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Sex ratio response of the parasitoid wasp Muscidifurax raptor to other females

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Summary. This study examines the sex ratio response of the parasitoid wasp Muscidifurax raptor to conspecific and confamilial females in relation to two groups of functional sex ratio models, local mate competition and host quality models. In some but not all experiments, M. raptor females produced a greater proportion of sons in the presence of a conspecific female than when alone, and this sex ratio effect carried over for a day after the females were isolated from each other. M. raptor females also produced a greater proportion of sons in the presence of a female of the confamilial parasitoid Spalangia cameroni than when alone (although only on the second day of exposure to S. cameroni, not on the first). M. raptor's sex ratio increase in the presence of conspecifics is consistent with local mate competition models but not with host quality models because the presence of a conspecific female did not cause there to be more, and thus potentially smaller, offspring developing per host. In contrast, the presence of a S. cameroni female did cause there to be more offspring developing per host than when a M. raptor female was alone; thus, M. raptor's sex ratio increase in the presence of S. cameroni may be explained by host quality models. An alternative explanation for the sex ratio increase in response to confamilials is that only a sex ratio response to conspecifics may be adaptive, due to local mate competition; but M. raptor females may be unable to distinguish between conspecific and S. cameroni females.

Key words: Sex ratio, Parasitoid wasps, Local mate competition

Many environmental factors have been shown to influence the offspring sex ratios produced by parasitoid wasps (reviewed in King 1987, 1992). Here we examine the sex ratio response of the parasitoid wasp Muscidifurax raptor to the presence of

conspecific and confamilial females and discuss our results in terms of two major groups of natural selection sex ratio models, local mate competition (LMC) models (Hamilton 1967) and host quality models (Charnov 1979; Charnov et al. 1981). The sex ratio response of parasitoid females to conspecifics is usually discussed in terms of local mate competition (LMC) theory (Hamilton 1967). The theory predicts that mothers should produce a greater proportion of sons when in the presence of other females than when alone (e.g., Hamilton 1967). Original LMC models assumed structured populations, with mating at the site of emergence, followed by female dispersal to new patches of hosts for oviposition. Recent LMC models indicate that an increased proportion of sons in the presence of another female is predicted even when not all mating is at the site of emergence (Nunney and Luck 1988).

Although sex ratio response to conspecifics is usually discussed in terms of LMC theory, host quality models may also apply when multiple offspring can develop in a single host (Waage 1982; Werren 1983; King 1992). Host quality models predict that a greater proportion of sons will be produced under conditions that will result in smaller offspring (Charnov 1979; Charnov et al. 1981). The assumption is that being small will be less disadvantageous to the reproductive success of males than of females. One situation that may result in smaller offspring is when a greater number of offspring develop in a host, as when multiple females oviposit in a host.

Muscidifurax raptor parasitizes the pupal stage of various fly species (Rueda and Axtell 1985). Unfortunately, there are no field observations as to where mating takes place. There is the potential for mating at the emergence site since M. raptor's hosts are sometimes clumped (personal observation), and male and female emergence times overlap (Legner 1969). However, that males can fly suggests that some of the mating may take place away from the emergence site. M. raptor is described as a solitary species (Rueda and Axtell 1985), meaning that usually only one offspring completes development on a host; however, even in the field, multiple offspring may develop on a single host five percent or more of the time (Propp and Morgan 1985).

We use two types of information to distinguish between LMC and host quality models in M. raptor. One distinction between the two types of models is that LMC models predict a greater proportion of sons in response to conspecific, but not allospecific, females (assuming females can distinguish between the two types of females); whereas host quality models can predict a greater proportion of sons in response to either type of female (King 1987). Another distinction is that host quality models predict a greater proportion of sons in response to females only when the presence (or previous presence) of another female causes an increased number of parasitoid offspring to develop on each host. In contrast, LMC models predict an increased proportion of sons even when another female's presence has no effect on the number of parasitoid offspring developing on a single host.

In order to make these distinctions, we examine how the offspring sex ratio of M. raptor females is affected 1) by the presence of conspecific females, 2) by having been with a conspecific female on previous day(s), and 3) by the presence of female Spalangia cameroni, a confamilial and naturally co-occurring solitary species (e.g., Butler et al. 1981; Mullens et al. 1986; Meyer et al. 1991). In each of these three situations we examine whether the presence (or previous presence) of another female

causes an increased number of parasitoid offspring to develop on each host.

Materials and methods

General methods

The M. raptor used in this study were from a colony established in 1990 from wasps that emerged from Musca domestica pupae collected in DeKalb, Illinois. The S. cameroni used in this study were from a colony established in 1985 with wasps that emerged from M. domestica and Stomoxys calcitrans pupae collected in Delphi, Indiana (King 1991). Both wasp colonies were maintained using M. domestica as hosts. Voucher specimens of M. raptor and S. cameroni are in collections at the Illinois Natural History Survey and the Purdue University Department of Entomology, respectively.

Each female used in experiments was newly emerged (less than two days old) and had been isolated in a test tube prior to her emergence so that she had no prior contact with other females. Prior to use in an experiment, each M. raptor female was paired with a male and observed to mate. The S. cameroni used in experiments were unmated. All experiments were conducted using M. domestica as hosts, at 23-28°C, 24L. Host pupae used in experiments were produced following the procedure in King (1988) for large hosts and were less than 2 d old. Females were given hosts in glass shell vials (70 mm high by 20 mm diameter) with cotton plugs or in 1 oz plastic vials (40 mm high by 36 mm top diameter by 27 mm bottom diameter). A streak of honey was provided on the side of each vial as food for the female(s). We did three experiments. After each experiment, we determined the number and sex of emerging offspring and counted the number of hosts with emergence holes.

Within each experiment we compared treatments in terms of the offspring sex ratio and number of offspring per female M. raptor and the number of wasp offspring per host with an emergence hole. Number of offspring per host with an emergence hole refers to the number of wasps per successfully parasitized host; it equals one when only one wasp emerges per host and is greater than one when more than one wasp emerges per host. Statistical analyses were done with SPSS-PC version 3.1 (Norusis 1988). When normality and homogeneity of variance assumptions were met, pairwise comparisons of treatments were by t-tests using pooled variances. Comparisons were by Mann-Whitney U tests when these assumptions were not met. Because t-tests are robust to deviations from these assumptions (Scheffé 1959), we used $\alpha = 0.001$ for tests of these assumptions, whereas we used $\alpha = 0.05$ for comparisons of means. One-tailed tests were used to compare sex ratios and number of wasp offspring per host with an emergence hole. (Two-tailed P values are given if the direction of difference is opposite to that predicted). Two-tailed tests were used to compare number of offspring per female.

Pseudovirgins (females that copulated but produced only sons) are excluded from the results presented here. Such females accounted for about 4% of all females and their exclusion did not affect statistical significance of the results at $\alpha = 0.05$, except where noted.

Experiments

The first experiment consisted of two parts. On day one we tested whether paired M. raptor females produce a greater proportion of sons than do solitary M. raptor females. In the solitary treatment one female was placed in a vial with 30 hosts for 24 hours; in the paired treatment two females were placed in a vial with 30 hosts for 24 hours. On day two, we tested whether previous exposure to another female affected a female's subsequent sex ratio response when alone. Females in the paired treatment were isolated; each female in both treatments received ten hosts for another 24 hours. Treatments were compared on each day. Values for the previously-paired treatment of the second day were calculated from the average values of the two previously-paired females.

The second experiment was similar to the first. It was designed after results of the first and third experiment suggested that a response to other females may require more than one day of exposure to other females (See Results). Solitary or paired females were given 30 hosts for each of three days. Then on the fourth and fifth days, paired females were isolated, and each female in both treatments was given ten hosts each day. To determine whether solitary and paired M. raptor females produce different sex ratios, the two treatments were compared on the first three days by MANOVA (multivariate analysis of variance) with sex ratio on days one, two and three as the three response variables and treatment (solitary or paired) as a between-subjects factor. Number of offspring per female was analyzed in the same way. Number of offspring per emergence hole was compared between treatments separately on each day because assumptions of normality were not met on all days.

To determine whether there was a carryover effect of previous exposure to another female and whether it lasted more than one day, the two treatments (consistently solitary and previously-paired) were also compared for the fourth and fifth days. Comparisons of number of offspring per female were by MANOVA. Comparisons of sex ratio and number of offspring per emergence hole were by paired comparisons on each day because assumptions of normality were not met. Values for the previously-paired treatment on the fourth and fifth days were calculated from the average values of the two previously-paired females.

The third experiment was designed to test whether M. raptor females respond to S. cameroni females. In one treatment a female M. raptor was placed alone in a vial; in the other treatment both a female M. raptor and a female S. cameroni were placed in a vial. In each treatment female(s) received 30 hosts for each of two days. The two treatments were compared by MANOVA with sex ratios on days one and two as the response variables and treatment as a between-subjects factor. Number of offspring per female was analyzed in the same way. Number of offspring per emergence hole was compared between treatments separately for each day because it did not meet the assumption of normality.

Results

In the first experiment there was no significant difference between paired and solitary females in proportion of sons, number of offspring per female, or number of offspring per host with an emergence hole (Table 1). Likewise, when paired females in experiment one were subsequently isolated, they did not differ from consistently

solitary females in sex ratio or in number of offspring per host with an emergence hole, although number of offspring per females were greater for previously paired females (Table 1). (Number of offspring per female was not significantly larger for previously paired females when pseudovirgins were included in the analysis (mean \pm s.e. (n): 3.3 ± 0.42 (22) versus 4.2 ± 0.32 (21); $t = 1.67$, $P = 0.10$.)

In contrast, in the second experiment there was a significant overall difference between paired and solitary females in proportion of sons and number of offspring per female, although not in number of offspring per host with an emergence hole (Table 2). There was a significantly greater proportion of sons from paired than from solitary females on day two, although not on days one or three. Number of offspring per female was significantly lower from paired than from solitary females on all three days. Paired females did not produce significantly more offspring per host than solitary females on any of the three days.

When paired females were isolated on day four, they still produced a greater proportion of sons than did consistently solitary females, although the two treatments no longer differed in number of offspring per female (Table 2). On day five, the two treatments did not differ in either sex ratio or number of offspring per female. There were no differences between treatments in number of offspring per host with an emergence hole for either day four or day five.

Muscidifurax raptor females produced a greater proportion of sons and more offspring when with S. cameroni than when alone. Also, there were more wasp offspring (M. raptor and S. cameroni combined) per host with an emergence hole in the treatment with S. cameroni (Table 3). The difference in sex ratio was significant only on day two; the difference in number of offspring per female was significant only on day one; and the difference in number of offspring per host with an emergence hole was significant on both days.

Discussion

Muscidifurax raptor females produced a greater proportion of sons in the presence of another female than when alone in some, but not all, situations. They produced a greater proportion of sons in the presence of a conspecific female in experiment two, in which females were paired for three days, but not in experiment one, in which females were paired for just one day. But in experiment two the effect was statistically significant only on day two, not on days one or three. The effect of another female's presence on sex ratio in experiment two carried over for a day after the females were isolated. M. raptor females also produced a greater proportion of sons when paired with S. cameroni than when alone; but again sex ratio was affected only on day two, not on day one.

When the sex ratios of M. raptor females increased in the presence of other females, it was probably the result of maternal manipulation of offspring sex ratio at fertilization rather than differential mortality of the sexes during development due to competition for resources on a host. There is no evidence of differential mortality of the sexes in M. raptor when hosts have been parasitized by just one female (Antolin 1992; Seidl and King unpublished) or in M. zaraptor when two or three parasitoid offspring have been placed on a single host (Wylie 1971).

If increasing proportion of sons in response to conspecific females is adaptive in M. raptor, LMC theory is a better explanation than host quality models. LMC theory may explain not only M. raptor's sex ratio response to conspecific females, but also its female-biased sex ratios (Hamilton 1967). The greater proportion of sons from paired conspecific females than from solitary females is not predicted by the host quality models because the greater proportion of sons was not associated with more, and thus smaller, offspring developing on each host (Table 2).

Production of an increased proportion of sons in the presence of conspecific females has been found in most species of parasitoid wasp that have been examined (King 1992). The pattern has been found in five other geographic strains of M. raptor besides the one studied here (Antolin 1992) and in eight of the nine other solitary species besides M. raptor that have been examined, including the congener M. zaraptor and the confamilial S. cameroni (Kuno 1962; Viktorov 1968, Schwartz and Gerling 1974; Kumar and Tripathi 1987; Abidi et al. 1988; Strand 1988; Markwick 1974; Wylie 1979; King 1989; but see van Dijken et al. 1989). Females produce a greater proportion of sons in response to conspecific females not only in most species of parasitoid wasps (references in King 1987, 1992 and above), but also in fig wasps (Frank 1985; Herre 1985, 1987) and mites (references in Charnov 1982).

Production of a greater proportion of sons even after subsequent isolation from other females has been tested for, and found, in only two other species besides M. raptor: the parasitoid wasps Trissolcus grandis and Telenomus heliothidis (Viktorov 1968; Strand 1988). Such a carryover effect indicates that a female's response to other females is not due simply to encountering already parasitized hosts.

In contrast to M. raptor's sex ratio response to conspecifics, the sex ratio response to S. cameroni cannot be explained by LMC theory, which predicts a sex ratio increase only in response to conspecific females. However, M. raptor females may be unable to distinguish between conspecific and allospecific females.

M. raptor's sex ratio response to S. cameroni can be explained by host quality effects. The presence of S. cameroni increases the number of offspring developing per host, which may affect the fitness of M. raptor (e.g., by making them smaller or by affecting development time). If an increased number of offspring per host has a more detrimental effect on the reproductive success of female than of male M. raptor, then there will be selection on females to produce a greater proportion of sons in the presence of S. cameroni (Waage 1982; Werren 1983). There is some evidence that being smaller has a detrimental effect on the reproductive success of both female and male wasps (Seidl and King unpublished); however it is not clear whether the detrimental effect is greater for females than for males.

Similar to M. raptor, in the confamilial parasitoid Nasonia vitripennis, females increase the proportion of sons that they oviposit in response to both conspecifically-parasitized hosts and hosts parasitized by two confamilial species (Wylie 1973).

Although increases in sex ratio in response to other females may be adaptive, as explained by local mate competition and/or host quality models, that M. raptor's sex ratio response to other females only occurred in some experiments, on only some days, is puzzling and is not explained by current sex ratio models. A day effect on sex ratio response to other females has not been looked for in any other species of parasitoid

wasps.

In contrast to the reduction in number of offspring per female in the presence of a conspecific in experiment two, number of offspring per female actually increased in the presence of S. cameroni in experiment three. One hypothesis for the greater offspring production of M. raptor females in the presence of S. cameroni is that M. raptor may use oviposition holes drilled by S. cameroni females. Within a host, Muscidifurax may then outcompete Spalangia because, relative to Spalangia, Muscidifurax larvae develop faster and are more likely to eat parasitoid eggs within the host (Wylie 1972; Markwick 1974).

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Table 1. Proportion of sons, number of offspring per female, and number of offspring per host with an emergence hole for M. raptor in experiment one
 A) on day one when females were either paired or solitary and
 B) on day two when the previously-paired or solitary females were solitary.

| Female treatment | Proportion of sons | | # offspring per female | | # offspring per host | |
|-----------------------|--------------------|----|------------------------|----|----------------------|----|
| | Mean \pm s.e. | n | Mean \pm s.e. | n | Mean \pm s.e. | n |
| A) day one | | | | | | |
| paired | 0.29 \pm 0.036 | 17 | 3.8 \pm 0.59 | 18 | 1.02 \pm 0.026 | 17 |
| solitary | 0.37 \pm 0.076 | 17 | 3.1 \pm 0.55 | 21 | 1.00 \pm 0.000 | 17 |
| | t = 0.89 | | t = 0.85 | | U = 144.5 | |
| | 2-t P = 0.38 | | 2-t P = 0.40 | | 1-t P = 0.50 | |
| B) day two | | | | | | |
| previously paired | 0.16 \pm 0.040 | 16 | 4.6 \pm 0.32 | 17 | 1.01 \pm 0.007 | 16 |
| consistently solitary | 0.14 \pm 0.038 | 19 | 3.4 \pm 0.43 | 21 | 1.00 \pm 0.000 | 19 |
| | U = 135.0 | | t = 2.13 | | U = 133.0 | |
| | 1-t P = 0.28 | | 2-t P = 0.03 | | 1-t P = 0.06 | |

2-t indicates a two-tailed test, 1-t a one-tailed test;
 n is the number of replicates of each treatment

Table 2. Proportion of sons, number of offspring per female, and number of offspring per host with an emergence hole for paired and solitary M. raptor in experiment two

A) on the first three days when females were either paired or solitary and
 B) on the fourth and fifth days when the previously-paired or solitary females were solitary.

| Female treatment | Proportion ¹ of sons | | # offspring ² per female | | # offspring ³ per host | |
|-----------------------|---------------------------------|----|-------------------------------------|----|-----------------------------------|----|
| | Mean \pm s.e. | n | Mean \pm s.e. | n | Mean \pm s.e. | n |
| A) | | | | | | |
| Day 1: | | | | | | |
| paired | 0.26 \pm 0.024 | 40 | 5.4 \pm 0.24 | 40 | 1.01 \pm 0.006 | 36 |
| solitary | 0.20 \pm 0.023 | 39 | 6.4 \pm 0.45 | 40 | 1.05 \pm 0.019 | 34 |
| Day 2: | | | | | | |
| paired | 0.24 \pm 0.016 | 40 | 7.0 \pm 0.29 | 40 | 1.02 \pm 0.007 | 36 |
| solitary | 0.16 \pm 0.014 | 39 | 11.1 \pm 0.49 | 40 | 1.02 \pm 0.014 | 34 |
| Day 3: | | | | | | |
| paired | 0.19 \pm 0.016 | 40 | 7.5 \pm 0.33 | 40 | 1.03 \pm 0.013 | 36 |
| solitary | 0.15 \pm 0.014 | 39 | 11.1 \pm 0.69 | 40 | 1.02 \pm 0.010 | 34 |
| B) | | | | | | |
| Day 4: | | | | | | |
| previously paired | 0.11 \pm 0.028 | 15 | 7.3 \pm 0.47 | 15 | 1.03 \pm 0.011 | 15 |
| consistently solitary | 0.06 \pm 0.016 | 16 | 7.8 \pm 0.55 | 16 | 1.02 \pm 0.013 | 16 |
| Day 5: | | | | | | |
| previously paired | 0.13 \pm 0.035 | 13 | 5.9 \pm 0.66 | 15 | 1.02 \pm 0.011 | 13 |
| consistently solitary | 0.13 \pm 0.035 | 16 | 6.2 \pm 0.45 | 16 | 1.01 \pm 0.008 | 16 |

2-t indicates a two-tailed test, 1-t a one-tailed test;
 n is the number of replicates of each treatment
 paired versus solitary females on days 1-3

¹ for sex ratio, multivariate $F_{3,75} = 6.03$, $P = 0.001$

univariate F-tests:

day 1: $F_{1,77} = 3.60$, $P = 0.06$

day 2: $F_{1,77} = 13.21$, $P = 0.001$

day 3: $F_{1,77} = 3.01$, $P = 0.09$

² for number of offspring per female, multivariate $F_{3,76} = 25.84$, $P < 0.001$

univariate F-tests:

day 1: $F_{1,77} = 4.07$, $P = 0.05$

day 2: $F_{1,77} = 51.04$, $P < 0.001$

day 3: $F_{1,77} = 21.51$, $P < 0.001$

³ for number of offspring per host with emergence hole

day 1: $U = 509.0$, 2-t $P = 0.07$

day 2: $U = 605.0$, 1-t $P = 0.46$

day 3: $U = 571.5$, 1-t $P = 0.25$

Table 2. continued

previously paired versus consistently solitary females on days 4-5

¹ for sex ratio,

day 4: $t = 1.72$, 1-t $P = 0.05$

day 5: $U = 101.5$, 1-t $P = 0.46$

² for number of offspring per female, multivariate $F_{2,28} = 0.19$, $P = 0.83$

univariate F-tests:

day 4: $F_{1,29} = 0.33$, $P = 0.57$

day 5: $F_{1,29} = 0.17$, $P = 0.69$

³ for number of offspring per host with emergence hole

day 4: $t = 0.34$, 1-t $P = 0.37$

day 5: $U = 87.5$, 1-t $P = 0.12$

Table 3. M. raptor's proportion of sons and number of offspring per female and the number of offspring (M. raptor and S. cameroni combined) per host with an emergence hole when M. raptor was with S. cameroni and when M. raptor was alone in experiment three.

| Female Treatment | Proportion ¹ of sons | | # offspring ² per female | | # offspring ³ per host | |
|-------------------------|---------------------------------|----|-------------------------------------|----|-----------------------------------|----|
| | Mean ± s.e. | n | Mean ± s.e. | n | Mean ± s.e. | n |
| Day 1: | | | | | | |
| with <u>S. cameroni</u> | 0.34 ± 0.040 | 29 | 10.8 ± 0.91 | 31 | 1.19 ± 0.028 | 31 |
| lone <u>M. raptor</u> | 0.28 ± 0.033 | 29 | 6.0 ± 0.64 | 31 | 1.04 ± 0.016 | 29 |
| Day 2: | | | | | | |
| with <u>S. cameroni</u> | 0.30 ± 0.036 | 30 | 10.2 ± 0.79 | 31 | 1.11 ± 0.024 | 31 |
| lone <u>M. raptor</u> | 0.21 ± 0.025 | 29 | 9.3 ± 0.89 | 31 | 1.06 ± 0.016 | 29 |

2-t indicates a two-tailed test, 1-t a one-tailed test;
n is the number of replicates of each treatment

¹ for sex ratio, multivariate $F_{2,54} = 3.35$, $P = 0.04$

univariate F-tests:

day 1: $F_{1,55} = 1.38$, $P = 0.25$

day 2: $F_{1,55} = 4.10$, $P = 0.05$

² for number of offspring per female, multivariate $F_{2,59} = 9.31$, $P < 0.001$

univariate F-tests:

day 1: $F_{1,60} = 18.51$, $P < 0.01$

day 2: $F_{1,60} = 0.66$, $P = 0.42$

³ for number of offspring per host with emergence hole

day 1: $U = 181.5$, 1-t $P < 0.001$

day 2: $U = 343.5$, 1-t $P = 0.05$