POPULATION GENETICS OF SOCIAL HYMENOPTERA WITH WORKER PRODUCED MALES

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SUMMARY

In many social Hymenoptera, particularly the bees and wasps, a proportion, ψ , of the males are produced by the workers. Using deterministic theory for a single locus it is shown that having worker produced males affects the speed of approach to Hardy-Weinberg equilibrium, the equilibrium gene frequency under mutation with counter-selection, the speed of elimination of a deleterious allele and the rate of advance of an advantageous gene. Equilibrium gene frequencies of a balanced polymorphism are shifted by a positive value of ψ if there are differences between the male viabilities. For certain male and female viabilities polymorphisms can either be extinguished or generated by having worker produced males. The approach to linkage equilibrium at two loci is either accelerated or retarded, though by not very much, depending on the value of ψ , and the recombination rate.

1. INTRODUCTION

In social Hymenoptera colonies are usually founded by a single fertilised queen who lays all of the female eggs and a certain proportion of the male eggs. In the honeybee virtually all of the males come from the queen as is the case with many ant species (Oster and Wilson, 1978). However, in many eusocial insects the workers have fully functioning ovaries and contribute a considerable proportion of the males. Contel and Kerr (1976) using genetic evidence estimated that 39 per cent of the males were sons of workers in a population of the stingless bee *Melipona subnitida*. Mixed male parentage is also common in wasps. Montagner found that there was a great variability between *Vespula* colonies; in some the queen was responsible for all of the males but in others she produced none, while in about half of the colonies examined the workers produced 75 per cent of the males (Spradbery, 1973). Worker oviposition commonly occurs in bumble bees; Zucchi estimates that in *Bombus atratus* workers lay 90 per cent of the male eggs (Michener, 1974), and in *B. melanopygus* genetic evidence indicates that the workers are the parents of about 40 per cent of the males though there is considerable intercolony variability (R. C. Plowright and R. E. Owen, unpublished data).

Hamilton's (1964) kin selection theory predicts that workers will be selected to raise their own sons, and this has stimulated collection of data on this question and a good deal of theoretical work on the consequences of this for the evolution of the social insects (e.g., Trivers and Hare, 1976; Oster, Eshel and Cohen, 1977).

However, the effect that worker produced males have on the population genetics of the social Hymenoptera has remained essentially unexplored.

Hymenoptera have a haplo-diploid genetic system and so their population genetics is, in general, the same as for sex-linked genes in diplo-diploids. It differs on account of the absence of interactions between sex-linked and autosomal loci in the male haploids (Crozier, 1977) and because the biology permits such phenomena as worker produced males which have no counterpart in sex-linked genetics of diplo-diploid species.

In this paper only deterministic theory will be employed because the assumptions of a large panmictic population are quite well realised in the social Hymenoptera. Analysis will be confined to discrete non-overlapping generations. This is a realistic assumption for wasps (Vespinae, Polistinae), bumble bees (genus *Bombus*) and honeybees (*Apis*) of the temperate zones. In the tropics where breeding is less seasonal overlapping generations occur and the exact results will not apply; however, the conclusions as regards the directions of gene frequency change etc. caused by having worker produced males will still be valid. The object is to present the effects of the mixed origin of males on some aspects of hymenopteran population genetics.

2. APPROACH TO HARDY-WEINBERG EQUILIBRIUM

Assume a gene locus g with alleles g_1 and g_2 initially at different frequencies in the two sexes. Let a proportion ψ of the males in a colony be produced by workers and $(1 - \psi)$ by the queen. The gene frequencies in each generation are shown in fig. 1. The male gene frequency in the second generation is $P' = (1 - \psi)p + \frac{1}{2}\psi(p + P)$ and the female gene frequency is $p' = \frac{1}{2}(p + P)$. Therefore $P' - p' = -\frac{1}{2}(1 - \psi)(P - p)$. Thus the gene frequency

FIG. 1.—Gene frequencies after one generation of random mating if they are initially different in the two sexes and there is no selection. The worker's genotype frequencies are also shown. The second generation of young queens and the worker produced males have the same gene frequencies as the workers.

difference between the sexes is reduced by the factor $[-\frac{1}{2}(1-\psi)]$ in each generation as opposed to $(-\frac{1}{2})$, which applies in the usual diploid sex-linked case or when $\psi = 0$. Similarly the difference in the t th generation is given by

$$P - p = (-\frac{1}{2})^t (1 - \psi)^t (P - p).$$

If $\psi = 1$, then equilibrium is attained immediately in the next generation, as in the diploid autosomal case. The effect of a positive value of ψ of any magnitude is to increase the speed of approach to equilibrium; though the gene frequency oscillations still occur at all values of ψ except 1. Note also that the relationship $(2 - \psi)p' + P' = (2 - \psi)p + P$ holds, *i.e.*, the quantity $(2 - \psi)p + P$ is conserved from generation to generation. This is of significance in section 5.

3. EQUILIBRIUM BETWEEN MUTATION AND SELECTION

Assume that the gene g_2 mutates to g_1 at rate μ per gene per generation. Back mutation is neglected. Suppose that g_1 is heterozygously expressed. Let the relative viabilities be

$$\begin{array}{cccccc} \text{♀♀} & g_1g_1 & g_1g_2 & g_2g_2 & \text{♂♂} & g_1 & g_2 \\ & 1 - S_{11} & 1 - S_{12} & 1 & & 1 - S_1 & 1 \end{array}$$

where $0 \leq S_{11}, S_{12} \leq 1$, and $0 \leq S_1 \leq 1$.

Then the genotypic frequencies after selection are

$$\begin{array}{ccc} \text{♀♀} & g_1g_1 & g_1g_2 & g_2g_2 \\ (1 - S_{11})pP/W & (1 - S_{12})(pQ + qP)/W & qQ/W \end{array}$$

where $W = 1 - S_{12}(p + P) - (S_{11} - 2S_{12})pP$;

$$\begin{array}{ccc} \text{♂♂} & g_1 & g_2 \\ \frac{(1 - S_1)[(1 - \psi)p + \frac{1}{2}\psi(p + P)]}{1 - S_1[(1 - \psi)p + \frac{1}{2}\psi(p + P)]} & \frac{(1 - \psi)q + \frac{1}{2}\psi(q + Q)}{1 - S_1[(1 - \psi)p + \frac{1}{2}\psi(p + P)]} \end{array}$$

The effect of mutation is to multiply the frequencies of the g_2 gene by $(1 - \mu)$, thus if mutation and extinction are in balance, then in the females the gene g_2 is at frequency

$$q = \frac{(1 - \mu)[\frac{1}{2}(1 - S_{12})(pQ + qP) + qQ]}{1 - S_{12}(p - P) - (S_{11} - 2S_{12})pP}, \quad (1)$$

while its frequency in the males is

$$Q = \frac{(1 - \mu)[(1 - \psi)q + \frac{1}{2}\psi(q + Q)]}{1 - S_1[(1 - \psi)p + \frac{1}{2}\psi(p + P)]}. \quad (2)$$

Writing $q = 1 - p$, $Q = 1 - P$, and neglecting terms of the order of p^2 , P^2 and pP , *i.e.*, terms of order μ^2 , we obtain from equation (1) the simplified relation

$$P = (p + S_{12}p - 2\mu)/(1 - S_{12}). \quad (3)$$

Similarly from equation (2) we obtain

$$1 - S_1(p - \frac{1}{2}\psi p) = 1 - p + \frac{1}{2}\psi p - \mu + P(\frac{1}{2}\psi S_1 - \frac{1}{2}\psi + 1). \quad (4)$$

Substituting (3) into (4) and rearranging gives the equilibrium value for

$$p = \frac{3\mu - \mu[S_{12} + \psi(1 - S_1)]}{S_1 + 2S_{12} - S_1S_{12} - \psi S_{12}}. \quad (5)$$

Substituting (5) in (3) gives the male equilibrium frequency

$$P = \frac{3\mu(1 + S_{12}) - \mu[S_{12} + \psi(1 - S_1)](1 + S_{12})}{(1 - S_{12})(S_1 + 2S_{12} - S_1S_{12} - \psi S_{12})} - \frac{2\mu}{(1 - S_{12})}. \quad (6)$$

The effect of ψ is not immediately obvious. However, differentiating p with respect to ψ shows that $dp/d\psi$ has the same sign as the expression $(3 - S_{12})S_{12} - (1 - S_1)(S_1 + 2S_{12} - S_1S_{12})$, and is therefore positive provided that $S_{12}^2 - (1 + 3S_1 - S_1^2)S_{12} + S_1(1 - S_1)$ is negative, which is the case if $S_1 > S_0$, where

$$2S_0 = (1 + 3S_1 - S_1^2) - \sqrt{(1 + 3S_1 + S_1^2)^2 - \psi S_1(1 - S_1)}.$$

Thus the effect of worker produced males is to increase p and also P , when $S > S_0$. If $S_1 = S_0$ then the equilibrium gene frequencies are independent of the value of ψ , and if $S_1 < S_0$ then they decrease as ψ increases.

If g_1 is recessive in females, then $S_{12} = 0$ and the equilibrium frequencies (5) and (6) become $p = [3\mu - \psi(1 - S_1)\mu]/S_1$ and $P = p - 2\mu$. If $\psi = 0$, then $p = 3\mu/S_1$ which is the standard result (Haldane, 1935) and $P = (3\mu/S_1) - 2\mu$. The frequencies P and p differ because they are the gene frequencies in the adults. This asymmetry between the sexes is not usually noted in sex-linked theory because they are not considered separately. In this case ψ decreases p and P , and thus it decreases the genetic load on the population. Taking $P = p$, the load based on the loss of individuals is

$$\begin{aligned} L &= \frac{1}{2}(S_1p + S_{11}P^2) \\ &\approx 1.5\mu - \frac{1}{2}\psi(1 - S_1)\mu, \end{aligned}$$

and based on the loss of the genetic material it is

$$L = \frac{1}{3}(S_1p + 2S_{11}p^2) \approx \mu - \frac{1}{3}\psi(1 - S_1)\mu.$$

When $\psi = 0$ these equations reduce to the standard forms as given by Crozier (1976).

For the case where the g_1 gene is recessive and only expressed in the females it can be shown that

$$P \approx \sqrt{\left(\frac{3\mu}{2S_{11}}\right)\left(\frac{2 - \psi}{2 + \psi}\right)}$$

and the effect of increasing the value of ψ is to reduce the equilibrium frequency of p .

4. ELIMINATION OF DELETERIOUS ALLELES

We consider the most general case of an unconditionally disadvantageous gene with viabilities g_1g_1 , $1 - S_{11}$; g_1g_2 , $1 - S_{12}$; g_2g_2 , 1 ; g_1 ,

$1 - S_1$; g_2 , 1. The gene frequencies after one generation of selection are:

$$p' = \frac{(1 - S_{11})pP + (1 - S_{12})[\frac{1}{2}(p + P) - pP]}{1 - S_{12}(p + P) - (S_{11} - 2S_{12})pP},$$

$$P' = \frac{(1 - S_1)[(1 - \psi)p + \frac{1}{2}\psi(p + P)]}{1 - S_1[(1 - \psi)p + \frac{1}{2}\psi(p + P)]}.$$

The rate of extinction of g_1 is determined to a high degree of accuracy by the equations resulting when second order terms in p and P (*i.e.*, squares and products) are neglected. Since S_{11} disappears when the product pP is omitted the rate of extinction effectively depends only on the heterozygous and hemizygous disadvantages S_{12} and S_1 . Dropping the second order terms we have

$$p' = \frac{1}{2}(1 - S_{12})(p + P)$$

$$P' = (1 - S_1)[(1 - \frac{1}{2}\psi)p + \frac{1}{2}\psi P].$$

Solving the eigenvalue equation

$$\begin{vmatrix} \frac{1}{2}(1 - S_{12}) - \lambda & \frac{1}{2}(1 - S_{12}) \\ (1 - S_1)(1 - \frac{1}{2}\psi) & \frac{1}{2}\psi(1 - S_1) - \lambda \end{vmatrix} = 0,$$

we obtain the roots. The process of elimination of g_1 is governed by the larger root λ_1 , where

$$4\lambda_1 = (1 - S_{12}) + \psi(1 - S_1) + \sqrt{[(1 - S_{12}) + \psi(1 - S_1)]^2 + 8(1 - S_{12})(1 - S_1)(1 - \psi)}.$$

The smaller root λ_2 is given by changing the sign of the radical. To ascertain the effect of having worker produced males let $\kappa = (1 - S_{12})/(1 - S_1)$. The cases $S_1 < S_{12}$, $S_1 = S_{12}$, $S_1 > S_{12}$ then correspond respectively to $\kappa < 1$, $\kappa = 1$ and $\kappa > 1$. We find that $4\lambda_1/(1 - S_1) = \kappa + \psi + \sqrt{[(3 - \psi)^2 + 8\kappa(1 - \kappa)]}$, it follows that if $S_1 = S_{12}$ and $\kappa = 1$, then λ_1 is independent of ψ , being simply equal to the relative viability $(1 - S_1)$. Otherwise

$$\frac{4}{(1 - S_1)} \frac{d\lambda_1}{d\psi} = 1 + \frac{(\psi - 3\kappa)}{\sqrt{[(\psi - 3\kappa)^2 + 8\kappa(1 - \kappa)]}}.$$

If $S_1 < S_{12}$, then $d\lambda_1/d\psi$ is positive because the second term above is positive if $\kappa \leq \frac{1}{3}\psi$, and if $\frac{1}{3}\psi < \kappa < 1$ it is negative but less than unity. Hence if $S_1 < S_{12}$ (*i.e.*, when g_1 is relatively less disadvantageous in the males than in the females) then λ_1 increases with increasing values of ψ . That is, having worker produced males reduces the rate of elimination of a deleterious allele. If $S_1 > S_{12}$ then $d\lambda_1/d\psi$ is negative because the second term above is negative and exceeds unity. Thus λ_1 diminishes as ψ increases, *i.e.*, the presence of worker males increases the rate of elimination of a gene which is relatively more disadvantageous in the males than in the females, as expected intuitively.

5. THE SPREAD OF AN ADVANTAGEOUS ALLELE

In this section we will investigate the effect of worker produced males on the spread of an advantageous allele that has a small additive effect on

fitness. We seek an expression to describe the rate of change of gene frequency which is analogous to that of the autosomal diploid case, $dp/dt \approx 2pq\alpha$ (Fisher, 1930), where α is the average effect of the allele. Unlike Hartl (1972) we do not assume dosage compensation (*i.e.*, that the fitness of each hemizygous male is identical to that of the corresponding female) nor that the gene frequencies in each sex are equal.

For five genotypes the relative viabilities are

	♀♀	g_1g_1	g_1g_2	g_2g_2	♂♂	g_1	g_2
		w_{11}	w_{12}	w_{22}		v_1	v_2
or		$1 + m_{11}$	$1 + m_{12}$	$1 + m_{22}$		$1 + m_1$	$1 + m_2$

Considering slow selection only, we obtain an expression for changes in gene frequencies in terms of fitness values. Thus for the females

$$Wp' = \frac{1}{2}(p + P) + m_{11}pP + \frac{1}{2}m_{12}(pQ + qP) \quad (7)$$

$$Wq' = \frac{1}{2}(q + Q) + \frac{1}{2}m_{12}(pQ + qP) + m_{22}qQ \quad (8)$$

with

$$\begin{aligned} W &= 1 + (m_{11}p + m_{12}q)P + (m_{12}p + m_{22}q)Q \\ &= 1 + T - \alpha(p - P), \end{aligned}$$

where

$$T = m_{11}p^2 + 2m_{12}pq + m_{22}q^2$$

and

$$\alpha = (m_{11} - m_{12})p + (m_{12} - m_{22})q.$$

Subtracting (8) from (7) gives

$$\begin{aligned} W(p' - q') &= (p - q) - (p - P) + m_{11}pP - m_{22}qQ \\ &= (p - q) - (p - P) + m_{11}p^2 - m_{22}q^2 - (m_{11}p + m_{22}q)(p - P). \end{aligned} \quad (9)$$

Therefore, because

$$\begin{aligned} 1/W &= 1/[1 + T - \alpha(p - P)] \\ &= 1 - T + \alpha(p - P) + O(m^2), \end{aligned}$$

where $O(m^2)$ denotes terms which are of the second degree in m and so are ignored under the hypothesis of slow selection, (9) reduces to

$$p' - q' = (p - q) - (p - P) + 2pq\alpha + \phi(p - P) - \alpha(p - P)^2 + O(m^2),$$

where $\phi = T + \alpha(p - q) - (m_{11}p + m_{22}q)$. Because $q = 1 - p$, $q' = 1 - p'$ we have

$$p' - p = pq\alpha - \frac{1}{2}(p - P) + \frac{1}{2}\phi(p - P) - \frac{1}{2}\alpha(p - P)^2 + O(m^2). \quad (10)$$

Similarly for the males we have

$$VP' = (1 - \psi)(1 + m_1)p + \frac{1}{2}\psi(1 + m_1)(P + p),$$

$$VQ' = (1 - \psi)(1 + m_2)q + \frac{1}{2}\psi(1 + m_2)(Q + q),$$

or

$$VP' = p + m_1 p - \frac{1}{2}\psi(p - P)(1 + m_1), \quad (11)$$

$$VQ' = q + m_2 q - \frac{1}{2}\psi(q - Q)(1 + m_2), \quad (12)$$

where

$$V = 1 + m_1 p + m_2 q + \frac{1}{2}\psi(m_2 - m_1)(p - P).$$

Therefore, subtracting (12) from (11) gives

$$V(P' - Q') = (p - q) + (m_1 p - m_2 q) - \frac{1}{2}\psi(2 + m_1 + m_2)(p - P). \quad (13)$$

Multiplying (13) by $1/V$, we obtain

$$P' - Q' = p - q + 2pq\beta - \psi(p - P) - \psi(m_1 + m_2)(p - P) + O(m^2), \quad (14)$$

where $\beta = m_1 - m_2$. Substituting $2P' - 1$ for $P' - Q'$ in (14) gives

$$P' = p - pq\beta - \frac{1}{2}\psi(p - P) - \frac{1}{2}\psi(m_1 + m_2)(p - P) + O(m^2),$$

and because $p = P + (p - P)$, it follows that

$$P' - P = pq\beta + (p - P) - \frac{1}{2}\psi(p - P) - \frac{1}{2}\psi(m_1 + m_2)(p - P) + O(m^2). \quad (15)$$

Note that α and β are equal to the β and γ respectively of Hartl (1971, 1972). Adding the gene frequency changes in females, equation (10), and males, equation (15), and weighing the contribution of the sexes appropriately, gives the overall effect:

$$2(p' - p) + (P' - P) = (2\alpha + \beta)pq - \frac{1}{2}\psi(p - P) + \phi(p - P) - \alpha(p - P)^2 + O(m^2). \quad (16)$$

Thus worker produced males influence the rate of change of the "overall gene frequency" $(2p + P)$ only when there is frequency disequilibrium between the sexes, *i.e.*, p and P are unequal. This is because the term $\frac{1}{2}\psi(p - P)$ in equation (16) equals 0 when $p = P$.

We noted in section 2 that the quantity $(2 - \psi)p + P$ is conserved in the absence of selection. Under the present assumption of slow selection we find that

$$\begin{aligned} [(2 - \psi)p' + P'] - [(2 - \psi)p + P] &= (2 - \psi)(p' - p) + (P' - P) \\ &= [(2 - \psi)\alpha + \beta]pq + O(m)(p - P) \\ &\quad + O(m)(p - P)^2 + O(m^2). \end{aligned}$$

Thus, even when $p = P$, the "weighted gene frequency" $(2 - \psi)p + P$ is not conserved but changes at the approximate rate $[(2 - \psi)\alpha + \beta]pq$ per generation. If α and β are both positive so that g_1 is advantageous in either sex, then $(2 - \psi)p + P$ increases. The quantity $(2 - \psi)\alpha + \beta$ may be thought of as the "weighted advantage" of g_1 the advantageous allele. We may expect that after a sufficiently long initial period the disequilibrium $(p - P)$ becomes, and remains, of the order m , in which case the increase per generation is

$$[(2 - \psi)\alpha + \beta]pq + O(m^2).$$

Therefore worker produced males actually slow the rate of increase of an advantageous allele having additive effects and under slow selection.

6. POLYMORPHISMS AT A SINGLE LOCUS

Assume viabilities

$$\begin{array}{cccccc} \text{♀♀} & g_1g_1 & g_1g_2 & g_2g_2 & \text{♂♂} & g_1 & g_2 \\ & w_{11}=a & w_{12}=h & w_{22}=b & & v_1 & v_2 \end{array}$$

with gene frequencies ♀: g_1, p ; g_2, q ; ♂: g_1, P ; g_2, Q . Let p_e, q_e ; P_e, Q_e and W_e, V_e denote equilibrium values where W_e and V_e are the mean viabilities given respectively by

$$\begin{aligned} W_e &= (aP_e + hQ_e)p_e + (hP_e + Q_e)q_e, \\ V_e &= (1 - \frac{1}{2}\psi)(v_1p_e + v_2q_e) + \frac{1}{2}\psi(v_1P_e + v_2Q_e). \end{aligned}$$

Then in a polymorphic equilibrium,

$$\begin{aligned} W_ep_e &= ap_eP_e + \frac{1}{2}h(p_eQ_e + q_eP_e), \\ W_eq_e &= \frac{1}{2}h(p_eQ_e + q_eP_e) + bq_eQ_e, \end{aligned} \quad (17)$$

and

$$\begin{aligned} V_eP_e &= v_1[(1 - \frac{1}{2}\psi)p_e + \frac{1}{2}P_e], \\ V_eQ_e &= v_2[(1 - \frac{1}{2}\psi)q_e + \frac{1}{2}Q_e], \end{aligned}$$

or by rearrangement

$$P_e = \frac{(1 - \frac{1}{2}\psi)v_1p_e}{V_e - \frac{1}{2}\psi v_1}, \quad (18a)$$

$$Q_e = \frac{(1 - \frac{1}{2}\psi)v_2q_e}{V_e - \frac{1}{2}\psi v_2}. \quad (18b)$$

Therefore, substituting equations (18) into (17) we get

$$\begin{aligned} \frac{W_ep_e}{(1 - \frac{1}{2}\psi)} &= \frac{ap_ev_1p_e}{V_e - \frac{1}{2}\psi v_1} + \frac{\frac{1}{2}hv_2p_eq_e}{V_e - \frac{1}{2}\psi v_2} + \frac{\frac{1}{2}hv_1p_eq_e}{V_e - \frac{1}{2}\psi}, \\ \frac{W_eq_e}{(1 - \frac{1}{2}\psi)} &= \frac{\frac{1}{2}hv_2p_eq_e}{V_e - \frac{1}{2}\psi v_2} + \frac{\frac{1}{2}hv_1p_eq_e}{V_e - \frac{1}{2}\psi v_1} + \frac{bq_ev_2q_e}{V_e - \frac{1}{2}\psi v_2}, \end{aligned}$$

which are equivalent to

$$V_eW_ep_e = (A^*p_e + H^*q_e)p_e, \quad V_eW_eq_e = (H^*p_e + B^*q_e)q_e,$$

where

$$\begin{aligned} A^* &= \frac{(1 - \frac{1}{2}\psi)V_e}{V_e - \frac{1}{2}\psi v_1}av_1, & B^* &= \frac{(1 - \frac{1}{2}\psi)V_e}{V_e - \frac{1}{2}\psi v_2}bv_2, \\ H^* &= \frac{(1 - \frac{1}{2}\psi)V_e}{V_e - \frac{1}{2}\psi v_1}(\frac{1}{2}hv_1) + \frac{(1 - \frac{1}{2}\psi)V_e}{V_e - \frac{1}{2}\psi v_2}(\frac{1}{2}hv_2). \end{aligned} \quad (19)$$

It follows that

$$p_e = \frac{H^* - B^*}{2H^* - A^* - B^*}, \quad (20a)$$

$$q_e = \frac{H^* - A^*}{2H^* - A^* - B^*}. \quad (20b)$$

If $\psi = 0$, then $A^* = a$, $B^* = b$ and $H^* = \frac{1}{2}h(v_1 + v_2)$. Since $a = w_{11}$, $h = w_{12}$, $b = w_{22}$ the equilibrium gene frequency equations reduce to their standard form as given in Edwards (1977). We also note that in the general case

$$\begin{aligned} V_e W_e &= A^* p_e + H^* q_e + H^* p_e + B^* q_e \\ &= (H^* - A^* B^*) / (2H^* - A^* - B^*). \end{aligned}$$

To obtain an expression for V_e we see that

$$\begin{aligned} \frac{2H^* - A^* - B^*}{(1 - \frac{1}{2}\psi)} &= \frac{(2H^* - A^* - B^*)(P_e - Q_e)}{(1 - \frac{1}{2}\psi)} = \frac{(1 - \frac{1}{2}\psi) V_e \frac{1}{2} h v_1^2}{(V_e - \frac{1}{2}\psi v_1)^2} \\ &+ \frac{(1 - \frac{1}{2}\psi) V_e (h - a - b) v_1 v_2}{(V_e - \frac{1}{2}\psi v_1)(V_e - \frac{1}{2}\psi v_2)} + \frac{(1 - \frac{1}{2}\psi) V_e \frac{1}{2} h v_2^2}{(V_e - \frac{1}{2}\psi v_2)^2}. \end{aligned}$$

The left hand side of the equation is also equal to

$$\frac{v_1(h-a)V_e}{V_e - \frac{1}{2}\psi v_1} + \frac{v_2(h-b)V_e}{V_e - \frac{1}{2}\psi v_2},$$

so by equating and rearranging, we get

$$\begin{aligned} \frac{v_1(h-a)}{V_e - \frac{1}{2}\psi v_1} + \frac{v_2(h-b)}{V_e - \frac{1}{2}\psi v_2} &= (1 - \frac{1}{2}\psi) \left[\frac{\frac{1}{2} h v_1^2}{(V_e - \frac{1}{2}\psi v_1)^2} \right. \\ &\left. + \frac{(h-a-b)v_1 v_2}{(V_e - \frac{1}{2}\psi v_1)(V_e - \frac{1}{2}\psi v_2)} + \frac{\frac{1}{2} h v_2^2}{(V_e - \frac{1}{2}\psi v_2)^2} \right]. \end{aligned} \quad (21)$$

Equation (21) can be put in the form of $f(V_e) = 0$, where

$$\begin{aligned} f(V_e) &= (V_e - \frac{1}{2}\psi v_1)(V_e - \frac{1}{2}\psi v_2) [v_1(h-a)(V_e - \frac{1}{2}\psi v_2 \\ &+ v_2(h-b)(V_e - \frac{1}{2}\psi v_1)] - (1 - \frac{1}{2}\psi) [\frac{1}{2} h v_1^2 (V_e - \frac{1}{2}\psi v_2)^2 \\ &+ (h-a-b)v_1 v_2 (V_e - \frac{1}{2}\psi v_1)(V_e - \frac{1}{2}\psi v_2) + \frac{1}{2} h v_2^2 (V_e - \frac{1}{2}\psi v_1)^2]. \end{aligned} \quad (22)$$

For the polymorphism to be stable, both roots of the quadratic equation $V_e W_e \lambda^2 - (V_e R + \frac{1}{2}\psi W_e U) \lambda - [SU - \frac{1}{2}\psi(R+S)U] = 0$ must be less than unity in absolute value, where

$$R = (aP_e + \frac{1}{2}hQ_e - \frac{1}{2}hP_e)q_e - (\frac{1}{2}hQ_e + \frac{1}{2}hP_e - bQ_e)P_e,$$

$$S = (a - 2h + b)p_e q_e + \frac{1}{2}h,$$

$$U = v_1 Q_e + v_2 P_e.$$

A necessary and sufficient set of conditions for stability is that the "stability coefficient",

$$\frac{(V_e R + S U) + \frac{1}{2} U [W_e - (R + S)]}{V_e W_e} \quad (23)$$

is positive and less than unity. The larger the value of the coefficient, up to unity, the longer it takes the system to return to equilibrium after a perturbation. Proof of this and a full analytical solution of the polymorphism equations will be given elsewhere (A. R. G. Owen and R. E. Owen, in preparation). For the purpose of this paper there is enough information to be able to investigate the effect of mixed male parentage on polymorphisms. To do this, numerical examples were worked out. First viability values a , h , b , and v_1 , v_2 were chosen, then an estimate of V_e was calculated which gave $f(V_e) = 0$, (equation 22) for each of eleven values of ψ . Equations (18), (19) and (20) were then used to calculate the equilibrium gene frequencies. The stability coefficient equation (23) was also calculated. The numerical examples are shown in table 1 and they illustrate the major effects that worker produced males have on polymorphism. Example (i) shows that even for modest values of ψ the equilibrium gene frequencies are shifted and in the direction, not surprisingly, of the male genotype with the greater viability. The system also remains stable. For a given set of female viabilities the shift in gene frequencies depends on the magnitude of the

TABLE 1

Numerical examples illustrating the effect of worker produced males on the equilibrium gene frequencies and stability of balanced polymorphisms. If the stability coefficient (calculated from equation 23) is less than 1.0 then the polymorphism is stable

Viabilities	Gene freqs.	ψ										
		0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
(i)												
$h = 10.0$	♀ p	0.750	0.758	0.766	0.774	0.782	0.791	0.800	0.810	0.820	0.830	0.841
$a = 5.0$	q	0.250	0.242	0.234	0.226	0.218	0.209	0.200	0.190	0.180	0.170	0.159
$b = 5.0$	♂ P	0.900	0.905	0.914	0.921	0.928	0.935	0.942	0.948	0.954	0.960	0.965
$v_1 = 3.0$	Q	0.100	0.095	0.086	0.079	0.072	0.065	0.058	0.052	0.046	0.040	0.035
$v_2 = 1.0$	Stability	0.769	0.779	0.788	0.798	0.808	0.818	0.828	0.837	0.848	0.858	0.868
(ii)												
$h = 10.0$	♀ p	0.517	0.518	0.519	0.520	0.522	0.523	0.525	0.526	0.529	0.531	0.534
$a = 5.0$	q	0.483	0.482	0.481	0.480	0.487	0.477	0.475	0.474	0.471	0.469	0.466
$b = 5.0$	♂ P	0.534	0.535	0.537	0.540	0.543	0.546	0.549	0.553	0.557	0.562	0.573
$v_1 = 3.0$	Q	0.466	0.465	0.463	0.460	0.457	0.454	0.451	0.447	0.443	0.438	0.427
$v_2 = 2.8$	Stability	0.667	0.683	0.700	0.717	0.734	0.750	0.767	0.783	0.800	0.816	0.837
(iii)												
$h = 5.0$	♀ p	0.900	0.908	0.916	0.924	0.933	0.943	0.953	0.963	0.975	0.987	1.000
$a = 3.0$	q	0.100	0.092	0.084	0.076	0.067	0.057	0.047	0.037	0.025	0.013	0.000
$b = 1.0$	♂ P	0.964	0.968	0.972	0.976	0.980	0.984	0.988	0.991	0.994	0.997	1.000
$v_1 = 3.0$	Q	0.036	0.032	0.028	0.024	0.020	0.016	0.012	0.009	0.006	0.003	0.000
$v_2 = 1.0$	Stability	0.901	0.910	0.920	0.929	0.939	0.948	0.958	0.968	0.978	0.989	1.000
(iv)												
$h = 1.82$	♀ p	0.000	0.213	0.296	0.353	0.397	0.433	0.464	0.491	0.511	0.536	0.555
$a = 0.5$	q	1.000	0.787	0.704	0.647	0.603	0.567	0.536	0.509	0.489	0.464	0.445
$b = 10.0$	♂ P	0.000	0.760	0.844	0.884	0.909	0.926	0.939	0.950	0.922	0.967	0.970
$v_1 = 10.0$	Q	1.000	0.240	0.156	0.116	0.091	0.074	0.061	0.050	0.078	0.033	0.030
$v_2 = 1.0$	Stability	1.000	0.833	0.767	0.725	0.695	0.673	0.655	0.642	0.622	0.622	0.614

difference in viability between the males and illustrated by the comparison between examples (i) and (ii). Sufficient magnitude of ψ can also cause a polymorphism to be extinguished: example (iii). For this to occur one of the alleles must be reasonably near fixation. The most interesting effect of having worker males is to cause stable polymorphisms to be generated from a non-polymorphic situation as shown in example (iv). With the viabilities chosen $A^* = 5.0$, $B^* = 10.0$ and $H^* = 10.0$, so that $p_e = P_e = 0.00$ and $q_e = Q_e = 1.00$ when $\psi = 0$. However, because the viabilities are asymmetrical between the sexes ($a < b$, $v_1 > v_2$) a polymorphism results when $\psi > 0$.

It is well-known that in situations like this, where the fitness of the corresponding hemizygotes and homozygotes differ in opposite directions, a stable polymorphism can result with $\psi = 0$ even if the female heterozygote is less fit than the mean of the homozygotes (Bennet, 1957; Haldane and Jayakar, 1964; Li, 1967). However, as can be seen from example (iv) the conditions are relaxed when there are worker produced males. Thus to get a polymorphism when $\psi > 0$, v_1 need only equal b rather than be greater than b which is required when $\psi = 0$. Worker produced males have no effect on a polymorphism when there is no selection among the males ($v_1 = v_2$). In this case which is the same when $\psi = 0$, equations (20) reduce to the standard diplo-diploid form and the gene frequencies are the same in the two sexes (Li, 1967). However, as can be seen from table 1, worker produced males have an effect whether there is complete dosage compensation ($v_1 = a$, $v_2 = b$) or lack of it ($v_1 \neq a$, $v_2 \neq b$). In fact it is a distinct possibility that the viabilities of the corresponding male and female genotypes could differ considerably since in many social hymenopteran groups the sexes have quite different life styles and may be exposed to different and often opposing selection pressures. For instance, queen bumble bees and wasps are physiologically adapted for hibernation during the winter while males live for only a few weeks at the end of the summer. Similarly, males are automimics of their sisters who are protected by their stings (Plowright and Owen, 1980) and are therefore selected to resemble them closely; but there also may exist opposing selective pressures on the same characters (hair length and colour, etc.) which work to reduce the resemblance (Stiles, 1979). Thus situations like example (iv) (table 1) may be quite likely. It is, of course, well-known that opposing selection in the two sexes of diplo-diploids can cause polymorphisms (Owen, 1953) and there are a number of examples (e.g., Turner, 1968).

7. APPROACH TO EQUILIBRIUM AT TWO LOCI

Assuming two loci with two alleles per locus denoted by $A_1, a_1; A_2, a_2$, let the four types of gametes have frequencies

	A_1A_2	a_1a_2	A_1a_2	a_1A_2
♀♀	x_1	x_2	x_3	x_4
♂♂	y_1	y_2	y_3	y_4

where $x_1 + x_2 + x_3 + x_4 = y_1 + y_2 + y_3 + y_4 = 1$. The frequencies of the 16 offspring genotypes are given by the terms in the expansion of $(x_1 + x_2 + x_3 + x_4)$

($y_1 + y_2 + y_3 + y_4$). Calculating the gametic frequencies in the next generation with recombination rate c we find that

$$\begin{aligned}x'_1 &= \frac{1}{2}x_1 + \frac{1}{2}y_1 - \frac{1}{2}cI, \\x'_2 &= \frac{1}{2}x_2 + \frac{1}{2}y_2 - \frac{1}{2}cI, \\x'_3 &= \frac{1}{2}x_3 + \frac{1}{2}y_3 + \frac{1}{2}cI, \\x'_4 &= \frac{1}{2}x_4 + \frac{1}{2}y_4 + \frac{1}{2}cI,\end{aligned}\tag{24}$$

and

$$\begin{aligned}y'_1 &= (1 - \psi)x_1 + \psi x'_1, \\y'_2 &= (1 - \psi)x_2 + \psi x'_2, \\y'_3 &= (1 - \psi)x_3 + \psi x'_3, \\y'_4 &= (1 - \psi)x_4 + \psi x'_4.\end{aligned}\tag{25}$$

In haplo-diploidy we have not only the coefficient of linkage disequilibrium $D = x_1x_2 - x_3x_4$, but also $I = x_1y_1 + x_2y_1 - x_3y_4 - x_4y_3$, the "coefficient of linkage-frequency disequilibrium", between the sexes. I has a maximum value of 0.5 while D has a maximum of 0.25. If $x_1 = y_1$, $x_2 = y_2$, $x_3 = y_3$, $x_4 = y_4$ then $I = 2D$. We are interested in finding the rate at which both D and I tend to zero. To find the speed of approach to equilibrium we need to find and solve the recurrence relations for I and D . Dealing with I first,

$$I' = x'_1y'_2 + x'_2y'_1 - x'_3y'_4 - x'_4y'_3.\tag{26}$$

By substituting equations (24) and (25) in (26) we get

$$I' = (1 - \frac{1}{2}\psi)D + \frac{1}{2}I - \frac{1}{2}c(1 - \psi)I + \frac{1}{2}\psi(y_1y_2 - y_3y_4).\tag{27}$$

Now calculating ($y'_1y'_2 - y'_3y'_4$) using equations (25) we obtain

$$y'_1y'_2 - y'_3y'_4 = (1 - \psi)^2D + \psi(1 - \psi)(D + \frac{1}{4}I) + \psi^2D'.\tag{28}$$

Priming (27) and substituting (28) into it gives

$$I'' = (1 - \frac{1}{2}\psi - \frac{1}{2}\psi^3)D' + \frac{1}{2}\psi(1 - \psi)D + \frac{1}{2}I' - \frac{1}{2}c(1 - \psi)I' + \frac{1}{8}\psi^2(1 - \psi)I.\tag{29}$$

Next we calculate D' from equations (24),

$$x'_1x'_2 - x'_3x'_4 = \frac{1}{4}(x_1x_2 - x_3x_4) + \frac{1}{4}(y_1y_2 - y_3y_4) + \frac{1}{4}I' - \frac{1}{2}cI'.\tag{30}$$

By priming equation (30) and substituting (28) into it we obtain

$$D'' = \frac{1}{4}(1 - \psi^2)D' + \frac{1}{4}(1 - \psi)D + \frac{1}{4}(1 - 2c)I' + \frac{1}{16}\psi(1 - \psi)I'.\tag{31}$$

We have, therefore, recurrence relations for D and I each of which involves both D and I .

By successively priming and substituting equations (29) and (31) into each other I can be eliminated to give a fourth-order equation in D which has a corresponding eigenvalue equation:

$$\begin{aligned}\lambda^4 - [\frac{3}{4}(1 - \frac{1}{3}\psi^2) - \frac{1}{2}c(1 - \psi)]\lambda^3 - [(\frac{1}{4} - \frac{1}{2}c)(1 - \frac{1}{2}\psi + \frac{1}{2}\psi^3) \\ + \frac{1}{8}c(1 - \psi)(1 + \psi^2) + (1 - \psi)(\frac{1}{4} + \frac{1}{16}\psi + \frac{3}{32}\psi^2 + \frac{1}{32}\psi^4) \\ - \frac{1}{8}(1 + \psi^2)]\lambda^2 - [(1 - \psi)\{\frac{1}{8}\psi(1 - 2c) - \frac{1}{32}\psi^2(1 + \psi^2) - \frac{1}{8}\} \\ + (1 - \psi^2)(\frac{1}{32}\psi^2 + \frac{1}{8}c)]\lambda + \frac{1}{32}\psi^2(1 - \psi)^2 = 0.\end{aligned}\tag{32}$$

The roots of the equation give the speed of approach to linkage equilibrium. Specifically the value of D in the t th generation is $D_t = k_1\lambda_1^t + k_2\lambda_2^t + k_3\lambda_3^t + k_4\lambda_4^t$ where k_1, k_2, k_3, k_4 are constants. If $|\lambda_1| > |\lambda_2|, |\lambda_3|, |\lambda_4|$ then $D \approx k_1\lambda_1^t$ when t is large. That is, the largest root, λ_1 , is the one that effectively determines the rate of approach to equilibrium when it takes more than a few generations to be reached. The smaller the value of λ_1 then the faster the approach to equilibrium.

Both D and I decrease at the same rate. For comparison the corresponding result for the autosomal diplo-diploid case is, as is well-known, $D_t = D_0(1-c)^t$, where the constant D_0 is the initial value of D . The constant k_1 is more complicated because it depends on D_0, I_0 and the λ 's, though in principle it can be calculated. However, we are more interested in finding the value of λ_1 , which depends solely on the values of c and ψ . Instead of solving equation (32) λ_1 can be found by iterating equations (29) and (31) and is equal to their ratio once it has become effectively constant. This was done for a range of ψ and c values to find the magnitude of the effect that worker produced males cause. It is apparent from table 2 that for a given

TABLE 2

The major root governing the speed of approach to equilibrium at two loci for various values of c and ψ . This is the rate at which D and I become zero and it is the same for both. An asterisk denotes that the values of D and I oscillate around zero (see text)

c	ψ										
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0.01	0.993	0.988	0.983	0.979	0.976	0.974	0.973	0.976	0.978	0.985	0.995
0.05	0.996	0.962	0.959	0.956	0.953	0.952	0.952	0.954	0.958	0.964	0.974
0.10	0.933	0.929	0.927	0.925	0.924	0.924	0.925	0.927	0.931	0.938	0.947
0.15	0.898	0.896	0.895	0.895	0.894	0.894	0.896	0.899	0.904	0.910	0.918
0.20	0.863	0.862	0.861	0.861	0.862	0.864	0.866	0.870	0.874	0.880	0.887
0.25	0.828	0.827	0.827	0.828	0.829	0.832	0.835	0.838	0.843	0.848	0.854
0.30	0.792	0.791	0.791	0.793	0.795	0.798	0.801	0.805	0.809	0.812	0.816
0.35	0.755	0.754	0.754	0.756	0.758	0.761	0.764	0.768	0.771	0.773	0.774
0.40	0.718	0.716	0.715	0.716	0.719	0.721	0.724	0.727	0.728	0.728	0.724
0.45	0.680	0.676	0.674	0.674	0.675	0.677	0.679	0.680	0.678	0.672	0.658
0.50	0.640	0.633	0.629	0.627	0.626	0.625	0.624	0.620	0.611	0.591	0.500
0.55	0.600	0.588	0.578	0.571	0.564	0.556	0.545	0.520	*	*	*

value of c the effect is not very large. For $c < 0.45$ intermediate values of ψ accelerate the approach to equilibrium but at high values of ψ the approach is retarded. For $c > 0.45$ worker produced males always increase the speed with which equilibrium is attained, but it never equals or exceeds the speed in the corresponding autosomal diplo-diploid case.

Recombination rates in excess of 0.5 are theoretically possible (Owen, 1949) and examples have been found for sex-linked genes in diploids (Wright, 1947). Without seeking to investigate the question in detail it is sufficient to note that for sufficiently large values of ψ values of c in excess of 0.5 have the effect of rendering more complicated the mode by which D and I tend to zero. For example, with $\psi = 0.8$ and $c = 0.55$, although equilibrium is approached more swiftly than when $c = 0.50$, the values of D and I oscillate around zero, changing sign about every 25 generations.

The result for $\psi = 0$ (corresponding to the normal sex-linked case in diplo-diploids) is worth deriving here because the method used is different

from those previously published (Wright, 1933; Bennett, 1963). When $\psi = 0$ equation (29) reduces to $I'' = D' + \frac{1}{2}(1-c)I'$, equation (31) reduces to $D'' = \frac{1}{4}D' + \frac{1}{4}D + \frac{1}{4}(1-2c)I'$, and the eigenvalue equation (32) becomes $[\lambda^3 - (\frac{3}{4} - \frac{1}{2}c)\lambda^2 - \frac{3}{8}(1-c)\lambda + \frac{1}{8}(1-c)] = 0$, which has roots

$$\lambda_1 = \frac{1}{4}[(1-c) + \sqrt{(1-c)(9-c)}],$$

$$\lambda_2 = \frac{1}{2}(1-c) - \frac{1}{4}[(1-c) + \sqrt{(1-c)(9-c)}],$$

$$\lambda_3 = \frac{1}{2}c,$$

as given by Bennett (1963). The first column of table 2 for $\psi = 0$ gives the values of λ_1 ; for example, when $c = 0.5$, $\lambda_1 = \frac{1}{4}(0.5 + \sqrt{4.25}) = 0.640$.

For a haplo-diploid species the rate of approach to linkage equilibrium is about two-thirds that of a diplo-diploid species with the same recombination rate (Bennett, 1963), and the presence of worker produced males has only a marginal effect.

8. DISCUSSION

The main conclusion reached is that worker produced males affect most aspects of social hymenopteran population genetics. The direction of this effect is not, in most cases, intuitively obvious and the equations involving ψ

TABLE 3

Summary of the effects of worker produced males on some aspects of the population genetics of the social Hymenoptera

Aspect	Conditions	Effect
Approach to Hardy-Weinberg equilibrium	—	Rate increased
Equilibrium between mutation and selection	$S_1 = S_0$ $S_1 > S_0$ $S_1 < S_0$ $S_{12} = 0$	No change in p_e, P_e p_e, P_e increased p_e, P_e decreased p_e, P_e decreased, genetic load decreased
Elimination of deleterious alleles	$S_{12} = 0$ and sex-limited $S_1 = S_{12}$ $S_1 < S_{12}$ $S_1 > S_{12}$	p_e decreased No change in rate Rate decreased Rate increased
Spread of an advantageous allele	$p \neq P$	Rate of gene frequency change slowed
Balanced polymorphism	—	P_e, p_e shifted in favour of male genotype with greatest viability. Dependant on relative viabilities polymorphisms extinguished or generated
Approach to linkage equilibrium at two loci	$c < 0.45$ $c > 0.45$ $c = 0.55$ and $\psi \geq 0.8$	Moderate values of ψ increases rate; high values decrease rate Rate increased Oscillations of D and I around zero

are often complex and substantially modified from their standard forms. A summary of the population genetic consequences of worker produced males, as analysed here, is given in table 3. Positive values of ψ usually have an effect whether the population is in equilibrium or not and also in most instances when the gene frequencies in the sexes are equal or unequal.

A particularly interesting consequence of having worker produced males is that in the hymenopteran species in which they occur there may be a marginally higher frequency of polymorphisms than in those species that do not have mixed male parentage. This is because under certain selective regimes quite low values of ψ can generate polymorphisms whereas high values, which are less likely to occur, are required to extinguish them (see table 1). Comparison could be made between social and solitary hymenoptera or between a particular social species and its social parasite which has no worker caste and hence no worker produced males. For instance, in Britain many species of the parasitic genus *Psithyrus* are highly host specific on the true bumble bees *Bombus*. Some species in fact only attack one host species; for example *P. barbutellus* on *B. hortorum*, *P. rupestris* on *B. lapidarius*, *P. vestalis* on *B. terrestris*, *P. bohemicus* on *B. lucorum* (Plowright and Owen, 1980). The parasite is subjected to almost the same environmental influences as the host because it is necessarily found within the same geographical area and its brood is attended to by workers of the host species in their nest. Differences between the host and parasite in polymorphism frequencies, etc., therefore could be due to having worker produced males in the host species.

The analysis given in this paper indicates that future experimental and theoretical work concerning the population genetics of the social hymenoptera should take into account the effect of mixed male parentage. Many of the results are applicable to haplo-diploid species of mites where males are initially produced and then mate with females of their mothers' generation.

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