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# Sex Ratio Manipulation by Parasitoid Wasps

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### Introduction

A mother's ability to pass on her genes to future generations is significantly affected by her offspring sex ratio (proportion of male offspring), and so offspring sex ratio is expected to be under strong selection (e.g., Fisher 1930; Hamilton 1967; Werren and Charnov 1978; Charnov 1982). The particular sex ratio favored may vary according to environmental conditions; in which case, selection may favor mothers with the ability to manipulate sex ratio in response to current environmental conditions. Two environmental conditions that may affect what sex ratio a mother should produce are (1) the amount of resources that will be available to her offspring (e.g., Trivers and Willard 1973; Charnov 1979; Charnov et al. 1981) and (2) the number of mothers present (e.g., Hamilton 1967, 1979).

The theory for sex ratio manipulation in response to environmental conditions is applicable to a wide range of organisms. However, haplodiploid parasitoid wasps are particularly good organisms for testing the theory. Females store sperm in a spermathecal capsule. As an egg passes through the oviduct a female may or may not release sperm; eggs passing through unfertilized will develop into sons while fertilized eggs will develop into daughters (Flanders 1956). Thus by controlling egg fertilization, mothers can control their offspring sex ratios.

Another reason that parasitoid wasps have received so much attention in the study of sex ratio manipulation is that a number of species can be reared in the laboratory in large numbers, and some of the environmental conditions to which females are expected to respond can be manipulated and measured. Also, knowing what factors affect a mother's offspring sex ratio has practical applications. Many of the hosts used by parasitoid wasps are agricultural pests, and releases of parasitoids may help control these pests (e.g., Legner and Brydon 1966; Legner and Dietrick 1974). Knowing what factors

influence sex ratio is important to successfully rear parasitoids for release (Waage 1986).

Relationships between sex ratios of parasitoid wasps and environmental conditions were noted by entomologists as early as the 1900s (reviewed in Clausen 1939; Flanders 1939). Since then, considerable progress has been made both in the development of sex ratio theory (Charnov 1982) and in the amassing of data on parasitoid wasp sex ratios (compare, for example, Waage 1986 and King 1987, to Clausen 1939; Flanders 1939 and 1946). The goal of this chapter is to outline some general patterns of sex ratio manipulation among parasitoid wasps and to suggest how these patterns relate to current sex ratio theory. I discuss sex ratio manipulation in response to two environmental conditions—host size and number of ovipositing females present. Adaptive manipulation of sex ratio in response to these factors is predicted by two basic groups of sex ratio manipulation models—host quality models and local mate competition (LMC) models. (Host quality models are sometimes referred to more specifically as host size models when host size is the aspect of host quality under consideration.) After briefly explaining the models, I will discuss some of the empirical support for them. Specifically, I will focus on general qualitative predictions and examine (1) the taxonomic distribution of parasitoid wasp species exhibiting the predicted patterns, (2) expected ecological correlates of sex ratio manipulation, (3) the role of differential mortality of the sexes, and (4) data on the assumptions of the models. I will end by briefly outlining some potential limitations on a female's ability to manipulate her offspring sex ratio in an adaptive manner. Throughout this chapter, methodological problems of testing sex ratio manipulation models in parasitoid wasps are considered, and possible solutions are suggested.

I am focusing on sex ratio manipulation in response to host size and number of females present for two reasons. First, there are data on a sufficient number of species to make some at least tentative generalizations. Second, the theory is fairly well developed for explaining how relationships between sex ratios and these two factors may result from adaptive manipulation. In contrast, some of the other factors that influence offspring sex ratios of parasitoid wasps (reviewed in King, 1987) are most likely not adaptive but rather may be just by-products of the mechanism of sex determination (e.g., effects of parental age due to sperm depletion) or nonadaptive effects of differential mortality of the sexes.

I focus here on qualitative predictions of the sex ratio manipulation models. At present there generally are not sufficient data on the assumptions of the models to make quantitative predictions. (See "Models' Assumptions" and "Limitations on Sex Ratio Manipulation" below.) Also, even if the data were available, life history differences would result in the quantitative pre-

ditions varying among species, and my goal is to look for some general trends among species.

### Sex Ratio Manipulation Models

#### Response to Host Size

The host quality models are mathematical evolutionary models which were developed to explain how maternal manipulation of offspring sex ratio in response to host characteristics such as host size may be adaptive (Charnov 1979; Charnov et al. 1981; Werren 1984a). A basic prediction of these models, and the prediction I focus on in this chapter, is that mothers should oviposit a greater proportion of daughters in large than in small hosts (Fig. 12.1A).

A critical assumption is that developing on a large host confers more to the ultimate reproductive success of females than of males (Fig. 12.1B). Charnov et al. (1981) suggested that host size may have a greater effect on female than on male reproductive success if host size is positively correlated with wasp size (Fig. 12.1C) and if wasp size increases the reproductive success of females more than the reproductive success of males (Fig. 12.1D). The idea is that a small male may still be able to inseminate as many females as a larger male, but a small female may not be able to produce as many offspring as a larger female. Alternatively, host size may have a differential effect on reproductive success of females vs. males through other avenues, such as an effect on development time. (See section on "Models' Assumptions".)

Sex ratio manipulation in response to host size has been examined primarily in solitary species of parasitoid wasps. In solitary species, by definition, only one offspring develops per host. Thus the quantity of resources available to a developing wasp should be closely correlated to the size of its host. Sex ratio manipulation in response to host size may also occur in facultatively gregarious and gregarious species (respectively, one to a few and many offspring develop per host). In gregarious and facultatively gregarious species, however, the expected relationship between host size and resources available to a developing wasp is complicated by the ability of mothers to adjust clutch size in response to host size. If mothers increase clutch size with increasing host size, as is commonly the case (King 1987), the quantity of resources available to a developing wasp will not necessarily be related to host size. If resource per wasp is not related to host size, sex ratio manipulation in response to host size is not expected.

#### Response to Other Mothers

Local mate competition (LMC) models predict what offspring sex ratio a mother should produce given the number of other mothers present (e.g.,

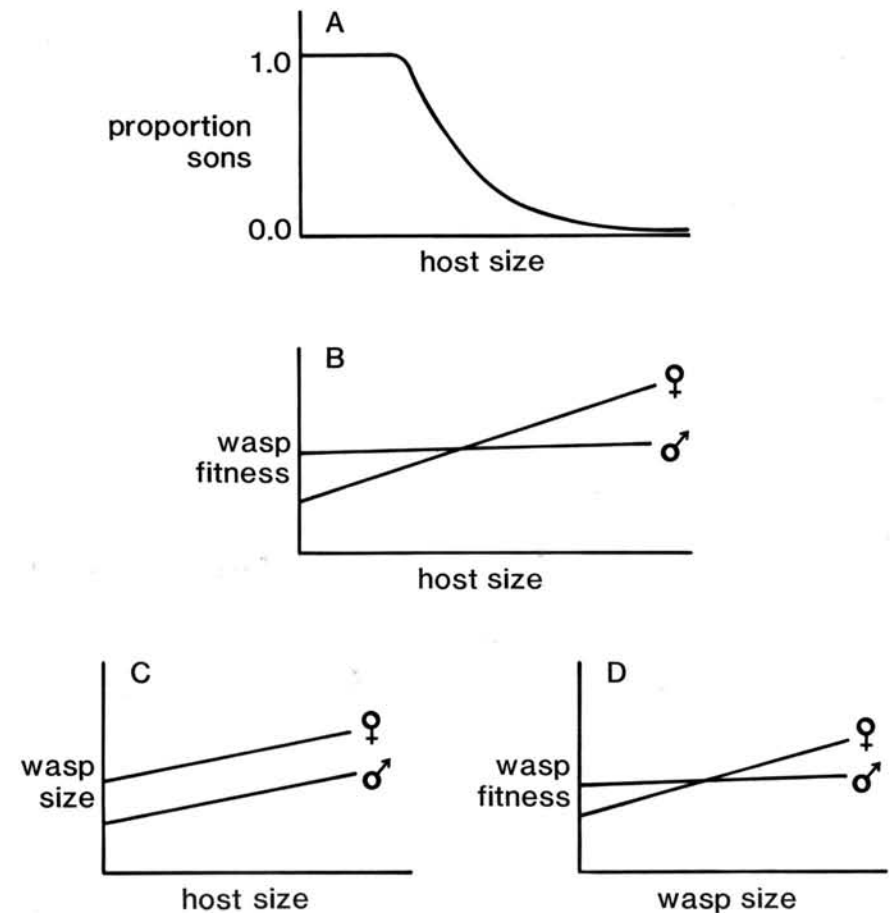


Figure 12.1. Diagrammatic example of host size model (Charnov et al. 1981): prediction (A), critical assumption (B), and one-way critical assumption may be met (C and D).

Hamilton 1967, 1979). LMC theory was designed for species in which hosts are in "patches": offspring mate within the patch from which they emerge; hence within patches there is competition among males for mates ("local mate competition"). Mated female offspring then disperse to new patches of hosts to oviposit. For gregarious species, a "patch" can consist of any number of hosts, including just a single host; for solitary species, a "patch" consists of a clump of two or more hosts. A general prediction of LMC models, and the one I focus on in this chapter, is that mothers should produce a greater proportion of sons when in a patch with other ovipositing females than when alone.

Though LMC ideas for parasitoid wasps are frequently discussed in terms of gregarious species, in some ways, solitary species are more straightforward for testing the models. In gregarious species, the pattern of a greater proportion of sons when more mothers are present might be explained not only by LMC models, but also or instead, by a version of the host quality models (Waage 1982; Werren 1984b; Taylor, manuscript). The idea is that when there are more mothers at a patch of hosts, more eggs will be laid in each host, and so emerging offspring will be smaller. If being small is more detrimental to the reproductive success of females than males, there will be selection for parasitoid mothers to produce a greater proportion of sons in response to the number of mothers present regardless of the presence or absence of LMC (Taylor, manuscript). King (1987, in press) and Taylor (manuscript) suggest some ways of distinguishing between LMC and host quality models for gregarious species.

## Empirical Support

### Methods

The tallies of species given here are based on studies found in an extensive, though not exhaustive, search of the literature. In considering these tallies, it is important to keep in mind that (1) there are more than 100,000 known species of parasitoid wasps and probably at least that many more unknown species (Hopper 1984; van den Bosch et al. 1982) and (2) the parasitoid wasps that are studied and the results that are reported may not be representative samples.

One of the difficulties in doing studies based on published literature is in obtaining basic information on the species of interest. It would be useful if papers consistently provided information on whether a species is solitary, gregarious, or facultatively gregarious; the family to which the species belongs (particularly for species outside of North America and recently described species; North American species described prior to about 1976 can generally be found in Krombein et al. 1979); and the stage of the host attacked (egg, larva, pupa).

### Predictions of the Models

#### Taxonomic distribution

Of 75 species for which there is information on the relationship between host size at the time of oviposition and offspring sex ratio, 53 species exhibit a greater proportion of sons in small than in large hosts. These 53 species

Table 12.1. 53 of 75 parasitoid wasp species in 13 families show some evidence of a greater proportion of sons emerging from hosts parasitized when small than from hosts parasitized when large.

EULOPHIDAE	15 of 17 species
ICHNEUMONIDAE	13 of 16 species
PTEROMALIDAE	7 of 11 species
BRACONIDAE	6 of 13 species
APHIDIIDAE	2 of 5 species
ENCYRTIDAE	3 of 3 species
APHELINIDAE	1 of 2 species
TRICHOGRAMMATIDAE	1 of 2 species
CHALCIDAE	1 of 1 species
DIAPRIIDAE	1 of 1 species
EURYTOMIDAE	1 of 1 species
TIPHIIDAE	1 of 1 species
TORYMIDAE	1 of 1 species
BETHYLIDAE	0 of 1 species

References in Table 1 of King 1989a; also Askew and Shaw 1979; Flanders and Oatman 1982; Nechols and Kikuchi 1985; Hu et al. 1986; Dijkstra 1986; Fuester et al. 1987; Mackauer and Kambhampati 1988; Ooi 1988; Wright and Kerr 1988; Gunasena et al. 1989; Knight and Croft 1989; Barrett and Brunner 1990; Fox et al. 1990; Ridgway and Mahr 1990a,b; Fujii and Khin Mar Wai 1990; Heinz and Parrella 1990; Fuester and Taylor 1991; Seidl and King, manuscript.

come from 13 different families, though primarily from the Eulophidae and the Ichneumonidae (Table 12.1).

The effect of number of mothers present on offspring sex ratio has been examined in fewer parasitoid wasps than has the effect of host size. Of 19 species, 16 exhibit a greater proportion of sons when more mothers are present. These 16 species are in five different families, though primarily in the family Pteromalidae (Table 12.2).

Table 12.2. Sixteen of 19 parasitoid wasp species in five families show some evidence of a greater proportion of sons emerging when more mothers are present (references in text).

PTEROMALIDAE	7 of 7 species
SCELIONIDAE	3 of 3 species
TRICHOGRAMMATIDAE	3 of 3 species
APHIDIIDAE	2 of 2 species
EULOPHIDAE	1 of 2 species
BETHYLIDAE	0 of 1 species
BRACONIDAE	0 of 1 species

### Ecological correlates

#### Response to host size

Are there any ecological differences between species that exhibit the patterns predicted by sex ratio manipulation models and species that do not? Parasitoids exhibiting host-size-dependent sex ratios include parasitoids of eggs, oothecae, nymphs, larvae, and pupae. Waage (1982) suggested that host-size-dependent sex ratios should occur in idiophytic but not koinophytic species of parasitoids. Idiophytic species are parasitoids of nongrowing hosts, i.e., egg or pupal parasitoids or larval parasitoids that paralyze their hosts. Koinophytic species are parasitoids of growing hosts, i.e., larval parasitoids that do not paralyze their hosts (Haeselbarth 1979). A test of Waage's hypothesis shows that among solitary species of parasitoid wasps, a significantly greater proportion of idiophytic than of koinophytic species exhibit host-size-dependent sex ratios (King 1989a). Thus, Waage's hypothesis is supported in a general way, though there are exceptions, including *Heterospilus prosopidis*, a koinophytic parasitoid that does manipulate sex ratio in response to host size (Charnov et al. 1981; Jones 1982), and *Spalangia endius*, an idiophytic parasitoid that does not manipulate sex ratio in response to host size (Donaldson and Walter 1984, King 1991b). For further discussion of Waage's hypothesis and why some exceptions are expected, see King (1989a).

Another expected ecological correlate of host-size-dependent sex ratios is the solitary habit. As explained above, host-size-dependent sex ratios are expected to be more prevalent among solitary species than among gregarious species. Available evidence suggests that this may be the case. Among idiophytic species, solitary species have the greatest proportion of species exhibiting host-size-dependent sex ratios, followed by facultatively gregarious species, with gregarious species having the smallest proportion (King 1989a). The number of gregarious species examined is small.

In some species, experimental design may have affected whether or not host-size-dependent sex ratios were found. Specifically, in some studies females were each presented with multiple host sizes, either simultaneously or sequentially; in other studies each female was presented with only a single host size. Presenting each female with more than one host size simultaneously is the most straightforward test for host-size-dependent sex ratios for two reasons. Simultaneous presentation may make host-size-dependent sex ratios easier to detect statistically because it avoids the problem of large between-mother variation in offspring sex ratio. In addition, with simultaneous presentation, host-size-dependent sex ratios are always expected (provided the assumption of a differential effect of host size on male vs. female reproductive success is met) (Table 12.3). In contrast, in the other situations, whether or not host-size-dependent sex ratios are expected also depends on

Table 12.3. Whether host-size-dependent sex ratios are expected (+) or not (-) depends on how multiple host sizes are presented to females and how host size is judged by females. (See text for further explanation).

Presentation of Host Sizes	How Females Judge Host Size	
	Absolute Terms	Relative Terms
Simultaneous	+	+
Sequential	+	+/-*
1 size per female	+	-

\*Dependent on memory capabilities

whether females can remember the distribution of host sizes previously encountered and whether there has been selection on females to judge host size in absolute or relative terms (discussed below and in Charnov et al. 1981; Jones 1982; Charnov 1982; King 1991a) (Table 12.3). If a female judges host size in absolute terms, she produces a constant, but different, sex ratio in each host size independent of other host sizes she has encountered. If a female judges host size in relative terms, the sex ratio she produces from a given host size depends on the other host sizes she has encountered; and if she encounters only a single host size, she produces the same sex ratio regardless of what the single host size is (Charnov et al. 1981; Werren 1984a).

It has been suggested that temporal variation in the host size distribution will select for females that judge in relative terms (Charnov et al. 1981; Jones 1982; King 1991a). At present, to my knowledge, there is information on temporal variation in host size distribution in nature for only one species of parasitoid wasp, *Spalangia cameroni* (King 1991a). For this species, there is significant temporal variation in host size distribution, and consistent with this, females were found to judge host size in relative terms. Other species that judge host size in relative terms include *Pimpla instigator* and *Diglyphus begini* (Chewyreu 1913 in Charnov 1982; Heinz and Parrella 1990). In contrast, *Heterospilus prosopidis* females judge in absolute terms (Charnov et al. 1981; Jones 1982). *Lariophagus distinguendus* and *Anisopteromalus calandrarum* judge host size in both relative and absolute terms: the sex ratio from a given host size varies according to what other host sizes have been encountered; yet when different females each encounter only one host size, sex ratio still varies among females according to host size (van den Assem 1971; van den Assem et al. 1984; Werren and Simbolotti 1989).

#### Response to other mothers

The parasitoids exhibiting a positive relationship between offspring sex ratio and number of mothers present include parasitoids of eggs, larvae,

pupae, and oothecae. All eight solitary species examined and both facultatively gregarious species examined exhibit a positive relationship (*Trichogramma japonicum* [Kuno 1962], *Trissolcus grandis* [Viktorov 1968], *Telenomus remus* [Schwartz and Gerling 1974], *Muscidifurax zaraptor* [Wylie 1979], *Trioxys indicus* [Kumar and Tripathi 1987], *Diaeretiella rapae* [Abidi et al. 1988], *Telenomus heliothidis* [Strand 1988], and *Spalangia cameroni* [King 1989b]; and *Trichogramma evanescens* [Salt 1936; Waage and Lane 1984] and *Trichogramma lutea* [Kfir 1982]). Six of nine gregarious species examined exhibit a positive relationship (*Nasonia vitripennis* [Velthuis et al. 1965; Walker 1967; Werren 1983; Orzack and Parker 1986; but see below], *N. giraulti* [King and Skinner 1991a], *Eupteromalus dubius* [Wylie 1976b], *Dinarmus vagabundus* [Rojas-Rousse et al. 1983], *Tetrastichus hagenowii* [Narasimham 1984], and *Pteromalus puparum* [Takagi 1985]). A prevalence of sex ratio manipulation in response to number of mothers present is expected in solitary species if hosts of many solitary species are clumped. At least five of the eight solitary species that have been examined parasitize hosts that are sometimes clumped, and thus these species are expected to experience local mate competition (*Spalangia cameroni* and *Muscidifurax zaraptor* [pers. observ.]; *Telenomus remus* [Gerling 1972]; *T. heliothidis* [Strand 1988]; and *Trichogramma japonicum* [Clausen 1978]).

*Bracon hebetor*, *Melittobia* spp., *Goniozus legneri*, and some strains of *Nasonia vitripennis* are apparently the only parasitoid wasps examined that have not shown a positive relationship between female number and offspring sex ratio (Galloway and Grant 1989; P. Wilhem 1986—pers. comm. Univ. Leiden, Netherlands, in Werren 1987; Legner and Warkentin 1988; Orzack and Parker 1986; Orzack et al. 1991). All four species are gregarious. *Bracon hebetor* in fact shows a negative relationship. Galloway and Grant (1989) suggest that *B. hebetor* may fit a host quality model rather than the LMC model (discussed further below under "Models' Assumptions").

#### *The Role of Differential Mortality of the Sexes*

The sex ratio patterns predicted by the sex ratio manipulation models are predicted to result from maternal manipulation of egg fertilization. Alternatively, the same sex ratio patterns may result from differential mortality of the sexes. For example, mothers may be ovipositing the same proportion of sons in small as in large hosts, but there may be greater survivorship of sons than of daughters in small hosts. In most parasitoid wasps, females are on average larger than males and so may require more resources to complete development (Hurlbutt 1987). Luckily, there are several ways to rule out differential mortality of the sexes as the cause of a sex ratio pattern (reviewed in King 1987). For some species, direct observations of the oviposition behavior of females allow determination of offspring sex ratio at oviposition (e.g., Suzuki et al. 1984). If differential mortality of the sexes

can be ruled out, then we know that females are manipulating offspring sex ratio at the time of oviposition.

Among the species exhibiting a greater proportion of sons in smaller hosts, differential mortality has been ruled out as the cause of the pattern for twelve species in six families: Ichneumonidae—2 species, Pteromalidae—4 species, Aphelinidae—1 species, Braconidae—2 species, Eulophidae—2 species, Tiphidae—1 species (Kishi 1970; Sandlan 1979; van den Assem 1971; King 1988; Fujii and Khin Mar Wai 1990; Luck and Podoler 1985; Charnov et al. 1981; Jones 1982; Flanders and Oatman 1982; Dijkstra 1986; Heinz and Parrella 1990; Brunson 1938). Thus in these species of parasitoid wasps, mothers are known to be manipulating offspring sex ratio in response to host size as predicted by the host size models. These twelve species include nine idiophytic and three koinophytic parasitoids.

Differential mortality has been ruled out as the cause of the relationship between offspring sex ratio and number of mothers present for nine species in three families: Pteromalidae—5 species, Scelionidae—3 species, Trichogrammatidae—1 species (Walker 1967; Wylie 1971, 1976b, 1979; King and Skinner 1991a; Viktorov and Kochetova 1973; van Welzen and Waage 1987; Strand 1988; Waage and Lane 1984).

In experimental tests of the relationship between number of mothers present and offspring sex ratio, the confounding problem of differential mortality of the sexes can be reduced or eliminated. Mothers can be prevented from laying so many offspring in a single host that there is reduced survivorship of those offspring. For example, females may be allowed to disperse (e.g., Werren 1983); however, it is then less clear whether the sex ratio is in response to the initial number of mothers or fewer (King and Skinner 1991a). Other solutions are to present mothers with many hosts or to present hosts for a shorter time period. This must be balanced by the concern to have few enough hosts and a long enough time period for mothers to interact. Another solution is to look just at sex ratios from hosts oviposited in once (e.g., van Welzen and Waage 1987). If there is a sex ratio increase in such hosts when multiple females are present, it indicates that the sex ratio increase is not just a result of differential mortality of the sexes. However, the lack of an increase in this situation does not rule out the existence of a sex ratio response to other females. In some species the mechanism by which females increase their sex ratios in response to other females may be by increasing sex ratio only when parasitizing previously parasitized hosts.

#### *Response to Both Host Size and Other Mothers*

The solitary parasitoid *Spalangia cameroni* is apparently the only species that has been shown to manipulate offspring sex ratio in response to both host size and number of mothers present (King 1988, 1989b). The gregarious species *Tetrastichus hagenowii* exhibits the patterns predicted by both

groups of models (Narasimham 1984); however, differential mortality of the sexes has not been ruled out as the cause. Interactions between sex ratio manipulation in response to host size or quality and LMC have been examined theoretically (Werren 1984a; Werren and Simbolotti 1989; Taylor, manuscript), but have received little empirical attention (Werren and Simbolotti 1989).

#### Models' Assumptions

Though the qualitative patterns predicted by the sex ratio manipulation models have been demonstrated in some species of parasitoid wasps, tests of the models' assumptions are scarce. (See also "Limitations on Sex Ratio Manipulation" below.) For sex ratio manipulation in response to host size, there are data on the effect of host size and/or wasp size on the reproductive success of males relative to females for only four species. All four of these species are solitary and oviposit a greater proportion of daughters on larger hosts (van den Assem 1971; Jones 1982; King 1988; Heinz 1991). For three of the four species, the braconid *Heterospilus prosopidis*, the pteromalid *Lariophagus distinguendus*, and the eulophid *Diglyphus begini*, host size or wasp size has a positive effect on aspects of both male and female reproductive success, but it has been suggested that females are more positively affected than males (Jones 1982; van den Assem et al. 1989; Heinz 1991). In contrast, experiments with the pteromalid *Spalangia cameroni* have shown no effect of host size through wasp size on aspects of either male or female reproductive success. A greater effect of host size on female than on male reproductive success may possibly occur for *S. cameroni* through a negative effect of host size on female wasp development time (King 1988), discussed below. Clearly we need to test further the effects of host size and of wasp body size on reproductive success of males relative to females.

In explaining how sex ratio manipulation in response to host size may have been selected for, the emphasis has traditionally been on host size differentially affecting male and female reproductive success through an effect on wasp size. However, regardless of whether host size affects wasp size, there may be selection to manipulate offspring sex in response to host size. This is because a differential effect of host size on female vs. male reproductive success can occur through avenues other than just wasp size, e.g., through an effect of host size on wasp development time (King 1987). Host size may have a differential effect on the development time of males vs. females (e.g., *S. cameroni*, King 1988); or the effect on development time may be independent of sex, but decreased development time may have a greater effect on the reproductive success of one sex than the other. Decreased development time might increase a wasp's reproductive success by decreasing generation time, by decreasing the period of exposure to pre-

dation and parasitism while the wasp is developing (King 1988), or by increasing access to mates.

Determining the relative importance of parasitoid size vs. development time in selecting for sex ratio manipulation in response to host size may be difficult. Controlling for wasp sex, a positive effect of host size on parasitoid wasp size has been demonstrated in almost all species examined, with only a few exceptions (Table 2 in King 1989a; also Mackauer and Kambhampati 1988, Wright and Kerr 1988, Cronin and Gill 1989, Gunasena et al. 1989, Heinz and Parrella 1989, and Hebert and Cloutier 1990). The relationship between host size and development time of male and of female wasps has been reported for less than a dozen species of parasitoid wasps, and the results have not been consistent: for 2 species no relationship for either sex (Sandlan 1982; Liu Shu-sheng 1985); for 2 species a positive relationship for both sexes (van den Assem 1971; Podoler and Mendel 1979); for 5 species a negative relationship for both sexes (Flanders and Oatman 1982; Nechols and Kikuchi 1985; Hagvar and Hofsvang 1986; Hebert and Cloutier 1990; Allen and Keller 1991); for 1 species, no relationship for males and a negative relationship for females (King 1988) and for 1 species, no relationship for males and a positive relationship for females (Seidl and King, manuscript). Among parasitoid wasp species examined so far, there is not a consistent relationship between the presence of host-size-dependent sex ratios and the presence of a relationship of host size with either parasitoid size or parasitoid development time. Effects of host size on wasp size and development time may be difficult to separate because the two variables may not be independent (e.g., Liu Shu-sheng 1985).

Insight on the relative importance of size vs. development time might be provided by parasitoid species in which offspring delay feeding within the host until a particular host stage or size has been reached. In such species, I would expect host size at the time of oviposition and size of emerging parasitoid offspring to be independent. However, I would expect parasitoids oviposited in smaller hosts to take significantly longer to reach adulthood. Therefore, if an effect of host size on parasitoid development time can select for manipulation in response to host size, I would expect to find host-size-dependent sex ratios in these species. There are parasitoid wasp species that remain in first instar until a particular host stage is reached (e.g., Finney et al. 1947; Flanders and Oatman 1982; Avilla and Albajes 1984); however, I do not know if there are any species in which feeding by the parasitoid is delayed until the host has grown to a particular size.

Data on the assumptions of LMC models are likewise needed. For example, in the original models it was assumed that sons mate only in the patch where they emerge; that after mating, daughters disperse to new oviposition sites; and that oviposition in a patch is synchronous among mothers. Unfortunately, studies with relevant data on male and female dispersal pat-

terns and oviposition patterns in the field are lacking. In gregarious species in which mating occurs within the host, clearly there can be local mate competition (e.g., Suzuki and Hiehata, 1985). What proportion of matings take place at the site of emergence in other species is not known. Theoretically the general pattern of increasing sex ratio with more mothers present should hold even with some oviposition asynchrony and some mating after male dispersal (Nunney and Luck 1988). The rate of increase in offspring sex ratio with increasing number of ovipositing mothers is expected to be less, however.

Level of inbreeding is another parameter of LMC models for which data are usually lacking. However, again the qualitative prediction of an increase in the proportion of sons with increasing numbers of ovipositing mothers is expected even under different levels of inbreeding (Herre 1985).

The effects of changing other parameters of LMC models have also been explored, e.g., parameters such as the variance and distribution in the number of ovipositing mothers (Nishimura, manuscript; see also "Limitations on Sex Ratio Manipulation" and Godfray 1990). Such theoretical explorations should help us to decide not only what information is needed to quantitatively predict sex ratio response, but also how accurately quantitative predictions can be made with the type of information that empiricists can practically obtain.

As mentioned earlier, positive relationships between number of mothers and offspring sex ratios have traditionally been explained by LMC theory but in gregarious species may also or instead be explained by a host quality model. The assumption of this host quality model for gregarious species, that crowding has a differential effect on male and female fitness, has not been well tested. Based on Grosch (1948), Galloway and Grant (1989) suggest for *Bracon hebetor* (a gregarious species) that although small size negatively affects aspects of both male and female fitness, females are less affected than males. One way to discount the LMC or host quality model for a species is to determine experimentally that critical assumptions of one of the models are inappropriate. Another way to distinguish between LMC models and the host quality model for gregarious species is to test predictions that are specific to one or the other (e.g., Werren 1980, 1984b; King, in press; Taylor, manuscript).

### Limitations on Sex Ratio Manipulation

It is clear that in at least some species of parasitoid wasps, females manipulate their offspring sex ratios in response to environmental conditions. However, there are several potential limitations on such manipulation, including extrachromosomal factors, sperm availability, clutch size, lack of genetic variation, and behavioral constraints, which may prevent manipu-

lation or just change the specific sex ratio values produced. Natural selection models of sex ratio manipulation have generally assumed the absence of these limitations. These limitations are discussed in turn below.

Extrachromosomal factors that influence offspring sex ratio have been found in *Nasonia vitripennis* (Saul 1961; Werren et al. 1981, 1986, 1987; Skinner 1982, 1985; Nur et al. 1988). These factors cause the production of either very female-biased or very male-biased sex ratios, and so their presence affects the specific sex ratio values produced. However, as long as females are producing at least some offspring of each sex, females are expected to meet the qualitative predictions of the sex ratio manipulation models. *Nasonia vitripennis* females without extrachromosomal factors manipulate offspring sex ratio in response to number of mothers present (e.g., Werren 1983), and there is some evidence that females with a factor do also. Examining either females without any extrachromosomal factors or females with a factor (*msr* factor), eight females on four hosts produce a significantly greater proportion of sons than one female on one host (sign tests on data in Figure 5.3 of Skinner 1983,  $P < 0.01$ ).

Sperm availability can influence the specific sex ratio values females produce (females with few sperm producing more male-biased sex ratios). However, manipulation should be prevented only in the extreme and obvious case of females lacking sperm. Lack of sperm occurs if females produce offspring while they are unmated or if they run out of sperm. Sperm depletion may be less of a problem in species that will mate multiply (e.g., *Goniozus gallicola*, Gordh, 1976). Information on how commonly females go unmated or run out of sperm in nature is scarce. (But see Godfray 1988; Hardy and Godfray 1990.) The presence of females constrained to produce particular sex ratios, e.g., due to sperm limitation or to extrachromosomal factors, may also cause selection on the sex ratios of unconstrained females (Godfray 1990). However, Godfray (1990) has shown for LMC models that if LMC is strong, the effect of constrained females is predicted to be small.

Selection to produce a particular clutch size may influence the exact sex ratios that females produce (Williams 1979). For example, with a clutch size of two, females can produce only one of three sex ratios. However, females should still be able to meet qualitative predictions of adaptive sex ratio manipulation models.

Lack of the necessary genetic variation may prevent the evolution of manipulation in some species. Genetic variation in sex ratio manipulation has not been well studied, but there is some evidence of variation both within genera and within a species. *Aphidius* and *Spalangia* both contain some species that do exhibit host-size-dependent sex ratios and some species that do not (Cloutier et al. 1981; Liu Shu-sheng 1985; Wellings et al. 1986; Legner 1969; Donaldson and Walter 1984; King 1988). Within a species, genetic

variation for sex ratio manipulation has been demonstrated in *Nasonia vitripennis* (Orzack and Parker 1986; Orzack et al. 1991).

The types and location of the cues that females use to measure host size and to detect the presence of other females may constrain sex ratio manipulation. For example, if females measure host size on the basis of external dimensions (as suggested by a study on clutch size manipulation in the parasitoid wasp *Trichogramma minutum*—(Schmidt and Smith 1987), and hosts are sometimes partially buried, females may appear to make “mistakes.” As another example, in parasitizing adult hosts, *Aphidius smithi* mothers sometimes parasitize embryos within the adult host (Mackauer and Kambhampati 1988). Females that have developed on embryos produce significantly fewer offspring than females developing on adult hosts; yet mothers do not appear to manipulate offspring sex ratio in response to whether they are parasitizing an embryo or an adult. Mackauer and Kambhampati (1988) suggest that *A. smithi* mothers may simply “not perceive aphid embryos as distinct hosts.”

For sex ratio manipulation in response to number of mothers present, adaptive manipulation may be constrained by whether or not a female can detect that other females are or were present. In at least one species of parasitoid wasp, females detect the earlier presence of other females based on trace odors left on the surrounding substrate by those females (*Trissolcus grandis* [Viktorov and Kochetova 1973], but not *Nasonia vitripennis* [Wylie 1976a], *Spalangia cameroni* [King 1989b], or *Muscidifurax raptor* [King, unpubl. data]). If the odors dissipate, females may fail to increase the proportion of sons they produce. In some species, females detect the presence of other females at least in part by encounters with already-parasitized hosts (*Nasonia vitripennis* [Wylie 1966; Holmes 1972; Werren 1980], but not *Trichogramma evanescens* [van den Dijken and Waage 1987] or *Telenomus heliothidis* [Strand 1988]). In *N. vitripennis* a female's ability to determine that a host has already been parasitized depends on her ovipositing close to the previous female's oviposition site (King and Skinner 1991b). Even when a female can detect the presence or absence of other females, she still may not be able to distinguish the number of females. Failure to distinguish the number of females may result from the lack of a simple mechanism and/or from weak or no selection to make such a distinction (Herre 1987).

The failure of *N. vitripennis* females to respond to the sex ratio of the previous female's offspring, as LMC theory predicts they will (Werren 1980), also may be a behavioral constraint. There may be no simple means by which a female can determine the sex of the previous female's offspring.

## Summary

At least some parasitoid wasp species manipulate offspring sex ratio in response to environmental conditions. Most, but not all, species of parasitoid

wasps that have been examined produce a greater proportion of sons in smaller hosts, as predicted by host quality models. The more than 50 species meeting this prediction come from 13 different families and include primarily solitary species, but also some gregarious and facultatively gregarious species. Species meeting the prediction include primarily parasitoids of non-growing hosts, but also some parasitoids of growing hosts.

In addition, most, but not all, species of parasitoid wasps that have been examined produce a greater proportion of sons in the presence of other mothers than when alone, as predicted both by LMC models and by a host quality model for gregarious species. The 16 species meeting this prediction come from five different families and include both solitary and gregarious species. Most, if not all, of these solitary species parasitize clumped hosts.

Differential mortality of the sexes has been ruled out as the cause of the relationships between sex ratio and host size and between sex ratio and number of mothers for twelve and nine species, respectively. Thus, in these species, mothers are known to be manipulating their offspring sex ratios in response to environmental conditions.

In order to understand the evolution of sex ratio manipulation in parasitoid wasps, we need more empirical information regarding the assumptions of models of adaptive manipulation. Insufficient data on the assumptions of sex ratio models, including the extent to which limitations on manipulation occur, mean that quantitative predictions about sex ratio manipulation are tentative at best. Fortunately, the models' qualitative predictions appear to be somewhat robust to the assumptions. We do, however, need continued theoretical exploration of how changing the assumptions of sex ratio models affects the predictions.

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