A Field Study of Host Size Effects on Sex Ratio of the Parasitoid Wasp Spalangia cameroni

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ABSTRACT.--I examined aspects of Charnov et al.'s (1981) host-size model for the parasitoid wasp Spalangia cameroni, using collections of fly pupae (hosts) from a poultry house. The model predicts that female parasitoid wasps should emerge from larger hosts than males. This prediction was supported for two collection dates in which only one host species, house flies, was parasitized by S. cameroni. The prediction was not supported either within host species or combining host species for the collection date in which both house flies and stable flies were parasitized. In fact, female S. cameroni emerged from smaller stable fly pupae than did males. The prediction of the host-size model also was not supported on a between host species basis. Though stable fly pupae are significantly smaller than house fly pupae, the sex ratio (proportion of males) of S. cameroni emerging from stable flies was not significantly greater than from house flies. Contrary to expectations, field data showed no positive relationship between host size and female wasp size either within or between host species. Laboratory experiments indicated that female S. cameroni judge host size relative to the size of other hosts encountered, as predicted based on the significant temporal variation found in the host size distribution in the field.

INTRODUCTION
        Individuals within a species may adopt different reproductive tactics such as breeding early versus late in the breeding season, producing different numbers or sizes of litters per year, and employing territorial versus nonterritorial behavior to obtain mates (see references in Alcock, 1979; Cade, 1980; Rubenstein, 1980). Another reproductive tactic, and the one this paper deals with, is manipulation of offspring sex ratio (proportion of males). One variable which may affect the sex ratio that a female produces is the amount of resources she will be able to provide her offspring. This

idea was first suggested for polygynous mammals by Trivers and Willard (1973).

A variation on the Trivers and Willard hypothesis has been formally developed for solitary parasitoid wasps and is referred to as the host size or host quality model (Charnov, 1979; Charnov et al., 1981). Most parasitoid wasps have haplodiploid sex determination whereby unfertilized eggs develop into sons and fertilized eggs into daughters. This provides mothers a means of controlling offspring sex ratio by adjusting the ratio of unfertilized to fertilized eggs at oviposition. Parasitoid wasps provision their offspring with food by ovipositing in or on a host (typically an insect). In solitary species only one offspring is produced per host. Thus, the size of a host generally should be a good relative measure of the quantity of resources available to an offspring. If developing in or on a large host contributes more to the ultimate reproductive success of females than of males, then mothers should lay primarily daughters in large hosts and sons in small hosts (Charnov et al., 1981). One way that there may be a greater effect of host size on females than on males is if wasp size increases with host size and wasp size increases the reproductive success of females more than that of males (Charnov et al., 1981). The host-size model prediction of a greater proportion of male parasitoids emerging from small than from large hosts has been supported in the majority of parasitoid wasp species examined, most of the data coming from laboratory studies (reviewed in King, 1987; King, 1989a). However, it is not at all clear that a positive effect of host size on wasp size is what has selected for host-size-dependent sex ratios (see Discussion).

When mothers manipulate sex ratio in response to host size, they may judge host size relative to the size of other hosts that they have encountered or in absolute terms (Charnov et al., 1981; Jones, 1982). If a female judges host size in absolute terms, her decision as to whether to fertilize an egg will depend only on the size of the host she is parasitizing, independent of the overall size distribution of hosts. However, if a female judges host size in relative terms, her decision as to whether to fertilize an egg will depend on the size of the host she is parasitizing relative to the size of other hosts she parasitizes (van den Assem, 1971; Charnov et al., 1981).

Whether selection will favor females that judge host size in relative terms over females that judge size in absolute terms depends on the temporal variation in host size distribution (Charnov et al., 1981; Jones, 1982). If host size distribution varies widely among wasp generations, selection may favor females that judge host size in relative terms. If host size distribution is fairly constant across generations, there may be no such selection.

This paper reports results of a field study on a poultry house population of the solitary parasitoid wasp Spalangia cameroni Perkins (Hymenoptera: Pteromalidae), which parasitizes pupae of various dipteran species (Rueda and Axtell, 1985). This apparently is the first field study designed specifically to examine the host-size model. Using field data, I look at three aspects of this model: (1) the relationship between host size and sex ratio of emerging wasps, (2) the relationship between host size and size of emerging wasps for each sex, and (3) the amount of temporal variation in the host sizes an ovipositing female is likely to encounter. In addition, through laboratory experiments, I determine whether females judge host size in relative or absolute terms.

Interpretation of results from field studies such as this one are frequently less clear cut than interpretation of results from laboratory experiments. Nevertheless, field studies are essential to understanding sex ratios in nature. In this study, field data

show that laboratory findings (King, 1988) are not simply artifacts of laboratory conditions. In addition, the field data raise interesting new questions about some of the complexities of sex ratios in S. cameroni.

MATERIALS AND METHODS

I collected fly pupae weekly from 28 May to 12 November 1985 from an enclosed, shallow-pit, egg-layer poultry house in Delphi, Indiana (the Hilltop poultry house described in Merchant, 1984). The hens' manure falls through their wire cages into shallow, dirt-bottom troughs directly below the cages. Fly larvae feed on the manure and then pupate in it. The fly pupae are hosts to several species of parasitoid wasps (Merchant, 1984 and below).

I collected fly pupae with pupal traps (Hogsette and Butler, 1981), which were buried just below the surface of the manure (see Hurlbutt, 1987 for further details). This paper deals only with Spalangia cameroni. Other species of parasitoid wasps which emerged from the fly pupae were S. endius Walker, S. nigroaena Curtis, and Muscidifurax raptor Girault and Sanders (Hymenoptera: Pteromalidae) (King, in press). Wasp species were identified following Boucek (1963) and Rueda and Axtell (1985) and fly species following Skidmore (1985).

Widths of fly pupae were measured to the nearest 0.05 mm at 360 X. Head widths of emerging wasps were measured using a microprojector and a digitizer pad. Head width was used because it is positively correlated with other measures of size, including weight (King, 1988), yet is not affected by feeding experience, as weight is. Outliers in size, dwarf wasps were defined as wasps of less than 0.50 mm head width. They are reported but are excluded from statistical analyses (p. 338, Dunn and Clark, 1974).

Whether ovipositing females judge host size in absolute or relative terms was determined by laboratory experiments. A colony of S. cameroni was established on house fly pupae. Female wasps used in experiments were recent emergents, had been observed to mate, and were given honey on which to feed. Small and large house fly pupae were produced by adjusting the amount of food per volume of fly eggs. (See King (1988) for further details.) In experiment one, I compared wasp offspring sex ratios from small hosts between two treatments--14 small hosts presented daily to each female versus 7 small hosts presented along with 7 large hosts daily to each female. In experiment two, I compared offspring sex ratios of wasps emerging from large hosts between two treatments--14 large hosts presented daily to each female versus 7 large hosts presented along with 7 small hosts daily to each female. Mean width of large hosts is 2.75 mm + 0.006 s.e., n = 189; mean width of small hosts is 2.24 mm + 0.014 s.e., n = 140 (King, 1988). Statistical analyses used the mother as the sampling unit.

If females judge host size in absolute terms, offspring sex ratios will not differ between treatments for a given host size. If females judge host size in relative terms, a host will be judged as large (and so have an increased chance of having a female rather than a male wasp oviposited in it) only when it is with smaller hosts, and a host will be judged as small (and so have an increased chance of having a male rather than a female wasp oviposited in it) only when it is with larger hosts. Thus, if females judge in relative terms, the proportion of male offspring from large hosts will be lower in the treatment in which both small and large hosts are presented, and the proportion

of male offspring from small hosts will be higher in the treatment in which both small and large hosts are presented.

RESULTS
        I restricted analyses involving parasitized pupae to the three collection dates for which there were more than 10 pupae parasitized by S. cameroni--September 3, September 10, and October 29. The highest percent parasitism by S. cameroni was September 10, with 8.4%. Percent parasitism by parasitoid wasp species other than S. cameroni was less than 6% on September 3 and September 10 and less than 1% on October 29. Across all dates, 35% of the S. cameroni that emerged (N = 301) were males. There were no significant differences in sex ratio among the three collection dates discussed above (G test of heterogeneity, G = 0.79, P > 0.50, df = 2).

Effect of host size and species on wasp sex ratio. -- For the September 3rd and October 29th collections, S. cameroni emerged only from house fly pupae. For both dates, the pupae from which females emerged were significantly larger than the pupae from which males emerged (Table 1).
        In contrast to the September 3 and October 29 collections, for the September 10 collection, only 69% of the pupae parasitized by S. cameroni were house flies (Musca domestica L. (Muscidae)); 30% were stable flies (Stomoxys calcitrans (L.) (Muscidae)), and less than 2% were an unidentified fly species. Stable fly pupae are similar in shape to house fly pupae, but are significantly smaller (2.26 + 0.022, (n = 24) versus 2.76 + 0.029 (n= 42) mm width, September 10 collection, Mann-Whitney U = 30.5, P < 0.001; see also Skidmore, 1985). Either across all host species combined or just for house flies, for the September 10 collection there was no significant difference in the size of hosts from which female versus male S. cameroni emerged (Table 1). Looking just at stable flies, there was a significant difference, but not in the expected direction: stable flies from which female S. cameroni emerged were significantly smaller than stable flies from which males emerged (Table 1).
   For the September 10 collection, in addition to looking across and within host species at the prediction of the host-size model, I also looked between host species. Despite stable fly pupae being on average smaller than house fly pupae, the sex ratio of S. cameroni emerging from fly pupae was independent of fly species (33% male wasps from stable flies, n = 18; 29% from house flies, n = 42; G test of heterogeneity, G = 0.13, P = 0.71, df = 1).

Effect of host size and species on wasp size. -- There was a significant positive relationship between house fly host size and emerging S. cameroni size for males (r = 0.23, P = 0.05, excludes one dwarf male from 2.90 mm wide host) though not a significant relationship for females (r = 0.14, P = 0.11). Note that host width explained only a small percentage of the variation in wasp head width (less than 5%). For stable fly hosts there was no indication of a positive relationship between host size and emerging S. cameroni size for either males ($r_{s = -0.16, P = 0.38}$) or females ($_r$s = -0.05, P = 0.45, excludes one dwarf female from 2.30 mm wide host).
        Despite stable fly pupae being significantly smaller than house fly pupae, the

head widths of wasps emerging from stable fly pupae were not significantly smaller than from house fly pupae for either male S. cameroni (0.61 mm + 0.005 s.e., n = 6 versus 0.61 mm + 0.005 s.e., n = 12) or females (0.58 mm + 0.006 s.e., n = 11, excludes one dwarf female versus 0.58 mm + 0.003 s.e., n = 30).

Temporal variation in host size distribution. -- The size of fly pupae available to S. cameroni, as estimated from parasitized and unparasitized fly pupae, varied significantly through time. This was true across all dates from May 28 to November 12 (Kruskal-Wallis test: H = 334.06, P < 0.001) (King, in press), as well as between August 6 and October 29, when S. cameroni was consistently present in the collections (Kruskal-Wallis test: H = 175.16, P < 0.001). Fly pupae from the September 10 sample were significantly smaller than pupae from either September 3 or October 29 (Kruskal-Wallis test: H = 15.88, P < 0.001 and H = 18.82, P < 0.001, respectively). There was no significant difference in pupal size between September 3 and October 29 (Kruskal- Wallis test: H = 1.24, P = 0.27).

The small mean size of fly pupae on September 10 was in part due to a higher percentage of stable fly pupae. Thirty-four percent of the September 10 fly pupae were stable flies. Only 2% of the September 3 and 5% of the October 29 fly pupae were stable flies. There was no significant difference in house fly pupal size for September 3 versus September 10 (width of 2.77 mm + 0.022 s.e., n = 60 versus 2.76 mm + 0.029 s.e., n = 42, Kruskal-Wallis test: H = 0.30, P = 0.59). House fly pupae from October 29 (2.83 mm width + 0.033 s.e., n = 59) were significantly larger than from either September 3 or September 10 (Kruskal-Wallis test: H = 3.81, P = 0.05 and H = 5.06, P = 0.03, respectively).

How ovipositing females judge host size. -- Mothers appear to judge host size on a relative basis (Table 2). The proportion of males emerging was lower from large hosts when both large hosts and small hosts were presented than when large hosts were presented alone. Similarly, the proportion of males emerging was higher from small hosts when both small hosts and large hosts were presented than when small hosts were presented alone.

DISCUSSION
Effect of host size and species on wasp sex ratio. -- Among most species of parasitoid wasps which have been examined, females emerge from larger hosts than males, as predicted by the host-size model (reviewed in King, 1987, 1989a). This is true both within host species and between host species of different sizes. However, most of these data are from laboratory studies.

In this study, the host-size model prediction of females emerging from larger hosts than males was supported for the two collection dates, September 3 and October 29, in which only one host species, the house fly, was parasitized. This result is consistent with laboratory experiments with house flies as hosts (King, 1988). In laboratory experiments, female S. cameroni emerging from larger house fly hosts than males results from maternal manipulation of offspring sex rather than from differential mortality of daughters in small hosts (King, 1988).

The results from the collection date for which S. cameroni emerged from both house fly and stable fly pupae (i.e., September 10) differed from the results of the

September 3rd and October 29th collections and from the laboratory results. For September 10, looking across (i.e., all species combined), within, and between host species, the only significant host size difference between male and female S. cameroni was opposite that predicted by the host-size model: males emerged from significantly larger, not smaller, stable fly pupae than did females. Within a host species, male wasps emerging from larger hosts than females, as observed for S. cameroni from stable flies, has been reported for only one other parasitoid wasp, the solitary species Macrocentrus ancylivorus (Finney et al., 1947). The September 10 results suggest that to S. cameroni, a given size of stable fly pupae is not equivalent to the same-sized house fly pupae. It will be interesting to test S. cameroni's sex ratio and body size response to stable flies in the laboratory under controlled conditions.

Throughout this paper, I have focussed on the host-size model prediction of a greater proportion of males from small than from large hosts. The reason for doing this is that this is a robust prediction. What actual sex ratio values are predicted depends on a number of unmeasured parameters, such as the level of local mate competition, the level of inbreeding, and the relative effect of host size on male versus female reproductive success (Werren, 1984).

Another prediction of the host-size model is a male-biased overall sex ratio if there is no local mate competition (Charnov et al., 1981; Werren, 1984). However, S. cameroni appears to experience local mate competition (King, 1989b), and this can explain its female-biased overall sex ratio (Werren, 1984).

Effect of host size on wasp size. -- The host-size model prediction of a greater proportion of sons from small than from large hosts is based on the assumption that host size has a more positive effect on the reproductive success of female wasps than of males (Charnov et al., 1981). This assumption, however, has seldom been tested (but see Charnov et al., 1981; Jones, 1982; King, 1988; van den Assem et al., 1989). Charnov et al. (1981) suggested that host size may affect wasp reproductive success through a positive effect of host size on wasp size and a more positive effect of wasp size on female than on male reproductive success. The idea is that body size may have a greater effect on a female's ability to produce eggs or offspring than on a male's ability to obtain mates.

In the laboratory, house fly pupal size has a positive effect on both male and female S. cameroni size (King, 1988). However, in this field study I found no significant positive effect for females. In laboratory experiments with S. cameroni, Legner (1969) found no significant effect of house fly pupal size on either female or male weight. However, Legner's study differed from both my field and laboratory study in host dimensions and in strain of S. cameroni (King, 1988).

That host size explained such a small percentage of the variation in S. cameroni size in this study suggests that other factors also were affecting wasp size. These factors may include: host age, multiple parasitism, temperature, and wasp genotype (Gerling and Legner, 1968; Kuno, 1962; Abdelrahman, 1974; Nealis et al., 1984). Effects of host age, multiple parasitism, and temperature may account for some of the differences between field and laboratory results as these variables were under greater control in the laboratory experiments than in the field.

In terms of the host-size model, the lack of an effect of host size on S. cameroni female body size in this study suggests either that (1) though not always

strongly present, there has been a positive effect of host size on female S. cameroni size often enough to select for sex ratio manipulation in response to host size or (2) that a positive effect of host size on female body size is not what has selected for sex ratio manipulation in response to host size in S. cameroni. To date, laboratory experiments with S. cameroni have shown no effect of wasp size on a female's production of offspring or her longevity (King, 1988). The assumption of the model, that host size has a greater effect on the reproductive success of females than of males, may be satisfied, not by an effect of host size on wasp size, but through an effect on some other aspect of the wasp (e.g., wasp development time; King, 1988). Laboratory experiments indicate that female S. cameroni have shorter development times when developing on larger hosts, but that host size does not affect male development time (King, 1988).

Temporal variation in host size distribution. -- Given that female S. cameroni do manipulate offspring sex ratio in response to host size for house flies as hosts, are females judging host size in absolute or in relative terms? Charnov et al. (1981) state that ovipositing females should judge host size in relative terms when the host size distribution varies among wasp generations, provided the distribution does not vary within generations. I suggest that if the distribution varies among generations, females should judge host size in relative terms regardless of within generation variation. I make this suggestion for two reasons: (1) If wasp generations overlap, it is unlikely that there will be temporal variation in the distribution of host sizes only among generations and not within generations, and (2) To judge host size in relative terms, a female must assess the host size distribution. If there is temporal variation within generations, a female will not be able to predict the host size distribution of her entire lifetime. However, she may still judge the distribution on a shorter time scale.

In this study there was significant temporal variation in host size distribution even over short time periods (e.g., September 3 to September 10). (S. cameroni develop in 31 to 40 days at 23C (personal observation).) Because of the temporal variation in host size distribution, it was predicted that ovipositing S. cameroni females should judge host size in relative terms. Results of laboratory experiments supported this prediction.

Temporal variation in host size distributions in the field has not been examined for any other parasitoid wasp to my knowledge. Whether females judge host size in absolute terms or relative to the size of other hosts encountered has been examined for only a few other species of parasitoid wasps. Pimpla instigator and Lariophagus distinguendus females judge host size in relative terms (Chewyreuv, 1913 in Clausen, 1939; van den Assem, 1971; Charnov et al., 1981). Heterospilis prosopidis females seem to evaluate hosts primarily in absolute terms (Charnov et al., 1981; Jones, 1982). Spalangia cameroni is apparently the first species for which there is now information both on temporal variation in host size distribution in the field and on how females judge host size.

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TABLE 1.--Mean + s.e. (n) width (mm) of fly pupae from which female versus male Spalangia cameroni emerged.

Date	Fly Spp.[a]	Host Size of Female Wasps	Host Size of Male Wasps	Test Comparison[b]
Sep 3	HF	2.80 + 0.013 (122)	2.69 + 0.024 (57)	t = 4.11, P < 0.001
Oct 29	HF	3.03 + 0.083 (7)	2.89 + 0.043 (5)	U = 5.5, P = 0.03
Sep 10	ALL	2.51 + 0.042 (43)	2.56 + 0.053 (18)	t = 0.73, P = 0.23
Sep 10	HF	2.64 + 0.037 (30)	2.68 + 0.028 (12)	t = 0.69, P = 0.25
Sep 10	SF	2.17 + 0.020 (12)	2.30 + 0.075 (6)	U = 15.0, P = 0.04

[a]HF = house flies, SF = stable flies, ALL = all fly species present
[b]t-tests and Mann-Whitney U tests

TABLE 2.--Mean + s.e. proportion of male S. cameroni emerging from house fly hosts in two laboratory experiments

Experiment I		Experiment II	
Small hosts (When alone)	Small hosts (When with large hosts)	Large hosts (When alone)	Large hosts (When with small hosts)
0.27 + 0.039	0.35 + 0.048	0.38 + 0.041	0.15 + 0.039
n = 27	n = 27	n = 48	n = 26
U = 263.5, P = 0.04		U = 225.5, P < 0.001	