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### ABSTRACT

Laboratory and field studies on about 100 species in sixteen families indicate that several factors can influence offspring sex ratios in parasitoid wasps. For many species, offspring sex ratio increases with one or more of the following: 1) maternal age at ovipositing or the amount of time since insemination, 2) the age of the male parent or the number of times he has copulated, 3) extreme temperature, 4) decreasing host size, age, or quality, 5) female wasp density, and 6) the number of progeny per host. Other factors which have been shown to affect offspring sex ratios in some species include: 1) number of hours since insemination, 2) genetic factors, 3) maternal size, 4) maternal diet, 5) polyembryony, 6) photoperiod and relative humidity, 7) host sex, and 8) host density.

These factors may affect offspring sex ratios through females manipulating fertilization of their eggs or through other mechanisms such as differential mortality or changes in sperm availability. Theoretical development has focused primarily on females manipulating their offspring sex ratios in response to host size and/or to female density. Host size models predict a negative relationship between offspring sex ratio and host size. These models assume that host size has a greater effect on the reproductive success of females than of males. LMC models predict a positive relationship between offspring sex ratio and female density. A major assumption of these models is that males mate primarily in their natal area. For each model, most of the species examined meet the model's general prediction. However, the models have been rigorously tested for only a few species. Such testing requires supporting data on the assumptions made and examination of alternative explanations, particularly sex ratio differences due to differential mortality.

### INTRODUCTION

The haplodiploid sex determination system of most parasitoid wasps provides females a means to control offspring sex ratio (ratio of male progeny to female progeny) because they can adjust the proportion of fertilized eggs at oviposition. Do females adjust the proportion of eggs they fertilize? What factors determine the final sex ratio of emerging wasps?

Knowing what factors influence offspring sex ratio is important for developing and testing sex ratio theories as well as for practical applications in biological control (Caltagirone, 1981; Legner et al., 1982; Legner and Badgley, 1982; Kido et al., 1983). Parasitoid wasps provision their young with food by ovipositing in or on a host, typically an insect. Upon hatching, the wasp larva feeds on the host, usually killing it prior to the wasp's pupation. Because a few males can fertilize many females, female-biased broods are beneficial in terms of biological control.

The topic of offspring sex ratios in parasitoid wasps was reviewed earlier by Flanders (1939, 1946) and Kochetova (1977). However, most current theories on this topic have been developed since then, and many additional field and laboratory studies have been done (some of these are reviewed in Charnov, 1982). In this paper I review about 100 species in sixteen families. The factors which may influence offspring sex ratio can be divided into four groups: parental characteristics, environmental characteristics, host characteristics, and factors influencing local mate competition (LMC). For each factor I give relevant species examples. I also discuss possible mechanistic and evolutionary causes of observed patterns of offspring sex ratios.

Most of the data available on offspring sex ratios of parasitoid wasps is from laboratory

studies. This is because of the difficulty of doing field studies and because of the need to rear greater proportions of females in the laboratory for release as biological control agents. However, knowing what the wasps do in nature becomes important when the wasps are released and when answering evolutionary questions. Some limitations of laboratory studies in terms of knowing what parasitoid wasps do in nature are discussed.

When statistics were not reported in a study but sufficient data were presented, I analyzed the data with nonparametric tests (Sokal and Rohlf, 1969). Pooling decisions were based on log linear analyses (Brown, 1977).

## **PARENTAL CHARACTERISTICS**

### **Delay Between Emergence and Insemination**

If a long duration between emergence and mating indicates a shortage of males in the population, selection should favor mothers which increase offspring sex ratio with increasing duration (Werren and Charnov, 1978). Mechanistically, duration between emergence and mating may affect offspring sex ratio in two ways. One, unmated females produce only sons. Mated females can produce both sons and daughters. Thus the number of offspring that females produce prior to insemination may affect their lifetime offspring sex ratios. Two, the delay between emergence and mating may affect offspring sex ratios even if virgin females do not oviposit. For Bracon hebetor (Rotary and Gerling, 1973) and for Campoletis perdistinctus (Hoelscher and Vinson, 1971), however, longer durations between emergence and mating are correlated with lower, not higher, offspring sex ratios after mating. The significance of this is not clear.

### **Number of Times a Female Has Mated**

Though single matings by females seems to be the rule in parasitoid wasps (Matthews, 1982), occasionally, females of some species mate multiply. Multiple insemination has no significant effect on the offspring sex ratios of Dahlbominus fuscipennis (Wilkes, 1963). For Macrocentrus ancylivorus, multiple insemination prior to oviposition can decrease the number of female progeny produced. In the laboratory a female M. ancylivorus may obtain up to eight spermatophores in her oviduct as a result of multiple mating. These block the passage of sperm from the spermatophores into the spermatheca. When the female begins ovipositing, the spermatophores are emitted and the female usually deposits only unfertilized eggs (Flanders, 1956). Multiple mating may be restricted to the laboratory. It is unknown whether females mate multiply in nature.

### **Maternal and Paternal Age**

For most species examined, females produce higher offspring sex ratios later in life than they do early in life (Table 1). Such increases in sex ratio may result from sperm depletion or from reduced sperm viability. Older Goniozus gallicola females produce only sons but when given the opportunity will remate and resume production of daughters (Gordh, 1976). In contrast, though older Aphytis melinus females also produce exclusively sons, they will not remate (Abdelrahman, 1974a). Whether sperm depleted females of other parasitoid wasp species remate has not been tested.

Not all species of parasitoid wasps always exhibit an increase in offspring sex ratio with

maternal age. Three species show no consistent change in offspring sex ratio with maternal age (Table 1). Experiments on two species, Anisopteromalus calandrae and Opius concolor, suggest that older females produce lower offspring sex ratios (Table 1). For O. concolor this relationship exists only when females oviposit on small hosts. One explanation is that females may prefer to oviposit sons on small hosts and daughters on large hosts (see "Host Size"). Hence, when presented only with small hosts, they may oviposit primarily sons, saving daughters in anticipation of encountering large hosts. When no large hosts are encountered for an extended period of time, females may begin to oviposit daughters (Assem et al., 1984).

In one species examined, Aphytis melinus, a positive relationship between sex ratio and maternal age exists only for large females. This result may be due to a positive relationship between female size and longevity. Because small females do not live as long as large females (Abdelrahman, 1974a), small females may never become sperm limited. Large females may live sufficiently long to outlast their sperm supplies.

The age of a female's mate also may affect her offspring sex ratio if his sperm supply diminishes with age. In the laboratory, older Dahlbominus fuscipennis males inseminate fewer females than they do when they first emerge. The females they do inseminate produce higher offspring sex ratios (Wilkes, 1963). Similarly, in at least seven other species, offspring sex ratio increases with the number of times the male has previously mated (Table 2). The time period between matings may affect this relationship. Pachycrepoideus vindemiae males exhibit sperm depletion when they mate with multiple females in rapid succession. However, they replenish their sperm supplies after about thirty minutes (Nadel and Luck, 1985).

Whether maternal and/or paternal age affects offspring sex ratios for a particular species will depend in part on whether sperm becomes limiting for females and males, respectively. To determine whether sperm depletion is likely to occur in nature or whether it is an artifact of laboratory conditions, the following information needs to be collected on wasps in the wild: longevity of both sexes, ovipositing frequency of females, and mating frequency of males.

### **Egg Order**

A female may oviposit exclusively male eggs, not only when a long time has elapsed since insemination, but also immediately after insemination (Aphidius smithi (Mackauer, 1976), Nasonia vitripennis (van den Assem and Feuth-DeBruijn, 1977), Orgilus jenniae (Flanders and Oatman, 1982)). The latter phenomenon presumably results because of time required for sperm to reach the spermatheca (Wilkes, 1965).

For at least eleven species, within any oviposition bout, females oviposit fertilized and unfertilized eggs in a particular sequence (Table 3). The sequence varies among species. Sometimes it even varies within species according to the female's ovipositing rate (e.g., Copidosoma truncatellum (Leiby, 1926; Bracon hebetor (= Microbracon hebetor) (Flanders, 1956)). It is not clear why, in an evolutionary sense, species differ in the sequence of unfertilized and fertilized eggs they produce.

### **Maternal Size**

Maternal size affects offspring sex ratio for some species of parasitoid wasps examined. In Aphytis melinus, sex ratio increases with maternal age for large but not small females (See "Maternal and Paternal Age" above). Thus lifetime offspring sex ratios are lower for small females. Similarly, medium and small Trichogramma brevicapillum females produce lower sex ratios than large females (Pak and Oatman, 1982). Unlike with Aphytis melinus though, this

pattern did not result from a maternal age effect on sex ratios. In contrast to both A. melinus and T. brevicapillum, for Telenomus fariai and Spalangia cameroni, there is no significant relationship between maternal size and offspring sex ratio (Rabinovich, 1970b; Hurlbutt, 1987a). For Nasonia vitripennis the effect of maternal size on offspring sex ratio depends on the host species. When ovipositing on flesh flies, there is no effect (S. Skinner, pers. comm.). When ovipositing on house flies, large females produce significantly lower offspring sex ratios than do small females (Wylie, 1966) ( $G = 21.13$ ,  $p < 0.001$ ). I suspect that on house flies the relationship results from differential mortality of daughters: percent survival of offspring from egg to maturity was lower for small females than for large ones.

### Maternal Diet

Maternal diet is another factor which may affect a female's offspring sex ratio. Female Bracon hebetor feeding on hosts and honey produce significantly higher offspring sex ratios than do females feeding only on hosts (Rotary and Gerling, 1973). This may be due to the increased longevity of females given honey: in this species, older females produce exclusively sons (Rotary and Gerling, 1973). Maternal diet does not seem to affect offspring sex ratios of Itoplectis conquisitor (House, 1980).

### Genetics

Offspring sex ratio has been demonstrated to be a heritable trait in several parasitoid wasp species. Artificial selection has altered sex ratio in Mastrus carpocapsae (= Aenoplex carpocapsae) (Simmonds, 1947), Caraphractus cinctus (Jackson, 1958), Dahlbominus fuscipennis (Wilkes, 1964), and Nasonia vitripennis (Parker and Orzack, 1985).

The artificially selected "sex ratio" strain of Dahlbominus fuscipennis produces only about 5% daughters as compared to the wild stock which produces about 90% daughters. The sex ratio trait is passed through females to sons and may be related to spermatozoa morphology. Both normal and "sex ratio" males produce both sinistrally coiled and dextrally coiled sperm. However, sinistrally coiled sperm seem to be incapable of fertilizing eggs (Wilkes and Lee, 1965). Unfortunately, there is no direct evidence that sex ratio strain males produce predominately sinistrally coiled sperm. However, the ratio of sinistrally to dextrally coiled spermatozoa is greater in the spermathecae of sex ratio strain females than in the spermathecae of wild stock females (Lee and Wilkes, 1965).

In Nasonia vitripennis, offspring sex ratios are influenced by nuclear genes (Parker and Orzack, 1985) as well as by at least four extrachromosomally-inherited factors (Saul, 1961 and below). Of the three extrachromosomally-inherited factors known to affect offspring sex ratios in natural populations, one factor, maternal-sex-ratio, is inherited through the mother and causes extremely female-biased broods (Skinner, 1982). Another factor, paternal-sex-ratio (Werren et al., 1981), causes a male's mate to produce only sons via the loss of paternal chromosomes in fertilized eggs (Werren and van den Assem, 1986; Skinner, 1987). The third factor, son-killer, a bacterium, is transmitted both maternally and contagiously. It affects the sex ratio by killing male embryos (Skinner, 1985; Werren et al., 1986).

### Polyembryony

For the wasp species discussed so far, little distinction has been made between the ratio of unfertilized eggs to fertilized eggs and the ratio of emerging males to emerging females. However, in polyembryonic wasp species, in which one egg gives rise to multiple offspring, the

offspring sex ratio may differ from the initial ratio of unfertilized eggs to fertilized eggs. For example, fertilized eggs of Macrocentrus ancyliivorous produce twice as many embryos as do unfertilized eggs (Flanders, 1956); and fertilized eggs of Platygaster hiemalis and P. variabilis usually produce many embryos, whereas unfertilized eggs usually produce only one embryo (Leiby, 1926). Multiple division of fertilized (female) eggs might be beneficial to females if their sperm supplies are limited. If, in these species, males usually mate before dispersing, the low production of males relative to females is also consistent with LMC theory (See section on "Factors Influencing Local Mate Competition").

## ENVIRONMENTAL CHARACTERISTICS

### Photoperiod

Photoperiod has been shown to affect offspring sex ratio of Pteromalus puparum (Bouletreau, 1976) and Campoletis perdistinctus (Hoelscher and Vinson, 1971). The effect is probably not due to differential mortality of the sexes, at least for P. puparum: female fecundity was the same for both photoperiods examined (Bouletreau, 1976).

### Temperature and Relative Humidity

The effect of temperature on offspring sex ratio has been examined in at least fourteen species of parasitoid wasps (Table 4). Usually, offspring sex ratios are highest at extreme temperatures. A temperature effect may occur when the parent wasps are exposed as larvae, pupae, or adults. It also may occur when the offspring are exposed. Not all species are affected at all stages (Euchalcidia caryobori) (Hanna, 1935), and the duration of exposure may influence the effect (Muscidifurax raptor (DeBach, 1943), Dahlbominus fuliginosus (Wilkes, 1959), M. raptor and Spalangia endius (Legner, 1976)). Mechanistically, extreme temperatures may affect offspring sex ratios by 1) sterilizing males (E. caryobori (Hanna, 1935), D. fuliginosus (Wilkes, 1959)); 2) increasing rate of movement to the point that mating is hindered (Aphidius testaceipes, Praon aguti (Sekhar, 1957); D. fuliginosus (Wilkes, 1963)); 3) decreasing the rate of movement to the point that mating is rare (D. fuliginosus (Wilkes, 1963)); 4) incapacitating sperm (Flanders, 1956; Wilkes, 1963); 5) causing the rate of oviposition to exceed the rate of sperm discharge (Flanders, 1946); 6) causing differential mortality of male and female offspring (D. fuliginosus (Wilkes, 1959)).

Relative humidity is another environmental factor which may affect offspring sex ratio (Table 4). Its effect varies among species, and the effect may change with temperature (e.g., M. zaraptor (Legner, 1977)).

Temperature-induced and relative humidity-induced changes in sex ratio which are found in the laboratory are not necessarily adaptive responses. In nature, wasps may avoid such extreme temperatures and humidities, e.g., by microhabitat selection.

Alternatively, variations in temperature, humidity, and photoperiod may affect offspring sex ratio because they are used as seasonal cues. It may be adaptive for females to vary offspring sex ratio seasonally if the relative reproductive success of males vs females differs seasonally (Werren and Charnov, 1978). Seasonal variation in offspring sex ratios has been observed in Tetrastichus galactopus (Nealis, 1983) and Pteromalus puparum (Takagi, 1987).

## HOST CHARACTERISTICS

The relationship between host size and offspring sex ratios of parasitoid wasps has been explored mathematically by Charnov et al. (1981) (see also Charnov, 1979). Their host size model predicts that mothers will vary the sex of their offspring according to host size if host size differentially affects the reproductive success of sons vs daughters. Such host size effects can be partitioned into two components: the relationship between host size and final offspring size and the relationship between offspring size and reproductive success.

Females should lay primarily daughters in large hosts and sons in small hosts if developing in or on large hosts confers more to the reproductive success of females than of males. At the extremes this may occur in two ways. One, a given increase in host size results in a greater increase in wasp size for females than for males, and a given increase in wasp size results in the same or greater increase in reproductive success for a female as for a male. Two, a given increase in host size results in the same increase in the size of the emerging wasp regardless of the wasp's sex; but a given increase in wasp size results in a greater increase in reproductive success for females than for males.

The relationship between host size and sex of emerging wasp(s) has been examined for many species of parasitoid wasps (see below); however, few studies have examined, for males relative to females, the relationships between host size and wasp size and between wasp size and lifetime reproductive success.

### Effect of Host Size on Wasp Size

A positive correlation between host size and wasp size has been demonstrated for some species of solitary wasps. (In solitary species, only one wasp develops successfully per host, whereas in gregarious species more than one develops per host.) For the solitary species Hyposoter exiguae (Jowyk and Smilowitz, 1978) and Roptrocercus xylophagorum (Samson, 1984), the percent increase in size from small to large hosts is greater for females than for males. However, for Apanteles rubecula and for Spalangia cameroni in the laboratory, the percent increase is independent of sex (Nealis et al., 1984; Nealis, pers. comm.; Legner, 1969; Hurlbutt, 1987a). In contrast to these examples, the size of Spalangia endius females (Donaldson and Walter, 1984) and probably males (Donaldson, pers. comm.) does not vary with host size.

For gregarious species the relationship between host size and size of emerging wasps is complicated by the number of wasps developing per host. If a female of a gregarious species produces the same number of offspring in a large host as in a small host, then offspring from a large host are expected to be of greater individual size than offspring from a small host. However, if a female lays more eggs in a large host than in a small host, as is often the case (Table 5), then the wasp offspring from large hosts could be the same size or smaller than those from small hosts. For the gregarious species Pteromalus puparum there is no correlation between host size and weight of emerging male or female wasp offspring (Lasota and Kok, 1986a). For Aphytis melinus and Aphytis lingnanensis host size and female wasp size are positively correlated. Male wasps were not studied (Opp and Luck, 1986).

### Effect of Wasp Size on Wasp Reproductive Success

There is some information on the relationship between wasp size and reproductive success for both solitary and gregarious species. Large size may be advantageous for both males and females. For females, large size usually correlates with increased offspring production (Table 6). Large size may also improve a female's ability to obtain hosts (Lariophagus distinguendus (van

den Assem, 1971), *Brachymeria intermedia* (Rotheray et al., 1984)). For males, large size may improve the ability to obtain effective matings (*Nasonia vitripennis* (van den Assem, 1976; Grant et al., 1980)) and may increase sperm production. Large size may also increase longevity (for females: *Nasonia vitripennis* (Wylie, 1966), *Aphytis melinus* (Abdelrahman, 1974a), *Coccygomimus turionellae* (Sandlan, 1979); for females and males: *C. cinctus* (Jackson, 1966), *G. himalayensis* (Shiga and Nakanishi, 1968a), *Lariophagus distinguendus* (van den Assem, 1971; Charnov et al., 1981), *Trichogramma evanescens* (Waage and Ng, 1984), but not *Spalangia cameroni* (Hurlbutt, 1987a).

There are also some advantages to being small, such as reduced development time and hence earlier emergence. This may be more important for males than for females because males mate multiply whereas females usually mate only once (Matthews, 1982). By emerging early a male may increase the number of virgin females he can potentially fertilize. This is especially true for species in which males defend emergence sites, and in which there is a prior ownership advantage (e.g., *Asolcus basalus* (Wilson, 1961)).

If male development is faster in small than in large hosts, selection may favor females laying sons primarily in small hosts. Looking at five species of pupal parasitoids, Legner (1969) found that male development was faster in small than in large hosts, but only at some host densities. In contrast, for *Orgilus jenniae*, a larval parasitoid, both males and females develop more quickly in large than in small hosts (Flanders and Oatman, 1982). For *Spalangia cameroni*, females develop more quickly in large than in small hosts, but male development time is independent of host size (Hurlbutt, 1987a). There are other data on the relationship between development time and host size; but usually not for males and females separately. Thus when shorter development times of wasps in smaller hosts is reported, more than one explanation is possible. It may be that males take less time to develop on small than on large hosts. Alternatively, it could be because males generally have shorter development times than females, regardless of host size; and a greater percentage of males are oviposited in small than in large hosts.

Determining the relative effect of host size on the reproductive success of male vs female wasps is difficult. Laboratory experiments only provide estimates of components of reproductive success. The small size and mobility of many species of parasitoid wasps makes it difficult to look at their reproductive success in the field.

Under the host size model, mothers control sex ratio by ovipositing either fertilized or unfertilized eggs according to host size. However, a relationship between host size and offspring sex ratio can also occur if one, there is differential mortality of developing wasps by sex and two, mortality varies with host size. In most species of parasitoid wasps, females are larger than males (Hurlbutt, 1987b) and so may have greater energy requirements. Thus in a small host a female larva may be more likely to starve than would a male larva.

### **Effects of Host Size, Age, Sex, and Species on Wasp Sex Ratio**

Empirically, host size has been shown to influence offspring sex ratios for many species of parasitoid wasps. For most species studied, the sex ratio of wasps emerging from large hosts is lower than from small hosts, though there are exceptions (Table 7).

Host age (or instar) is sometimes used by scientists as a measure of host size because of a positive correlation between the two variables. For most species which have been examined, offspring sex ratio decreases with increasing host age (Table 8). For *Trichogramma japonicum* and *T. semifumatum*, the lower sex ratio of wasps emerging from older hosts than from younger ones is not due to the older hosts being larger. Both species are egg parasitoids, and the host

eggs probably do not grow as they age. For another egg parasitoid, Telenomus fariai, there is no consistent relationship between host age and offspring sex ratio (Rabinovich, 1970a). In contrast to the above examples, for Nasonia vitripennis, the sex ratio of wasps emerging from older hosts is higher than from younger hosts (Wylie, 1963). However, as with the egg parasitoids, host age should not be positively correlated with host size: hosts are parasitized when in the pupal stage. For N. vitripennis the increase in sex ratio with increasing host age may result from superparasitism (an excess of wasps oviposited on each host) causing differential mortality of daughters. Superparasitism is greater in old than in young hosts (Wylie, 1963).

Effects of host sex on offspring sex ratio probably result from differences in host size. For at least four parasitoid wasp species the sex ratio of wasps emerging from male hosts is higher than from female hosts: Apechthis ontario and Phaeogenes hariolus (McGugan, 1955); Exenterus amictorius and E. nigrifrons (Lyons, 1977) ( $G = 17.84$ ,  $p < 0.001$  and  $G = 74.26$ ,  $p < 0.001$ ). In all these experiments, the male hosts were smaller than the female hosts. In contrast to these four wasp species, when Gregopimpla himalayensis parasitizes Maracosoma neustria testacea, host sex does not affect the wasp sex ratio though host males are smaller than host females (Shiga and Nakanishi, 1968a). Similarly, when Pteromalus puparum parasitizes Artogeia rapae, host sex does not affect the wasp sex ratio though host males are larger than host females (Lasota and Kok, 1986a,b). For at least P. puparum, however, there was no significant effect of host size on wasp size for either male or female wasps (Lasota and Kok, 1986a).

Other investigators have compared offspring sex ratios using different host species of various sizes. For ten of twelve parasitoid wasp species studied, lower sex ratios are associated with larger host species (Table 9). For all ten of these species, the relationship between host species and offspring sex is not obligatory. However, for some species in the family Aphelinidae the relationship is obligatory (Walter, 1983). These species are referred to as heterotrophic parasitoids (Walter, 1983); the mother oviposits only fertilized eggs in homopteran hosts and only unfertilized eggs in lepidopteran eggs. Thus the relative abundance of the two types of hosts may influence the wasp's offspring sex ratio. In other species, referred to as heteronomous hyperparasitoids (Walter, 1983), the mother oviposits fertilized eggs in unparasitized homopteran hosts and unfertilized eggs in homopteran hosts containing the larvae or pupae of chalcidoid wasps. The offspring sex ratios of heteronomous hyperparasitoids may be affected by host density and by the density of other chalcidoid wasps. When host densities are low and the density of other chalcidoid wasps is high, an ovipositing female will encounter a large proportion of parasitized hosts and so will produce a more male-biased offspring sex ratio. The evolutionary significance of heterotrophy and heteronomous hyperparasitism is not clear.

Relationships between offspring sex ratio and host size as measured by host age, sex, or species may be due to quantitative or qualitative differences in hosts. Qualitative differences include differences in nutritional makeup and in length or rate of development. If host quality differentially affects reproductive success of male and female wasps, mothers should oviposit the more positively affected sex in higher quality hosts. Evidence that host quality may affect offspring sex ratio comes from Pachycrepoideus vindemiae (van Alphen and Thunnissen, 1983) and Aphytis melinus (Abdelrahman, 1974b).

It is unclear why some species are exceptions to the pattern of increasing sex ratio with decreasing host size. For example, Macrocentrus ancylivorus is a solitary species and females tend to be larger than males; yet a greater percentage of females emerge from small hosts than from large hosts (Finney et al., 1947). Perhaps large hosts are more often superparasitized than small hosts, and there is differential female mortality in superparasitized hosts. Muscidifurax

raptor is also solitary, and females tend to be larger than males (Legner, 1976); yet the sex ratio of wasps emerging from small and large hosts is the same. This is not a result of differential mortality (Wylie, 1967). Gregopimpla himalayensis females are also larger than males. The species is gregarious, but there is no significant difference in the number of eggs laid on small (male) vs large (female) hosts (Shiga and Nakanishi, 1968a); therefore, the wasps from large hosts are probably larger than those from small hosts. Nevertheless, there is no significant relationship between host size and the sex ratio of emerging wasps.

### **Manipulation vs Differential Mortality**

As mentioned earlier, a relationship between sex ratio and host size may result from selective oviposition by mothers or from differential mortality. Few studies address this distinction. Of the more than forty studies in Tables 7, 8, and 9, in which an effect on offspring sex ratio was demonstrated, for only eight studies was differential mortality ruled out as a causal factor: 1) and 2) In Tiphia popilliavora, the same sex ratio of wasps was obtained from wasp eggs transferred from third instar hosts to second instar hosts as from eggs laid directly on third instars (Brunson, 1938). In Aphytis lingnanensis immature wasps from both small and large hosts were transferred to large hosts to develop (Luck and Podoler, 1985). 3) and 4) In Dolichomitus sp. (Kishi, 1970) and in Lariophagus distinguendus (van den Assem, 1971) mortality was too low to have caused the observed differences in sex ratio among different-sized hosts. 5) and 6) In Coccygomimus turionellae and Spalangia cameroni, there was no difference between the number of wasps emerging from hosts parasitized by virgin females (produce only sons) and from hosts parasitized by mated females (produce sons and daughters) (Sandlan, 1979; Hurlbutt, 1987a). 7) and 8) In Heterospilus prosopidis (Charnov et al., 1981; Jones, 1982), and in Leiophron uniformis (Debolt, 1981), host mortality did not consistently increase with decreasing host size.

In these solitary species for which differential mortality has been ruled out, females are selectively ovipositing fertilized eggs in large hosts and unfertilized eggs in small hosts. Further support for such maternal control comes from experiments on Coccygomimus turionellae (Aubert, 1961 in Sandlan, 1979). Hosts of different sizes were hidden in large or small artificial cocoons. Regardless of actual host size, primarily female wasps emerged from large cocoons and male wasps from small cocoons.

### **How Females Judge Host Size**

For species in which females vary offspring sex relative to host size, is host size evaluated on a relative or absolute basis (Charnov et al., 1981; Jones, 1982)? In other words, will medium-sized hosts be considered large when just medium and small hosts are present but considered small when just medium and large hosts are present? Judging host size on a relative basis allows a female to produce a given offspring sex ratio independent of changes in the distribution of available host sizes. How host size is judged may depend on the amount of temporal variation in the host size distribution. If the distribution is essentially constant across wasp generations, the ability to judge host size on a relative basis may not confer a reproductive advantage. How females judge host size has been examined for only a few species, and the results have not been consistent. For Pimpla instigator (Chewyreu, 1913 in Clausen, 1939), Lariophagus distinguendus (van den Assem, 1971; Charnov et al., 1981), and Spalangia cameroni (Hurlbutt, 1987a), ovipositing females judge host size on a relative basis. However, for Heterospilus prosopidis, host size seems to be judged primarily in absolute terms (Charnov et al., 1981; Jones, 1982).

## FACTORS INFLUENCING LOCAL MATE COMPETITION (LMC)

### LMC Theory

Three interrelated factors may affect offspring sex ratios of parasitoid wasps: female wasp density, the number of times an individual host is parasitized, and host density. Local mate competition (LMC) theory (Hamilton, 1967) is one way of relating these factors to variation in offspring sex ratios. (See Charnov, 1982 for a recent review; Frank, 1986 for additional LMC theory references.) This theory predicts that isolated females should produce primarily daughters with only enough sons to inseminate those daughters. The reasoning is that if a female is not near other ovipositing females, she will pass on the same number of genes regardless of which son mates (assuming all her sons are equally fit). If she produces more sons than are required to provide enough sperm for her daughters, her sons will just be competing among themselves for mates; and she will have wasted energy that she could have used to produce daughters. Competition among sisters for mates is not considered a problem because females usually only mate once, whereas males mate many times (Matthews, 1982). Thus females are considered to be the limiting sex. When more than one ovipositing female is present, females should lay more sons. A female's sons will no longer be competing just among themselves but will be competing with nonsibling males as well. In this situation, the more sons a female produces, the greater the probability that one of her sons, and not some other female's son, will inseminate a given female. As the number of ovipositing females increases, the offspring sex ratio should asymptotically approach a value less than or equal to one, depending on the level of inbreeding (Herre, 1985).

LMC theory was originally couched in terms of the number of female wasps contributing offspring in a given patch. However, it can also be discussed in terms of superparasitism and host density. The term superparasitism refers both to one female ovipositing repeatedly in a single host and to more than one female ovipositing in a single host. Though both types of superparasitism may affect wasp sex ratios, only the latter type is relevant to LMC theory; and it is relevant only when the wasp is a gregarious species. Because parasitoid wasps usually mate immediately after emergence (Flanders, 1946; Matthews, 1982), in gregarious species most matings are expected to occur between individuals emerging from the same host. If a female oviposits in an unparasitized host and no other females subsequently oviposit in that host, there will be mate competition among the brothers. If a female oviposits in a previously parasitized host, her sons will be competing not only with brothers but also with other males. Thus females should lay a greater percent of sons in parasitized hosts than in nonparasitized hosts (Suzuki and Iwasa, 1980; Werren, 1980a). Increasing female density relative to host density is predicted to affect offspring sex ratio because the number of hosts which are parasitized by more than one female should increase.

The relative number of offspring laid by the first vs second female also should affect the sex ratio produced by the second female (Werren, 1980a,b; Suzuki and Iwasa, 1980). As the ratio of second female's offspring to first female's offspring increases, the second female's offspring sex ratio should decrease. Otherwise, competition among her sons will increase as the ratio of the second female's sons to the first female's daughters increases. There is some experimental evidence of such a change in offspring sex ratio for *Nasonia vitripennis* (Werren, 1980a but see Orzack, 1986).

### Superparasitism

Showing that density of female wasps, superparasitism, or host density correlates with the expected sex ratio bias is not a complete test of LMC theory. The sex ratio bias could also result from differential mortality associated with superparasitism. Superparasitism may result in the death of some or all of the wasp offspring either through a host reaction (e.g., encapsulation of the "extra offspring" (Puttler, 1961)), through starvation, or through aggression among wasp larvae (Chow and Mackauer, 1984). If mortality is greater in superparasitized hosts than in singly parasitized hosts and if there is differential mortality of the sexes, superparasitism will shift offspring sex ratios toward the sex suffering less mortality. In some species there is differential female mortality: Bracon gelechia (Narayanan and Subba Rao, 1955); B. hebetor (Rotary and Gerling, 1973); Trichogramma chilonis in hosts parasitized by two females, though not in hosts parasitized by only one female (Suzuki et al., 1984). In some species there is differential male mortality: Psuedeucoila bochei (Jenni, 1951 in Jackson, 1966); Aphytis melinus (Abdelrahman, 1974a). In other species there is no differential mortality by sex: Muscidifurax raptor, Spalangia cameroni (Wylie, 1971), Bracon lineatellae (= Habrobracon lineatellae) (Laing and Caltagirone, 1969).

Laboratory experiments which demonstrate differential mortality of the sexes in superparasitized hosts are relevant to natural situations only when rates of superparasitism are at natural levels. Rates tend to be high in experiments when ovipositing wasps are confined with few hosts for long periods. However, this problem can be alleviated by using containers which allow the wasps to leave the hosts at will (Werren, 1983), by increasing the number of hosts or by decreasing the duration of host exposure.

Another way in which superparasitism may affect offspring sex ratio is related to the host size model (see section on "Host Characteristics"). Though the host size model was designed for solitary species, it can also be applied to gregarious species when a wasp's size is related to the size of the host from which it emerged. Wasps emerging from superparasitized hosts are smaller than those emerging from singly parasitized hosts (e.g., Trichogramma evanescens (Chacko, 1969), Tetrastichus hagenowii (Narasimham, 1984), Nasonia vitripennis (Werren, 1984b), Ptecomalus puparum (Takagi, 1985), Anaphes sordidatus (Collins and Grafius, 1986)). If the greater sex ratio in superparasitized vs singly parasitized hosts occurs only when the superparasitism is by more than one female, LMC theory is the best explanation. However, when the pattern occurs regardless of whether the superparasitism is by one or by more than one female, further experiments are needed to show whether the host size model or differential mortality is the best explanation.

### **Female Density**

Several studies have examined how density of female wasps, superparasitism, and host density affect offspring sex ratios. For eleven of thirteen species studied, a greater density of female wasps results in a greater offspring sex ratio (Table 10). For Trissolcus grandis, this effect of the presence of other females on offspring sex ratios persists even after the other females have been removed (Viktorov, 1968), and the effect can be induced just by trace odors of other females (Viktorov and Kochetova, 1973). This is not true for Nasonia vitripennis (Wylie, 1976a) and has not been looked at in other species.

Evidence that a positive relationship between female wasp density and offspring sex ratio may sometimes result from superparasitism associated with differential female mortality comes from Trichogramma evanescens, T. japonicum and Tetrastichus hagenowii. For these species, increasing the female density increases the number of offspring per host. For Trichogramma

evanescens, host mortality--and thus, presumably, wasp offspring mortality--increases (Salt, 1936); for Trichogramma japonicum (Kuno, 1962) and Tetrastichus hagenowii (Narasimham, 1984), mortality of the wasp offspring increases. In all three species it is not known whether the mortality is differential with respect to sex.

Unlike most other species examined (Table 10), Bracon hebetor shows no consistent increase in offspring sex ratio as female density increases (Reinert and King, 1971). However, female densities used in this study--50, 100, 150...400-- are much higher than in the other studies. According to LMC theory, the rate of change in sex ratio will decrease with increasing number of foundresses. From a density of 50 to 400 foundresses, the percent of female offspring is expected to decrease by only 1.1% (Hamilton, 1979). This small a change would not be detected in B. hebetor.

### Number of Offspring Per Host

Further evidence that superparasitism can affect offspring sex ratios comes from species for which a greater number of offspring per host results in a greater offspring sex ratio (Table 11). For Bracon gelechiae and B. hebetor, the increase in the sex ratio of wasps emerging from superparasitized hosts probably results from differential mortality of females. For both species, percent mortality increases as the number of offspring per host increases (Narayanan and Subba Rao, 1955; Benson, 1973). Furthermore, artificially spreading the eggs of B. hebetor across the host's body eliminates the relationship between the number of offspring per host and their mortality. It also eliminates the relationship between the number of offspring per host and the sex ratio of emerging wasps (Benson, 1973). In contrast, the positive relationship observed in Gregopimpla himalayensis does not result from differential mortality (Shiga and Nakanishi, 1968b).

For Trichogramma lutea, when only one parasite develops per host, it is usually a female. When two to five develop per host, there is a negative relationship between offspring sex ratio and the number of parasites developing per host, probably because females usually lay one unfertilized egg and the rest fertilized eggs (Kfir, 1982).

In contrast to the above examples, for Nasonia vitripennis and Goniozus emigratus the number of wasps developing in each host does not affect the sex ratio of the emerging wasps (Table 11). Larvae within a host were all from one female; therefore, LMC theory predictions are not relevant. The host size model would apply only if wasp size varied with host size. More eggs were laid in larger hosts, but no data were given on how wasp size was affected (Holmes, 1970 in 1972; Green et al., 1982).

Nasonia vitripennis females can recognize when a host has already been parasitized though this ability may be imperfect (Orzack, 1986). When ovipositing on previously parasitized hosts, some genotypes increase the proportion of sons laid (Wylie, 1966; Holmes, 1972). The magnitude of increase varies genotypically (Orzack and Parker, 1986). The increase in percent sons laid on parasitized vs unparasitized hosts occurs even when the host was previously parasitized by a competing species (Wylie, 1973). This does not fit with LMC theory. However, females may be unable to distinguish between hosts which have been parasitized by conspecifics and hosts parasitized by other species. An alternative explanation is the host size model. Unlike for N. vitripennis, for Trichogramma chilonis the sex ratio of eggs laid by lone females is not significantly different in unparasitized hosts and hosts already parasitized by one female (Suzuki et al., 1984).

## Host Density

The relationship between host density and offspring sex ratio is not consistent across species or even within species across studies (Table 12). For *Gryon atriscapus* and *Trichogramma evanescens* the negative relationship between offspring sex ratio and host density may be because females tend to lay male eggs first in an oviposition bout and then lay primarily female eggs for a while (Waage and Ng, 1984). Thus the shorter the oviposition bout (as is expected at low densities), the greater the offspring sex ratio. Jackson (1958) suggested another explanation, that rapid ovipositing at high host densities, e. g., *Spalangia endius* (Legner, 1967), may stimulate the spermatheca to release sperm. However, available data do not support this explanation. Offspring sex ratio does not change significantly with host density for *S. endius* (Table 12). Furthermore, rate of ovipositing does not affect offspring sex ratios, at least for *Lariophagus distinguendus* (van den Assem, 1971).

Indirect evidence that host density affects offspring sex ratios of parasitoid wasps comes from studies in which females are deprived of hosts for long periods. Presumably, such deprivation should simulate low host density. For *Caraphractus cinctus*, females deposit more female eggs when hosts are provided in rapid succession than when hosts are only provided intermittently (Jackson, 1958, 1966). In contrast, for *Coccygomimus turionellae* the offspring sex ratio decreases as the timespan over which the females are without hosts increases (Sandlan, 1979). Likewise, *Muscidifurax zaraptor* females deprived of hosts for 18 hours produce significantly lower offspring sex ratios than do females not deprived of hosts (Wylie, 1979).

## INTERACTIONS AMONG FACTORS

For many of the factors I have discussed, the effect on offspring sex ratio may vary depending on the state of other factors. The interaction between host size (or quality) and LMC has been considered theoretically (Werren, 1984a). As discussed in previous sections, there is some empirical evidence of an interaction between the following factors in regards to their effects on offspring sex ratios: 1) maternal age and size, 2) maternal age and host size, 3) host size and the habitat of the wasp population, 4) host size and density, 5) host age and whether or not hosts are superparasitized, and 6) wasp genotype and whether or not hosts are superparasitized.

Interactions offer an explanation for the differences among studies as to the effect of a given factor on offspring sex ratio. For example, studies on host size have not all used the same host density. Thus, if there is an interaction between host size and host density, the effect of host size on offspring sex ratio may vary among studies.

## CONCLUSIONS

Many factors influence the offspring sex ratio a female parasitoid wasp produces. The relationship between each factor and offspring sex ratio is not consistent across all species. However, for most factors some generalizations can be made. A female's offspring sex ratio usually increases with 1) her age at ovipositing or the amount of time since insemination, 2) the age of her mate or the number of times he has copulated, 3) extreme temperatures, 4) decreasing host size, age, or quality, 5) the number of other female wasps present, and 6) the number of progeny per host. Other factors which have been shown to affect offspring sex ratios in at least some species of parasitoid wasps include: 1) closeness to the time of insemination on a short time scale, 2) genetic factors, 3) maternal size, 4) maternal diet, 5) polyembryony, 6) photoperiod and relative humidity, 7) host sex, and 8) host density.

It is important to keep in mind that most of the data reviewed come from laboratory studies,

so caution must be exercised in extrapolating the results to what wasps do in nature. Hopefully, future studies will relate lab results to natural situations. In natural environments do males live long enough and mate frequently enough to run out of sperm? Do females live long enough and encounter hosts frequently enough to deplete the sperm supplies in their spermathecae? How prevalent is superparasitism? Do females vary offspring sex ratios seasonally? Are the densities of female wasps and of hosts used in laboratory studies representative of natural densities?

Another area which needs to be addressed in future studies is the mechanism by which each factor affects offspring sex ratios. In particular, are differences in offspring sex ratios a result of differential mortality or of female ovipositional behavior? Differential mortality has been ruled out in only a small fraction of studies.

Further testing of sex ratio models is also needed. Though there is empirical support for the predictions of Charnov et al.'s (1981) host size model, more data on the assumptions of the model are needed. What is the effect of host size both on wasp size and on wasp reproductive success for males relative to females? For species studied in relation to female density, superparasitism, and host density, an unsolved question is whether the relationship between each factor and offspring sex ratio is best explained by LMC, by the host size model, by differential mortality, or by some other model.

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TABLE 1

The relationship between offspring sex ratio and maternal age or time since insemination. A "+" indicates a positive relationship; a "-", a negative relationship; "nd", a nondirectional relationship; and "none", no relationship. When statistical analyses were presented or when sufficient information was provided for me to analyze the data statistically, S ( $P < 0.05$ ) or NS ( $P > 0.05$ ) is indicated.

Wasp Species	Relationship	Reference
Anisopteromalus calandrae		van den Assem et al., 1984
ovipositing on:		
only young (small) hosts	- S *1	
only old (large) hosts	- S *2	
young and old hosts (y:o)		
15:85	NS *3	
45:55	nd S *4	
55:45	NS *5	
70:30	nd S *6	
85:15	NS *7	
Aphidius nigripes	+ S	Cloutier et al., 1981
A. testaceipes	+ S *8	Sekhar, 1957
A. urticae	+ S	Dranfield, 1979
Aphytis melinus		Abdelrahman, 1974a
small females	none	
large females	+	
Brachymeria intermedia	S *9	Barbosa and Frongillo, 1979
Bracon hebetor	+	Rotary and Gerling, 1973
B. lineatellae (=Habrobracon lineatellae)	+	Laing and Caltagirone, 1969
Chrysocharis laricinellae	+	Quednau, 1967
Coccygomimus turionellae	+ S	Sandlan, 1979
Dahlbominus fuscipennis (=D. fuliginosus)	NS *10	Wilkes, 1963
Dibrachys boarmiae	+ S *11	Guelel, 1982
Euplectpus laphygmae	none	Gerling and Limon, 1976
Glyptapanteles flavicoxis	+ S	Cui et al., 1986
Goniozus emigratus	+	Gordh and Hawkins, 1981
Leptopilina bouvardi	+	Kopelman and Chabora, 1986

Muscidifurax zaraptor	+ S	Coats, 1976
Nasonia vitripennis	+	Velthuis et al., 1965
	+	Legner and Gerling, 1967
Opius concolor		Avilla and Albajes, 1984
ovipositing only on:		
young (small) hosts	- S	
old (large) hosts	NS	
Orgilus jenniae		Flanders and Oatman, 1982
Praon aguti	+ S *12	Sekhar, 1957
Roptrocercus xylophagorum	none	Samson, 1984
Spalangia cameroni	+	Legner and Gerling, 1967;
	+	Hurlbutt, 1987a
NS		Moon et al., 1982
Telenomus calvus	+	Orr et al., 1986
T. remus	+	Schwartz and Gerling, 1974
Trichogramma japonicum	+	Vu Quang Con, 1986
T. minutum	+ S	Houseweart et al., 1983

\*1  $G = 127.12$ ,  $p < 0.001$ ;  $r_s = -0.79$ ,  $p < 0.01$

(data from Table 1 in van den Assem et al., 1984)

\*2  $G = 31.74$ ,  $p < 0.001$ ;  $r_s = -0.58$ ,  $p < 0.05$

(data from Table 1 in van den Assem et al., 1984)

\*3  $G = 3.89$ ,  $p = 0.87$ ;  $r_s = -0.52$ ,  $p > 0.05$

(data from Table IV in van den Assem et al., 1984)

\*4  $G = 19.89$ ,  $p = 0.01$ ; however, the relationship is nondirectional:  $r_s = 0.20$ ,  $p > 0.05$

\*5  $G = 5.87$ ,  $p = 0.66$ ;  $r_s = -0.20$ ,  $p > 0.05$

\*6  $G = 15.70$ ,  $p = 0.05$ ; however the relationship is nondirectional:  $r_s = 0.20$ ,  $p > 0.05$

\*7  $G = 8.45$ ,  $p = 0.39$ ;  $r_s = 0.05$ ,  $p > 0.05$

\*8  $G = 58.23$ ,  $p < 0.001$  (combining last 4 days to remove zeros)  
 $r_s = 0.79$ ,  $p < 0.05$

\*9  $G = 7.12$ ,  $p = 0.03$ ; a posteriori G-tests (Sokal and Rohlf, 1969) show that the sex ratio increased from week 2 to week 1 to week 6, but only weeks 2 and 6 differed significantly at

the alpha = 0.05 level.

\*10  $G = 5.24$ ,  $p = 0.51$

\*11  $G = 1782.38$ ,  $p < 0.001$  (combining last 3 days to remove zeros)  
 $r_s = 1.00$ ,  $p < 0.01$

\*12  $G = 63.04$ ,  $p < 0.001$  (combining last 4 days to remove zeros)  
 $r_s = 0.71$ ,  $p < 0.05$

TABLE 2

The relationship between the number of times a male has mated and his mate's offspring sex ratio. Symbols explained in Table 1.

Wasp Species	Relationship	Reference
<i>Aphidius matricariae</i>	+ S *1	Vevai, 1942
<i>A. smithi</i>	+	Wiackowski, 1962
<i>A. testaceipes</i>	+ S *2	Sekhar, 1957
<i>Aphytis lingnanensis</i>	+ S	Gordh and DeBach, 1976
<i>Pachycrepoideus vindemiae</i>	+ S *3	Nadel and Luck, 1985
<i>Praon aguti</i>	+ S *4	Sekhar, 1957
<i>P. palitans</i>	+	Schlinger and Hall, 1960
<i>Spalangia cameroni</i>	+ S	Hurlbutt, 1987a

\*1  $G = 121.43$ ,  $p < 0.001$   $r_s = 0.74$ ,  $p < 0.01$

\*2  $G = 106.16$ ,  $p < 0.001$ ;  $r_s = 0.75$ ,  $p < 0.01$

\*3  $G = 4168.02$ ,  $p < 0.001$ ;  $r_s = 1.00$ ,  $p < 0.01$

\*4  $G = 98.96$ ,  $p < 0.001$ ;  $r_s = 0.79$ ,  $p < 0.01$

TABLE 3

Species which exhibit a sequence effect of unfertilized and fertilized eggs within a single period of ovipositing.

Wasp Species	Reference
<i>Anisopteromalus calandrae</i>	Waage, 1982a
<i>Anthrenus fuscus</i>	Mertins, 1985
<i>Bracon hebetor</i>	Flanders, 1956
<i>Cephalonomia tarsalis</i>	Powell, 1938
<i>Copidosoma truncatellum</i>	Leiby, 1926
<i>Gryon atriscapus</i>	Waage, 1982b
<i>Heterospilus prosopidis</i>	Waage, 1982a
<i>Laelius pedatus</i>	Mertins, 1980
<i>L. utilis</i>	Mertins, 1985
<i>Trichogramma chilonis</i>	Suzuki et al., 1984
<i>T. evanescens</i>	Waage and Ng, 1984
<i>T. sp.</i>	Flanders, 1939, 1946

TABLE 4

Wasp species in which the effect of temperature (T) and/or relative humidity (RH) on offspring sex ratios has been examined.

Wasp species	Factor	Reference
<i>Agathis gibbosa</i>	T, RH	Odebiyi and Oatman, 1977
<i>A. unicolor</i>	T, RH	Odebiyi and Oatman, 1977
<i>Aphytis lingnanensis</i>	T	DeBach and Argyriou, 1966
<i>A. melinus</i>	T	DeBach and Argyriou, 1966; Hoffman and Kennet, 1985
<i>Camponotus perdistinctus</i>	T	Hoelscher and Vinson, 1971
<i>Euchalcidia caryobori</i>	T	Hanna, 1935
<i>Hyposoter exiguae</i>	T	Browning and Oatman, 1981
<i>Microplitis brassicae</i>	T	Browning and Oatman, 1985
<i>Muscidifurax raptor</i>	T, RH	DeBach, 1943; Legner, 1976, 1977
<i>M. zaraptor</i>	T, RH	Legner, 1976, 1977
<i>Nasonia vitripennis</i>	T	DeBach, 1943
<i>Spalangia cameroni</i>	T, RH	Legner, 1977
<i>S. endius</i>	T, RH	Legner, 1976, 1977
<i>Trissolcus grandis</i>	T	Kochetova, 1977

TABLE 5

The relationship between the number of wasps developing per host and host size. Symbols explained in Table 1.

Wasp Species	Relationship	Reference
<i>Aphytis melinus</i>	+	Abdelrahman, 1973
<i>Dahlbominus fuscipennis</i>	+ S	Wilkes, 1963
<i>Goniozus emigratus</i>	+ S +	Gordh and Hawkins, 1981 Green et al., 1982
<i>Hyssopus thymus</i>	+ S	Purrington and Uleman, 1972
<i>Nasonia vitripennis</i>	+	Holmes, 1970 in 1972;
	+	Grant et al., 1980
	+	Wylie, 1967
<i>Pteromalus puparum</i>	+ S	Takagi, 1986
<i>Tetrastichus galactopus</i>	+	Nealis, 1983
<i>Trichogramma embryophagum</i>	+	Klomp and Teerink, 1962
<i>T. semifumatum</i>	+	Taylor and Stern, 1971

TABLE 6

The relationship between female size and egg or offspring production.  
Symbols explained in Table 1.

Wasp Species	Relationship	Reference
<i>Apanteles rubecula</i>	+ S	Nealis et al., 1984
<i>Aphytis lingnanensis</i>	+ S	Opp and Luck, 1986
<i>A. melinus</i>	+ S	Opp and Luck, 1986
<i>Biosteres longicaudatus</i>	+	Lawrence, 1981
<i>Bracon hebetor</i>	+	Benson, 1973
<i>Caraphractus cinctus</i> <i>luctuosa</i> + S *1	+ Iwata, 1966	Jackson, 1966 <i>Coccygomimus</i>
<i>C. parnarae</i>	NS *2	Iwata, 1966
<i>C. pluto</i>	+ S *3	Iwata, 1966
<i>C. turionellae</i>	NS	Sandlan, 1979
<i>Gregopimpla himalayensis</i>	+ S	Shiga and Nakanishi, 1968a
<i>Nasonia vitripennis</i>	+ S + S	King and Hopkins, 1963; Velthuis et al., 1965
<i>Pteromalus puparum</i>	+ S	Takagi, 1985
<i>Spalangia cameroni</i>	NS	Hurlbutt, 1987a
<i>Tetrastichus hagenowii</i>	+	Narasimham, 1984
<i>Trichogramma evanescens</i>	+ S	Waage and Ng, 1984

\*1  $r = 0.57$ ,  $p = 0.01$  (head width vs number of oocytes)

\*2  $r = 0.39$ ,  $p = 0.20$  (head width vs number of oocytes)

\*3  $r = 0.60$ ,  $p = 0.04$  (head width vs number of oocytes)

TABLE 7

The relationship between host size and the sex ratio of emerging wasps. Symbols explained in Table 1.

Wasp Species	Relationship	Reference
<i>Alysia manducator</i>	- S	Holdaway and Smith, 1933
<i>Aphytis lingnanensis</i>	- S	Luck and Podoler, 1985
<i>A. proclia</i>		Sumaroka, 1967
steppe population	- S *1	
foothill population	- S *2	
mountain population	NS *3	
<i>Brachymeria intermedia</i>	- S	Barbosa and Frongillo, 1979
<i>Bracon rhyacioniae</i>	-	Goyer and Schenk, 1970
<i>Campoplex</i> sp.	-	Clausen, 1939
<i>Cecidostiba</i> sp.	-	Deyrup and Gara, 1978
<i>Coccygomimus turionellae</i>	- S *4	Sandlan, 1979
<i>Coeloides brunneri</i>	- S	Ryan and Rudinsky, 1962
<i>Dahlbominus fuscipennis</i>		Wilkes, 1963
experiment 1	- S	
experiment 2	NS	
<i>Dolichomitus</i> sp.	-	Kishi, 1970
<i>Ecphylus</i> sp.	-	Deyrup and Gara, 1978
<i>Exenterus</i> sp.	-	Clausen, 1939
<i>Goniozus emigratus</i>	NS	Green et al., 1982
<i>Itoplectis cristatae</i>	-	Nozato, 1969
<i>Lariophagus distinguendus</i>	- S *5	van den Assem, 1971
	-	Charnov et al., 1981
<i>Leiophron uniformis</i>	- S *6	Debolt, 1981
<i>Macrocentrus ancylivorus</i>	+	Finney et al., 1947
<i>Metaphycus helvolus</i>	-	Flanders, 1946
<i>Muscidifurax raptor</i>	NS	Wylie, 1967;
	NS *7	Legner, 1969
<i>Nasonia vitripennis</i>	NS	Wylie, 1967

<i>Opius concolor</i>	- S *8	Avilla and Albajes, 1984
<i>Phaenopria occidentalis</i>		Legner, 1969
high host density	- S *9	
low host density	- S *10	
<i>Pteromalus puparum</i>	none	Takagi, 1986
<i>Roptrocercus xylophagorum</i>	- S	Samson, 1984
<i>Spalangia cameroni</i>		Legner, 1969
host (house fly) density:		
high	NS *11	
low	+ S *12	
in the field:		Hurlbutt, 1987a
stable fly	+ S	
house fly	- S	
in the lab:		
house fly	- S	
<i>S. drosophilae</i>	NS *13	Legner, 1969
<i>Spalangia endius</i>	NS	Donaldson and Walter, 1984
<i>Spalangia nigra</i>		Legner, 1969
high host density	- S *14	
low host density	- S *15	
<i>Spathius sequoiae</i>	-	Deyrup and Gara, 1978
<i>Tetrastichus hagenowii</i>	-	Narasimham, 1984

\*1 G = 16.46, p < 0.001  
 \*2 G = 4.41, p = 0.04  
 \*3 G = 0.90, p = 0.34  
 \*4 G = 12.65, p < 0.001  
 \*5 G = 77.64, p < 0.001  
 \*6 G = 8.98, p = 0.03  
 \*7 G = 0.43, p = 0.51  
 \*8 G = 184.99, p < 0.001

\*9 G = 22.61, p < 0.001  
 \*10 G = 4.58, p = 0.03  
 \*11 G = 1.35, p = 0.25  
 \*12 G = 5.14, p = 0.02  
 \*13 G = 3.34, p = 0.07  
 \*14 G = 11.14, p < 0.001  
 \*15 G = 19.06, p < 0.001

TABLE 8

The relationship between host age and the sex ratio of emerging wasps.  
Symbols explained in Table 1.

Wasp Species	Relationship	Reference
Anisopteromalus calandrae	- S - S	van den Assem et al., 1984; Kistler, 1986
Aphidius ervi	- S	Wellings et al., 1986
A. nigripes		Cloutier et al., 1981
female given 60 hosts every 24 hours	nd S	
female allowed to attack each host only once	- S	
Elasmus hispidarum	-	Taylor, 1937 in Clausen, 1939
Heterospilus prosopidis		
host species:		
Callosobruchus chinensis	- S	Jones, 1982
Zabrotes subfasciatus	-	Kistler, 1986
Lariophagus distinguendus	- S *1	van den Assem, 1971
Leiophron uniformis	S *2	Debolt, 1981
Microplitis croceipes	NS	Hopper and King, 1984
Nasonia virtipennis	+ S	Wylie, 1963
Pleurotropis parvulus	-	Taylor, 1937 in Clausen, 1939
Telenomus fariai	none	Rabinovich, 1970a
Tiphia popilliavora		Brunson, 1938
given young and old hosts:		
simultaneously	- S *3	
on alternate days	- S *4	
Trichogramma japonicum	-	Vu Quang Con, 1986
T. semifumatum	-	Taylor and Stern, 1971

\*1  $G = 172.90$ ,  $p < 0.001$ ;  $r_s = -0.70$ ,  $p < 0.01$  (data from Table II  
in van den Assem, 1971)

$G = 63.70$ ,  $p < 0.001$ ; (data from Table III in van den Assem, 1971)

\*2  $G = 8.98$ ,  $p = 0.03$ ; a posteriori G-tests (Sokal and Rohlf, 1969)

show that sex ratio increases from host instar 4 to 2 to 1 to 3, but at  $\alpha = 0.05$  the difference was only significant between instars 4 and 3.

\*3  $G = 251.38, p = 0.00$

\*4  $G = 171.55, p = 0.00$

TABLE 9

The relationship between host species size and the sex ratio of emerging wasps.

Wasp Species	Relationship	Reference
<i>Alysia manducator</i>	- S	Holdaway and Smith, 1933
<i>Dolichomitus</i> sp.	-	Kishi, 1970
<i>Echthromorpha hyalina</i>	-	Seyrig, 1935 in Clausen, 1939
<i>Eurytoma morio</i>	- S *1	Mendel, 1986
<i>Metacolus unifasciatus</i>	- S *2	Mendel, 1986
<i>Pimpla instigator</i> 1939	-	Chewyreu, 1913 in Clausen, 1939
<i>P. maculiscaposa</i>	-	Seyrig, 1935 in Clausen, 1939
<i>P. turionellae</i>	- S *3	Arthur and Wylie, 1959
<i>Pteromalus puparum</i>	none	Takagi, 1986
<i>Spalangia cameroni</i>	NS	Hurlbutt, 1987a
<i>Tetrastichus hagenowii</i>	-	Narasimham, 1984
<i>Trichogramma minutum</i>	- S *4	Houseweart et al., 1983
<i>T. semifumatum</i>		Taylor and Stern, 1971
sizes of host species (length X width, mm <sup>2</sup> ):		
0.24, 0.26, 0.30, 0.48	nd *5	
0.18, 0.26	+ *6	

\*1  $G = 69.53$ ,  $p < 0.001$

\*2  $G = 60.00$ ,  $p < 0.001$

\*3  $G = 53.72$ ,  $p < 0.001$ ;  $r_s = 0.89$ ,  $p < 0.01$

\*4  $G = 15.97$ ,  $p < 0.001$

\*5 Experiment Va in Taylor and Stern, 1971

\*6 Experiments Ia and Ib in Taylor and Stern, 1971

TABLE 10

The relationship between the density of female wasps and the sex ratio of their offspring. Symbols explained in Table 1.

Wasp Species	Relationship	Reference
<i>Biosteres longicaudatus</i>	+	Lawrence, 1981
<i>Bracon hebetor</i>	nd	Reinert and King, 1971
<i>Dinarmus vagabundus</i>	+	Rojas-Rousse et al., 1983
<i>Eupteromalus dubius</i>	+ S *1	Wylie, 1976b
<i>Nasonia vitripennis</i>	+ S *2	Velthuis et al., 1965
+ Walker, 1967	+ S	Werren, 1983
<i>Pteromalus puparum</i>	+	Takagi, 1985, 1986
<i>Spalangia cameroni</i>	NS	Hurlbutt, 1987a
<i>Telenomus remus</i>	+ S *3	Schwartz and Gerling, 1974
<i>Tetrastichus hagenowii</i>	+	Narasimham, 1984
<i>Trichogramma evanescens</i>	+ S *4	Salt, 1936
<i>T. japonicum</i>	+ S *5	Kuno, 1962
<i>T. lutea</i>	+	Kfir, 1982
<i>Trissolcus grandis</i>	+	Viktorov, 1968

\*1  $G = 242.88, p < 0.001$

\*2  $G = 151.23, p < 0.001; r_s = 1.00, p < 0.01$

\*3  $G = 54.60, p < 0.001$  (1 female vs 5 to 8 females)

\*4  $G = 142.12, p < 0.001; r_s = 1.00, p < 0.01$

\*5  $G = 11.09, p = 0.05; r_s = 1.00, p < 0.01$

TABLE 11

The relationship between the number of wasps developing per host and the sex ratio of the wasps. Symbols explained in Table 1.

Wasp Species	Relationship	Reference
<i>Aphytis melinus</i>	+ S	Abdelrahman, 1974b
<i>Bracon hebetor</i>	+ S	Benson, 1973
<i>B. gelechia</i> (=Microbracon gelechia) Rao, 1955	+ +	Narayanan and Subba
<i>Eupteromalus dubius</i>	+ S *1	Wylie, 1976b
<i>Goniozus emigratus</i>	NS	Green et al., 1982
<i>Gregopimpla himalayensis</i>	+ S *2	Shiga and Nakanishi, 1968a
<i>Nasonia vitripennis</i>	none	Holmes, 1970 in 1972
<i>Pediobius foveolatus</i>	+	Stevens et al., 1977
<i>Pteromalus puparum</i>	+	Takagi, 1985
<i>Tetrastichus hagenowii</i>	+	Narasimham, 1984
<i>Trichogramma brevicapillum</i>	+ S	Pak and Oatman, 1982
<i>T. lutea</i>	nd	Kfir, 1982

\*1  $G = 242.88, p < 0.001$

\*2  $G = 22.28, p < 0.001$

TABLE 12

The relationship between host density and the sex ratio of emerging wasps. Symbols explained in Table 1.

Wasp Species	Relationship	Reference
Aphidius smithi	+	Wiackowski, 1962
A. urticae	none	Dranfield, 1979
A. uzbeckistanicus	none	Dranfield, 1979
Coccophagus ochraceus	+	Flanders, 1956
Gryon atriscapus	NS *1	Waage, 1982b
Leiophron uniformis	S *2	Debolt, 1981
Muscidifurax raptor	NS *3	Legner, 1967
	NS *4	Legner, 1969
Phaenopria occidentalis		Legner, 1969
female wasps given:		
small hosts	- S *5	
large hosts	NS *6	
Spalangia cameroni	NS *7	Legner, 1967
female wasps given:		Legner, 1969
small hosts	NS *8	
large hosts	- S *9	
S. drosophilae	NS *10	Legner, 1969
S. endius	NS *11	Legner, 1967
	NS	Donaldson and Walter, 1984
S. nigra		Legner, 1969
female wasps given:		
small hosts	NS *12	
large hosts	+ *13	
Trichogramma brevicapillum	-	Pak and Oatman, 1982
T. evanescens	- S	Waage and Ng, 1984
T. japonicum	- S	Vu Quang Con, 1986

\*1  $G = 5.38$ ,  $p = 0.07$

\*2  $G = 15.54$ ,  $p = 0.001$ ; a posteriori G-tests (Sokal and Rohlf, 1969) show that sex ratio increases as host density goes from 50 to 25 to 100 to 75, but the only significant difference at

alpha = 0.05 was between 50 hosts and both 100 and 75 hosts.

\*3 G = 5.53, p = 0.15 (California and Uruguay populations)

\*4 G = 0.14, p = 0.71

\*5 G = 12.42, p < 0.001

\*6 G = 0.58, p = 0.45

\*7 G = 2.38, p = 0.50

\*8 G = 0.54, p = 0.40

\*9 G = 8.76, p = 0.003

\*10 G = 0.00, p = 1.00

\*11 G = 0.51, p = 0.92

\*12 G = 1.72, p = 0.19

\*13 G = 13.07, p < 0.001