

OFFSPRING SEX RATIOS OF *BRACON PHYLACTEOPHAGUS* AS INFLUENCED BY HOST SIZE AND MATERNAL AGE

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(Received for publication 23 November 1990; revision 20 December 1990)

ABSTRACT

Laboratory studies of *Bracon phylacteophagus* Austin (Hym : Braconidae) showed that significantly higher offspring sex ratios (male : female) were produced from small hosts than from large hosts and evidence suggests that selective oviposition was the main factor influencing this relationship. Females produced a higher ratio of male offspring later in life than they did earlier in life from large hosts.

Keywords: sex ratios; host size; maternal age; *Phylacteophaga froggatti*; *Bracon phylacteophagus*.

INTRODUCTION

Bracon phylacteophagus, a parasite of *Phylacteophaga froggatti* Riek (Hym : Pergidae), eucalyptus leaf-mining sawfly, was imported from Australia and successfully laboratory-reared, released, and established in New Zealand in 1988 and 1989 (Faulds 1990). With braconids, female progeny are produced from fertilised eggs and male progeny from unfertilised eggs. To explain the 4.6 : 1.0 male to female sex ratio of progeny of laboratory-mated females, compared with 1 : 1 and 1.5 : 1.0 found in Australian field populations in 1987 and 1988, Faulds (1990) suggested that the number of times a female mates may be important. This suggestion was based on the fact that after the initial exposure to males, laboratory females had no further mating opportunities. By contrast, females in the field have the opportunity to mate often as oviposition progresses. It was also thought that host size might influence offspring sex ratios when, after a large reduction in sawfly numbers at Maungatapu 1 year after release of the parasite, most sawfly larvae were parasitised while still small and the great majority of emergences from these hosts were males.

In 1990 the progeny of some field-collected females were laboratory reared to determine if host size would influence offspring sex ratios. As these field-collected females could have mated several times, this experiment did not have the constraints of a single mating.

METHODS

Eight field-collected females were released into individual plastic cups in quarantine room rearing conditions as described by Faulds (1990). Leaves containing only either large (>9 mm) or small (<5 mm) sawfly larvae were taped to the inside of the cups. After 2 days the leaves were removed from the cups into 200 x 250-mm clear plastic bags. Fresh sawfly-infested leaves were then added. A foliage change was made every 2 days and at each foliage change the host size was alternated between large and small hosts. Occasionally when small larvae were not available large larvae were used on consecutive foliage changes. The number and sex of emerging adults collected daily from the plastic bags were recorded.

A chi-square test was used to compare the frequency of male and female emergences for different host sizes and female parent ages.

RESULTS

For all eight females higher offspring sex ratios (male : female) were produced from small hosts than from large hosts, and more offspring were reared from large hosts than from small hosts (Table 1).

Females produced significantly higher offspring sex ratios later than earlier in life from large hosts but not from small ones (Tables 2 and 3).

No parasite mortality was seen.

TABLE 1—Offspring produced from large and small hosts. Frequency of male and female emergences for different host size (large v. small host) chi-square = 77.2, $p = 0.0001$ (highly significant)

Female No.	Large host			Small host		
	No. offspring		Ratio	No. offspring		Ratio
	Male	Female		Male	Female	
1	9	14	0.64:1	17	0	∞:1
2	15	23	0.65:1	25	6	4.17:1
3	5	18	0.28:1	9	8	1.12:1
4	17	28	0.61:1	24	4	6.00:1
5	25	15	1.67:1	32	2	16.00:1
6	16	8	2.00:1	20	3	6.67:1
7	26	16	1.62:1	31	2	15.50:1
8	16	25	0.64:1	23	6	3.83:1
Totals	129	147		181	31	

TABLE 2—Offspring produced early in life and late in life from large hosts. Frequency of male and female emergences for different female parent ages (early v. late life) chi-square = 14.8, $p = 0.001$ (highly significant)

Female No.	Early life			Late life		
	First half of total emergences			Second half of total emergences		
	Male	Female	Ratio	Male	Female	Ratio
1	4	7	0.57:1	5	7	0.71:1
2*	7	13	0.54:1	8	10	0.80:1
3	0	11	0.00:1	5	7	0.71:1
4	6	17	0.35:1	11	11	1.00:1
5	11	9	1.22:1	14	6	2.33:1
6	4	8	0.50:1	12	0	α :1
7*	12	10	1.20:1	14	6	2.33:1
8	5	15	0.33:1	11	10	1.10:1
Totals	49	90		80	57	

* The uneven division into "first half, second half" is due to emergences occurring on the same day at the halfway point being grouped together.

TABLE 3—Offspring produced early in life and late in life from small hosts. Frequency of male and female emergences for different female parent ages (early v. late life) chi-square = 3.5, $p = 0.062$ (not significant)

Female No.	Early life			Late life		
	First half of total emergences			Second half of total emergences		
	Male	Female	Ratio	Male	Female	Ratio
1	8	0	α :1	9	0	α :1
2	11	4	2.75:1	14	2	7.00:1
3	4	4	1.00:1	5	4	1.25:1
4	11	3	3.67:1	13	1	13.00:1
5	16	1	16.00:1	16	1	16.00:1
6	9	3	3.00:1	11	0	α :1
7	14	2	7.00:1	17	0	α :1
8	11	3	3.67:1	12	3	4.00:1
Totals	84	20		97	11	

DISCUSSION

Host size does influence offspring sex ratios for many species of parasitoid wasps, and for most species studied the offspring sex ratio (male : female) from small hosts is greater than from large hosts. However, few studies have demonstrated whether this relationship is a result of selective oviposition or differential mortality (King 1987). While this study did not aim to address this distinction there were some indications that with *B. phylacteophagus* the relationship is more a result of selective oviposition. Firstly, no obvious signs of parasite mortality were seen. Secondly, although more *B. phylacteophagus* were reared from large hosts than from small hosts this was probably due to many of the small hosts being below the minimum size required by the parasite. Farrell & New (1980) found that only *P. froggatti*

larvae in the last two instars, pupae and prepupae are attacked. To clearly distinguish between large and small hosts nearly all the small *P. froggatti* used in this study were at an earlier stage. Although small hosts were attacked, demonstrating that Farrell & New's "minimum host size" is not exact, at least in laboratory conditions, many of the small hosts were probably unsuitable. Also, the occasional use of large hosts on consecutive foliage changes when small hosts were unavailable could account for some of the greater number of offspring produced from large hosts.

Finally, even if the lower number of emergences from small hosts was due to differential mortality, and this mortality was regarded as female mortality, the sex ratio of progeny reared from small hosts was still significantly higher than from large hosts (chi-square = 19.9, $p = 0.001$).

For field-collected females in this study the ratio of male to female progeny from large hosts was 0.88 : 1.0 (range from 0.28 : 1.0 to 2 : 1). By comparison, Faulds (1990) found that for laboratory-mated females the ratio was greater than 3.4 : 1.0 except for one female where the ratio was 2 : 1. Whenever possible (i.e., nearly always) large hosts only were exposed to these laboratory-mated females. Logically, offspring sex ratios should have been higher for field-collected females than for laboratory-mated females. In laboratory conditions females produce higher offspring sex ratios later than earlier in life and some of the field-collected females would have oviposited before capture (average progeny for laboratory-mated females = 92 (Faulds 1990); average progeny for field-collected females = 61). Because the conditions for host exposure and rearing were identical in both studies the difference in these ratios can be explained only by an occurrence prior to the females going into the rearing room. One such explanation could be the suggestion by Faulds (1990) that for females more than one mating is required to produce low offspring sex ratios. While females in the field can mate often as oviposition progresses, laboratory-mated females did not have this opportunity.

King (1987) concluded that females of most species of parasitoid wasps produce higher offspring sex ratios later in life than they do early in life and that this may be a result of sperm depletion or reduced sperm viability. If, as suggested by Faulds (1990), *B. phylacteophagus* females in the field mate often as oviposition progresses, thus topping up their sperm supply, an increase in offspring sex ratios later in life would only occur when populations were low and there were not enough males present for further mating. Also, if more than one mating by females is necessary for low or at least 1 : 1 offspring sex ratios, it means either that the female cannot store enough sperm at any one time to fertilise 50% of her eggs, or that the male does not transfer enough sperm at any one mating to fertilise 50% of the eggs. Because all females except one produced some female offspring later in life it is doubtful if the production of higher offspring sex ratios then was a result of reduced sperm viability.

In this study two factors which have been shown to influence offspring sex ratios of *B. phylacteophagus* in laboratory conditions are host size and maternal age, and there are some indications that the latter could be related to the number of times a female mates.

ACKNOWLEDGMENTS

I wish to thank L. Bulman for the statistical analyses.

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