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Labile Sex Ratios in Wasps and Bees

Life history influences the ratio of male and female offspring

John H. Werren

A common theme in the impressive diversity of life is the division of reproduction into male function (production of small gametes) and female function (production of large gametes). This simple fact of life has profound implications.

How does natural selection determine allocation of energy and other resources to male versus female function in a species? This question of sex-allocation selection can be applied to a wide range of reproductive systems (Charnov 1982). For a hermaphroditic plant, it asks about the allocation to pollen versus allocation to ovules. For species of fish that change sex, it must consider the timing of the sex shift and the reproductive effort put into each sex. For an insect with separate sexes, it is a question about sex ratios of a female's progeny.

In this article, I describe recent work on sex allocation in wasps and bees. Wasps and bees do not change sex, as do some plants and other animals. However, they have an impressive ability to control the sex of their offspring (*facultative* or *labile* sex-ratio control), and do so in some amazing ways. Insights gained from studies of these insects apply to many other reproductive systems.

Bee and wasp life histories

Wasps and bees, which belong to the insect order Hymenoptera, are excellent organisms for testing sex-allocation theory. The hymenoptera have a special form of sex determination, called haplodiploidy, which allows control over the sex ratio. Female offspring develop from fertilized (diploid) eggs, whereas male offspring develop from unfertilized (haploid) eggs. Therefore, female bees and wasps can control the sex among offspring by controlling sperm access to eggs. In female hymenoptera, sperm is stored in the spermathecal organ after mating, and sperm is then released from this organ to allow fertilization. Many hymenoptera are known to alter their sex ratio in response to environmental circumstances (Clausen 1939).

Wasps and bees have an impressive ability to control the sex of their offspring

Another feature of the wasps and bees that makes them useful for testing sex-allocation theory is the diversity of their natural histories. Most people are familiar with the social wasps and bees, such as hornets, yellow jackets, and honeybees. Such species have highly organized social groups in which only one or a few individuals reproduce, while other individuals (e.g., workers) assist in colony activities.

Nonsocial wasps and bees include muddaubers, leafcutter bees, and potter wasps. Females of these species have individual nests—underground, in twigs, or constructed with mud—where they lay eggs and provide them with food. The habits of these nonsocial insects are generally believed to be the primitive condition preceding the evolution of sociality.

Parasitic wasps and bees represent by far the most common hymenopteran life-style. Females of these species typically lay their eggs on or in the eggs or larvae of other insects. The offspring then develop by feeding on and eventually killing their host. Parasitic hymenoptera are abundant, and extremely important in regulating insect populations. Still other hymenoptera have larvae that feed on plants.

I will consider four life-history factors that influence sex ratios in bees and wasps: population structure, resource quality, seasonality, and patterns of inheritance. The phenomena described here can be generalized to many other species that have labile sex ratios.

Population structure

Natural selection acts very differently on autosomal genes in random-mating populations than in populations spatially subdivided into many local groups. Fisher (1930) was the first to observe that autosomal sex-ratio selection is frequency dependent. He predicted that natural selection favors "equal investment" of resources in male and female offspring in large random mating populations. This investment results in a 1:1 primary sex

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Wasps are excellent research subjects for the testing of sex-allocation theory.

ratio (i.e., at conception) for species in which the cost of producing a son or daughter is equal. Fisher's conclusion has been repeatedly confirmed mathematically.

Hamilton (1967) observed that altering the assumption of random mating leads to quite different results. Many species have populations that are divided into local groups where mating takes place among the progeny of only a few parents. Hamilton found that for a specific kind of population structure, where individuals mate in local groups but the females then disperse each generation to found new groups, female-biased sex ratios result. Such a population structure would be common, for instance, in insects that lay their eggs on a temporary food resource, requiring dispersal of the progeny to new resources after mating. The females establishing new groups are referred to as *foundresses*.

The evolution of different sex ratios in structured populations can be interpreted in terms of either individual selection or group selection (Colwell 1981). I will discuss only individual selection here. Three factors favor production of female-biased sex ratios by foundresses in local mating populations (Frank 1985, Grafen 1984, Taylor 1981, Werren 1983).

First, there is local mate competition among the foundress' sons. Because mating occurs in relatively small groups before dispersal, her sons compete among themselves for a limited number of mates. Increasing the number of sons would therefore not greatly increase the number of sets of grandchildren. This situation contrasts with a large random-mating population, in which one mother's sons would compete primarily with the sons of other mothers.

Second, in small groups there is a local mate advantage of producing daughters, since these daughters are potential mates for sons. However, sibling matings in some species result in inbreeding depression. In these cases, the local mate "advantage" may actually be a disadvantage.

Third, there may be a difference in the genetic relatedness of a foundress to her sons versus daughters. Clearly, if a foundress gene is more likely to occur in a daughter than in a son, then the transmission of that gene to future generations is increased if the

1%–2% sons) but do not alter sex ratio with foundress number.[1]

We do not expect that all wasp species will show facultative sex ratios. For many species, foundress number may not be variable enough to select for a facultative sex ratio strategy. (This may be the case in *Mellitobia*.) Alternatively, foundress number may be highly variable, but individual foundresses cannot tell what the number is. In either case, the optimal sex ratio is expected to evolve in response to average degree of inbreeding and foundress number. One should be able to predict the average sex ratio in a species without facultative sex-ratio control using these parameters. Whether Hamilton's (1967) theory can adequately explain sex-ratio differences between species without sex-ratio control is relatively untested (Waage 1982).

Superparasitism. The wasp *N. vitripennis* demonstrates an additional facultative sex-ratio behavior of interest. The female typically lays 20–40 eggs into a host and offspring develop gregariously. The fly hosts are sometimes individually dispersed in nature, when the fly larva crawls away from its carcass before pupation. The first wasp to encounter such an isolated host produces a strongly female-biased sex ratio (approximately five percent sons), consistent with Hamilton's theory. However, if a second wasp encounters this host, she can detect that it has been previously parasitized. If she also attacks this host (called superparasitism), the second female lays fewer eggs and produces a greater proportion of sons than did the first. Superparasitism is similar to a two-foundress situation except that brood sizes differ between the two females and the second wasp "knows" that there are two foundresses, whereas the first wasp did not have this knowledge.

The optimal sex ratios for the first and second wasp have been predicted in a natural selection model that assumes high egg-to-adult survival for both broods and synchronous emergence and mating between both broods. These assumptions have been verified (Werren 1980).

[1]P. Wilhelm, 1986. Personal communication. University of Leiden, Netherlands.

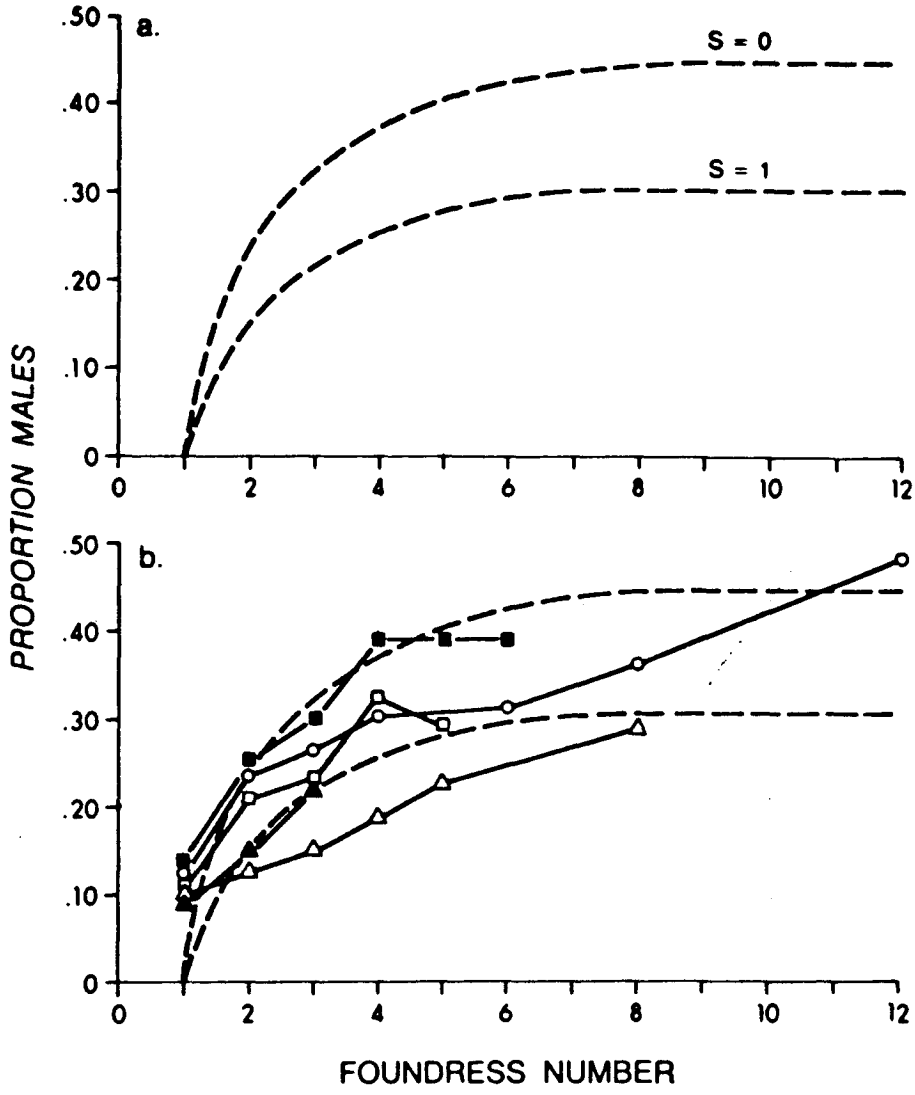

Figure 1. a. The optimal sex ratios are shown as a function of number of foundresses establishing local mating populations. The upper curve shows the optimal sex ratio in an outbred haplodiploid species ($S = 0$) and the lower curve for an inbred haplodiploid species ($S = 1$). In general, sex ratios are biased against males when foundress number is small, but increase toward 1:1 (50% sons) with an increasing number of foundresses per patch. b. The observed sex ratio for five different wasp species are shown. These are *Pegoscapus assuetus* (△), *Tetrapus costaricensis* (■), *Blastophaga* sp. 1 (□), *Blastophaga* sp. 2 (▲), and *Nasonia vitripennis* (○). Data from Frank (1985), Herre (1985), and Werren (1983).

What should the first wasp do, given that superparasitism may occur? Bounds can easily be placed on the first wasp's sex-ratio behavior. If superparasitism is rare, then the first wasp is relatively unaffected by it and should produce just enough sons to inseminate her daughters. If superparasitism always occurs and both wasps lay the same number of eggs, then this is just Hamilton's (1967) $N = 2$ situation, and the first wasp should produce approximately 25% sons. So, even with superparasitism, the first wasp's sex ratio varies only between 5% and 25% sons.

In contrast, the optimal strategy for the second wasp is much more variable. Her optimal sex ratio is a function of the number of eggs she lays (T = number of eggs of second female/number of eggs of first female) and the sex ratio produced by the first wasp. When both wasps lay the same number of eggs, then $T = 1$. As shown in Figure 2a, the optimal sex ratio of the second wasp is very sensitive to relative brood size. When she lays relatively few eggs into the host, she should produce 100% sons, but if

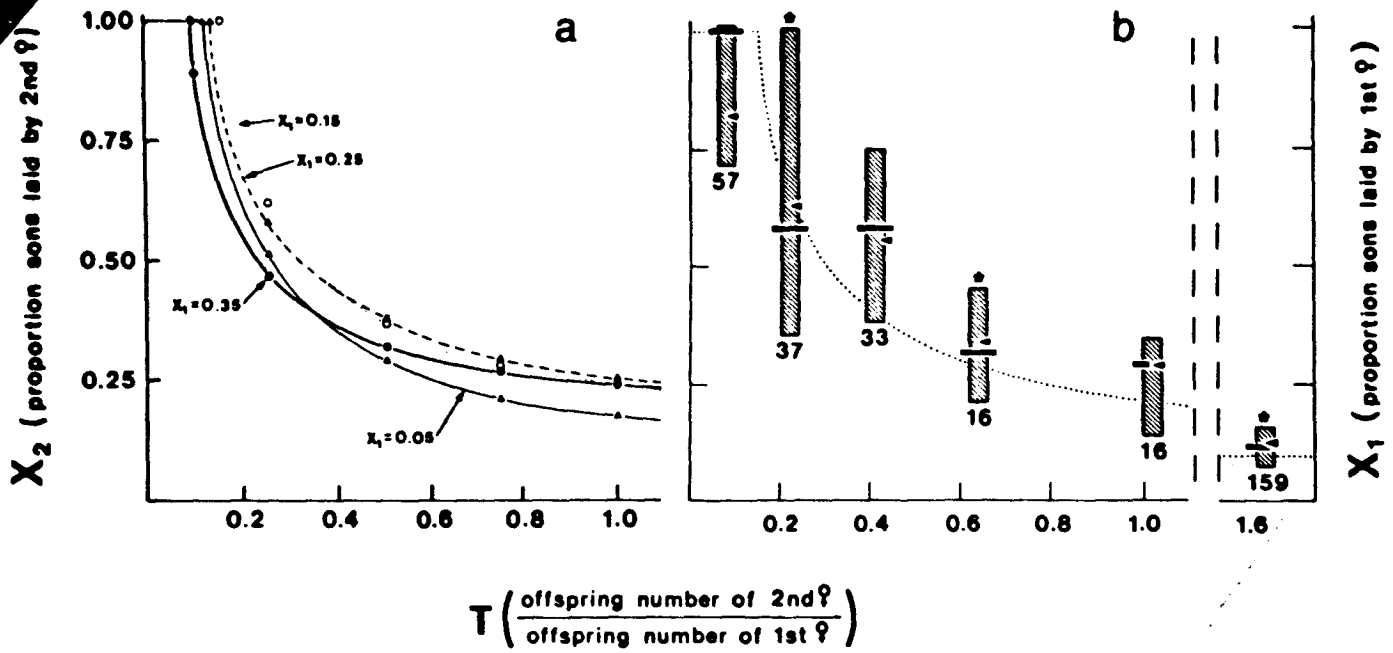

Figure 2. a. The predicted optimal sex ratio of a second wasp parasitizing an isolated host is shown as a function of her brood size relative to that of the first wasp. Generally, the second wasp should produce all sons when laying few eggs, but employ a female bias when laying a larger number of eggs into the host. The curves were calculated from an optimality model. b. Data from *N. vitripennis* that support the prediction outlined above. The dotted curve is the expected sex ratio. The black horizontal bars are the median sex ratio and the shaded vertical bars show the distribution of the first 25% of data to either side of the median. The stars indicate differences signifiant at the 0.001 level. Expected and observed sex ratios for the first wasp are shown at the left.

she lays more eggs into the host, her optimal sex ratio declines rapidly to approximately 25% sons.

Why is the second wasp's sex ratio so strongly influenced by the number of eggs she lays on the host? The answer is best understood by considering a numerical example. This example counts "sets of grandchildren" that a second wasp would get by producing different sex ratios. Sets of grandchildren are achieved both through sons and through daughters. There is no inbreeding depression in *Nasonia*.

Suppose the first wasp typically produced 1 son and 20 daughters. Now suppose the second wasp laid one egg on the host. If she made that egg a son, on average that son would get half of the 20 matings from the host, or ten sets of grandchildren. However, if that one egg were a daughter, the second wasp would only get one set of grandchildren. Obviously, it pays to make a son.

Now, suppose the second wasp laid ten eggs on the host. If she produced all sons she would get 10/11 of 20 matings, or 18 sets. Producing all daughters yields only ten sets. For a mixed sex ratio of 40% sons, she would get 4/5 of 26 matings from sons plus 6 sets from daughters, or 27 sets—the maximal return for ten eggs. Clearly, it pays to produce a mixed sex ratio under these conditions.

The numerical example does not include such complexities as genetic relatedness or inbreeding depression, but it does capture the essential features. There is not a great deal of difference between 4/5 and 10/11 of the matings, i.e., a parent does not gain much by producing six additional sons. This effect is the essence of local mate competition. In addition, by producing six more daughters, there are that many more potential mates available for sons, i.e., local mate advantage. These interacting forces favor the wasp to adjust its sex ratio in response to brood size.

This model has been tested in the laboratory using genetically marked strains. Figure 2b shows the remarkable ability of this parasitic wasp to adjust its sex ratio in response to relative brood size. The wasp produces mostly sons when the relative brood size is small and mostly daughters when the relative brood size is large. The predicted curve is shown by the dotted line, with the median sex ratio and first quartile (25% of data) to either side of the median shown for five brood-size categories.

The general fit between observed and predicted sex ratios is striking. However, there is also a great deal of variation from the median value. The wasp is clearly not producing a precise sex ratio in response to relative brood size, and the natural selection model does not explain this variation (Orzack and Parker 1986).

There are several possible explanations. Selection may be weak or variable for this character and therefore the response has not canalized, i.e. become relatively insensitive to environmental variation. Alternatively, the wasp may be unable to precisely control its sex ratio or to accurately assess relative brood size. The wasp may also be responding to other factors (such as host quality) not assessed by the experimenter. Current data suggest that the wasp does not accurately assess relative brood size, and therefore she alters her sex ratio in response to her absolute brood size.

Studies of sex-ratio responses to population structure have been remarkably successful in predicting

eneral quantitative patterns of sex ratio behavior, but so far have not adequately explained variation in the patterns.

Resource quality

The resources that a parent provides for offspring can vary in quality. If that variation affects the fitness of males and females differently, then natural selection can act so that parents alter sex allocation in response to resource quality (Charnov 1979, Trivers and Willard 1973). There is ample evidence that wasps and bees do just this.

Consider host size in parasitic wasps. Many wasp species lay single eggs within a host, and the size of the developing wasp is constrained by the size of its host, i.e., large hosts produce large wasps and small hosts produce small wasps. Now suppose that size has a major effect on the fitness of one sex, but not on the fitness of the other. For example, in many parasitic wasps size has a major effect on female fitness because large females can produce more eggs over their lifetime (Charnov et al. 1981). In wasps where males do not physically compete with each other for mates, size seems to have much less effect on male fitness.

It is easy to see that in such a species, wasp parents are selectively favored to produce daughters in large hosts and sons in small hosts. However, it is not that simple. Obviously, if only large hosts were available, it would become profitable to put sons in large hosts also. Thus, the actual sex ratio to be produced depends in a complex manner on the distribution of host sizes.

Host size effects on sex ratio have been documented in many parasitic wasp species (Clausen 1939). One complicating factor is that females may be less likely to survive in small hosts than in large hosts, thus creating a sex-ratio shift. However, in many species it has been unequivocally demonstrated that females alter their primary sex ratio in response to host size (Charnov 1982).

Theoretical treatments have investigated in more detail how a parent should adjust its sex ratio to resource quality (Charnov 1979, Charnov et al. 1981, Werren 1984). As applied to host size, these models make two general predictions. First, host size is relative. What is a large host in one situation may be a small host in another. Therefore, the sex ratio produced on a host should depend not on its absolute size, but on its relative size. Generally, more males should be produced when the host is relatively small and more females when it is relatively large.

The second prediction is that the frequency of any host size in the population affects the optimal sex ratio to be produced on it. For example, when small hosts are rare a wasp should put mostly males into them, but when small hosts are common, a greater proportion of females should be put in them. Why? Because there is less profit in producing excess sons relative to (even) small daughters when the population is glutted with males from small hosts. Wasps should alter their sex ratio on any host size based upon the perceived distribution in the population.

How do these models perform in experiments? Only a few species have been examined in detail, with mixed results. One case that shows the effect of relative host size is the wasp *Lariophagus distinguendus*, which attacks larvae of the common granary weevil. In a group of weevil larvae, the wasp produces mostly daughters on a host of a particular size when that host is large compared with the others available and mostly sons when the same host size is relatively small (Charnov et al. 1981, van den Assem 1971).

L. distinguendus also alters sex ratios in response to the frequency of large and small hosts, generally producing more females on small hosts when they are relatively more common. *Anisopteromalus calandrae*, another parasite of granary beetles, also adjusts sex ratio on hosts based on the frequency of large and small hosts encountered (van den Assem et al. 1984).

In contrast, although the wasp *Heterospilus prospoides* (also a parasite of larval weevils) lays more sons on small hosts and more daughters on large hosts, it does not adjust sex ratio in response to relative host size. Nor does it respond to frequency of host sizes (Jones 1982). Which species respond to changes in frequency of host sizes and relative host size, and which species do not, may reflect which wasp species meet the assumptions of the models.

A crucial assumption is that the wasp can somehow perceive the overall distribution of host sizes parasitized in the population. The most likely way for a wasp to do this is to respond to its own parasitization experience. There is good evidence that individuals in certain species alter sex ratio based on prior experience (van den Assem et al. 1984). The crucial question then becomes to what extent does the experience of any individual correlate with the overall parasitization in the population?

Obviously, each individual in a population will not parasitize the same host size distribution. Both sampling and spatial variation are expected. In species with a weak correlation between individual and population experience, there would be no selective advantage for individuals to alter sex ratio with experience. One might then expect the pattern observed in *H. prospoides*. On the other hand, in species where host size changes seasonally, there could be a reasonable correlation between individual and population trends, which would favor a wasp to adjust sex ratio according to its experience.

Many of these species, such as *L. distinguendus*, may also be subject to local mate competition (Werren 1984). In a small local population there is a stronger correlation between individual and population experience because any single foundress contributes a large proportion to the local population.

Many other aspects of resource quality can affect wasps and bees. For example, females of certain solitary bees and wasps construct cells within crevices (such as hollowed-out twigs) where they place an egg and pollen, for food. This behavior is called trap-nesting. The adult size of the resulting offspring is constrained by cell diameter and the amount of food put into the cell.

Considerable data have been collected on some trap-nesting bee species because they are important in pollination of agricultural crops such as alfalfa (Tepidino and Parker 1987). A consistent pattern is that males are produced in small trap nests and fe-

males in large trap nests (Charnov 1982, Tepidino and Parker 1987). A similar pattern occurs in solitary wasps that build nest cells of different sizes (Freeman 1981).

Size affects the fitness of males and females differently in many species. The same basic principles outlined here for parasitic wasps also apply to such diverse groups as orchids, nematodes, mollusks, shrimp, and labroid fishes (Charnov 1982). In all these species, one sex benefits more from being large than does the other sex, and each shows some form of labile sex allocation. Indeed, the basic condition of size benefiting one sex more than the other is likely to be met in so many species that a true quandary is why more species do not show labile sex allocation (Policansky 1982, Warner 1978).

Seasonality

In some cases, seasonality can influence optimal sex allocation (Werren and Charnov 1978). For example, consider a species in which individuals have at most two reproductive periods in their lifetime, one in the spring and one in the autumn. Under these circumstances natural selection can favor individuals that produce different sex ratios in the spring and autumn. Two conditions are necessary for this to occur, overlap in generations and asymmetry in this overlap between the sexes.

These conditions are best understood by taking an extreme example. Suppose that males and females born in spring reproduce in the autumn, but cannot overwinter and therefore die. Of those born in the autumn, females reproduce in the spring and then die, while males reproduce in the spring and some survive to reproduce again the following autumn (Figure 3).

In this example only males have an overlap in the generations, but similar results follow if both males and females have overlap, as long as there is some asymmetry in the degree of overlap. Natural selection favors parents that produce a male bias in autumn and a female bias in spring. If the overlap from autumn males is large, then large deviations in sex ratio can be favored. Fitness of sons from the spring generation is devalued by the reproductive competition they face in the autumn from males from the previous year.

Seger (1983) found that facultative sex-ratio shifts are also expected when more complicated (and realistic) seasonal life histories are considered. He showed that seasonal life histories common to some solitary bees favors production of a female bias in the autumn generation.

Other presocial hymenopteran species have life histories that select for male-biased sex ratios in the autumn generation. Data on several of these species clearly show a seasonal sex-ratio shift, as seen in Table 1.

Seger also made the important observation that seasonal sex ratio shifts can predispose a presocial bee or wasp to evolve sociality. Due to the inheritance pattern of haplodiploidy, female hymenopterans are genetically more related to their sisters (sharing 3/4 of their genes) than to their own offspring (sharing 1/2 of their genes), and they are less related to brothers (sharing only 1/4 of their genes) (Hamilton 1964).

As a result of this relationship, natural selection will favor females that remain and assist their mother in rearing of offspring, rather than going off to rear their own offspring, if they can preferentially invest in sisters rather than brothers (Trivers and Hare 1976). If a presocial wasp or bee produces a female-biased sex ratio late in the season, then natural selection predisposes the daughters produced earlier to remain as workers. Supporting this view, Seger (1983) has found that primitively eusocial

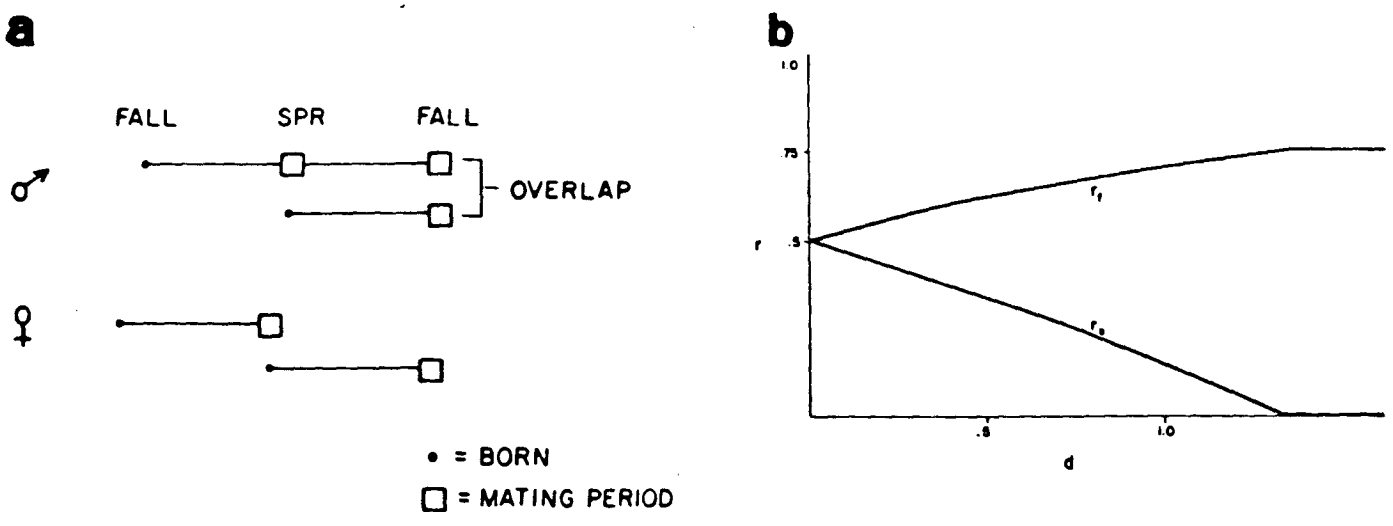

Figure 3. a. Hypothetical life history is shown that favors a seasonal shift in the sex ratio, (●) indicates birth and (□) indicates reproduction. Males and females born in the spring reproduce in the autumn, but cannot overwinter and therefore die. Of individuals born in the autumn (and overwinter), females reproduce only once, but males are longer lived and reproduce in spring and autumn. Therefore, a parent is favored to produce a male bias in autumn and a female bias in the spring. b. Theoretically, the degree of the bias (r = proportion sons) depends upon the amount of overlap (d) between autumn- and spring-born males. Overlap is defined as $d = N_a S_a / N_s S_s$ where N_a is the number of individuals born in the autumn, N_s is the number of individuals born in the spring, S_a is the survival of autumn-born males to the next autumn, and S_s is the survival of spring-born males to the next autumn.

pecies typically have life history patterns that favor female-biased sex ratios later in the season.

From a primitive social situation, more complex sociality could then evolve—for example, the evolution of sterile castes. In complex social species (e.g., honeybees and ants), there is potential conflict between the queen and workers over sex allocation, and some biologists believe that this type of conflict may be important in the maintenance of sociality (Trivers and Hare 1976). The role of sex allocation in the evolution and maintenance of insect sociality is very controversial (Andersson 1984, Evans 1977). Sex ratios in presocial and social Hymenoptera therefore promise to be an area of active research in the future.

Table 1. Sex ratios from field populations of various solitary wasps and bees with two reproductive periods are shown. Many of these species have significant seasonal shifts in sex ratio, as predicted by theory. Sex ratio is expressed as number of males/number of females. Data from Seger (1983).

	Early season	Late season	P
Pompilidae			
Dipogon sayi	0.36 (33)	0.55 (11)	(0.3)
Eumenidae			
Ancistrocerus antilope	0.33 (12)	0.84 (31)	0.002
A. antilope	0.09 (76)	0.67 (103)	0.0005
A. catskill albophaleratus	0.30 (254)	0.85 (40)	0.0005
Euodynerus foraminatus	0.50 (133)	0.52 (56)	(0.3)
E. foraminatus	0.47 (552)	0.52 (318)	(0.2)
E. leucomelas	0.32 (44)	0.54 (28)	(0.06)
Sphecidae			
Pemphredon lethifer	0.32 (111)	0.59 (533)	0.0005
Passaloecus ithacae	0.29 (28)	0.31 (70)	(0.8)
Megachilidae			
Megachile relativa	0.32 (115)	0.54 (331)	0.001
M. mendica	0.70 (33)	0.54 (76)	(0.2)
M. inermis	0.17 (6)	0.88 (17)	0.01

Patterns of inheritance

Most theories of sex-ratio evolution either implicitly or explicitly assume autosomal genetic control over the sex ratio. Autosomal genes reside on the chromosomes and are transmitted to future generations through both sexes. As a result, selection favors a balance between male and female production.

In contrast, cytoplasmic genes are typically inherited within the egg cytoplasm. Virtually every known case of cytoplasmic inheritance, from mitochondria and chloroplasts to intracellular symbionts, occurs through the female line (Grun 1976). This asymmetric transmission of inheritance creates strong selective pressure for cytoplasmic genes that distort sex ratio toward female production, since this is the only sex that transmits the cytoplasmic genes to future generations.

As a result, there is genetic conflict between cytoplasmic genes and chromosomal genes over sex allocation. Cytoplasmically inherited factors that change the sex ratio of eggs, alter sex determination, or kill males are found in such diverse organisms as mites, isopods, mosquitoes, fruitflies, parasitic wasps, and plants (Uyenoyama and Feldman 1978). Most of these factors are microorganisms, such as rickettsia, spiroplasms, microsporidia, and viruses, that reside in the host cytoplasm.

There is a second source of genetic conflict over sex allocation. Meiotic drive occurs when one chromosome is overrepresented relative to its homolog among gametes of an individual. In species with two sex chromosomes (e.g., X and Y), any gene on a sex chromosome that increased its frequency at the expense of the other chromosome in the gametes would be strongly favored by natural selection, and thus cause a distortion in the sex ratio (Hamilton 1967). Such sex chromosome drives have been found in nature (Uyenoyama and Feldman 1978).

There is very strong selective pressure on all three kinds of genetic elements—autosomal genes, sex-linked genes, and cytoplasmic factors—to produce different sex ratios. As a result of this, gene wars over sex allocation are inevitable. We do not know how these genetic conflicts are resolved. It is generally believed that autosomal genes control allocation, but the existence of meiotic drive and cytoplasmic sex ratio distortion in a wide range of taxa indicates that autosomes do not always triumph.

An extensive assemblage of sex-ratio distorters occurs in the parasitic wasp *N. vitripennis* (Huger et al. 1985, Skinner 1982, 1983, 1985, Werren and van den Assem 1986, Werren et al. 1981, 1986). This fascinating system has three extrachromosomal factors, each of which distorts the sex ratio in a different way. Approximately 26% of females in natural populations carry at least one of these factors.

Maternal sex ratio *(msr)* is a maternally transmitted factor that causes wasps to produce nearly 100% daughters. Sonkiller *(sk)* is a maternally and infectiously transmitted bacterium that causes male eggs to die.

The third factor, paternal sex ratio *(psr)*, is the most unusual of all. Although most known cases of cytoplasmic inheritance are maternally transmitted, *psr* is paternally transmitted and causes the production of all-male families. The factor is transmitted to fertilized eggs with the sperm, but then causes destruction of the paternal chromosomes. The resulting egg is therefore haploid and develops into a male. Since *psr* is paternally inherited, the production of all-male families greatly enhances its transmission to future generations. By contrast, the fitness of chromosomal genes in *psr* males is severely reduced because the chromosomes are destroyed by *psr*. Therefore, there is obviously strong genetic conflict between the *psr* factor and the chromosomal genome. Such sex-ratio distorters may eventually serve to provide useful biological agents for controlling pests.

Conclusions

Sex allocation is a fundamental characteristic of sexual species. It is an area where evolutionary theory can be tested quantitatively. Sex allocation is relatively easy to quantify in most organisms, and we have a basic understanding of the selective processes operating on it.

One unifying principle that applies to all sex allocation systems is that of asymmetric transmission. Whenever genes have a higher transmission through one sex than the other (e.g., due to population structure, seasonality, resource quality, or patterns of inheritance), selection will favor genes that increase production of that sex.

What can be concluded about sex allocation in wasps and bees? Many species of wasps and bees can control the sex of their offspring because of their haplodiploid sex determination. Great progress has been made in recent years in characterizing sex allocation in this group. Qualitative, and in some cases quantitative, predictions have been substantiated for sex-allocation models relating to population structure, resource quality, seasonality, and patterns of inheritance. Indeed, the wasps and bees have provided some of the clearest demonstrations of how selection acts upon sex allocation.

However, other aspects of these systems are not adequately explained by current theory. For example, the variations that exist between species in sex allocation have not been explained. In addition, little is known of the mechanisms involved in labile sex ratios. Not surprisingly, as scientists learn more about these systems, more questions appear to be generated than answered. Nevertheless, sex allocation promises to be an area where rigorous tests can be performed on quantitative theories of evolutionary adaptation.

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References cited

Andersson, M. 1984. The evolution of eusociality. *Annu. Rev. Ecol. Syst.* 15: 165–189.

Charnov, E. L. 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. *Am. Nat.* 113: 465–480.

_____ 1982. *The Theory of Sex Allocation.* Princeton University Press, Princeton, NJ.

Charnov, E. L., R. L. Los-den Hartogh, W. T. Jones, and J. van den Assem. 1981. Sex ratio evolution in a variable environment. *Nature* 289: 27–33.

Clausen, C. D. 1939. The effect of host size upon the sex ratio of Hymenopterous parasites and its relation to methods of rearing and colonization. *J. NY Entomol. Soc.* 47: 1–9.

Colwell, R. K. 1981. Group selection is implicated in the evolution of female-biased sex ratios. *Nature* 290: 401–404.

Evans, H. E. 1977. Extrinsic versus intrinsic factors in the evolution of insect sociality. *BioScience* 27: 613–617.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection.* Oxford University Press, New York.

Frank, S. A. 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution* 39: 949–964.

Freeman, B. E. 1981. Parental investment and its ecological consequences in the solitary wasp, *Scehphron assimile* (Dahlborn) (Sphecidae). *Behav. Ecol. Sociobiol.* 9: 261–268.

Grafen, A. 1984. Natural selection, kin selection and group selection. Pages 62–84 in J. R. Krebs and N. B. Davis, eds. Behavioural Ecology: an Evolutionary Approach, 2nd ed. Blackwell Scientific Publ., Oxford, UK.

Grun, P. 1976. *Cytoplasmic Genetics and Evolution.* Columbia University Press, New York.

Hamilton, W. D. 1964. The genetical evolution of social behavior, I & II. *J. Theor. Biol.* 7: 1–52.

_____ 1967. Extraordinary sex ratios. *Science* 156: 477–488.

Herre, E. A. 1985. Sex ratio adjustment in fig wasps. *Science* 228: 896–898.

Huger, A., S. W. Skinner, and J. H. Werren. 1985. Bacterial infections associated with the son-killer trait in the parasitoid wasp, *Nasonia* (= *Mormoniella*) *vitripennis*. *J. Invest. Pathol.* 46: 272–280.

Jones, W. T. 1982. Sex ratio and host size in a parasitoid wasp. *Behav. Ecol. Sociobiol.* 10: 207–210.

Orzack, S. H., and E. D. Parker, Jr. 1986. Sex-ratio control in a parasitic wasp, *Nasonia vitripennis*. I. genetic variation in facultative sex-ratio adjustment. *Evolution* 40(2): 331–340.

Policansky, D. 1982. Sex change in plants and animals. *Annu. Rev. Ecol. Syst.* 13: 471–495.

Seger, J. 1983. Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature* 301: 59–62.

Skinner, S. W. 1982. Maternally inherited sex ratio in the parasitoid wasp, *Nasonia vitripennis*. *Science* 215: 1133–1134.

_____ 1983. Extrachromosomal sex ratio factors in the parasitoid wasp, *Nasonia* (= *Mormoniella*) *vitripennis*. Ph.D. dissertation, University of Utah, Salt Lake City.

_____ 1985. Son-killer: a third extrachromosomal factor affecting sex ratio in the parasitoid wasp, *Nasonia* (= *Mormoniella*) *vitripennis*. *Genetics* 109: 745–754.

Suzuki, Y., and U. Iwasa. 1980. A sex ratio theory of gregarious parasitoids. *Res. Popul. Ecol.* 22: 366–382.

Taylor, P. D. 1981. Intra-sex and inter-sex sibling interactions as sex ratio determinants. *Nature* 291: 64–66.

Tepidino, V. J., and F. D. Parker. 1987. Alternation of sex ratio in a partially bivoltine bee, *Megachile rotindata* (Hymenopteria: Megachilidae). *Ann. Entomol. Soc. Am.*, in press.

Trivers, R. L., and H. Hare. 1976. Haplodiploidy and the evolution of social insects. *Science* 191: 249–263.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90–92.

Uyenoyama, M. K., and M. W. Feldman. 1978. The genetics of sex ratio distortion by cytoplasmic infection under maternal and contagious transmission: an epidemiological study. *Theor. Popul. Biol.* 14: 471–497.

van den Assem, J. 1971. Some experiments on sex ratio and sex regulation in the Pteromalid *Lariophagous distinguendus*. *Neth. J. Zool.* 21: 373–402.

van den Assem, J., F. A. Putters, and Th. C. Prins. 1984. Host quality effects on sex ratio of the parasitic wasp *Anisopteromalus calandrae* (Chalcidoidea, Pteromalidae). *Neth. J. Zool.* 34: 33–62.

Waage, J. K. 1982. Sib-mating and sex ratio strategies in scelionid wasps. *Ecol. Entomol.* 7: 103–112.

Warner, R. R. 1978. The evolution of hermaphroditism and unisexuality in aquatic and terrestrial vertebrates. Pages 78–101 in *Contrasts in Behavior.* E. Reese, ed. Wiley Interscience, New York.

Werren, J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* 208: 1157–1159.

_____ 1983. Sex ratio evolution under local mate competition in a parasitic wasp. *Evolution* 37: 116–124.

_____ 1984. A model for sex ratio selection in parasitic wasps: local mate competition and host quality effects. *Neth. J. Zool.* 34: 81–96.

Werren, J. H., and E. L. Charnov. 1978. Facultative sex ratios and population dynamics. *Nature* 272: 349–350.

Werren, J. H., S. W. Skinner, and E. L. Charnov. 1981. Paternal inheritance of a *daughterless* sex ratio factor. *Nature* 293: 467–468.

Werren, J. H., S. W. Skinner, and A. Huger. 1986. Male-killing bacteria in a parasitic wasp. *Science* 231: 990–992.

Werren, J. H., and J. van den Assem. 1986. Experimental analysis of a paternally inherited extrachromosomal factor. *Genetics* 114: 217–233.