

This is an electronic version of the article published as
King, B.H. 1996. Sex ratio responses to other parasitoid wasps: multiple adaptive explanations.
Behavioural Ecology and Sociobiology 39:367-374. The original publication is available at
www.springerlink.com.

B. H. KING

Sex ratio responses to other parasitoid wasps: multiple adaptive explanations

B. H. King, Department of Biological Sciences, Northern Illinois University, DeKalb,
IL 60115, U.S.A.

Fax: (815) 753-0461

Internet: bking@niu.edu

Abstract In an effort to distinguish among adaptive models and to improve our understanding of behavioral mechanisms of sex ratio manipulation, this study examines sex ratio response to other wasps in the solitary parasitoid wasp *Spalangia cameroni*. Relative to when alone, females produced a greater proportion of sons in the presence of conspecifics, regardless of whether the conspecifics were female or male. In addition, females produced a greater proportion of sons after a day with a conspecific male, and after a day with a conspecific female but only if the females had been ovipositing. Relative to when alone, females did not produce a greater proportion of sons in the presence of females of the confamilial *Muscidifurax raptor* or in response to hosts that had already been parasitized by a conspecific. A combination of evolutionary models may explain *S. cameroni*'s sex ratios. An increased proportion of sons in response to conspecific females is common among parasitoid wasps and is usually explained by local mate competition (LMC) theory. However, such a response is also consistent with the perturbation model, although not with the constrained females model. The response to conspecific males is not consistent with LMC theory or the perturbation model but is consistent with the constrained females model.

Key words Sex ratio · Local mate competition · Behavioral mechanism · Parasitoid wasp

Introduction

Sex ratio manipulation is a common phenomenon in a range of taxa (e.g., references in Charnov 1982; Clutton-Brock and Iason 1986) but has been especially well-documented in parasitoid wasps (reviewed in Waage 1986; King 1987, 1993a; Godfray 1994). However, most studies have focussed on one of two explanations for common

sex ratio patterns, local mate competition theory (e.g., Hamilton 1967) or host quality theory (e.g., Charnov 1979); and other alternative adaptive explanations have not been well-examined (King 1993a). Studies of the behavioral mechanisms by which females assess the environment for sex ratio manipulation have been done with a relatively small number of parasitoids (reviewed in Godfray 1994).

Here, I attempt to distinguish among adaptive explanations for sex ratio response to other females and to examine behavioral mechanisms, using the parasitoid wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae). Production of a greater proportion of sons in the presence of another female versus when alone has been found in most parasitoid wasps that have been examined (reviewed in King 1987, 1993a), including *S. cameroni* (King 1989). In *S. cameroni* and some other species the pattern has been shown to be a result of maternal manipulation of offspring sex at oviposition and not a result of differential mortality of the sexes. Female wasps can control offspring sex at oviposition by controlling egg fertilization: unfertilized eggs develop into sons and fertilized eggs into daughters.

I examine how generalized *S. cameroni*'s response to females is. Do females respond only to females or also to males? Do females respond only to conspecific females or also to females of the confamilial *Muscidifurax raptor*, with whom they naturally co-occur (e.g., Butler et al. 1981; Meyer et al. 1991)? Does the effect on sex ratio of having been with a conspecific persist after the conspecific is no longer present? Is there an effect of having been in the presence of a conspecific even when not ovipositing? Is there an effect of physical contact? Do females respond only to the physical presence of a female or also to hosts that have been parasitized by another conspecific female? Knowing if and how females respond to other wasps is important both for evaluating adaptive models and for understanding behavioral mechanisms of sex ratio manipulation.

Local mate competition (LMC) theory is the traditional explanation for the production of an increased proportion of sons in response to other females in parasitoid wasps (described below). However, a version of host quality theory could also explain such a sex ratio response (described below). Additionally, what appears to be a response to number or density of females may be better or additionally explained as a response to adult sex ratio: A female who has encountered not only the male with whom she mated but also other female(s) may perceive a more female-biased population sex ratio than a female who has encountered no other wasp except the male with whom she mated. Two adaptive sex ratio models, the perturbation model and the constrained females model predict an offspring sex ratio response to adult sex ratio, although they make opposite predictions.

I evaluate these four adaptive models for offspring sex ratio response to other wasps by comparing offspring sex ratios produced by mated females in response to other wasps relative to when alone (Table 1). First, I briefly describe each of the four models (predictions and assumptions summarized in Tables 1 and 2, respectively).

LMC models assume a subdivided population structure with mating primarily at the natal patch, followed by female dispersal to new oviposition patches (e.g., Hamilton 1967; reviewed in Antolin 1993). Relative to when alone in a patch, when a female is with another female, her sons will compete not only with each other but also

with the other female's sons, hence the predicted increase in proportion of sons in response to other females. Some mating by males outside of the natal patch and asynchronous oviposition both reduce, but do not eliminate, the predicted increase in proportion of sons (Nunney and Luck 1988).

The perturbation model predicts selection for parents that adjust sex ratio inversely in response to adult sex ratio (Werren and Charnov 1978). The perturbation model assumes overlapping generations and temporal variation in relative fitness of the sexes, such as will occur with perturbations of population sex ratio. The generations must overlap so that the sex ratio experienced by the parents is relevant to the sex ratio that the offspring experience.

The constrained females model predicts that an increased abundance of virgin females will select for mated females to produce a decreased proportion of sons (Godfray 1990). In most parasitoid wasps, when virgin females reproduce, they are constrained to produce sons -- because of haplodiploid sex determination. Thus, the greater the proportion of females that are virgin, the greater the proportion of male offspring expected in the population in the next generation. More virgin females may result if there is a shortage of males, which might be indicated by a more female-biased population sex ratio. If the proportion of virgin females varies, there may be selection for facultative sex ratio response by individual females (Godfray and Hardy 1993).

A version of host quality theory, which I refer to as the crowding model, can predict a response to conspecifics and/or heterospecifics (Waage 1982a; A. D. Taylor unpublished). The crowding model predicts a greater proportion of sons when more mothers are present under the following conditions: 1) more mothers at a patch of host(s) results in more eggs being laid in each host, 2) more eggs per host results in smaller offspring, and 3) being small is more detrimental to the reproductive success of females than males. This prediction holds regardless of the presence or absence of LMC (A. D. Taylor unpublished). This model was designed for gregarious species, i.e., species in which multiple offspring develop on a single host.

Available data suggest that *S. cameroni* meets assumptions of LMC theory, the constrained females model, and perhaps the perturbation model, but not the crowding model (Table 2). *S. cameroni* parasitizes the pupal stage of various fly species (Rueda and Axtell 1985). A female drills through a host puparium with her ovipositor and lays an egg on the pupa within. The wasp larva hatches in about two days and then feeds on the fly pupa, eventually killing it (Gerling and Legner 1968). With rare exception, only one offspring completes development on each host; i.e., *S. cameroni* is a solitary species. Hosts are sometimes clumped in the field (personal observation). Some males leave the natal site unmated, and males can be found at host pupae that are in a stage suitable for oviposition (Myint and Walter 1990). Thus, although traditionally sex ratio response has only been examined in response to other females, in *S. cameroni*, females may interact at oviposition sites with males as well.

Both LMC theory and the perturbation model predict that a greater proportion of sons should be produced in response to other females, but the models differ in predicted response to males (Table 1). In response to more males, LMC theory does not predict a response; whereas the perturbation model predicts a decreased proportion of sons. The sex ratio responses predicted by the constrained females model differ

from the other models both for response to females and for response to males: the constrained females model predicts a decreased proportion of sons in response to females and an increased proportion of sons in response to males. Only the crowding model predicts a response to both conspecific and heterospecific females, but it applies to gregarious species, not solitary ones such as *S. cameroni* (Table 2).

Methods

General Methods

The *Spalangia cameroni* used in this study were from a colony established in 1985 with wasps that emerged from *Musca domestica* and *Stomoxys calcitrans* pupae collected in Indiana, U.S.A (King 1991). The *Muscidifurax raptor* were from a colony established in 1990 with wasps that emerged from *Musca domestica* pupae collected in DeKalb Co., Illinois, U.S.A. The experiments were performed in 1993 and 1994; a long time in culture does not appear to affect *S. cameroni*'s sex ratio behavior (King 1994). The wasp colonies were maintained at 23-28°C, 24L using *M. domestica*, a natural host species (King 1988). Voucher specimens of *S. cameroni* and *Muscidifurax raptor* are in the insect collections at Purdue University's Department of Entomology and the Illinois Natural History Survey, respectively.

Hosts were produced following the procedure in King (1988) for large hosts. When presented to the wasps, hosts were less than 24 h old (timed from the initiation of pupal tanning).

Within a day of emerging, virgin females and virgin males were paired and mating was observed. Pairing duration was variable, usually less than an hour. All wasps had just mated for the first time within hours of being used in an experiment. Females had no other previous contact with wasps. Females were presented with hosts in small plastic vials (40 mm high by 36 mm top diameter by 27 mm bottom diameter) for 24 h with a drop of honey on the vial wall for food.

I estimated offspring sex ratio at oviposition from sex ratio at emergence. There is no evidence of differential mortality of the sexes during development in *S. cameroni*, even when multiple offspring compete on a single host (Wylie 1971; King 1988, 1990).

The Experiments

The first experiment involved four treatments: 1) one *S. cameroni* female, 2) two *S. cameroni* females, 3) one *S. cameroni* female and one *M. raptor* female, and 4) one *S. cameroni* female and four conspecific males. In all but two replicates of the treatment with four conspecific males, the males included the male with whom the female had just mated. All of the males and females had just mated. In each treatment the wasp(s) received 30 hosts for 24 h. After flies emerged, the remaining fly pupae were isolated in individual test tubes for further development of any wasp offspring. This was necessary to ensure that emerging *M. raptor*, which take about a week less to develop than *S. cameroni* (personal observation), would not hyperparasitize any of the hosts from which wasps had not yet emerged (Mandeville et al. 1990; personal observation). I compared sex ratio and offspring production of *S. cameroni* when alone versus when with each other type of wasp. In the treatment with two females, offspring sex ratio

was pooled across both females.

In the second experiment, I examined the effect of having oviposited in the presence of another female conspecific or a female *M. raptor* versus having oviposited alone on the previous day. On the first day, females were either alone or with another female (a conspecific or a *M. raptor*) and were given 30 hosts for 24 h, as in the previous experiment. On the second day, females from all three treatments were alone, and each was given 15 hosts for 24 h. (To avoid pseudoreplication, on the second day one female was randomly chosen from the treatment with a pair of conspecific females). I compared second day sex ratios and offspring production between females that had been alone both days and females that had been with another female on the first day but alone on the second day.

In the third experiment, to determine the effect of having been with another wasp, for the 24 h prior to being given 30 hosts, a female was either in a vial with another female, with a male (her mate), or alone. I compared the sex ratio and offspring production of females that had consistently been alone to females that had been with a male and to females that had been with a female.

To determine the effect of prior physical contact, immediately upon being given 30 hosts, a female was either touched five times with a small paint brush or was not touched. I compared the sex ratio and offspring production of females that had been touched to those that had not.

I looked indirectly at the response to hosts exposed to another female (Table 3). It was not possible to look directly at a female's response to already parasitized hosts because there was no genetic marker that would allow offspring to be matched to their mothers. The difference between the experimental and control treatments was that the second female in the experimental treatment received hosts that had been exposed to another female, whereas in the control the hosts that the second female received had not been exposed to another female. Controlling for effects of host age turned out to be unnecessary: sex ratio did not differ between 0-day-old and 1-day-old hosts in the control (see Results). Thus, I compared the sex ratio and offspring production from hosts exposed to one female (the control) versus hosts exposed to two females sequentially (the experimental treatment).

Statistical Analyses

I used SPSS-PC version 3.1 for statistical analyses (Norusis 1988). Mean \pm SE are presented.

In the last three experiments and in most replicates of the first and second experiment, the treatments were temporally blocked, that is replicates of each treatment were run simultaneously. I did this to control for variation in laboratory conditions such as temperature and humidity. Within each replicate, I attempted to further match treatments in terms of size and age of hosts. Nevertheless, treatments within replicates were not correlated for sex ratio or for most clutch size comparisons, indicating no block effect. In order to increase power, I compared treatment effects by two sample tests when there was no correlation and by paired tests when there was a significant correlation (Zar 1984, p. 152). Comparisons were by t-tests, or if assumptions of normality were not met, Mann-Whitney U tests.

Two-tailed P values are indicated by "2t", one-tailed values by "1t". In the first experiment, sex ratio of one versus two conspecific females was compared by a 1-tailed test because a greater proportion of sons from the latter has already been shown (King 1989); this comparison was performed just as a control. Comparison of the sex ratio of a female alone versus with *M. raptor* was 1-tailed because the models predict no effect or a greater proportion of sons with a confamilial. In the first experiment, comparison of the sex ratio of a female alone versus with male conspecifics was 2-tailed because the sex ratio models predict opposite results (Table 1). Because both significant results in the first experiment were for a greater proportion of sons when with another wasp (Table 4), in subsequent experiments, I used 1-tailed tests in the same direction.

I included pseudovirgins (females that produced only sons despite having mated). However, excluding identifiable pseudovirgins did not affect conclusions.

Results

In the first experiment, pairs of *S. cameroni* females produced a significantly greater proportion of sons than lone *S. cameroni* females, despite the presence of a pseudovirgin in the lone female treatment (Table 4). (Without the pseudovirgin, 0.23 of the offspring were male in the lone female treatment.) *S. cameroni* females with *S. cameroni* males also produced a significantly greater proportion of sons than lone *S. cameroni* females (Table 4).

S. cameroni females with *M. raptor* did not produce a greater proportion of sons than lone *S. cameroni* females (Table 4). When with a *M. raptor* female, *S. cameroni*'s sex ratio was not related to the number of *M. raptor* offspring produced ($r = 0.06$, $n = 28$, 1t $P = 0.38$). Comparing replicates in which some versus no *M. raptor* offspring were produced, *S. cameroni*'s sex ratio did not differ (Mann-Whitney $U = 75.0$, $n_1 = 16$, $n_2 = 12$, 2t $P = 0.33$). When *M. raptor* produced offspring, the average was 2.8 ± 0.5 , range 1-7, $n = 16$.

Being with another wasp reduced a female's clutch size regardless of whether she was with males or a female, *S. cameroni* or *M. raptor* (Table 4). Fewer *S. cameroni* offspring were produced when *M. raptor* also produced offspring (10.4 ± 1.2 versus 13.2 ± 0.7 ; $t = 1.77$, $df = 28$, 1t $P = 0.04$).

In the second experiment, females that had oviposited with another conspecific female the previous day produced a greater proportion of sons than females that had been alone continuously (0.30 ± 0.04 versus 0.18 ± 0.03 , Mann-Whitney $U = 117.5$, $n_1 = 23$, $n_2 = 22$, 1t $P = 0.001$), but did not differ in number of offspring produced (paired $t = 0.88$, $df = 22$, 2t $P = 0.39$). Females that had oviposited with a *M. raptor* female for the previous day did not differ from females that had been alone continuously in proportion of sons (0.185 ± 0.04 versus 0.180 ± 0.03 , Mann-Whitney $U = 372.5$, $n_1 = 36$, $n_2 = 22$, 1t $P = 0.35$) or in offspring production ($t = 0.34$, $df = 59$, 2t $P = 0.74$).

In the third experiment, females that had been alone did not differ in proportion of sons from females that had been with another female but without hosts the previous day (0.21 ± 0.02 versus 0.23 ± 0.01 , $t = 1.15$, $df = 57$, 1t $P = 0.13$). However, females that had been alone produced a lower proportion of sons than

females that had been with a male (0.21 ± 0.02 versus 0.26 ± 0.02 , $t = 1.91$, $df = 57$, $1t P = 0.03$). Females that had been alone did not differ in clutch size (14.7 ± 0.9) either from females that had been with another female but without hosts the previous day (16.1 ± 0.6 , paired $t = 1.63$, $df = 28$, $2t P = 0.11$) or from females that had been with a male (15.7 ± 0.6 , $t = 0.93$, $df = 57$, $2t P = 0.36$).

There was no significant difference between contacted and noncontacted females in either proportion of sons or clutch size (0.27 ± 0.04 versus 0.22 ± 0.02 , Mann-Whitney $U = 257.5$, $n_1 = 24$, $n_2 = 24$, $1t P = 0.26$; 15.0 ± 0.7 versus 15.2 ± 0.7 ; $t = 0.17$, $df = 46$, $1t P = 0.43$).

Females that were given hosts that had previously been exposed to another female did parasitize additional hosts: more offspring emerged from such doubly-exposed hosts than from 0-day-old hosts exposed to one female (21.4 ± 0.6 versus 15.7 ± 0.77 ; $t = 5.89$, $df = 78$, $1t P < 0.001$). Sex ratios from 0-day-old and 1-day-old hosts did not differ (0.25 ± 0.03 versus 0.29 ± 0.03 ; Mann-Whitney $U = 625.5$, $n_1 = 40$, $n_2 = 37$, $2t P = 0.24$), so samples were combined. Sex ratios from doubly-exposed hosts were not significantly different from sex ratios from singly-exposed hosts (0.25 ± 0.02 versus 0.27 ± 0.02 ; Mann-Whitney $U = 1446.0$, $n_1 = 40$, $n_2 = 77$, $2t P = 0.59$).

Discussion

Relative to when alone, *S. cameroni* females produced a greater proportion of sons not only in the presence of conspecific females but also in the presence of conspecific males, after a day with a conspecific male, and after a day of ovipositing with a conspecific female. In contrast, there was no sex ratio response to the presence of confamilial *M. raptor* females, to having been with a conspecific female the previous day without ovipositing, or to hosts that had already been parasitized by a conspecific. The greater proportion of sons in the presence of a conspecific female strengthens conclusions from a previous study (King 1989).

Evolutionary Mechanisms

A combination of evolutionary models may explain *S. cameroni*'s sex ratio responses to other wasps.

LMC theory appears to be relevant to *S. cameroni* based on a combination of the facultative sex ratio response to other females and the observed mating structure, which involves partial sibmating (Myint and Walter 1990). The absence of a response to confamilials also is consistent with LMC theory. However, the increased proportion of sons in response to males which was observed here is not consistent with LMC.

As the oldest of the four adaptive models discussed here, LMC theory has received the most attention in terms of both theoretical and empirical development (Charnov 1982; Godfray 1994). LMC theory is also supported in some other parasitoid wasps, by within and between species sex ratio patterns and by support for the assumption of full or partial sibmating (reviewed in Godfray 1994).

The perturbation model predicts *S. cameroni*'s increased proportion of sons in response to conspecific females and the absence of a response to confamilials, but does not predict the increased proportion of sons in response to males. Additional data on assumptions of the perturbation model would aid in assessing its relevance for *S.*

cameroni. Laboratory data suggest some overlap of generations (Table 2), an assumption of the perturbation model. However, this overlap should be viewed with caution because male longevity may be unnaturally elongated by male inactivity in such experiments. Field data on male longevity would be more convincing, although admittedly difficult to obtain. There is indirect support for the assumption that population adult sex ratio varies temporally, but direct measurement of temporal variation remains to be made.

The constrained females model predicts the increased proportion of sons in response to males and the absence of a response to confamilials, but does not predict the increased proportion of sons in response to conspecific females. Two assumptions of the model remain to be tested for *S. cameroni*: temporal variation in proportion of virgin females and a negative relationship between the proportion of adults that are male and the proportion of females that remain virgin (see Godfray and Hardy 1993 for methodology). Development of a constrained females model with low levels of local mating also would be helpful because most species, including *S. cameroni*, do not have fully local mating (Myint and Walter 1990; Hardy 1994). For models with extreme local mating see Godfray (1990).

To better evaluate both the perturbation model and the constrained females model, data on the effect of latency to mate on offspring sex ratio would also be useful. In my experiments, I have assumed that females perceive population sex ratios by the sex ratio of adults that they encounter. Alternatively, females might perceive population sex ratios by their latency to mate, a greater latency indicating a less male-biased sex ratio (Charnov 1982). This has not been examined in *S. cameroni*. But two other parasitoid wasps, a braconid and an ichneumonid, both produce a greater proportion of daughters with greater latency (Rotary and Gerling 1973; Hoelscher and Vinson 1971). This pattern is contrary to the perturbation model but consistent with the constrained females model.

Aside from data on the effect of number of mothers on offspring sex ratio, data relevant to the perturbation model and constrained females model are scant for other parasitoid wasps. In contrast to *S. cameroni*, the solitary pupal parasitoid wasp *Brachymeria intermedia* (Chalcididae) generally decreases the proportion of sons it produces when in the presence of an increasing proportion of adult males, consistent with the perturbation model (Mohamed and Coppel 1986). In the gregarious parasitoid wasp *N. vitripennis*, the proportion of males that a female produces is significantly increased by three hours of exposure to three conspecific males, though not to one or two conspecific males (Wylie 1966, 1976).

The relationship between adult sex ratio and offspring sex ratio is also variable among other types of organisms, regardless of whether one looks at adult sex ratio directly (Sharpe and Wyatt 1974; references in Werren and Charnov 1978; Charnov 1982; McLain and Marsh 1990) or at delayed mating or fertilization, which may indicate a low proportion of adult males (references in Werren and Charnov 1978; Charnov 1982).

Suggestions for future research include further development of models that include multiple adaptive mechanisms for sex ratio manipulation, and more empirical studies attempting to distinguish among adaptive models, e.g., by examining the effects

of adult sex ratio, mating latency, and frequency of virgin females on offspring sex ratios. In addition, the possibility of phylogenetic constraints on sex ratios and sex ratio manipulation in this and other species needs to be investigated as it remains largely unexplored.

Proximal Mechanisms

One behavioral mechanism for producing a greater proportion of sons in the presence of another female is the "interference mechanism": in a given oviposition bout, females oviposit sons first, followed by daughters, and they oviposit fewer total offspring in the presence than in the absence of another female (Waage 1982a, b). This mechanism has been documented in a few parasitoid wasp species (Waage and Lane 1984; van Welzen and Waage 1987). In *S. cameroni*, consistent with this mechanism, the presence of a female or male conspecific, causes females to oviposit a greater proportion of sons and fewer total offspring (Table 4). Other data on *S. cameroni*, however, do not support this interference mechanism. *M. raptor* interrupts *S. cameroni*'s oviposition (King and Lee 1994) and causes a reduction in offspring production, yet *S. cameroni* exhibits no sex ratio response to *M. raptor*. A day's exposure to a male or an ovipositing conspecific female causes no offspring reduction but does cause a sex ratio response.

Another mechanism by which females might modify sex ratio is by changing the sequence of son and daughter production in the presence versus absence of conspecifics (van Welzen and Waage 1987; King 1993b). The sequence in which daughters and sons are oviposited has not been examined in *S. cameroni*.

S. cameroni's sex ratio response to the presence of another female must be a response to the female's presence since there was no response to encounters with already parasitized hosts. The sex ratio from hosts exposed sequentially to two females was not significantly greater than from hosts parasitized only by one female. "Second" *S. cameroni* females did parasitize hosts that had already been exposed to another female: they produced about six offspring to the first female's sixteen. Looking at a composite sex ratio from both the second female and the first is not as powerful as examining only the second female's sex ratio. Nevertheless, the results were not even in the predicted direction.

S. cameroni's sex ratio response to males is not from sperm clogging the oviduct and interfering with fertilization, as in the parasitoid wasp *Macrocentrus ancylivorus* (Braconidae) (Flanders 1956). Female *S. cameroni* only mate once (Hurlbutt 1987).

S. cameroni's sex ratio response to male and female conspecifics is probably not just through physical contact. Courtship involves considerable contact, and an *S. cameroni* male will readily mount, court, and try to copulate with mated females, including females with whom he successfully mated (Hurlbutt 1987). However, there was no effect of contact in my study (although contact was brief and not throughout the period of oviposition). In addition, if just contact is the cue, females might have been expected to respond to *M. raptor*, yet did not, in terms of sex ratio. Interactions between *M. raptor* and *S. cameroni* involve interruption of each others' oviposition and physical contact (King and Lee 1994). *S. cameroni* probably receives as much or more

interference from *M. raptor* as from conspecific females: *M. raptor* is more aggressive than *S. cameroni* (King and Lee 1994).

The generality of sex ratio response to other females has not been well-examined in many other parasitoid wasps. In the mostly solitary confamilial *M. raptor*, females produce a greater proportion of sons in response to both conspecifics and *S. cameroni* under some, but not all, conditions (King and Seidl 1993). In *Nasonia vitripennis*, which is a gregarious confamilial, a female increases the proportion of sons that she produces when with conspecific female(s), even if the female is newly emerged and hence not ovipositing (Wylie 1966), and when with three conspecific males, although not when with just one or two conspecific males. A *N. vitripennis* female does not significantly increase the proportion of sons that she produces when she is with a glued down conspecific female or an ovipositing *S. cameroni* female or *S. cameroni* male (Wylie 1976).

Production of a greater proportion of sons even after subsequent isolation from other females has been tested for, and found, in three other parasitoid wasps besides *S. cameroni*: *Trissolcus grandis* (Scelionidae), *Telenomus heliothidis* (Scelionidae), and *M. raptor* (Viktorov 1968; Strand 1988; King and Seidl 1993).

Acknowledgments I thank J. Cline for assisting with fly colony maintenance; J. Cline, H. Dixon, and K. Lindley for counting wasps; R. King, T. Bittner, J. Cline, M. Napoleon, A. Queral, C. Trombino, J. Turmo for comments on this manuscript. This research was supported by the Graduate School and the Department of Biological Sciences at Northern Illinois University.

References

- Antolin MF (1993) Genetics of biased sex ratios in subdivided populations: models, assumptions, and evidence. In: Futuyma D, Antonovics, J (eds) Oxford survey of evolutionary biology. Oxford Press, pp 239-282
- Butler JF, Escher RL, Hogsette JA (1981) Natural parasite levels in house flies, stable flies, and horn flies in Florida. In: Proceedings of the workshop on status of biological control of filth flies. United States Department of Agriculture, pp 61-79
- Charnov EL (1979) The genetical evolution of patterns of sexuality: Darwinian fitness. *Am Nat* 113:465-480
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton, New Jersey
- Clutton-Brock TH, Iason GR (1986) Sex ratio variation in mammals. *Q Rev Biol* 61:339-374
- Flanders SE (1956) The mechanisms of sex ratio regulation in the parasitic Hymenoptera. *Insectes Soc* 3:325-334
- Gerling D, Legner EF (1968) Developmental history and reproduction of *Spalangia cameroni*, parasite of synanthropic flies. *Ann Entomol Soc Am* 61:1436-1443
- Godfray HCJ (1990) The causes and consequences of constrained sex allocation in haplodiploid animals. *J Evol Biol* 3:3-17
- Godfray HCJ (1994) Parasitoids. Princeton University Press, Princeton, New Jersey

- Godfray HCJ, Hardy ICW (1993) Sex ratio and virginity in haplodiploid insects. In: Wrensch DL, Ebbert M (eds) Evolution and diversity of sex ratio in insects and mites. Chapman and Hall, New York, pp 402-417
- Hamilton WD (1967) Extraordinary sex ratios. *Science* 156:477-488
- Hardy ICW (1994) Sex ratio and mating structure in the parasitoid Hymenoptera. *Oikos* 69:3-20
- Hoelscher CE, Vinson SB (1971) The sex ratio of a hymenopterous parasitoid, *Camponotus perdistinctus*, as affected by photoperiod, mating, and temperature. *Ann Entomol Soc* 64:1373-1376
- Hurlbutt BL (1987) Sex ratio in a parasitoid wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae). PhD dissertation. Purdue University, West Lafayette, IN.
- King BH (1987) Offspring sex ratios in parasitoid wasps. *Q Rev Biol* 62:367--396
- King BH (1988) Sex-ratio manipulation in response to host size by the parasitoid wasp *Spalangia cameroni*: a laboratory study. *Evolution* 42:1190--1198
- King BH (1989) A test of local mate competition theory with a solitary species of parasitoid wasp *Spalangia cameroni*. *Oikos* 55:50-54
- King BH (1990) Sex ratio manipulation by the parasitoid wasp *Spalangia cameroni* in response to host age: a test of the host-size model. *Evol Ecol* 4:149-156
- King BH (1991) A field study of host size effects on sex ratio of the parasitoid wasp *Spalangia cameroni*. *Am Midl Nat* 125:10-17
- King BH (1993a) Sex ratio manipulation by parasitoid wasps. In: Wrensch DL, Ebbert M (eds) Evolution and diversity of sex ratio in insects and mites. Chapman and Hall, New York, pp 418--441
- King BH (1993b) Sequence of offspring sex production in the parasitoid wasp *Nasonia vitripennis* in response to unparasitized versus parasitized hosts. *Anim Behav* 45:1236-1238
- King BH (1994) How do female parasitoid wasps assess host size during sex-ratio manipulation? *Anim Behav* 48:511-518
- King BH (1996) Fitness effects of sex ratio response to host quality and size in the parasitoid wasp *Spalangia cameroni*. *Behav Ecol* 7:35-42
- King BH, Lee HE (1994) Test of the adaptiveness of sex ratio manipulation in a parasitoid wasp. *Behav Ecol Sociobiol* 35:437-443
- King BH, Seidl SE (1993) Sex ratio response of the parasitoid wasp *Muscidifurax raptor* to other females. *Oecologia* 94:428-433
- Mandeville JD, Mullens BA (1990) Host species and size as factors in parasitism by *Muscidifurax* spp. and *Spalangia* spp. (Hymenoptera: Pteromalidae) in the field. *Ann Entomol Soc Am* 83:1074-1083
- McLain DK, Marsh NB (1990) Individual sex ratio adjustment in response to the operational sex ratio in the southern green stinkbug. *Evolution* 44:1018-1025
- Meyer JA, Schultz TA, Collar C, Mullens BA (1991) Relative abundance of stable fly and house fly (Diptera: Muscidae) pupal parasites (Hymenoptera: Pteromalidae; Coleoptera: Staphylinidae) on confinement dairies in California. *Environ Entomol* 20:915-921
- Mohamed MA, Coppel HC (1986) Sex ratio regulation in *Brachymeria intermedia*, a pupal gypsy moth parasitoid. *Can J Zool* 64:1412-1415

- Myint WW, Walter GH (1990) Behaviour of *Spalangia cameroni* males and sex ratio theory. *Oikos* 59:163-174
- Norusis MJ (1988) SPSS/PC+ advanced statistics V2.0. SPSS Inc., Chicago
- Nunney L, Luck RF (1988) Factors influencing the optimum sex ratio in a structured population. *Theor Popul Biol* 33:1-30
- Rotary N, Gerling D (1973) The influence of some external factors upon the sex ratio of *Bracon hebetor* Say (Hymenoptera: Braconidae). *Environ Entomol* 2:134-138
- Rueda LM, Axtell RC (1985) Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and other muscoid flies associated with poultry and livestock manure. Technical Bulletin 278. North Carolina Agricultural Research Service, North Carolina State University
- Sharpe RM, Wyatt AC (1974) Sex ratio and weaning bodyweight differences in the offspring of unisexually- and bisexually-reared cross-fostered rats. *Lab Anim* 8:61-69
- Strand MR (1988) Variable sex ratio strategy of *Telenomus heliothidis* (Hymenoptera: Scelionidae): adaptation to host and conspecific density. *Oecologia* 77:219-224
- Viktorov GA (1968) Influence of density on the sex ratio in *Trissolcus grandis* Thoms (Hymenoptera, Scelionidae). *Zool Zh* 4:1035-1039
- Waage JK (1982a) Sex ratio and population dynamics of natural enemies--some possible interactions. *Ann Appl Biol* 101:159-164
- Waage JK (1982b) Sib-mating and sex ratio strategies in scelionid wasps. *Ecol Entomol* 7:103-112
- Waage JK (1986) Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In: Waage JK, Greathead D (eds) *Insect Parasitoids*. Academic Press, London, pp 63-95
- Waage JK, Lane JA (1984) The reproductive strategy of a parasitic wasp. II. Sex allocation and local mate competition in *Trichogramma evanescens*. *J Anim Ecol* 53:417-426
- van Welzen CRL, Waage JK (1987) Adaptive responses to local mate competition by the parasitoid, *Telenomus remus*. *Behav Ecol Sociobiol* 21:359-365
- Werren JH, Charnov EL (1978) Facultative sex ratios and population dynamics. *Nature* 272:349-350
- Wylie HG (1966) Some mechanisms that affect the sex ratio of *Nasonia vitripennis* (Walk.) (Hymenoptera: Pteromalidae) reared from superparasitized housefly pupae. *Can Entomol* 98:645-653
- Wylie HG (1971) Observations on intraspecific larval competition in three hymenopterous parasites of fly puparia. *Can Entomol* 103:137-142
- Wylie HG (1976) Interference among females of *Nasonia vitripennis* (Hymenoptera: Pteromalidae) and its effect on sex ratios of their progeny. *Can Entomol* 108:655-661
- Zar JH (1984) *Biostatistical analysis*, 2nd edn. Prentice-Hall, Englewood Cliffs

Table 1. Models predicting sex ratio responses to other wasps relative to when alone.
 < % ♂ = lower proportion of sons than when alone
 > % ♂ = greater proportion of sons than when alone

Model	Sex ratio response to:		
	♂ conspp	♀ conspp	♀ confamilial
LMC	none	> % ♂	none
Perturbation	< % ♂	> % ♂	none
Constrained ♀s	> % ♂	< % ♂	none
Crowding	none	> % ♂	> % ♂

Table 2. Assumptions of models predicting sex ratio responses to other wasps and relevant data on *S. cameroni*.

Model	Important assumptions and data on <i>S. cameroni</i>
LMC (Hamilton 1967; reviewed in Antolin 1993)	Some local mating, followed by female dispersal to new oviposition patches <i>S. cameroni</i> has some sibmating at the natal site, but most males and females disperse soon after emergence, prior to mating (Myint & Walter 1990).
Perturbation (Werren and Charnov 1978)	<p>Overlapping generations</p> <p><i>S. cameroni</i> in the laboratory: (unpublished data from experiments in King 1988) Males develop in 32 days (± 0.1 s.e., range 30-35, n = 88) and with little activity live 40 days (± 3 s.e., range 8-59, n = 18). Females develop in 35 days (± 0.1 s.e., range 32-41, n = 246) and reproduce for 30 days (± 1 s.e., range 14-44, n = 31).</p> <p>Temporal variation in adult population sex ratio</p> <p><i>S. cameroni</i> adult sex ratio presumably varies temporally: relative development time of the sexes varies with host species (King 1996), and relative abundance of host species varies temporally (e.g., King 1991).</p>

Table 2. continued

Model	Important assumptions and data on <i>S. cameroni</i>
Constrained Females (Godfray 1990; Godfray and Hardy 1993)	Variation in proportion of virgin females e.g., as a result of variation in adult sex ratio (see Introduction). <i>S. cameroni</i> 's adult sex ratio presumably varies (see Perturbation model) Virgin females readily reproduce, producing sons <i>S. cameroni</i> virgins produce as many offspring as mated females but only sons (King 1988)
Crowding (Waage 1982a; A. D. Taylor unpublished)	Offspring from multiple females can develop per host <i>S. cameroni</i> is a solitary species. Greater negative effect of crowding on female than male fitness (e.g, via reduction in offspring size)

Table 3. Experimental design to test the response to hosts already exposed to another female relative to the response to unexposed hosts.

	Experimental Treatment	Control
day 1	0-day-old hosts are given to ♀ A	0-day-old hosts are given to ♀ C
day 2	hosts (now 1-day old) that were exposed to ♀ A are given to ♀ B	unparasitized 1-day-old hosts are given to ♀ D

Table 4. Proportion of sons and clutch size per *S. cameroni* female in the presence of other wasps relative to when alone.

Treatment	Proportion of Sons		Clutch Size Per SC ♀	
	Mean ± SE (Range)	n	Mean ± SE (Range)	n
1 SC ♀	0.26 ± 0.03 (0.00-1.00)	34	14.4 ± 0.6 (7-23)	34
2 SC ♀s	0.29 ± 0.02 (0.00-0.58)	28	9.7 ± 0.5 (0.5-12)	28
1 SC ♀ with 4 SC ♂	0.32 ± 0.03 (0.00-0.64)	29	11.6 ± 0.6 (4-17)	29
1 SC ♀ with 1 MR ♀	0.21 ± 0.02 (0.00-0.50)	28	11.5 ± 0.8 (0-18)	30

SC = *S. cameroni*, MR = *M. raptor*.

Proportion of Sons:

1 SC ♀ versus 2 SC ♀: Mann-Whitney U = 349.0, 1t P = 0.04

1 SC ♀ versus 1 SC ♀ + 1 MR ♀: Mann-Whitney U = 391.5, 2t P = 0.23

1 SC ♀ versus 1 SC ♀ + 4 SC ♂: Mann-Whitney U = 331.5, 2t P = 0.02

Clutch Size:

1 SC ♀ versus 2 SC ♀: Mann-Whitney U = 116.5, 1t P < 0.001

1 SC ♀ versus 1 SC ♀ + 1 MR ♀: Mann-Whitney U = 322.5, 1t P = 0.01

1 SC ♀ versus 1 SC ♀ + 4 SC ♂: t = 3.38, 1t P = 0.001