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Fitness consequences of body-size-dependent host species selection in a generalist ectoparasitoid

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Abstract In insect parasitoids, offspring fitness is strongly influenced by the adult female's choice of host, particularly in ectoparasitoids that attack non-growing host stages. We quantified the fitness consequences of size-dependent host species selection in *Dirhinus giffardii*, a solitary ectoparasitoid of tephritid fruit fly pupae. We first showed a positive correlation between the size of emerged *D. giffardii* wasps and the size of their host fruit fly species (in order of decreasing size): *Bactrocera latifrons*, *B. cucurbitae*, *B. dorsalis* or *Ceratitis capitata*. We then manipulated individual wasps to show that the parasitoid preferred to attack the largest (*B. latifrons*) to the smallest (*C. capitata*) host species when provided with a choice, and laid a greater proportion of female eggs in *B. latifrons* than in *C. capitata*. There were no differences in developmental time or offspring survival between individuals reared from these two host species. Finally, we compared the foraging efficiency of large versus small wasps (reared from *B. latifrons* vs *C. capitata*) under two different laboratory conditions: high versus low host habitat quality, given that realized fecundity in parasitoids may be influenced by either egg-limited or time-limited factors. Under both conditions, large wasps parasitized more hosts than did small ones as a consequence of high searching efficiency in the host-poor habitat, and high capacity for adjusting egg maturation in response to host availability in the host-rich habitat. Considering the flexibility of body growth, the apparent lack of cost of achieving large body size in either development or survival, and the strong dependence of realized reproductive success on a female's size, we argue that body size may be a key to understanding evolution of host species selection in ectoparasitoids. We also discuss constraints

upon the evolution of size-dependent host species selection in parasitoids.

Keywords Body size · Egg maturation · Host selection · Parasitoids · Sex allocation

Introduction

Body size is one of the most apparent life-history traits of every organism, and often relates to reproductive success in animals (Clutton-Brock 1988). Insect parasitoids are ideal model systems for examining the relationship between adult body size and reproductive outcome (Godfray 1994). Females of many polyphagous or oligophagous parasitoids may encounter a variety of host species that substantially differ in size. Both theoretical predictions and empirical studies show that female wasps generally benefit most from developing in large hosts, as the size of emerged parasitoids is often positively correlated with the size of its natal hosts (Charnov et al. 1980; Charnov and Stephens 1988; King and Charnov 1988; Godfray 1994; King and Lee 1994; West et al. 1996; Otto and Mackauer 1998; Napoleon and King 1999; Teder et al. 1999; Morris and Fellowes 2002). This is particularly true for generalist parasitoids that attack non-growing host stages (e.g. Ueno 1998a, 1998b).

The body size of adult parasitoids is positively correlated with many other fitness components, such as adult longevity and fecundity for females and mating ability for males (Visser 1994; Kazmer and Luck 1995; West et al. 1996; Ellers et al. 1998; Otto and Mackauer 1998; Ueno 1998b; Eijs and van Alphen 1999; Sagarra et al. 2001; Ellers and Jervis 2003; Jervis et al. 2003). Larger female parasitoids often have higher mature eggload, and live longer due to larger energy reserves than smaller females (e.g. Eijs and van Alphen 1999; Sagarra et al. 2001). Large females also have higher dispersal and patch-finding ability in the field (Visser 1994; Kazmer and Luck 1995; West et al. 1996; Bennett and Hoffmann 1998; Ellers et al. 1998). Therefore, many studies take body size

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as the easiest proxy for real fitness in parasitoids (see Roitberg et al. 2001 for a review).

However, a bigger body may not always be advantageous in insect parasitoids. The fitness gain from being large may come at the cost of prolonged developmental time or increased juvenile mortality (Sequeira and Mackauer 1992; Harvey et al. 1994; Petersen and Hardy 1996; Harvey and Strand 2002). As a result, some endoparasitoids may favor rapid development over size, while others favor size over developmental time (see Harvey and Strand 2002).

Other factors influencing body-size-dependent host selection may include host resistance and host quality. The specificity of host resistance and parasitoid virulence is often a key factor influencing host species selection in endoparasitoids (e.g. Rolff and Karljeveld 2001; Lapchin 2002). In some cases, host quality may not increase with host size (e.g. Harvey et al. 2004). Even in some solitary ectoparasitoids, when the host resources are in surplus supply the host size may not be a good predictor of the wasp's size (Wang and Messing 2004a). Thus, a final determination between body size and fitness would depend on the degree of physiological and nutritional compatibility between the host and the parasitoid. To be beneficial for large body size as a result of body-size-dependent host selection in insects, there must exist a greater benefit than cost in achieving a large body (Leather 1988; Rivero and West 2002; Tammaru et al. 2002).

Another critical factor in the development of a comprehensive theory linking size-dependent host species selection and its consequences for offspring fitness is to quantify female size-related variations in behavioral, physiological and ecological abilities. There must be a positive correlation between body size and realized fitness, as assumed in many evolutionary models of parasitoid behavior (Charnov et al. 1980; Visser 1994; Klingenberg and Spence 1997; Roitberg et al. 2001). Many studies on size–fitness relationships in female parasitoids are based on the estimation of mature eggload at emergence, or on lifetime reproductive success when given unlimited hosts with or without access to food (see Visser 1994; Roitberg et al. 2001 for reviews). There may be many other factors influencing a female parasitoid's reproductive success under more natural settings. Besides female size-based dispersal ability, extrinsic mortality, and exploitative competitive ability (Visser 1994; Petersen and Hardy 1996; West et al. 1996; Ellers et al. 1998; Rivero and West 2002), the most important factors that influence female parasitoid foraging success may be its searching efficiency, and the ability to adjust egg production in response to changing environmental conditions. Many evolutionary interpretations of parasitoid behavior have assumed that females are either time-limited or egg-limited (Godfray 1994; Rosenheim 1999). Time limitation occurs when parasitoids die before they can deposit all the eggs that they can mature. Egg limitation occurs when parasitoids run out of eggs before they die in synovigenic species (a parasitoid able to mature eggs throughout part or all of their adult lives). Both egg- and time-limitation factors

could preclude a positive increase on the number of ovipositions by large females in highly variable environments. The critical issue is: how does a parasitoid deal with these factors in response to changing host availability? (Papaj 2000). Many synovigenic parasitoid species exhibit behavioral plasticity to adjust egg production in response to variations in host-habitat quality (Ellers and Jervis 2003; Wang and Messing 2003). Ellers and Jervis (2003) showed that the ovigeny index (i.e. percentage of mature eggs at adult emergence relative to the maximum potential egg production over lifetime) tends to decline with increasing body size across parasitoid species. Thus, large females may have a higher capacity to mature eggs quickly in host-rich habitats and search more efficiently in host-poor habitats, although this has not been addressed in previous studies.

The current study addresses the fitness consequences of body-size-dependent host species selection by *Dirhinus giffardii* Silvestri (Hymenoptera: Chalcididae), a solitary ectoparasitoid attacking pupae of many tephritid fruit fly species. We focus on the comparison of realized reproductive outcome of different-sized females reared from different-sized host species under two different conditions of host availability, given that there may exist either time- or egg-limitation on the parasitoids' foraging success. *D. giffardii* is native to West Africa, where its co-evolved host is the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). It has been introduced into over 20 countries for biological control of tephritid fruit fly pests, such as *C. capitata* in Hawaii during the early 1900s (Wharton 1989). The parasitoid has been reported to attack a number of other tephritid species (Noyes 2002), including tephritids of Asian origin in Hawaii: the oriental fruit fly *Bactrocera dorsalis* (Hendel) and the melon fly *B. cucurbitae* (Coquillett).

D. giffardii was selected as a model system because of several special life-history and behavioral traits ideal for quantifying the fitness consequences of body-size-dependent host species selection. Firstly, *D. giffardii* is a generalist parasitoid. Because most its hosts are polyphagous tephritid species that vary significantly in size, host species selection behavior by *D. giffardii* may have important consequences for the size-fitness relationship of its offspring. Secondly, like other ectoparasitoids (Godfray 1994; Quicke 1997), female *D. giffardii* produce only a few large eggs at a time, and have relatively low fecundity (Dresner 1954; Podoler and Mazor 1981). Egg-limitation is likely to occur in this parasitoid. Thirdly, there may be a high searching cost for this parasitoid. Fruit fly larvae pupate on or under the soil surface, and female *D. giffardii* search for hosts by walking over the soil surface (Dresner 1954). Once a female encounters a host, she examines the host with her antennae and drills into the shell of the host puparium (the hardened exoskeleton of the fly's last larval stage) and lays an egg into the space between the host pupa and the puparium if the host is suitable. Laying an egg by *D. giffardii* can take up to 30 min (Wang and Messing, unpublished data). Finally, unlike endoparasitoids that place their eggs in the host hemolymph where

the eggs may face a complex host immune response (Lapchin 2002), the pupal ectoparasitoid acts like a predator and does not need to overcome internal and physical host defenses.

We first tested whether the size of emerged *D. giffardii* adults is positively correlated with the size of the four host tephritid fruit fly species in Hawaii: *C. capitata*, *B. dorsalis*, *B. cucurbitae* and the Malaysian fruit fly, *B. latifrons* (Hendel) in Hawaii. We then examined whether the parasitoid preferred to attack large rather than small host species, and lay a greater proportion of female eggs in larger host species in a choice experiment, and whether body size was traded off against other fitness parameters such as developmental time and juvenile mortality. Finally, we quantified the effect of female size as a result of host species selection on its foraging capacity, defined as searching efficiency and the ability to adjust egg maturation in response to host availability.

Methods

Hosts and parasitoids

The four different-sized fruit fly species, *C. capitata*, *B. dorsalis*, *B. cucurbitae* and *B. latifrons*, were provided by the USDA-ARS Pacific Basin Agricultural Research Center, Honolulu, Hawaii, where they were reared using standard wheat-based artificial diets (Tanaka et al. 1969). Eggs of each species were incubated on artificial diets in plastic containers (20×12×4 cm), and shipped from the rearing laboratory to the Kauai Agricultural Research Center (KARC), where this study was conducted. The fly eggs were reared under standard laboratory conditions (23±1°C, 65±10% RH, LD 12:12 h, 3,500 lx) at KARC, until fly larvae started to pupate, when each rearing container was placed inside a holding box (45×30×15 cm) containing 1.5 cm of sand in which the flies pupated. Thus, host puparia were easily collected from the boxes for experiments and culture of *D. giffardii*.

A laboratory population of *D. giffardii* was initially established at a laboratory in the University of Hawaii at Manoa, Honolulu, from field collections of parasitized fruit fly puparia, and was later transferred to and reared at KARC. The wasps used in this study were reared on different host species according to the requirement of each experiment. Emerged wasps were held in screen cages (30×30×30 cm) at an approximate 1:1 sex ratio with water and honey provided. Because the parasitoid prefers to attack >2-day-old host puparia in which the fly pupa has fully formed within its puparium (Wang and Messing 2004b), all rearing and experiments used 2- to 3-day-old host puparia, and were conducted under the same laboratory conditions described above.

Effect of host species on the size of emerged wasps

The parasitoid was first reared on each of the four host species for at least one generation before it was used for the test on each corresponding host species. Prior to each test, individuals from a sample of 50 puparia of each host species were measured for maximum body length and width using a calibrated binocular microscope. Because host shape of the *Bactrocera* and *Ceratitis* species was slightly different (the former was more slender), we also estimated puparium volume as an additional measure of size using the following formula:

$$V = 4/3\pi \times (l/2) \times (w/2)^2 \quad (1)$$

where *V* is the volume of a prolate ellipsoid puparium with length *l* and width *w* (Otto and Mackauer 1998).

For the test of each host species, 100 host puparia were carefully chosen under a microscope to reduce within-species variation in size, and placed in a Petri dish (9 cm diameter). The Petri dish was then placed into a cage holding 50 1-week-old mated female wasps for 24 h, with water and honey provided. This exposure resulted in about 50–60% parasitism, with less than 5% superparasitism. All exposed hosts were transferred to a container (4.5×9.5×5 cm) with screened holes until the adult flies or wasps emerged. Upon emergence, all adult wasps were chilled in a refrigerator (6–7°C) for 12 h and then individually measured for maximum body length and width under a microscope. Preliminary tests found that body length was strongly correlated with dry body weight (dry wasps were weighed on an electronic microbalance) [Weight (mg)=1.5 length (mm)–4.0, length >2.7 mm, *n*=100, *r*²=0.98]. For convenience we used body length as a measure of wasp size.

The experiment was replicated until at least 100 wasps of each sex from each host species were obtained. The size of 100 female and male wasps reared from each of the four host species was measured and compared.

Host species selection and its effect on offspring fitness and sex allocation

Based on results from the above experiment, we then used the largest (*B. latifrons*) and smallest (*C. capitata*) host species to examine the parasitoid's host species selection and the consequences on offspring fitness components as well as sex allocation in relation to host species size, by manipulating individual female wasps' behavior in a choice experiment. A wet tissue paper was spread over a Petri dish (9 cm diameter), and covered with 1.5 cm of sand. This was used to keep the sand moist to prevent host puparium desiccation during the experiment. Five puparia of each host species (ten pupae total) were placed together over the sand. The Petri dish was then placed into a screen cage (9.5×10.5×13 cm) with water and honey provided. A single female wasp (1 week old, mated and naive for oviposition experience) was then introduced into the cage for 36 h. The experiment was replicated 37 times.

All puparia used in this experiment were standardized with regard to size and age for each species (4.5–4.7 mm long and 1.9–2.1 mm wide for *C. capitata*; and 5.2–5.4 mm long and 2.1–2.3 mm wide for *B. latifrons*) to control within-species size variation. It has been shown in some parasitoids that rearing experience of immature wasps will influence the adult parasitoid's host selection, and a parasitoid's offspring tends to select its natal hosts (e.g. Morris and Fellowes 2002). In order to avoid this possible bias we used wasps that were not reared from *C. capitata* nor *B. latifrons*, but from *B. dorsalis* for this test, and were standardized for a length range of 3.6–3.8 mm.

All exposed puparia were individually reared in small containers until the adult flies or wasps emerged. Meanwhile, as a control 50 unexposed puparia of each fly species were reared under the same laboratory conditions. The developmental time and sex of all emerged wasps were recorded twice a day, and the body size of each wasp was measured. Mortality of the exposed hosts was low: from a total of 185 exposed puparia of each species, only 7 *C. capitata* and 7 *B. latifrons* puparia died before fly or wasp emergence. All dead puparia were reconstituted in water for 1–2 days and dissected under a stereomicroscope to determine the presence or absence of recognizable immature parasitoid cadavers and pharate adults. The dead parasitoid eggs and larvae were normally attached to the host surface and were easy to recognize. The immature mortality of the parasitoids in each host species was corrected based on the control mortality, which was 1% for *C. capitata* and 2% for *B. latifrons*. Adult emergence rate was estimated as the number of emerged adults to the total wasps that developed to adulthood from each rearing host.

Because the immature mortality of the parasitoid was low in both host species (5 of 76 parasitized hosts from *C. capitata*; and 5 of 106 parasitized hosts from *B. latifrons*) in this experiment, and self-superparasitism by *D. giffardii* did not occur, we estimated the parasitoid's primary offspring sex allocation based on the sex ratio

of emerged and unemerged adult wasps. In one replicate only male wasps emerged; this replicate was discarded because of the possibility that the female wasp used might not have been inseminated. Thus, there was at least one female offspring reared from each replicate. In two replicates only the *B. latifrons* puparia were attacked, while in another two replicates the offspring mortality was relatively high. These four replicates were also excluded from the analysis of offspring sex ratio. Sex ratio was thus estimated based on 32 replicates in which mortality of the immature wasps was less than 1% ($0.78 \pm 1.6\%$ in *C. capitata* and $0.53 \pm 1.7\%$ in *B. latifrons*).

In addition, 40 female wasps reared from each host species were dissected to measure their ovipositor length. In order to determine if there is a trade-off between developmental time and body size, the relationship between adult size and developmental time was further analyzed for individual wasps that emerged from the same host fly species.

Female size and foraging capacity

We hypothesize that the realized fecundity of this synovigenic parasitoid would be influenced by egg supply or egg maturation rate when foraging in a host-rich habitat, and limited by searching efficiency when foraging in a host-poor habitat, with both constraints related to individual female body size.

The experiment consisted of four treatments using large or small females foraging in host-rich or host-poor habitats. The large female wasps were reared from *B. latifrons*, while the small females were reared from *C. capitata*. We first conducted a test to investigate the egg maturation dynamics of the different-sized females. Females of each group were held together with approximately the same number of males in a cage supplied with honey and water for 1–8 days after emergence. Fifteen to 20 females from each of five age groups (0, 2, 4, 6, 8 days old) and each of the two size groups were dissected to count their mature eggload and immature but recognizable eggs. All females dissected were chosen under a microscope to ensure an approximate body size within the same size group.

Because mature eggload of the naive females increased with age and peaked 6 days after emergence when deprived of hosts (see Results), in the next experiment we used 6-day-old females that had about six mature eggs in large females and four eggs in small females. All wasps used were again selected under a microscope for minimal variation in size within each group (4.0–4.2 mm long for the large females and 3.5–3.7 mm long for the small ones).

The experiment was conducted in a cage (9.5×10.5×13 cm) with screened openings on two sides and the lid. As in the above experiment, we first spread wet tissue paper on the bottom of the cage and then covered the paper with 2 cm of sand. In the host-rich habitat treatment, six *C. capitata* puparia were half-buried in the middle of the experimental perimeter. In contrast, in the host-poor habitat treatment, three *C. capitata* puparia were half-buried over three linear sites (one in the middle, and two in separate edges of the perimeter). Water and a droplet of honey were provided inside the cage. A single female wasp was released into each cage for 24 h. In order to further determine if the parasitoid's foraging efficiency was influenced by egg supply and rate of egg maturation, the experiment was continued on the second day, i.e. after the first 24-h exposure we replaced the exposed hosts with the same number

of unparasitized hosts for each treatment. After another 24 h, the wasp was removed and dissected immediately to count its mature and immature but recognizable eggs. All the exposed hosts were dissected within 2 days to determine the presence of parasitoid eggs. The experiment was repeated 20 times for each wasp size and host habitat treatment.

We estimated relative egg maturation rate of the experimental females during the 2-day exposure under the two different habitat conditions based on the number of eggs laid (*El*) during the exposure, mature egg load after the exposure (day 8) (*E*), and the mean mature eggload on day 6 (*E*₆) and day 8 (*E*₈) of the control female wasps without exposure to hosts since their emergence:

$$\text{Egg maturation rate (control)} = (E_8 - E_6)/2 \quad (2)$$

$$\text{Egg maturation rate (treatment)} = (El + E - E_6)/2 \quad (3)$$

We assumed that egg resorption within the 2 days was negligible, as sugar resources were provided and dissection showed the absence of partially resorbed eggs in the ovaries (completely resorbed eggs with only chorion remnants and partly resorbed with broken bodies).

Data analysis

All data analyses, including linear regression for relationships, one-way ANOVA for comparisons of two means, and ANOVA Tukey HSD test for multiple comparisons of mean values were performed using JMP 4.1 (SAS, Cary, N.C.). Proportional data were arcsin square root transformed before the tests. In order to test the possible interaction effect between female wasp size and host habitat quality, data on the parasitoid's foraging capacity were subjected to two-way ANOVA (JMP 4.1). Because some of offspring in the host selection test shared the same mothers, for testing the possible effect of the parasitoid origin on its size and developmental time, we chose the mothers who produced at least more than two offspring of the same sex from the same host species and ran an extra two-way analysis of variance by incorporating both host species and the origin of the parasitoid as response variables.

Results

The four host species (*C. capitata*, *B. dorsalis*, *B. cucurbitae* and *B. latifrons*) were significantly different in body size (length: $F_{3,196}=104.8$, $P<0.001$; width: $F_{3,196}=34.2$, $P<0.001$; volume: $F_{3,196}=59.9$, $P<0.001$) (Table 1). *B. latifrons* was the longest while *C. capitata* was the shortest. There was no significant difference in body width among the three *Bactrocera* species, and all of these *Bactrocera* were wider than *C. capitata*. As a result, *C. capitata* was the smallest species in terms of body volume, followed by *B. dorsalis*, and there was no difference between *B. latifrons* and *B. cucurbitae* (Table 1).

Table 1 Effect of host size of tephritid fruit fly species on the size of emerging *Dirhinus gijardii*. Values (mean ±SE) followed by the same letter within each column were not significantly different (ANOVA, Tukey HSD test, $P>0.05$)

Host species	Host body size (mm)				Wasp body length (mm)		
	<i>n</i>	Length	Width	Volume	<i>n</i>	Female	Male
<i>Ceratitis capitata</i>	50	4.59±0.03 a	2.04±0.01 a	1.02±0.01 a	100	3.60±0.02 a	3.31±0.03 a
<i>Bactrocera dorsalis</i>	50	4.85±0.03 b	2.25±0.01 b	1.31±0.02 b	100	3.72±0.02 b	3.48±0.01 b
<i>B. cucurbitae</i>	50	5.02±0.03 c	2.31±0.02 b	1.43±0.03 c	100	3.83±0.02 c	3.66±0.02 c
<i>B. latifrons</i>	50	5.35±0.03 d	2.27±0.03 b	1.49±0.04 c	100	4.13±0.02 d	3.93±0.02 d

Table 2 Host species selection by *D. giffardii* and its consequence on the parasitoid's offspring survival and developmental time. Values (mean \pm SE) followed by the same letter within each column

Host species	n	No. of hosts parasitized	% Immature mortality	% Adult emergence rate	Development time (days)			
					n	Female	n	Male
<i>C. capitata</i>	37	2.1 \pm 0.2 a	6.1 \pm 4.0 a	99.1 \pm 0.9 a	35	38.9 \pm 0.2 a	35	36.6 \pm 0.2 a
<i>B. latifrons</i>	37	2.9 \pm 0.2 b	2.3 \pm 3.6 a	100 \pm 0.0 a	64	39.3 \pm 0.2 a	34	36.0 \pm 0.2 a

The size of emerging *D. giffardii* adults was influenced by the size of its host species (female: $F_{3,396}=128.3$, $P<0.001$; male: $F_{3,396}=195.8$, $P<0.001$). Body length of both female and male wasps increased with the length of host species (Table 1), and females were always larger than males from all host species: *C. capitata* ($F_{1,199}=39.2$, $P<0.001$), *B. dorsalis* ($F_{1,199}=40.4$, $P<0.001$), *B. cucurbitae* ($F_{1,199}=185.2$, $P<0.001$), or *B. latifrons* ($F_{1,199}=120.6$, $P<0.001$).

When provided with a choice between the largest (*B. latifrons*) and smallest (*C. capitata*) host species, *D. giffardii* preferred to attack the largest ($F_{1,73}=11.1$, $P<0.001$; Table 2), and laid a significantly greater proportion of female eggs in the larger hosts (61 \pm 6%, $n=35$) than in the smaller hosts (39 \pm 6%, $n=35$; $F_{1,73}=9.3$, $P<0.01$). Again, female (4.2 \pm 0.02 mm, $n=64$) and male (3.9 \pm 0.04 mm, $n=34$) wasps that developed from *B. latifrons* were significantly larger than female (3.6 \pm 0.03 mm, $n=35$) and male (3.4 \pm 0.02 mm, $n=35$) wasps reared from *C. capitata* (female: $F_{1,98}=179.6$, $P<0.001$; male: $F_{1,68}=102.9$, $P<0.001$). The large females had significantly longer ovipositors (1.0 \pm 0.01 mm, $n=40$) than the small females (0.9 \pm 0.01 mm, $n=40$; $F_{1,79}=91.4$, $P<0.001$). Although some individuals shared the same mothers, the origin of the parasitoids did not influence the size or development time (29 different mothers among females, all $P>0.05$; 21 different mothers for males, all $P>0.05$). There were no significant differences in juvenile mortality ($F_{1,73}=0.1$, $P=0.80$), adult emergence rate ($F_{1,73}=1.0$, $P=0.32$) or developmental time of females ($F_{1,98}=1.1$, $P=0.29$), or males ($F_{1,68}=3.8$, $P=0.06$), between the individuals reared from the two host species (Table 2). From the same host species, females were always larger than males and developed slower than males in *C. capitata* (size: $F_{1,69}=8.1$, $P<0.01$; developmental time: $F_{1,69}=61.2$, $P<0.001$) and *B. latifrons* (size: $F_{1,97}=6.7$, $P<0.01$; developmental time: $F_{1,97}=154.6$, $P<0.001$). There was no relationship between body size of individual adults and developmental time of *D. giffardii* in either females or males developed from either *B. latifrons* (linear regression, female wasps: $r^2<0.0001$, $n=64$, $P=0.99$; male wasps: $r^2=0.05$, $n=34$, $P=0.22$) or *C. capitata* (linear regression, female wasps: $r^2=0.01$, $n=35$, $P=0.56$; male wasps: $r^2=0.003$, $n=35$, $P=0.77$), suggesting that the parasitoid grew faster in the large than in the small hosts.

D. giffardii emerged with few mature eggs (Fig. 1). When deprived of hosts but provided with food, mature eggload increased with age following a power function (large female: eggload = 2.31 age^{0.39}, $r^2=0.95$; small fe-

were not significantly different (one-way, ANOVA, $P>0.05$). Immature mortality was corrected based on the control mortality of unexposed hosts

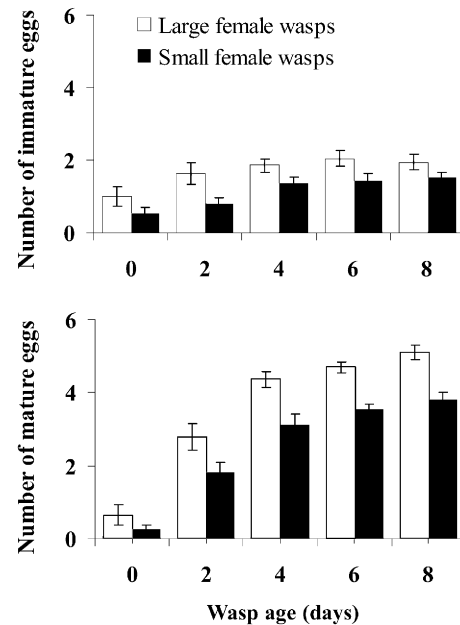


Fig. 1 Egg maturation dynamics in relation to body size of female *Dirhinus giffardii* when deprived of hosts but provided with food. Bars refer to mean (\pm SE) immature eggs and mature eggs per female ($n=15$ –20 for each age group)

male: eggload = 1.45 age^{0.48}, $r^2=0.99$), and reached a peak 6–8 days post-emergence in both large and small female wasps (Fig. 1). On average the large females produced 0.20 eggs/day while the small females produced 0.14 eggs/day during the sixth and eighth days post-emergence. Within the same age group, the large females always had a significantly greater number of mature eggs than the small ones (Fig. 1). The number of immature eggs also increased with age in the large ($F_{4,77}=2.9$, $P=0.03$) and small ($F_{4,77}=7.9$, $P<0.001$) females (Fig. 1). Eggs matured rapidly during the first 2 days, as the number of immature eggs in the second age group was significantly higher than the youngest wasps and then slowed down after 2–3 days; there were no differences in the number of immature eggs among the last three age groups in both large and small females (Fig. 1). Overall, immature eggload in the large females was also higher than in the small females (Fig. 1). No obvious egg resorption was observed during dissection, suggesting that the abdominal cavity of the parasitoid may limit further production of mature eggs when deprived of hosts.

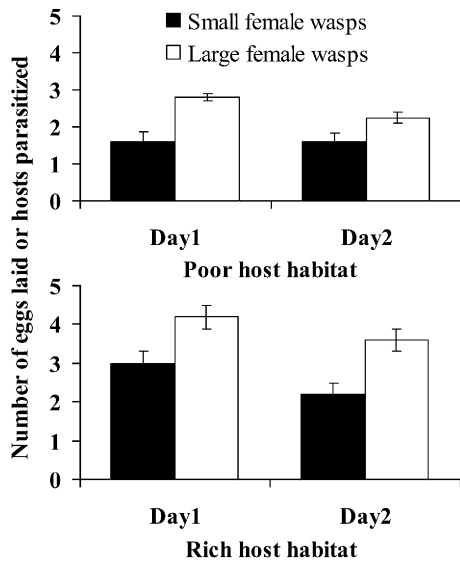


Fig. 2 Female wasp size and foraging success in *D. giffardii* under two different conditions of host density and distribution: host-rich habitat (six hosts per day per female with clustered host distribution) and host-poor habitat (three hosts per day per female with discrete host distribution). Bars refer to mean (\pm SE) number of eggs laid or hosts parasitized per female during the first day ($n=20$) and second day exposure ($n=20$)

Under both conditions of host availability, for 2 consecutive days the large females laid more eggs than the small females each day (Fig. 2; Table 3). As a result, the large females laid more eggs during the 2-day exposure in both the host-rich habitat ($F_{1,39}=18.0$, $P<0.001$) and the host-poor habitat ($F_{1,39}=15.9$, $P<0.001$). Self-superpara-

sitism was not found during dissection. The number of ovipositions was thus consistent with the number of hosts parasitized.

During the 2-day exposure large females parasitized $65\pm3\%$ (mean \pm SE) of the 12 hosts presented in the host-rich habitat, significantly higher than that of small females ($43\pm4\%$) in the same quality habitat ($F_{1,39}=18.1$, $P<0.001$). In the host-poor habitat, large females parasitized $84\pm4\%$ of the six hosts presented, also significantly higher than that of small females ($53\pm7\%$) ($F_{1,39}=15.6$, $P<0.001$).

After the 2-day exposure to hosts, larger females still carried a significantly greater number of mature eggs than did small females in the poor habitat (Fig. 3; Table 3; $F_{1,38}=6.4$, $P=0.02$). However, there was no significant difference between the large and small females in the number of immature eggs after the 2-day exposure to hosts in either habitats (Fig. 3; Table 3). In contrast to the number of unparasitized hosts by the end of exposure, in the host-rich habitat the small females suffered more from egg supply than the large females, while in the host-poor habitat, the small females were less effective than the large females in finding hosts, as a higher percentage of mature eggs were laid by the large females than by the small females (Table 3; Fig. 4).

Overall, in both habitats the large females produced a greater number of mature eggs or their eggs matured more rapidly than those of the small females (Fig. 4; Table 3). In contrast to the egg maturation rate of the females that were denied access to hosts, oviposition triggered egg maturation in both the large and small females. No significant interaction effect of female size and host habitat

Table 3 Results of two-way ANOVA testing the effects of female size of *D. giffardii* and host habitat quality on the parasitoid's searching efficiency and egg maturation rate

Measurements	Source	df	MS	F	P
Number of eggs laid (day 1)	Size	1	28.8	21.2	<0.001*
	Habitat	1	39.2	28.9	<0.001*
	Size \times habitat	1	<0.01	<0.01	1.000
	Error	76	1.36	—	—
Number of eggs laid (day 2)	Size	1	21.0	17.3	<0.001*
	Habitat	1	19.0	15.6	<0.001*
	Size \times habitat	1	2.81	2.31	0.133
	Error	76	1.22	—	—
Mature eggload after exposure	Size	1	6.61	6.21	0.015*
	Habitat	1	2.81	2.64	0.108
	Size \times habitat	1	3.61	3.39	0.069
	Error	76	1.06	—	—
Number of mature eggs produced	Size	1	156.8	43.9	<0.001*
	Habitat	1	80.0	22.4	<0.001*
	Size \times habitat	1	0.05	0.01	0.906
	Error	76	3.56	—	—
Percentage of mature eggs laid	Size	1	3.53	6.73	0.011*
	Habitat	1	0.86	1.64	0.204
	Size \times habitat	1	0.22	0.42	0.519
	Error	76	0.52	—	—
Egg maturation rate (eggs/female per day)	Size	1	13.6	15.3	<0.001*
	Habitat	1	20.0	22.4	<0.001*
	Size \times habitat	1	0.01	0.01	0.906
	Error	76	0.89	—	—

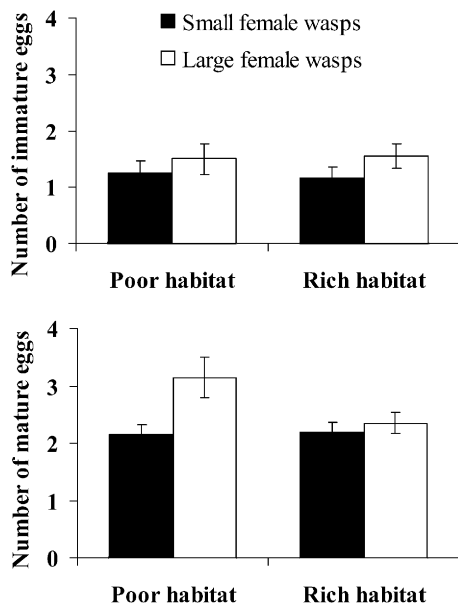


Fig. 3 Mean (\pm SE) number of mature ($n=20$) and immature ($n=20$) eggload of per female *D. giffardii* after 2-day exposure in host-rich habitat and host-poor habitat (see Fig. 2 for the description of host habitat)

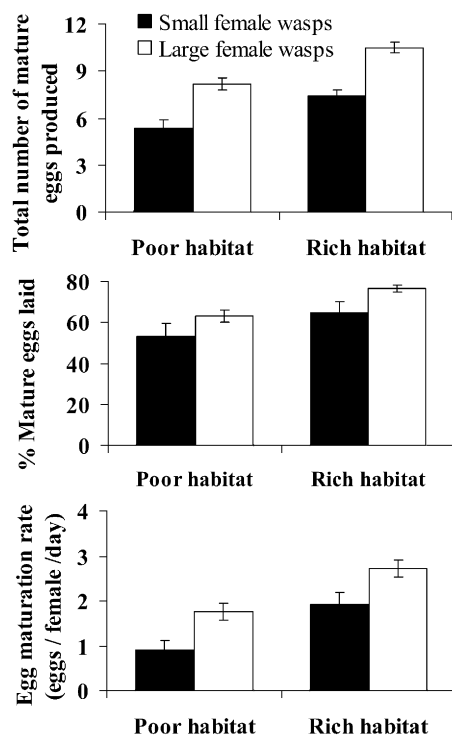


Fig. 4 Egg production and maturation rate of large vs small female *D. giffardii* in response to host habitat quality (see Fig. 2 for the description of host habitat). Bars refer to mean (\pm SE) number of total mature eggs produced per female ($n=20$), percentage of mature eggs laid during a 2-day exposure ($n=20$), and egg maturation rate (eggs/female per day) ($n=20$)

quality on the parasitoid's searching capacity or egg maturation rate was found (Table 3).

Discussion

Body-size-dependent host selection and sex allocation

Body size is a central element in current theories of life-history evolution (Fox and Czesak 2000; Lafferty and Kuris 2002). This study clearly confirms a body-size-dependent host species selection and a positive correlation between the size of host species and emerged parasitoids in *D. giffardii*, as predicted by host-size models (Charnov et al. 1980), and as shown in studies of other parasitoids (e.g. King and Charnov 1988; Teder et al. 1999; Sagarra et al. 2001). When it switched from the coevolved and small *C. capitata* to the non-coevolved but larger *Bactrocera* species, the parasitoid could successfully develop without apparent costs to offspring development or survival, and with a fitness advantage deriving from larger body size. It was observed that the parasitoid consumed almost all the host resource when emerged from the host puparia of either species, i.e. it was able to achieve maximum fitness gains when the hosts were relatively large. *D. giffardii* can also develop as a facultative hyperparasitoid on a number of other fruit fly parasitoids, and adult *D. giffardii* that developed from these smaller secondary host species (i.e. parasitoids) were smaller, than those developing on the relatively large *C. capitata*, but developmental time of both male and female *D. giffardii* was also unaffected by the host species (Wang and Messing 2004b). All of these findings reflect the plasticity of body growth in this generalist parasitoid. The lack of any pattern of dependence of developmental time on size suggests that *D. giffardii* grows faster on large host species than on small host species, as predicted by development models for parasitoids developing in a fixed resource system (Mackauer and Sequeira 1993; Otto and Mackauer 1998). It also suggests that there was no apparent trade-off between body size and developmental time in *D. giffardii*, although a simple phenotypic trade-off may vary in response to selection and environmental variation (see Roff et al. 2002).

It seems plausible for generalist parasitoids like *D. giffardii* that the lack of cost in achieving a large body, combined with the fitness advantage of being large should drive the evolution of body size, which should eventually result in the selection of large host species; large variation in size across many host species should be a basis for natural selection to operate on generalist parasitoids. Then, why do most generalist ectoparasitoids not evolve to large body size? There may exist other counterbalancing selective forces. First, as small and short-lived animals, a parasitoid's life expectancy in nature may be hours rather than days or weeks (e.g. Ellers et al. 1998; Rosenheim 1998). With such a short life expectancy, parasitoids may experience the environment as more stochastic, as they typically sample only a few patches in

their lifetime (Ellers et al. 1998; Ellers and Jervis 2003). Second, there is within-species variation in host size in many polyphagous host species. For example, *B. dorsalis* puparia were significantly larger when reared on papaya fruit than on an artificial diet, and when reared under low-density conditions than under high-density conditions (Wang and Messing, unpublished data). Third, the existence of flexibility in body growth, on the one hand, can allow generalist parasitoids to attack an expanded host range; but on the other hand, favoring a large host species can narrow host availability. Thus, all these factors could impose constraints on the evolution of host species selection.

In addition, physiological or physical capacity may impose limits on the minimum size of hosts and the maximum size of some generalist ectoparasitoids. For example, it was observed in *Pachycrepoideus vindemmiae* Rondani (an ectoparasitoid attacking pupae of many cyclorrhaphous Diptera) that there was no significant difference in offspring survival of *P. vindemmiae* that developed in *C. capitata* versus *Drosophila melanogaster* Meigen, and parasitizing *C. capitata* gave the wasps the advantage of larger body size (Wang and Messing 2004a). However, *P. vindemmiae* prefer to attack *D. melanogaster* rather than *C. capitata*. *D. melanogaster* has a thinner puparium shell than that of a large host such as *Musca domestica* L. (comparable to *C. capitata*) (Morris and Fellowes 2002). It may be easier for *P. vindemmiae* to drill through the thinner host puparia than through the larger host puparia (Morris and Fellowes 2002; Wang and Messing 2004a). In this case, there may be costs in selecting large hosts in terms of host handling time. These interactions could be further complicated by natal host species, for example, *P. vindemmiae* reared from *M. domestica* tended to be larger and had higher attack rates than those reared from *D. melanogaster* (Morris and Fellowes 2002). Although *P. vindemmiae* can successfully develop from a range of small host species like *Drosophila* to a large host species like *B. latifrons* (the latter species is over 20 fold larger in mass than the former), it could only consume a small portion of the host tissue when developing in *B. latifrons* (Wang and Messing 2004b). Host species size thus may not be a suitable proxy of host quality for this parasitoid, when it is surplus to the parasitoid's requirements.

The observed result of host size-dependent sex ratio in this study was due to offspring sex manipulation by *Dirhinus giffardii* females in response to host species size, rather than a result of differential sex-specific mortality of the males versus females. As predicted by theoretical models (Charnov et al. 1980), *D. giffardii* placed more female offspring in large host species, as done by other parasitoids (King and Charnov 1988; Heinz 1993; King and Lee 1994; Ueno 1998a, 1998b; Napoleon and King 1999). This prediction assumes that females gain relatively more in fitness from increased size than males. Although the fitness advantage of being large for males was less clear, the size of male *D. giffardii* was also positively related to the size of the natal host species

(Table 1). If size improves the ability of a male to mate, this will add additional advantage to size-dependent host species selection (van den Assem 1989).

Size-dependent foraging capacity

Host selection behavior has important consequences for the size–fitness relationship in parasitoids (Petersen and Hardy 1996; Roitberg et al. 2001). Here, we extend this common finding by evaluating whether the consequence of size-dependent host selection by *D. giffardii* translates into a measurable fitness advantage for large females. This was the case when the realized fecundity was measured under two different foraging environments. As shown, there is a remarkably strong fecundity advantage of being large for female *D. giffardii* under both host-rich and host-poor habitats.

Our current understanding of dynamic oviposition behavior in parasitoids has often neglected the underlying mechanism or physiology associated with ovarian developmental dynamics in relation to host use (Papaj 2000). A critical issue in parasitoid behavioral ecology is to understand how a synovigenic parasitoid like *D. giffardii* dynamically adjusts the rate of egg maturation in response to changing host availability. Our current study shows that large female *D. giffardii* not only have a higher number of mature eggs at eclosion than smaller females, as in other synovigenic parasitoids (Visser 1994), but also are more capable of optimally adjusting egg production in response to habitat quality. To our knowledge, this is the first identified example of the rate of egg maturation in parasitoids being not only greatly affected by the availability of hosts but also by female size. In contrast to the control wasps, oviposition overwhelmingly triggered egg maturation in *D. giffardii*. When the wasps were deprived of hosts, even large *D. giffardii* females produced few eggs at a time and virtually shut down egg maturation after 6–8 days post-eclosion. The oviposition-mediated mechanism of egg maturation ensures the maximum probability of conferring reproductive plasticity (Ellers and Jervis 2003; Wang and Messing 2003), as theory predicts that a parasitoid would lose fitness if producing excessive eggs when foraging in poor quality habitats (Rosenheim 1999). Small females of *D. giffardii* basically suffer from egg-limitation in high host density environments, but are generally time-limited in low host density environments. In our protocol, we used the realistic scenario of host puparia buried in sand. The parasitoid was observed to often dig in the sand using its powerful forelegs in order to examine an entire host. The strong forelegs of large females are probably more effective than those of smaller females for handling and digging hosts. As a result, foraging capacity is positively related to female size in *D. giffardii*.

There may be many opportunities for other environmental factors to obscure the positive relationship between realized fecundity and female body size. What we did not consider in this study is the parasitoid's dispersal

ability and its ability to withstand adverse weather conditions under natural settings. It has been shown in the laboratory that larger female wasps of the taxonomically close species *Dirhinus pachycerus* Masi lived longer than smaller ones (Bai 1990). There may also exist differences in exploitative competitive ability between large and small wasps (e.g. Petersen and Hardy 1996). However, this selection, if adaptive, should favor large hosts and would add fitness benefits to large females, particularly at low resource environments. If this holds true for *D. giffardii*, the fitness benefits of being large will be even more substantial.

In conclusion, it is beneficial for *D. giffardii* to use large hosts because of a positive relationship between the wasp size and the size of natal host species, and a fitness gain as a result of body-size-dependent host species selection. We argue that body size is a key to understanding evolution of host species selection. Due to the behavioral and ecological simplicity of the ectoparasitoid, *D. giffardii* provides a model system in which it is feasible to quantify the fitness consequences of body-size-dependent host species selection, and will contribute to our understanding of optimal host selection under body size constraints in other generalist parasitoids. This study may provide a foundation for such lines of research by documenting that host selection can have a positive effect on a parasitoid's fitness under laboratory settings. Although we chose the simplest scenario, one can readily imagine more realistic scenarios, including a larger number of hosts and spatial and temporal variance of host availability. For example, instead of clustered or even distribution, hosts may be randomly distributed. Thus, our experiments represent one extreme within a wide range of possibilities, one that would maximize our chances of finding positive effects of body size on searching capacity. To further understand the evolution and ecology of host selection, we must document how and to what extent selection affects fitness under natural conditions.

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