EVOLUTION OF SEX RATIOS IN SOCIAL HYMENOPTERA: KIN SELECTION, LOCAL MATE COMPETITION, POLYANDRY AND KIN RECOGNITION*

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ABSTRACT

A model is constructed to study the effect of local mate competition and multiple mating on the optimum allocation of resources between the male and female reproductive brood in social hymenopteran colonies from the 'points of view' of the queen (parental manipulation theory) as well as the workers (kin selection theory). Competition between pairs of alleles specifying different sex investment ratios is investigated in a game theoretic frame work. All other things being equal, local mate competition shifts the sex allocation ratio in favour of females both under queen and worker control. While multiple mating has no effect on the queen's optimum investment ratio, it leads to a relatively male biased investment ratio under worker control. Under queen control a true ESS does not exists but the 'best' strategy is merely immune from extinction. A true ESS exists under worker control in colonies with singly mated queens but there is an asymmetry between the dominant and recessive alleles so that for some values of sex ratio a recessive allele goes to fixation but a dominant allele with the same properties fails to do so. Under multiple mating, again, a true ESS does not exist but a frequency

dependent region emerges. The best strategy here is one that is guaranteed fixation against any competing allele with a lower relative frequency. Our results emphasise the need to determine levels of local mate competition and multiple mating before drawing any conclusions regarding the outcome of queen-worker conflict in social hymenoptera . Multiple mating followed by sperm mixing, both of which are known to occur in social Lymenoptera, lower average genetic relatedness between workers and their reproductive sisters. This not only shifts the optimum sex ratio from the workers 'point of view' in favour of males but also poses problems for kin selection theory. We show that kin recognition resulting in the ability to invest in full but not in half sisters reverts the sex ratio back to that in the case of single mating and thus completely overcomes the hurdles for the operation of kin selection.

1. INTRODUCTION

Fisher (1930) showed that in outbreeding populations natural selection would favour equal parental investment in offspring of each sex. If the population is inbreeding however, competition for females is predominantly between brothers (local mate competition) so that natural selection favours a female biased sex ratio (Hamilton, 1967). In the extreme case, when there is complete sib-mating, a parent 'should' produce just enough sons necessary to inseminate all the daughters. These predictions of Fisher and Hamilton have been repeatedly verified, both theoretically and empirically (Charnov, 1982; Metcalf, 1980; Owen, 1983; Werren, 1980; 1983). Indeed the theory of sex allocation has in recent years become a cornerstone of evolutionary biology, a status achieved primarily because of the success with which precise quantitative and empirically testable predictions have been made (Charnov, 1982).

The theory of sex allocation has assumed importance for yet another reason. Predictions concerning sex allocation appear to be powerful in choosing between competing theories purporting to explain the evolution of sociality in insects.

A hidden assumption in Fisher's argument of equal allocation between the two sexes is that a parent is equally related to his or her sons and daughters. In haplodiploid social insects such as wasps, bees and ants, sterile female workers often feed and care for their siblings instead of producing their own offspring. Haplodiploidy, a genetic system where males arise from haploid unfertilized eggs and females from fertilized, diploid eggs, creates asymmetries in genetic relatedness. Females are related to their sisters by 3/4 and to their brothers by 1/4. This asymmetry is in fact an important factor in favour of Hamilton's (1964a,b) theory of the evolution of social behaviour because it genetically predisposes a hymenopteran worker towards the evolution of sterility. Trivers and Hare (1976) argued however that a worker gains nothing in fitness if she invested equally in brothers and sisters because her average relatedness to her siblings is 1/2, the same as her average relatedness to her own offspring. Sterility in workers would be selected if they can capitalise on the asymmetries in genetic relatedness by investing in their sisters and brothers in the ratio 3:1. In other words when workers invest in siblings who are related to them in the ratio 3:1 natural selection would favour a ratio of allocation paralleling the ratio of relatedness. The queen who is fertile and who produces the sons and daughters would on the contrary favour an equal investment in brood of the two sexes in her colony. In this context there would be a conflict of interests between the queen and the workers in the optimum ratio of allocation of resources between brood of the two sexes.

The theory of kin selection argues that workers are sterile and act altruistically towards their sibs because this is the strategy that maximises their inclusive fitness. Inclusive fitness of an individual may be defined as its total contribution to the gene pool of the next generation obtained both by the production of offspring and by aiding genetic relatives. The theory of parental manipulation (Alexander, 1974) on the other hand suggests that workers are sterile because they are manipulated into this state by their parents. The two theories make mutually opposing predictions regarding the expected allocation between the two sexes in the reproductive brood in social hymenopteran colonies. If kin selection is responsible for worker sterility and altruism, then the workers should win in the conflict over the investment ratio and the resultant sex-investment ratio observed should be 3:1. If worker sterility and altruism are a consequence of parental manipulation instead, queens should be successful in manipulating the workers into investing equally in reproductives of the two sexes and a 1:1 ratio of investment is expected. Trivers and Hare (1976) weighed male and female reproductives in a number of social hymenopteran colonies and showed that the observed ratios of investment were significantly closer to 3:1 than 1:1 and concluded that their data are uniquely explained by kin selection theory.

The predictions and conclusions of Trivers and Hare (1976)depend on the assumption that the social insects under consideration are outbreeding and that the queens mate only once. Under inbreeding or local mate competition (LMC), the queens too would prefer a female biased investment ratio (Hamilton, 1967) and the 3:1 ratio seen by Trivers and Hare may have nothing to do with workers realising their optimum investment ratio as opposed to the queens' optimum value (Alexander and Sherman, 1977). Similarly if the queens mate with more than one male then the relatedness between the workers and the reproductive sisters they rear will no longer be 3/4 but distributed anywhere between 3/4 (full sisters) and 1/4 (half sisters). Under these conditions the predictions used by Trivers and Hare (1976) are no longer valid (Alexander and Sherman, 1977). Both LMC and multiple mating by queens are known to occur in social hymenoptera although their intensities might vary widely (Alexander and Sherman, 1977; Page and Metcalf, 1982; Crozier, 1980). While multiple mating has long been recognised to be common in hymenoptera (see Wilson, 1971) it has often been assumed that sperms from different males clump in the spermatheca of the females leading to use of sperm from a single male for extended periods of time (see Orlove, 1975, for example). However, in the only case where careful investigation has gone into this question it is clear that sperms do not clump (Page and Metcalf, 1982).

When multiple mating results in a lowered average genetic relatedness between workers and reproductives in a colony this not only alters the expected sex-investment ratio from the workers 'point of view' but may also be considered as a factor against kin selection (Hamilton 1964b; Wilson 1971). It may be argued however that 'workers can circumvent the problem of multiple insemination' by kin recognition leading in full sisters but not in half-sisters (Page and Metcalf, 1982).

In recent years a number of theoretical investigations relating to the evolution of sex ratios in social hymenoptera have been undertaken. Stimulated in part by the work of Trivers and Hare (1976) who predicted a 3:1 investment ratio under worker control and a 1:1 ratio under queen control, several authors have confirmed these predictions by rigorous methods (Oster, Eshel and Cohen, 1977; McNair, 1978; Craig, 1980; Uyenoyama and Bengtsson, 1981; Charnov, 1980). Other factors such as LMC and worker-queen conflict have also occassionally been considered (Taylor and Bulmer, 1980; Oster, Eshel and Cohen, 1977, Bulmer, 1981, Benford, 1978). Our intention here is to simultaneously consider the effects of LMC, polyandry and kin recognition and generate predictions regarding optimum sex allocation ratios in the frame work of kin selection theory and parental manipulation theory.

2. THE MODEL

Consider a large population of social insect colonies. Each colony is initiated by a single inseminated female (queen) who first produces an undefined number of female offspring who act as workers. These workers care for and feed the reproductive male and female offspring subsequently produced by the queen. (The reproductive brood). Allocation of resources between production of workers and reproductives is another problem but we shall not be concerned with that here. Here we shall also not worry about the workers and refer only to the reproductives as offspring or sons and daughters. After the emergence of the reproductive offspring, the queen dies. Of both the male and female offspring, a fraction d disperses away from the natal nest and joins a mating aggregate. The dispersing fraction of reproductives from each colony joins this aggregate where random mating takes place (outbreeding). A fraction $1-d$ of male and female offspring remains at the natal nest site and undergoes sib mating (inbreeding). After matimg all the males die and each inseminated female initiates a separate new colony. Thus d parametrises local mate competition. A value of unity for d indicates complete outbreeding while a value of zero implies total inbreeding.

Let a single locus with two alleles A(dominant) and B(recessive) specify the investment ratio between the two sexes. For simplicity let us assume that the investment ratio is directly translated into sex ratio. Thus individuals of the genotype AA and AB produce a fraction r_A of males among their reproductive progeny while individuals of the genotype BB produce a fraction r_B males.

Queen control of investment ratios

Even if the optimum investment ratio is different for the queen and the workers, the queen could in principle manipulate the workers into feeding her reproductive offspring in the ratio optimum for her. This is modelled by adjusting the sex ratio of reproductive offspring according to the genotype of the queen.

If queens mate only once there would be six types of inseminated females, AA.A, AA.B, AB.A, AB.B, BB.A, BB.B (where the first two letters refer to the queen's genotype and the third letter refers to the genotype of the male she has mated with i.e., of the sperm stored in her spermatheca). Consider inseminated females of the genotype AA.A. These females produce r_A sons and $1-r_A$ daughters. Of these dr_A sons and $d(1-r_A)$ daughters disperse. $(1-d)r_A$ sons and $(1-d)(1-r_A)$ daughters stay at the nest and undergo sib mating to result in $(1-d)(1-r_A)$ inseminated females of the genotype AA.A. Similarly, in a colony initiated by an inseminated female of type AB.A, $\frac{r_A}{2}$ sons each of type A and B and $\frac{1-r_A}{2}$ daughters each of type AA and AB are produced. Of these, $\frac{dr_A}{2}$ sons each of type A and B and $\frac{d(1-r_A)}{2}$ daughters each of type AA and AB disperse while $\frac{(1-d)(r_A)}{2}$ sons each of type A and B and $\frac{(1-d)(1-r_A)}{2}$ daughters each of type AA and AB stay on at the nest. After sib mating four types of inseminated females result, AA.A, AA.B, AB.A and AB.B, each in frequency $\frac{(1-d)(1-r_A)}{4}$.

From a knowledge of the frequencies $(f_1, f_2 \ldots . f_6)$ of each of the types of inseminated females initiating colonies in any one generation, one can calculate the total frequencies of each type of male and female offspring arriving at the mating aggregate. Now, assuming random mating we can compute the frequencies of each type of inseminated female produced as a result of outbreeding.

Thus knowing the frequencies of each type of inseminated females in one generation, we can compute the frequencies of each type of inseminated females at the next generation as

$$\begin{pmatrix} f_1(t+1) \\ \vdots \\ \vdots \\ \vdots \\ \vdots \\ f_6(t+1) \end{pmatrix} = [A] \begin{pmatrix} f_1(t) \\ \vdots \\ \vdots \\ \vdots \\ \vdots \\ f_6(t) \end{pmatrix} \quad \ldots 1$$

where the elements of A are functions of r_A, r_B, d as well as $f_1(t) \ldots f_6(t)$. Since the frequencies of the six types of females should add up to unity, the dynamics of the system is described by a 5x5 matrix. (For a detailed description of this methodology, see Charnov, 1982).

In a system of 2 alleles A and B, the two obvious steady states correspond to populations consisting only of A(frequency of allele A, $f_A=1.0$) and only of B($f_B=1.0$). The resistance of each of these steady states to invasion by the other allele is investigated by a stability analysis of the system of difference equations (1). If the dominant eigenvalue of the matrix describing the dynamics of a small perterbation about a steady state is greater than unity then that steady state is unstable (can be invaded). Conversely if the eigenvalue is less than unity than that steady state is stable (cannot be invaded). If $f_A=1.0$ is stable and $f_B=1.0$ is unstable this indicates that A would be selected for and go to fixation. Both $f_A=1.0$ and$f_B=1.0$ being stable indicates a frequency dependent selection (who ever establishes himself first wins). Finally, if both $f_A=1.0$ as well as $f_B=1.0$ are unstable this indicates coexistance of the two alleles.

For different values of r_A (the proportion of males specified by the dominant allele), r_B(the proportion of males specified by the recessive allele) and d the dynamics of the system is investigated to determine which of the above conditions prevail, viz., one of the two alleles going to fixation, the two alleles coexisting or frequency dependent selection.

Worker control of investment ratios

Trivers and Hare (1976) assumed that 'the offspring is capable of acting counter to its parents' 'best interests' and thus workers should be able to feed the reproductive brood in the ratio that optimises their inclusive fitness. Once again, making the simplifying assumption that investment ratios are directly translated into sex ratios, this is modelled simply by adjusting the sex ratio of the reproductive brood in accordance with the genotype of the workers. For instances queens of the type AB.B will produce workers of the type AB and BB in equal proportions. Although some have considered the possibility of workers of one genotype behaviourally dominating over workers of other genotypes (Charnov, 1978; Craig, 1980; Pamilo, 1982; Bulmer, 1983) we agree with Bulmer (1983) that additivity seems biologically more meaningful. Thus in a colony with AB and BB workers in equal numbers, the proportion of males in the reproductive brood is taken to be $\frac{r_A + r_B}{2}$. Thus $\frac{r_A + r_B}{4}$ males each of types A and B and $1/2\ (1 - \frac{r_A + r_B}{2})$ females each of type AB and BB are produced in a colony initiated by an inseminated female of type AB.B.

Polyandry

When queens mate with more than one male, they are assumed to mate with males of different genotypes in the proportion that males of these genotypes are represented in the population (at the nest site in the case of sibmating or at the mating aggregate in the case of out breeding). Equal number of sperms of each mate are assumed to be stored in the spermatheca which are then used randomly. Thus in a system of 2 alleles, if every female mates twice there would be 9 types of inseminated females, AA.A.A, AA.A.B., AA.B.B., AB.A.A., AB.A.B., AB.B.B., BB.A.A., BB.A.B., BB.B.B. where the first two letters refer to the genotype of the female and the last two letters refer to the genotypes of the 2 males she has mated with. Similarly one can write down the genotypes of inseminated females for any specified number of matings. For different numbers of mating we have investigated the outcome of competition between alternate sex ratio alleles both under queen and worker control.

Kin-recognition

In the previous section the workers were assumed to invest in all brothers and sisters irrespective of their relatedness (i.e. full-sisters and half-sisters were not distinguished). Here it is assumed that workers can distinguish genetic relatedness and will invest in their full-sisters but not in their half sisters. As for investment in brothers, multiple mating by the queen does not make any difference as there can be no half-brothers in a haplodiploid system. In a colony initiated by a female of the type AA.A.B. (where the first two letters refer to the genotype of the female and the last two letters refer to the genotype of the two males she has mated with) there would be daughters of two genotypes AA and AB, each type being full-sisters amongst themselves but half-sisters of each other. Hence we assume that AA females would invest only in AA females and brothers while AB females would invest only in AB females and brothers. In a colony founded by a female of the type AB.A.A. on the other hand, there would still be two lines of full sisters but both would contain equal numbers of females of the genotype AA and AB. In other words full-sisters and half-sisters are decided by which father the sperm has come from and not by the genotype with reference to the alleles A and B in our model; these alleles are merely sex-investment ratio determining alleles. We assume therefore that both AA and AB females would invest in males on the one hand and equally in AA and AB females on the **other.** In contrast, in a colony founded by females of the type AB.A.B. there would again be two lines of full sisters one consisting of AA and AB females and the other of BB and AB females. While each type of worker will allocate resources between brothers and sisters depending on its genotype, resources meant for the sisters will be subdivided in the following manner. AA workers will invest equally in AA females and 50 % of the AB females who are their full sisters. BB females will similarly invest in BB females and the remaining 50 % of AB females who are their full sisters. As for AB females, the first 50 % who are full-sisters of AA females will invest equally in AA females and in that 50 % of AB females who are their full sisters. Similarly the other 50 % of AB females who are full sisters of BB females will invest equally in BB females and the remaining 50 % of AB females who are their full sisters. Using this formulation ~~one~~ we have investigated the outcome of competition between alternate sex ratio alleles under worker control when kin recognition is present.

3. RESULTS

A. Evolutionarily Stable Strategies

What sex investment strategies would be favoured by Natural Selection? We should look for those strategies which would go to fixation against competition from any other strategy. This can be readily done by a glance at the fate maps which present the results of competition between pairs of genotypes specifying different sex investment ratios. We illustrate this with the schematic diagrams in Fig.1 where values on the abscissa are proportions of male offspring specified by the dominant allele A and those on the ordinate by the recessive allele B. The diagonal is an equifitness line where the two alleles are indistinguishable. As described earlier, when the dominant eigenvalues (λ) is greater than 1, the resident allele can be invaded whereas if it is less than 1 it cannot be invaded. The set of pairs of r_A and r_B which correspond to $\lambda = 1$ thus forms a boundary between regions of stability and instability. Two such lines along with the diagonal divide the coordinate space into three kinds of regions (Fig.1) viz.A, where the dominant allele A goes to fixation, B, where the recessive allele B goes to fixation and C, where the two alleles coexist.

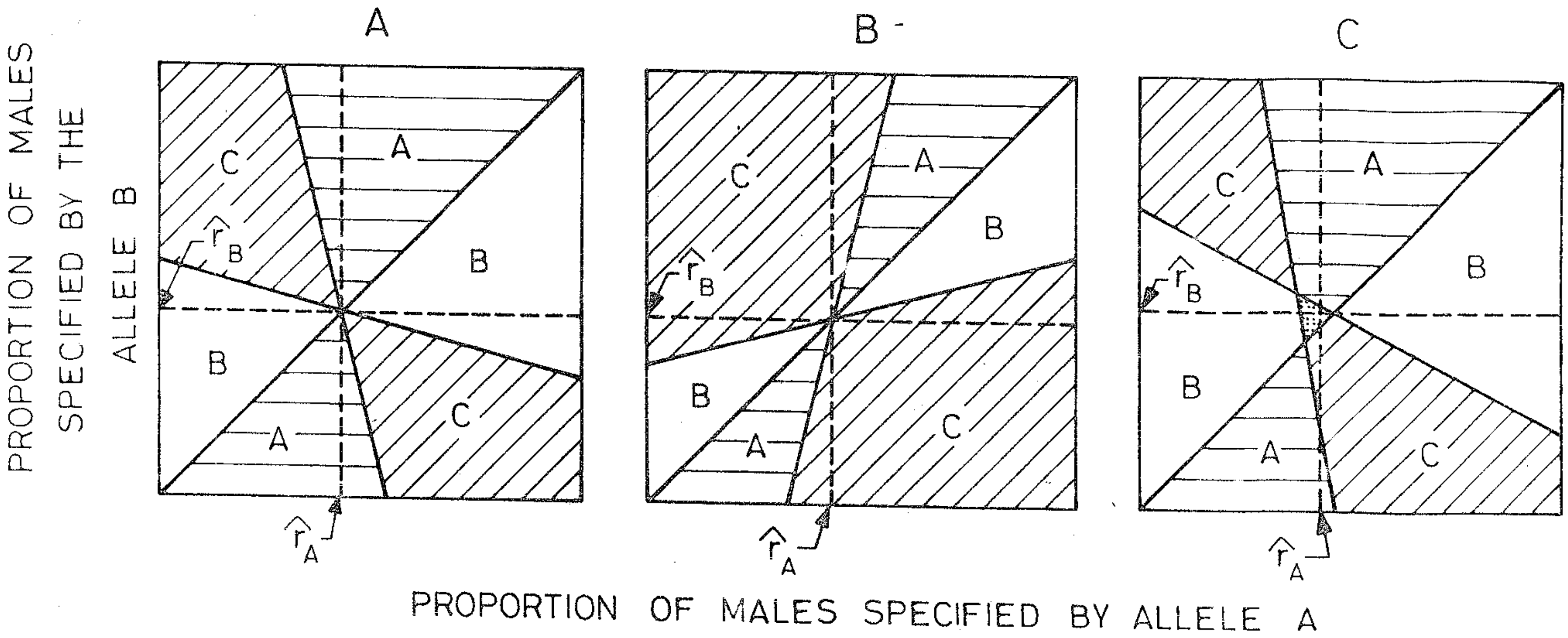

Figure 1 : Illustrative,fate maps showing schematically (A)ESS of the coexistence kind, (B)True ESS and (C)ESS of the frequency dependence kind. In the coordinate space of the proportion of males specified by two alleles, A is the area where allele A goes to fixation, B, the area where allele B goes to fixation and C where the two alleles coexist and f, the region of frequency dependence. r_A is the ESS for allele A and r_B the ESS for allele B.

To see which strategy will be favoured by natural selection notice from Fig.1A that when the dominant allele takes a value $\widehat{r}_A$ it would go to fixation irrespective of the value taken by the other allele. In other words this value of $\widehat{r}_A$ represents an evolutionarily stable strategy (ESS) (Maynard Smith 1964; for a lucid introduction to the concept of ESS, see Maynard Smith 1983).

It is possible however that no true ESS may exist. In Fig.1B for instance, whatever value one of the alleles takes, there is always a strategy open for the competing allele to invade. Notice that in Fig.1B if the allele A takes the value $\widehat{r}_A$ it may be invaded but never eliminated altogether, no matter what value is taken by the allele B. We shall henceforth call this an ESS of the coexistence kind. When the two lines separating regions of stability and instability do not intersect the diagonal at the same point there emerges a fourth kind of region in the co-ordinate space, a region of frequency dependence denoted by f in Fig.Ic. In this region that allele goes to fixation which has a higher initial frequency. Now if allele A takes the value $\widehat{r}_A$ it is stable against invasion by any mate competition (d) . A typical fate map (Fig.2) (at d=0.5 i.e., where half the offspring disperse before mating while the other half undergo sib mating) shows that the pattern is similar to that depicted in Fig.1B where no true ESS is possible but only an ESS of the coexistence kind. This means that a population need not necessarily consist of a unique strategy but that more than one strategy may coexist leading to the possibility of sex ratio polymorphism.

Variations of this ESS (of the coexistence kind) with levels of LMC (Fig.3) show that the results are as expected from the work of Fisher and Hamilton. Under complete outbreeding (d=1.0) an equal investment in males and females is predicted. As the level of LMC increases the optim ratio becomes increasingly female biased. The quantitative relationship[+] between the ESS and d in Fig.3 is described by

$$r = \frac{d(1+d)}{3+d} \qquad \ldots 2$$

[+] We have not derived this and the subsequent equations analytically as the algebra involved is extremely tedius. However the equations reproduce the corresponding curves exactly.

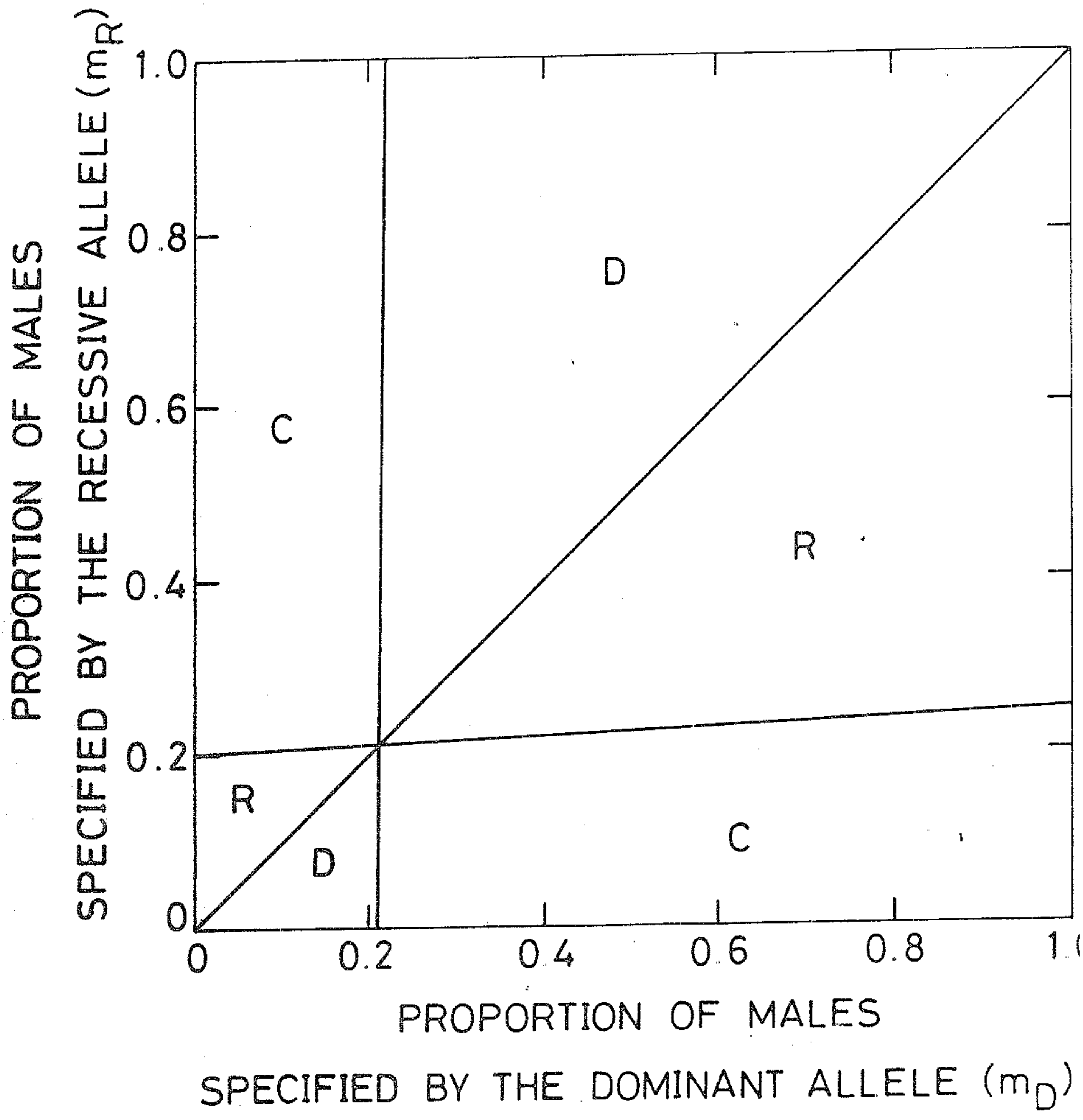

Figure 2 : Fate map for competition between a dominant and recessive allele specifying different sex ratios. Queen control.

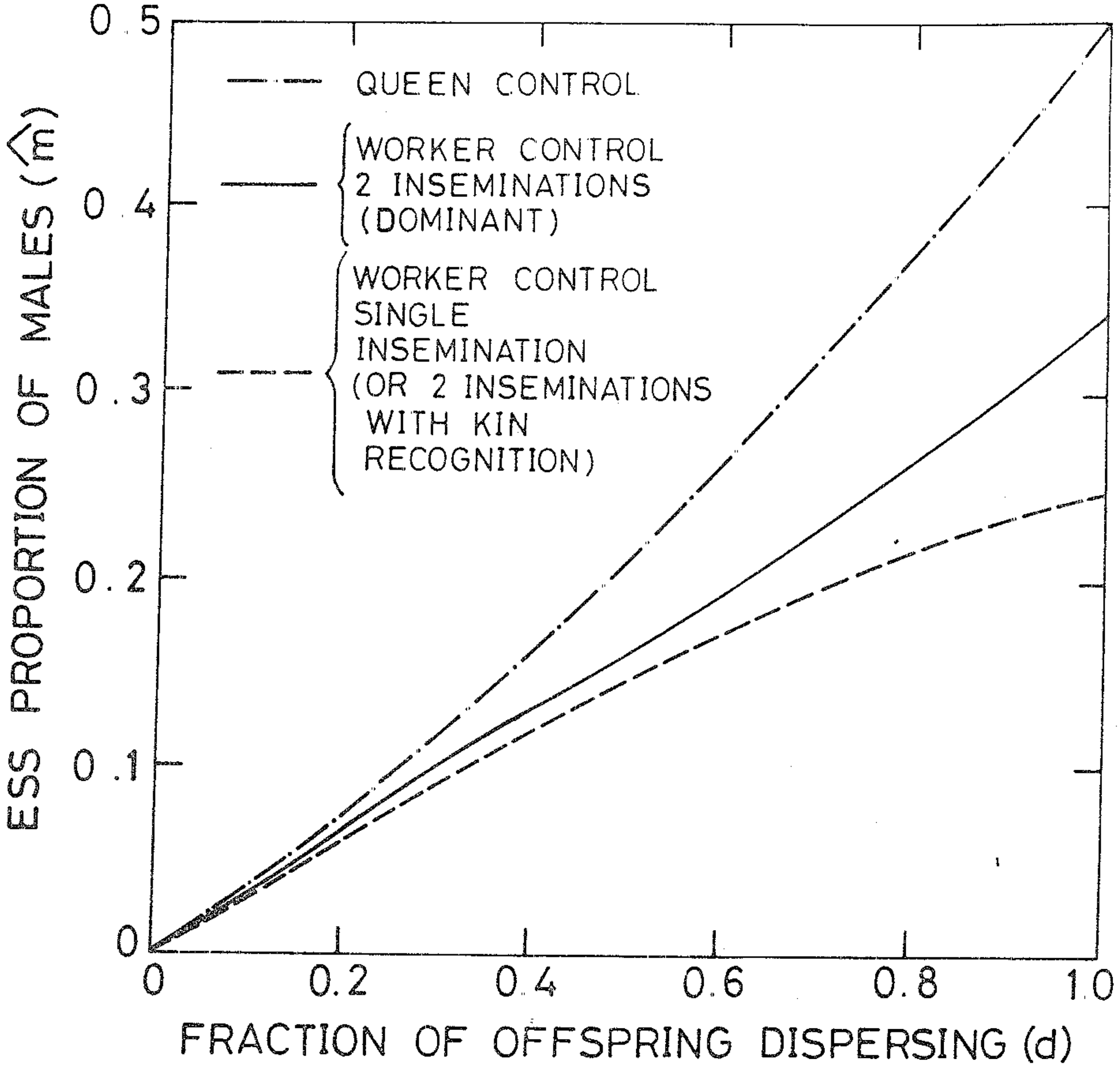

Figure 3 : ESS proportion of males ($\hat{m}$) is plotted as a function of fraction of offspring dispersing (d)

2. When workers control the Ratio of Investment

Now let us consider the situation when workers rather than queens decide the optimum ratio of allocation of resources between the two sexes. Once again in colonies with singly mated queens we have studied competition, under different levels of local mate competition, between alleles specifying different sex allocation ratios. A typical fate map (at d=0.5) (Fig.4) shows that the pattern is similar to that depicted in Fig.1A where a true ESS exists. Notice however that the fate map is asymmetrical with the regions where the dominant allele goes to fixation being smaller than that where the recessive allele goes to fixation. For instance, (Fig.4) a recessive allele producing 10 percent males always eliminates a dominant allele that produces 50 percent males. On the other hand if the allele specifying 10 percent males is dominant and the allele specifying 50 percent males is recessive then both alleles coexist at frequencies of 0.734 and 0.256 for the dominant and recessive alleles respectively (Table 1 columns 1-4). In other words a recessive allele goes to fixation while a dominant allele with the same properties fails to do so.

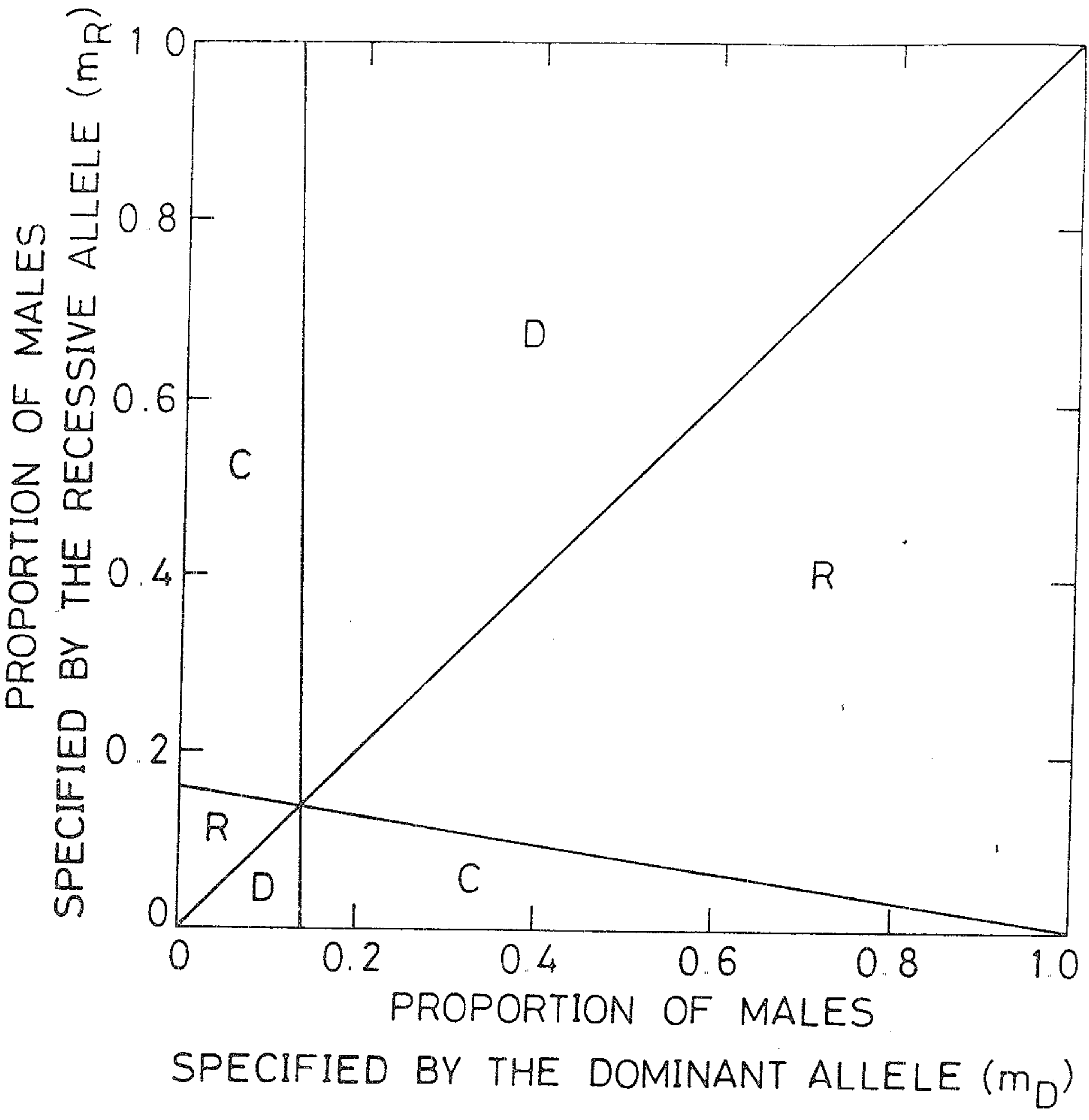

Figure 4 : Fate map for competition between dominant and recessive alleles specifying sex ratios. Worker control in colonies with single inseminated queens or double insemination with kin recognition.

TABLE - 1

Proportion of males specified by Genotypes		Equilibrium frequency of Alleles		Proportion of males observed at equilibrium	
Dominant Allele	Recessive Allele	Dominant Allele	Recessive Allele	Dominant Allele	Recessive Allele
0.5	0.1	0.0	1.0	-	0.1
0.1	0.5	0.734	0.266	0.120	0.198
0.7	0.1	0.0	1.0	-	0.1
0.1	0.7	0.804	0.196	0.118	0.206

This rather surprising result can perhaps be understood when we consider how the sex ratio is determined in colonies having more than one genotype. For example in a system of 2 alleles and each colony being initiated by one singly inseminated female, there would be six types of colonies (Table 2 Row 1). From the genotypes of the queens and the genotype of her mate we can write down the genotypic composition of the reproductive brood as well as workers in each type of colony. (Table 2, Rows 2,3 and 4). Some colonies are pure with respect to A or B while others have a substantial representation of both alleles. Let the allele A be advantageous compared to B. When A is dominant, the phenotypic sex ratio corresponds to that advantageous value specified by A, both in the colonies with pure A as well as to some extent in the mixed colonies (Table 2, Row 5). Thus some of this advantage is also confered on the allele B as a result of which it is never completely eliminated. On the contrary when A is recessive the phenotypic sex ratio corresponds to this value only in the pure A colonies so that none of the advantage is lost to the allele B (Table 1 Row 6). In such a situation A is therefore able to eliminate B altogether. Such an asymmetry between

TABLE - 2

Genotype of Inseminated Queen	AA.A[+]	AA.B	AB.A	AB.B	BB.A	BB.B
Genotype of male reproductive offspring	A	A	A or B	A or B	B	B
Genotype of Female Reproductive offspring	AA	AB	AA or AB	AB or BB	AB	BB
Genotype of worker offspring	AA	AB	AA or AB	AB or BB	AB	BB
Sex ratio of reproductives when A is dominant	r_A	r_A	r_A	$\frac{r_A+r_B}{2}$	r_A	r_B
Sex ratio of Reproductives when A is recessive	r_A	r_B	$\frac{r_A+r_B}{2}$	r_B	r_B	r_B

[+] The first two letters refer to the genotype of the queen while the third letter refers to the genotype of the male she has mated with i.e., the sperm she carries in her spermatheca.

a dominant and recessive allele seems therefore to be because of the fact that the advantageous dominant allele also biases the sex ratio of the other allele in the favoured direction whereas a recessive allele does not do so. If this argument were correct one would predict that when A is dominant and the two allele coexist, the phenotypic sex ratio of B at equilibrium should be closer to that specified by A (advantageous) rather than by B (disadvantageous). This is indeed what is seen when we look at the phenotypic sex ratios of the two coexisting alleles at equilibrium (Table 1, column 5 and 6).

We saw in the previous section that local mate competition leads to a female biased sex ratio under queen control. When workers control the ratio of investment this optimum sex ratio is even more female biased (Fig.3). The quantitative relationship between ESS sex ratio and levels of LMC (d) is described by

$$r = \frac{d}{3+d} \qquad \ldots 3$$

In the absence of LMC (d=1.0) the optimum sex ratio under worker control is 3:1 in favour of females as predicted by Trivers and Hare (1976).

C. Polyandry

When queens mate with males of more than one genotype their daughters would no longer be all full sisters of each other. Since some of the daughters of the queen become reproductives and others worker, the genetic relationship between an average worker and the average reproductive would not be 3/4 as in the case of single mating but lower. The optimum sex ratio from the workers point of view would therefore be different as a consequence of polyandry. The genetic relationship between the queen and her daughters however is not altered by multiple mating. The optimum sex ratio from the queen's 'point of view' is therefore not altered by polyandry.

As expected, our analysis shows that the results remain unaltered under polyandry when queens control the ratio of investment. On the other hand there are striking differences in the results under worker control. Considering the case of 2 matings we have studied the competition of alleles specifying different sex ratios, once again under different levels of LMC. The results (Fig.5) show that the fate maps are now similar to that shown in Fig.IC where a region of frequency dependence emerges. This leads to an ESS

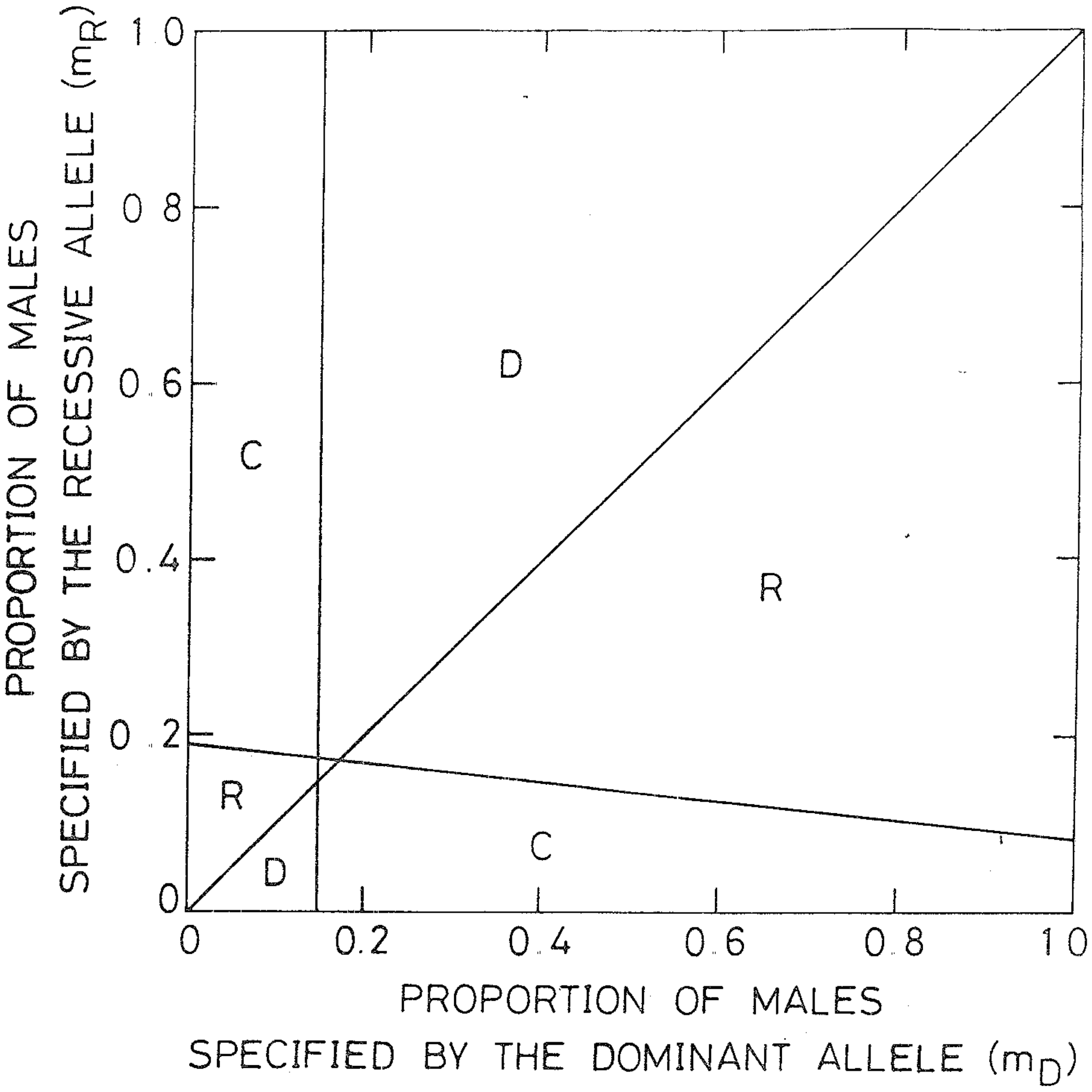

Figure 5 : Fate map for competition between a dominant and a recessive allele specifying different sex ratios. Worker control in colonies with doubly inseminated queens.

of the frequency dependence kind. Besides, the ESS for the dominant allele is different (although slightly) from that for the recessive allele. The kind of asymmetry between the dominant and recessive alleles seen in the single mating case still persists although considerably reduced. This is probably because with an increase in the number of inseminations, the varieties of colonies with respect to their genotypic composition increases. As a result, even for the recessive alleles, its advantage is no longer as strictly confined to itself as before.

When the ESS is plotted as a function of the levels of LMC (fig.3) we see that for any given value of d the optimum sex ratio under worker control with doubly inseminated queens is more female biased than the case of queen control but more male biased than the case of worker control with singly inseminated queens. As the number of inseminations that the queen has undergone increases, the optimum sex ratio under worker control becomes increasingly male biased and asymptotically approaches the corresponding value under queen control for that particular value of d (Fig.6)

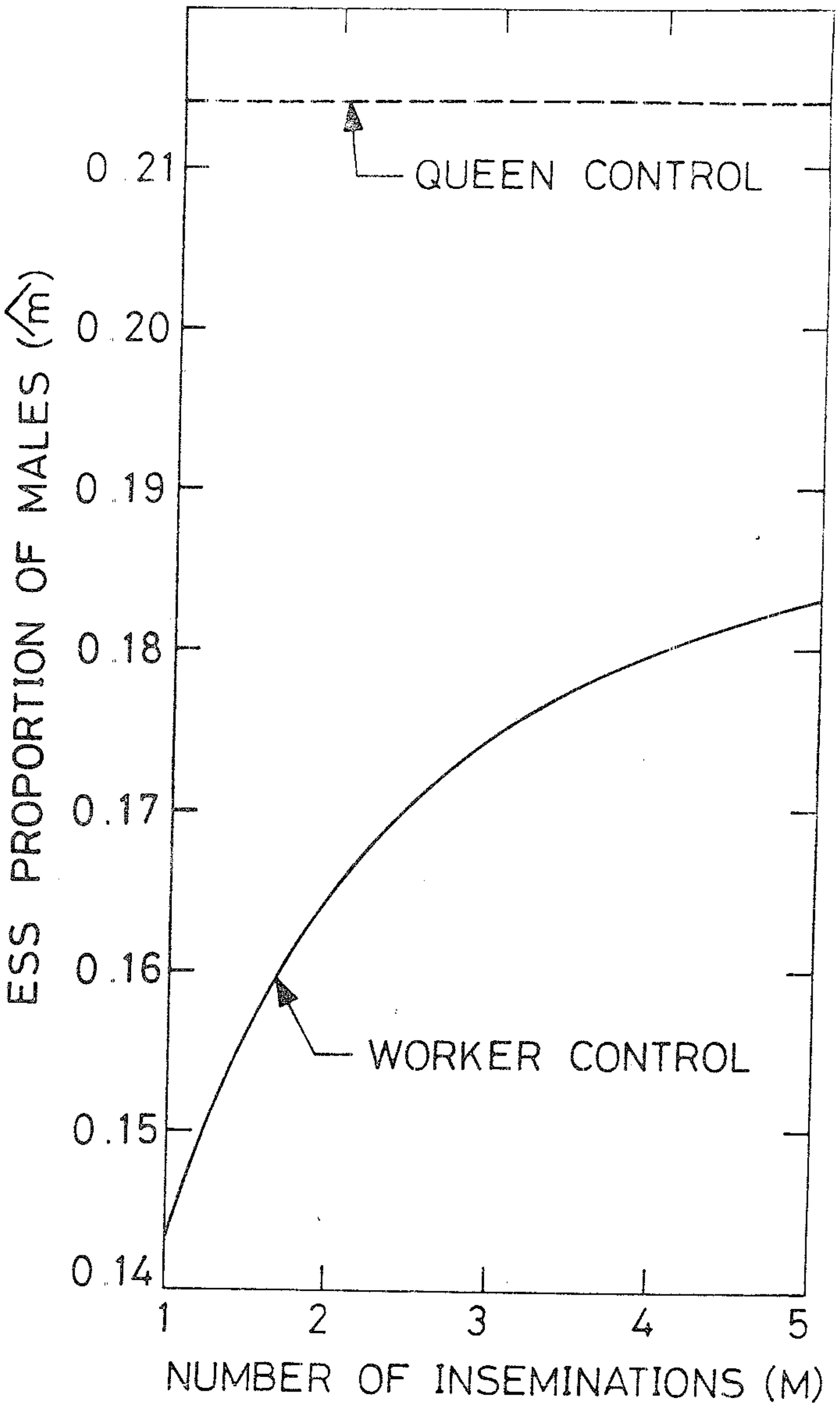

Figure 6 : ESS proportion of males ($\hat{m}$) is plotted as a function of number of inseminations (M).

Kin-recognition

The optimum sex ratio under worker control is less female biased when the queen mates more than once because the colony would now contain more than one line of full sisters. This reduces the average relatedness between a worker and a reproductive female. If by means of kin recognition each worker only invested in its brothers and full sisters one would expect that the optimum sex ratio would be similar to the case where the queen mates only once. We find in fact that under conditions of kin recognition in a colony with doubly mated queens the fate map and the ESS vs d plot are identical to the case where the queens mate only once (Fig.3 and 4).

4. DISCUSSION

The social insects provide a very attractive model system to explore the evolution of sociality in animals. In consequence considerable theoretical work has gone into this question, and several theories have been proposed primarily to explain the evolution of sterile castes in social insects. Trivers and Hare (1976) used the theory of sex allocation and derived powerful predictions to distinguish between two such theories viz. Kin Selection and Parental manipulation and also presented empirical evidence seemingly in overwhelming support of Kin Selection Theory. Their conclusion unfortunately remains equivocal as a result of their failure to take into consideration two additional factors, LMC and polyandry either in their model or in their data (Alexander and Sherman, 1977).

Nonetheless we find their approach of using the concept of sex allocation to derive mutually exclusive predictions in the frame work kin selection on the one hand and parental manipulation on the other very attractive. We have therefore reinvestigated this question at the theoretical level taking LMC and polyandry explicitly into consideration. We have calculated the optimum sex, allocation ratios from the points of view of the queen (parental manipulation) and workers (kin selection) at different levels of LMC and polyandry. All other things being equal LMC makes the sex ratio increasingly female biased under both situations. Polyandry however has no influence on the sex ratio under queen control but leads to a relatively male biased sex ratio under worker control.

In investigating competition between alleles specifying different sex investment ratios we have normally considered the two competing alleles to be a dominant-recessive pair. Considering them to be codominant however does not qualitatively alter any of our conclusions although the fate maps, as one might expect, become symmetrical.

A rather unexpected result to emerge from our studies is an asymmetry between the dominant and recessive alleles such that for a particular pair of sex ratio strategies one of them would go to fixation if it is recessive but not if it is dominant. In the latter case it would coexist with its competitor. We have sought to explain this phenomenon by showing that an advantageous dominant allele does not go to fixation because it also biases the sex ratio of its competitor while a recessive alleles effect on the phenotypic sex ratio is largely confined to itself. We would like to point out that if this explanation were correct it would have wider implications for the evolution of altruistic behaviour; in fact for any trait that makes its bearer behave altruistically towards a conspectic without regard to the degree of genetic relatedness.

Maynard Smith (1964) has introduced the concept of Evolutionarily stable strategy which is defined as that strategy which is unbeatable by any other strategy. In our analysis we found two additional kinds of evolutionarily stable strategies namely that of the coexistence kind which guarantees its bearer at least coexistence with any possible competitor and of the frequency dependence kind which guarantees its bearer fixation against any competitor provided it is the first to arrive. In our present analysis these two additional kinds of ESSs may be taken to be true ESSs for all practical purposes. In Fig.2 showing the ESS of the coexistance kind, the frequency of the competiter to the ESS falls off very sharply as we move away from the ESS itself. Similarly in Fig.5 representing ESS of the frequency dependence kind, the region of frequency dependence is very small. While small in magnitude these are by no means artefacts and might well turn out to be phenomena of greater significance in other situations.

Taylor and Bulmer (1980) have modelled a scenario of a number of patches, each being colonised by one or more inseminated females, and the offspring mating within the patch before dispersal. Working only within the context of queen control they derive a relationship between the optimum investment ratio (r) and number of females (n) colonising a patch.

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

Here LMC is a function of n. In a patch colonised by n females, the proportion of offspring of any female undergoing sib mating would be $\frac{1}{n}$ which is equivalent to 1-d in our model. Equating d to $\frac{n-1}{n}$ equation (4) is equivalent to our expression for the optimum sex ratio under queen control (equation 2). It must be pointed that Hamilton (1979) has also arrived at the same expression while modelling dimorphism in fig wasps.

As expected the ability to recognise kin and invest differentially in full sisters as opposed to half sisters completly counteracts in effects of multiple mating. This result therefore suggests that multiple mating need not necessarily pose any problems for the operation of kin selection. On the other hand the fact that kin recognition is possible does not automatically provide evidence for kin selection. Even under multiple mating and kin recognition different sex ratios are expected under queen (parental manipulation) and worker (kin selection) control.

Our results emphasise the need to determine the probable levels of LMC and multiple mating and the possibility of workers differentially investing in full sisters as opposed to half sisters under field conditions before drawing any conclusions regarding the outcome of worker queen conflict in social insect colonies. Consider for instance a 3:1 ratio being considered as evidence of worker control (Trivers and Hare, 1976). Notice from our results in Fig.3 that a 3:1 ratio is predicted (i) under worker control for complete outbreeding and single mating, (ii) under queen control for d=0.57 as well as (iii) under worker control with doubly mated queens for d=0.75. (iv) as well as under worker control for complete out-breeding and double mating but with Kin recognition. At the present time field data on LMC and polyandry in social hymenoptera are rather scanty. Kin-recognition has been repeatedly demonstrated (Greenberg, 1979; Getz and Smith 1983; Breed, 1981; Klahnand Gamboa, 1983) but the ability to distinguish between full and half sisters within a single colony has never been demonstrated so far. An empirical study designed to simultaneously gather quantitative information on sex investment ratios, LMC, multiple mating and kin recognition is now essential and well within the realm of possibility due to the increasing application of electrophoretic methods. (Metcalf, 1980). We would like to point out however that factors other than LMC and parental manipulation and kin recognition may also significantly affect the sex ratio. It may also therefore be necessary to take these into account. Significant among such additional factors might be worker oviposition (Benford 1978; Owen and Plowright, 1982) orphaned colonies producing male biased sex ratios leading to female biased sex ratios among the remaining queenright colonies (Owen, Rodd and Plowright, 1980), multilocus control of sex ratio leading to sex ratio polymorphism (Pamilo, 1982) and fluctuating sex ratios because of populations being away from equilibrium (Herbers 1979; McNair, 1978).

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