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REPRODUCTIVE DYNAMICS AND OFFSPRING ALLOCATION IN FIG WASPS

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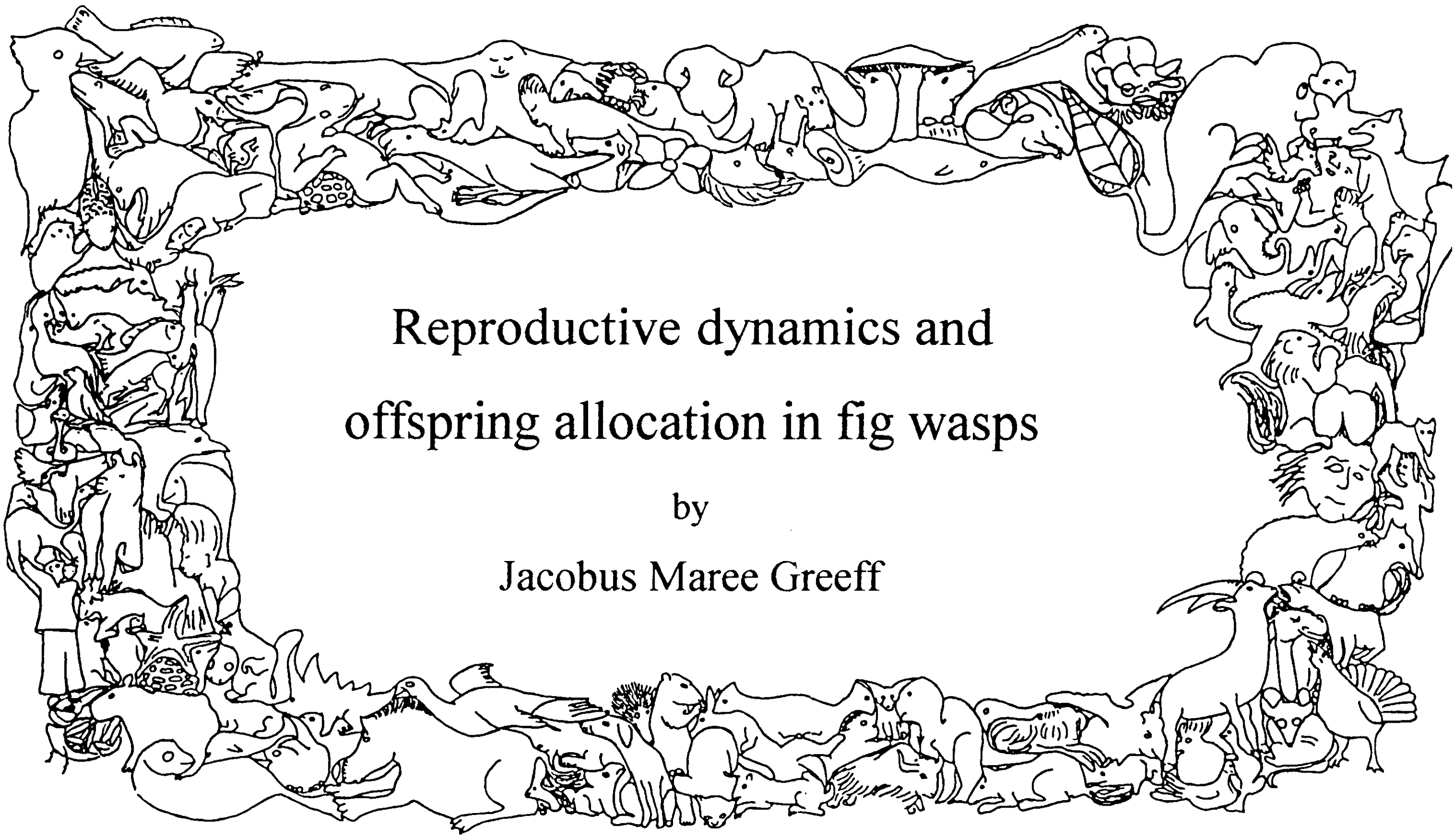

Reproductive dynamics and offspring allocation in fig wasps

by

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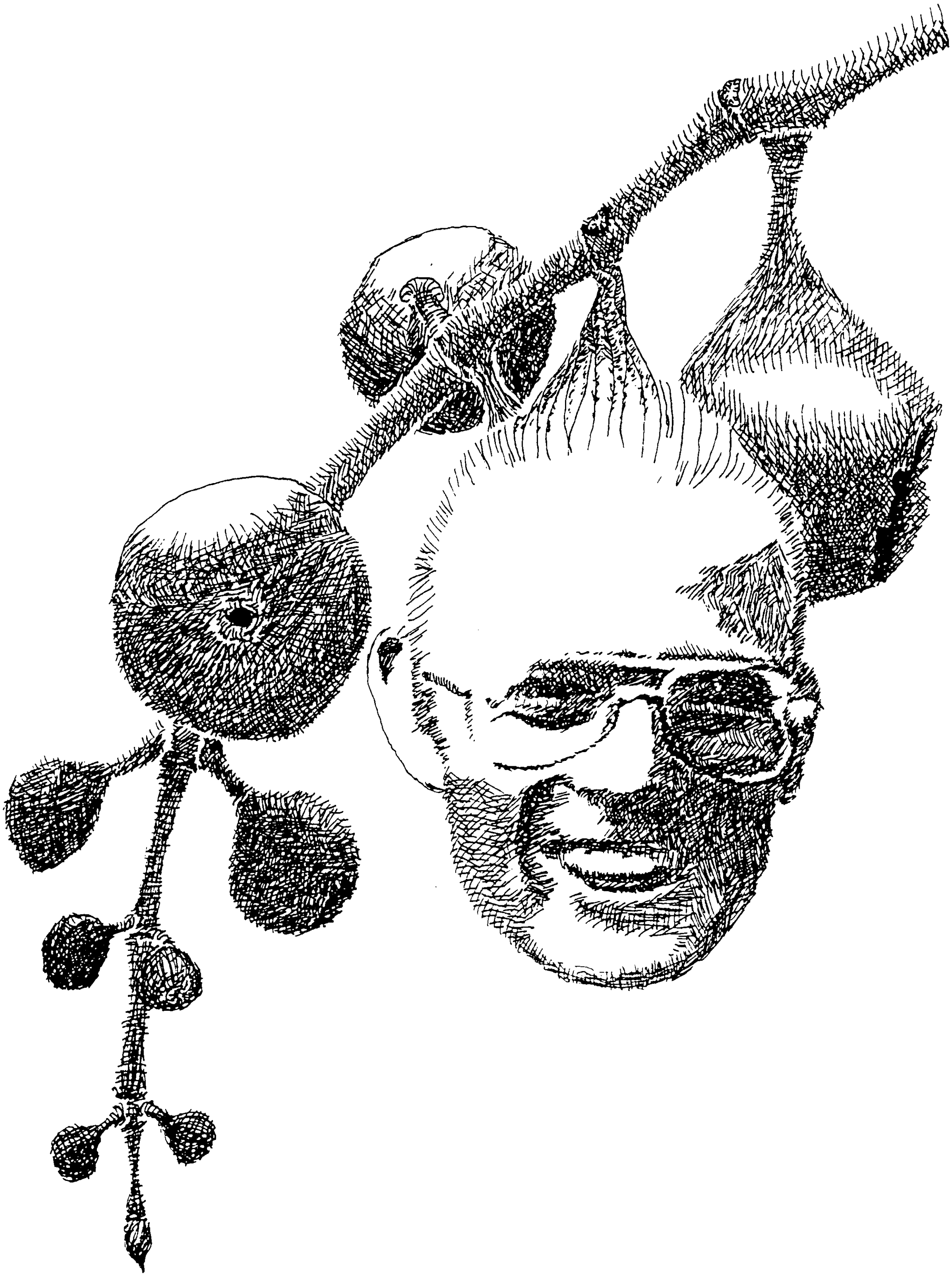
"Ek het oral op die aarde rondgegrawe
grawe grawe hande in die hare, o ja
want ek is honger"
Johannes Kerkorrel



Abstract

This thesis considers problems in sex ratio theory, especially those posed by fig wasps. In structured populations with male dimorphisms for dispersal, optimal sex ratios depends on the frequencies of the morphs. Species with relatively more dispersing males should have relatively less female biased sex ratios when foundress number is kept constant. The frequencies of male morphs are affected by two factors. Firstly, the proportion of females that can be mated by either. Secondly, the frequency of the non-dispersing male morph decreases as the likelihood of local mate competition against brothers increases.

Females are envisioned to adjust their sex ratios to the average relatedness of daughters to mothers. If females can determine their relatedness to their mates, they can conditionally adjust their sex ratios to more accurate estimates of their daughter's relatedness to them. Sibmated females should produce more female biased sex ratios than outbred females (except when very high inbreeding depression occurs) resulting in a split sex allocation pattern in the population. Split sex ratios are conducive to the evolution of eusociality.

When female fig wasps simultaneously adjust their sex ratio and clutch size, a dichotomous oviposition pattern should evolve. Females either produce large very female biased clutches or one male egg clutches. This allocation strategy reduces the relatedness of males sharing figs, which in turn, allows the evolution of fatal fighting in certain wasp species.

Local mate competition models normally assume that females can produce exact sex ratios. When females' sex ratios are imprecise and varies randomly it may affect the average predictions of models. It is shown that variation, unless extremely high, will not affect the predicted sex ratios.

Pollinating females are able to oviposit sequentially. This can affect the predicted optimal sex ratios by skewing the relative reproductive contributions of initial and subsequent foundresses. Second females have more information than the first ones and can produce a conditionally optimal sex ratio. Contrastingly, the first females need to produce sex ratios that have to be optimal for a variety of foundress numbers. Such average strategies can explain the variation in single foundress data.

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1. Introduction

The study of sex ratios is fascinating. Like so many other fields, it was Darwin who first recognised the general problem. Since then the field has grown immensely, with several books reviewing the subject (Charnov 1982; Karlin and Lessard 1986; Pamilo and Crozier 1996; Wrensch and Ebbert 1993). In addition, sex ratio studies have interacted fruitfully with other disciplines, often creating the mathematical medium for realising and developing fundamental evolutionary concepts (Table 1). Moreover, theoretical predictions have been qualitatively and frequently, quantitatively accurate (Godfray and Werren 1996). Seen from a purely theoretical viewpoint, sex ratio studies have and continues to be a field worthy of enquiry.

Fig wasps were introduced to the study of sex ratios and behavioural ecology by Hamilton (1979). In this and subsequent studies of sex ratios (Frank 1985a; Herre 1985, 1987, 1989; Nefdt 1989), fig wasps have turned out to be a text book example, where data closely fit model predictions (Godfray 1994; Werren 1987). Hamilton (1979) also recognised a number of other phenomena which begged explanations. One such phenomenon is the male dimorphism of many fig wasp species. He argued that frequency dependant selection can sustain the dimorphism in the morphology and mating behaviour of males. Fig wasps have also been an important model organism for a number of other evolutionary problems unrelated to sex ratios (Table 2). Despite all this attention, many questions remain unanswered, some of which I address in this work.

In South Africa a number of evolutionary biologists tend to be highly critical of the pre-eminent importance of natural selection and hence of the optimisation methods used in this thesis. There also exists a general aversion to and apathy about the importance of modelling in evolutionary biology. This apathy is reflected in the dearth of modelling papers presented at the annual Symposia of the Zoological Society of Southern Africa and during informal conversations with staff and students. In these circles, the assumptions of this approach are often misunderstood leading to the erroneous invalidation of the field of inquiry. I thus find it necessary to explicitly state and explain the assumptions that are important when using these techniques. I therefore use this introductory chapter to briefly overview the optimisation research program, evolutionary game theory and inclusive fitness, in addition to fig wasp sex ratios.

Table 1. A few examples of concepts that were created or developed through the study of sex ratios.

Unbeatable sex ratio strategy - precursor to evolutionary stable strategy (Hamilton 1967)
Parent-offspring conflict (Trivers and Hare 1976)
Relationship of group selection to inclusive fitness (Colwell 1981; Frank 1985a; Nunney 1985)
Continuous stable strategy - distinction between m- and δ-stability (Eshel 1981; Taylor 1989)
Evolution of eusociality (Iwasa 1981; Grafen 1986)
Sex determination (Bull 1983)
Expansion of Price's equation to hierarchical selection (Frank 1986a)
Virginity and constrained sex allocation (Godfray 1988)

Table 2. Important topics that use fig wasps as model species, but are unrelated to sex ratio studies

Coevolution (Herre 1989, 1993; Janzen 1970; Wiebes 1970)
Fatal fighting & male morphology (Hamilton 1979; Murray 1987, 1989, 1990; Vincent 1991)
Evolution of Dieocy (Kjellberg et al. 1987; Godfray and Grafen 1991)
Mutualism (Bronstein 1989; Bronstein and McKey 1989; Nefdt and Compton 1996)

Forces and factors in evolution

Darwin (1859) laid the foundations for evolutionary theory by identifying the process of natural selection. In so doing, he created a frame of mind to interpret nature. Although the process of evolution, as opposed to *de novo* creation, is no longer contentious among biologists, the importance of the process and outcome of natural selection are still hotly debated. Darwin identified several factors that are important in understanding variation in nature. One of these was the importance of history, which he used in his argument against creationism. He felt that the constraining element of historicity can explain "why nature is prodigal in variety, though niggard in innovation" (Darwin 1859, 445). This notion, that animals are constrained by their present form and past evolution to evolve in only certain directions, is very relevant to the use of optimality theory. However, Darwin is most strongly identified with the concept of natural selection. There is no question that he felt natural selection to be an extremely important cause of evolution: "If then we have under nature variability and a powerful agent always ready to act and select, why should we doubt that variations in any way useful to beings ... would be preserved, accumulated and inherited?" (Darwin 1859, 443).

Darwin's argument can be summarised as follows; there is variability in phenotypes and their reproductive potentials, the phenotypes of offspring correlate with that of their parents (laws of inheritance) and more individuals are created than can possibly survive. Given these three tenets, it follows that those phenotypes (A) that survive and reproduce better than others (B) will contribute more to future generations, and since phenotypes are inherited, the A phenotypes will become predominant. Darwin also argued that new varieties or modifications continue to be produced and are thus the "wood to keep the fire burning". Clearly, Darwin had an appreciation of the importance of inheritance and the production of new variation (mutation). One of the difficulties felt by Darwin was the blending nature of inheritance, i.e. the phenomenon that the phenotype of an offspring is often halfway between that of the two parents. Such blending will "dilute" variants that are biased in the advantageous direction and eventually nullify the effect of natural selection. This difficulty was resolved with the rediscovery of Mendel's theory of particulate inheritance. Mendel showed that phenotypes are inherited in discrete packages that are not blended with each other, but remain intact. Mendelism and Darwinism were combined by Fisher, Haldane and Wright to give the New

Synthesis. This synthesis was basically the same as Darwin's, except that we have a clearer understanding of how inheritance actually operates. Consequently, it is possible to calculate how natural selection on an allele for a specific phenotype may be influenced by various factors, such as epistasis, linkage, pleiotropy, genetic drift, migration and mutation.

It may be important to incorporate the genic interactions and regulation of gene expression into population genetic models. Kauffman (1993) showed that if systems of genes have a high connectivity (when the activity at one gene is affected by a large number of other genes and in turn affects the expression of a large number of other genes), natural selection will not be very effective because selection on one allele affects that of others. The general importance of his models still needs to be confirmed and will depend on the prevalence of the high connectivity he envisions. In fact, Kauffman's models may explain why the large scale, random interactions between loci may never evolve in the first place (Levinton 1996).

It is also important to note that natural selection is not just important in causing changes in gene frequencies, but also stabilises them (Williams 1992; Reeve and Sherman 1993).

> "I regard it as unfortunate that the theory of natural selection was first developed as an explanation of change. It is much more important as an explanation for the maintenance of adaptation." (Williams 1966, 54)

Now we have the ingredients to model and predict variation in nature given certain relationships between genotype and phenotype. If we can determine the identities and functions of genes that affect a trait, we can predict and study its evolution. However, we seldom know exactly how genes interact to produce specific phenotypes and this sort of inquiry will be both slow and not easy to extrapolate (Grafen 1984). It is of course possible to model certain types of genes, but predictions may depend in unknown ways on the assumptions and interactions between the genetic constitution of the trait and population phenomena (compare Kirkpatrick and Bull 1987 and Nordborg 1991). The underlying mechanisms of genetic models may often be concealed whereas phenotypic models may yield more general answers that are more easily interpreted (Lloyd 1977). Phenotypic models have become very popular in the search for faster and more general or "global" answers for specific groups of traits. This research methodology has recently been described as the optimisation research program (ORP) by Mitchell and Valone (1990).

Optimisation research program

> "When we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond his comprehension; when we regard every production of nature as one which has had a history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, nearly in the same way as when we look at any great mechanical invention as the summing up of the labour, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting, I speak from experience, will the study of natural history become!" (Darwin 1859, 456)

We take to heart these words of Darwin and view organisms - or rather their phenotypes - in terms of their contribution to the fitness of the individual (Maynard Smith 1978), an exercise Charnov (1982) calls "selection thinking". The basis for this approach is that when traits affect fitness they can be expected to have undergone changes due to natural selection subject to constraints (Krebs and McCleery 1984; Maynard Smith 1978; Mitchell and Valone 1990; Parker and Maynard Smith 1990; Stearns and Schmid-Hempel 1987). The aim is thus to uncover the selective forces and historical constraints that may have shaped a trait.

Two points need to be made here: 1) we do not assume, as is often alleged, that all traits are optimal, merely that specific traits are optimal given certain constraints (Krebs and McCleery 1984; Maynard Smith 1978; Mitchell and Valone 1990; Parker and Maynard Smith 1990; Stearns and Schmid-Hempel 1987; Williams 1985). Selection thinking forces one to concentrate on traits that are likely to affect fitness (Maynard Smith 1978). For instance, even though the lines on the palms of our hands may affect our lives dramatically, depending on how much one believes in palmistry, I do not expect any evolutionary biologist to explain these in terms of natural selection. A reasonable critique may thus be that only traits that are important to fitness are studied and others neglected. However, I am not sure that this is a negative point. 2) We do not ignore the effects of historical constraints. In fact they are of paramount importance in delineating the dynamics and boundary conditions of models (see especially Stearns and Schmid-Hempel 1987); without historical constraints, animals would be expected to live forever and produce infinite amounts of offspring clonally (Maynard Smith 1978; in fact such predictions also assume some constraints (Lewontin 1978)). Strictly speaking a trait can therefore only be locally optimal. Historical constraints are also important in that they can prevent a certain optimal state being reached because the starting conditions may canalise the trait in a different direction (Charnov 1982; Maynard Smith 1978).

I subscribe to Mitchell and Valone's (1990) description of the ORP in terms of a scientific research program *sensu* Lakatos (1978; as cited in Mitchell and Valone 1990). A scientific research program can be seen as having a hierarchy of assumptions. A number of these, the hard core assumptions, are the starting point and are most important. However, these are not under scrutiny by practitioners of the program. For an assumption to be part of the hard core, it must have previously proven helpful in many different situations. The ORP has two hard core assumptions that separate it from other branches of evolutionary inquiry (Mitchell and Valone 1990).

The first is the phenotypic gambit (Grafen 1984; Krebs and McCleery 1984; Lloyd 1977; Maynard Smith 1978; Mitchell and Valone 1990; Parker and Maynard Smith 1990; Stearns and Schmid-Hempel 1987): "the relative fitness of strategies near locally stable equilibria are not qualitatively influenced by the transmission properties of the strategies" (Mitchell and Valone 1990). This assumption allows us to ignore the genetics determining the property and to focus solely on the phenotype (Lloyd 1977). The belief is that, in cases where the genetic determination is not able to support the true breeding phenotype, selection will be directed towards the actual genetic determination mechanism (Grafen 1984). Hence, we assume that these genetic constraints will be rare or, at most, transient. Furthermore, it should be kept in mind that there may be many ways to achieve a specific strategy genetically, even though a specific genotype may only specify one strategy. Hence, traits may be quasi-independent (Lewontin 1978), i.e. although selection on a specific gene may affect the desirable trait but also an undesirable trait, other options may exist to achieve the same effect.

The second hard core assumption is that most populations of strategies are at or close to a locally stable equilibrium (Mitchell and Valone 1990, Stearns and Schmid-Hempel 1987). Based on this assumption we seek to find empirical verification of predicted phenomena.

Without this assumption, it is impossible to reject or even confirm models. A possible problem with this assumption is that environments are constantly changing and thus animals may not be close to the local optimum. However, animals move, following appropriate conditions. More importantly, the most important environment for traits is that of the other characters of the organism themselves. An animals is therefore a suite of coevolved characters which should not change as frequently and easily (Stearns and Schmid-Hempel 1987).

The hard core assumptions do not make any testable predictions on their own. Therefore, we need protective belt (or model) assumptions which can be subjected to empirical tests. The actual modelling starts with the model assumptions. The researcher needs to decide which traits can be considered as constraints and which as variables (Stearns and Schmid-Hempel 1987). In behavioural models, informational constraints also play an integral role (Boomsma and Grafen 1991; Parker and Maynard Smith 1990; Stubblefield and Seger 1990; Taylor and Crespi 1994). Constraints do not preclude adaptations but characterise them (Mitchell and Valone 1990). Next, a number of plausible strategies needs to be identified and it needs to be specified how each affects fitness (fitness functions). Although the term fitness is used very loosely here, it is defined precisely in each model. One problem with these definitions is that they are often surrogates for Darwinian or inclusive fitness; feeding efficiency for instance. In such cases, the surrogate currency may be problematic and itself subject to falsification. In sex ratio studies one works directly with the inclusive fitness, thus largely avoiding this currency problem. There are three basic types of model in which fitness functions have specific characteristics. Maynard Smith (1978) classified these as: 1) optimisation, where a strategy needs to be optimised in an environment with no competitors; 2) games, where the environment includes other "players" also trying to optimise their strategies and, lastly, 3) games of inclusive fitness, where some of the players have genes in common. Since sex ratios are games of inclusive fitness, I will expand more on game theory and inclusive fitness below. Once the model assumptions have been made, predictions can be produced that can be tested empirically. Note that a specific model cannot be wrong (excluding mistakes due to negligence of the modeller), just inappropriate.

A test of a model's appropriateness is the next step. This can and should be done at two levels. Firstly, the model assumptions can be tested directly; secondly, the accuracy of model predictions can be tested. If the model explains the data well, we can claim that we have identified at least some of the major selective forces acting on the trait. Note that the match between data and predictions is not just a mere correlation; the fact that the assumptions are causally linked to the predictions suggests that we understand the actual evolutionary mechanism (Endler 1986). Another model with different parameters may also explain the data well. In fact, a lack of alternative models may be a shortfall of the ORP (Stearns and Schmid-Hempel 1987). Also, statistical tests are designed to reject null hypotheses, so that proper statistical tables need to be compiled to accept null hypotheses (Parker and Maynard Smith 1990).

When the model fails to explain the data, it can be as a result of three things: firstly, the core assumptions may be wrong. Even though this may be the case and the specific trait may not be under selection, it will be insane (Williams 1985) to reject the core assumption. In no other scientific field of inquiry is rejection of the hard core required; why should it be the case in evolutionary biology? Secondly, the model assumptions about constraints and fitness functions may be wrong, i.e. the model may be inappropriate. In this case, the model should be re-evaluated and new parameters incorporated and constraints considered. Note that these adjustments are not mere *ad hoc* adjustments to salvage the hard core assumptions because they predict new test cases (Williams 1985; Mitchell and Valone 1990). The adjustments can only be called *ad hoc* if they restrict the model's field of application. For instance, on realising that sex ratios in organisms that mate locally are female biased and not equality, Hamilton (1967) did not claim that Fisher (1930) was correct except for cases where mating is not random. Rather, he incorporated the mating pattern into the model to make new predictions which could be tested. The readjustment of models should thus be seen as a quest to get closer to the relevant factors and not as an attempt to save the hard core assumptions. Several studies of sex ratios have, in fact, argued that their data do not support the notion that sex ratios are adjusted to optimise fitness, i.e. they rejected the hard core assumption (Donaldson and Walter 1991; Nadel and Luck 1992). Subsequently, other workers (Godfray and Hunter 1992; Hunter and Godfray 1995; Taylor 1993) showed that Donaldson and Walter (1991) and Nadel and Luck (1992) had compared their data to inappropriate models. Thirdly, the data might be wrong. This last option is not often acknowledged but may be very important in behavioural studies. For instance, the "same" stimulus might be given to animals; however, this stimulus might not be perceived to be the same by the animals. Furthermore, in sex ratio studies, the primary sex ratio (which is the trait under consideration) may be impossible to determine, with researchers settling for secondary sex ratios. It should be kept in mind that "quantification can set back the cause of science by giving a false air of great certainty of conclusion" (Grafen 1987).

How good should the fit between models and data be? Recently, Orzack and Sober (1994) proposed that, if models quantitatively predict results, then we can assume that natural selection is the only important force affecting the trait. However, I have never heard it claimed from within the ORP that confirmation means that natural selection is the only important factor (Brown 1982). In fact, such an assumption completely ignores the emphasis on historical constraint. Furthermore, they make heavy going of individual variation around the optimality point, arguing that such variation undermines an important assumption of optimality models. But as we have seen, "no-variation " is not an important assumption; in fact Houston and McNamara (1985) and Yoshimura and Shields (1987) have shown that individual variation can be an important constraint that can be incorporated into models. Individual variation can affect the predictions of optimality models. Natural variation in strategies can be non-adaptive noise or it can be fine scale variation in optimality points for individuals (Parker and Maynard Smith 1990). It is also important to note that selective pressure decreases as an optimality point is reached and one may thus expect some variation (Parker and Maynard Smith 1990). Finally, Parker and Maynard Smith (1990) point out that if the estimated model parameters have variance, why should predictions not have variance too? Since variation is not a hard core assumption of the ORP, Orzack and Sober's (1994) obsession with the phenomenon of individual variation in order to topple the ORP, seems illogical. The ORP "will be abandoned if and when we learn of a better device for coping with ...phenomena" (Williams 1985).

The ORP does not claim that traits arise because of natural selection and Gould and Lewontin's (1978) criticism about the origin of traits seems mis-directed. The importance of current utility has been convincingly argued for (Clutton-Brock and Harvey 1978; Reeve and Sherman 1993). In fact, it has been argued recently that the reason(s) for the origin of a trait is basically indeterminable (Frumhoff and Reeve 1994; Leroi *et al.* 1994).

Although the ORP is an extremely useful way to address evolutionary questions, it certainly has shortfalls, especially with regard to genetic peculiarities such as Fisher's runaway sexual selection. The field of enquiry should thus determine which type of model, optimality or a genetic/quantitative, should be used. However, by using both these approaches it may be possible to obtain an idea of the mechanism of genetic determination of a trait.

Although data plays an important role in matching models to reality, it is not necessarily the end goal of all models. Modelling *per se* has merit in that it forces one to think systematically about a problem and identify important factors that might otherwise be overlooked. It can also show how traits may have evolved together (Iwasa 1983) and create the language for future models (see Frank's (1996) discussion of Price (1970)). The rigor of models also makes the claims about local adaptation precise and explicit and the ORP cannot be accused of haphazardly erecting "just so" stories to explain data. The method also clarifies the relation between constraints and adaptation (Stearns and Schmid-Hempel 1987). The strong predictive power of the ORP has the ability to direct future research. "The study passes from the realm of natural history to that of science when the investigator postulates an undocumented remainder of a strategy" (Williams 1985).

Evolutionary games theory

Lewontin (1961) was the first to propose that games theory could be useful in an evolutionary context. He argued that it could be used at a species level to search for the unbeatable strategies species may play against each other. The reason he suggested games theory was because he felt it could give a more global answer to problems than specific genetic models could. This is, of course, exactly the same reason why we use it today at an individual level. Interestingly, Lewontin is one of the most important critics of the ORP (Gould and Lewontin 1979; Rose et al. 1984) and Maynard Smith, the patron of evolutionary game theory, has denounced Lewontin's (1961) suggestions as group selectionist (Maynard Smith 1976).

The current use of game theory stems from a number of studies that considered frequency dependent selection, especially Hamilton's 1967 paper (for history see Maynard Smith 1976, 1982; Parker 1984; Frank 1996). Maynard Smith (1982) consolidated these ideas and the concept of an evolutionary stable strategy (ESS) was born. Games can either be between two individuals or between one individual and the rest of the population. Sex ratio games fall into the second class. In such a game, an ESS is a strategy which, when adopted by all the members of the population, is not invadable by other (mutant) strategies. For traits that are continuously variable the fitness of a mutant adopting strategy v against a population that plays u, can be written down as the function $w(u, v)$. The ESS strategy v^* can then be found by solving for v^* in equation (1)

$$\left.\frac{\partial w}{\partial u}\right|_{u=v=v^*} = 0 \tag{1}$$

Provided that

$$\left.\frac{\partial^2 w}{\partial u^2}\right|_{u=v=v^*} < 0 \tag{2}$$

This condition ensures that v^* obtained from equation (1) is a maximum (Maynard Smith 1982). Eshel (1983) pointed out that not all ESS's that comply to equations (1) and (2) are evolutionary attainable. When a population close to the ESS evolves towards it, and not away from it, the ESS is a continuously stable strategy (CSS). An ESS is a CSS when

$$\left.\frac{\partial^2 w}{\partial u \partial v} + \frac{\partial^2 w}{\partial v^2}\right|_{u=v=v^*} < 0 \tag{3}$$

This condition ensures that a mutation that is closer to the ESS than the current population strategy, will increase. Taylor (1989) found it useful to describe an equilibrium point as m-stable (equation 3) or/and δ-stable (equation 2). Christiansen (1991) argued that only m-stability is of evolutionary importance and that δ-stability or the normal ESS condition is only important in separating the types of dynamics one can expect around an m-stable point. Except for the model in chapter 3, the equilibria I investigated are all m-stable. Most theoretical discussions do not explicitly address the possibility that the left hand side of equation (2) can be zero. The model presented in chapter 3 has this attribute and I call it a weak ESS after Uyenoyama and Bengtsson (1982). It is thus possible for mutants to accumulate in this system as long as this does not adjust the average population value. However, in reality, the assumption of an infinite population size made in chapter 3 is violated and (2) is negative, even if only marginally so. In this regard, the model in chapter 3 resembles Fishers sex ratio model as described by Taylor (1989).

Inclusive fitness and reproductive value

Hamilton (1963, 1964) introduced the concept of inclusive fitness as a heuristic tool to deal with selection on genes that affect the fitness of its carrier and that of relatives. The basic notion is that an allele increasing the reproduction of individuals containing the same allele will have an inflated fitness called inclusive fitness as a result of its social consequences. Although it is easy to see, at least in retrospect, that changes in the frequency of such a gene depend on inclusive fitness rather than only the individual's own fitness, the exact details of inclusive fitness are harder to understand.

Hamilton (1964) proposed an estimate of relatedness (measure of genetic similarity), equal to Wright's coefficient of relationship between individuals, which summarises the actions of kin selection. Subsequently, Hamilton (1970) and other workers (Crozier 1970; Grafen 1985; Michod and Hamilton 1981; Queller 1984, 1992; Seger 1981; Taylor 1989) showed that this initial estimate only held for a given number of restrictive assumptions, the most limiting being that no inbreeding may occur. Since the sex ratio models considered here are all concerned with inbreeding populations, I use the more appropriate regression coefficient of relatedness (Hamilton 1970, 1972). For this estimate to work, we must assume additive gene action and weak selection (Taylor 1989). In haplodiploid taxa, such as fig wasps, the relatedness of sons to mothers is always 1 (Crozier 1970), whereas that of daughters to mothers depend on the amount of inbreeding. When a female mates with a brother or other related male, her daughters will receive genes identical by descent to her from her mate as well as from herself. Hence, inbreeding increase the relatedness of daughters to their mothers. Inbreeding depression reduces the relatedness between daughters and their mothers because inbred individuals contribute less to successive generations (Greeff and Taylor in press). Complimentary sex determination is common in many hymenopterans (Cook and Crozier 1995) and it leads to inbreeding depression in female offspring.

In certain circumstances, relatedness alone is not sufficient to summarise selection on such "social" genes. Certain genetic systems or life history patterns may cause one sex to be more efficient at transmitting the social gene than the other (Benford 1978; Hamilton 1972; Seger 1983). This ability is called the reproductive value of the sex (Taylor 1989) and in haplodiploid species, such as fig wasps, the reproductive value of the female subpopulation is twice that of male subpopulation because females transmit their genes to sons and daughters whereas males only have daughters. We can correct relatedness coefficients by multiplying them with the appropriate reproductive values.

The sex ratio can affect the reproductive success of the sexes (Hamilton 1972; Taylor 1989). For instance, when the sex ratio is female biased, males may fertilise many females and will transmit their genes relatively better than females. The relation of this effect to any sex ratio model is obvious and is just the reverse side of the argument by Fisher, described below. This effect can be combined with the reproductive value of the sex, to give the reproductive value of the indivddual (Taylor 1989).

Lastly, the effect of the gene on the fitness of different individuals may not be the same and this needs to be incorporated when necessary. In sex ratio models, the trait under selection is the sex ratio a female produces. The effect of the behaviour will thus be incorporated in the adjustments of the previous paragraph. However, certain cases are more tricky and require special treatment. For instance, Denver and Taylor (1995) showed that inbreeding depression lowers the reproductive value of a sibmating as compared to an outbreeding event. When a numerical increase in one sex increases the probability of sibmating more than for the other sex, these factors need to be taken into consideration (see chapter 3).

In sex ratio studies, the behaviour under consideration is how a mother divides her resources between sons and daughters. Hence, a system of valuation of sons and daughters incorporating all the points related above must be constructed in order to find an evolutionary stable sex allocation ratio. Furthermore, the payoff of certain sex ratio strategies commonly depends on the strategies of other females making it necessary to frame the models in terms of games theory.

Sex ratios

The field of sex ratios is immense and here I briefly outline its history and certain key concepts that are of importance to the work presented here. In 1871, Darwin asked why it is that the sex ratio (proportion of sons) of so many species is close to one half. The question really is how natural selection would act in a species with a biased sex ratio so as to return the sex ratio to equality. Darwin gave an argument which holds for monogamous species with sons and daughters being equally costly: in a population where the sex ratio is biased towards sex A, some of the parent's resources invested in A offspring will be wasted because they will not be mated. The target of selection would thus be the maximum number of offspring mated. Darwin suggested two ways in which this can be achieved: 1) parents can either skew their sex ratio to the other side to ensure that more offspring are mated, or 2) parents can reduce the number of offspring, but invest more per capita resources in the overproduced sex. These stronger individuals should thus be more likely to become mated. However, Darwin (1874) retracted his argument in the second edition of his book with the oft quoted words, "I now see that the whole problem is so intricate that it is safer to leave the solution for the future". He could not determine how the sex ratio of an individual's offspring can affect that individual's fitness.

This problem went unresolved for 56 years until Fisher (1930) proposed a solution. He realised that the quantity under selection was the reproductive value, which he defined as the extent to which an individual of a certain age will contribute to the ancestry of future generations. Hence, when we value sons and daughters, we should do so in terms of the number of grandchildren they will ultimately produce. He argued that, at the time when offspring become independent of their parents, the reproductive value of males and females should be equal because children receive half their genes from fathers and half from mothers (except haplodiploids, as discussed above). Therefore, parental investment should be selected so that it is equal for the two sexes at the time when offspring become independent. If this is not so, parents who invest more in the sex that is under-invested receive more reproductive value per unit investment. Natural selection then restores the equality of the sex investment. The important shift here is towards investment; hence, if males are more costly to produce, a female biased numerical sex ratio will be evolutionary stable. The other distinction is the separation in time before and after independence of the young. For instance, a male biased mortality before independence will bias the conception ratio towards males, whereas a male biased mortality after independence will not affect the investment ratios.

Over the next 37 years, relatively little progress occurred; a number of models were developed to explain Fisher's argument. In 1966, Williams said: "I would regard the problem of sex ratio as solved". Only a year later, Hamilton (1967) opened a whole new can of worms with his "extraordinary sex ratios" by exposing a number of implicit assumptions in Fisher's argument. Firstly, he pointed out that the reproductive values of genes expressed on X- and Y-chromosomes are not equal for the two sexes. For genes on a Y-chromosome, only the heterogametic sex have any reproductive value; for genes on a X-chromosome (or all the genes of haplodiploids) the sex with only one X-chromosome (or male haplodiploids) are half as valuable as the opposite sex. Secondly, he pointed out that the mating population is often not panmictic but is subdivided into smaller local groups within which matings are random. Such local groups are often the result of females that oviposit their eggs in clusters. The young hatch and mate with their sibs. If we assume that males can fertilise many females and that females' reproductive success do not depend on the number of matings they have, the reproductive success of a mother is correlated with the sum of the number of daughters she has and the number of matings her sons secure. If we assume that males and females are equally costly (as may be the case in many invertebrates with no parental care), that females mate randomly in a patch and that n females oviposit an equal amount of eggs per patch, Hamilton (1967) found the ESS sex ratio to be $(n-1)/2n$. When n equals 1 the prediction is a sex ratio of zero, but mothers actually need to produce just enough sons to mate with all their daughters. As n rises this ratio increases towards ½, i.e. as the local population includes more of the total population, the sex ratio approaches the Fisherian ratio for one large panmicitc population. The reason for this effect is that when the number of ovipositing females (n) is low, brothers mostly compete amongst themselves for mating opportunities and females do better to shift some resources to females who do not compete. This effect is called local mate competition (LMC) and Taylor (1981) showed that in this type of population, the skew in sex ratio actually occurs for two reasons: it reduces competition between brothers and also increases male mating success due to the increased number of sisters.

Hamilton (1972, 1979) improved his model in an application to fig wasps. He included the relatedness asymmetry for haplodiploid species which he previously neglected. In outbreeding haplodiploids, the asymmetry in reproductive value and relatedness of the sexes cancel each other, but when inbreeding occurs, such as in LMC models, these asymmetries have to be incorporated. The correct predicted sex ratio is then $(n-1)(2n-1)/(n(4n-1))$. In a more clearly presented genetic model, Taylor and Bulmer (1980) obtained the same prediction for an LMC model.

Bulmer and Taylor (1980) developed a model for asymmetrically dispersing sexes in a structured population. Different dispersal patterns lead to different intensities of competition between kin of the same sex and result in optimal sex ratios that are biased towards the more dispersive sex.

Werren (1980) explored another dimension suggested by Hamilton (1979). When females contribute unequal numbers of eggs to the local population, the sex ratios will be dependent on the clutch size because competition between brothers and the effect of extra sisters on brothers can be enhanced or dampened when the clutch is respectively larger or smaller than average. This idea has been further explored for different clutch sizes resulting from different fecundities (Frank 1985a; Stubblefield and Seger 1990; Yamaguchi 1985). Related to this is the problem of simultaneous optimisation of clutch size and sex ratios (Nagelkerke 1994). Here, the optimal decisions depend heavily on the playoff between other factors that determine clutch size and its dependence on the sex ratio.

Frank (1985a) and Herre (1985), both working on fig wasps, showed that when n is variable the optimal sex ratio is given by $(n\text{-}1)(2\tilde{n}\text{-}1)/(n(4\tilde{n}\text{-}1))$ with $\tilde{n}$ equal to the harmonic mean number of foundresses per patch. This results from the fact that when sex ratios are adjusted to variable foundress number, patches with fewer foundresses contribute more females per mother than patches with more foundresses. Since these females are more inbred, the estimate of the relatedness asymmetry needs to be adjusted.

Information usage and facultative sex ratio shifts is important in sex ratio models (Werren 1987). Females may respond to relatedness of females on a patch (Frank 1985a; Taylor and Crespi 1994) or to the average relatedness of fellow nest mates (Boomsma and Grafen 1991; Chan and Bourke 1994; Sundström 1994 and many other studies), number of females sharing a patch (Frank 1985a; Hamilton 1979; Herre 1985) and relative contributions of offspring to a patch (Werren 1980; Stubblefield and Seger 1990).

Fig wasps

Fig wasps are hymenopterans and are therefore believed to have a haplodiploid genetic system (haploid males and diploid females). This genetic system allows females to manipulate the sex ratio of their young by either fertilising an egg, leading to a female, or by withholding sperm, leading to a male. Furthermore, they are chalcidoids and are therefore believed not to have complimentary sex determination (CSD; Cook 1993; Cook and Crozier 1995). With CSD, inbreeding leads to high mortality of female offspring or the production of diploid males. The absence of CSD means that mating systems involving inbreeding, such as in many fig wasps, can evolve.

Fig wasp oviposition and mating patterns are extremely varied. On the grounds of their oviposition behaviour, we can divide them into two categories: internally and externally ovipositing species. This distinction is helpful in that it separates two life history patterns that require very different models for oviposition behaviour.

Internally ovipositing fig wasps

Internally ovipositing species comprise the pollinators and a number of other galling wasps. One or more mated females of these species enter a fig through its very narrow passage, the ostiole, and are trapped inside the fig. Once inside, they lay their eggs in the ovules of some of the florets and pollinate the florets. These females therefore have to lay all their eggs in the same fig and can optimise their fitness by adjusting their sex ratios and by maximising the number of eggs they can lay. Each egg develops in its own gall and the eclosure of full-grown wasps from their galls is synchronous, with males eclosing before females. The males search for galls containing females and fertilise them. Once most of the females have been fertilised, males start to excavate a tunnel through the fig's wall through which the females and other wasp species can escape from the fig. Since the mating takes place inside the fig, a local mating pattern results. Furthermore, females are believed to settle randomly on figs to form "new" patches and to enter the figs almost simultaneously. Since developing wasps obtain most of their resources from the gall, the investment in a single male and female is likely to be equal. The pollinating species are thus perfect candidates for the LMC models.

A number of studies using pollinating fig wasps (Frank 1985a; Hamilton 1979; Herre 1985, 1987, 1989; Nefdt 1989) found good qualitative correspondence between model predictions and data and, in some cases, the fit was quantitatively accurate. Firstly, figs with more foundresses (higher n), had less female biased sex ratios. The wasps can therefore facultatively adjust their sex ratio to the number of females that oviposit in the fig. Secondly, species with lower $\tilde{n}$ produced lower sex ratios for any given number of foundresses, suggesting that the average amount of inbreeding also affects these traits. These models therefore suggest that both n and $\tilde{n}$ are important in shaping the oviposition behaviour of females. Herre's (1987) data suggest that females' ability to facultatively alter their sex ratios is not perfectly developed and that females may have a strategy which is a slight compromise for different values of n. The adjustability should therefore be seen as a constraint and not as is suggested by Herre *et al.* (1996) as a failure of natural selection. Herre (1987) found that 1) species that experience a more varied environment are able to adjust their sex ratio better, 2) that those species with a more constant environment had a sex ratio that is well adjusted for the more common situation and is adjusted in the correct direction for the less common foundress number but not as far as predicted. Hamilton (1979) and Frank (1985a) both found more female biased ratios than predicted and suggested and incorporated a number of factors that might play a role but which have been ignored in models (Table 3 lists a few of these). The model can then be adjusted until it fits the data. In these cases, the additional assumptions need to be tested to prevent an *ad hoc* situation.

Another point of attention is the sex ratio of single foundresses. The model predicts just enough males to fertilise all the females, but since no data have been collected on actual fertilising ability, no predictions can be made. The males are not only needed to fertilise females, but have to construct the exit hole, without which, the females will be trapped inside the fig. The determining factor will thus be the more demanding requirement. Furthermore, if there is a mortality factor, selection should favour an even more male biased ratio to prevent the worst-case scenario of no exit hole despite the occurrence of increased mate competition between brothers.

The variation in individual sex ratios and our inability to measure the exact contributions of different females has been attacked as a weak link in fig wasp sex ratios (Herre *et al.* 1996; Orzack 1995).

Externally ovipositing fig wasps

Externally ovipositing fig wasps lay their eggs from the outside of the figs with very long ovipositors. Some of these species are peculiar in that their males are dimorphic and that certain types of males exhibit extreme fatal fighting (Hamilton 1979). Research on these species has therefore concentrated on male dimorphisms and fighting (Hamilton 1979; Murray 1987, 1989, 1990; Vincent 1991), but recently also on their host relationships (Compton and van Noort 1992), community ecology (Compton et al. 1994; Compton and Hawkins 1992;

Table 3 Other factors that may also be important in determining pollinating fig wasp sex ratios (first two by Hamilton (1979) and all but first by Frank (1985a)).

Advantage of genetic variability - affects the relatedness asymmetry
Varied clutch sizes - results in lower effective n and $\tilde{n}$
Non random settling of females - decreases effective n and $\tilde{n}$
Non random mating and mate competition - decreases effective n and $\tilde{n}$
Genetic recognition among foundresses - conditional adjustment to actual genetic variance

Hawkins and Compton 1992) and effects on the mutualism between pollinating species and fig trees (Bronstein 1991; West and Herre 1994; Kerdelhué and Rasplus 1996).

Hamilton (1979) found that the frequencies of the male morphs correspond with the frequencies of females available to each morph. Frequency dependant selection may therefore keep this dimorphism stable. He argued that the concentration of females in defendable areas, such as figs, can be the driving force behind fatal fighting, whereas high relatedness between males may prohibit this. Hamilton proceeded to argue that sex ratios might reflect the mating structure and thus relatedness in figs. One may therefore expect a decrease in the tendency to fight as sex ratios decrease. Murray (1987, 1989) tested this hypothesis within a specific species but could not confirm this relationship. Vincent (1991) compared the incidence and magnitude of fighting to the exact place of mating within the fig. She found a very good correlation between the two, indicating that the mating site is the more important component selecting for fighting by influencing the actual defendability of the female "resource".

An important difference relating to oviposition behaviour and offspring allocation in these species is the fact that females can optimise both their sex ratio and their clutch size. Furthermore, different male morphs normally have alternative mating strategies in which dispersal before mating is asymmetric for the two morphs, resulting in an asymmetry in mate competition between brothers of each morph. These behavioural factors have not been incorporated into models.

Aims

The aim of this study is to extend sex ratio theory to externally ovipositing fig wasps and their specific life histories (Chapters 2 - 4) and to address some problems that relate to pollinating fig wasps (Chapter 5 - 6). I use inclusive fitness and games theory (described above) to obtain evolutionary stable strategies. In some cases, an analytical solution could not be found and numerical computer simulations were used.

The first life history trait that is addressed is how alternative mating strategies (a result of male dimorphisms) might affect sex allocation in externally ovipositing species. Two aspects that can result are addressed in chapters 2 and 3 respectively. Firstly, since the two morphs have different dispersal abilities, sib competition between males of the two morphs will be different. Such a difference should lead to skews in sex ratios, depending on the frequency of either morph. Because morph determination can occur as a result of genes expressed in the mother or in the son, there is also the potential for parent-offspring conflict regarding the frequencies of the morphs. In chapter 2, I address these questions and test it using Hamilton's (1979) data. A second possibility is that the mating site may confer information to the female on her relatedness to her mate. For instance, when a female mates outside a fig with a winged male, she is very likely to be unrelated to that male. On the other hand, when a female mates inside the fig, there is a possibility that it can be a brother. If this information can be used, it can lead to sex ratios that are more precisely adjusted to the relatedness asymmetry. This possibility is explored in a simplified model and its ramifications to the evolution of eusociality and empirical tests are considered in chapter 3.

An assumption made in the models in chapters 2 and 3, and in Hamilton's (1979) application of the sex ratio-mating structure correlation, is that clutch size is constant for different females. In chapter 4, I consider oviposition behaviour when both clutch size and sex ratio can be optimised simultaneously for species with monomorphic males. Predictions are made for sex ratios when different information is available to females. The model's results are used to predict relatedness patterns in figs and understand the evolution of fighting.

In chapter 5, I determine the importance of variation/inaccuracy of sex ratios in the optimal predictions of LMC models. The results are discussed in the light of some recent criticism (Orzack 1993, 1995) of empirical sex ratio work.

In chapter 6, I investigate the assumption that pollinating fig wasps enter figs almost simultaneously. The results suggest another reason for one of the trends observed by Herre (1987) for single foundress sex ratios.

2. Offspring Allocation in Structured Populations with Dimorphic Males ♣

Summary

Many fig wasp species have dimorphic males. These males often mate in different localities, the one typically disperses before mating whereas the other does not disperse. Hamilton (1979) developed a model for offspring allocation in dimorphic fig wasps, but he assumed that females only lay a single egg per fig. This assumption is not realistic and precludes any effects local mate competition (LMC) may exert on morph abundance. I develop a model without these restrictions and show that the optimal proportions of each morph is determined by two parameters. Firstly, the proportion of the non-dispersing morph is affected by the average number of females that oviposit in a patch. This effect is due to the negative correlation between LMC between brothers and the number of females that oviposit in a patch. Secondly, the proportions of both male morphs correlate with the expected proportion of females which will mate with each morph. The separation of the two parameters generalizes the model to any other species which is spatially structured and which has two male morphs or even two alternative mating strategies. A comparison of two models show that parent-offspring conflict involving morph ratios will not have far reaching consequences. I test these models using Hamilton's (1979) data and both models accurately predict the variation in morph ratios in six species of dimorphic fig wasps.

♣ Slightly adjusted from Greeff, J.M. 1995. Offspring allocation in structured populations with dimorphic males. *Evolutionary Ecology* **9:** 550-558

Introduction

Fig wasps have a high incidence of male dimorphism (Vincent, 1991). Gadgil (1972) showed that frequency dependent sexual selection can lead to such stable dimorphisms. In other words, an increase in the numbers of the one morph, relative to the other reduces the average success of the first morph. This situation is typical of many of the dimorphic species of fig wasps (Hamilton, 1979). In fig wasps, the two morphs mate in different locations: I define males that are *Confined* to the fig in which they hatch out and mate with females as they emerge from their galls as type C, and males that *Disperse* from the figs (normally winged) and mate with females that did not mate within the figs as type D. These unmated females originate from male-less figs and from figs where all the males have already died, either because of fighting or old age (J.M. Greeff, unpub. data). Hence, due to frequency dependent sexual selection, the evolutionary stable ratio (ESS *sensu* Maynard Smith, 1982) of the two male morphs will be equal to the ratio of the females that can be mated outside the figs to those that are mated inside. This is exactly what Hamilton (1979) found.

Hamilton (1967) showed that deviations from the 50:50 sex ratio can be expected when the mating population is spatially structured. The female bias in his 1967 model results from competition between related males for mating opportunities (coined local mating competition, LMC). The effect of LMC and inbreeding in biasing the sex ratio has been demonstrated repeatedly for pollinating fig wasps (Hamilton, 1979; Frank, 1985a; Herre, 1985; Nefdt, 1989). Hamilton (1979) modeled a population with two male morphs having life histories resembling those described above. He assumed that the number of females which use the same fig is described by a Poisson distribution and, more importantly, that females lay only one egg on a specific fig and then move on to another. It follows that wasp species with lower densities will have a higher proportion of figs on which only one female oviposits resulting in higher proportions of female-only figs. The expected mating opportunity of D males is thus higher for species of wasps with lower densities, and a negative correlation between wasp density and morph D is therefore expected. Strictly speaking this population (Hamilton , 1979) is not structured in the sense of Hamilton (1967) and as a result the expected sex ratio for all species will be ½.

A restrictive assumption in Hamilton's (1979) model is that females lay only one egg per fig. In fact, selection may favor bigger clutches. Frank (1986b) showed that the value of a daughter to a female is not simply equal to the number of alleles identical by descent, but added to this is the alleles identical by descent obtained from her mate. The relevance of Frank's (1986b) proof can be explained as follows. The fitness of males depends on the number of females they mate with, but the analogous situation for females is not true. In other words the fitness of females does not depend on the number of males they share the fig with. A female who lays a bigger clutch, with a female biased sex ratio, therefore has the same fitness gain per daughter as a female laying only a single female egg. But, she has higher fitness gains through her sons, because their mating opportunities have increased. Therefore, by laying bigger clutches, females can exploit their daughters' complete value (*sensu* Frank, 1986b). I first alleviate this restriction on clutch size by developing a new model and then I test this model with Hamilton's original data (1979).

Models

I present two models. In the first, females control their offspring sex ratio whereas the morph ratio is under male control, and in the second females control both the offspring sex and male morph ratios. Females move through the fig tree and lay clutches of a constant size on each fig. Any number of unrelated females may oviposit on a specific fig. The model is not based an a specific distribution of females that oviposit per fig, rather we shall see that the harmonic mean number of females ovipositing per fig is sufficient. This value can be calculated for any given distribution. C males mate at random with females in their natal fig, whereas D males leave the figs and mate with unrelated females. The proportion of females that can be mated to D males is j and the proportion that can be mated to C males is $1 - j$. I assume that all females mate. Let R_m and R_f be a female's relatedness to her male and female offspring respectively. For haplodiploid species $R_m = 1$ and $R_f = (1+3F)/(2+2F)$ (Hamilton, 1972), where F is the inbreeding coefficient. For diploid species $R_m = R_f$. Let v_m and v_f respectively be the reproductive values (*sensu* Taylor, 1988) of the male and female subpopulations. In haplodiploids $2v_m = v_f$ and in diploids $v_m = v_f$ (Taylor, 1988).

To find the evolutionary stable sex and morph ratios we need to investigate the fitness of a rare mutant. By using differentiation we can then find the strategy that is uninvadable by any rare mutant (Maynard Smith, 1982).

Females control the sex ratio only (model 1)

Let N be the total number of females which oviposit in a specific fig and let the mutant female lay a sex ratio (males/total) t, whereas all the other females lay a sex ratio of T. A fixed proportion of each female's male offspring develop into morph C and the remainder develop into morph D. These proportions are governed by the availability of females to the male types, that is, if j females are available for mating with D males, a proportion j of the males of each clutch will be type D and $1 - j$ will be type C.

We can now calculate the mutant female's fitness through a C son (w_c) in this fig as the product of his relatedness to her, the value of a male and his expected number of matings:

$$w_c = R_m v_m (1 - j)((1 - t) + (N - 1)(1 - T))/(t + (N - 1)T). \tag{1}$$

Similarly the mutant female's fitness through a D son (w_d) in this fig is:

$$w_d = R_m v_m (1 - j)(1 - T)/T. \tag{2}$$

The mutant female's fitness through a daughter (w_f) in this fig is the product of her relatedness to daughters and the value of females:

$$w_f = R_f v_f. \tag{3}$$

The mutant female's total fitness gain from this specific fig (w) normalized to one egg is thus proportional to

$$w = t w_c + t w_d + (1 - t) w_f. \tag{4}$$

The female's lifetime fitness (W) is the summation of w for all the figs she oviposits in. Using Equations 1-4 we can write W down as:

$$W = \sum_{N=1}^{N\,\max} P_N \left[R_m\, v_m \left[\frac{t(1-j)(N - NT + T - t)}{t + NT - T} + \frac{tj(1-T)}{T} \right] + R_f v_f (1-t) \right] \tag{5}$$

where P_N is the proportion of figs with N ovipositing females.

To find the ES sex ratio we need to investigate

$$\left.\frac{\partial W}{\partial t}\right|_{t=T} = \left[\frac{(1-j)(1-t)-k(1-j)+j(1-t)}{t}\right] R_m v_m - R_f v_f = 0 \qquad (6)$$

(Maynard Smith, 1982), where k is the reciprocal of the harmonic mean number of females that oviposit per fig. Suzuki and Iwasa (1980) showed that if a is the probability of sibmating, F is equal to $a/(4 - 3a)$ in a haplodiploid population. Hence, R_f for haplodiploid species is $1/(2 - a)$. In this model the probability of sibmating is $k(1 - j)$ and R_f is thus $1/(2 - k(1 - j))$. By substituting the appropriate values for R and v into (6) and solving for t the ES sex ratio is obtained as

$$t = \frac{(1-k(1-j))(2-k(1-j))}{4-k(1-j)} \qquad (7)$$

for haplodiploid species and

$$t = \frac{1-k(1-j)}{2} \qquad (8)$$

for diploid species. If j is set equal to 0 in Equations 7 and 8, we obtain the general result for the optimal sex ratio predicted by partial sibmating where k is the probability that the female mates with a sib (Taylor, 1993) and we obtain the optimal sex ratio for patch-structured models where $k = 1/N$ (Hamilton, 1967, 1979; Taylor and Bulmer, 1980).

Females control both the sex and morph ratio (model 2)

In this model the organism's life history is the same as in the previous except that the proportion of the two types of males is not under male control. Rather, a female oviposits a clutch, a proportion r of which develop into C males and s into D males. The remainder, $1 - r - s$, of the clutch develop into females. In this case the offspring sex ratio is $r + s$, and the values from the previous model that correspond to r and s are $(1 - j)t$ and jt (this is wrong, see correction at end of chapter).

A similar approach as above gives a female's lifetime fitness (W) as

$$W = \sum_{N=1}^{N\max} P_N \left[R_m v_m \left[\frac{r(1-j)(N - NR - NS + R + S - r - s)}{r + NR - R} + \frac{sj(1-R-S)}{S} \right] + R_f v_f (1 - r - s) \right] \quad (9)$$

where R and S are, respectively, the proportion of C and D males in the clutches of the other females. To find the ES ratios we need to investigate

$$\left.\frac{\partial W}{\partial r}\right|_{\substack{r=R \\ s=S}} = \left[\frac{(1-j)(1-r-s) - k(1-j)(1-s)}{r} \right] R_m v_m - R_f v_f = 0 \quad (10)$$

and

$$\left.\frac{\partial W}{\partial s}\right|_{\substack{r=R \\ s=S}} = \left[\frac{j(1-r-s)}{s} - k(1-j) \right] R_m v_m - R_f v_f = 0 \quad (11)$$

From Equation 10 we can solve for

$$s = \frac{R_m v_m (1-j)(1-r-k) - rR_f v_f}{R_m v_m (1-k)(1-j)} \quad (12)$$

and

$$r = \frac{R_m v_m (1-j)(1-s)(1-k)}{R_m v_m (1-j) + R_f v_f} \quad (13)$$

From Equation 11 we can solve for

$$s = \frac{R_m v_m j(1-r)}{R_f v_f + R_m v_m (j + k(1-j))} \tag{14}$$

and

$$r = \frac{R_m v_m (j(1-s) - ks(1-j)) - R_f v_f s}{R_m v_m j} \tag{15}$$

By setting equal the right hand sides of Equations 12 and 14 and those of Equations 13 and 15 respectively and by substituting the appropriate values of R and v we obtain the ES ratios as

$$r = \frac{(1-j)(1-k)(2-k(1-j))}{4-k(1-j)} \tag{16}$$

and

$$s = \frac{j(2-k(1-j))}{4-k(1-j)} \tag{17}$$

for haplodiploid species and

$$r = \frac{(1-j)(1-k)}{2} \tag{18}$$

and

$$s = \frac{j}{2} \tag{19}$$

for diploid species.

Equations 7, 16 and 17 can be used to illustrate the effects of j and k on the optimal ratios graphically (Fig. 1).

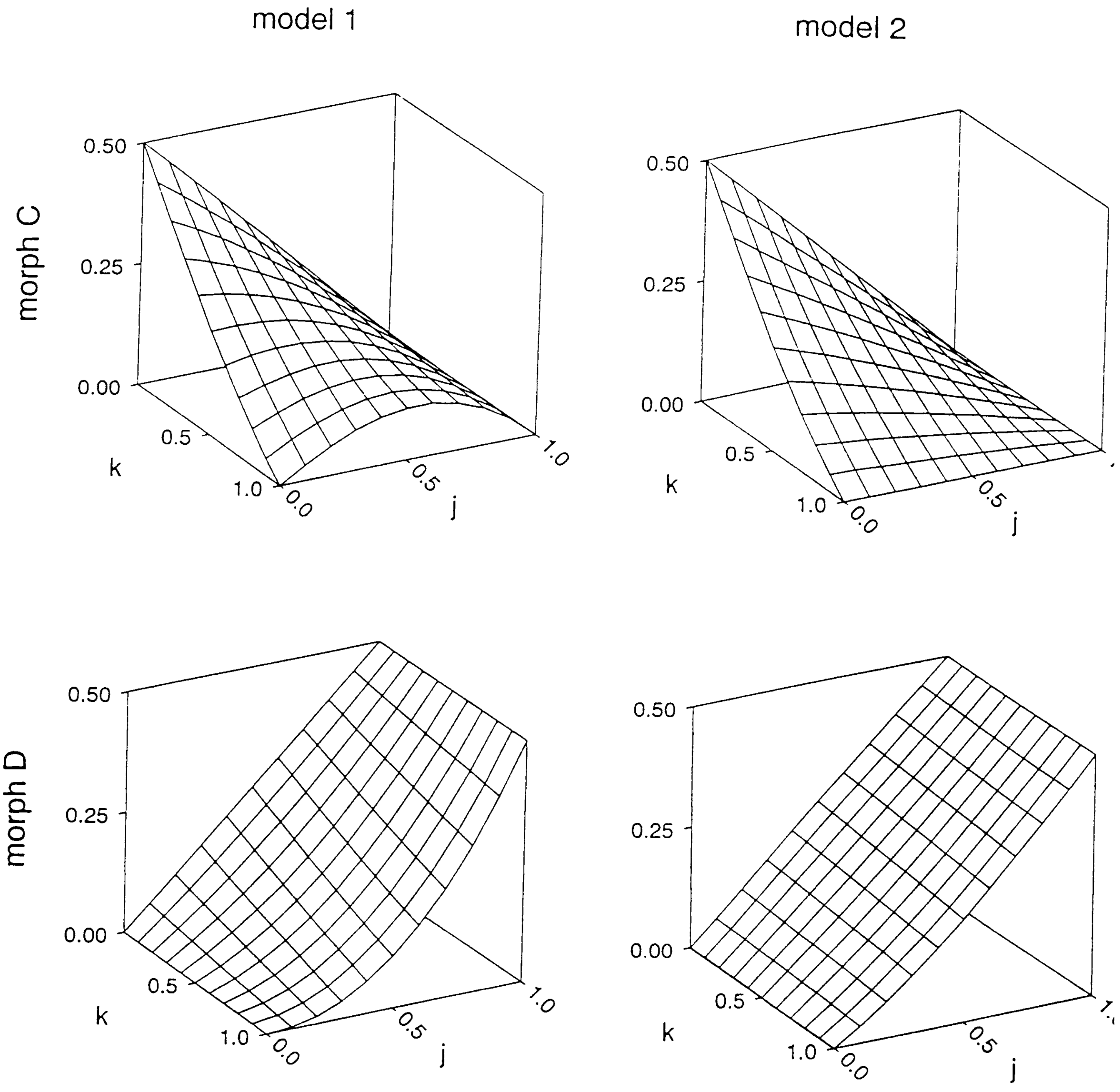

Figure 1. The proportions of the offspring, predicted to be C and D males for models 1 and 2 as functions of *k* and *j* (model 1's predictions for the C morph is slightly higher and D slightly lower than that of the corrected plot, see correction at end of chapter).

Comparisons to Hamilton's model and data

To compare these models with that of Hamilton (1979), we need a common frame of reference. Hamilton's model is based on the Poisson distribution and is specified entirely by the Poisson parameter λ. It is possible to obtain values of k by choosing the right λ. Using λ we can calculate his M (the mean number of males per fig) as $\lambda/(2(1 - e^{-\lambda}))$. Then, using M, b (his s, the proportion of males that are morph C) can be obtained by choosing values that satisfy the equality $(1-b) = e^{-bM}$. j is then simply equal to $1 - b$. Using this method it is possible to see how j and k are related to each other and how the morph ratio is affected by j (Fig. 2).

To test the model developed here with Hamilton's (1979) data j and k have to be calculated. First, assume that the Poisson distribution describes the oviposition behavior of the females. Then, values of λ for the six species can be chosen such that $e^{-\lambda}$ equals the proportion of figs without wasps. Using λ, k was numerically calculated for figs that contain wasps. If females that mate with D males originate from maleless figs only we can set j equal to the proportion of females that eclose in maleless figs. The predicted values of r and s can then be calculated using Equations 7, 16 and 17 and compared to the actual values (Fig. 3).

Results and Discussion

The Models

The difference between these models (Fig. 1) and that of Hamilton (1979, Fig. 2) can broadly be explained by the fact that LMC, inbreeding, sib-mating and parent-offspring conflict are all excluded in his model by assuming that females lay one egg per fig. The fact that k and j are both determined by the Poisson parameter restricts the values of j and k to the line in figure 2 as opposed to the complete surface (Fig. 1). Also, although k varies in figure 2 it must be realized that k in itself does not cause any selective pressures on the abundance of the morphs. Whereas, in the models developed here, k reflects the intensity of LMC between C males, k does not reflect the LMC in Hamilton's (1979) model. The only source of selection in Hamilton's model is thus j. Because morph D's optimal abundance is only slightly affected by k, Hamilton's (1979) model gives very similarly predictions for the optimal value of s as mine. However, k affects r dramatically and

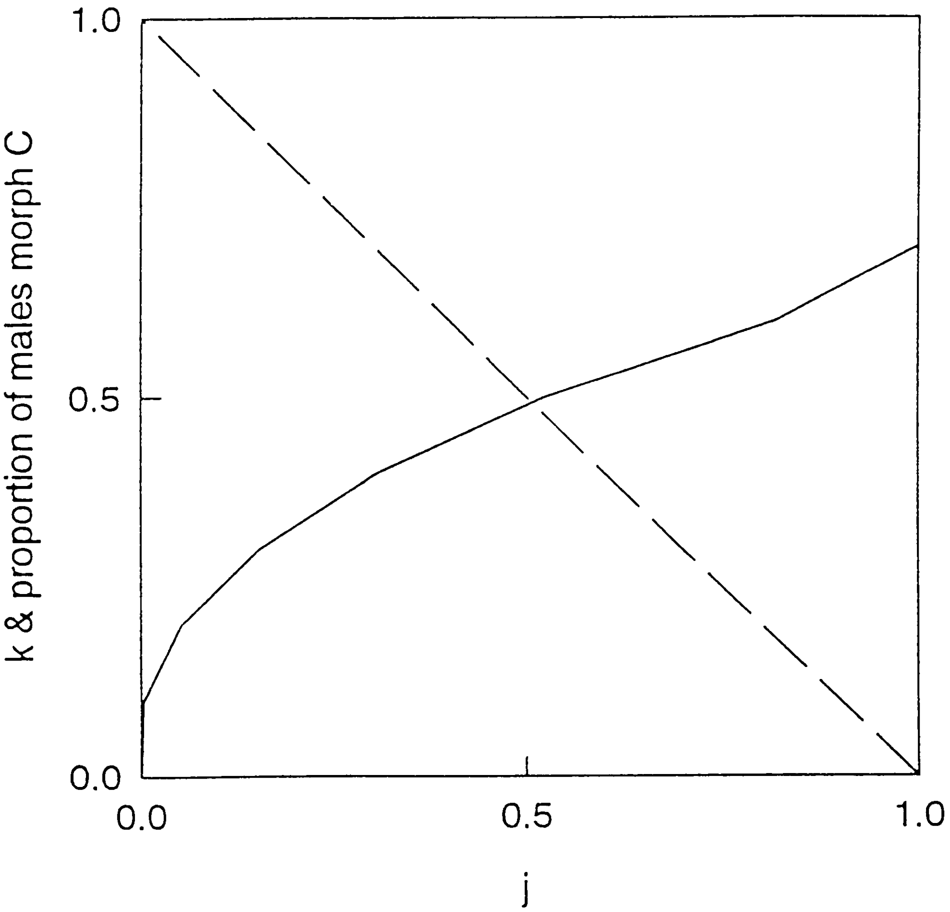

Figure 2. The proportions of the offspring, predicted to be C males (dashed line) by Hamilton's (1979) model as a function of *j* and the relation between *k* and *j* in his model (solid line).

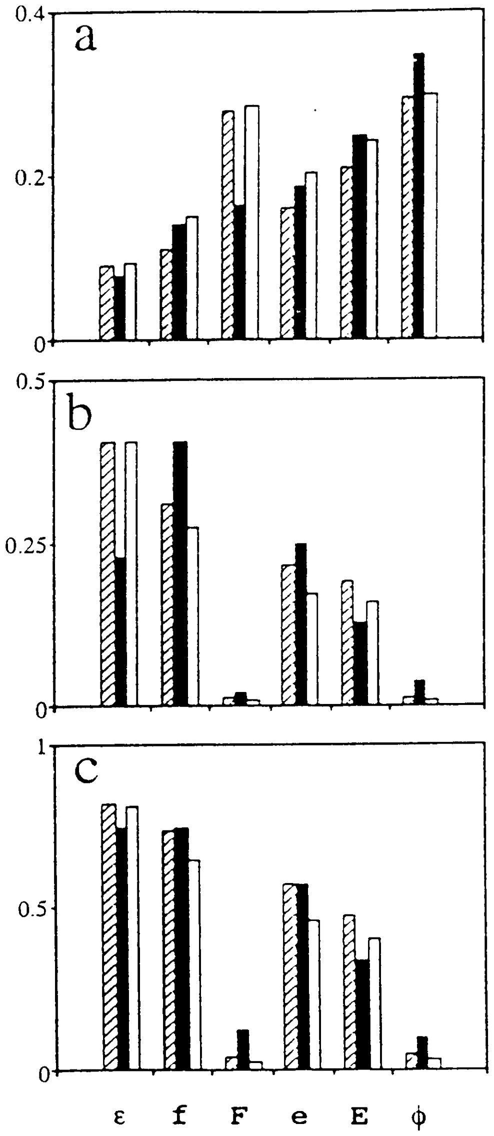

Figure 3. The predicted and observed proportion of the morphs for 6 species of fig wasps: e, f, F, e, E and f. a. C/(males+females), b. D/(males+females) and c D/males. The filled bars = observed, clear bars = model 1 and hatched bars = model 2.

Hamilton's (1979) model and mine only give the same predictions for when $k = 0$. Models 1 and 2 can thus be applied more generally than Hamilton's (1979).

Bulmer and Taylor (1980) showed that the sex ratio should be skewed to the sex that disperses more randomly. Given that the two male morphs have the same expected mating success, these two models predict a similar bias towards the male morph that disperses before mating.

The predictions of the two models do not differ markedly. In general, C males experience LMC and their ratio decreases as k, a measure of the extent of LMC, increases. Since the number of females they can mate with decreases as j increases, the optimal ratio of the morph also declines as j increases. D males, on the other hand, are not affected by LMC and therefore their ESS is only slightly affected by k. This effect is a result of a pay-off from investment in females, because the value of females increases at higher levels of inbreeding. This effect of k also has an effect on C males, but it is completely overshadowed by the effect of LMC. As opposed to C males, D males' access to the 'resource' of females increases with j and their ratio increases with j. Because D males do not experience LMC, they have a higher ratio over most of the area covered by the graph. The increase in a son's mating success due to extra daughters decline as j increases, resulting in a lower female biased sex ratio. j also decreases the amount of inbreeding, and since females become less related to their female offspring as the population is more outbred (Herre, 1985), this leads to a further decrease in females as j increases or k decreases.

The two models give the same values for the sex ratio, but they differ slightly in their predictions of the morph ratio. Except for the extreme values of j and at $k = 0$, model 2 predicts slightly higher values for morph D and lower values for C than model 1. This difference is because D males are more valuable to females than their actual mating potential (but see correction). The parent-offspring conflict concerning morph allocation is therefore not very important, but it increases as j nears 0.5 and as k increases. The availability of females and the size of local populations is important for males which mate locally. In the case of males which disperse before mating the availability of females is of vital importance, while the importance of the local population size is small.

For diploid populations the predictions are very similar and the differences are a result of the differences in relatedness and value of the two sexes.

When clutch sizes are small, r, s and t cannot be any magnitude because they rely on integer numbers of eggs. Hence, the models do not accurately predict the optimal ratios of small clutches accurately.

Both models fit the data equally well. There are significant correlations between the observed proportions of morph C and D (C/(males+females) and D/(males+females)) and the predictions of the two models (Spearman's $r = 0.829$, $p = 0.05$ for all comparisons). The observed proportions of males, morph D (D/males) is also significantly correlated to the models' predictions (Spearman's $r = 0.943$, $p < 0.05$ for both cases). The fact that rarer species have more winged males (D) is thus due to the fact that there are more females to mate with them *and* because type C males become less fit as fewer females oviposit in the same fig.

Although it is theoretically possible to measure whether morph determination is controlled by the female or by the males themselves, no clear cut picture emerges from figure 3. It could be argued that morph determination differs between species, but because the values for j and k are only approximate estimates, caution should be taken in interpreting figure 3 too literally. In order to determine the ultimate cause of morph determination, accurate estimates of j and k are required.

CORRECTION

Male dispersal dimorphism, local mate competition and frequencies of morphs.♣

In sex allocation problems it is commonly assumed that the mother determines the sex of her offspring, especially in the hymenoptera (but see Hawkes 1992). I recently investigated the effects of a male dimorphism for dispersal on female allocation when the population is structured (Greeff 1995): oviposition patches are founded by a variable number of females - the harmonic mean number equal to $1/k$; one male morph is **C**onstrained and mate locally whereas the other morph **D**isperse from the oviposition patch. Such a dimorphism may be the result of genes expressed in the mother or in the son. Hence, their might be mother-son conflict over the ratio of D and C males. Interestingly, there is no mother-son conflict over the sex ratio in partial sibmating models (Uyenoyama and Bengtsson 1982). Unfortunately, the calculation of the morph ratio under son control in my previous attempt failed to incorporate all the relevant parameters and here I would like to rectify this mistake for haplodiploid species.

Assume that there are $(1 - j)$ females that can be mated locally and j females that can be mated by D males. We will thus expect the males in the population to adopt either strategy, dispersing or not, in reference to j and $(1 - j)$. However, males that do not disperse, are more likely to compete against brothers than the average male. Hence, competition between similar genes in C males will lead to their Evolutionary Stable frequency being less than j. This effect will be operative regardless of whether the genes act in the mother or the son. Previously I overlooked its importance in "son control".

For haplodiploid taxa (Greeff 1995) the ES frequency of the C morph (r = C/(males + females), when determined by genes in the mother, is

$$r = \frac{2 - k(1-j)}{4 - k(1-j)} \cdot (1-j)(1-k) \qquad (1)$$

and that of the D morph (s = D/(males + females)) is

$$s = \frac{2 - k(1-j)}{4 - k(1-j)} \cdot j. \qquad (2)$$

♣ Modified version in Press: Greeff, J.M. 1997. Local mate competition, sperm usage and alternative mating strategies. *Evolutionary Ecology* in press.

When the mother determines the sex only, the ES sex ratio (t = males/(males + females)) is

$$t = \frac{2-k(1-j)}{4-k(1-j)} \cdot \left[(1-j)(1-k)+j\right]. \quad . \tag{3}$$

The first term in each of these equations is equal to

$$\frac{R_m\, v_m}{R_m\, v_m + R_f\, v_f}, \tag{4}$$

with R_i equal to the relatedness of a sex i (**m**ale or **f**emale) offspring to the mother and v_i equal to the reproductive value of sex i. This term is thus a valuation of sons by mothers in terms of their genetic ability.

The remainder of the terms is an expectation of mating success of males. Mothers adjust the ratio of C males by the likelihood of not competing with brothers (1-k) in (1). Notice that $t = r + s$ and that the square bracket in (3) is equal to (1 - k(1 - j)), which is the probability of outbreeding.

What proportion of the males in (3) should disperse before mating and what proportion should mate locally? In my previous attempt to answer this question I argued that (1 - j) males would mate locally and j males would disperse. This assumption is wrong, because locally mating males compete against brothers. Males should therefore adjust their probability of dispersal according to the extent of local mate competition in addition to j and 1 - j. If selection is weak and mutations have a small effect the success of a rare allele, **a**, determining the probability of male dispersal in a population with an allele **A** is proportional to

$$w \propto \sum_{N=1}^{N\,\max} P_N \frac{(1-j)N(1+F)u}{(1+F)(u-v)+2Nv} + \frac{j(1+F)(1-u)}{2(1-v)}, \tag{5}$$

where the proportion of males carrying the **a** and **A** allele staying, being u and v respectively, with P_N equal to the proportion of patches containing N foundress females and F equal to the inbreeding coefficient.

The ES phenotype of the allele at this locus can be found by solving for v^* in equation (6) below

$$\left.\frac{\partial w}{\partial u}\right|_{u=v=v^*} = \frac{1+F}{4v^*(1-v^*)} \cdot \left[(1-j)(1-v^*)(2-k(1+F)) - 2v^*j\right] = 0. \tag{6}$$

yielding

$$v^* = (1-j)\cdot\frac{2-k(1+F)}{2-k(1+F)(1-j)}. \tag{7}$$

When selection is weak and mutations have a small effect F is equal to $k(1-j)/[4-3k(1-j)]$ giving

$$v^* = \frac{(1-j)(4-5k+3jk+k^2-jk^2)}{(4-5k+5jk+k^2-2jk^2+j^2k^2)} \tag{8}$$

Under son-control, we can see from (7) that, as under mother-control (1), the mating opportunity of locally mating males, $(1-j)$, is decreased by the second term to allow for competition between similar genes. The similarity between brothers is affected by the number of females ovipositing on the patch (k); as k decreases the probability of competing against a brother decreases. The second term of (7) approaches 1 as k approaches 0. Genetic similarity of brothers also depends on the inbreeding coefficient of the mother and therefore increases in F leads to a reduction in the correction term. The correction term leads to a slight downward adjustment of the C morph and upward adjustment of the D morph frequencies from my previous predictions. Because similar forces act on genes expressed in mothers and sons the mother-son conflict regarding the ratio of male morphs is very low with mothers adjusting the ratio slightly more to local mate competition.

3. Alternative mating strategies, partial sibmating and split sex ratios in haplodiploid species ♣

Abstract

It is shown that when females can adjust their offspring sex ratios conditionally to the identity of their mates, i.e. sib or non-sib, split sex ratios are expected. These split sex ratios result from variation in relatedness between females and their daughters. Haplodiploid females' relatedness to their daughters increases as their relatedness to their mates increases. Therefore, sibmated females' optimal progeny sex ratio is more female biased than that of outbred females. Inbreeding depression that can result from complimentary sex determination (CSD) is also considered. The genetic load caused by CSD can be so costly to sibmated females that they switch to the production of males only. The evolutionarily stable sex ratios for a sibmating model is found to be of a weak type. These weak equilibria and split sex ratios can lead to high variation about the mean and are an incentive for further studies on sex ratio variation in conjunction with mating behaviour. The occurrence of split sex ratios in haplodiploid taxa is important because it favours the evolution of eusociality. Partial local mating and alternative mating strategies can thus eventually lead to the evolution of eusociality.

♣ Published paper: Greeff, J.M. 1996. Alternative mating strategies, partial local mating and split sex ratios in haplodiploid species. *Journal of Evolutionary Biology* **9**: 855-869

Introduction

General trends in sex allocation have shown that the sex ratio of offspring is normally adjusted so that mothers' inclusive fitness is maximized (Charnov, 1982; Werren, 1987; Godfray, 1994; excluding eusocial insects). The success of offspring sex ratio strategies depends on a number of ecological and genetic factors and we aim to identify the important factors causing the observed variation in sex ratios. Furthermore, the variation in sex ratio is an important selective force on mating strategies (Clutton-Brock and Parker, 1992) and it plays a key role in the evolution of eusociality (Iwasa, 1981; Grafen, 1986).

Offspring sex allocation strategies are commonly affected by local mate competition (LMC) between related males (Hamilton, 1967) and by relatedness asymmetries (Hamilton, 1979). LMC arises when brothers compete for mating opportunities and results in relatively lower investment by a mother in male than in female offspring (Hamilton, 1967). Asymmetries in the relatedness of daughters to mothers as compared to the relatedness of sons to mothers is unique to haplodiploid taxa. These asymmetries can result from inbreeding: Daughters receive genes both from their fathers and mothers whereas sons only receive genes from their mothers. Thus when a female and her mate are related, their daughters receive genes from both the mother and the father that are identical by descent to those of the mother. As a result the relatedness of the daughter to her mother increases as the relatedness of the father to the mother increases. Since males only receive genes from their mothers, inbreeding does not alter a son's relatedness to his mother. Hence, inbreeding in haplodiploid taxa has the effect of making the optimal sex ratio more female biased (Herre, 1985).

Inbreeding depression can bias the primary sex allocation towards males by decreasing the value of sibmatings (Denver and Taylor, 1995) and by decreasing the relatedness between daughters and their mothers (Greeff and Taylor, in press). This effect excludes the effects on the secondary sex ratio due to female mortality (Smith and Shaw, 1980) or diploid males (Cook and Crozier, 1995).

Another set of important factors affecting sex ratio strategies is the information the female has about her environment and herself. Factors falling in this class are: the number of other females ovipositing in a local patch (Hamilton, 1979), the relatedness of a female to other females ovipositing in a local patch (Taylor and Crespi, 1994), the relative clutch size of the female (Suzuki and Iwasa, 1980; Werren, 1980), the quality of the host (Godfray, 1994) and in eusocial insects: the number of males the queen mated with (Boomsma and Grafen, 1990, 1991) and the number of queens in the colony (Chan and Bourke, 1994; Evans, 1995).

Most approaches to predicting optimal sex allocation strategies use the mean relatedness of daughters to their mothers. In many conditions this is the most plausible and biologically realistic approach. However, it is not always the case. Closely related individuals commonly mature in the same location. In such situations females eclosing together with their brothers sibmate if they mate before dispersal and are likely to outbreed if they disperse before mating (I call this type of mating pattern - partial local mating, PLM, after Hardy, 1994). Two haplodiploid taxa that display PLM are fig wasps with dimorphic males (Hamilton, 1979; Vincent, 1991; Greeff, 1995) and hymenopteran parasitoids (Myint and Walter, 1990; King and Skinner, 1991a; Nadel and Luck, 1992; Ikawa *et al.*, 1993; Hardy, 1994). It may be possible that a female can obtain information about her relatedness to her mate from her own mating behaviour. In fact, Ode *et al.* (1995) found that *Bracon hebetor* females did not mate with males that hatched from the same host as themselves. They were thus able to use this environmental cue to avoid mating with brothers. From variation in sex ratio investment of ants, Sundström (1994) and Evans (1995) argued that these ants could estimate their relatedness to their fellow colony members using genetic cues. Therefore, females may even be able to obtain knowledge about kinship relations from genetic cues.

This paper investigates the possibility that females of haplodiploid taxa respond conditionally to variation in relatedness to their mates when making sex allocation decisions. This approach is interesting because it connects alternative mating strategies to split sex ratio evolution and ultimately to the evolution of eusociality. I use a partial sibmating model and inclusive fitness arguments to investigate the problem. Uyenoyama and Bengtsson (1982) and Denver and Taylor (1995) investigated similar models, but they did not allow for conditional sex ratio responses. Uyenoyama and Bengtsson's (1982) genetic models showed that the evolutionarily stable (ES) sex ratio strategy they found is of a weak form: a population will evolve towards the equilibrium, but once there, there will be no selection against other sex ratio strategies. It is thus of interest to see whether this inclusive fitness approach will also indicate a weak equilibria.

The Model

Imagine a very large haplodiploid population in which females deposit clutches of constant size. Only one female oviposits at a specific location and there is thus no multiple foundress clutches. A proportion α of the females of each clutch sibmates, with $0<\alpha<1$ (see appendix, p 105, for a list of abbreviations). The remaining females mate at random to males from the population. The following sections are based on this mating structure.

The basic model in which it is assumed that all the females produce the same sex ratio (daughters/(sons + daughters)), r, and diploid offspring suffer an inbreeding penalty, s, has been investigated (Denver and Taylor, 1995; Greeff and Taylor, in press). Here I show that the equilibrium for s equal to 0, is of a weak nature and this model is then extended by allowing sibmated females to produce a sex ratio of i that can be different from outbred females' sex ratio of u. I assume that the diploid offspring of sibmated females suffer an inbreeding depression penalty and only a proportion, $1 - s$, of their diploid offspring will survive.

Before I calculate the optimal values of i and u, the effects of i, u and s on relatedness and the reproductive values of sibmating and outbreeding need to be calculated.

Equilibrium characteristics of r

Uyenoyama and Bengtsson (1982) and Denver and Taylor showed that the ES sex ratio r is equal to $(2+2\alpha-\alpha^2)/(4-\alpha)$, when $s = 0$. We can calculate the fitness, $W(\rho,R)$, of a mutant female producing a sex ratio of ρ in a population producing a sex ratio R as the sum of her fitness gains through sons and daughters. Her fitness gains through sons is equal to the product of the number of sons, their expected mating success, their relatedness to her and the reproductive value of males, v_m. v_m is half the value of v_f (reproductive value of females) because males only pass their genes on to females whereas females pass their genes on to both sexes. We need to do this for males that mate with sisters as well as males that mate with unrelated females. The mutant's fitness gains through her daughters is in turn equal to the product of the number of daughters, their relatedness to her and the value of females. Setting $v_m = ½$ and $v_f = 1$, and with a daughters relatedness to her mother equal to $1/(2-\alpha)$ (Uyenoyama and Bengtsson, 1982) and a son's equal to 1, we obtain

$$W(\rho,R) = \tfrac{1}{2}[\alpha\rho + (1 - \rho)R(1 - \alpha)/(1 - R) + 2\rho/(2 - \alpha)]. \tag{1}$$

If $W(R,R)$ is equal to the fitness of a female following the population strategy, we can investigate what type of ES ratio r is by inspecting,

$$2\{W(R,R) - W(\rho,R)\} = (R - \rho)[r - R]/((2 - \alpha)(1 - R)). \tag{2}$$

When R equals r, the term in square brackets is equal to zero and the fitness of all possible strategies would thus be equal. Also, as R approaches r, the difference between a mutant's fitness and the fitness of an average female decreases and hence the selective pressure on the sex ratio will decrease as the goal, r is approached.

Relatedness

In this section I quantify the variation in relatedness in the population. If we consider one locus with alleles ⊙ ≠ ○ ≠ ◎, where the three symbols denote alleles not identical by descent. Based on genotype and mating behaviour we can identify six mating types (Table 1) - two resulting from outbreeding events (capitals) and four resulting from sibmatings (small letters). From the mating types and the identities of the offspring we can write six recursion equations for the expected proportions of these mating types in the next generation given α, s, i and u as

$$\mathrm{A}' = (1 - \alpha)[\mathrm{A}u + \mathrm{a}i(1 - s) + \mathrm{B}u + \mathrm{b}i(1 - s) + \mathrm{c}i(1 - s)\tfrac{1}{2}]/t, \tag{3A}$$

$$\mathrm{B}' = (1 - \alpha)[\mathrm{c}i(1 - s)\tfrac{1}{2} + \mathrm{d}i(1 - s)]/t, \tag{3B}$$

$$\mathrm{a}' = \alpha[\mathrm{A}u + \mathrm{a}i(1 - s)]/2t, \tag{3C}$$

$$\mathrm{b}' = \alpha \mathrm{c}i(1 - s)/4t, \tag{3D}$$

$$\mathrm{c}' = \alpha[(\mathrm{A}u + (\mathrm{a} + \mathrm{c})i(1 - s))\tfrac{1}{2} + \mathrm{B}u + \mathrm{b}i(1 - s)]/t \tag{3E}$$

and

$$\mathrm{d}' = \alpha[\mathrm{c}i(1 - s)\tfrac{1}{4} + \mathrm{d}i(1 - s)]/t, \tag{3F}$$

with $t = \alpha i(1 - s) + (1 - \alpha)u$.

Table 1. The six mating types and the relatedness (G_d) between the female and her daughters for each type. Capitals indicate outbreeding events and small letters, sibmatings.

mating types male x female	G_d
A. ⊙ x ◎○	½
B. ⊙ x ◎◎	½
a. ⊙ x ◎○	½
b. ⊙ x ◎◎	½
c. ⊙ x ⊙◎	1
d. ⊙ x ⊙⊙	1

We can find the equilibrium ratios of the six types of matings as the right eigenvector for eigenvalue 1.

$$\frac{4(1-\alpha)[2u(1-\alpha)+\alpha i(1-s)]}{\alpha^2 i(1-s)}$$

$$\frac{2u(1-\alpha)+\alpha i(1-s)}{\alpha u}$$

$$\frac{4u(1-\alpha)}{\alpha i(1-s)}$$

$$1$$

$$\frac{4[u(1-\alpha)+\alpha i(1-s)]}{\alpha i(1-s)}$$

$$\frac{u(1-\alpha)+\alpha i(1-s)}{u(1-\alpha)}$$

In this paper the word "relatedness" refers to the pedigree coefficient of relationship as defined by Pamilo and Crozier (1982). The average relatedness of a daughter to her mother (G_a) can be calculated as the sum of the products of the proportion of each mating type and the specific relatedness of a daughter to her mother of that mating type (Table 1):

$$G_a = \frac{u(2+\alpha)(1-\alpha)+\alpha i(1-s)(1+\alpha)}{2[2u(1-\alpha)+\alpha i(1-s)]} \tag{4}$$

For the basic model, i.e. when $i = u = r$, G_a is

$$G_a = \frac{2-\alpha s(1+\alpha)}{2[2-\alpha(1-s)]} \tag{5}$$

(Fig. 1). However, notice that the daughters of females who mated with non-sibling males (a proportion of 1 - α of all the females) are related to their mothers by a ½ only (G_o).

Conversely, daughters of those females that did sibmate are related to their mothers by more than equations (4) and (5). The average relatedness of a daughter to her sibmated mother can be calculated as the sum of the products of the proportion of each of the small letter mating types and the specific relatedness of a daughter to her mother of that mating type:

$$G_s = \frac{3u(1-\alpha) + 2\alpha i(1-s)}{2[2u(1-\alpha) + \alpha i(1-s)]} \tag{6}$$

For the basic model, i.e. when $i = u = r$, G_s is

$$G_s = \frac{3-\alpha(1+2s)}{2[2-\alpha(1+s)]} \tag{7}$$

(Fig. 1). G_s varies from ¾ when there is no sibmating up to 1 if α is 1. Inbreeding depression causes a decrease in these relatedness estimates (Fig. 1; Greeff and Taylor, in press).

The value of a sibmating and an outbreeding event

When sibmated and outbred mothers produce different sex ratios and sibmated mother's daughters suffer from inbreeding depression a sibmating event and a non-sibmating event do not have the same capacity to propagate genes to future generations. Therefore we need to weight a sibmating event by V_s and an outbreeding event with V_o, the reproductive values of sibmating and outbreeding events respectively (Denver and Taylor, 1995).

I closely follow Denver and Taylor (1995) to derive V_s and V_o. If a female produces K offspring per clutch we can calculate the number of female and male offspring as:

$$m_s = K(1 - i), \tag{8A}$$

$$m_o = K(1 - u), \tag{8B}$$

$$f_s = Ki(1 - s) \tag{8C}$$

and

$$f_o = Ku, \tag{8D}$$

which is the number of male (m) and female (f) offspring a sibmated (subscript s) and an outbred (subscript o) female produce respectively.

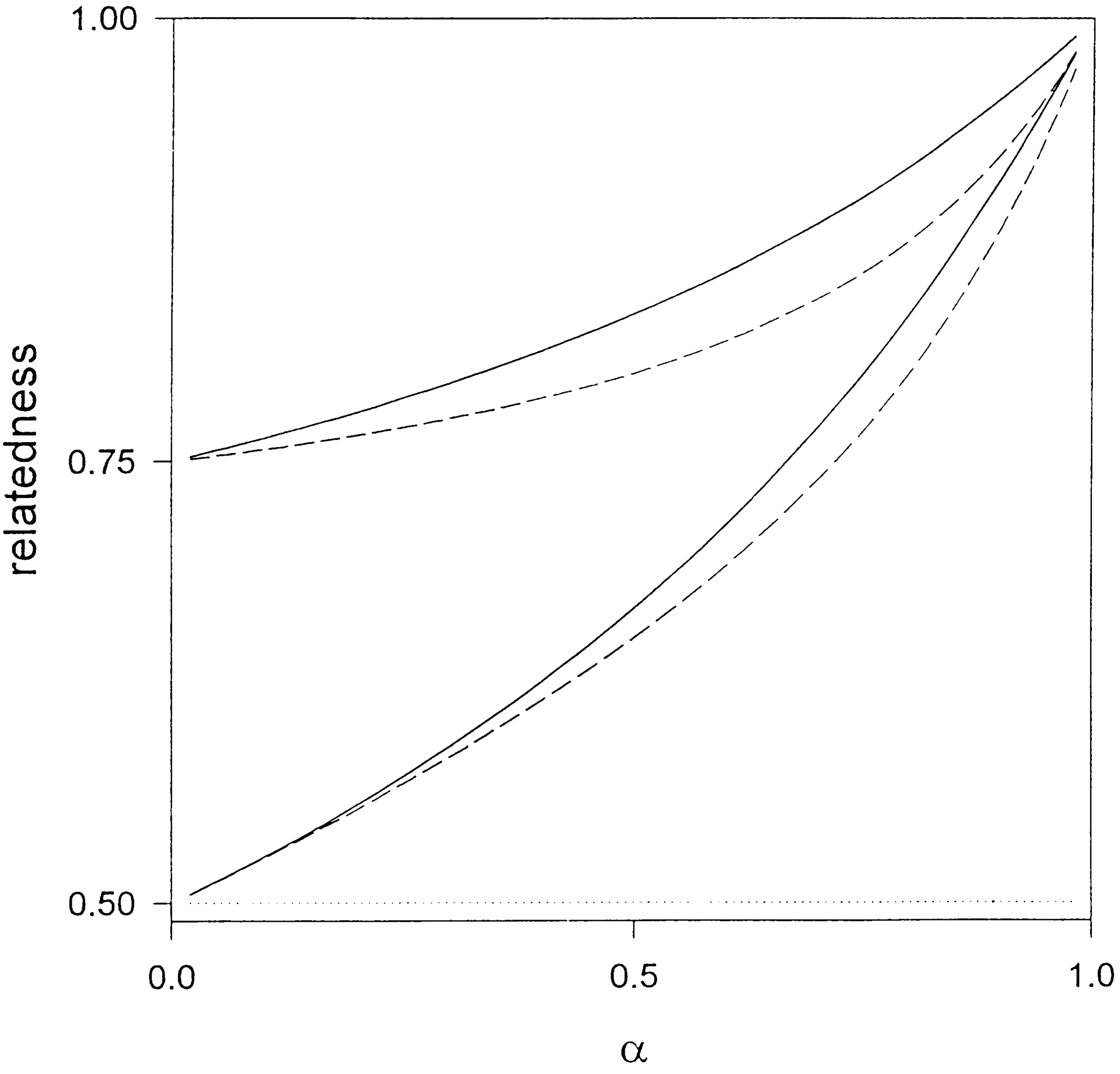

Fig. 1. The average relatedness of daughters of sibmated (G_s; the pair of lines starting at 0.75), outbred (G_o; dotted line) and combined females (G_a; the pair of lines starting at 0.5) to their mothers against the probability of sibmating, α. The solid lines are for when $s = 0$ and the dashed lines, for when $s = 0.5$.

If we normalize so that each female produces only one daughter we obtain, $\alpha f_s + (1 - \alpha)f_o = 1$, and using (8C) and (8D) it follows that $K = 1/[\alpha i(1 - s)+(1 - \alpha)u]$. By summing the product of each mating type and the number of offspring of each mating type (Denver and Taylor, 1995) the recursion equations for reproductive values of a single sibmating and a single outbreeding can be written down as

$$V_s' = \alpha f_s V_s + (1-\alpha)f_s v_f V_o + \frac{m_s(1-\alpha)}{\alpha m_s + (1-\alpha)m_o} v_m V_o \tag{9A}$$

and

$$V_o' = \alpha f_o V_o + (1-\alpha)f_o v_f V_o + \frac{m_o(1-\alpha)}{\alpha m_s + (1-\alpha)m_o} v_m V_o \tag{9B}$$

with $v_m = 1/3$ and $v_f = 2/3$, equal to the reproductive value of a male and a female respectively (Hamilton, 1972; Taylor, 1988). By inspecting the right eigenvector for the eigenvalue 1 of the transition matrix the equilibrium ratio V_o:V_s can now be obtained as

$$1 : \frac{-3\alpha i^2 + 2i + u + \alpha(i-u) - 3iu(1-\alpha) + is[3\alpha i - 2 - \alpha + 2u(1-\alpha)]}{3u[1 - \alpha i - u(1-\alpha)]} \tag{10}$$

ES split sex ratios - Conditional adjustment to G_s and G_o

When all the females of the population produce one sex ratio, regardless of whether they sibmated or bred out this ES sex ratio r is equal to (Greeff and Taylor, in press)

$$r = \frac{3(2 + 2\alpha - \alpha^2) - \alpha s(11 + 8\alpha - \alpha^2 - 4\alpha s - 4\alpha^2 s - \alpha^3 s)}{3(4-\alpha) - \alpha s(14 + 5\alpha - \alpha^2 - 4\alpha s - 4\alpha^2 s - \alpha^3 s} \tag{11}$$

Daughters of outbred mothers are less related to their mothers than the average relatedness of daughters to mothers, whereas the opposite is true for daughters of sibmated mothers (Fig. 1). If the population is close to or on r we can expect mutations causing outbred females to produce slightly more male biased sex ratios than r to be at a selective advantage. Similarly, mutations causing sibmated females to produce slightly more female biased sex ratios than r will be at a selective advantage (Fig. 2). This divergent selection will then continue till the system reaches a new equilibrium. We find this equilibrium next.

One additional son increases an outbred and a sibmated mother's inclusive fitness by

$$w_m = (1-\alpha)\frac{\alpha i(1-s)+(1-\alpha)u}{\alpha(1-i)+(1-\alpha)(1-u)}V_o G_m v_m \ , \tag{12}$$

with G_m, the son's relatedness to his mother equal to 1. Note that a son only increases his mother's inclusive fitness if he outbreeds, when a son breeds with his sister he reduces his brothers' mating opportunities. w_m is simply the product of the number of matings each male can expect, the reproductive value of the mating type, the reproductive value of a male and the son's relatedness to his mother. One additional daughter increases an outbred female's fitness by

$$w_{fo} = (1 - \alpha)V_o G_o v_f + \alpha V_s(G_o v_f + G_m v_m) \tag{13}$$

and an inbred female's fitness by

$$w_{fs} = (1 - s)[(1 - \alpha)V_o G_s v_f + \alpha V_s(G_s v_f + G_m v_m)] \tag{14}$$

When a daughter outbreeds she increases her mother's fitness by the product of the reproductive value of an outbreeding, the reproductive value of a female and the relatedness of the daughter to her mother. When the female sibmates, she additionally increase her mother's fitness by increasing the mating opportunities of her brothers. In calculating w_{fs} these increases need to be weighted by the expected survival of the additional daughter (1 - s). The sex ratio will be at equilibrium when $w_m = w_{fo}$ for outbred females and $w_m = w_{fs}$ for inbred females. Using (12) and (13) we find the ES sex ratio, u, of outbred females as

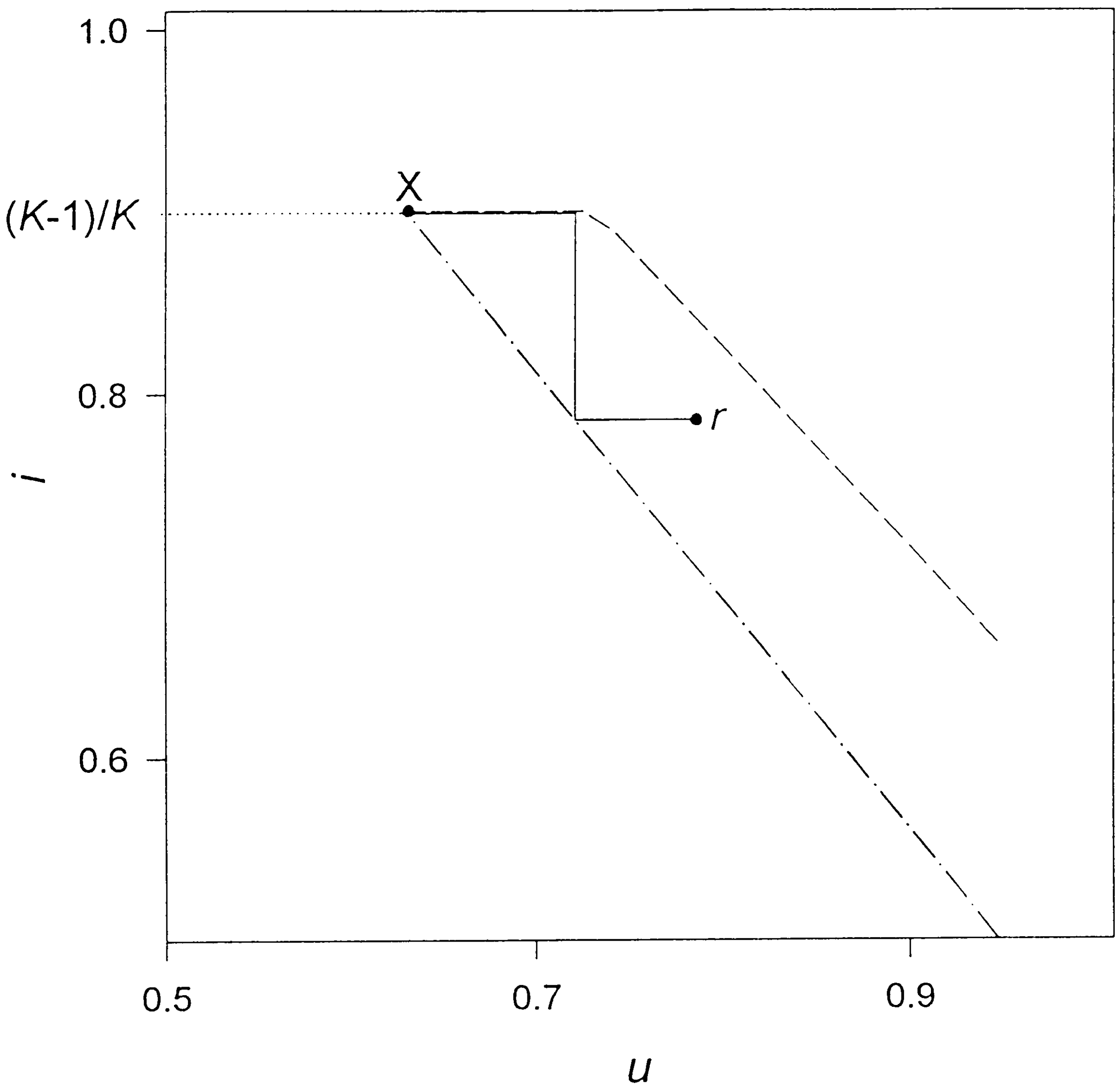

Fig. 2. The optimal value of i in terms of u (dashed) and the optimal value of u in terms of i (dash-dot) when $s = 0$ and $\alpha = 0.5$. r is the ES for the non-split sex ratio and the solid lines show how the computer simulation finds X, the ES split sex ratio. The dotted line indicates where the maximum sex ratio, $(K\text{-}1)/K$, is.

$$u = \frac{3 + 2\alpha - 12\alpha i + 7\alpha is + \sqrt{[\alpha^2(4 - 24i^2s + 49i^2s^2 - 20is) - \alpha(54is + 24i + 12) + 9]}}{12(1-\alpha)} \tag{15}$$

To find the ES i, I use (12) and (14), but because the roots could not be found analytically, an alternative approach is necessary. To find the ES i for a specific u, we set i equal to r. We then systematically increase or decrease i till $w_m = w_{fs}$ or till i has reached its maximum or minimum. It is important to notice that equations (12) and (14) assume that a sibmated female produces at least enough sons to mate with all her daughters (as in Hamilton's 1967 model). If we assume that a male can mate with a very large number of females and that clutches are not larger than this number, the maximum value of i is $(K - 1)/K$. Taking the above into consideration we can calculate the ES i in terms of u and the ES u in terms of i. When these are plotted against each other (Fig. 2) we can see how the system will evolve to an equilibrium. Starting from r, i will be selected upwards and u towards the left, till the point X is reached. To systematically find the equilibrium point of the model over a range of values for α and s a computer program was used that followed the solid line till X was reached (Fig. 2).

Assuming that K is ten the ES i, u and r in terms of α and s is given in Fig. 3. When s is equal to 0 or 0.25 (Fig. 3a and 3b), i is the most female biased sex ratio possible $(K - 1)/K$, and u and r increases as α increases, r being more female biased than u. When s is equal to ½ (Fig. 3c), the equilibrium state of i and u is dramatically different. u increases together with α till the most female biased ratio is reached. On the other hand the ES value for i is the most male biased ratio possible for low α and when α exceeds about 0.4, i increases rapidly as α increases until the most female biased ratio is reached.

Discussion

Sex ratio variation

This inclusive fitness argument corroborates Uyenoyama and Bengtsson's (1982) original finding that the ES sex ratio r in a sibmating model is of a weak type. In this case the population evolves towards the ESS, but as it nears the ESS the selective pressure, driving the population decreases until it eventually equals zero at the ESS. This largely ignored

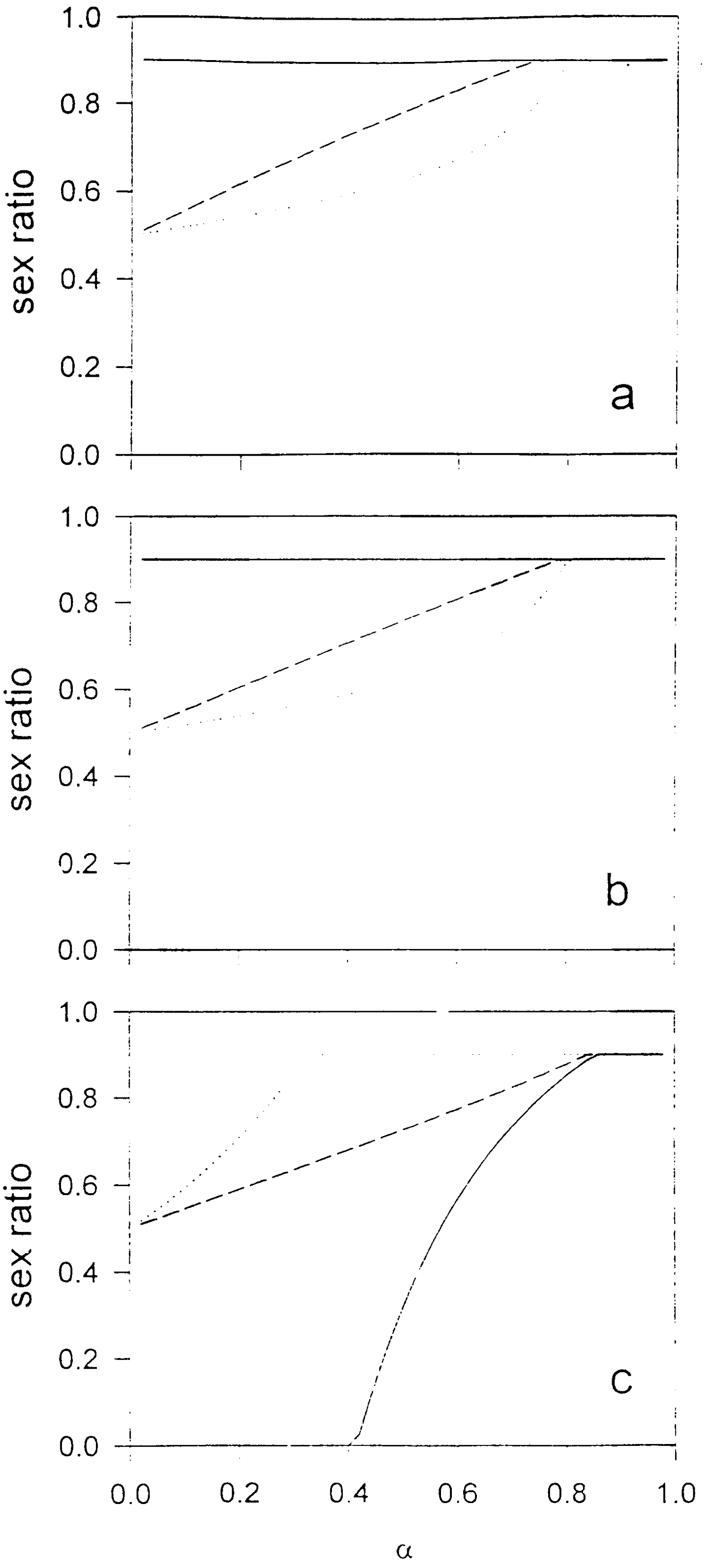

Fig. 3. The evolutionarily stable sex ratios (proportion of daughters) for *i* (solid), *u* (dotted) and *r* (dashed) as a function of α with $K = 10$ and $s = 0$ (a), $s = 0.25$ (b) and $s = 0.5$ (c).

phenomenon is important because it means that one would expect considerable variation around the expected ESS (variation which may otherwise be unexplained).

The reason why sibmating models have weak equilibria whereas LMC models have strong ones, is because the probability of sibmating in a clutch and the sex ratio of the clutch is not correlated in the former, but is in the latter. Hence, in a sibmating model, a mutant female in a population at equilibrium, will exactly compensate losses through one sex by gains in the other. Which one of the two models is more suitable for a particular species depends on how frequently the probability of sibmating correlates with the sex ratio of the clutch. Information on oviposition and mating behaviour is thus of fundamental importance in tests of sex ratio models.

Furthermore, this model introduces split sex ratios as an additional source of variation. The possible adaptive nature of variation in sex ratios reinforces Hardy's (1992) conclusion that the variation (distribution) of sex ratios requires more study. Large variation in observed sex ratios (Owen, 1983; Orzack *et al.*, 1991) does not necessarily mean that the ESS approach is wrong or just approximately right.

Split sex ratios

The split sex ratios predicted in this model result from a split in the relatedness between females and their daughters and is thus conceptually similar to the model of Boomsma and Grafen (1990, 1991) where split sex ratios occur in eusocial Hymenoptera due to differences in relatedness between workers and their sisters. However, in their model differences in relatedness occur because of variation in the number of males to which the queen is mated.

We will first consider the cases where s is equal to 0 and ¼. In many chalcidoid wasps there is indeed no apparent cost to inbreeding (Cook, 1993) and an s of zero will not be unrealistic. When s equals ¼, it corresponds to the inbreeding depression expected when complimentary sex determination (CSD) is influenced by two loci. Since daughters of sibmated females are more related to their mothers than their brothers (Fig. 1), sibmated females invest as much of their resources in daughters as possible. Even though a quarter of the daughters of a sibmated mother may die (when s = ¼) and even though the reproductive value of a sibmating is less than that of an outbreeding she still gains more fitness by investing most of her resources into daughters (Fig. 3a and 3b). Sibmated females are thus selected to produce just enough males to mate with the proportion of their daughters that will sibmate, allocating the remainder into females.

On the other hand, $G_m v_m = G_o v_f$ and outbred females' optimal ratio of the two sexes only depends on their sons' expected mating success. As α increases a larger proportion of a female's daughters will sibmate, and by investing more in daughters a female increases the mating success of her sons. This effect of α is very similar to that of LMC. When α decreases there are more females available that will outbreed and males can expect a higher mating success. These two effects due to α cause u to increase as α increases (Fig. 3).

When CSD is determined at only one locus we can expect a genetic load (s) equal to a half. In this case the load exerted on the overall value of daughters by a sibmated female, overshadows the higher relatedness value between mother and daughter (when α is small). The very high inbreeding depression also reduces V_s substantially and it is on average less than half that of V_o. Hence, at low values of α sibmated females do not expend any energy on daughters. As a result sibmated females produce males only and they "flood" the population with males and this means that the expected mating success of the average male drops. Now the optimal strategy for outbred females, for whom $G_m v_m = G_o v_f$, is to produce more female biased sex ratios than $\underline{r}$. Hence they counter the decrease in male mating success by producing fewer males. When α increases further, the mating opportunities of males to unrelated females will decrease even more and the outbred females will produce still more female biased sex ratios.

As α increases the mating success of a mother's sons becomes more dependant on the number of sisters they have. Hence, the increases in fitness due to an extra daughter increases. Additionally, the relatedness of a daughter to her sibmated mother increases as α increases. At higher values of α, these two effects of α overcome the negative effect of s and sibmated females starts to lay female eggs too. Thus, high levels of inbreeding depression leads to a reverse in the split sex ratio, with sibmated females producing more male biased sex ratios and outbred females more female biased sex ratios.

Eusociality

The existence of split sex ratios is important because it is one of the conditions that favours the evolution of eusocial behaviour via kin-selection (Grafen, 1986). Iwasa (1981) and

Godfray and Grafen (1988) showed that the regular occurrence of unmated haplodiploid females can lead to split sex allocation and Seger (1983) showed that solitary bivoltine hymenopteran species also produce split sex ratios. The sex allocation strategy described here is thus a third pathway leading to split sex ratios which may favour eusocial evolution. If females found nests on their own and PLM occurs, females will be selected to produce spilt sex ratios, setting the stage for the increase of genes causing individuals to rear sibs in preference to founding their own nests. Since this prediction of split sex ratios due to sibmating is restricted to haplodiploid taxa it fits the observation that eusociality is found more often in haplodiploid taxa than diploid taxa (Hamilton, 1964; Crespi, 1992).

Assumptions and tests

The extent to which these models apply to reality depends on females' ability to perceive variation in relatedness, either passively (e.g. using mating behaviour as a cue (*Ode et al.*, 1995) or actively (e.g. using genetic cues, Sundström, 1994; Evans, 1995). Male dispersal to localities where females eclose (Nadel and Luck, 1992) reduces the accuracy with which females can passively estimate their mate's relatedness to them. However, the numerous advantages of the ability to recognize kin may select for this ability.

This model ignores the important effects of host quality and size that has been shown, both empirically and theoretically, to be important in parasitoid oviposition (Werren, 1987; Hardy, 1994). However, this model still predicts a split in sex ratios of sibmated and outbred females given that the hosts are of equal quality or size. The model assumes that the sex ratio of a clutch and the proportion of sibmating are independent. A common example of such a violation is when more than one female oviposits in the same breeding patch. However, provided that females can actively determine whether they mated to a brother or not, this model can be extended to incorporate multiple foundressess. In this case α will be affected by the number of females to a patch, i.e. α will decrease as the number of mothers increases. α will now also be affected by i and u.

Although fig wasps display PLM (Hamilton, 1979; Vincent, 1991; Greeff, 1995) they commonly have multiple foundresses, therefore violating an important assumption of this model. However, many of the rarer species with dimorphic males, like *Camarothorax mutabilis* (Vincent and Compton, 1992), are good candidates to test this model. Another group this model will be useful for is the parasitoid Hymenoptera, in which PLM may be very common (Myint and Walter, 1990; King and Skinner, 1991a; Nadel and Luck, 1992; Ikawa *et al*., 1993; Hardy, 1994), but in which superparasitism may not be as frequent.

The split sex ratios predicted here, warns that future empirical tests using parasitoids, must plan their breeding programs so as to avoid mixing data of sibmated and outbred females. For instance a breeding program where the tested females are all outbred may yield a more male biased sex ratio than would be expected for the average female. The detection of split sex ratios in these taxa will be evidence for the wasps' ability to recognize kin.

4. Offspring allocation in externally ovipositing fig wasps with varying clutch size and sex ratio ♣

Abstract

The simultaneous optimization of clutch size and sex ratio is a tricky problem. Unless parameters such as host size or fecundity exist to pin down the optimal clutch size, this problem remains elusive to analytical analysis. This is because the fitness landscape with respect to clutch size and sex ratio does not have one single evolutionary stable peak towards which the population can evolve. To solve the problem I introduce a computer simulation to optimize both clutch size and sex ratio using externally ovipositing fig wasps as a model taxon. The simulation approach allows the use of integer numbers of eggs rather than assuming that females can produce any sex ratio between 0 and 1. When females have no information about the patches on which they oviposit they produce either large clutches with a strong female bias or clutches of a single male egg. When females have complete knowledge of their oviposition site, a set of conditional substrategies is evolutionary stable. Like above, these substrategies are either big clutches with a female bias or clutches consisting of a single male egg. This dichotomous oviposition pattern results in unrelated males sharing a fig, a condition conducive to the evolution of fatal fighting. Selection on female oviposition strategies may therefore be an important driving force behind high levels of fighting observed between male fig wasps.

♣ In press: Greeff, J.M. Offspring allocation in externally ovipositing fig wasps with varying clutch size and sex ratio. *Behavioral Ecology* in press.

Introduction

Externally ovipositing fig wasps lay their eggs from the outside of the fig fruit (syconium) with long ovipositors which they drill through the fruit's skin (Bronstein, 1991; Murray, 1987; Ulenberg and Nübel, 1982; West and Herre, 1994). They either gall the syconium tissue on the inside of the fruit or parasitize other wasp species, developing inside the fig (Bronstein, 1988; Compton and van Noort, 1992). Externally ovipositing fig wasps pose a number of unique and interesting questions regarding offspring allocation, distinct from those posed by pollinating fig wasps (Frank, 1985a; Hamilton, 1979; Herre, 1985, 1987).

One of these is how the occurrence of male dimorphism for dispersal affects the sex ratio (Greeff, 1995, in press; Hamilton, 1979). Another question relates to the fact that, unlike most pollinating fig wasps, externally ovipositing females are able to oviposit in many figs (Hamilton, 1979; Murray, 1989). In this paper I show how the externally ovipositing fig wasps' ability to move from fig to fig whilst ovipositing, affects their offspring allocation.

I consider externally ovipositing species with monomorphic males (198 species from a data base of 333 species Vincent, 1991) which mate in their natal fig. Mated females disperse from their natal tree to trees with receptive fruit. This mating and oviposition behavior leads to two ways in which selection can affect the optimal sex ratio.

Firstly, local mate competition (LMC) between sons for access to receptive females (Hamilton, 1967) biases the optimal sex ratio towards daughters who do not reduce each other's fitness by competing amongst themselves (Bulmer and Taylor, 1980). The intensity of LMC between brothers is proportional to the ratio of related to unrelated males that are competing for matings in the patch. Hence, as the number of ovipositing females increases (Hamilton, 1964) and as a specific female's clutch size decreases in comparison to the other females' on the patch (Suzuki and Iwasa, 1980; Werren, 1980), the LMC between her sons will decrease.

Secondly, sibmating can be common and it creates a relatedness asymmetry between sons and their mothers as compared to daughters to their mothers (Hamilton, 1972). The relatedness of hymenopteran females to their mother is elevated by increases in inbreeding whereas that of males is unaffected (Hamilton, 1972). The optimal strategy is thus to increase investment in females as inbreeding increases (Herre, 1985).

The fig tree with its large fruit crops forms a natural cluster of compartmentalized oviposition sites. Since each wasp develops in its own gall (Murray, 1990), the number of wasps developing in a fruit is believed not to affect the eclosing wasp's size and vitality. In addition, the figs into which females oviposit are probably not saturated with eggs (Hawkins and Compton, 1992). These two factors lead to the incorporation of the following model assumptions: Firstly, the likelihood that a female oviposits on a fig is unaffected by the number of other wasps which have already oviposited on that fig. Secondly, once a suitable tree has been located, searching time (owing to the females' lack of choosiness of oviposition sites and to the synchronized maturation and close proximity of figs to each other) is not important in their decision making process.

Based on these life history characteristics and assumptions the problem can be stated as follows: Females have to optimize the clutch sizes and sex ratios they produce in different figs. Keeping in mind that 1) the optimization of these two behaviors must occur simultaneously because they are interdependent (Godfray, 1986; Stubblefield and Seger, 1990; Nagelkerke, 1994; Yamaguchi, 1985); and 2) that a games theory approach is necessary because one to many females may oviposit in a patch, with each female's behavior affecting the fitness of the other females.

Recently Nagelkerke (1994) worked on a very similar problem, modelling simultaneous optimization of egg distribution and sex allocation in predatory mites. However, he made two confounding assumptions which I try to alleviate here. The first is that females do not produce clutches consisting of one sex only and the second that females can produce any conceivable sex ratio (males/(males+females)) between 0 and 1. Since females can only produce integer numbers of sons and daughters, this assumption can become unrealistic, especially when small clutches are produced.

By using a computer simulation rather than the normal analytical approach, I allow for clutches consisting of a single sex, only integer numbers of eggs are considered and the haplodiploid genetic system is assumed. I first develop a model for **uninformed** females. These females have no knowledge of how many other females also utilized the specific fig she selected for oviposition. This model is then extended to allow for females (**informed**) having complete knowledge of the specific fig's history.

The analysis predicts a few stereotyped oviposition behaviors which leads to specific variation in sex ratios, clutch sizes and relatedness.

Model

In order to optimize a behavior, the units of its measure need to be specified. Here a unit that encompasses both clutch size and sex ratio is needed. Assume that during the female's life time, she lays a total of κ eggs. If she followed the strategy that gave her the maximum fitness for all her eggs, it means that this strategy also maximizes her fitness per egg. In other words, a female should group and allocate sex to her eggs in such a way that each egg yields the maximum fitness returns for that specific patch type. Hence, like Nagelkerke (1994), I will use fitness per egg as the quantity that must be optimized.

Analytical analysis of this problem shows that the fitness landscape does not have one peak to which the population can evolve, but that it is saddle shaped. I first illustrate this problem and then use a simulation approach to circumvent it.

Analytical Approach

Assume a female lays y male and x female eggs, with $x + y = K$ and $y = rK$. Furthermore, her brood is equal to a proportion t of the total of M conspecific eggs in the patch. The sex ratio of the other eggs in the patch is s.

To calculate the fitness of a hymenopteran female we need to appreciate that the reproductive value of females (v_f) is twice as much as that for males (v_m; because males only pass their genes on to the females in the next generation, whereas females pass their genes on to both sexes) and that the relatedness of a son to his mother (R_m) is 1, but that of daughters to their mother (R_f) is $(1+3F)/(2+2F)$, where F is the inbreeding coefficient (Hamilton, 1972).

A female's fitness through all her sons from a specific patch is the product of the number of sons, the expected number of matings per male, her relatedness to her sons and the reproductive value of males. This can be written as

$$w_m = rtM \frac{(1-r)tM + (1-s)(1-t)M}{rtM + s(1-t)M} \cdot 1 \cdot \frac{1}{2}$$

Similarly, a female's fitness through all her daughters from a specific patch is the product of the number of daughters, the relatedness of the female to her daughters and the reproductive value of females, expressed as

$$w_f = (1-r)tM\frac{1+3F}{2(1+F)}\cdot 1$$

We can therefore calculate a female's fitness per egg (w) as the sum of w_m and w_f divided by her clutch size:

$$w = \tfrac{1}{2}\left[\frac{r}{rt+s-st} - r + \frac{(1-r)(1+3F)}{1+F}\right] \tag{1}$$

Herre (1985) derived a similar equation. From (1) it can be seen that the fitness of a strategy depends on four parameters. Three of these, her sex ratio (r), relative clutch size (t) and inbreeding coefficient (F), are potentially under the female's direct control. By selecting to mate with sibs or non-sibs, females can use F to optimize their sex ratio (Greeff, in press). However, here I will assume that females cannot make this distinction and that they respond to the average value of F. The sex ratio of the patch on which the female will oviposit (s), may potentially be "controlled" by the selection of certain patches, but this option is not allowed in the model.

To obtain the optimal clutch size I investigate equation (1)'s partial derivative to t (Maynard Smith, 1982; Parker, 1984).

$$\left.\frac{\partial w}{\partial t}\right| = \frac{r(s-r)}{(rt+s-st)^2} \tag{2}$$

From (2) it can be seen that the sign of the slope of w along t is independent of t. There is thus no maximum value of t between 0 and 1. Furthermore, the slope is zero when $r = 0$ or $r = s$. This means that clutch size will not have any effect on fitness when a female produces a female only clutch, or when her sex ratio is exactly equal to that of the patch she visits. When her sex ratio is between 0 and the sex ratio of the patch (s), the slope is positive, and the optimal clutch size will be the biggest possible. Conversely, if she produces a more male biased sex ratio than the patch's ($r > s$), the slope is negative and the smallest possible clutch will be optimal.

To obtain the optimal sex ratio we set equation (1)'s partial derivative to r equal to zero (Maynard Smith, 1982; Parker, 1984)

$$\left.\frac{\partial w}{\partial r}\right| = \tfrac{1}{2}\left[\frac{s(1-t)}{(rt+s-st)^2} - 1 - \frac{1+3F}{1+F}\right] = 0$$

and solving for r gives

$$r = \frac{\sqrt{\dfrac{s(1-t)(1+F)}{2(1+2F)}} - s(1-t)}{t}. \tag{3}$$

Since the second partial differential of (1) to r is smaller than zero, (3) is a maximum (Parker, 1984). Equation (3) is similar to that of Werren (1980) except that it takes into account that male and female offspring have different reproductive values and relatednessess to their mother. Equation (3) predicts an increase in the optimal sex ratio as the relative clutch size (t) decreases, as long as s is smaller than 0.92 (determined numerically by substituting values; a condition which should always hold since s will not go above 0.5). In line with Herre (1985) the optimal sex ratio decreases as the inbreeding coefficient (F) increases. Further, the optimal sex ratio increases with the sex ratio of the patch (s) as long as s is smaller than the threshold value of $(1+F)/(8(1-t)(1+2F))$. Beyond this threshold r decreases as s increases. Hence, when a female is confronted with a specific patch, the optimal sex ratio will, depending on the magnitude of s and F, either be a proportionately large clutch with a low sex ratio, or a small clutch with a high sex ratio.

The fact that values of t and r are restricted also needs to be considered. r is restricted because integer numbers of eggs are laid, resulting in a limited amount of possible sex ratios. t is restricted by both the maximum number of eggs and the minimum number of eggs a female can lay. For example, if there are only two eggs in the fig, the female can lay a minimum proportion t, of 1/3.

This analytical approach can tell us how females should act given a particular set of values for s and F. But it is not possible to tell what patterns one can expect when inspecting the wasps that emerge from figs. These patterns will be the end product of many such decisions, shaped by a long history. To determine the result of such interactions I use the following simulations.

Simulations

I made a number of simplifying assumptions in these simulations: (1) the Poisson distribution with variable λ describes the distribution of the number of females that oviposit on patches. (2) Assuming that a maximum of 20 females can oviposit on a patch we can calculate the average number of wasps per patch and the proportion of empty patches. (3) Females never oviposit more than one clutch on the same patch and (4) they lay a maximum of Ω eggs per patch.

Since the inbreeding coefficient and oviposition behavior of females affect each other, *F* was recalculated after a strategy changed.

Uninformed Females

In this model females do not have any information about the figs they oviposit on. Nagelkerke (1994) showed that there is no single evolutionary stable strategy (ESS sensu Maynard Smith, 1982) for this situation. Hence, if an ESS exists, it has to be a mixed ESS, where a proportion of the clutches is of one type and the remainder another. Based on the analytical analyses it is expected that such a mixed ESS will consist either of a small clutch size with a high sex ratio or of a large clutch size with a low sex ratio.

I chose the alternatives to be a clutch of either the maximum size consisting of one male egg and Ω-1 female eggs (A), or a clutch of one male egg (B). If the proportion of A females is *p*, the binomial expansion, in conjunction with the Poisson distribution can be used to calculate the proportion of patches with each type of female. The fitness of each strategy is calculated as above as

$$w_A = \sum_{n=1}^{20}\sum_{a=1}^{n}\left[\left[\frac{P_n D_{na} a}{\sum_{n=1}^{20}\sum_{a=1}^{n} P_n D_{na} a}\right]\left[\frac{R_f v_f x + R_m v_m \frac{ax}{n}}{1+x}\right]\right]$$

and

$$w_B = \sum_{n=1}^{20}\sum_{b=1}^{n}\left[\left[\frac{P_n D_{nb} b}{\sum_{n=1}^{20}\sum_{b=1}^{n} P_n D_{nb} b}\right]\left[\frac{(n-b)xR_m v_m}{n}\right]\right]$$

where P_n is the zero truncated Poisson probability of a patch with n females, a and b are respectively the number of A and B females on the patch, x is the number of female eggs an A female produce per patch and D_{ij} is the binomial probability of a patch containing i females and j of them being the specific type of female (A/B) given p.

The equilibrium is obtained by increasing the value of p, till w_A is equal to w_B. Then all the mutant strategies consisting of Ω or less eggs were tested against this equilibrium, assuming a trinomial distribution describes the frequency at which the mutant, A, and B females occur.

Informed Females

To examine how and whether females' perceptive abilities may affect their oviposition behavior, a model is developed in which females arrive sequentially at the patches and can determine the exact contents of a patch. These females can use the information obtained from the fig to react conditionally to the specific patch. She can thus have a strategy comprising substrategies, each of which is the best for a particular patch she encounters and oviposits on. A female has a strategy set composed of twenty substrategies, each conditional on the number of females that had oviposited previously.

Computer simulations as described by Houston and McNamara (1987) were used to find the ESS. Optimization is done step-wise for each substrategy. To find the optimal substrategy the fitness of a mutant which acts the same as the rest of the population for all but the substrategy that is being optimized is calculated. The best mutant substrategy is then used as the population substrategy for the next round. The substrategy for the female that arrives first is optimized first, then the second and so on till the last substrategy, whereafter the process is iterated till substrategies are stable. Following the same rationale as in the analytical model, the fitness of a mutant strategy for the ith female to arrive at the patch can be calculated as:

$$w_i = \frac{\sum_{n=i}^{20} P_n \left[x_i R_f v_f + R_m v_m y_i \frac{\sum_{i=1}^{n} x_i}{\sum_{i=1}^{n} y_i} \right]}{(y_i + x_i)\sum_{n=i}^{20} P_n}$$

where y_i and x_i are respectively the number of male and female eggs the ith female produces.

The program was run for Ω equal to 3,4,5,6,7,8,9 and 10 eggs and at values for λ equal to 0.1, 0.5, 1.0, 2.5 and 5.

Results and discussion

Uninformed Females

The relationship between numbers of eggs in a fig to the sex ratio is represented in Figure 1. The equilibrium frequency (p) of A females decreases as the maximum number of eggs a female will lay on one fig (Ω) increases (Figure 2). This is because A females produce more daughters at higher Ω and the sex ratio is thus more female biased, allowing more B females' sons to exploit these extra females. As the population density (λ) increases the proportion of A females (*p*) decreases (Figure 3), because the chances of being a single foundress is reduced, decreasing the mating success of the sons of A females and decreasing the risk that the sons of B females share the patch with other males only.

The fitness of uninformed females decreases as the population density (λ) increases (Figure 3), because more females "parasitise" A females. The fitness of uninformed females is unaffected by Ω, the maximum number of eggs a female lays on any one fig (Figure 2).

Note that the relatedness between males sharing a fig is zero, because they have no brothers in that fig, whereas the relatedness between females is a decreasing function of the number of females.

Informed females

The best strategy for the first female is to lay one male egg, and Ω-1 female eggs, except

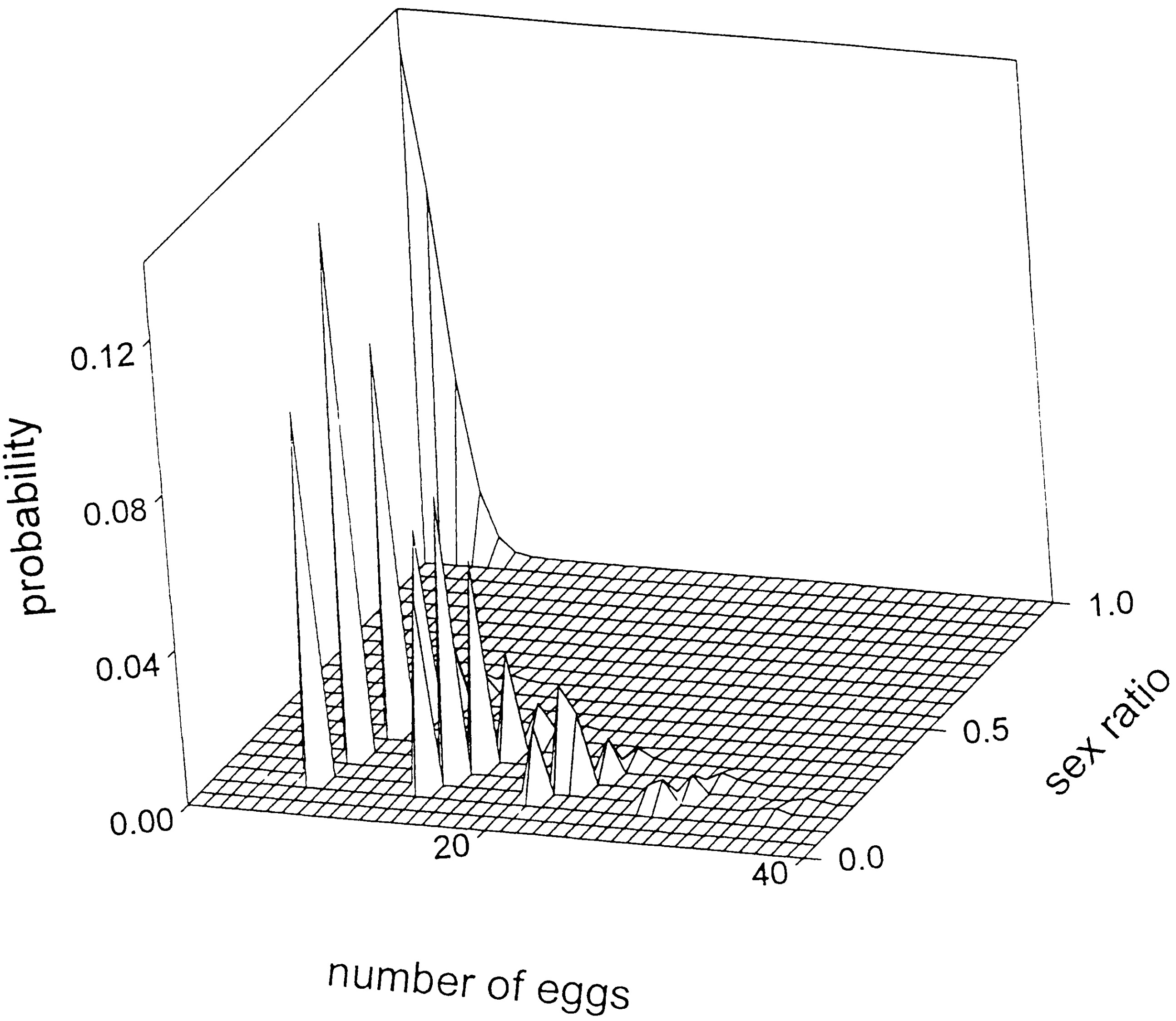

Figure 1

The proportion of patches containing a certain number of eggs with a specific sex ratio for uninformed females with $\Omega = 7$ and λ equal to 2.5. The clumped peaks correspond to a given number of females laying mostly female broods, with varying numbers of females laying a single male egg.

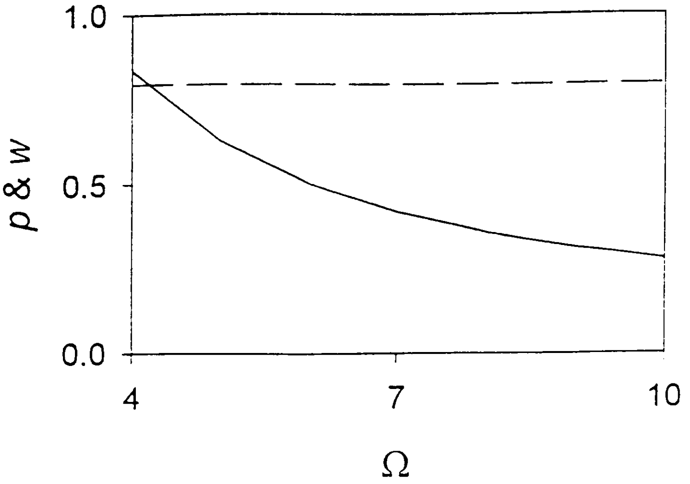

Figure 2

The fitness (broken) and equilibrium value of p (solid) against Ω for uninformed females with λ equal to 2.5.

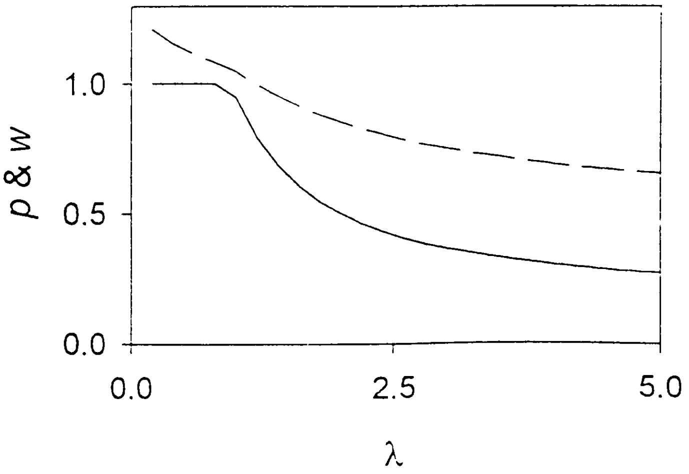

Figure 3

The fitness (broken) and equilibrium value of p (solid) against λ for uninformed females with Ω equal to 7.

for where $\Omega = 10$ or 9 and $\lambda = 5$ when it was two sons. The remaining females then produce two types of clutches, normally alternating with each other. Since the first female produced a large, female biased clutch, the second and sometimes third, fourth and fifth females are pushed to the side of the saddle where small, male biased clutches are the best substrategy. These females cause the sex ratio to become more male biased (Figure 4), eventually reaching a threshold value where the next female is pushed to the other side of the saddle where a large, female biased clutch is the best substrategy. This strategy is again one male egg and Ω-1 female eggs, when Ω is smaller than or equal to 5. When Ω is more than 5, females normally lay two male eggs and Ω-2 female eggs and when Ω is 10 and λ is 5, some females produce clutches with three male eggs and the remainder females.

The resulting pattern in sex ratio variation is quite different from that for uninformed females (compare Figure 1 to Figure 4). In the informed population the sex ratio increases as the number of eggs in a specific fig increases, whereas it decreases in an uninformed population. The threshold sex ratio at which subsequent females will produce a clutch of one male egg decreases as λ decreases (Figure 4c-e). This is because females are more likely to be alone on the patch and inbreeding will thus be higher for lower values of λ. As Ω increases (Figure 4a-c) the sex ratios of females producing big clutches become more female biased and therefore the number of subsequent females that can produce a single male egg only is higher, i.e. it takes longer to reach the threshold (Figure 4).

Generally, the fitness of the first and other female producing females, increase as Ω increases and λ decreases (Figure 4). Females ovipositing a single male egg directly after a female biased substrategy have a higher fitness than the preceding female, but the subsequent single-male-egg females' fitness is less (Figure 4). The fitness of uninformed females are generally close to that of informed females with equal λ and Ω.

The relatedness between males and females sharing a patch can be calculated (Figure 5). As in uninformed females, females from the same fig are groups of sisters for which relatedness starts off very high and decreases as the number of groups of sisters increases. Most males are produced by females who lay one male egg per patch. Therefore, in contrast to females, males are either not related to each other at all, or in cases where some females produced clutches with two male eggs, some males may have a single male relative in the fig (Figure 5). If females did not follow this dichotomous oviposition pattern, but all produced clutches of the same size and sex ratio, the relatedness among males would be much higher,

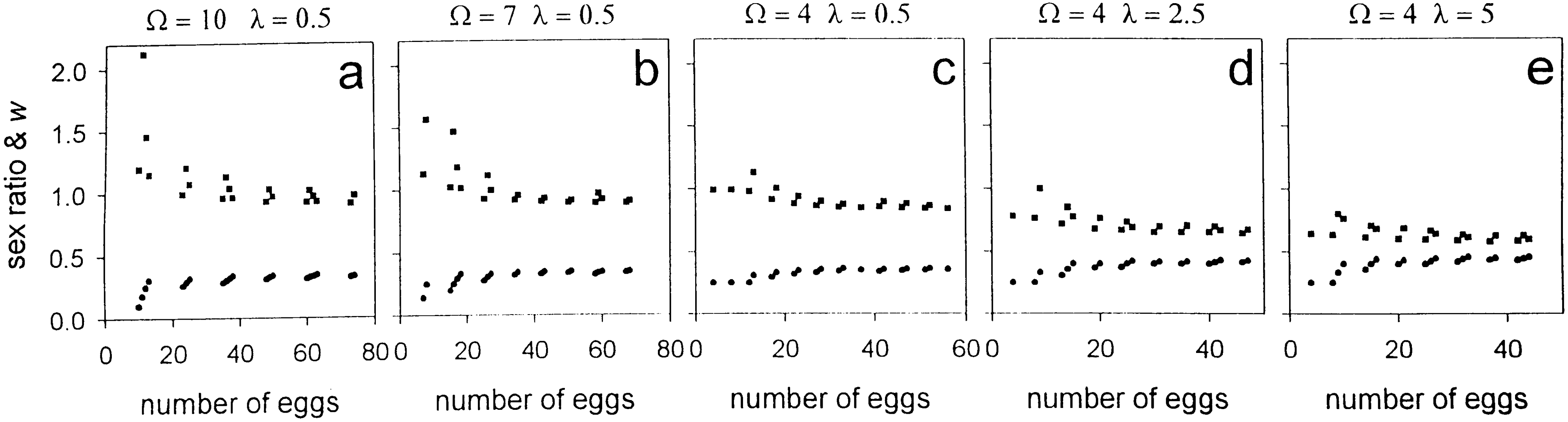

Figure 4

The predicted variation in sex ratios (circles) against the number of eggs in the patch and the fitness per egg of the females producing the sex ratios (squares) for informed females.

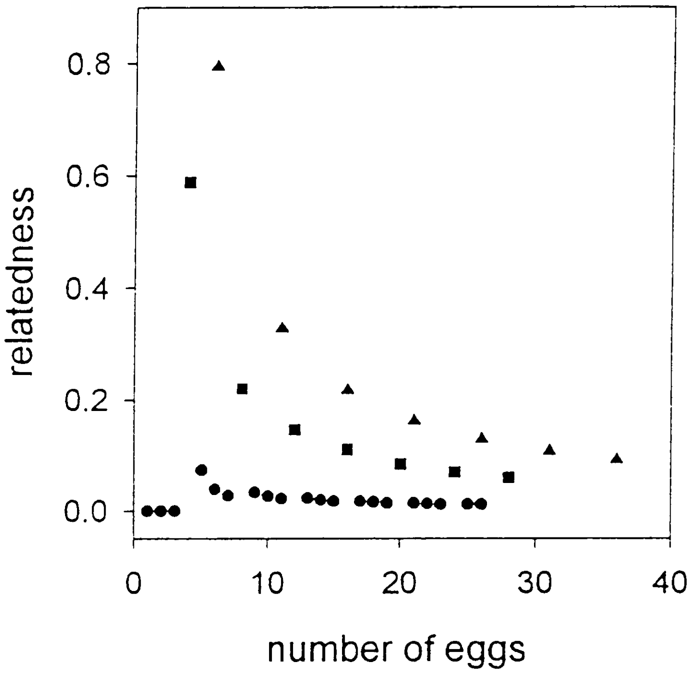

Figure 5

The relatedness between females (triangles) and between males (squares and circles) against the number of that sex individuals hatching in a patch when $\Omega = 7$ and $\lambda = 2.5$ for informed females when monandry is assumed. The substrategy of the females are in sequence, 1 male 6 females, 1 male, 1 male, 2 males 5 females, 1 male, 1 male, 2 males 5 females etc. The circles are the model's prediction and the squares are the expected relatedness if all females produce a clutch of 4 males and 5 females, resulting in the same total number of males.

and would as for females, decrease as the number of males in the patch increases (Figure 5).

General

The dichotomy in oviposition behavior results because the optimal clutch size is either the maximal or the minimal size, depending on the sex ratio of the clutch and the other eggs in the patch. Hence, although the specific strategies of females may differ as the model parameters differ, there are really only two types of substrategies: one male egg, or a big, female biased clutch.

An implicit assumption of the informed female model is that selection on one substrategy does not have an effect on other substrategies. Orzack & Parker (1986) showed that selection for increased sex ratio in one type of host did not alter the sex ratios for other types of hosts, suggesting that this assumption may be reasonable.

When λ equals 0.1, 0.5, 1 and 2.5, informed females with bigger clutches had a higher fitness, but when λ equals 5, the fitness of female-producing females did not increase unidirectionaly with Ω. Hence, for informed females at lower values of λ, maximum clutch size is under a runaway selection to increase. Contrastingly, the fitness of uninformed females is not affected by clutch size. Two factors may oppose the runaway process. Rubenstein (1982) showed that high predation risk can select for females that disperse their eggs into several nests. Fig trees have many seed predators, that often consume the complete contents of the fig including the fig wasps (pers. obs.). This predation may counter selection for bigger clutch sizes. The second factor may simply be the number of mature eggs the female has available (Compton et al., 1994). Many of these wasps are synovigenic and it may often happen that a female only has a limited number of eggs available.

Females' perceptive abilities may lead to the undermining of the assumption that the settling events of females are independent of each other. If females can discriminate between different figs they can also actively search for or avoid certain figs. Many parasitoids have been shown to evaluate the quality of their hosts (King and Skinner, 1991b) and fig wasps may also be able to do so. Even a limited ability to determine patch characteristics will be beneficial. By investigating Figure 4, one can see that if females avoid ovipositing in figs with many eggs or with high sex ratios they may indeed increase their fitness. The degree to which they can do so will depend on the availability of figs with low numbers of eggs and low sex ratios. As these figs become more scarce, the amount of energy and time expended on searching for them starts to outweigh the benefits a female receives by laying her eggs in a "high quality" fig. If most females adopt this type of strategy, the "high quality" figs will quickly become depleted, increasing the cost of searching. If searching cost were included in the model, female choosiness and searching times will have values such that the blocks in Figure 4 fall on a horizontal line.

Another condition where the assumption that females can oviposit on all figs is problematic is in species which parasitize very rare species. In these cases females may spend a great deal of time finding their hosts and the amount of energy a female has to spend on a fig containing hosts cannot only depend on sex ratios. These females can be expected to lay big clutches in figs containing their host species (Skinner, 1985; Parker and Courtney, 1984; Iwasa et al., 1984).

Murray (1987) found a correlation between sex ratios and the total number of *Philotrypesis pilosa* wasps which resembles that expected for totally informed females (his figure 2). He (Murray, 1987) argued that the positive correlation between sex ratio and the number of wasps in the fig is an indication of the degree of male relatedness within the fig. In contrast, my models suggest that males sharing a fig are unrelated to most, if not all the males in that fig, regardless of the sex ratio. Hence, the fact that Murray (1987, 1989) found no correlation between sex ratio in the fig and fighting intensity between males may be no surprise. In terms of my models his observations makes sense, because sex ratio may not indicate relatedness. Selection on females to lay optimal clutches could thus have caused a structuring of the male population that favours the evolution of fatal fighting between males, a frequent phenomenon in fig wasps (Frank, 1987; Hamilton, 1979; Murray, 1987, 1989, 1990; Vincent, 1991).

In line with various authors (Gray and Kennedy, 1994; Stubblefield and Seger, 1990; Taylor and Crespi, 1994; Nagelkerke, 1994) who showed that the perceptive ability of animals affects their optimal behavior, the two models predict distinct patterns in the variation of sex ratios. By comparing observed patterns to the models we can investigate wether females use information from the figs to allocate their resources.

The most important result of this study is the prediction of dimorphic oviposition behavior of females. This phenomenon can be tested by studying the relatedness between females and between males sharing figs.

List of abbreviations

A	oviposition strategy of 1 male egg and Ω-1 female eggs
a	no. of females that follow strategy A on a patch
B	oviposition strategy of 1 male egg
b	no. of females that follow strategy B on a patch
D_{ij}	binomial probability that j of the i females that oviposits on a patch followed the focal strategy
F	inbreeding coefficient
K	clutch size
λ	Poisson variable (measure of population density)
M	total no. of eggs in a patch
Ω	maximum no. of eggs a female lays in a patch
p	proportion of times that strategy A is adopted
P_n	zero truncated Poisson probability of a patch with n females
r	sex ratio of focal female
R_f	relatedness of daughter to mother
R_m	relatedness of son to mother
s	sex ratio of a patch excluding the focal females eggs
t	relative clutch size of focal female
v_f	reproductive value of a female
v_m	reproductive value of a male
w	fitness per egg
w_A	fitness per egg of the average A strategy
w_B	fitness per egg of the average B strategy
w_f	fitness through daughters on a patch
w_i	fitness per egg of the ith female to arrive at patch
w_m	fitness through sons on a patch
x	no. of female eggs
x_i	no. of female eggs laid by ith female
y	no. of male eggs
y_i	no. of male eggs laid by ith female

5. Variation in optimal sex ratios: a sheep in wolf's clothing ♣

In contrast to Godfray and Werren's (1996) tale of victory for sex ratio studies, Orzack (1993) has expressed a much more pessimistic view. Optimal sex ratio models predict that all females in the same environment should produce exactly the same evolutionary stable sex ratio (ESS). Orzack (1993, 1995) and Orzack and Sober (1994a, 1994b) argued that tests of optimality models fail to test whether all individuals of a population falls on the predicted monomorphic optimum. Tests normally compare the population mean to model predictions and "ignore" variation around the optimum. Here, I analyze the effect of such variation on the predictions of local mate competition (LMC) models. The model suggests that Orzack's (1993) skepticism regarding sex ratio studies may be somewhat inflated.

The core assumption of the optimization research program is that organisms are optimal given a certain set of constraints (Mitchell and Valone 1990). By building, testing and re-building models, "the selective forces and the historical constraints operating" (Parker and Maynard Smith 1990) can be identified (Krebs and McCleery 1984). Houston and McNamara (1985) and Yoshimura and Shields (1987) argued that variation in behavior can be incorporated as a constraint in optimality models. In fact, since predictions that allow for variation in behavior can yield results different from those that do not, consideration of the effect of variation is essential.

Variation has been considered in two types of sex ratio models. The first is in models with weak equilibria. Weak equilibria are predicted in partial sib mating models (Uyenoyama and Bengtsson 1982; Greeff 1996) and in large randomly mating populations (Shaw and Mohler 1953). When a population is on a weak equilibrium, all mutants are selectively neutral and can invade. Therefore, some variation is expected around the predicted optimum. To understand the dynamics of variation in these cases, specific genetic models are required

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♣ Manuscript submitted as a Note: Greeff, J.M. Variation in optimal sex ratios: a sheep in wolf's clothing.

(Bodmer and Edwards 1960; Taylor and Sauer 1980). Secondly, variation in sex ratios caused by random deaths has been considered for LMC models with a single foundress (Green et al. 1982; Nagelkerke and Hardy 1994). In these models, a single haplodiploid female oviposits her clutch in a locality and mating takes place between brothers and sisters before dispersal. Females that fail to mate will only be able to lay male eggs which will ultimately be doomed (Heimpel 1994). Females therefore produce "insurance" males to reduce the risk of their daughters being unmated.

Sex ratios predicted by Hamilton's (1967) LMC models are strong equilibria and variation around their optima is not selectively neutral when the population is at the optimum. Selection is thus expected to reduce the variance and, consequently variation has become a less important focus of attention (but see Hardy 1992). However, inspection of the fitness function of mutants in a LMC model suggests another way in which variation can affect optimal predictions. I first illustrate this effect and then quantify its influence on the optimal sex ratio.

Asymmetric fitness function

Consider a typical LMC model where groups of n haplodiploid females oviposit in patches. Their offspring mate within the patch and daughters disperse randomly to found new patches. In this scenario, the optimal sex ratio (r) is (Hamilton 1979; Taylor and Bulmer 1980):

$$r = \frac{(n-1)(2n-1)}{n(4n-1)} \tag{1}$$

The fitness of a mutant female producing a sex ratio s in a population with a sex ratio r can be calculated as the sum of her fitness gains through sons and daughters. Her fitness through sons is equal to the product of the number of females they inseminate, their relatedness to her (R_m) and the reproductive value of males (v_m) (Hamilton 1972). Her fitness through daughters is equal to the product of the number of daughters, their relatedness to her (R_f) and the reproductive value of females (v_f). Normalizing to a single offspring, we can express her fitness as:

$$w = \frac{s((n-1)(1-r)+(1-s))}{(n-1)r+s} \cdot R_m v_m + (1-s) R_f v_f \qquad (2)$$

w can be calculated by substituting *r* from equation (1) and the appropriate values of *n*, *R* and *v* (fig. 1). The optimal sex ratio (*r*, heavy line) becomes more female biased as the foundress number (*n*) decreases. Since *w* decreases away from *r*, *r* is a strong ESS as opposed to the weak equilibrium that results when n includes the whole population. *w* is asymmetric around *r* (fig. 1). Hence, mutants that vary to one side of the optimum are "penalized" more than mutants deviating by the same amount towards the other side. The reason for this asymmetry is that the extra sons of mutants that produce more male biased sex ratios can capitalize on the female biased equilibrium sex ratio. Therefore, the asymmetry is more pronounced at low *n* where sex ratios are most skewed and the fitness of mutants deviating from the optimum is more reduced than at higher *n*.

When there is variation in phenotypes, asymmetrical fitness functions result in mean optimal strategies that deviate to the side on which penalties increase at a lower rate (Williams 1992). The deviation is advantageous because it buffers the more harmful effects of variation to the side of the optimum where the fitness function declines more rapidly. Therefore, variation in sex ratios will cause more male biased sex ratios to be optimal than models that do not allow for variation. Since the asymmetry is most pronounced when *n* equals two, the effect of variation in the optimal sex ratio should be greatest when only two females oviposit in a patch. I therefore model the case where two females oviposit per patch.

Model

I assess the effect of variation about the mean sex ratio for two distributions with different variances: a uniform distribution with a high variance and negative kurtosis and a binomial distribution with a lower variance. The optimal exact sex ratio for two foundresses is ≈ 0.214. I assume that the sex ratio varies symmetrically about the mean sex ratio. The range of the variation was investigated for up to 0.4 in the binomial and 0.5 in the uniform model (table 1). These ranges ensure that all patches have sex ratios greater than zero and the effect of

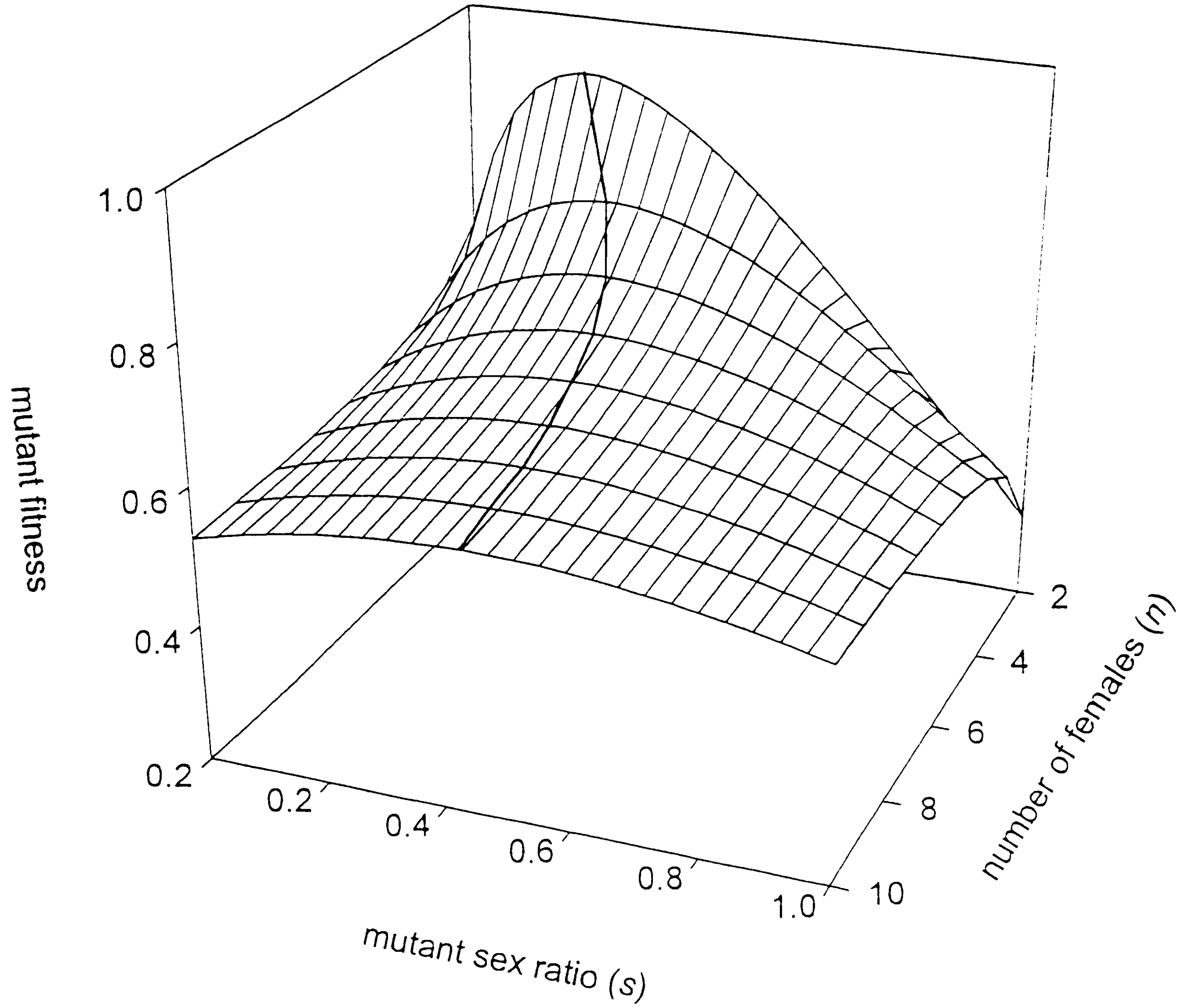

FIG. 1.- The fitness of a mutant producing the exact sex ratio, *s*, when the population produces the optimal sex ratio *r* (indicated by heavy line).

variation due to patches with no males (Nagelkerke and Hardy 1994) can be disregarded. To incorporate variation in the sex ratio I adjust equation (2) as follows:

$$w = \sum_i \sum_j P_{ij} \left[\frac{(s+j)(2-(r+i)-(s+j))}{r+i+s+j} R_m v_m + (1-(s+j)) R_f v_f \right] \qquad (3)$$

with i and j equal to the random deviation from the mean sex ratios of r and s respectively. P_{ij} is the probability that a mutant female with a sex ratio of $(s + j)$ shares a patch with a female with a sex ratio of $(r + i)$. To find the ESS, equation (3) is differentiated to s:

$$\left.\frac{\partial w}{\partial s}\right|_{s=r} = \sum_i \sum_j P_{ij} \left[\frac{2r(1-2(r+i+j)) + 2i(1-j) - i^2 - j^2}{(2r+i+j)^2} R_m v_m - R_f v_f \right] = 0 \qquad (4)$$

The values of r satisfying equation (4) were found numerically (table 1, see Appendix).

Results and discussion

Binomial variation around the mean sex ratio evaluated here does not affect the optimal sex ratio in any detectable manner (table 1). On the other hand, uniform variance has, as expected, a larger effect. In this model, the optimal sex ratio varies up to 0.055 from the optimum predicted by equation (1). This low shift - an order of magnitude less than the range of variation - indicates that the asymmetry in fig. 1 is not of great importance.

Since the fitness function of mutant strategies needs to be calculated before the optimum can be found, it is easy to test for asymmetry of this curve (as was done above). If asymmetry is detected, the model can then be extended to incorporate the effects of variation. For sex ratios, variation has to be highly platykurtic to result in any detectable deviations from the expected optimum predicted by equation (1). Since the two foundress case is expected to yield the greatest deviation for sex ratio problems (fig. 1), this model suggests that variation in sex ratios should not be considered a serious violation of the assumption that sex ratios are exact.

The model does not address the mechanism that causes variation *per se*, just the shape

Table 1

The optimal sex ratio when variation in the precision of the sex ratio is considered.

range about mean sex ratio	optimal sex ratio under two different distributions	
	binomial	uniform
0.02	0.215	0.215
0.10	0.215	0.215
0.20	0.215	0.225
0.30	0.215	0.235
0.40	0.215	0.250
0.50	*	0.270

* For the model of binomial variation, 0.5 is so high that sex ratios of 0 occur which is not considered in the model.

of the variation. Hence, it is not claimed that the variation is understood, but only that its effect on the optimal strategy is. Understanding the causes of variation (Orzack 1986, 1990; Antolin 1992a, 1992b) is important in itself but its exact relevance to optimality models needs to be clarified.

The aim of optimality models is to identify the factors and constraints that result in equilibria and not the equilibrium points *per se*, as some researchers believe (Moore and Boake 1994; Orzack and Sober 1994a, 1994b). For the model presented above, the uniform results suggest that the approach of the sex ratio towards the monomorphic optimum of 0.214 depends on variation about the mean sex ratio. Evolution towards the optimum will thus go hand in hand with the reduction of variance in sex ratios and more accurate sex determination.

Optimality models can tell us much about evolutionary transitions and how the evolution of one trait may affect that of another (Iwasa 1981). It is necessary to restate that optimality models can not only incorporate constraints, but rely upon them to be built (Maynard Smith 1978; Mitchell and Valone 1990). By considering the variation in a phenotype as yet another constraint, we may settle on a more realistic picture of evolution (Houston and McNamara 1985; Yoshimura and Shields 1987).

Appendix

For numerical analyses of equation (4), the following definitions and calculations were used: P_{ij} is the product of P_i and P_j, the probabilities of the deviations being equal to i and j, respectively. If the total range of variation in the sex ratios is $2m$ and females lay clutches of h eggs, the variation involves $2mh$ offspring. The deviation from s, i, can then be calculated as $(p/h - m)$ with p equal to the integers from 0 to $2mh$. The probability distribution of p is equal to $1/(2mh + 1)$ for all p in the uniform distribution and is $C_p^{2mh} \cdot 0.5^{2mh}$ for the binomial distribution. The proportion of females mated to brothers (k) can then be calculated as $\Sigma_i \Sigma_j P_{ij}\{[2s(1 - s - i - j) + i + j - i^2 - j^2]/[2(1 - s)(2s + i + j)]\}$ and the relatedness of a daughter to her mother (R_f) is then equal to $1/(2 - k)$ (Hamilton 1972). The relatedness of sons to their mothers is 1 (Hamilton 1972) and the reproductive value of males (v_m) is half that of females (v_f) (Price 1970). I assume that females lay 200 eggs, giving an accuracy of 0.005 (1/200) for sex ratios.

6. Sequential oviposition and optimal sex ratios in pollinating fig wasps ♣

The optimal progeny sex ratio produced by a mother depends on the amount of competition between same sexed sibs (Hamilton, 1967; Clark, 1978) and on the mother's relatedness to each sex (Hamilton, 1979; Herre, 1985). In haplodiploid species where the mating population is structured in groups of related individuals, two phenomena of importance occur: (1) brothers compete against each other for mating opportunities, referred to as local mating competition or LMC (Hamilton, 1967) and (2) sib-mating occurs, which results in mothers being more related to daughters than sons (Hamilton, 1972; Herre, 1985). Due to these two factors optimal sex ratios become more female biased as relatedness in the local mating population increases.

Agaonine fig wasps (Hymenoptera : Agaonidae : Agaoninae) have provided a useful empirical system for testing models of sex ratio optimization. Their usefulness is due to various aspects of their natural history, which is characterized by a mutualism with plants of the genus *Ficus* (Moraceae). *Ficus* inflorescences are shaped like a hollow ball, lined on the inside with hundreds or thousands of unisexual flowers. When the female flowers are ready to be pollinated, attractive volatiles are released (Ware *et al.*, 1993) and the bracts lining the ostiole (a bract-lined tunnel) loosen to allow the female wasps to squeeze their way through (Galil, 1977). The duration of volatile release and ostiole opening are linked to pollinator entry. Un-entered figs can remain attractive for several weeks, whereas after a single pollinator had entered syconia of *F. carica* and *F. aurea* they were found to remain attractive for a maximum of four days (Khadari *et al.*, 1995).

Once one or more pollen-bearing mated fig wasp females (foundresses) have passed through the ostiole they reach the lumen of the fruit, where they pollinate the fig flowers and

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lay their eggs inside a proportion of the ovules. Females have a short adult life span of just one to three days (Kjellberg *et al.*, 1988; Compton *et al.*, 1994) and typically die inside the fruit. The length of the period between entry of the first wasp and the fig flowers becoming unsuitable for oviposition is not known. The offspring develop to maturity in the galled ovules, whereupon the male wasps emerge, chew holes in the females' galls and mate with them. After mating, the males chew an exit hole through the wall of the fig, allowing the females to emerge, *en masse*. This phase of adult wasp activity is short, and usually concentrated within a few hours (Ware & Compton, 1994).

Since a foundress typically oviposits in a single fig, her sons will compete for mating opportunities. The extent of this competition depends on the number of foundress females that entered the fig: the more foundresses the less the LMC. If we assume that in cases of multiple foundresses (1) females enter the fig effectively simultaneously and (2) they lay the same amount of eggs, fig wasps become good subjects for testing sex ratio theory.

Making these two assumptions, the effects of LMC have been confirmed in numerous species, with sex ratios becoming less female biased as the number of ovipositing females sharing a fig increases (Frank, 1985a; Herre, 1985, 1989; Nefdt, 1989; Herre *et al*,. in press). In this note we investigate these assumptions. We demonstrate that sequential oviposition by foundress fig wasps can take place, and examine the relative contributions of initial and subsequent foundresses to combined progeny totals. We then discuss optimal sex ratio predictions in such circumstances and from an analysis of data of Herre (1987) we conclude that progeny sex ratios produced by the first foundresses that enter figs may be adjusted in anticipation of additional females entering the same fig subsequently.

Materials and methods

The experiments were carried out using *Ceratosolen capensis* Grandi, a fig wasp that pollinates *Ficus sur* Forssk. trees, growing in the 1820 Settlers Botanical Gardens in Grahamstown, Eastern Cape Province, South Africa. Females display sex ratio adjustment to foundress number, in accordance with Herre's 1985 model (Nefdt, 1989; Herre *et al.*, in press). Compton *et al.* (1994) found that adult females maintained in mesh-topped plastic vials at moderate temperatures (20°C) and high humidities, survived an average of 52 hours (maximum 72 hours) and that provision of a 10% sucrose solution did not increase longevity, suggesting that adults do not feed. The wasps became moribund several hours before death. They contain an average of 238 (range of 180 - 370) eggs (Nefdt 1989).

To estimate the longevity of females inside figs, newly eclosed *C. capensis* females (between 1 and 5) were introduced into bagged *F. sur* figs *in situ* by placing them at the ostioles with a fine brush. The figs were examined 24 hours later.

To obtain a lower limit for the total duration of oviposition we estimated oviposition rates. Ten *C. capensis* females were introduced individually into unpollinated figs. The figs were then removed to the laboratory where they were split open and the females observed for periods of up to an hour using a dissection microscope illuminated by a low-intensity fibre-optics 'cold' light. Indirect estimates of oviposition rates by the females were obtained by timing the frequency of style probing with their ovipositors, and by recording the frequency of pollination events, which appear synchronised with oviposition. Oviposition rates shortly after entry in to the figs was assumed to be maximal.

Finally, to determine whether a second female can enter a fig and oviposit viable eggs 24 hours after the first, we allowed newly emerged, individual *C. capensis* females to enter 20 previously-bagged, receptive figs, and the figs were re-bagged. Second females (newly emerged) were allowed to enter into 10 of the figs 24 hours later, while the remaining figs acted as controls. The figs were then bagged again, to prevent further pollination or parasitism of the wasp progeny, and left on the tree to ripen. After two months the figs began to soften, indicating that the wasp progeny were about to emerge. The figs were picked and placed singly into bottles with nylon mesh tops. The emerged wasps were sexed and counted and the figs dissected to find any wasps remaining inside the figs. Unfortunately, the progeny of first and second females cannot be separated.

Results

Of thirteen females that entered 7 figs, 2 were dead, 7 moribund and 4 were still laying eggs 24 hours later. Therefore, most oviposition occured within the first 24 hours of arrival inside a fig.

Recently-introduced females continued to lay eggs for up to several hours after the figs were split open. Their oviposition behaviour is highly consistent, and even when females were moved around they continued in a seemingly normal fashion. Females probed an average of 70.0 flowers per hour, whereas pollination events were less frequent, averaging 26.0 per hour. Every pollination event was immediately preceded by a very pronounced deep probing of the style. The female kept the entire length of her ovipositor inserted for a few seconds. The number of pollination events was therefore synchronised with oviposition and provided an estimate of average oviposition rate. On this basis, females were estimated to require around nine hours to lay an entire egg load, if oviposition was maintained at these rates. As females appear to preferentially utilise shorter styled flowers first (Nefdt & Compton, in press), which are likely to take less time to penetrate, nine hours is likely to be a lower limit for the time required to complete oviposition.

All 10 of the females that were placed on figs that had been entered 24 hours previously by other females successfully entered the figs. Wasp progeny from seven control figs and nine experimental figs (with second foundresses) were reared successfully. Control figs with a single foundress contained an average of 243.0 wasp progeny (SD = 59.2), while the figs which received a second wasp produced an average of 581.8 wasp progeny (SD = 108.6). Females entering figs 24 hours after the first foundresses were therefore able to lay just as many eggs as the first females (Kruskal Wallis Z = 1.53, P = 0.125, comparing numbers of progeny when two foundresses were present with twice the progeny when one was present).

The average sex ratio of the progeny resulting from a single foundress was 0.13 males (SD = 0.02), while in the figs with a second foundress added 24 hours later the combined sex ratio of the first and second female averaged 0.14 males (SD = 0.03). This difference is not significant (Mann Whitney U = 29.5, P > 0.05).

Discussion

We have shown that *C. capensis* females can enter figs 24 hours after an earlier female has entered, at a time when the first foundresses were often moribund or dead. These females were also able to lay a full egg load, resulting in an effectively sequential oviposition pattern, contrary to the assumptions of current models.

Nefdt (1989) showed that, in *C. capensis*, the number of offspring produced per foundress was reduced as the number of foundresses per fig increased beyond two, apparently due to resultant shortages in oviposition sites. When three or more females of this species enter sequentially this will mean that they cannot all lay their full egg loads, and earlier females will contribute disproportionately more to the overall number of progeny. Therefore, the second assumption of current models, that foundress females sharing a fig contribute equal numbers of progeny, may also not apply in all cases.

Having established that oviposition by fig wasps sharing figs with other foundresses may be partially or entirely sequential, and that contributions to the total number of progeny can vary between females, what are the consequences for their optimal sex ratio adjustment?

When two females oviposit in sequence, contribute equal numbers of progeny to the total brood, and their offspring eclose simultaneously, the optimal sex ratios (the proportion of males) for the second females is higher than that of the first female (Suzuki & Iwasa, 1980; Werren, 1980). Where fig wasps conform to these criteria it can be shown that the optimal sex ratio of a second female, s_2, with equal clutch size to the first is

$$s_2 = \sqrt{\frac{s_1(1+F)}{1+2F}} - s_1 \qquad (1)$$

where s_1 is the first female's sex ratio and F is the inbreeding coefficient (unpublished calculations). If F is set to zero, this is equivalent to Werren's (1980) equation for equal clutch sizes. For *C. capensis*, F is equal to 0.595 (Nefdt 1989) and s_1 is equal to 0.13. Inserting these values into equation (1) gives an optimal sex ratio of 0.18 for the second females. We would thus predict a slight increase to 0.155 in the combined sex ratios of figs with two females that produce equal numbers of progeny. The small increase we detected in our experiment was in this direction but not statistically significant. Nefdt (1989) found that when 2 *C. capensis* females entered a fig simultaneously, they produced a sex ratio of 0.20. That we did not observe this large increase suggests that the wasps may need to interact in order to adjust their sex ratios.

Werren (1980) and Suzuki & Iwasa (1980) argued that in conditions where a host is parasitized by either one, or two females in sequence, the first females' sex ratios should correlate positively with the probability of superparasitism (a phenomenon analogous to a second female entering and ovipositing inside a fig after the first has completed oviposition). The proportion of single foundresses in a species should covary negatively with the probability of sequential oviposition. We can therefore test the hypothesis with fig wasps, using Herre's (1987) data from New World species. In support of their predictions, there is a significant negative correlation between the proportion of fruits with single foundress broods and the proportion of males in single foundress broods (Spearman Correlation Coefficient, Rs = -0.664, n = 13, P = 0.013; Fig. 1). This suggests that the first females that enter figs may make adjustments for the possibility that subsequent females will also be ovipositing in the same figs. Sequential oviposition may therefore be influencing between-species variation in single foundress sex ratios. Alternative explanations for variation in single foundress sex ratios are nonetheless available. Herre (1987), for example, argued that wasps should lay sex ratios that are closer to optimality under those conditions experienced most frequently by the wasps, hence he expected the same negative correlation. Sex ratios produced by male foundresses might also reflect the need by the wasps to ensure that sufficient male progeny are available to produce an exit hole for the females (Herre *et al.*, 1996) or to fertilize all the females (Hamilton, 1970). These factors may well act in concert.

Our experimental results show that optimal sex ratio selection in fig wasps may be more complex than previously thought. However, we have only shown that sequential ovipositing is possible, and its prevalence in natural populations remains to be determined.

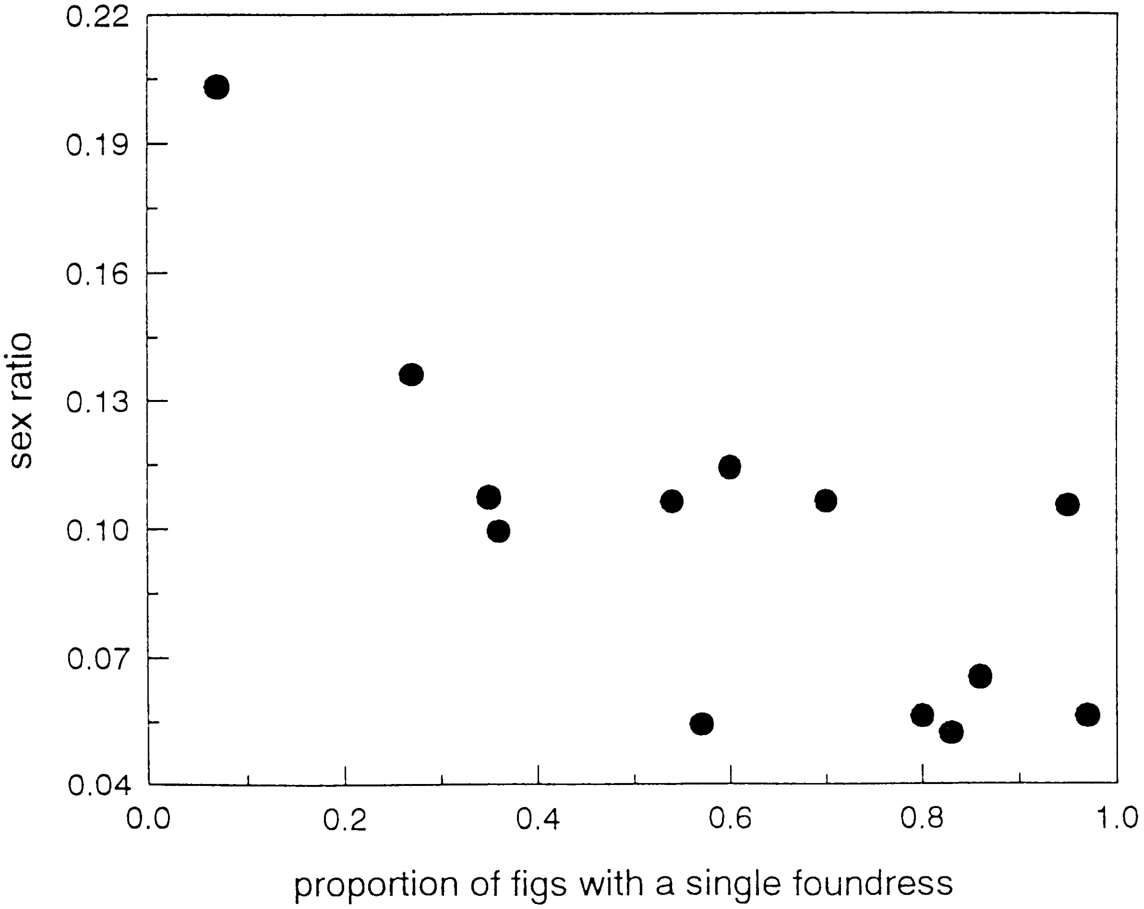

Fig. 1. Between-species comparisons of the proportions of figs with single foundress broods in relation to the mean proportion of males produced by lone foundresses. Data for 13 species of Neotropical fig wasps from Herre (1987).

7. Conclusions

Due to the diversity of fig wasp mating and oviposition systems their offspring allocation strategies allow for much comparative work. It is useful to distinguish between externally and internally ovipositing species. I concentrated mainly on externally ovipositing fig wasps which present us with a number of interesting life history traits that shape sex allocation. Sex allocation shapes the population genetically so as to predispose species to evolve in certain directions - fighting, eusociality and sibmating (see below). The models developed here give some direction and suggestions for future fig wasp work. The findings, especially those of chapter 3, resulted in general conclusions about allocation theory that other workers need to keep in mind when testing theories.

Externally ovipositing species

The females of externally ovipositing species can lay their eggs in a number of figs and mating may take place at several locations inside or outside the fig. Male morphology correlates very well with mating site and males are specialised to either mate inside the fig or to disperse before mating outside the figs (Vincent 1991). Males that disperse are routinely winged whereas locally mating males are apterous. Some species have dimorphic males with one morph being an active disperser whereas the other mates locally in the fig (Hamilton 1979). Some of the morphs that mate inside the fig are extremely aggressive and routinely kill conspecific males in their quest for mating opportunities. Since the mating pattern is an important factor in determining allocation strategies I investigate the relationships between mating patterns and oviposition behaviour and the work suggests that female oviposition strategies can in turn shape male behaviour.

Dimorphic males: a male perspective

The determination of the sex of offspring is believed to be controlled by the female who, by controlling the muscles of her spermatheca, can either prohibit fertilisation of an egg or fertilise it respectively. The optimisation of the sex ratio is thus treated from the perspective of the mother (but see Hawkes 1992). The genes that affect morph determination may either be expressed in mothers or their sons. Hence a model needs to consider expression of these genes at either of these two levels.

Females allocate resources to offspring in such a way that competition between her own offspring are minimised: investing in offspring that are more likely to compete against each other than against random individuals only serves to increase the strife between similar genes. A female should also value her offspring in terms of their expected mating success, allocating more resources to offspring with a higher expected mating success. Considering fig wasp with dimorphic males (chapter 2) we can expect that mothers will allocate resources to the two types of sons in accordance to their expected mating success, i.e. the proportion of females that will mate with either. Furthermore, the female should reduce the amount of energy invested in males that mate locally as the amount of competition between brothers increases. The dispersing males do not compete against brothers. When the genes determining the morphs are expressed in males, the success of such genes also depends on the expected reproductive success of the two types of males and on the amount of competition with similar genes. Therefore local mate competition (LMC) between brothers should also bias the morph ratio towards the dispersing morph, but to a lesser extent than for the case when the gene is expressed in the mother.

The model predictions fit the data collected by Hamilton (1979) very well and better than his model. It suggests that the problem is understood. The only difference between the models is that Hamilton assumed that females lay only one egg per fig whereas I assumed that females lay bigger clutches of constant size. His assumption eliminates all possibilities for LMC because brothers never share a fig. However, too much comfort should not be taken in the good fit because a number of assumptions still need to be scrutinised. The assumption of constant clutch size may by wrong, especially in the light of chapter 4 (see below) which suggests a dichotomy in clutch sizes. I also assume that the proportion of females that can be mated by either type of male is independent of the proportion of the male types. In practice the mating "strategy" of females seems to be an artefact of whether there are any living males present inside the fig. When there are, they are mate inside, when not, they have to mate outside. In turn the number of live males depends on the extent of male fights, on the duration of female eclosure and on mortality rates of males. We can expect at least the latter phenomenon to produce a correlation between the number of local mating males in a fig and the number of females that will mate inside the fig. These two assumptions need to be clarified before any final confidence can be placed in the models. It is also not known if females mate only to dispersing males when they fail to mate inside the fig. It is potentially possible that females may mate more than once, but behavioural data suggest (Greeff unpublished data) that females become unattractive to males very soon after their first mating.

Dimorphic males: a female perspective

In the previous section the occurrence of male dispersal was investigated with a perspective of male mating success and local mate competition between brothers. In this section the focus is turned to the female. Females are believed to adjust their sex ratios to the average inbreeding coefficient in the population. The inbreeding coefficient determines the average relatedness of a daughter to her mother. Hence, more inbred populations have more female biased sex ratios because daughters are more related to their mothers. However, the specific relatedness of a daughter to her mother varies in the population as do the inbreeding coefficient, and the sex ratios produced by mothers are thus a best reply to average conditions, rather than specific adjustments to relatedness. Females who are able to adjust their sex ratios to a more accurate measure of relatedness will have higher fitness. Such information may be obtained from the male's morphology or from the mating site.

In a very simplified model (chapter 3), I show that split sex ratios evolve when a female can distinguish between brothers and non-brothers, with sibmated females producing more female biased sex ratios because they are more related to their daughters than outbred females. Although the model assumptions are very restrictive, I expect similar adjustments for more complex structured populations with females gauging their allocations to daughters by their relatedness to their mates. Boomsma and Grafen (1991) predicted similar splits for eusocial insects where the relatedness of workers to nest mates varied due to different levels of polyandry of the queens. In these cases workers adjust the sex ratio of the sexuals produced from the colony with respect to their average relatedness to nest mates, or the genetic variance in the colony.

These findings have a number of interesting repercussions. Firstly, split sex allocations predisposes a taxon towards the evolution of eusociality in haplodiploids. The ability of females to determine the relatedness of mates may bias a taxon into becoming eusocial. However, haplodiploid eusocial taxon mostly have complimentary sex determination (Cook 1993) which causes a high degree of inbreeding depression. In these taxa, CSD is likely to reduce the extent of inbreeding to such an extent that the process will not be given a chance to start the evolutionary trajectory. Secondly, a general trend in wasps to facultatively manipulate their offspring sex ratios in a way proportional to their relatedness to their mate can result in variation in data when the relatedness to mate is not controlled for. It will be interesting to see if these conditional adjustments are as common as the split sex ratios in eusocial insects. It will be easy to test this general prediction on fig wasps and other parasitoids. Thirdly, a male has more offspring per sibmating event than per outbreeding event, because males are only related to daughters. Hence, males may be expected to follow sibmating strategies more often than the availability of females will predict. For the model I investigate, very few males are expected to sibmate, because it will reduce the mating success of other sibmating brothers enormously. However, in LMC models this effect may shape the incidence of sibmating as opposed to outbreeding. When multiple matings occur the accuracy with which females can adjust their sex ratios should be decreased.

Clutch size and sex ratio with monomorphic local mating males

Hamilton's model assumed that females lay only one egg per fig. Daughters increase their mother's reproductive success by reproducing, but can also increase their brother's mating opportunities (Taylor 1981; Frank 1986b). Hence, females that lay daughter eggs together with sons may have higher success than females who lay single eggs. Hence, in the previous two sections it was assumed that females produce larger clutches, but of constant size. Here I determine whether we can expect clutches to have a constant size.

Analytical models are fairly unsuccessful at solving this problem because the optimal clutch size does not depend on the clutch size itself but rather on the sex ratios of the focal female and of the patch. Hence, specific models need to be constructed to identify trends that can be expected. First a model is developed in which females have no information regarding the fig they oviposit on and second the model is extended to allow females to have complete information of the content of the figs (chapter 4).

The models predict that clutch sizes should not be monotonic in the population, but it is under diverging selection to be either as big as possible or as small as possible. However, linked to clutch size is the sex ratio. Bigger clutches will only be favoured if they are more female biased and smaller clutches when they are more male biased. The end result is a dichotomous oviposition strategy with females producing either large very female biased clutches or one male-egg clutches. When females have no information about the figs on which they oviposit they adopt these two strategies at equilibrium frequencies. When females have information regarding the fig they facultatively shift between the two strategies depending on the fig's content.

This prediction has several ramifications that also affect the previous two models. Firstly, males sharing a fig are very seldom sibs, whereas females are. Low relatedness between brothers will not prevent the evolution of fatal fighting. Hence, any other force selecting for fatal fighting will not be barred by relatedness and the high incidence of fatal fighting can be understood. Furthermore, variation in sex ratios of figs should not be interpreted as an estimate of the relatedness between brothers as Hamilton (1979) and Murray (1989) assumed.

Secondly, the exact relevance of this model to the model presented in chapter 2 has not been computed. But the occurrence of females producing single male eggs, leading to lower relatedness between males, should increase the incidence of males that mate locally, since LMC will be reduced between brothers. The occurrence of dispersing males causes extra females to increase the mating success of their brothers to a lesser degree, which may select for less female biased sex ratios. However, these are mere speculations and specific modelling will need to be directed at this multidimensional problem.

The predictions of this model can be tested by estimating the relatedness of males sharing figs and comparing this to that of females. Before such data are available it will be impossible to determine population genetic structure by inference from sex ratio variation.

Internally ovipositing species

Internally ovipositing species, which include the pollinating species, are the ones who have received most attention with regards to their sex ratios. The beauty of these pollinating species is their relatively simple life history which resembles the model assumptions of LMC models very well. Females enter figs fairly simultaneously to found oviposition patches. They lay all their eggs inside one fig and all the mating takes place, presumably at random (but see Frank 1985b), between the hatchlings of the specific fig. Here I address two separate issues regarding the interpretation of sex ratio data and the assumptions of models.

Sex ratio variation

Exactly how variation in sex ratio should be treated is unclear. It can either mean that there are constraints preventing it from being perfectly adjusted, or it can be a result of fine tuned conditional responses of females such as investigated in chapter 3 (also see chapter 1). If variation is the result of non-adaptive noise, it is important to test the optimality model's sensitivity to variation ,since variation can lead to different optimal predictions. I examine a two foundress local mate competition model in which variation can be expected to give the biggest deviation between optimal predictions allowing variation and those that do not. It is found that the variation needs to be substantial to cause any change in the predictions. It is important to notice that such variation should be interpreted as yet another constraint on sex allocation and not as a failure of adaptation as Herre *et al.* (1996) suggest and as Orzack and Sober (1994a, 1994b) would insist upon.

Sequential ovipositing

The data suggest that the assumption that females enter very shortly after each other should be questioned. However, only the possibility of sequential oviposition has been illustrated and further experiments will need to determine its incidence. If sequential ovipositing occurs routinely in fig wasps it will mean that the first foundress to enter a fig will not produce a sex ratio that is the best for a single foundress. She should produce a more male biased sex ratio, to cushion for the cases when second and later females are still going to enter. This prediction is supported by data. It might become necessary to identify the offspring of specific mothers to further advance sex ratio studies on pollinating species.

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9. Appendix

List of abbreviations for chapter 3

α	proportion of the females of each clutch that sibmates
f_o	number of female offspring produced by an outbred female
f_s	number of female offspring produced by a sibmated female
G_a	average relatedness of a daughter to her mother
G_m	relatedness of a son to his mother
G_o	relatedness of a daughter to her outbred mother
G_s	relatedness of a daughter to her sibmated mother
i	sex ratio (proportion of daughters) produced by sibmated females
K	number of offspring a female produce
m_o	number of male offspring produced by an outbred female
m_s	number of male offspring produced by a sibmated female
ρ	sex ratio produced by a mutant female unconditionally of mating behaviour
r	ES sex ratio produced by females where sex ratio is not conditional on mating behaviour
R	non-mutant females' sex ratio (unconditional to mating behaviour)
s	inbreeding depression (proportion of brood that dies)
u	sex ratio produced by out bred females
v_f	reproductive value of the female subpopulation
v_m	reproductive value of the male subpopulation
V_o	reproductive value of an outbreeding event
V_s	reproductive value of a sibmating event
w_{fo}	inclusive fitness value of one additional daughter to her outbred mother
w_m	inclusive fitness value of one additional son to his mother
w_{fs}	inclusive fitness value of one additional daughter to her sibmated mother
W	inclusive fitness of a strategy