relatively specialized parasitoid, particularly well adapted to the apple habitat (Hausmann, Mattiacci & Dorn 2005), and both host- and host habitat-related cues are used in host location (Mattiacci, Hütter & Dorn 1999).

So far, many studies on the behavioural ecology of parasitoids, especially gregarious parasitoids, have concluded that host size is equal to host quality. The central question being addressed in this study is whether host size alone is an adequate predictor of host quality. To evaluate this hypothesis, we examined the influence of two different host species on the reproductive success of the parasitoid. We compared the parasitoid's performance quantitatively in terms of development time, longevity, lifetime fecundity and clutch size. Host species effects on the performance of the subsequent parasitoid generation are discussed.

Materials and methods

PARASITOID AND HOST CULTURES

The initial colony of *H. pallidus* was provided in 1996 by T. Unruh (USDA-ARS Research Laboratory, Wapato, WA, USA), and originated from France. Following detection of this parasitoid in Switzerland (Tschudi-Rein et al. 2004) the colony was refreshed by the introduction of field-collected adults and maintained as a single colony. Starting from this single colony, two strains were obtained by rearing the parasitoids on two different hosts. One strain was reared on *C. pomonella* hosts (CP strain), the other on *C. molesta* hosts (CM strain).

The CM parasitoid strain was maintained on last instar *C. molesta* caterpillars and the CP parasitoid strain on last instar *C. pomonella* caterpillars. Both host species had been reared on a wheatgerm-based artificial diet (Huber, Benz & Schmid 1972). Newly hatched first instar caterpillars were placed individually into a plastic box (18 × 18 × 10 mm) filled with 3·4 g of artificial diet. Boxes containing *C. pomonella* hosts and *C. molesta* hosts, respectively, were kept at 25° ± 2 °C, 60 ± 10% RH and 16 h light : h dark. The caterpillars were offered to 4–7-day-old mated female parasitoids. In the permanent rearing, host caterpillars were offered to the female wasp in glass vials (10 cm length, 2·8 cm diameter) at a ratio of two parasitoids per host.

Because plant cues offered during the ontogenesis of the parasitoid are of crucial importance for the behavioural

efficiency of the emerged wasps (Gandolfi, Mattiacci & Dorn 2003b), a small piece of fresh apple (Gandolfi, Mattiacci & Dorn 2003a) was added to the vial and a drop of undiluted honey served as food source to the parental female. The vials were closed with a piece of thin-meshed net. The ovipositing parental females were removed from the vial one week later. Parasitized caterpillars were kept under standardized laboratory conditions at a temperature of $24° ± 2 °C$, RH of $60\% ± 10\%$ and a light regime of 16 h light : 8 h dark until the emergence of the parasitoid's progeny 14–17 days later. Upon emergence, progeny was removed from the vial and transferred to a Plexiglas cage, respectively ($25 × 25 × 25$ cm), where they were fed with honey and water.

INFLUENCE OF HOST SPECIES ON IMMATURE DEVELOPMENT TIME

The duration of immature development of the parasitoid was studied on both hosts, *C. molesta* and *C. pomonella*. A single medium-sized host larva (*C. molesta* 15–25 mg, *C. pomonella* 40–80 mg) was offered in a glass vial (10 cm length, 2·8 cm diameter) to a 4–7-day-old, mated *H. pallidus* female. A droplet of honey served as food source. Experiments on *C. molesta* were conducted with parasitoids of the CM strain and those on *C. pomonella* with parasitoids from the CP strain. Every 24 h, we recorded the duration of host attack until oviposition took place and the development time of the egg, larval and pupal stages. From these observations the complete development time was calculated. Because eggs and larvae are very small and extremely delicate, development of the larvae was observed under the microscope through the glass vials without disturbing the developing brood. Temperature and relative humidity were as described above.

INFLUENCE OF HOST SPECIES, HOST FOOD AND PARASITOID WEIGHT ON ADULT FEMALE FITNESS

Female longevity and lifetime fecundity were measured to describe parasitoid fitness in relation to the two host species. To determine the effect of host species on the fitness of the parasitoid, longevity was studied in relation to the host species on which the brood had developed and in relation to the female size (0·35–0·66 mg fresh pupal weight). To determine the influence of the first trophic level (the host's nutritional source) on the fitness of the third trophic level (parasitoid), female longevity was checked daily after emergence in the absence of the host for four groups of 42 individuals (standardized by age and handling, but variable in size). The first group of test parasitoids developed on *C. molesta* caterpillars that had been reared on an artificial diet; the second group developed on *C. molesta* caterpillars that had been reared on apple fruits. The third and fourth groups developed on *C. pomonella* caterpillars that had been reared either on an artificial diet or on apple fruits. Prior to the experiments, pupae were weighed in order to minimize handling effects on adult performance. Afterwards, each pupa was put singly into a glass vial and a droplet of honey served as food source for the emerging adult.

Potential fecundity was determined by exposing 15 medium-sized female *H. pallidus* females (0·35–0·55 mg fresh pupal weight) individually to medium-sized host larvae (*C. molesta* 13–21 mg, *C. pomonella* 20–45 mg) of each host species in a Plexiglas Petri dish (3 cm diameter) and supplied with a droplet of undiluted honey. Parasitoids used in these experiments derived from the CM and the CP strain. Upon successful oviposition, eggs were counted and the female wasp was kept with the brood for an additional 2 days for brood guarding (Zaviezo & Mills 1999) and to allow the maturation of a new set of eggs (Tschudi-Rein & Dorn 2001). Thereafter, the female was removed and offered a new host caterpillar. This procedure was repeated until the parasitoid's death.

Potential lifetime fecundity was estimated by multiplying the average number of eggs a female laid per clutch with the total number of hosts attacked by the most successful female of the sample (Zaviezo & Mills 1999).

INFLUENCE OF HOST SIZE AND SPECIES ON PARASITOID CLUTCH SIZE

To evaluate the influence of the host species and weight on the clutch size of *H. pallidus*, caterpillars of different size within each species (*C. pomonella*: 8–100 mg, *C. molesta*: 2–25 mg fresh weight) were offered to individual naive *H. pallidus* females, standardized by age (4–7 days old) and handling (honey-fed) and of similar size (0·48–0·52 mg fresh pupal weight). Parasitoids used in these experiments were derived from the two different parasitoid strains. Parasitoids of the CP strain were offered *C. pomonella* caterpillars, those of the CM strain *C. molesta* caterpillars for oviposition. Host caterpillars were divided into two groups according to larval instars. For *C. molesta*, group 1 comprised third instar caterpillars ranging from 2·2 mg to 13·3 mg in body weight. The second group consisted of fourth instar caterpillars that ranged from 6·1 mg to 25·4 mg in size. Analogously, *C. pomonella* larvae were classified into two groups: group 1 comprised fourth instar caterpillars between 8·3 mg up to 49·7 mg of weight. Group 2 included all fifth instar caterpillars, which were larger than 26·4 mg. Larval instars were determined by measuring the head capsule width (Weitzner & Whalone 1987). A single host caterpillar and a single parasitoid female were placed into a glass vial. Because any manipulation on the developing brood leads to severe losses in emerging adults, parasitoid larvae completed development without any interference. Upon successful development, the number of emerging parasitoid adults was counted and their sex ratio was determined.

RELATIONSHIP BETWEEN HOST SPECIES, HOST SIZE, CLUTCH SIZE AND OFFSPRING SIZE

To check for possible adaptive differences in the respective parasitoid strain, a cross-experiment was conducted. Parasitoids that had been reared on *C. molesta* for many generations were offered *C. pomonella* hosts for parasitism; parasitoids reared on *C. pomonella* developed on *C. molesta* hosts for one generation. Resulting offspring were counted and weighed.

To determine the influence of host species, host size and clutch size on parasitoid offspring size, *C. molesta* and *C. pomonella* hosts of different size were offered individually to a single parasitoid female. Females were standardized by age (4–7 days old), nutrition (honey-fed) and size (0·50 ± 2 mg of fresh pupal weight). Upon successful development, parasitoid pupae were removed from the dead host and offspring body size was determined by weighing each pupa. Clutch size was defined as number of pupae.

STATISTICAL ANALYSIS

Data were analysed using parametric statistics. In cases where the assumptions of normality and homogeneity of variance were not met, nonparametric tests were used. To analyse the influence of the host species on the development time of the parasitoid, we used a Mann–Whitney *U*-test. The influence of host species and host body size was assessed using two-way analysis of variance (ANOVA). For all tests a threshold level of $P < 0.05$ was used.

Results

INFLUENCE OF HOST SPECIES ON IMMATURE DEVELOPMENT TIME

The overall time required to complete development (from egg stage to adult emergence) amounted to 16·03 ± 1·20 SD days for *H. pallidus* parasitoids reared on *C. pomonella* and 15·71 ± 0·825 SD days for those reared on *C. molesta*. The Mann–Whitney *U*-test indicated a significant difference in the overall development time of the parasitoids on the two host species ($Z = -1.971$, $P < 0.05$). The shorter development time is in favour of the CM strain and can be attributed to the significantly shorter embryonic development time (*U*-test: $Z = -2.241$, $P < 0.05$) on *C. molesta* hosts.

Female *H. pallidus* from both strains spent almost the same time on probing, host paralysis and oviposition on *C. molesta* (2·05 days ± 0·53 SD) as on *C. pomonella* (2·10 days ± 0·57 SD) caterpillars, respectively. Their host handling time was not significantly different ($Z = -0.727$, $P = 0.47$) between the two *Cydia* host species. Time needed from egg deposition until egg hatching was similar on *C. molesta* (1·08 days ± 0·28 SD) and on *C. pomonella* hosts (1·23 days ± 0·43 SD). Also, the time needed to complete larval development

was not influenced significantly by host species ($Z = -0.749$, $P = 0.45$). The parasitoid brood required a similar amount of time on *C. molesta* (4·98 days ± 0·79 SD) as on *C. pomonella* (5·08 days ± 0·96 SD) to complete immature development. The pupal stage also lasted for a similar time ($Z = -0.113$, $P = 0.91$) on *C. molesta* (7·6 days ± 0·91 SD) as on *C. pomonella* caterpillars (7·62 days ± 0·90 SD).

INFLUENCE OF HOST SPECIES, HOST'S FOOD AND PARASITOID WEIGHT ON ADULT FEMALE FITNESS

The diet of the host caterpillar did not influence significantly the longevity of the parasitoid female. No significant difference in longevity was detected between parasitoids that had been reared on host caterpillar fed with the artificial diet or apple (CM strain: $t = -0.622$, d.f. = 82, $P = 0.536$, CP strain: $t = -1.941$, d.f. = 82, $P = 0.056$). Similarly, there was no significant difference in female longevity between parasitoid females emerging from the two host species ($t = -0.443$, d.f. = 71, $P = 0.659$). Parasitoid females that had developed on *C. molesta* caterpillars lived for an average of 43·45 days (± 15·24 SD, $n = 33$), whereas those that had developed on *C. pomonella* caterpillars lived on average for 41·59 days (± 15·24 SD, $n = 41$).

For *C. molesta*-reared parasitoids, the average number of eggs laid in a lifetime on *C. molesta* hosts (55·85 ± 21·25 SD, $n = 14$) did not differ significantly from those that *C. pomonella* reared parasitoids laid on *C. pomonella* hosts (53·93 ± 14·62 SD, $n = 14$) ($t = -0.278$, d.f. = 26, $P = 0.78$).

INFLUENCE OF HOST SIZE AND SPECIES ON PARASITOID CLUTCH SIZE

Clutch size increased with host size and the relationship (Fig. 1) is well described by a linear regression for
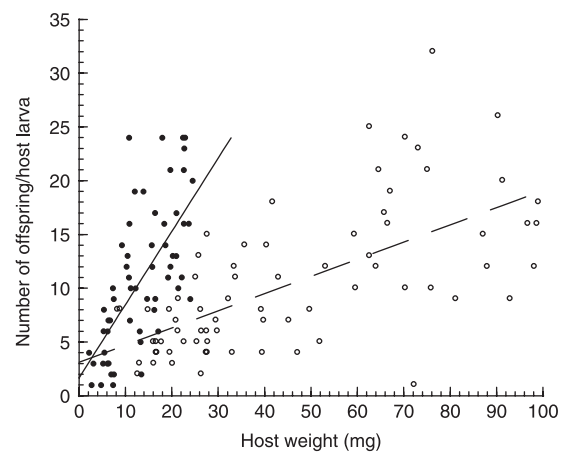
Fig. 1. Relationship between clutch size of the parasitoid *H. pallidus*, estimated as number of pupae that completed development on the host *C. molesta* (●) or *C. pomonella* (○) and host larval fresh weight. Linear regression analysis for parasitoids reared on *C. molesta*: solid line; on *C. pomonella*: dotted line.

Table 1. Results of two-way ANOVA testing for the relationship between host species (*Cydia molesta* and *C. pomonella*) and host body size (in mg) affecting clutch size

	d.f.	MS	F	P
Host species	1	14·71	0·6	= 0·44
Host body size	1	1761·43	71·71	< 0·001
Host species × host body size	1	677·23	27·57	< 0·001
Error	133	24·56		

Fig. 2. Number of *H. pallidus* offspring produced per mg host larval weight for *C. molesta* and *C. pomonella*. Different letters indicate that there is a significant difference between the number of offspring produced per host larva and the host species involved.

both host species (*C. molesta*: $R^2 = 0.458$, $F = 51.536$, d.f. = 1, $P < 0.001$, *C. pomonella*: $R^2 = 0.418$, $F = 51.456$, d.f. = 1, $P < 0.001$). On both host species, significantly more parasitoids developed on large host caterpillars [CP strain ($t = -5.663$, d.f. = 72, $P < 0.001$), CM strain ($t = -4.588$, d.f. = 61, $P < 0.001$)] than on smaller ones. The two-way ANOVA showed that the factors significantly influencing the clutch size are the size of the host caterpillars and the interaction between host body size and the host species (summarized in Table 1). The mean number of parasitoid offspring produced on *C. molesta* hosts (11·03 mg ± 5·89 SD, $n = 63$) did not differ significantly from the mean number of offspring produced per *C. pomonella* host caterpillars (11·34 mg ± 6·56 SD, $n = 74$), despite the fact that *C. molesta* caterpillars are on average much smaller (13·75 mg ± 6·5 SD) than *C. pomonella* caterpillars (45·26 mg ± 26·57 SD) (*U*-test: $Z = -8.303$, $P < 0.001$).

For both host species, offspring sex ratios were heavily female-biased with the number of males in a clutch varying from zero to two (median: 1). There was no significant difference in the number of males per clutch between parasitoids that had developed on *C. molesta* hosts (0·93, $n = 91$) and those that developed on *C. pomonella* hosts (0·94, $n = 113$) ($t = -0.1$, d.f. = 199, $P > 0.05$).

RELATIONSHIP BETWEEN HOST SPECIES, HOST SIZE, CLUTCH SIZE AND OFFSPRING SIZE

On last instar *C. molesta* caterpillars (15–30 mg) an average of 10·68 ± 4·68 ($n = 34$) parasitoids developed per host, on fifth instar *C. pomonella* caterpillars (25–100 mg) 10·53 ± 5·9 parasitoids developed per host ($n = 36$). The cross-experiment revealed that parasitoids adapt progeny to the host's quality that they encountered irrespective of the host upon which the parasitoid had developed originally. These results document that continuous rearing on a given host does not lead to the formation of parasitoid races adapted to a specific host, and that the method used to test the influence of host size and species is valid for the purpose of the study.

To control for slight differences in the size of the host caterpillar within a size category of a host species group, parasitoid clutch size was expressed as number of female offspring per mg fresh host weight. Similarly,
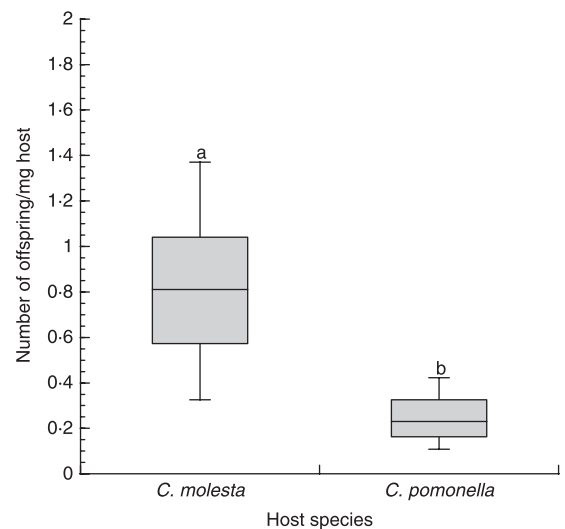
mean daughter size was characterized as mean daughter weight per mg host larval weight. The number of offspring produced per mg host (Fig. 2) was significantly higher on *C. molesta* host larvae (0·82 ± 3·8 SD, $n = 31$) than on *C. pomonella* hosts (0·27 ± 0·18 SD, $n = 43$) ($Z = -6.044$, $P < 0.001$).

Host species did have a significant influence not only on the number of offspring produced per host larva, but also on the daughter's weight. Even though parasitoids do adjust clutch size according to host size in both species, the mean weight of the daughters per mg host weight was significantly higher in *C. molesta* (0·03 mg ± 0·18 SD) than in *C. pomonella* hosts (0·015 mg ± 0·009 SD, $t = -4.808$, d.f. = 72, $P < 0.001$) (Fig. 3).

Mean daughter size was influenced positively by host size in the case of *C. molesta* hosts ($R^2 = 0.323$, $F = 13.836$, $P < 0.01$), accounting for 32·3% of the variance (Fig. 4). Fresh pupal weight increased with increasing host size, regardless of the clutch size. In contrary, there was no relationship when *C. pomonella* was the host. Here, mean parasitoid offspring body size stayed constant over all the different host stages ($R^2 = -0.024$, $F = 0.07$, $P > 0.05$), ranging from 8·3 mg to 98·7 mg (Fig. 4). With *C. molesta*, not only the number of offspring produced per host increases with increasing host size, but also individual progeny gains in weight as host size increases, whereas in the case of *C. pomonella* only clutch size increases with increasing host size.

Discussion

The principles of clutch size adjustment in response to host size have been demonstrated for a variety of gregarious parasitoid species (Lemasurier 1987; Hardy *et al.* 1992; Zaviezo & Mills 2000). These adjustments
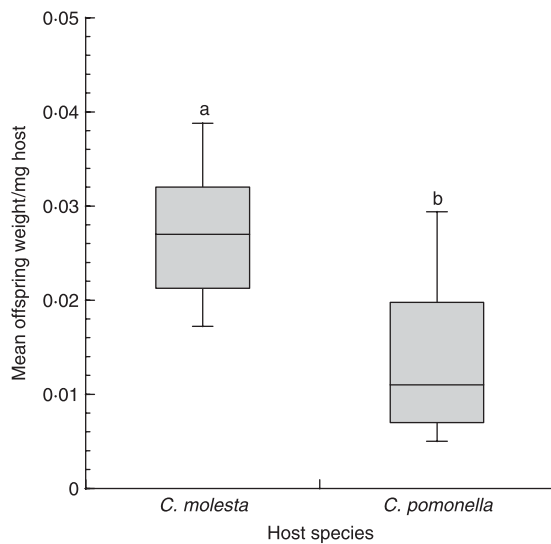
Fig. 3. Relationship between host species and mean offspring weight, expressed as offspring weight per mg host. For the two species the median is illustrated. Different letters indicate that there is a significant difference between the number of offspring produced per host larva and the host species involved.
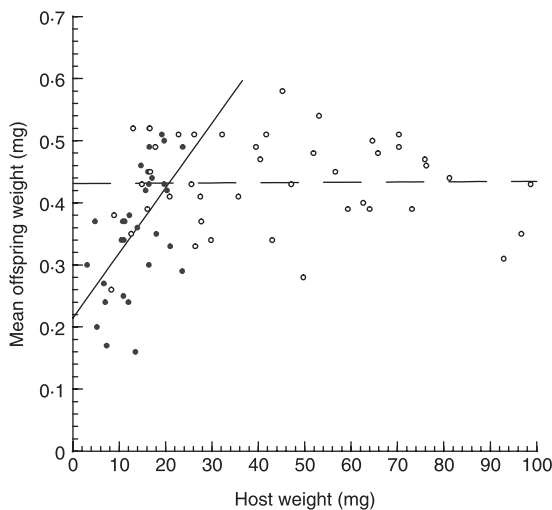
Fig. 4. Relationship between host size, expressed as host weight and the mean offspring size of *H. pallidus*, estimated as number of pupae that completed development on *C. molesta* (●) and *C. pomonella* (○) hosts.

have been considered adaptive, such that larger hosts are assumed to provide a greater amount of nutrients to the developing brood than smaller hosts (Hardy *et al*. 1992; Zaviezo & Mills 2000; Bell *et al*. 2005). Contrary to expectations, *H. pallidus* displayed a different behaviour of clutch size adjustments in the two host species of the same genus. Last instar *C. pomonella* larvae weighing 50–100 mg yielded the same number of parasitoid offspring as last instar *C. molesta* larvae weighing 16–25 mg, despite the fact that the difference in host weight is approximately fourfold. As a consequence, parasitoids developing on *C. molesta* have lower *per capita* food availability, which could translate into smaller

offspring size. Alternatively, the parasitoid's offspring might be able to adjust nutrient uptake to the availability of host resources. If this regulation mechanism applies, equal offspring size, regardless of host size, should be noted. However, larger parasitoids were produced per weight unit of food resource on *C. molesta* hosts compared to *C. pomonella* hosts. These results provide evidence that host quality is not only determined by host size. Rather, host nutrients seem to differ in the two host species, with *C. molesta* being more rewarding in some way for the parasitoid. Thus, nutrient uptake and conversion might not be equal in the two species. Our results show that offspring size increased with host size for *C. molesta* hosts. In contrast, for parasitoids that had developed on *C. pomonella* clutch size increased with host size, but offspring weight was constant over the examined host weight range. In our study, clutch size was not constrained by egg load itself, as 4-day-old honey-fed *H. pallidus* females produce an average egg load of 20 (Tschudi-Rein & Dorn 2001).

Sex allocation theory predicts that smaller hosts (of inferior quality) yield fewer female offspring than large hosts (Bertschy *et al*. 2000). This assumption presumes that females lose relatively more in fitness when being small compared to males (Charnov 1982). In our study, *C. molesta* hosts did not yield more male offspring than the larger *C. pomonella* hosts. This corroborates the hypothesis that *C. molesta* has a different qualitative value in terms of nutrients.

Ovipositing females seem to be able to estimate subtle differences in host quality. These differences in quality could be the result of a reduced number of eggs laid on *C. pomonella* caterpillars or of a higher mortality of parasitoid larvae on *C. pomonella* hosts. Mortality during pre-imaginal development on *C. pomonella* hosts has been described as low (Zaviezo & Mills 2000), indicating that the differences observed are due to females accurately assessing the quality of an encountered host and adjusting clutch size accordingly. It appears that nutrient convertibility may be the crucial key to explain the observed differences in parasitoid offspring number and size. Our findings are in agreement with Sequeira & Mackauer (1992), who claim that quality is determined by the amount of nutrition available to the parasitoid and not necessarily by only the host's total mass. We therefore conclude that *H. pallidus* females are indeed able to evaluate precisely the nutritional quality of a given host and that host size is not the only factor determining clutch size decisions.

Quality and quantity of host tissue are probably the most important factors influencing parasitoid size. Adult female weight may influence fitness by affecting the searching efficiency, longevity and fecundity of the wasp (Godfray 1994). We investigated different aspects of parasitoid fitness with respect to host species and host diet. Our results indicate that neither the diet of the host caterpillars nor the host species influence the longevity of *H. pallidus*. These findings are of crucial importance, as longevity is proposed to be correlated

directly with parasitoid fitness (Waage 1986; Godfray 1994; Schmale *et al*. 2001). Furthermore, there was no positive correlation between parasitoid size and longevity for both parasitoid strains. If there had been a nutritional deficiency in one host species, not only a reduction in female parasitoid weight but also a reduced life span would be expected (Godfray 1994). Remarkably, our data revealed that lifetime fecundity of female parasitoids was not affected by host species. Even though the total number of eggs produced in a lifetime was generally low (*C. molesta* 55·85, *C. pomonella* 53·93) under the experimental conditions chosen compared to previously reported values (*C. pomonella* 31–218; Zaviezo & Mills 2000), they did not differ between the host species strains upon which the parasitoid had developed.

We therefore conclude that smaller parasitoids do not suffer from being small in terms of longevity and that host species do not affect the reproductive success of the parasitoid.

The ultimate goal of a successful parasitoid's strategy can be described as maximum biomass acquisition in the shortest possible developmental time (Sequeira & Mackauer 1992). The faster the development, the sooner offspring become sexually mature and can reproduce themselves (Godfray 1994). On the other hand, the time needed for optimal nutrient acquisition may be prolonged due to suboptimal host quality (Sequeira & Mackauer 1992) or simply because larger hosts take longer to be consumed by the parasitoid larvae (Mackauer & Sequeira 1993; Harvey *et al*. 1998). In many parasitoid species, females are larger than males and therefore require longer pre-imaginal development (Otto & Mackauer 1998; Bertschy *et al*. 2000; Zaviezo & Mills 2000). In *H. pallidus*, the development time of females was slightly different on the two host species. Contrary to the existing hypothesis, larvae took a few hours longer to complete pre-imaginal development on *C. pomonella* hosts compared to *C. molesta* hosts, even though *C. pomonella* caterpillars are larger. The above-mentioned difference in egg to adult developmental time is due mainly to differences in embryonic development, where *C. molesta* hosts seem to favour fast development. However, larval development time between immature parasitoids feeding on the two hosts was not different. Overall, the differences in development time is marginal compared to the extended time-period required for host location and host handling (Mattiacci *et al*. 1999) and is thus considered to be of minor biological significance.

Our study provides empirical evidence that the host–parasitoid relationship is far more complex than a simple relationship, where host size equals host quality as was so far assumed.

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