

A MODEL FOR SEX RATIO SELECTION IN PARASITIC WASPS: LOCAL MATE COMPETITION AND HOST QUALITY EFFECTS

by

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SUMMARY

Sex ratios are highly variable among parasitic wasps, and the adaptive significance of this variability is currently the subject of intensive study. A model is presented which combines two important effects upon sex ratio selection, (1) local mate competition and (2) host quality. It is proposed that these two effects occur commonly in parasitic wasp species. For species in which females benefit more (in fitness) than do males from large (or good) hosts, the model predicts:

- 1) Wasps should produce a greater proportion of sons on small (or poor) hosts than on large (or good) hosts.
- 2) The overall sex ratio should be either greater than or equal to the Hamiltonian sex ratio (*i.e.* the sex ratio dictated by local mate competition and inbreeding).
- 3) The overall sex ratio is characterized by three regions, a Hamiltonian sex ratio when few small (or poor) hosts are parasitized, a linearly increasing sex ratio when an intermediate proportion of smaller (or poor) hosts are parasitized, and then a declining sex ratio when many small (or poor) hosts are parasitized.
- 4) The degree of deviation from the Hamiltonian sex ratio depends on the relative fitness of daughters on small hosts. The less fit are small daughters, the greater an expected sex ratio increase at intermediate frequencies of smaller host parasitization.
- 5) When a single host size is parasitized, the Hamiltonian sex ratio should be produced.

The relevance of the model to various parasitic wasp life histories is discussed.

INTRODUCTION

Sex ratios have long been known to be highly variable in the parasitic Hymenoptera (CLAUSEN, 1940; FLANDERS, 1965). This variability has been explained as due to either differential mortality between the sexes or as control of the sex ratio by the parent. Due to haplodiploid sex determination (unfertilized eggs develop into males), Hymenoptera have potential control over the sex of offspring via control of sperm access to eggs, and numerous parasitic wasp species have anatomical features suggesting this control (FLANDERS, 1965). Therefore, parasitic

* "The views of the author do not purport to reflect the position of the Department of the Army or the Department of Defense," (para 4-3, AR 360-5).

wasps provide excellent material for testing ecological theories on the evolution of sex ratios (CHARNOV, 1982). In addition, the topic is of importance because the sex ratio of an organism can have a major impact upon its population dynamics. Understanding the sex ratio dynamics of certain wasp species is relevant to their use as biological control agents (LUCK & PODELER, 1982; HASSELL *et al.*, 1983), and can also assist in improving mass rearing programs (WAAGE & MING, 1983).

Recent studies indicate that at least in some wasp species, sex ratio is adaptively controlled. These studies have focused upon two factors, local mate competition (WERREN, 1980, 1983; WAAGE, 1982; HERRERA, 1984) and host quality (VAN DEN ASSEM, 1971; CHARNOV *et al.*, 1981; JONES, 1982), which have effects upon sex ratio selection in parasitic wasps.

Local mate competition (HAMILTON, 1967) occurs in populations which are subdivided into temporary local mating groups composed of the broods of a few parents. In general, the population structure selects for a female biased sex ratio because sons of a parent compete with each other for reproductive success within the local mating groups. Such a population structure is probably common in parasitic wasps which attack patchily distributed hosts and in which mating occurs upon or near the natal patch. Empirical studies support the relevance of local mate competition to parasitic wasps (GREEN *et al.*, 1983, and above). The effect is probably much more prevalent than previously appreciated.

Host quality variability also affects sex ratio selection. For example, consider host size. Suppose that large host size is more beneficial to the fitness of daughters than to sons. Selection would then favor wasps to lay more daughters in large hosts and more sons in small hosts (VAN DEN ASSEM, 1971). Host size effects are common in many wasp species (CLAUSEN, 1939). The concept applies equally well to other aspects of host quality which differentially effect fitness of the two sexes, such as host species (HOLDAWAY & SMITH, 1933), host age and previous parasitization (ALPHEN & THUNISSEN, 1983). An optimality model for sex ratio shifts with host quality has been developed by CHARNOV (1979) and CHARNOV *et al.* (1981).

The purpose of this paper is to explore the combined effects of local mate competition and host quality on sex ratio evolution in parasitic wasps. An optimality model is developed and the results are considered in relation to the various life history strategies of parasitic wasps.

MODEL

Consider the following life history: females of a solitary (one egg per host) wasp species attack patches of hosts composed of two host sizes, large and small. The total population is composed of many such patches. The fitness of male and female progeny differ depending upon whether they develop upon large or small hosts. Mating occurs among the progenies from the patch. Males then die and female progeny disperse in search of new hosts.

A mathematical approach similar to HAMILTON (1967) is utilized to determine the optimal sex ratio strategy on large and small hosts. The fitness of a rare-type foundress producing one sex ratio strategy in a population producing another strategy, is defined. Then the Evolutionary Stable Strategy (MAYNARD SMITH, 1976) is mathematically derived.

The inclusive fitness of a foundress is generally defined by (1) the relative fitnesses of her sons and daughters, (2) her genetic relatedness to sons and daughters, (3) her sex ratios on small and large hosts and the sex ratios of the other foundresses, and (4) the proportion of parasitized hosts which are small versus large. The following definitions are utilized:

- N = number of foundresses in a patch.
- r_s = proportion of sons produced on small hosts by the rare-type foundress.
- \hat{r}_s = proportion of sons produced on small hosts by the common-type foundress.
- r_l = proportion of sons produced on the large hosts by the rare-type foundress.
- \hat{r}_l = proportion of sons produced on the large hosts by the common-type foundress.
- W_m = fitness of male offspring on small hosts relative to fitness of males on large hosts.
- W_f = fitness of female offspring on small hosts relative to fitness of females on large hosts.
- g_m = genetic relatedness of foundress to male offspring.
- g_f = genetic relatedness of foundress to female offspring.
- p = proportion of parasitized hosts which are small.

It is assumed that each foundress parasitizes the same number of hosts and the same proportion of small hosts. Following HAMILTON (1967), the fitness of a rare-type foundress (W_T) can be written as:

$$W_T = g_m(p W_m r_s + (1-p)r_l) F/M + g_f(p W_f (1-r_s) + (1-p)(1-r_l)) \quad (1)$$

where F is the total production of female progeny in the patch and M is the total production of male progeny in the patch.

$$F = pW_f(1-r_s + (N-1)(1-\hat{r}_s)) + (1-p)(1-r_l + (N-1)(1-\hat{r}_l)) \quad (2)$$

$$M = pW_m(r_s + (N-1)\hat{r}_s) + (1-p)(r_l + (N-1)\hat{r}_l) \quad (3)$$

By differentiating formula (1) with respect to r_s , then setting $dW_T/dr_s = 0$, $r_s = \hat{r}_s$, $r_l = \hat{r}_l$, the optimal sex ratio on small hosts (r_s^*) is obtained:

$$r_s^* = \frac{W_m g_m (N-1)(W_f p + 1-p) - r_l (1-p)(W_m g_m (N-1) + W_f (N g_f + g_m))}{W_m W_f p N (g_m + g_f)} \quad (4)$$

Similarly, the optimal sex ratio on large hosts (r_l) is

$$r_l^* = \frac{g_m (N-1)(W_f p + 1-p) - r_s p (W_f g_m (N-1) + W_m (N g_f + g_m))}{N(1-p)(g_m + g_f)} \quad (5)$$

These two formulae must be simultaneously solved to determine the optimal sex ratio strategy (r_s, r_l) as a function of population structure (N), host quality effects (W_m, W_f , and p) and genetic relatedness (g_m, g_f). Although the formulae are cumbersome, they simplify as expected. Assuming genetic relatedness to be equal ($g_m = g_f = .5$), then:

- 1) When host size has no differential effect upon fitness ($W_m = W_f$), and a single sex ratio is produced, the Hamiltonian solution obtains: $r^* = (N-1)/2N$.
- 2) If there is only one host size (p approaches 0 or 1), then: $r^* = (N-1)/2N$.
- 3) Under very large population sizes ($N \rightarrow \infty$):

$$r_s^* \rightarrow (W_m(W_f p + 1-p) - r_l(1-p)(W_m + W_f))/(2W_m W_f p) \quad (6)$$

$$r_l^* \rightarrow (W_f p + 1-p - r_s p(W_f + W_m))/(2(1-p)) \quad (7)$$

which are equivalent to CHARNOV's (1979) solution for a large panmictic population.

Due to their complexity, formulae (4) and (5) are simultaneously solved by computer to provide the optimal host size sex ratio strategy (r_s^*, r_l^*) under local mate competition. Results are shown in figs. 1, 2 and 3. For simplicity, genetic relatedness is assumed equal towards male and female offspring ($g_m = g_f = .5$), which is the case for outbreeding populations. The general result of inbreeding in haplodiploid populations is to increase the relative relatedness to daughters (HAMILTON, 1978), thus favoring an increased sex ratio bias towards females. The effect is slight, however, in comparison to the impact of

local mate competition (HAMILTON, 1967, 1978). Following SUZUKI & IWASA (1980) it can be shown that the optimal sex ratio in a population subject to local mate competition and inbreeding is $r^* = g_s(N-1)/(g_s + g_f)N$. This simplifies to Hamilton's original solution ($r^* = (N-1)/2N$) when inbreeding is neglected, and to HAMILTON'S (1972) solution for haplodiploid organisms ($r^* = (n-1)(2n-1)/n(4n-1)$) when sib mating occurs at the assumed $1/n$ frequency. HERRERA (1984) derives a similar formula using different mathematical techniques and presents supporting data for inbreeding effects in fig wasps.

In fig. 1, relative male and female fitness on small hosts are held constant ($W_m = 1, W_f = .5$) and the effect of foundress number and proportion small parasitized hosts can be seen. Four different foundress number and proportion small parasitized hosts can be seen. Four different foundress numbers are used ($N = 2, 4, 8, 100$), with 100 foundresses approaching a large panmictic population. As can be seen, a more male biased sex ratio is favoured on small hosts and a more female biased sex ratio is favored on large hosts. The degree of bias

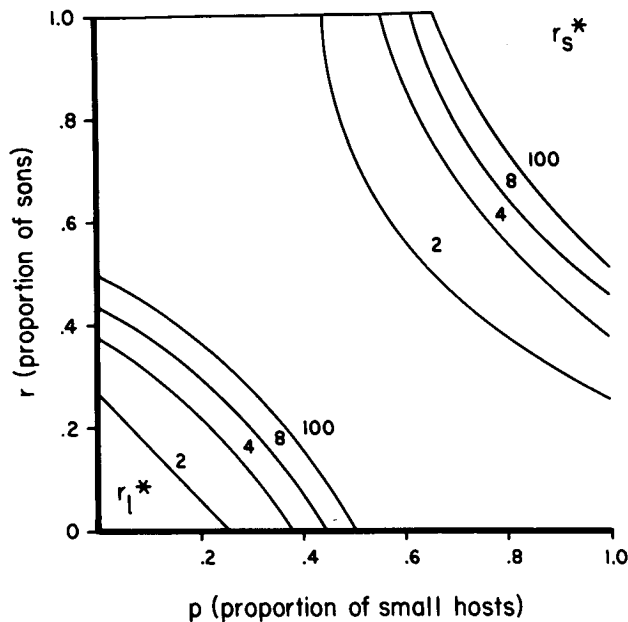


Fig. 1. The optimal sex ratios on small (r_s) and large (r_l) hosts are shown as a function to p , the proportion of small hosts among those parasitized in the patch. This is displayed for 2, 4, 8, and 100 foundresses. One hundred foundresses approximates a panmictic population. The relative fitness of males on small hosts (W_m) is 1.0, relative fitness of females on small hosts (W_f) is 0.50.

depends upon the number of foundresses in the patch. The fewer foundresses, the more female biased the sex ratio on large hosts and the sooner females are produced on small hosts with increasing 'p'.

The proportion of small parasitized hosts, p , has a clear influence on the sex ratios produced. For any set of r_s, r_l curves examined (e.g. $N=2$), three different regions can be discerned:

Region I; p is small, 100% sibs are produced on small hosts and sex ratio on large hosts declines with increasing p .

Region II; p is intermediate, 100% sons are produced on small hosts and 0% sons are produced on large hosts.

Region III; p is large, sex ratio on small hosts declines with increasing p and 0% sons are produced on large hosts.

When only one host size is used ($p=1$ or 0) the Hamiltonian sex ratio is produced. CHARNOV (1979) observed a similar pattern in his panmictic model.

The general pattern makes intuitive sense. When few small hosts are parasitized, a parent is selectively favored to put some sons in large hosts. As proportion of small parasitized hosts increases, a parent is favored to produce fewer sons on the large hosts, due to the preponderance of males in the smaller hosts and the greater relative value of large daughters. When more and more small hosts are parasitized, there comes a point where the parent is favored to begin producing some daughters in the smaller hosts, since the value of sons is diminished by the abundance of males and the value of daughters enhanced by their relative scarcity. At the extreme where there are very few large hosts to be parasitized, the wasp is effectively in a single host size situation and is favored to produce the Hamiltonian solution on small hosts.

Fig. 2 illustrates the dynamics of the overall sex ratio with these changing parameters. Male fitness on small hosts is set at $W_m=1$ and the overall sex ratio is shown for $W_f=.75$ or $.25$ and $N=2, 4$ and 100 . Again, the three regions can be discerned:

In *region I*, the overall sex ratio remains stable at Hamilton's solution, $r^*=(N-1)/2N$.

In *region II*, the sex ratio increases linearly with p , because 100% sons are produced on small hosts and 0% sons on large hosts. The degree of deviation from the Hamiltonian solution depends upon the value of daughters from small hosts. Where host size has a small effect upon daughter fitness ($W_f=.75$) region II is small and there is little deviation in overall sex ratio. In comparison, when small daughters have little fitness ($W_f=.25$), then region II is large and strongly male biased sex ratios can result.

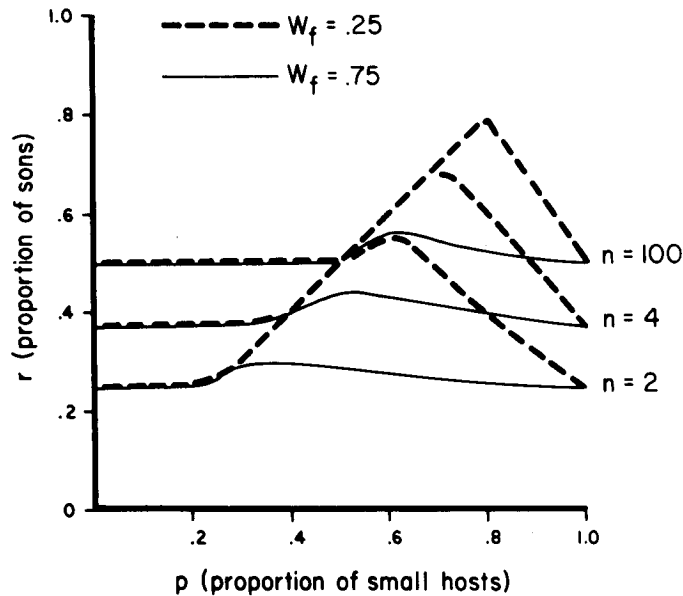


Fig. 2. The overall sex ratio in a patch is shown as a function of p , the proportion of small hosts among those parasitized. Foundress number (N) and the relative fitness of daughters on small hosts (W_f) are also varied. The figure shows that decreasing the fitness of daughters on small hosts causes a greater deviation from the Hamiltonian sex ratio, at intermediate values of p .

Region III is the area where the sex ratio on small hosts begins to decline with increasing p . Thus the overall sex ratio declines as well to again achieve the Hamiltonian solution at $p = 1$.

The figure shows that the overall sex ratio is either at the Hamiltonian solution, or it is more male biased. Therefore, we can predict that if a female bias occurs in a population, it is most likely due to local mate competition rather than to host quality effects. The amount of deviation from Hamilton's solution depends upon the fitness of daughters on small hosts. This is most likely correlated with host size, so we expect that when the difference between host sizes is small, there should be little deviation in overall sex ratios at intermediate p values, but when the difference in host sizes is large, larger deviations from Hamilton's solution should result.

Finally, fig. 3 shows further effects of varying W_f and W_m upon sex ratio selection. In the figure, r_s^* and r_l^* are shown when $N = 4$. Solid lines indicate the sex ratio when $W_m = 1$ for three different female

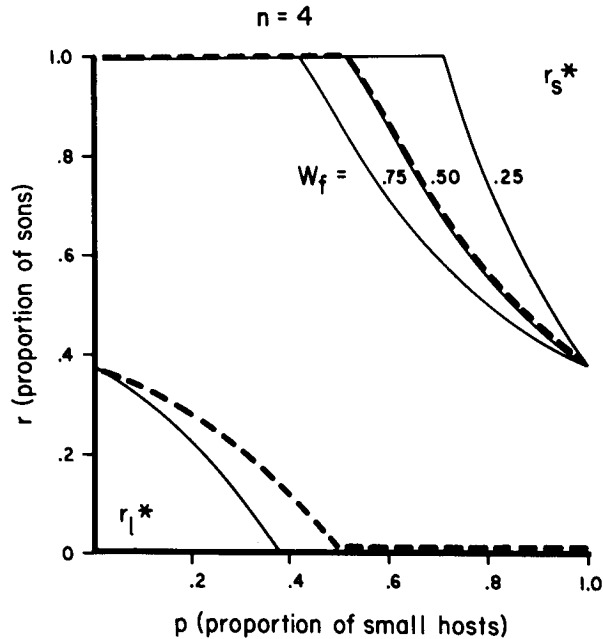


Fig. 3. The optimal sex ratio on small and large hosts are shown when foundress number is held constant ($N=4$) and the relative fitnesses of sons and daughters on small hosts is varied. Solid lines indicate the sex ratios when $W_m=1$ for three different female fitnesses. The dashed lines indicate sex ratios in the case where $W_m=.75$ and $W_f=.50$.

fitnesses ($W_f = .25, .50$ and $.75$). The dashed lines indicate sex ratio in the case where $W_m = .75$ and $W_f = .50$. The figure presents an interesting general phenomenon. When W_m is held constant and W_f is varied the r_s^* curve shifts, but the r_l^* curve does not. Surprisingly, the sex ratio on large hosts is insensitive to the relative fitness of females on small hosts. Similarly, if W_f is held constant and W_m is varied, the r_l curve shifts—*i.e.* the sex ratio on small hosts is insensitive to the relative fitness of males on small hosts, but is sensitive to the relative fitness of females on small hosts. The effect has implications for the evolution of sex ratios in parasitic wasps. In general, it is believed that male fitness is less influenced by host size than is female fitness (CHARNOV *et al.*, 1981). To the extent that this is true, the model predicts that the r_l curve should be relatively stable whereas the r_s^* curve should shift dramatically with changes in host size distribution (as they impact on male and female fitnesses). Shifts in the r_s^* curve will be towards a greater production of sons as W_f declines.

Assuming that male fitness is less sensitive to host size than female fitness, which is probably the case in most wasp species, the predictions of the model are summarized below:

- 1) Wasps should produce a greater proportion of sons on small hosts than on large hosts. The actual sex ratios produced will depend upon the level of local mate competition, relative fitnesses of sons and daughters on small hosts, level of inbreeding and proportion of small hosts parasitized.
- 2) The overall sex ratio should be either greater than or equal to the Hamiltonian sex ratio (*i.e.* the sex ratio dictated by local mate competition and inbreeding). Therefore, a female biased overall sex ratio suggests that the wasp species is subject to local mate competition.
- 3) The overall sex ratio can be characterized by three regions, a Hamiltonian sex ratio when p is low; a linearly increasing sex ratio (with respect to p) when p is intermediate; and a declining sex ratio back to the Hamiltonian solution when p is high.
- 4) The degree of deviation from the Hamiltonian sex ratio depends upon the relative fitness of daughters on small hosts. The less fit small daughters, the greater an expected sex ratio deviation in the intermediate p region.
- 5) As the fitness of daughters on small hosts is changed (*e.g.* by changes in size differences between large and small hosts), the expected sex ratio on large hosts (with respect to p) will *not* change, but the expected sex ratio on small hosts will change. Thus, a relatively fixed sex ratio response is expected on large hosts, but a dynamic sex ratio response is expected on small hosts.
- 6) When a single host size is parasitized in a patch ($p=1$ or 0) the Hamiltonian sex ratio should be produced.

Although the preceding model has been presented in terms of host size for convenience, the model applies equally well to other host quality characteristics which differentially effect male and female fitness. Therefore, host quality can be substituted for host size in the above presentation.

DISCUSSION

Both this model and that of CHARNOV (1979) show that the sex ratio strategy is strongly dependent upon 'p', the proportion of small hosts among those parasitized in a patch. When a wasp encounters a patch of hosts, she typically parasitizes some, but not all of the hosts before departing. Oftentimes, parasitic wasps preferentially parasitize larger hosts in a patch. Indeed, GREEN (1982) has developed an 'optimal

foraging' model for panmictic populations which predicts that large hosts should be preferentially parasitized. The same conclusion probably holds under local mate competition. The net effect is that typically a low proportion of smaller hosts will be parasitized under natural conditions. Only when (1) large hosts are uncommon, (2) wasp densities are high or (3) patch density is low, will foundresses more frequently parasitize the less desirable hosts. Of course, small and large hosts are relative terms. When the difference in host quality between host sizes is less pronounced, there will be less resistance to oviposition on the lower quality hosts.

In laboratory circumstances, where wasps are sometimes confined on hosts under high density, parasitizations of very small hosts can occur. The model would not apply to such artificial circumstances unless similar conditions are also encountered by the species in nature. High density situations also have the added complication that super-parasitization can occur, which can result in increased offspring mortality (VAN ALPHEN & NELL, 1982; LAWRENCE, 1981). Mortality can obscure sex ratio shifts which occur at the egg stage, making it more difficult to study the adaptive sex ratio. But mortality also acts as an added selective factor due to its effects upon the fitness terms of male and female progeny. Thus an increased daughter mortality on super-parasitized hosts is an added selective factor favoring increased laying of male eggs on those hosts.

A major question concerning the relevance of the model is to what extent local mate competition and host quality effects co-occur. The panmixia model of CHARNOV (1979) predicted that overall sex ratio will either be 50:50 or male biased for most wasp species. In contrast, most wasp species studied which show a host size effect have an overall female biased sex ratio. This is true of *Lariophagus distinguendus*, the solitary parasite of granary weevils used in the CHARNOV *et al.* (1981) study. Female biased sex ratios also typically occur in *Anisopteromalus calandrae* (VAN DEN ASSEM *et al.*, 1984), *Heterospilus prospoides* (JONES, 1982) and *Asobara tabida* (VAN ALPHEN & NELL, 1982), and a variety of other species with host quality effects (CLAUSEN, 1940; ARTHUR & WYLLIE, 1959). The model presented here predicts that an overall female biased sex ratio indicates local mate competition, *i.e.* that host size effects alone are not sufficient. As an exception, female biased sex ratios without local mate competition can be expected in species which lay males in the larger or better quality hosts. However, this is not typical for parasitic wasps (CHARNOV *et al.*, 1981). The existence of sex ratio distorting extrachromosomal factors (WERREN *et al.*, 1981; SKINNER, 1982) can also result in female sex ratios without local mate competition, although models indicate that such factors will not great-

ly influence the sex ratio strategies of uninfected wasps (WERREN & BULMER, *in prep.*).

The model predicts that, when a single host size is parasitized in a patch, the Hamiltonian sex ratio should be produced. Therefore, a constant sex ratio should be produced independent of host size when a single size is available in the patch. The prediction was not met in laboratory experiments with either *Lariophagus distinguendus* or *Heterospilus prospoides* (CHARNOV *et al.*, 1981). In both cases a relatively constant (female biased) sex ratio was produced when moderate to large hosts were used (around 15% male for *Lariophagus* and around 40% male for *Heterospilus*). However, when hosts at the small end of the acceptance spectrum were used, an increasingly male biased sex ratio resulted. There appears to be an innate tendency to lay sons in very small hosts, even when they are the only hosts available. It is very possible that patches of exclusively small hosts are rarely parasitized in nature, due to the foraging behavior of the wasp. Daughters emerging from the small hosts were of a very low quality and, at least in *Lariophagus*, the wasp was obviously reluctant to parasitize them. Thus the sex ratios produced on the preferred moderate to large hosts probably reflect a more normal behavior of the wasp. In testing these ecological models, the normal oviposition behavior of the wasp species being examined should be taken into account.

Evidence indicates that local mate competition is common in the parasitic wasps (WAAGE, 1982, 1983; GREEN *et al.*, 1982; WERREN, 1980, 1983). Local mate competition can be expected in species which (1) parasitize patchily distributed hosts (2) have low wasp density relative to patch density and (3) have mating upon or near the natal patch. Obviously, patchiness is another relative term used in the discussion, and is dependent upon the context and scale utilized. The coleopteran egg parasite *Caraphraactus cinctus* responds differently to eggs laid in rows versus singly, in a fashion which illustrates patch relativity (JACKSON, 1966). In nature, when encountering eggs of *Agatus bipustulatus* in rows the wasp will produce a strong excess of females, but when encountering single eggs of the same species, the wasp typically produces 1 male and 2 females. Thus, the wasp apparently perceives either a row of eggs or a single egg as a patch, depending upon the context. For local mate competition, host patchiness should be viewed relative to male wasp dispersal and the probability of male mating success with increasing distance from the natal patch. Local mate competition clearly occurs in species with short-lived or non-dispersing males, such as *Nasonia vitripennis* (WERREN, 1983). In other species subject to local mate competition, males may disperse from the natal patch after mating, but their opportunities for garnering mates outside the natal patch is relatively low.

Fluctuations in population density will effect the level of local mate competition in nature (CHARNOV, 1982). When wasp density is low relative to patch density, the likelihood is that only a limited number of foundresses will encounter any one patch, thus favoring local mate competition. When wasp density increases, greater panmixia will result. Many wasp species are probably subject to fluctuating densities such as seasonal changes in population size, and should therefore adjust sex ratio accordingly.

The particular life history of a wasp species will influence whether local mate competition and host quality effects co-occur. Parasitic wasps can be generally characterized as solitary, semi-gregarious or gregarious. Solitary wasps typically lay one egg per host, semi-gregarious can be roughly defined to lay one to a few eggs per host, and gregarious wasps lay many eggs per host. Host size effects upon sex ratio are very common in solitary species (CLAUSEN, 1939). This is to be expected, since the size of a host can have a very direct impact upon the size of the resulting wasp. Among the solitary species, sex ratio adaptations to host size are expected in pupal parasites, since the host does not grow further once parasitization has occurred. Similarly, host size adaptations are expected in larval parasites in which host development is terminated shortly after oviposition. In certain wasp taxa, oviposition occurs in the egg or larval stage, but wasp development is not completed until the host's last larval instar or pupal stage (CLAUSEN, 1940; ASKEW, 1971). Host size sex ratio adaptations are less likely to evolve here for the obvious reason that the ovipositing wasp is not in the position to assess the expected final size of the host. An exception to the above generalization would be those wasps which parasitize mixed species patches of hosts. Wasps may then shift sex ratio in response to host species.

In semi-gregarious species, the sex of one offspring in a host can greatly influence the fitness of the other progeny in the host, due to food limitation. WAAGE & MING (1983) has documented the phenomenon quite nicely in the egg parasite *Trichrogamma evanescens*. A single wasp consumes a significant proportion of the host. Males typically pupate at a smaller size than do females, so that they consume less food within the host, and leave more for the other offspring. Therefore, when 2-3 eggs are laid, the fitness of emerging offspring will be strongly influenced by whether those offspring are all male, all female or an intermediate sex ratio. WAAGE & MING (1983) developed a numerical model for the best combination sex ratio and egg number in a host by assuming that a single foundress parasitizes the patch. Similar circumstances may occur in the semi-gregarious scale parasites *Aphytis melinus* and *A. lingnanensis* (LUCK *et al.*, 1982), and in other semi-gregarious species (JACKSON, 1966; MERTENS, 1980).

In gregarious species a single wasp consumes a relatively small portion of the host, and therefore its sex typically has little impact upon the size of other offspring in the host. Similarly, host size will generally have less impact upon the fitness of emerging offspring, since the ovipositing wasp can adjust the number of eggs laid so as to decrease detrimental effects upon offspring size. The question of brood size regulation in gregarious parasites has been investigated by CHARNOV & SKINNER (1983).

Host quality effects are still possible in gregarious species. For example, when a wasp parasitizes a previously attacked host, her offspring can be smaller and less fit than those of the previous wasp (SUZUKI & IWASA, 1980). This host quality effect is in addition to local mate competition effects resulting from superparasitism (WERREN, 1980). In addition some host species may be more suitable than others for offspring development, thus resulting in larger offspring size (independent of the number of eggs laid). When two or more host species in a patch are suitable for oviposition, but vary in their quality, host quality sex ratio shifts can occur. This may be occurring with the wasp *Nasonia vitripennis* parasitizing mixed patches of blowflies and houseflies (GRANT, *pers. comm.*).

Certain wasp taxa have life histories which are unlikely to favor either local mate competition or host quality adaptations. Eucharitids and perilampids lay eggs upon foliage and produce planidial larvae which crawl upon suitable passing hosts (ASKEW, 1971). The hyperparasitic trigonalids lay eggs upon foliage where they are consumed by feeding caterpillars. If the caterpillar is subsequently parasitized by an ichneumon or tachinid, the hyperparasite will develop. In such cases the parent wasp does not actively choose the host of the offspring and host quality sex ratio adaptations cannot evolve. Local mate competition is less likely (although not impossible) since individual offspring are dispersed into the environment and are less likely to be associated with siblings. Sex ratios of 50:50 are therefore expected to be more prevalent in these taxa.

One final discussion of the model is in order. For a precise sex ratio adaptation to evolve along the lines envisioned by the model, individual wasps would have to reliably measure host size, foundress number and the proportion of different host sizes parasitized in a patch. There is ample evidence that many wasps have impressive capabilities to measure these parameters. *Lariophagus distinguendis* can detect host size (tunnel width) differences at least as small as 0.2 mm (CHARNOV *et al.*, 1981). The ability of *Anisopteromalus calandrae* to "remember" the size of previously parasitized hosts has been elucidated in a remarkable series of experiments by VAN DEN ASSEM *et*

al. (1984). Wasps such as *Nasonia vitripennis* (WERREN, 1980, 1983) and certain agaonid species (HERERRA, 1983) can assess the number of foundresses in a patch. However, in many species these parameters may be fluctuating too greatly over time and space to be accurately measured by individual wasps.

Foundress number need not be directly measured for a sex ratio strategy to evolve. Selection will presumably adjust sex ratio behavior to the average foundress number encountered if it cannot be directly assessed. Other wasp species may have a graduated response to single, few or many foundresses in a patch rather than a fine-tuned sex ratio shift. Similarly, if wasps cannot accurately assess the proportions of host sizes parasitized in a patch, then host size specific sex ratios could evolve, as observed in *Heterospilis prospoides* (CHARNOV *et al.*, 1981). The model presented here shows that the proportion of different host sizes parasitized can have a major impact upon the fitness of individual wasps. Therefore, when the parasitization experiences of individual wasps accurately reflect what is happening in the mating subpopulation, memory capabilities for host size distribution are expected to evolve.

Finally, it should be pointed out that the combined effects of local mate competition and resource quality are likely to be common in other arthropods such as bees, non-parasitic wasps, mites and aphids, and also in parasitic organisms which are subject to demic mating populations and within-deme variations in resource quality.

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REFERENCES

- ALPHEN, J. J. M. VAN & H. W. NELL, 1982. Superparasitism and host discrimination by *Asobara tabida* Nees (Braconidae: Alysiinae), a larval parasitoid of *Drosophilidae*. — *Neth. J. Zool.* **32**: 232-260.
- ALPHEN, J. J. M. VAN & I. THUNISSEN, 1983. Host selection and sex allocation by *Pachycrepoides vindemiae* Rondani (Pteromalidae) as a facultative hyperparasitoid of *Asobara tabida* Nees (Braconidae; Alysiinae) and *Leptopilina heterotoma* Thomson (Cynipoidea; Eucoilidae). — *Neth. J. Zool.* **32**: 497-514.
- ARTHUR, A. P. & H. G. WYLIE, 1959. Effects of host size on sex ratio, development time and size of *Pimpla turionella* (Hymenoptera: Ichneumonidae). — *Entomophaga* **4**: 297-301.
- ASKEW, R. R., 1971. *Parasitic Insect*. American Elsevier Publ. Co., New York.

- ASSEM, J. VAN DEN, 1971. Some experiments on sex ratio and sex regulation in the Pteromalid *Lariophagus distinguendus*. — Neth. J. Zool. **21**: 373-402.
- ASSEM, J. VAN DEN, F. A. PUTTERS & Th. C. PRINS, 1984. Host quality effects on sex ratio of the parasitic wasp *Anisopteromalus calandrae*. — Neth. J. Zool. **34**: 33-62.
- CHARNOV, E. L., 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. — Amer. Natur. **113**: 465-479.
- CHARNOV, E. L., R. L. LOS-DEN HARTOGH, W. T. JONES & J. VAN DEN ASSEM, 1981. Sex ratio evolution in a variable environment. — Nature **289**: 27-33.
- CHARNOV, E. L., 1982. *Sexual Allocation Theory*. Princeton University Press, Princeton, New Jersey.
- CHARNOV, E. L. & S. W. SKINNER, 1983. Evolution of host selection and clutch-size in parasitoid wasps. — Flor. Entomol. (*in press*).
- CLAUSEN, C. P., 1939. The effect of host size upon the sex ratio of hymenopterous parasites and its relation to methods of rearing and colonization. — J. N.Y. & ent. Soc. **47**: 1-9.
- CLAUDEN, C. P., 1940. *Entomophagous Insects*. McGraw Hill, New York.
- FLANDERS, S. E., 1965. On the sexuality and sex ratios of hymenopterous populations. — Amer. Natur. **93**: 489-494.
- GREEN, R. F., 1982. Optimal foraging and sex ratio in parasitic wasps. — J. theor. Biol. **95**: 43-48.
- GREEN, R. F., G. GORDH & B. HAWKINS, 1982. Precise sex ratios in highly inbred parasitic wasps. — Amer. Natur. **120**: 653-665.
- HAMILTON, W. D., 1967. Extraordinary sex ratios. — Science **156**: 477-488.
- HAMILTON, W. D., 1972. Altruism and related phenomena, mainly in social insects. — An. Rev. Ecol. Syst. **3**: 193-232.
- HAMILTON, W. D., 1978. Wingless and fighting males in fig wasps and other insects. In: Reproductive competition and selection in insects. M.S. Blum & N. A. Blum, eds. Academic Press, New York.
- HASELL, M. P., J. K. WAAGE & R. M. MAY, 1983. Variable parasitoid sex ratios and their effect on host-parasitoid dynamics. — J. an. Ecol. **52**: (*in press*).
- HERRERA, E. A., 1984. Adaptive sex-ratio in fig wasps. — Submitted to Science.
- HOLDAWAY, F. G. & H. F. SMITH, 1933. A relation between size of host puparia and sex ratio of *Alysia manducator* Pantzer. — Austr. J. exp. Biol. Med. Sci. **10**: 247-259.
- JACKSON, D. J., 1966. Observations on the biology of *Caraphractus cinctus* (Hymenoptera: Mymaridae), a parasitoid of the eggs of Dystiscidae (Coleoptera). — Trans. R. ent. Soc. Lond. **118**: 23-49.
- JONES, W. T., 1982. Sex ratio and host size in a parasitoid wasp. — Behav. Ecol. Sociobiol. **10**: 207-210.
- LAWRENCE, P. O., 1981. Interference competition and optimal host selection in the parasitic wasp, *Biosteres longicaudatus*. — Ann. ent. Soc. Amer. **74**: 540-544.
- LUCK, R. F., H. PODOLER & R. KFIR, 1982. Host selection and egg allocation behavior by *Aphytis melinus* and *A. lingnanensis*: comparison of two facultative gregarious parasitoids. — Ecol. Entom. **7**: 397-408.
- LUCK, R. F. & H. PODOLER, 1982. Competitive displacement of *Aphytis lingnanensis* by *A. melinus*: The role of host size and female progeny production. — Ecol. Entom. **7**: 409-421.
- MAYNARD SMITH, J., 1976. Evolution and the theory of games. — Amer. Sci. **64**: 41-45.
- MERTENS, J. W., 1980. Life history of *Laelius pedatus*, a gregarious bethylid ectoparasite of *Anthrenus verbasci*. — Ann. ent. Soc. Amer. **73**: 686-693.

- PUTTLER, B., 1961. Biology of *Hyposoter exiguae* (Hymenoptera: Ichneumonidae), a parasite of lepidopterous larvae. — *Ann. ent. Soc. Amer.* **54**: 25-30.
- SANDLAN, K., 1979. Sex ratio regulation in *Coccygomimus turionella* Linnaeus (Hymenoptera: Ichneumonidae) and its ecological implications. — *Ecol. Entomol.* **4**: 365-378.
- SKINNER, S. W., 1982. Maternal inheritance of a sex ratio factor in the parasitoid wasp, *Nasonia vitripennis*. — *Science* **215**: 1133-1134.
- SUZUKI, Y. & Y. IWASA, 1980. A sex ratio theory of gregarious parasitoids. — *Res. Pop. Ecol.* **22**: 366-382.
- WAAGE, J. K., 1982. Sib-mating and sex ratio strategies in scelionid wasps. — *Ecol. Entomol.* **7**: 103-112.
- WAAGE, J. K. & N. S. MING, 1983. The reproductive strategy of a parasitic wasp: I. Optimal progeny and sex allocation in *Trichogramma evanescens*. — *J. an. Ecol.*: (in press).
- WAAGE, J. K., 1983. The reproductive strategy of a parasitic wasp II. Sex allocation and local mate competition in *Trichogramma evanescens*. — *J. an. Ecol.*: (in press).
- WERREN, J. H., 1980. Sex ratio adaptations to local mate competition in a parasite wasp. — *Science* **208**: 1157-1160.
- WERREN, J. H., S. W. SKINNER & E. L. CHARNOV, 1981. Paternal inheritance of a daughterless sex ratio factor. — *Nature* **293**: 467-468.
- WERREN, J. H., 1983. Sex ratio evolution under local mate competition in a parasitic wasp. — *Evolution* **37**: 116-124.
- WERREN, J. H. & M. BULMER, 1983. The coevolution of autosomes and extra-chromosomal sex ratio factors. *Manuscript*.