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Host-size-dependent sex ratio in a parasitoid wasp

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Abstract Charnov's host-size model explains parasitoid host-size-dependent sex ratio as an adaptive consequence when there is a differential effect of host size on the offspring fitness of parasitoid males versus females. This article tests the predictions and the assumptions of the host-size model. The parasitoid wasp *Pimpla nipponica* Uchida (Hymenoptera: Ichneumonidae) laid more female eggs in larger or fresher host pupae when choice among hosts of different sizes or ages was allowed. Then, whether an asymmetrical effect of host size and age on the fitness of females versus males existed in *P. nipponica* was examined. Larger or fresher host pupae yielded larger wasps. Larger females lived longer, whereas male size did not influence male longevity. Large males mated successfully with relatively large females but failed with small females, whereas small males could mate successfully either with small or with large females. Thus, small-male advantages were found, and this held true even under male–male competition. Ovariole and egg numbers at any one time did not differ among females of different sizes. Larger females attained higher oviposition success and spent less time and energy for oviposition in hosts. Larger females produced more eggs from a single host meal. Taken together, females gained more, and males lost more, by being large. Host size and age thus asymmetrically affected the fitness of offspring males versus females through the relationships between host size or host age and wasp size, which means the basic assumption of the host-size model was satisfied. Therefore, sex ratio control by *P. nipponica* in response to host size and age is adaptive.

Key words Fitness · Host-size model · Mating success · Oviposition success · *Pimpla* · Host selection · Small male advantage

Introduction

Most hymenopteran parasitoids are haplodiploid (White 1973; Cook 1993) and have the potential for controlling offspring sex ratio by regulating sperm access to eggs (Flanders 1956). In fact, many studies have demonstrated that many species of parasitoid wasps can control offspring sex ratio in response to environmental variables (e.g., Hamilton 1967; Charnov 1982; King 1987, 1993; Waage 1986; Werren 1987; Godfray 1994). Many evolutionary hypotheses have been proposed to explain these sex ratio responses (e.g., Hamilton 1967; Suzuki and Iwasa 1980; Charnov 1982; Werren 1984; Frank 1985; Herre 1985; Godfray 1990, 1994; Antolin 1992; Hardy 1992, 1994; West and Herre 1998).

For parasitoid wasps, host quality, such as host size and age, is a significant factor that influences offspring sex ratio (Charnov 1982; King 1987, 1993). Host size, in particular, has been frequently found to correlate negatively with proportions of offspring males (Charnov et al. 1981; King 1987, 1988, 1993; Heinz and Parrella 1990; Ueno and Tanaka 1997; Antolin 1993; Ueno 1998a; but see also Galloway and Grant 1989; Cook et al. 1994; Antolin et al. 1995). The correlation between host size and parasitoid sex ratio results from sex ratio control by female wasps in response to host size (van Dijken et al. 1989; Antolin 1993; Ueno and Tanaka 1997; but see also Wellings et al. 1986).

Charnov et al. (1981) have first proposed, with a theoretical model, that host-size-dependent sex allocation by female parasitoids can evolve as an adaptive behavior if host size influences the fitness of males versus females asymmetrically (Fig. 1), a hypothesis primarily based on Charnov (1979). Such a host-size effect is assumed to emerge through relationships between host size and the size of resulting wasps and through relationships between wasp size and fitness (Fig. 1). The model is called a host-size model and is now accepted as a general theory for host-size-dependent sex ratio in parasitoid wasps (King 1993; Godfray 1994). Nevertheless, only a few studies have exam-

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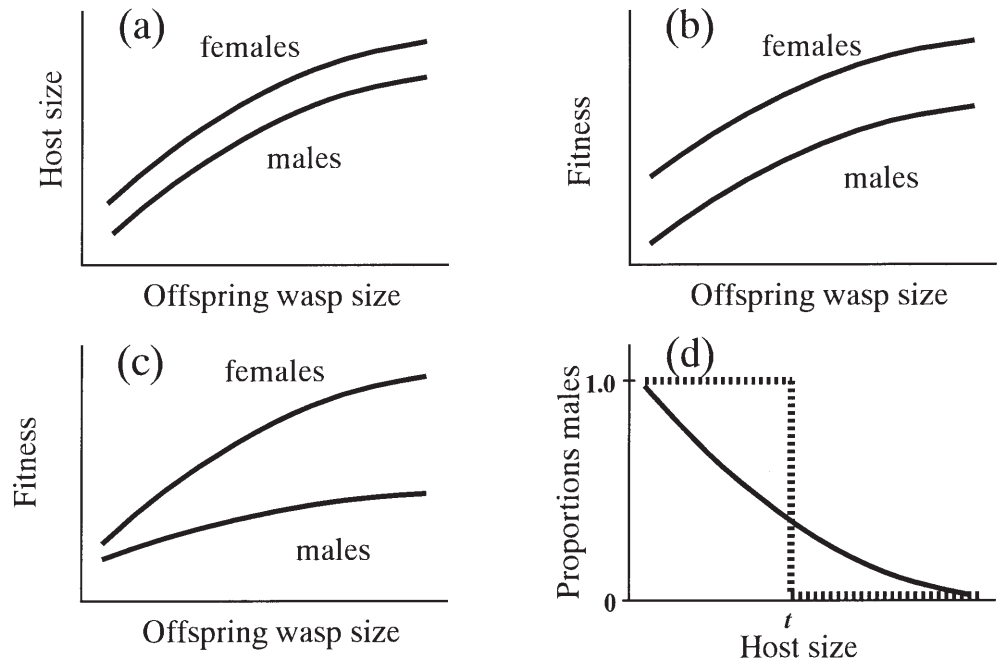


Fig. 1a–d. Basic assumptions and predictions of the host-size model. The first assumption of the model is that host size positively correlates with adult size (**a**), considered as the first step for the evolution of host-size-dependent sex ratio. The second assumption is that adult size influences their fitness and that adult size-related fitness functions differ between males and females (**c**). The model predicts that host-size-dependent sex ratio can evolve when the two assumptions are

satisfied: in case of **c**, proportions of males should decrease with host size (**d**) while, in case of **b**, such sex ratio patterns should not evolve. Also, the model predicts a sharp threshold in host size above which wasps lay only female eggs and below which only males (*dashed line* in **d**), whereas empirical studies in general show a gradual transition of sex ratio (**d**)

ined the basic assumption of the host-size model, i.e., the presence of a differential effect of host size on the fitness of males versus females.

To date, clear evidence for supporting the basic assumption of a host-size model is surprisingly rare; the evidence is given only in a few parasitoid species (Jones 1982; van den Assem et al. 1989; Heinz 1991; Ueno 1998a). In other parasitoids, the basic assumption of the host-size model was even contradicted (King 1988; Seidl and King 1993; Cook et al. 1994; King and King 1994; King and Lee 1994; Antolin et al. 1995). Do these facts suggest that host-size model cannot explain universally host-size-dependent sex ratio in parasitoid wasps? We can consider several reasons for the paucity of the evidence. Parasitoid fitness in relation to wasp body size is often complex and is difficult to measure, in particular, for males. These facts make it difficult to show clear quantitative relationships between wasp size and the reproductive success.

There may be some overlooked but significant size-related fitness components in parasitoid wasps. Further, laboratory fitness measures may not reflect realized fitness in the field (Kazmer and Luck 1995). Also, quantitative estimates of size-related fitness function on the basis of laboratory studies appear to underestimate the fitness penalties of being small in the field (Hardy et al. 1992; Godfray 1994; Visser 1994). Only a few field studies, however, have examined the reproductive success of adult parasitoids with regard to their size (Kazmer and Luck 1995; West et al.

1996). Thus, more data based on both laboratory and field studies need to be accumulated, and fitness components that have not been studied previously should be explored. By doing so, we need to clarify what are reliable estimates reflecting the relationship between parasitoid size and fitness.

Here I use the solitary endoparasitoid wasp *Pimpla nipponica* (= *Coccygomimus nipponicus*) Uchida (Hymenoptera: Ichneumonidae) experimentally to examine the adaptiveness of sex ratio control in response to host size. The reason I chose this species is that *P. nipponica* encounters a considerable range of host species that should differ in size because it is a polyphagous and multivoltine parasitoid of lepidopteran prepupae and pupae (Townes et al. 1965; Yasumatsu and Watanabe 1965; Ueno and Tanaka 1994). This wide variety of host size can cause strong selection for adaptive sex ratio control in response to host size (Charnov et al. 1981; King 1993).

In this article, I first tested if *P. nipponica* control offspring sex ratio in response to host size, and then examined whether the sex ratio control can be explained by the host-size model. For this purpose, I conducted a series of laboratory experiments to examine some fitness components of males and females. Also, I examined sex allocation responses by *P. nipponica* to host pupae of different ages enclosed in the cocoon, because the host-size model can be extended to any situations in which females encounter a variety of hosts that differ in quality. Although the size of

pupae of themselves does not change very much, older host pupae will contain fewer host resources for the developing parasitoids because host tissues are converted to sclerotized adult structures with increasing host pupal age. Hence, host pupae of different ages may produce wasp offspring that differ in size, a situation in which host-age-dependent sex ratio may evolve. I discuss here the sex allocation strategy and the body size-related fitness function in *P. nipponica* in the context of evolutionary theories about parasitoid sex ratio.

Materials and methods

General methods

Basic biology and rearing methods of *P. nipponica* are described in Ueno and Tanaka (1994). A colony of *P. nipponica* was reared on a laboratory host, *Galleria mellonella* (L.), and was maintained in the laboratory at $20 \pm 1^\circ\text{C}$ and 16:8 L:D. Newly emerged female wasps were placed individually in plastic cups ($10 \times 4.5\text{cm}$), together with a male, and provided with tissue paper saturated with a honey solution. A variety of hosts of different sizes were exposed to female wasps for parasitism. Parasitized hosts were collected and held at $25 \pm 1^\circ\text{C}$ and 16:8 L:D until wasp emergence. Newly emerged wasps were used for the following experiments. In my experiments, forewing length was used as the measure of adult wasp size. Also, *G. mellonella* was used as a test host.

Effect of host size on parasitoid sex ratio

First, I tested if host size influences the offspring sex ratio of *P. nipponica*. I collected newly emerged, mated females of 5.5- to 6.0-mm forewing length and placed them individually in plastic cups. I then placed tissue papers saturated with a honey solution in the cups, and replaced them twice a week thereafter. I presented each female with two hosts of different sizes (40–175 mg) for 1 h, and repeated this treatment for 7 days from 3 days after wasp emergence. These females were used for testing. I used a 10-day experimental period for each test female; thus, 11- to 20-day-old females were used. Preliminary observations showed that within these ages offspring sex ratio did not vary with female age. In this experiment, 20 females were used.

I offered randomly a variety of hosts of different sizes (40–175 mg) singly to test females and observed them for successful single oviposition. I took care to avoid superparasitism and host feeding. I determined single ovipositions in a host by observing a visible sign of the base of the ovipositor (Ueno 1995). I also recorded patterns of abdominal tip movements during oviposition, which can be used to predict the sex of deposited eggs (Ueno 1995). I used the movements to determine primary sex ratio, i.e., offspring sex ratio at oviposition. I collected hosts and kept them at $25 \pm 0.5^\circ\text{C}$ and 16:8 L:D. When wasps emerged, I recorded their sex.

Effect of host age on parasitoid sex ratio

I tested if host age influenced offspring sex ratio of *P. nipponica*. I collected newly formed 60- to 79-mg host cocoons and kept these hosts at $25 \pm 1^\circ\text{C}$ until the experiment. In this experiment, I used 0- to 3-day-old (fresh) and 7- to 9-day-old (old) host pupae and 14 newly emerged and mated females for testing. I allowed each test female access both to fresh and to old hosts every other day from 3 days after wasp emergence. Exposure time to hosts was 1 h. I used an 8-day experimental period for each test female. Every day, I presented 3 fresh and 3 old hosts to each test female in the cups and observed them for successful oviposition on the hosts. During oviposition, I observed abdominal tip movements of females under a binocular microscope, to determine primary sex ratio (see above). Hosts were removed as soon as they were parasitized and were then kept at $25 \pm 1^\circ\text{C}$ and 16:8 L:D until wasp emergence. Other experimental conditions were the same as in the first experiment.

Effect of host size or age on parasitoid size

The effect of host size and age on wasp size was assessed by using host pupae of a variety of sizes or of different ages. Host size and age classes were the same as in the sex ratio experiments. I offered unparasitized healthy host cocoons singly to female wasps in the cups and observed them for successful single oviposition. After oviposition, I removed hosts from the cups, and then kept them at $25 \pm 1^\circ\text{C}$ and 16:8 L:D until wasp emergence. Forewing length of emerged wasps was measured under a binocular microscope.

Wasp size and longevity

I conducted experiments to examine the effects of parasitoid wasp size on wasp longevity. Newly emerged parasitoid wasps were placed individually in plastic cups ($10 \times 4.5\text{cm}$). Tissue paper saturated with a honey solution or water was placed in the cups; thus, two experimental groups of wasps (with or without food) were established. The tissue papers were replaced twice a week thereafter. Female were allowed access to hosts every 3 days after emergence. These procedures were repeated until wasps died. The cups were kept at $20 \pm 1^\circ\text{C}$ and 16:8 L:D.

Male wasp size and mating success

Experiments were conducted to determine the effects of male wasp size on reproductive success. In these experiments, male mating success with females of different sizes was used as the measure of the reproductive success of males.

Newly emerged male parasitoids were individually placed in plastic cups with papers saturated with honey solution. Males aged 3–6 days old that had not mated previ-

ously were used for testing. Newly emerged females that differed in size were placed individually in the cups. Observations were started only when mounting behavior by males was observed. Successful intromission by males was recorded as successful mating. Trials were terminated after 10 min.

Next, I examined male mating success with females of different sizes under male–male competition. Male wasps with three different sizes, i.e., 5.1- to 5.5-, 6.0- to 6.4-, and 6.5- to 6.9-mm males (forewing length), were used as “small,” “medium,” and “large” males, respectively. Each of the three size classes of males was placed in the cup and female wasps 0–1 days old were singly entered into this cup. I observed which male wasp could first mate successfully. In this experiment, 5.0- to 5.5-mm or 6.0- to 6.5-mm females were used for testing.

Female wasp size and reproductive potential

In this experiment, the numbers of ovarioles or mature and immature eggs were used as the measures of the reproductive potential of females. Female wasps that emerged from hosts of different sizes were dissected under a binocular microscope. The numbers of ovarioles and mature and immature eggs were then counted and recorded and the forewing length measured. In this experiment, I used 49 females aged 11–16 days old that had been allowed access to hosts twice a week since 3 days after emergence. The other treatments were the same as in the sex ratio experiments.

Female wasp size and successful parasitism

The effects of female size on successful parasitism were determined by exposing fresh host pupae of 100–120 mg enclosed in the cocoon to female wasps of different sizes (4.5–6.9 mm). I offered hosts individually to female wasps aged 11–15 days old. I started observations when each female responded to a host. I noted whether the female successfully oviposited or gave up oviposition. Handling time (time spent on hosts) and the numbers of attacks (=drillings) required until successful oviposition or giving up were observed for each trial. The other treatments were the same as the sex ratio experiments.

Female wasp size and egg production efficiency

I examined the effects of female wasp size on egg production efficiency, i.e., the numbers of eggs produced per host meal (=host feeding). Newly emerged female wasps were individually placed in the cups and paired with males. After mating was observed, males were removed from the cups. From day 4 after wasp emergence, 3–4 hosts were offered singly to females every other day, and I observed whether oviposition or host feeding took place. This procedure was repeated for 2 weeks. In this experiment, the number of eggs oviposited between host feedings was used as the mea-

sure of egg production efficiency. I used 66 female wasps in this experiment.

Statistical analysis

Statistical analyses were made using JMP (1997) from SAS Institute and Statview-J version 4.5 (1995). In the analysis of mating success and oviposition success data, the sequential Bonferroni’s method (Rice 1989) was used for multiple comparisons after tablewide chi-squared tests had been made.

Results

Effect of host size on parasitoid sex ratio

One female among 20 test females died during the experimental period, and therefore sex ratio data from 19 females were analyzed. Both primary and secondary offspring sex ratio decreased with increasing host weight (Kendall’s rank correlation test after arcsin square root transformation; $Z = -2.82$, $n = 6$, $P = 0.0048$ for both primary and secondary sex ratios) (Fig. 2), suggesting that female wasps adjusted offspring sex ratio in response to host size and placed more female eggs in larger hosts.

Effect of host age on parasitoid sex ratio

Secondary offspring sex ratio from fresh hosts was significantly lower than that from old hosts (paired t -test

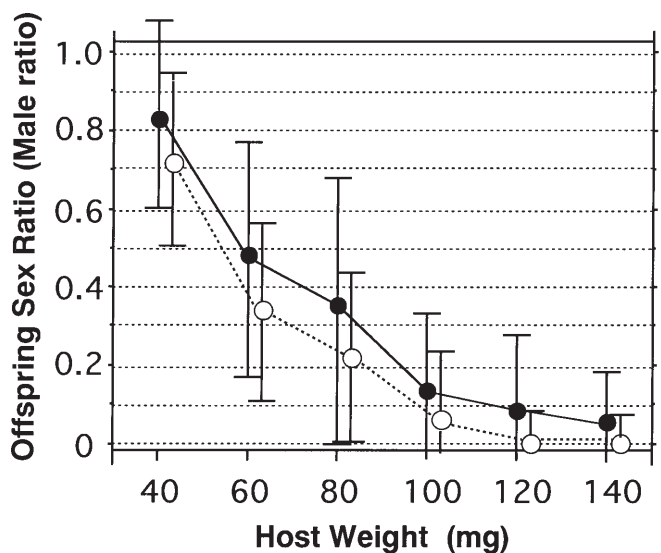


Fig. 2. Relationship between host weight and offspring sex ratio (proportions of males) (closed and open circles indicate secondary and primary sex ratios, respectively). Mean values are shown with SD. Mean sex ratio decreased significantly with increasing host weight (Kendall’s rank correlation test; $P < 0.01$). The results indicate that female *Pimpla nipponica* tend to allocate male eggs in relatively small hosts and female eggs in relatively large hosts

with arcsin square root transformation; $t = 3.28$, $df = 14$, $P = 0.008$) (Fig. 3). Also, the estimated primary offspring sex ratio from fresh hosts was lower than that from old hosts (paired t -test with arcsin square root transformation; $t = 4.22$, $df = 14$, $P = 0.0009$) (Fig. 3). These results indicate that female wasps tended to place male eggs in old host pupae and female eggs in fresh host pupae.

Effect of host size or age on parasitoid size

Forewing length of both offspring males and females increased significantly with increasing host weight [regression analysis; $n = 33$, $F = 68.53$, $df = 1$, $P < 0.0001$, $r^2 = 0.95$; forewing length (mm) = $0.02 \times \text{host weight} + 3.82$ for males; $n = 38$, $F = 43.71$, $df = 1$, $P < 0.0001$, $r^2 = 0.87$; forewing length (mm) = $0.02 \times \text{host weight} + 4.12$ for females], indicating that host size is a good measure for the amount of resources for parasitoid larvae.

Larger male and female parasitoids emerged from fresh than from old host pupae [mean \pm SD; 5.67 ± 0.29 mm ($n = 18$) vs. 5.11 ± 0.47 mm ($n = 21$) for males; 5.98 ± 0.28 mm ($n = 22$) vs. 4.84 ± 0.51 mm ($n = 16$) for females] (Scheffe's F -test; $F = 10.35$, $df = 1$, $P = 0.003$ for males; $F = 42.70$, $df = 1$, $P < 0.0001$ for females), indicating that host age is also a good measure for the amount of resources for the developing parasitoids.

Wasp size and longevity

For both male and female wasps, there was no significant relationship between wasp size and longevity when only water was provided (regression analysis; $F = 0.67$, $df = 1$, $P = 0.66$ for males; $F = 1.22$, $df = 1$, $P = 0.43$ for females). When wasps were provided with honey solution, female longevity increased significantly with increasing wasp size ($F = 7.26$, $r^2 = 0.16$, $P = 0.011$) but male longevity was

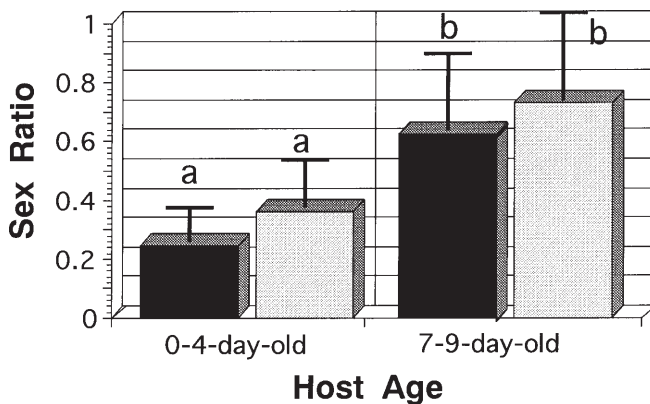


Fig. 3. Relationship between host age and offspring wasp sex ratio. Mean values are shown with SD. In both primary (back bars) and secondary (shaded bars) sex ratios, mean sex ratio from fresh hosts differed significantly from that from old hosts (paired t -test with arcsin square root transformation; $P < 0.01$). The results indicate that female *P. nipponica* tends to lay male eggs in old hosts and female eggs in fresh hosts

not influenced by wasp size ($F = 0.14$, $df = 1$, $P = 0.71$) (Fig. 4). These results suggested that wasp size can positively influence only female longevity, although the influence can differ depending on the environments that a wasp experiences.

Male wasp size and mating success

All tested males responded to females by vibrating the wings and by moving vigorously around the experimental cups. When they encountered females, males tried to mount the females, and mating attempts did not differ between small and large males. However, male size markedly influenced male mating success (Figs. 5 and 6). Small males enjoyed high mating success with females of different sizes in equal proportions (chi-squared test; $df = 3$, $P > 0.05$ for males of 3.75–4.49, 4.5–5.24, and 5.25–5.99 mm) (Figs. 5). In contrast, large males failed to mate successfully with relatively small females, and mating success differed depending on female size (chi-squared test; $df = 3$, $P < 0.05$, for males 6.00–6.74 and 6.75–7.5 mm) (Fig. 5).

Observations revealed that (1) large males had difficulty mounting relatively small females and (2) large males often

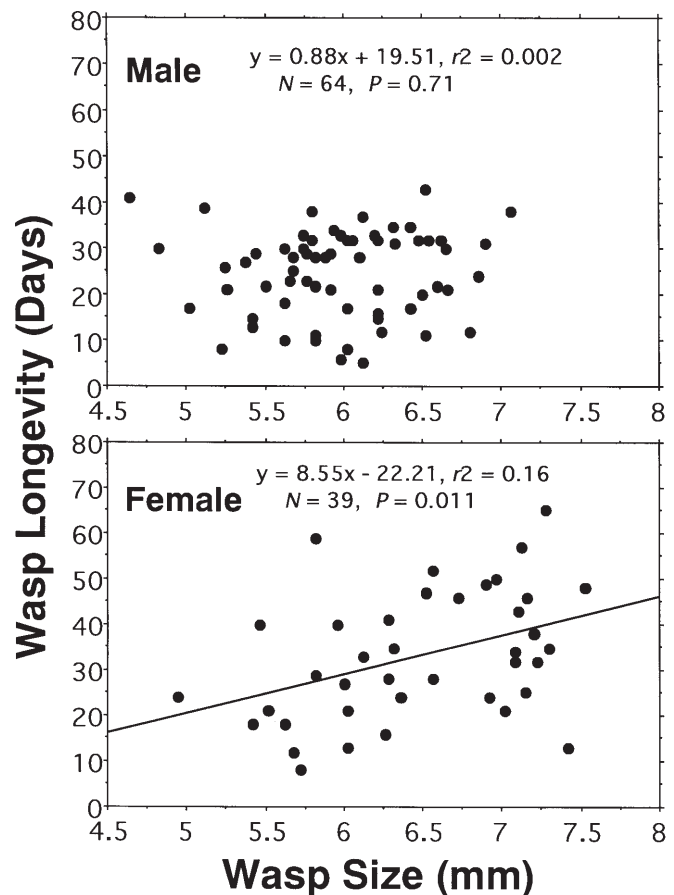


Fig. 4. Relationship between wasp size and longevity when wasps were provided with a honey solution as food. The relationship indicates that wasp size has a positive effect on female longevity under good food conditions

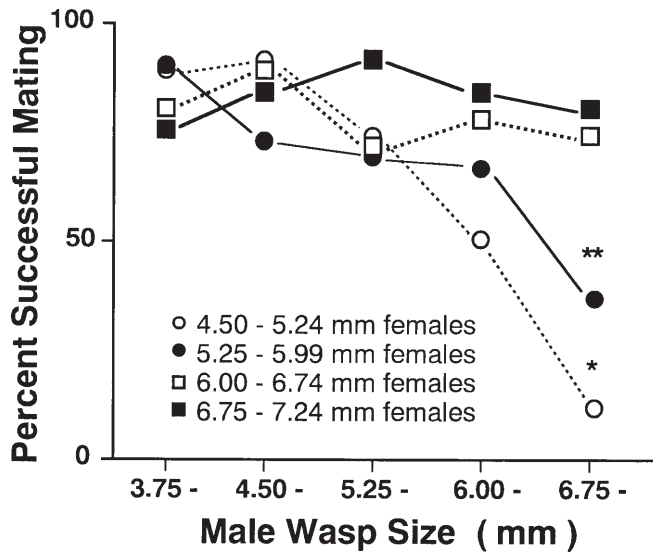


Fig. 5. Male mating success when female size varies. Stars indicate significant differences among the male size classes (chi-squared test; $df = 4$, $P < 0.05$). Smaller males succeed to mate equally with different-sized females while larger males fail to mate with relatively small females, showing that a small male advantage exists depending on the size of females available

had difficulty in keeping up with here the females when the females moved. Even when females stood still and tried to accept males, the females started to move if large males took a long time to mount successfully, resulting in failure of mating. Also, the size mismatch affected the stability of copulation; small females occasionally fell down after large males mounted, probably because the males were too heavy for the females. It appeared that females did not behave differently toward males of different sizes, suggesting female discrimination was not involved.

Further, male mating success differed depending on male size under male-male competition (Fig. 6). No physical male-male competition was observed. When females were relatively small, the smallest class of males (5.1–5.5 mm) showed the highest mating success among the three size classes of males (chi-squared test for heterogeneity; $\chi^2 = 14.9$, $df = 2$, $P = 0.0006$) (Fig. 6a). However, when females were relatively large, mating success did not differ among the size classes of males ($\chi^2 = 1.4$, $df = 2$, $P = 0.49$) (Fig. 6b). These results suggested that smaller males had advantages for mating either under a single pair situation or under male-male competition, although the advantages depended on counterpart female size.

Female wasp size and successful parasitism

All females responded to hosts and attacked the hosts. However, oviposition success was influenced by size (chi-squared test for heterogeneity; $\chi^2 = 33.29$, $df = 4$, $P < 0.0001$), and smaller female wasps had less ability to successfully oviposit than large females (Fig. 7a).

After the cases in which females gave up oviposition were excluded, mean numbers of drillings and time spent

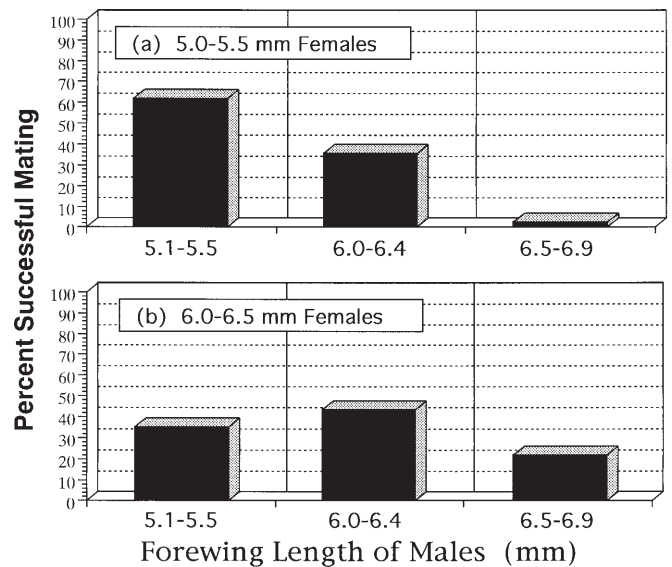


Fig. 6a–b. Male mating success under male-male competition. When females are relatively small, smaller males express higher mating success (a: chi-squared test; $df = 2$, $P < 0.05$), but when females are relatively large, no mating advantages in relation to male size are found (b: chi-squared test; $df = 2$, $P > 0.05$)

for oviposition were calculated. The numbers of drillings and handling time required for oviposition decreased significantly with increasing female wasp size (regression analysis; $F = 11.98$, $df = 1$, $r^2 = 0.15$, $P = 0.0009$ for drilling numbers; $F = 20.95$, $df = 1$, $r^2 = 0.24$, $P < 0.0001$ for handling time) (Fig. 7b,c), suggesting again that larger females can enjoy higher reproductive success.

The numbers of attacks, i.e., drilling with the ovipositor, and total handling time spent on hosts differed markedly between successful and unsuccessful oviposition (F -test; $F = 29.19$, $df = 1$, $P < 0.0001$ for attack numbers; $F = 28.88$, $df = 1$, $P < 0.0001$ for handling time) (Fig. 8). Therefore, when female wasps failed to oviposit in hosts, they suffered additional costs; i.e., their time and energy required for attacking and drilling a host were wasted.

Female wasp size and the reproductive potential

The numbers of ovarioles, mature, and immature eggs did not differ depending on female wasp size (regression analysis; $F = 3.37$, $df = 1$, $P = 0.074$ for ovariole numbers; $F = 1.54$, $df = 1$, $P = 0.23$ for mature egg numbers; $F = 1.56$, $df = 1$, $P = 0.22$ for immature egg numbers), suggesting the reproductive potential of females was not influenced by wasp size.

Female wasp size and egg production efficiency

Larger females had another advantage for reproduction. The number of eggs produced per host feeding increased significantly with increasing female size (regression analysis; $F = 6.96$, $df = 1$, $r^2 = 0.16$, $P = 0.011$) (Fig. 9). This

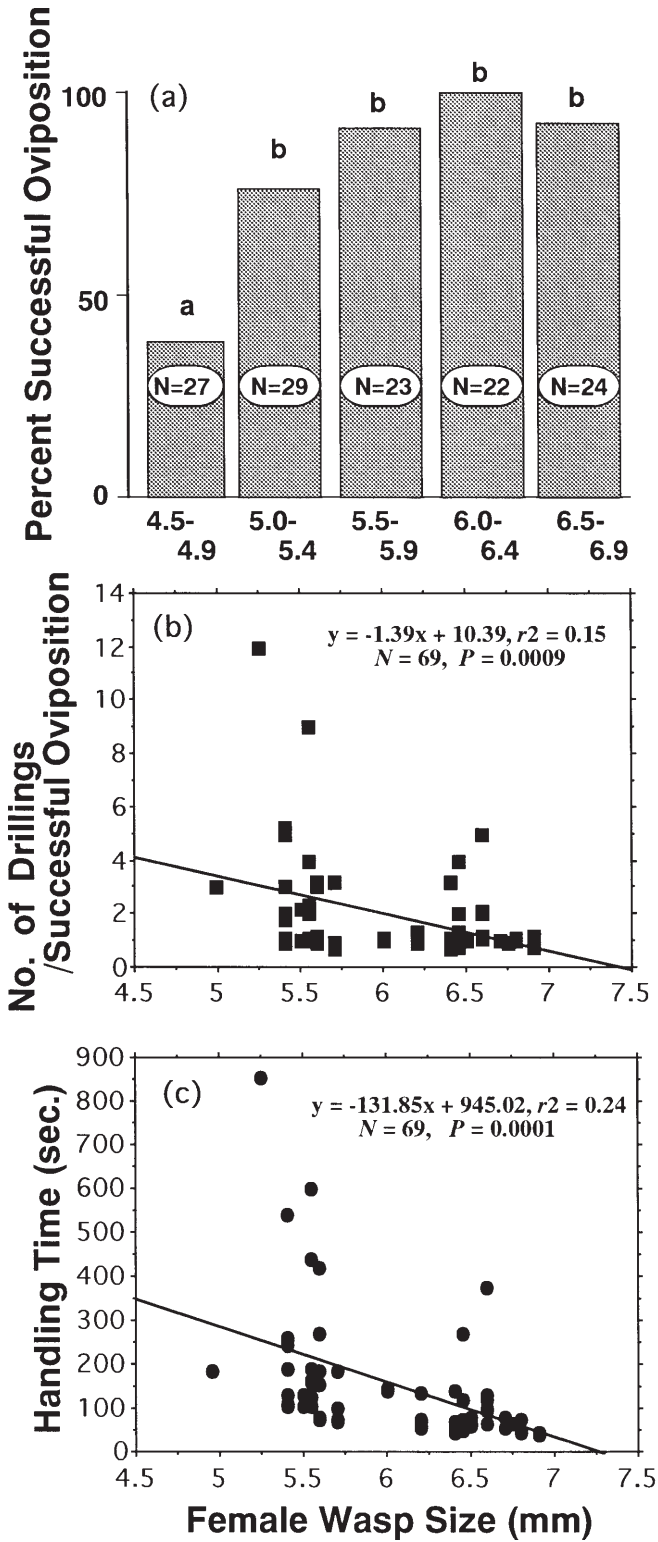


Fig. 7a-c. Relationships between female wasp size and degrees of successful oviposition in hosts (a), number of attacks (=drilling events) (b), and total handling time required for oviposition (c). Smaller females evidently have a lower ability to oviposit in hosts (chi-squared test with the sequential Bonferroni's method; $P < 0.05$) and require more time and energy for successful single oviposition (regression analysis; $P < 0.001$)

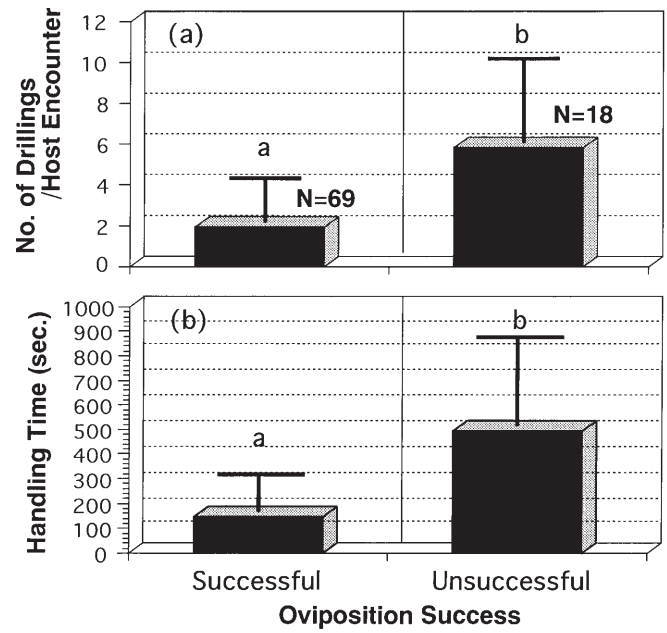


Fig. 8a,b. Numbers of attacks and total handling time per oviposition trial by female wasps in relation to success of oviposition. When females fail to oviposit in hosts and abandon oviposition, they suffer from time and energy costs without any reward, i.e., oviposition

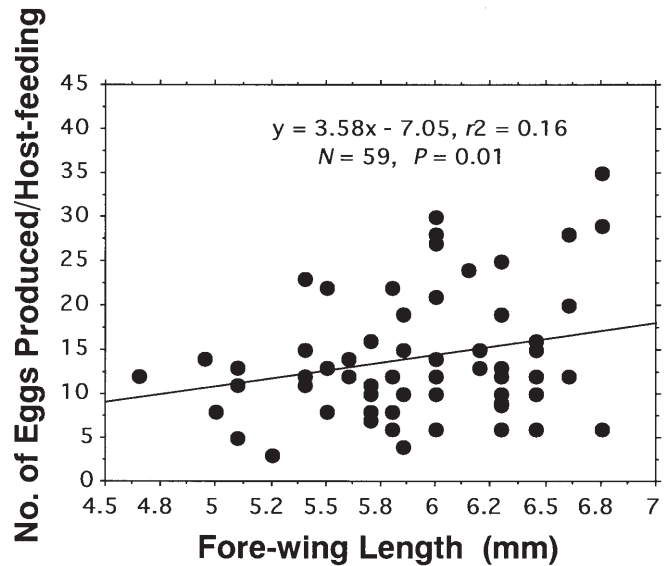


Fig. 9. Relationship between female wasp size (forewing length) and number of eggs produced per host feeding. Larger females can produce a greater number of eggs per host feeding

suggests that larger females have higher reproductive efficiencies.

Discussion

Male wasp size as a determinant of the fitness

Many empirical studies have assessed size-related female fitness whereas size-related male fitness has been much less extensively investigated, with the exception of the relationship between size and longevity (but see Antolin et al. 1995; Ode et al. 1996). However, measuring male fitness with regard to size is essential to testing the host-size model. In the present study, I have evaluated size-related fitness function of male *P. nipponica* by focusing on the relationships between size and longevity under good and poor food conditions and the relationships between size and mating success under single pair and male–male competition conditions.

Male longevity can be an indicator of the fitness of males because it should correlate with the opportunity of finding mates. In *P. nipponica*, male size did not influence male longevity regardless of availability of food (see Fig. 4). In this sense, male size does not influence the fitness of males. Male size, however, may be important if males fight for their mates or if the size influences mating success because of size-assortative mating or female choice. I have measured male mating success of *P. nipponica* with regard to male size by directly observing successful intromission by males. Two striking results have been obtained: (1) small males have greater mating success and (2) mating success of males depends largely on female size. Both these results are demonstrated for the first time in parasitoids.

I have shown an advantage of small size in male *P. nipponica* under the single pair condition; small males can mate successfully with any size classes of but large males fail to mate with small females (see Fig. 5). Such a small-male advantage appears to be a rather rare phenomenon in insects. Small-male advantages have been shown in relatively few insect species (McLachlan and Allen 1987; Steele and Partridge 1988; Fincke et al. 1997) whereas large-male advantages are much more frequently observed (Goldsmith 1987; Partridge et al. 1987; Yuval et al. 1993; Fincke et al. 1997), although males of different sizes can use different mating tactics (Goldsmith and Alcock 1993). The male's skill in quickly mounting and inserting their genitalia into females appears to be important in determining male mating success in *P. nipponica* (see Results).

It is likely that direct male–male competition leads to nonrandom mating with regard to male size. In some parasitoid wasps, physical combat among competitive males is observed (Hamilton 1979; Murray 1987, 1989; Eggleton 1990; van den Assem 1996). *P. nipponica* females are sexually receptive at emergence, and mating probably takes place near emergence sites. In the field, male wasps are found to aggregate at places near hosts (probably) containing female pupae (Ueno, personal observation). Thus,

direct male–male competition might take place at female emergence sites, and size-dependent mating success might be found. However, direct male–male competition is not observed in *P. nipponica* (see Results). Consequently, skillful small males mate first, and small-male advantages hold true even under male–male competition (see Fig. 6).

I have shown evidence that an advantage of small males over large males clearly depends on female size, and small males can have greater mating success with a wide variety of females differing in size (Figs. 5 and 6). Small males are likely to be successful in most conditions associated with host-size distributions, which may differ in places and seasons. At present, this kind of phenomenon is only known from two pimpline parasitoids, including *P. nipponica* (this study; also Ueno 1998a). Antolin et al. (1995) found in *Bracon hebetor* that male mating success did not depend on the size of available females. Advantages of small or large size in males may thus vary among parasitoid species.

Female wasp size as a determinant of the fitness

In the current study, I have assessed size-related fitness function of female *P. nipponica* by examining the relationships between size and longevity, reproductive potential, oviposition success, and egg production efficiency. In general, larger female parasitoids live longer (Sandlan 1979a; Waage and Ng 1984; van den Assem et al. 1989). Similarly, larger *P. nipponica* females live longer (Fig. 4), although such relationships may depend on food conditions, i.e., access to carbohydrate sources (Ode et al. 1996; West et al. 1996). By living longer they can encounter and oviposit in more hosts, suggesting that larger females may enjoy higher fitness.

An increase of female fecundity with increasing wasp size has been well documented mainly in many proovigenic parasitoid wasps (Waage and Godfray 1985). For synovigenic parasitoids such as *P. nipponica*, although fecundity at any one time may not correctly reflect lifetime fecundity, it might be a good measure for female reproductive potential. In *P. nipponica*, no significant difference was found between female size and the numbers of ovarioles, and mature and immature eggs, at least in my experimental conditions. However, because larger females live longer, lifetime fecundity will be greater in large females than in small females.

Lepidopteran pupae have highly hardened cuticles. In addition, they wiggle when attacked by parasitoids, preventing parasitoids from inserting the ovipositor (Cole 1959). Consequently, pupal parasitoids of Lepidoptera expend considerable time and energy to successfully drill into and penetrate the host pupal cuticle. It is likely that larger female parasitoids are more powerful and thus are more successful in ovipositing in a host. Being powerful may be an important determinant of female reproductive success. Surprisingly, few studies have examined this possibility, which I tested in the current study.

The results showed that large female *P. nipponica* have powerful oviposition success (see Fig. 7). Further, larger

individuals succeed in oviposition with fewer oviposition trials, i.e., drillings, and spend less time on handling a host on oviposition (Fig. 7), probably because they are more powerful. These results indicate that large females have higher fitness than small females. Additionally, a penalty of being small was found. Because smaller females more frequently fail to oviposit in a host, they waste energy and time without gaining the current chance of oviposition (Fig. 8). This kind of penalty has not been previously examined in parasitoids. However, if energy and time wasted by unsuccessful oviposition are overlooked, then the penalties of being small may be underestimated.

In many synovigenic parasitoids, feeding on a host as a means of obtaining nutrients, i.e., host feeding, is essential for continuous oogenesis (Sandlan 1979b; Jervis and Kidd 1986; Heimpel and Collier 1996; Jervis et al. 1996; Morales-Ramos et al. 1996; Ueno 1998b, 1999). *P. nipponica* requires host feeding for egg production, but hosts used for host feeding cannot be used as oviposition sites because they are heavily damaged by such feeding (Ueno 1997a). Thus, *P. nipponica* loses a current oviposition opportunity when it feeds on a host. By ingesting a greater amount of host materials from a single host, females will produce a greater number of eggs, allowing them to reduce the number of hosts used for feeding and to increase the number of hosts available for oviposition. Therefore, it will be advantageous to obtain host materials as much as possible. The maximum quantity of host materials that a female can feed on may depend on the female size. However, no study has examined this. In the present study, I tested this possibility. The results showed that larger females can produce a greater number of eggs per host meal (Fig. 9), suggesting that larger females can use a greater proportion of encountered hosts for oviposition. Part of the reason for the greater production of eggs per host feeding lies in their ability to gain and store greater resources from a single host feeding (Ueno, unpublished).

Countless numbers of studies have investigated the relationships between female parasitoid size and fitness, and most of them have demonstrated that larger females can have greater fitness (see King 1987). Similarly, by being large, female *P. nipponica* attain high reproductive success.

Sex ratio control in *P. nipponica* as a good example of host-size model

In *P. nipponica*, both primary and secondary offspring sex ratio decrease clearly with increasing host size (see Fig. 2). Therefore, the host-size-dependent sex ratio is caused by maternal manipulation of sex allocation in response to host size. Host-size-dependent sex allocation could be explained as an evolutionary consequence, if host size differently influences the fitness of males versus females (Charnov 1979; Charnov et al. 1981; see Fig. 1).

In many parasitoid species, the size of parasitoids correlates positively with the size of their hosts (King 1987; Ueno 1998a). Likewise, highly positive relationships were found between host size and offspring size in *P. nipponica* (see

Fig. 4). Host size, therefore, is a good estimate of the amount of host resources available for the developing parasitoids. This influence of host size on offspring wasp size has been considered as the first step for the evolution of host-size-dependent sex allocation (Charnov et al. 1981; King 1993).

Larger females of *P. nipponica* are clearly superior in their reproductive potential and in their ability to attack a host and produce eggs. The presence of positive effects of host size on the fitness of female wasps by itself is not a definitive cause for the evolution of host-size-dependent sex allocation, however. What is important is whether the marginal gain in fitness with adult size is greater for females than males. I have demonstrated that male *P. nipponica* lose more by being larger. Thus, being large has positive effects on the fitness of female wasps while it has negative effects on male wasps. Host size indirectly influences the fitness of males and females in a differential way. The basic assumption of the host-size model is satisfied in *P. nipponica*, which indicates that sex ratio control by *P. nipponica* in response to host size is adaptive.

The host-size model proposed by Charnov et al. (1981) primarily concerned adaptiveness of sex ratio control by parasitoid wasps in response to host size. This model can be applied to any sex ratio response to hosts of different types if host types influence the fitness of offspring males and females asymmetrically. The current literature suggests that the host-size model can be applied to sex ratio control by some pupal parasitoids in response to host age (King 1990; Ueno 1997b). Old host pupae produce smaller wasp offspring than do fresh host pupae. Thus, when females encounter hosts of different ages, they are selected to lay female eggs in fresh hosts. As expected, female *P. nipponica* lay more female eggs in fresher hosts (see Fig. 3). The host-age-dependent sex ratio in *P. nipponica* is thus explained by the host-size model. Because host cocoon morphology by itself does not change with age, *P. nipponica* must recognize cues other than the morphology. Female *P. nipponica* probably use chemicals on the cocoon surface to recognize host-age differences. Female *P. nipponica* may thus use two distinct cues, i.e., host size and chemicals, for sex allocation decisions.

The combination of selective advantages of small males and large females results in a strong selection that favors the evolution of host-size- or host-age-dependent sex allocation. In fact, *P. nipponica* shows clear sex ratio control in response to host size and age (see Figs. 2 and 3; Ueno and Tanaka 1997). In contrast, *Sparangia cameroni* and *Muscidifurax raptor*, solitary pupal parasitoids of Diptera, show significant but relatively weak sex ratio control in response to host size (King 1988; Seidl and King 1993). In these parasitoids, differential effects of host size on the fitness of males versus females are lacking or, if any, appear to be weak (King 1988, 1996; Seidl and King 1993; King and King 1994; King and Lee 1994). The pteromalid parasitoid *Lariophagus distinguendus* shows clear sex ratio control in response to host size. In this species, asymmetrical effects of adult size on the fitness between males and females are large (van den Assem et al. 1989). Thus, the degree of

asymmetrical effects of host size on male versus female offspring may influence the degree of sex ratio control by female parasitoids in response to host size.

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