J. Math. Biology (1981) 12: 355–362

Journal of
Mathematical
Biology

On the Survival Probability of a Slightly Advantageous Mutant Gene with a General Distribution of Progeny Size – A Branching Process Model*

Ilan Eshel*
Department of Statistics, Tel-Aviv University, Tel Aviv, Israel

Abstract. A branching process method is employed to study the survival probability of a slightly advantageous mutant gene with a general distribution of progeny size in a large population. A counter-example to a classic proposition is given. A somewhat weaker result is proved.

Key words: Branching process – Mutation – Extinction – Progeny size

1. Introduction

The extinction probability of an advantageous mutant gene in a large population depends not only on the fitness of the mutant, but also on the distribution of its progeny size, especially (Gillespie, 1974), on its variance. In the case of a Wright-Fisher model (see Fisher, 1930) with a slight advantage $s > 0$ for the new mutant, the extinction probability of the mutant is well known to be

$$u(s) = 1 - 2s + o(s). \tag{1.1}$$

This approximation is obtained either by a diffusion model (e.g. Kimura, 1964) or by a model of a branching process with a Poisson distribution of offspring (e.g. Ewens, 1969). When the distribution of offspring is arbitrary, it has been conjectured by Haldane (1928) and others, that the survival probability of a slightly advantageous mutant gene is proportional to the ratio between the selective advantage of the gene and the variance of its progeny size.

Employing a branching process with a general generating function $f(u) = Eu^X$ of the progeny size, Ewens (1969) has attempted to show that the extinction probability of the process, namely the smallest positive solution of the equation

$$f(u) = u \tag{1.2}$$

(e.g. see Harris, 1963), is approximated by

---

* Supported in part by NIH Grant 5R01 GM10452-18
Present address: Department of Mathematics, Stanford University, Stanford, CA 94305, USA

0303 – 6812/81/0012/0355/$01.60

$$u(s) = 1 - \frac{2s}{\sigma^2} + o\left(\frac{s}{\sigma^2}\right) \tag{1.3}$$

where $EX = 1 + s > 1$, $\operatorname{Var} X = \sigma^2$.

This result was obtained by replacing the left side of (1.2) by its three-term Taylor expansion around $u = 1$. Unfortunately, this method does not generally guarantee a valid approximation of the solution of (1.2), even if this solution is known to be close to 1. Moreover, we see that even if $s/\sigma^2 > 0$ is as small as we wish, $u(s)$ may not be close to 1 at all. In §2 we prove, on the contrary, that for any values $\sigma^2 > 0$ and $0 < u_0 < 1$ and for any $s > 0$ as small as we wish, there is a Galton-Watson process with $1 + s$ and σ^2 as the expectation and variance of the number of offspring born to a single parent and with u_0 as the extinction probability of the process.

It is shown, however, that if the whole distribution of the progeny size of a single parent is changed in a "smooth" way so that its expectation grows from 1 to $1 + s$, then the approximation (1.3) is valid.

The main purpose of this work is thus to find quite general conditions, hopefully fitting most conceivable biological circumstances, under which the approximation (1.3) is mathematically valid.

2. Counterexamples of the Approximation (1.3)

Example 1

Proposition. *For any given values of $\sigma^2 > 0$ and $0 < u_0 < 1$ and for any value $\varepsilon > 0$ sufficiently small, there is a Galton-Watson process with $1 + \varepsilon$ and σ^2 as the mean and the variance of the number of offspring born to a single parent, and with u_0 as the extinction probability of the process.*

Proof. Put

$$p_0 = \frac{\sigma^2 - \varepsilon + \varepsilon^2 - (N-1)(N-2)p_N}{2}, \tag{2.1}$$

$$p_2 = \frac{\sigma^2 + \varepsilon + \varepsilon^2 - N(N-1)p_N}{2}, \tag{2.2}$$

$$p_1 = 1 - p_0 - p_2 - p_N \tag{2.3}$$

where

$$p_N = \frac{(\sigma^2 + \varepsilon^2)(1 - u_0)^2 - \varepsilon(1 - u_0^2)}{(N-1)(N-2)(1-u_0)^2 - 2[(N-2)u_0 - (N-1)u_0^2 + u_0^N]} \tag{2.4}$$

and N is any natural number sufficiently large as to assure that the denominator is positive (note that the denominator tends to ∞ as $N \to \infty$).

If $\varepsilon > 0$ is sufficiently small, then the numerator of (2.4) is also positive and

$$p_N > 0. \tag{2.5}$$

Assume further

$$\varepsilon < \frac{1 - u_0}{2}. \tag{2.6}$$

From (2.4) it follows that for any fixed values of u_0, σ^2, and ε

$$\lim_{N\to\infty} (N-1)(N-2)p_N = \lim_{N\to\infty} N(N-1)p_N = \sigma^2 + \varepsilon^2 - \varepsilon\frac{1+u_0}{1-u_0}.$$

Hence, from (2.1) and (2.2) one readily gets

$$\lim_{N\to\infty} p_0 = \frac{\varepsilon u_0}{1-u_0} > 0, \tag{2.7}$$

$$\lim_{N\to\infty} p_2 = \frac{\varepsilon}{1-u_0} > 0. \tag{2.8}$$

From (2.3) and (2.6) it follows that

$$\lim_{N\to\infty} p_1 = \lim_{N\to\infty} (1 - p_0 - p_2 - p_N) = 1 - \frac{1+u_0}{1-u_0}\varepsilon > 0. \tag{2.9}$$

Thus, for $\varepsilon > 0$ sufficiently small and N sufficiently large we know that

$$f(u) = p_0 + p_1 u + p_2 u^2 + p_N u^N \tag{2.10}$$

is a probability generating function. From (2.1), (2.2), and (2.3) (independently of p_N) it follows that the mean of the distribution generated by (2.9) is

$$m = f'(1) = p_1 + 2p_2 + Np_N = 1 + \varepsilon. \tag{2.11}$$

The variance of this distribution is

$$f''(1) + f'(1) - [f'(1)]^2 = p_0(1+\varepsilon)^2 + p_1\varepsilon^2 + p_2(1-\varepsilon)^2 + p_N(N-1-\varepsilon) = \sigma^2 \tag{2.12}$$

Moreover, by a straightforward calculation we get

$$\begin{aligned} 2[f(u) - u] &= 2p_0(1-u) - 2p_2u(1-u) - 2p_Nu(1-u^{N-1}) \\ &= (\sigma^2 + \varepsilon^2)(1-u)^2 - \varepsilon(1-u^2) - \{(N-1)(N-2)(1-u)^2 \\ &\quad - 2[(N-2)u - (N-1)u^2 + u^N]\}p_N \end{aligned}$$

and for $u = u_0$, it follows from (2.4) that

$$f(u_0) - u_0 = 0.$$

But the equation $u = f(u)$ has, at the most, one solution at the interval (0, 1). Thus, u_0 is the smallest positive solution of this equation and u_0 is the extinction probability of a Galton-Watson process with $f(u)$ as the generating function of the number of offspring born to a single parent.

Indeed, example 1 is not intended to describe any realistic biological situation. It is suggested merely as a mathematical tool to disprove (1.3) as a general mathematical statement. It manifests the fact that the inaccuracy in (1.3) may not be minor; it may be of any order of magnitude.

Note, however, that regardless of immediate biological plausibility, the generating function (2.9) cannot possibly correspond to the distribution of copies produced by a single, rare (heterozygote) mutant in a randomly mated diploid population. The generating function of such a distribution must indeed be of the form

$$f(u) = \varphi\left(\frac{1+u}{2}\right) \tag{2.13}$$

where φ is a probability generating function, corresponding to the total number of viable offspring (mutant or non-mutant) reproduced by a single mutant parent. A question raised by the referee is, thus, whether deviations from (1.3) are limited to special, haploid situations. The following example is less dramatic, but somehow more realistic, satisfying (2.13) and therefore fitting to both haploid and diploid situations.

Example 2

Let the distribution of copies reproduced by a single mutant be determined by the generating function

$$f(u) = (1-\delta)e^{(1+\varepsilon)(u-1)} + \delta e^{(1+\lambda)(u-1)}. \tag{2.14}$$

This corresponds to a situation in which any mutant individual can fall into one out of two environmental situations. In each case it is bound to reproduce copies according to a Poisson law. However, the expected number of copies will be $1+\varepsilon$ in the first, and $1+\lambda$ in the second environmental situation.

Assuming $0<\delta<1$ and $\lambda>\varepsilon>0$, it is readily shown (and quite intuitively clear) that the mutation survival probability is an increasing function of both δ and λ. Especially, we know that it is at least $2\varepsilon + 0(\varepsilon)$, which is the value for $\delta = 0$ (or for $\lambda = \varepsilon$). But the mean and variance of (2.14) are

$$m = 1 + \varepsilon + \delta(\lambda - \varepsilon) \tag{2.15}$$

and

$$\sigma^2 = m + \delta(1-\delta)(\lambda-\varepsilon)^2, \tag{2.16}$$

respectively. Hence, if λ is very large and δ is very small, so that $\lambda\delta \to 0$ and $\lambda^2\delta \to \infty$, then $m \to 1+\varepsilon$, $\sigma^2 \to \infty$, and (1.3) yields an approximation $o(\varepsilon)$ as much smaller than ε as we wish for the mutation survival probability.

Moreover, for any fixed $1>\delta>0$ (not necessarily close to 0), and for λ large enough, the right side of (2.13) still tends to 0 as $\lambda \to \infty$, while the smaller positive solution of $f(u) = u$ is readily shown to be smaller than $1-\delta$, and the mutant survival probability is, therefore, larger than δ.

Remark. Both Examples 1 and 2 correspond to situations of rare mutants, propagating moderately most of the time, but being extremely successful under very rare conditions, admittedly not a very common situation in nature. Exact conditions for (1.3) to hold are studied in the next two sections and, it is suggested, cover most common natural situations.

3. A Model of Smooth Changes in the Distribution of the Property Size

We start with two examples of natural situations in which continuous changes in fitness are determined by specific continuous changes in the entire distribution of the progeny size of a single parent.

(i) *The Case of an Increased Viability*

If the effect of a new mutant is expressed in a change in the viability of its carrier, then the distribution of the number of *viable* offspring born to a single mutant parent is conveniently given by its generating function

$$\psi_\alpha(u) = \psi(1 - \alpha + \alpha u), \tag{3.1}$$

where

$$\psi(u) = \sum_{k=0}^{\infty} p_k u^k$$

is the probability generating function (p.g.f.) of the number of offspring newly born to a single adult individual.

The fitness of the mutant can be written as

$$1 + s(\alpha) = \alpha\psi'(1) \tag{3.2}$$

and small changes in the mutant fitness are determined by small parametric changes in the generating function ψ_α.

(ii) *A Case of Monotone-Likelihood Ratio Family of Progeny Size*

Let $\psi(u)$ be any non-degenerated p.g.f. and let $\psi(\alpha) < \infty$. Then

$$\psi_\alpha(u) = \frac{\psi(\alpha u)}{\psi(\alpha)} \tag{3.3}$$

is also a p.g.f.. $\{\psi_\alpha(u)\}$ represents a family of distributions, increasing geometrically in monotone likelihood; and the expectation $1 + s(\alpha)$ is, therefore, increasing with α. The positive and negative binomial distributions of a given order as well as the Geometric and Poisson families of distributions are all represented by the family-structure (3.3). Moreover, any probability g.f. belongs to some family of this sort. (For any g.f. ψ just define ψ_α as in (3.3) and set $\psi_0 = \psi$.)

We now generalize these two examples to a more general structure, hopefully covering most natural situations of continuous changes in fitness.

For $\alpha_0 \leqslant \alpha < \alpha_1$ (possibly $\alpha_1 = \infty$), let

$$\psi_\alpha(u) = \sum_{k=0}^{\infty} p_k(\alpha) u^k$$

be a probability generating function with

$$\sum_{k=0}^{\infty} k^2 p_k(\alpha) < \infty.$$

We assume

$$\psi'_{\alpha_0}(1) = 1 \qquad \text{i.e.,} \qquad EX_{\alpha_0} = 1 \qquad \text{where} \qquad \psi_\alpha(u) = Eu^{X_\alpha}, \tag{3.4}$$

$$\psi''_{\alpha_0}(1) = \sigma^2 > 0. \tag{3.5}$$

(3.6) The expectation $\psi'_\alpha(1) = 1 + s(\alpha)$ is an increasing function of α.

(3.7) For all $0 \leqslant u \leqslant 1$ and $\alpha_0 \leqslant \alpha < \alpha_1$, there exist continuous second derivatives $(\partial^2/\partial\alpha^2)\psi_\alpha(u)$ and $(\partial^2/\partial u\,\partial\alpha)\psi_\alpha(u)$ (including the appropriate left and right second derivatives at the edges).

Note that the assumptions (3.4) – (3.7) are all satisfied by the families $\psi_\alpha(u)$ described in the two examples given above.

We are now interested in the extinction probability $u(\alpha)$ of a Galton-Watson process with an individual progeny generating function $\psi_\alpha(u)$ when α is close to α_0 or, equivalently, when $s(\alpha) > 0$ is close to 0.

Since s is a continuous and increasing function of α with continuous second derivatives over $[\alpha_0, \alpha)$, a continuous change in the parameter α readily yields a family $\{\phi_s(u)\}_{0 \leqslant s < s(\alpha_1)}$ satisfying the conditions

$$\phi_{s(\alpha)}(u) = \psi_\alpha(u) \qquad \text{for all} \qquad \alpha_0 \leqslant \alpha < \alpha_1, \qquad 0 \leqslant u \leqslant 1, \tag{3.8}$$

$$\phi_0(u) \not\equiv u, \tag{3.9}$$

$$\phi'_s(1) = 1 + s. \tag{3.10}$$

(3.11) The second order derivatives $(\partial^2/\partial s^2)\phi_s(u)$ and $(\partial^2/\partial u\,\partial s)\phi_s(u)$ (including left and right second order derivative at the edges) exist and are continuous for all $0 \leqslant u \leqslant 1$, and $0 \leqslant s < s(\alpha_1)$.

4. Analysis of the Model

We know that for all $s \geqslant 0$, the extinction probability of a Galton-Watson process with the individual progeny generating function $\phi_s(u)$ is given by the smallest non-negative solution $u = u(s)$ of the equation

$$u = \phi_s(u). \tag{4.1}$$

We also know that for $s = 0$, (4.1) has a double solution $u(0) = 1$, while for any $s > 0$ it has a unique solution $u(s)$ in the interval $(0, 1)$, with an order of multiplicity 1. By implicit differentiation, (4.1) implies

$$u' = \frac{\partial}{\partial s}\phi_s(u) + u'\phi'_s(u). \tag{4.2}$$

For any supercritical g.f. $\phi(u)$, if u is the smallest non-negative solution of $u = \phi(u)$, then $\phi'(u) < 1$. Hence, for all $s > 0$, (4.2) may be written as

$$u' = \frac{\dfrac{\partial}{\partial s}\phi_s(u)}{1 - \phi_s'(u)}. \tag{4.3}$$

But from $\phi_s(1) \equiv 1$, it follows that for all $s \geqslant 0$,

$$\frac{\partial^2}{\partial s^2}\phi_s(1) = \frac{\partial}{\partial s}\phi_s(1) \equiv 0,$$

$(\partial/\partial s)\,\phi_s(V)$ and $(\partial^2/\partial s^2)\,\phi_s(V)$ are continuous functions of both V and s. It is readily shown that $\lim_{s\downarrow 0} u(s) = 1$, otherwise there is a value $\delta > 0$ and a sequence $s_i \to 0$ such that $u(s_i) < 1 - \delta$. In this case, it follows from (3.10) and the convexity of $\phi_{s_i}(u)$ that for all $1 - \delta \leqslant u \leqslant 1$

$$u \geqslant \phi_{s_i}(u) \geqslant u - (1 - u)s_i$$

thus, as $i \to \infty$, we have $\phi_{s_i}(u) \to u$ on one hand, and $\phi_{s_i}(u) \to \phi(u)$ on the other hand, in contrast to (3.9). We, therefore, have

$$\lim_{s\downarrow 0}\frac{\partial^2}{\partial s^2}\phi_s[u(s)] = \lim_{s\downarrow 0}\frac{\partial}{\partial s}\phi_s[u(s)] = 0. \tag{4.4}$$

Because $\phi_0'(1) = 1$, both numerator and denominator of (4.3) tend to 0 as $s \downarrow 0$. Now since $(\partial/\partial u)\phi_s(1) = 1 + s$

$$\lim_{s\downarrow 0}\frac{\partial^2}{\partial u\,\partial s}\phi_s(u) = 1 \tag{4.5}$$

is obtained in the same way as (4.4). Employing the l'Hospital theorem with (4.4) and (4.5), (4.3) becomes

$$\begin{aligned} u'(0) &= \frac{\lim\limits_{s\downarrow 0}\dfrac{\partial^2}{\partial s^2}\phi_s(u) + u'(0)\lim\limits_{s\downarrow 0}\dfrac{\partial^2}{\partial u\,\partial s}\phi_s(u)}{\lim\limits_{s\downarrow 0}\dfrac{\partial^2}{\partial u\,\partial s}\phi_s(u) + \phi_0''(1)u'(0)} \\ &= -\frac{u'(0)}{1 + \sigma^2 u'(0)}. \end{aligned} \tag{4.6}$$

where $u'(0)$ stands for the right derivative of $u(s)$ at $s = 0$ and $\sigma^2 = \phi_0''(1)$ $EX^2 - 1 = \operatorname{Var} X_0$.

The solution $u'(0) = 0$ of (4.6) corresponds to the constant solution $u(s) \equiv 1$ of (4.1). The other solution

$$u'(0) = -\frac{2}{\sigma^2} \tag{4.7}$$

corresponds to the smallest relevant solution of (4.1) over $s \geqslant 0$. When $s > 0$ is small, the survival probability of the process is therefore given by

$$1 - u(s) = \frac{2s}{\sigma^2} + o(s) \tag{4.8}$$

independently of the family, provided that this family satisfies the conditions (3.1)–(3.4).

5. Summary

A Galton-Watson process has been employed to study the extinction probability u of a slightly advantageous mutant gene. The widely accepted approximation

$$1 - u = \frac{2s}{\sigma^2} + o(s) \tag{1.3}$$

has been shown to be mathematically invalid. However, it has been proved to be valid for a rather rich set of families of progeny distributions, and (1.3), even though mathematically incorrect, may be accepted for most conceivable biological situations.

References

Evens, W. J.: Population Genetics. London: Methuen 1969

Fisher, R. A.: The genetical theory of natural selection. (Rev. 2nd ed.) New York: Dover 1930, 1958

Gillespie, J. H.: Natural selection for within-generation variance in offspring, number I: Genetics **76**, 601 – 606 (1974)

Gillespie, J. H.: Natural selection for within generation variance in offspring, Number II: Direct haploid model. Genetics **81**, (2), 403 – 413 (1975)

Haldane, J. B. S.: A mathematical theory of natural and artificial selection, Part V: Selection and mutation. Proc. Camb. Phil. Soc. **26**, 220 – 230 (1927)

Harris, T. E.: The theory of branching processes. Berlin: Springer 1963.

Kimura, N.: Diffusion models in population genetics. J. Appl. Probabil. **1**, 177 – 232 (1964)

Received October 9, 1980/Revised March 23, 1981

Reprinted from THEORETICAL POPULATION BIOLOGY
All Rights Reserved by Academic Press, New York and London

Vol. 12, No. 1, August 1977
Printed in Belgium

Worker–Queen Conflict and the Evolution of Social Insects*

G. OSTER*

University of California, Berkeley, California

I. ESHEL

Tel-Aviv University, Tel-Aviv, Israel

AND

D. COHEN

Hebrew University, Jerusalem, Israel

Received October 11, 1976

A general expression for the inclusive fitness of haplodiploids is developed. The optimal investment of colony resources in eusocial Hymenoptera is then derived by maximizing the inclusive fitnesses of workers and queens subject to an ergonomic constraint. Because of assymmetries in the coefficients of relatedness, there is a genotypic "conflict of interest" between the queen and her daughters. We show how the inclusive fitness formula can be used to investigate this situation and to determine who is controlling the colony investment policy. Finally, we show that the optimization of inclusive fitness is consistent with the equilibria of a detailed genetic model.

1. INTRODUCTION

In a recent paper, Trivers and Hare (1976) called attention to the possible role of worker–queen conflict in the evolution of eusociality in Hymenoptera. In particular, they concluded that in monogynous ants the investment of colony resources should be near a ratio of 3:1 in favor of females, a conclusion which their data appear to bear out. The importance of this work lies in its support for the genetic theory of the evolution of eusociality in Hymenoptera first proposed by Hamilton (1964). However, Trivers and Hare arrived at their deductions largely by verbal reasoning—occasionally a treacherous path in evolutionary theory. In this paper we would like to take one step toward

---

* Work supported by NSF Grant No. BMS-74-18897.

ISSN 0040-5809

quantifying their arguments, and in so doing perhaps illuminate some of the difficulties that must be surmounted before a comprehensive theory can be developed.

One of the principal difficulties in modeling the conflict between the workers and the mother queen lies in defining the inclusive fitness of each party. As we shall see, the "value" of a male or female offspring depends crucially on the current sex ratio in the community (i.e., collection of colonies). Thus, the colony population dynamics are tied inextricably to the dynamics of the whole community, so neither can be studied independently. Trivers and Hare confront this dilemma by restricting their attention to steady-state communities and invoking the sex ratio argument of Fisher (1958) (cf. also Hamilton, 1967) to assume that the community sex ratio has equilibrated. Unfortunately, it is difficult to justify Fisher's argument quantitatively; however, simple models which assume that the sex ratio is controlled by a single autosomal locus appear to support the conclusion in diploid populations (Eshel, 1972; Bodmer and Edwards, 1960; Spieth, 1974). Hamilton (1972) advances a verbal argument for a 1:1 ratio in haplodiploids. The community sex ratio plays a prominent role in our considerations here as well.

In Section 2 we define inclusive fitness of the workers and queens for steady-state community. This definition depends on obtaining an expression for "reproductive success" which reflects the community sex ratio.

In Section 3 we formulate the conflict between the workers and queen in a game-theoretic context and discuss the notion of competitive (Nash) equilibria in a general framework. In Section 4 a few special competitive situations are examined and the equilibria are computed. This yields the "optimal" investment and sex ratios which Trivers and Hare use to determine who is controlling the colony investment policy.

A larger issue in population genetics underlies our modeling efforts here. Throughout our discussion we assume without proof that natural selection operates so as to favor genes which increase an individual's inclusive fitness. While such optimization arguments are common in the ecological literature, it is by no means clear that natural selection can be viewed as an optimizing process in the long run. Indeed, it is easy to construct models in terms of gene frequencies for which no extremum principle can be constructed. Nevertheless, since it is virtually impossible to track genotype structure for polygenic characters, one still hopes that macroscopic quantities can be constructed which will give the general trend of evolutionary processes while averaging out the microscopic dynamics of gene frequencies. In this connection it is known that the classical fitness function of population genetics provides an extremum principle only in very restricted cases (cf. Shahshahani, 1976; Roughgarden, 1976). In Section 5 we offer some evidence that inclusive fitness may be a more broadly applicable "macrovariable" with which to track evolutionary trends (cf. Seger, 1976). We do this by constructing, in one special case, a microscopic model whereby the trait in question is governed by one locus/two alleles, and we show that the gene frequency equilibrium does indeed correspond to that inferred on the basis of inclusive fitness arguments. However, our macroscopic treatment is limited to equilibrium situations.

2. The Inclusive Fitness of Queens and Workers

2.1. Consider an individual who performs an act which changes her fitness, w_i, by an amount δw_i. If this act affects her relatives, then their fitness will change by amounts δw_j, where j indexes all those affected by the act. Hamilton (1964) proposed that the net effect of an act on the actor's genetic fitness be assessed by adding to δw_i the total of all the effects on the actor's relatives, δw_j, each discounted by their "degree of relatedness," r_{ij}:

$$\delta V_i = \delta W_i + \sum_j r_i \delta W_{ij} . \tag{2.1}$$

V_i is called the individual's "inclusive fitness," and the "relatedness" of two individuals can be defined as (Li, 1955):

$r_{ij} \triangleq$ expected fraction of i's genes which are identical
by descent to genes in j.

r_{ij} can be calculated by standard methods for haplodiploid populations (cf. Crozier, 1970). A complete discussion of the difficulties of computing r_{ij} explicitly can be found in Roughgarden (1978). For our purposes here we can consider the r_{ij}'s as phenomenological coefficients measuring the "degree of relatedness" between individuals. Figure 1 summarizes the relevant relationships between individual in a monogynous hymenopteran colony assuming no inbreeding and single insemination of the queen.

Notice that the relatedness between females is symmetric, $r_{ij} = r_{ji}$, while those between females and males is asymmetric, $r_{ij} \neq r_{ji}$. Moreover, $r_{ij} = 0$

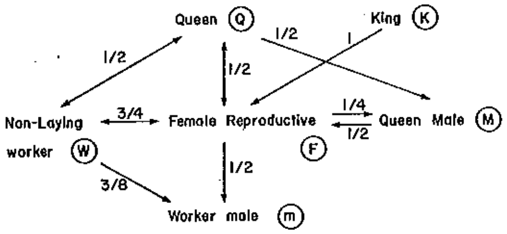

FIG. 1. Degree of relatedness, r_{ij}, among individuals in a monogynous, eusocial hymenopteran colony assuming no inbreeding and single queen insemination (corrections for these effects can be found in Hamilton (1972)). "Queen males" are sons of the queen and "worker males" are sons of laying workers.

between a king and his "sons." On the basis of these genetic relationships alone it appears that female workers should be biased toward aiding in rearing sisters and foregoing laying eggs of their own.[1] This would be in the queen's best interest since she would certainly prefer her own sons ($r = \frac{1}{2}$) to grandsons ($r = \frac{1}{4}$). However, Trivers noticed that the aforementioned asymmetry implies that the inclusive fitness of the workers and the queen are not identical, and therefore, might be maximized in different ways, leading to worker–queen conflict within the colony. It is the resolution of this conflict that we wish to investigate. First, using Eq. (2.1) and the data summarized in Fig. 1, let us formulate explicit expressions for the inclusive fitness of the queen and workers.

2.2. Denote by F the number of new queens produced by the founding queen of a colony during the reproductive phase. Since drones can be produced from either queen eggs or from worker eggs, we denote by M the number of queen sons and by m the number of worker sons. Two derived quantities we small need later are:

$$p \equiv \frac{M}{M+m} \qquad \text{the fraction of queen males} \tag{2.2}$$

$$\sigma \equiv \frac{M+m}{F} \qquad \text{the colony sex ratio} \tag{2.3}$$

so that the composition of the colony reproductives can be characterized by either the vector $\mathbf{N} = (N_1, N_2, N_3) \triangleq (F, M, m)$ or by (σ, p, N), where $N = \sum_{i=1}^{3} N_i$ is the total number of reproductives.

Next, we denote by S_F, S_M, and S_m the reproductive success of a *gene* in a new queen, queen male, and worker male, respectively. Henceforth, we assume that both queen males and worker males are equivalent with respect to their chances of siring a new colony: $S_M = S_m$. We define these quantities more exactly in a moment. First, we define the reproductive value of all individuals of type j to an individual i by

$$v_{ij} \triangleq r_{ij}S_j\,, N_j\,, \qquad j = F, M, m. \tag{2.4}$$

Then, the inclusive fitness of the queen can be defined as

$$\begin{aligned} V_Q = \sum_j v_{Qj} &= r_{QF}FS_F + r_{QM}MS_M + r_{QM}mS_m \\ &= \underbrace{\tfrac{1}{2}FS_F + \tfrac{1}{2}MS_M}_{W_Q} + \underbrace{\tfrac{1}{4}mS_m}_{r_{Qm}W_m} \end{aligned} \tag{2.5}$$

---

[1] Workers can lay only male eggs since prior to the reproductive phase of colony growth there are no males to fertilize them.

Comparing Eq. (2.5) with Eq. (2.6) we see that the "self-fitness," W_Q, comprises the first two terms and the "indirect fitness" is the third term. Similarly, the inclusive fitness of a worker is

$$V_W = \sum v_{Wj} = \underbrace{\tfrac{1}{2}\hat{m}S_m}_{W_W} + \underbrace{[\tfrac{3}{4}FS_F + \tfrac{1}{4}MS_M + \eta\tilde{m}S_m]}_{\sum r_{ij}W_j}. \tag{2.6}$$

Here $\hat{m}$ is the number of her sons (related to her by $r = \frac{1}{2}$) and $\hat{m}$ is the numbers of her nephews ($r = \frac{3}{8}$). For nonlaying workers, $w_w = 0$ and the only contribution to her genetic fitness is indirect via the quantity in brackets.

2.3. To proceed further we must derive expressions for S_F & $S_M = S_m$, the reproductive successes of females and males. A moment's reflection reveals that the probability of, say, a male founding a colony depends on the number of other males competing to mate with the new queens-to-be (we are assuming queens mate but once, a common circumstance in Hymenoptera). That is, reproductive success of an individual cannot be defined independently of the community sex ratio. Thus, the strategies required to increase the inclusive fitness of both the queen and workers depends on the community structure. Conversely, if the community is small enough that the reproductive output of a single colony significantly affects the community sex ratio, then the optimization of colony level fitness cannot be implemented independently of the community dynamics. Rather than attempt a comprehensive treatment of individual–colony–community level selection, we restrict ourselves to the special case of an equilibrium community. We denote by overbars quantities pertaining to the community as a whole, e.g., $\bar{\sigma} = (\overline{M} + \overline{m})/\overline{F}$ is the community sex ratio.

First, we give a precise definition for the reproductive success quantities introduced above:

$S^{\tau}_{M(F)}$ = the expected number of genes in generation τ (in both sexes) which are identical by descent to a particular gene in a male (female) in generation 0.

$S_M = \lim\limits_{\tau\to\infty} S_M{}^{\tau}$ = the expected reproductive success of a male.

This limit exists and can be shown to be unique (Lipow, 1977). Next, we consider a stable community consisting of n colonies where the community composition in generation t at nuptial flight time is given by $\overline{F} = \sum_{i=1}^{n} F_i$, $\overline{M} = \sum_{i=1}^{n} M_i$, $\overline{m} = \sum_{i=1}^{n} m_i$. The probability of a particular male founding a colony is just $n/(\overline{M} + \overline{m})$. Each such colony will produce, on the average, $\overline{F}/n$ female alates, $\overline{M}/n$ queen males, and $\overline{m}/n$ worker males. Each female will have, by definition, a reproductive success S_F and each male a reproductive success, S_M. (Note that $S_F^{\tau+1}$ is the expected number of genes passed on to the next generation by a female which succeeds in founding a colony in generation τ. The number of F's which succeed is just n.) Thus, we can write the following difference equation for $S_M{}^\tau$:

$$\begin{aligned} S_M^{\tau+1} &= \frac{n}{\bar{M}+\bar{m}}\left\{\frac{\bar{F}}{n}\, r_{MF} S_F{}^\tau + \frac{\bar{M}}{n}\, r_{MM} S_M{}^\tau + \frac{\bar{m}}{n}\, r_{Mm} S_M{}^\tau\right\} \\ &= \frac{1}{\bar{\sigma}}\cdot 1\, S_F{}^\tau + \bar{p}\cdot 0\cdot S_M{}^\tau + (1-\bar{p})\,\frac{1}{2}\, S_M{}^\tau. \end{aligned} \tag{2.7}$$

Asymptotically, $S_M{}^\tau \to S_M$, $S_F{}^\tau \to S_F$ (Lipow, 1977). Thus, we can solve Eq. (2.7) for the relative reproductive success of males and females:[2]

$$S \triangleq \frac{S_M}{S_F} = \frac{\bar{F}}{\bar{M}+(\bar{m}/2)} = \frac{2}{\bar{\sigma}(1+\bar{p})}. \tag{2.8}$$

In the case of a diploid population, Fisher's argument implies (e.g., Bodmer and Edwards, 1960) $S = 1/\bar{\sigma} = \bar{F}/\bar{M}$; here we see that the diploid value is modified by the factor $1 \leqslant 2/(1+\bar{p}) \leqslant 2$. This is due to the presence of worker males, m, which are "worth" only half of a queen male since they require one extra reproductive event.

An analogous expression for S_F could have been written using similar reasoning, but would yield the same expression for the relative reproductive success.

2.4. In order to derive expressions for S_M and S_F separately we must write another independent equation. Lipow (personal communication) has shown us a method for deriving such an equation in the equilibrium case. Imagine that, at time zero, we introduce into a steady-state community a collection of "marked" genes which we denote by "red" and "blue," according to the following scheme. Each female, being diploid, receives two red genes (or chromosomes); each queen male and each worker male, being haploid, receives one blue gene. The total number of these marked genes remains constant at $2\bar{F}+\bar{M}+\bar{m}$ since the population is stationary, but the "colors" redistribute themselves generation by generation throughout the population. We can write an equation for this redistribution by *defining* $S_F^{(t)}$ and $S_M^{(t)}$ to be the total number of individuals (of both sexes) in generation t whose marked genes are identical by descent to females (i.e., red) and males (i.e., blue) at $t = 0$, respectively.

---

[2] Benford (1976) has shown us an elegant alternative derivation of Eq. (2.8).

Since at $t = 0$, $2\bar{F}$ red genes were introduced along with $(\bar{M} + \bar{m})$ blue genes, we must have at generation t the relation

$$2\bar{F} + \bar{M} + \bar{m} = 2\bar{F}S_F^{(t)} + (\bar{M} + \bar{m})\, S_M^{(t)}. \tag{2.9}$$

Indeed, since this is just a conservation equation for chromosomes, it must hold for all t, and we have

$$2\bar{F} + \bar{M} + \bar{m} = 2\bar{F}S_F + (\bar{M} + \bar{m})\, S_M \tag{2.10}$$

or, dividing through by $(\bar{M} + \bar{m})$,

$$S_F = 1 + \frac{\bar{\sigma}}{2}(1 - S_M). \tag{2.11}$$

This equation is independent of (2.8) and can be used to obtain S_F and S_M separately,

$$S_F = \left(\frac{\bar{p}+1}{\bar{p}+2}\right)\left(\frac{\bar{\sigma}+2}{2}\right) = \frac{(2\bar{F} + \bar{M} + \bar{m})(2\bar{M} + \bar{m})}{(3\bar{M} + 2\bar{m})\, 2\bar{F}}, \tag{2.12}$$

$$S_M = \left(\frac{1}{\bar{p}+2}\right)\left(\frac{\bar{\sigma}+2}{\bar{\sigma}}\right) = \frac{2\bar{F} + \bar{M} + \bar{m}}{3\bar{M} + 2\bar{m}}. \tag{2.13}$$

However, as we shall see, only the relative reproductive success $S = S_M/S_F$ are required for our calculations.

2.5. Using Eq. (2.8) we can express V_Q and V_w in terms of either S_M or S_F,

$$V_Q = S_F\left[\frac{1}{2}F + \frac{S}{2}M + \frac{S}{4}m\right], \tag{2.14}$$

$$V_W = S_F\left[\frac{3}{4}F + \frac{S}{4}M + \frac{S}{2}\hat{m} + \frac{3}{8}S\tilde{m}\right]. \tag{2.15}$$

If we focus attention on a particular (average) worker, then we can define her average relatedness $\bar{r}$ to the worker brood: Let $m = \hat{m} + \tilde{m}$, $0 \leqslant q = m/m \leqslant 1$; then

$$\tfrac{3}{8} \leqslant \bar{r} = [\tfrac{1}{2}(1 - q) + \tfrac{3}{8}q] \leqslant \tfrac{1}{2}. \tag{2.16}$$

Then we can write Eq. (2.5) as

$$V_W = S_F\left[\frac{3}{3}F + \frac{S}{4}M + \bar{r}Sm\right], \qquad \frac{3}{8} \leqslant \bar{r} \leqslant \frac{1}{2}. \tag{2.17}$$

As Eqs. (2.14) and (2.17) show, the inclusive fitness of the queen and her daughters are functions of both colony and community quantities and, in general, they are not equal. Thus, we can indeed expect that some "conflict of interest" will arise with respect to how colony resources are allocated. Let us next investigate the nature of this conflict more deeply.

2.6. *Remark.* The general expression for inclusive fitness has the form:

$$V = \sum_{j=1}^{\text{all relative types}} r_j S_j N_j = \mathbf{r}^T \mathbf{S} \mathbf{N} \text{ (c.f. sect. 3.3).} \tag{2.18}$$

Several generalizations of this formula may be necessary in certain circumstances:

(a) The effective degree of relatedness, r_j, is increased by inbreeding, so that $r_j \leqslant r_j(\hat{F})$, where $\hat{F}$ is the coefficient of inbreeding (cf. Hamilton, 1972).

(b) The reproductive success, S_j, derived above assumed unrestricted mating over the whole population. If local mate competition is important, then S_j must be modified (and inbreeding may be important).

(c) N_j is the total expected number of relatives of type j. In models which account for age structure this can be calculated from demographic data alone, i.e., population mortality and birthrate schedules.

Hamilton (1967) and Alexander and Sherman (1977) have pointed out that local mate competition between males devalues sons with regard to the queen's inclusive fitness. This will have the effect of biasing sex ratios in favor of females by a mechanism independent of the relative values of r_j and thus independent of haplodiploidy. In our subsequent analysis, we ignore this effect.

In populations where inbreeding is important, there may be a genetic "cost" associated with excessive homozygosity (e.g., fecundity depression and/or mortality elevation). In such cases, Eq. (2.18) must be further modified by a factor $\varphi(\hat{F}) \leqslant 1$ which decreases the effective inclusive fitness.

Finally, we emphasize that expression (2.18) has been derived for a stationary population only. Considerable modifications must be made to treat the dynamic case.

3. OPTIMUM INVESTMENT RATIOS FOR QUEENS AND WORKERS

First, we examine the simplest case where one or the other party completely controls the situation, so that only one inclusive fitness is maximized. For example, in honeybees the workers control the queen's egg-laying according to the number of egg cells they construct. Moreover, in some cases they also control the sex ratio by varying the size of the egg cells: Male eggs are deposited by the queen in the larger cells, and female eggs in the smaller cells. On the other hand, in bumblebees, the queen is able to suppress worker egg-laying by aggressive behavior toward them. Let us examine the two extreme cases.

Throughout our discussion we adhere to the following assumptions:

(i) The community is in equilibrium, and all colonies in the community are identical in size.

Wilson (1975) and Cohen and Eshel (1976) have demonstrated that variations in colony composition can have profound effects on community evolution; however, we shall ignore this effect here.

(ii) The cost of rearing an egg to maturity is constant, and equal to C_F, C_M, and C_m calories for female, queen male, and workers males, respectively.

Because of economies of scale the true cost of brood rearing is surely different for small and large colonies (Oster and Wilson, 1978). However, by assumption (i) we have ignored the fact that the community is composed of colonies in various sizes and stages of their life cycle.

(iii) Since all colonies are assumed identical, and the community is at equilibrium, the total energetic resources of the community are shared equally by all colonies. Thus, each colony is subject to the same "budget constraint":

$$E = \sum_{i=1}^{3} C_i N_i = C_F F + C_M M + C_m m, \tag{3.1}$$

where E is the total energetic resources of the colony. Henceforth, we measure all costs as fractions of the total available energy, $\alpha = C_F/E$, $\beta = C_M/E$, $\gamma = C_m/E$:

$$\sum \alpha_i N_i = \alpha F + \beta M + \gamma m = 1. \tag{3.2}$$

Using the energetic constraint (3.2), the composition of the reproductive population $\mathbf{N} = (F, M, m) = ((1 - \beta M - \gamma m)/\alpha, M, m)$ can be represented in $\mathbb{R}^2$ in terms of either M and m or σ and p (cf. Fig. 2).

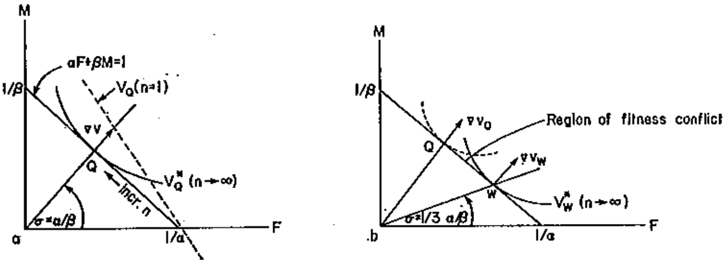

FIG. 2. The colony sex ratio which maximizes the queen's inclusive fitness. The point Q is the optimum sex ratio in a large community, where the V_Q contour is tangent to the ergonomic constraints.

3.1. *Queen control.* From Eq. (2.14) the queen's inclusive fitness is

$$V_Q(F, M, m; \bar{\sigma}) = S_F \left[\frac{1}{2} F + \frac{S}{2} M + \frac{S}{4} m\right]. \tag{3.3}$$

First, we compute the ratio of investment which maximizes the queen's fitness. In order to do this we must account for the dependence of the success ratio $S = 2/\bar{\sigma}(1 + \bar{p})$ on the size of the community. For our purposes we restrict our attention to the case of n colonies, each containing $M_i + m_i$ male and F_i female reproductives; so that $\bar{M} = \sum_{i=1}^{n} M_i$, $\bar{m} = \sum_{i=1}^{n} m_i$ & $\bar{F} = \sum_{i=1}^{n} F_i$. Each colony is subject to the identical ergonomic constraint $\alpha F_i + \beta M_i + \gamma m_i = 1$ so that we can write (3.3) for the ith colony:

$$V_Q^i = S_F \left[\left(\frac{1}{2} - \frac{S}{4}\frac{\alpha}{\gamma}\right) F_i + \left(\frac{S}{2} - \frac{S}{4}\frac{\beta}{\gamma}\right) M_i + \frac{S}{4\gamma}\right]. \tag{3.4}$$

From the second term we see that m's are preferred to M's only if $\beta > 2\gamma$, that is, $\beta/\gamma > 2 = r_{QM}/r_{Qm}$. While this is obvious a priori, there are situations where one or more workers do lay eggs despite the queen's preference, which affects the value of V_Q. For the moment, however, we continue with the a sumption of total queen control and set $m = 0$. (From the first term we see that F's are preferred to m's when $\gamma/\alpha > S/2 = 1/(\bar{\sigma}(1 + \bar{p}))$).

Thus, in the case of queen control we must solve the following nonlinear programming problem

$$\text{Max } V_Q^i(F_i, M_i, \bar{F}, \bar{M}) \tag{3.5a}$$

subject to

$$\alpha F_i + \beta M_i \leqslant 1, \qquad i = 1, 2, ..., n. \tag{3.5b}$$

In this case it is just as easy to substitute the ergonomic constraints into the fitness equation. Noting that $S = \bar{F}/\bar{M} = \sum_{i=1}^{n} F_i / \sum_{i=1}^{n} M_i = (n - \beta\bar{M})/(\alpha\bar{M})$, we obtain

$$V_Q^i = \frac{S_F}{2\alpha}\left[1 - 2\beta M_i + n\frac{M_i}{\bar{M}}\right]. \tag{3.6}$$

To find the maximum inclusive fitness we need only apply the chain rule and set

$$0 = \frac{dV_Q^i}{dM_i} = \frac{\partial V_Q^i}{\partial M_i} + \frac{\partial V_Q^i}{\partial \bar{M}}\frac{\partial \bar{M}}{\partial M_i} + \frac{\partial V_Q^i}{\partial S_F}\frac{\partial S_F}{\partial M_i}. \tag{3.7}$$

Since all colonies are assumed identical in this calculation, $\bar{M} = nM_i$. Furthermore, we are concerned only with the large community limit, $n \to \infty$ and for this case it can be shown that $\partial S_F/\partial M_i \sim O(1/n)$, and we can neglect that term in the chain rule. (Terms involving S, however, are not negligible.) Carrying out the differentiations we obtain

$$M_i = \frac{n-1}{n}\frac{1}{2\beta}, \qquad F_i = \frac{n+1}{n}\frac{1}{2\alpha} \tag{3.8}$$

so that

$$\sigma_i = \frac{\alpha}{\beta}\frac{n-1}{n+1}, \qquad i = 1,2,\ldots, n \tag{3.9}$$

Therefore, each colony's ratio of investment is

$$R_i^* = \frac{n-1}{n+1} = \frac{C_M M_i}{C_P F_i} \quad \& \quad \operatorname*{Lim}_{n\to\infty} R^*(n) = 1. \tag{3.10}$$

Thus $0 \leqslant R_i \leqslant 1$, and we can expect $R = 1$ only in the large community limit, $n \to \infty$. The situation is sketched in Fig. 2. In most ant species alates disperse widely, and the effective community size is generally $\sim 10^2$ or more (E. O. Wilson, personal communication). Therefore, in most cases $R \approx 1$, since R rises rapidly with n (however, see Wilson, 1963). The above calculation shows how R varies with community size. More importantly, it demonstrates that one cannot treat $\bar{\sigma}$ as a constant in Eq. (3.5). This would be tantamount to treating the community as one large colony which would yield, by Eq. (3.5), produce only fermales if $\alpha > 2\beta$. Mathematically, this is clearly inevitable. When $S =$ constant, V_Q is linear, and so we maximize the linear function, V_Q, over the linear ergonomic constraint set. Allowing the success ratio S to vary renders V_Q nonlinear, however, and thus admits a "mixed" strategy of both males and females.

The reason one cannot assume an infinite community at the outset is simply that

$$\operatorname*{Lim}_{n\to\infty} \frac{d}{dM_i} S(n) \neq \frac{d}{dM_i} \operatorname*{Lim}_{n\to\infty} S(n) \tag{3.11}$$

since the series defining $Sn = \sum_{i=1}^{n} F_i / \sum_{i=1}^{n} M_i + \frac{1}{2}\sum_{i=1}^{n} m_i$ does not converge (uniformly).

The assumption that all colonies are identical is also suspect since the uniform distribution may well be unstable (cf. Wilson, 1975). However, we cannot investigate stability of the optimum without introducing dynamical equations, and so we continue with our static analysis. (Indeed, there is no guarantee that the equilibrium of the dynamic equations corresponds to the fitness optimum; cf. Rocklin and Oster, 1976; Slatkin, 1976).

If, for some reason, the queen loses all control of male production to the workers so that only m's are produced, then an identical calculation shows that her optimum fitness is achieved when $R_Q^* = 1$.

3.2. *Worker control.* The case of total worker control of investment proceeds identically. Substituting the ergonomic constraint into Eq. (2.17), the worker's fitness is

$$V_W = S_F\left[\left(\frac{3}{4} - \frac{\bar{r}S\alpha}{\gamma}\right)F + \left(\frac{S}{4} - \frac{\bar{r}S\beta}{\gamma}\right)M + \frac{S\bar{r}}{\gamma}\right]. \tag{3.12}$$

The second term yields the condition for M's to be preferred to m's by the workers:

$$\gamma/\beta > 4\bar{r}, \qquad \tfrac{3}{8} \leqslant \bar{r} \leqslant \tfrac{1}{2}. \tag{3.13}$$

That is, worker sons (or nephews) are preferred to brothers unless the latter are at least 50% cheaper to produce. Assuming that all adult males are essentially identical, it is difficult to see how this could be the case since the only additional cost to a worker in raising a son vs a brother is the energy required to manufacture an egg. In some cases, however, laying workers cease to forage, thus depriving the colony of their energy profit, and conceivably this could raise the effective cost of worker males to the point where M's are more profitable. Let us proceed assuming that the workers always prefer m's ($M = 0$).

Once again we see that maximizing V_w with $S =$ constant subject only to the linear ergonomic constraint will always yield an extremum consisting of either all F's or all m's, depending on whether $\gamma/\alpha > \frac{4}{3}\bar{r}s$ (i.e., the first term in Eq. (3.12)). Therefore, we write Eq. (2.11) for the ith colony:

$$\begin{aligned} V_W{}^i &= S_F\left[\frac{3}{4}F_i + \bar{r}Sm_i\right] \\ &= \frac{S_F}{4\alpha}\left[3(1 - \gamma m_i) + 8\left(\frac{n - \gamma\bar{m}}{\bar{m}}\right)\bar{r}m_i\right]. \end{aligned}$$

Setting $dV_w{}^i/dm_i = 0$ yields for the investment ratio

$$R_i{}^* = \frac{8\bar{r}(n-1)}{3n + 8\bar{r}}, \tag{3.14}$$

which, for $n \to \infty$ becomes

$$\begin{aligned} R_i{}^* = 8\bar{r}/3 &= 1 \quad \bar{r} = \tfrac{3}{8} \quad \text{non-laying workers,} \\ &= \tfrac{4}{3} \quad \bar{r} = \tfrac{1}{2} \quad \text{laying workers.} \end{aligned} \tag{3.15}$$

Therefore, under worker control the colony investment ratio should be between 1 and $\frac{4}{3}$. From Eq. (4.12) we see that if the queen is forced to abdicate all the male production to a *few* of her daughters (so that, for the majority of workers $\bar{r} = \frac{3}{8}$), then both party's inclusive fitness is maximized at the same value of $R = 1$.

Trivers and Hare used the dry weight ratio as an estimate of R (although they caution that differences in caloric value and water content might bias this measure). In honeybees, males and females are nearly the same size, indicating $C_M/C_F \sim 1$. However, the sex ratio is frequently biased heavily in favor of males, despite the prediction of Eq. (3.15) that $\sigma \sim 1$. One possible explanation (other than invalidating the whole equilibrium theory) is that honeybee colonies reproduce mostly by "fission," or swarming. The new queen absconds the nest accompanied by a substantial cohort of workers. Thus, the risk she runs in starting a new colony is substantially lower than if she had to found a colony as a solitary queen. The males, on the other hand, must disperse singly and compete for other swarming queens—a much riskier enterprise than that faced by the queens. As S. Macevicz (personal communication) has pointed out, it appears reasonable to add to the cost of the reproductive females, $C_F F$, the cost of the worker entourage $C_w W$ which accompanies her at the time of swarming. Thus, the investment ratio should be modified to $R = C_M M/C_F F + C_w W$. With this correction the investment ratios in species wherein colonies reproduce by fission are brought more in line with kin selection theory, although a quantitative assessment is difficult.

This modification suggests another problem for the kin selection theory, however. Why should a worker join a swarm, thereby trading an average $\bar{r}$ of $\frac{1}{2}(\frac{3}{4} + \frac{1}{4}) = \frac{1}{2}$ for $\bar{r}$'s of $\frac{3}{8}$ (assuming that the new queen is fertilized by an unrelated male)?

Despite controlling the rearing of brood the workers may not be able to lay eggs themselves, either because of an inhibitory pheromone or by some form of queen dominance, as happens in bumblebees. Then the workers' fitness must be computed from

$$V_W = S_F[\tfrac{3}{4}F + \tfrac{1}{4}SM]. \tag{3.16}$$

Repeating the above calculation yields the investment ratio when all males are queen sons but the workers raise them in the proportions which maximize their inclusive fitness:

$$R^* = \frac{n-1}{3n+1}, \qquad \lim_{n\to\infty} R(n) = \frac{1}{3}. \tag{3.17}$$

3.3. We can derive a general expression for the optimum investment ratio, R^*, by solving the following programming problem:

$$\max_{\mathbf{N}}[\mathbf{r}^T\mathbf{S}(\bar{\mathbf{N}})\mathbf{N}] = V_l^*, \qquad l = Q, W \tag{3.18a}$$

subject to the constraints

$$\boldsymbol{\alpha}^T\mathbf{N} \leqslant 1, \qquad \mathbf{N} \geqslant 0. \tag{3.18b}$$

Here $\mathbf{N} = (F, M, m)$ is the colony composition, $\boldsymbol{\alpha} = (\alpha, \beta, \gamma)$ is the cost vector, $\mathbf{r}_l$ is the relatedness vector (r_{l1}, r_{l2}, r_{l3}) for the lth agent (Q or W) and

$$\mathbf{S}(\bar{\mathbf{N}}) = \begin{pmatrix} S_F(\bar{\mathbf{N}}) & 0 & 0 \\ 0 & S_M(\bar{\mathbf{N}}) & 0 \\ 0 & 0 & S_m(\bar{\mathbf{N}}) \end{pmatrix}$$

is the reproductive success matrix.

One can show (e.g., using Lagrange multipliers) that there is no extremum in the interior of the feasible set and that any optima must lie on the boundary $M = 0$ or $m = 0$. Thus, we can restrict our attention to the case $p = 0$ or 1 and solve the easier problem

$$\mathrm{Max}[S_F(r_{l1}X_1 + r_{l2}SX_2)] \tag{3.19a}$$

subject to

$$\alpha_1 X_1 + \alpha_2 X_2 = 1, \qquad X_1, X_2 \geqslant 0 \tag{3.19b}$$

Here the quantities X_1 & X_2 refer to females and males, respectively. If $m = 0$, $S = \sum_{i=1}^{n} F_i / \sum_{i=1}^{n} M_i$, while if $M = 0$, $S = \sum F_i / \frac{1}{2} \sum m_i$. Eliminating, say X_1, via the constraint, and setting $dV_1/dX_2 = 0$, we obtain for $n \to \infty$:

$$R_l{}^* = \sigma c = \left\{ \left[\frac{r_{l2}}{r_{l1}} \text{ when } m = 0 \right], \left[\frac{2r_{l1}}{r_{l2}} \text{ when } M = 0 \right] \right\}_{l=Q,W} \tag{3.20}$$

where c is the male/female cost ratio.

The expression for finite n is

$$R^*(n) \simeq r_2(n-1)/(r_2 + \nu n r_1), \tag{3.21}$$

where $\nu = 1$ if $m = 0$, $\nu = \frac{1}{2}$ if $M = 0$. In order for (3.21) to hold for small n, however, the r_{ij}'s must be modified to account for inbreeding. In an inbred colony females are related to daughters by $\frac{1}{2} \leqslant r_F \leqslant \frac{1}{2}((1 + 3F)/(1 + F))$, where $0 \leqslant F(n) \leqslant 1$ is the inbreeding coefficient (Hamilton, 1972). Therefore, investment in females may be considerably enhanced by inbreeding even if the queen controls investment.

3.4. In bumblebees the queen lays all the eggs for most of the reproductive phase, inhibiting worker egg-laying by dominance. However, toward the end of the season her egg-laying and domineering abilities seem to decline. Frequently, a single worker will commence to lay eggs of her own, while preventing other workers from laying by assuming the dominant attitudes of the queen. There may even be mutual egg destruction between the old queen and the laying worker. The net result is that, averaged over the reproductive season, $0 < p < 1$ ($p \sim 0.75$, C. Plowright, personal communication). In this case one would expect that the *measured* investment ratio, $\bar{R}$, would be intermediate between the optimum for the queen and workers. We can define an average $\bar{R}$ by

$$\bar{R} \triangleq \frac{c_M M + c_m m}{c_F F} = \sigma \bar{c}, \tag{3.22}$$

where $\bar{c}$ is the average cost ratio

$$\bar{c} = \frac{c_M P + c_m(1 - p)}{c_F}. \tag{3.23}$$

Trivers' data for several species of *Bombus* show $0.32 \leqslant \bar{c} \leqslant 0.85$, $1.14 \leqslant \sigma \leqslant 1.72$. According to the theory developed here, the optimum investment ratio, R^*, is bounded by

$$0.33 \leqslant R^* \leqslant 1.33.$$

3.5. Trivers and Hare observed that $\bar{R} \sim \frac{1}{3}$ for ants, indicating that the workers' were controlling the sex ratio while the queen controlled male production. However, in many species laying workers do contribute significantly to male production and values of p between 0 and 1 are common (Hamilton, 1972). From the viewpoint of optimizing inclusive fitness one way this can come about is if control shifts during the reproductive period from the queen to the workers. One scenario is that during the first part of the season $p = 1$ when the queen controls male production, but workers control rearing, $R = \frac{1}{3}$. Then, if the queen becomes senescent so that her egg production falls off or her capacity to inhibit laying workers declines, worker males commence being reared. The result is that at the time of the nuptial flight the male population is a mixture of queen males and worker males, and the net observed ratios of investment are neither the queen's nor the workers' optimum. Equation (3.22) is a "net," or season-averaged, investment ratio. If the community is in a steady state, then $\bar{R}$ is indeed the "equilibrium" ratio of investment; it is not an optimum for either party, but rather a sequential optimum for each party in turn. Therefore, it is misleading to call $\bar{R}$ a "preferred" ratio. Rather, $\bar{R}$ should be viewed as an index of which party in conflict has control of the situation.

If $\bar{R} = \frac{1}{3}$, then the workers control the rearing, but the queen controls male production. Values of $\frac{1}{3} < \bar{R} < 1$ could mean either that workers control both male production and rearing or that control of rearing has shifted from queen to workers at some point. Thus, values of p between 0 and 1 could reflect a shift of control from queen to workers during the reproductive period.

Another mechanism whereby mixed male broods may be optimal is if the ergonomic constraint is not linear. This could come about if the costs, C_F, C_M, and C_m were not constants but varied somehow with N, p, or σ. If laying workers are less diligent foragers than their nonlaying sisters, then the ergonomic constraint, E, is a function of p, which reflects the proportion of laying workers.

In such a case the constrained maximum problem (3.18) could yield an internal solution ($0 < p < 1$).

3.6. In the preceding section we derived the optimal ratio of investment for both the queen and workers if each party were to act unilaterally. We saw that only in the case where the queen laid all the female eggs and a few workers laid *all* the male eggs did their optimum investment ratios agree. In all other cases there is a conflict of fitness interests. The regions of disagreement are shown in Fig. 3. Outside the region, *ABCD*, both parties gain fitness by moving toward *ABCD*, and presumably natural selection will produce strategies which fall within this region. In our subsequent analysis we restrict ourselves to the more realistic case where $r_{wm} = \frac{3}{8}$, and so the region of conflict reduces to the triangular region *ABC*. The opposite extreme, $\bar{r} = \frac{1}{2}$, implies that each worker essentially tends to her own eggs, which contravenes the assumption of eusociality.

Table I summarizes the optimal investment ratios for the four cases computed above.

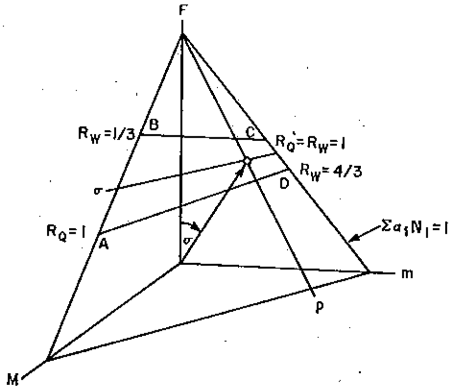

FIG. 3. The trapezoid *ABCD* represents the region of conflict between the queen and the workers. Only at vertex *c* do both party's investment ratios agree.

TABLE I

	$p = 1$ $(\gamma > 4\bar{r}\beta)$	$p = 0$ $(\gamma < 4\bar{r}\beta)$
Queen's optimal investment ratio, R_Q	1	1
Workers' optimal investment ratio, R_W	1/3	$1 \leqslant 8\bar{r}/3 \leqslant 4/3$

4. The Conflict between the Queen and Her Daughters

4.1. As Eqs. (2.14) and (2.15) show, the conflict of interest between the queen and the workers centers around the relative proportions of females, queen males, and worker males the colony will produce. The optimum inclusive fitnesses calculated in Section 3 assumed that male egg-laying (i.e., $p = M/(M + m)$) and brood rearing (i.e., $\sigma = (M + m)/F$) was totally controlled by one party or the other. Therefore, while the queen and workers might "disagree" over the values of p and σ, there was no real conflict. In order to formulate the conflict quantitatively we must be specific as to just how the changes alluded to in Eq. (2.1) are brought about. That is, we must parameterize the various strategies available to the queen and workers. We denote by $\mathbf{u} = (u_1, u_2, \ldots, u_n)$ & $\mathbf{v} = (v_1, v_2, \ldots, v_m)$ the strategy parameters of the queen and workers, respectively. For example, the queen can lay female or male eggs as she chooses. The workers, on the other hand, in addition to laying male eggs of their own, can determine which eggs are reared to adulthood since the care of the brood is entirely in their hands. In this case the following list comprises the strategy set for the queen and workers:

$$\begin{array}{cl} \begin{array}{c}\text{Queen strategy}\\ \mathbf{u}\end{array} & \left\{\begin{array}{l}\text{lay } u_1 \text{ female eggs}\\ \text{lay } u_2 \text{ male eggs}\\ \text{lay } v_4 \text{ worker eggs}\end{array}\right. \\[1em] \begin{array}{c}\text{Worker strategy}\\ \mathbf{v}\end{array} & \left\{\begin{array}{l}\text{raise to maturity } v_1 \text{ female eggs}\\ \text{raise to maturity } v_2 \text{ queen male eggs}\\ \text{raise to maturity } v_3 \text{ worker male eggs}\end{array}\right. \end{array} \tag{4.1}$$

One can imagine many additional strategies: (a) Both parties can kill progeny before maturation; (b) the queen may exert control over worker egg-laying via aggressive behavior or by an inhibitory pheromone; (c) conversely, the workers might control the queen's egg-laying (e.g., honeybees). In Fig. 4 we have sketched a schematic representation of the various strategy sets we will discuss.

4.2. Next we must determine the relations which govern how the strategy set $(\mathbf{u}, \mathbf{v})$ is translated into the adult reproductive population (F, M, m). That is, we must formulate the equations governing the demographic trajectory of the colony:

$$(\mathbf{u}, \mathbf{v}) \mapsto (F, M, m) = \mathbf{T}(\mathbf{u}, \mathbf{v}). \tag{4.2}$$

We call this transformation $\mathbf{T}$ (cf. Fig. 4).

It is clearly not feasible to deal with the situation in its full generality, and so we restrict ourselves to a few simple cases. Unless otherwise stated the assumptions given in Section 3.1 hold throughout our treatment.

4.3. To summarize, the situation as developed so far consists of three parts:

(1) The strategy vectors of the queen and workers $(\mathbf{u}, \mathbf{v})$ (considered as points in the "strategy space" $\Sigma = \mathbb{R}^n \times \mathbb{R}^m$).

(2) A set of demographic equations relating the strategy vectors $(\mathbf{u}, \mathbf{v})$ to the reproductive population $\mathbf{N} = (F, M, m) \in P$:

$$T: \Sigma \rightarrow P$$

$$(\mathbf{u}, \mathbf{v}) \mapsto \mathbf{N}$$

The budget constraint (3.3) restricts $\mathbf{N}$ to the simplex: $\Delta = \{\mathbf{N} \mid \Sigma \alpha_i N_i = 1\}$ on which either (M, m) or (σ, p) may be used as coordinates.

(3) A pair of "inclusive fitnesses" V_W, V_w defined on the population space, P:

$$\left.\begin{matrix} V_Q \\ V_w \end{matrix}\right\}: P \rightarrow \mathbb{R}.$$

This is illustrated schematically in Fig. 5.

4.4 *Remark.* Throughout our treatment we mostly use the "natural" coordinates (F, M, m) to locate colony composition points on the ergonomic constraint simplex in population space. Other coordinates are useful for certain purposes. The most common are the male ratio, p, and sex ratio, σ, (defined in Eqs. (2.2) and (2.3) and the fractional sex ratio $X \equiv (M + m)/(F + M + m) = (M + m)/N = \sigma/(1 + \sigma)$. Setting one of the functions p, σ, X, V_Q, or $V_W =$ constant defines a set of level contours on the ergonomic constraint simplex Δ; any pair of these contour sets can be used as coordinates on Δ to specify the colony composition. Thus, a point $\mathbf{x} = (F, M, m)$ is specified as well by (N, p, σ), (N, p, X), (E, V_Q, V_w), etc.

4.5. Now that the conflict of interest between the queen and her daughters has been formalized, we must turn to the question of how it can be resolved. That is, assuming that each party will be selected to adopt strategies which increase their respective inclusive fitnesses, how will the system evolve? In fact, we have to ask a more restrictive question. Since we have ignored dynamic aspects in our formulation, we are only equipped to enquire about possible equilibrium states of the system. Even with this restriction, however, it is not immediately apparent how to define an equilibrium in a situation such as ours where two parties are in conflict. One sensible notion of equilibrium which applies to our situation can be borrowed from game theory: the "Nash equilibrium." Roughly speaking, a strategy $(\mathbf{u}^*, \mathbf{v}^*)$ is a Nash point (or competitive equilibrium) if neither party in the conflict can improve his position providing his opponent does not change his strategy. Formally, a point $(\mathbf{u}^*, \mathbf{v}^*) \in \Sigma$ is a Nash point if the fitnesses ("payoffs" in the game) satisfy

$$V_Q(\mathbf{u}, \mathbf{v}^*) \leqslant V_Q(\mathbf{u}^*, \mathbf{v}^*), \tag{4.3a}$$

$$V_W(\mathbf{u}^*, \mathbf{v}) \leqslant V_W(\mathbf{u}^*, \mathbf{v}^*). \tag{4.3b}$$

If the strict inequality holds in (4.3), $(\mathbf{u}^*, \mathbf{v}^*)$ is called a "strong Nash" point.

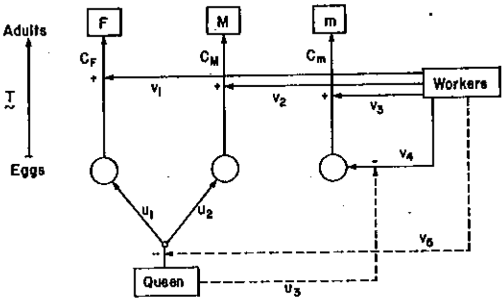

FIG. 4. The stategy sets of the queen and the workers. Queen stategies: u_1 = number of female eggs laid, u_2 = number of male eggs laid, u_3 = inhibitory effect on worker laying. Worker strategies: v_i $(i = 1, 2, 3)$ = effort allocated to raising females, queen males, and worker males, respectively; v_4 = number of worker eggs laid, v_5 = control of queen egg laying.

The Nash point can be illustrated graphically in the special case where each player has a single strategy (u, v). Then we can plot on Σ (the u–v strategy plane) level contours of $U_Q = \mathbf{T} \circ V_Q$ and $U_W = \mathbf{T} \circ V_W$. This is shown in Fig. 4 for an arbitrary set of functions U_W, U_Q. Consider first the U_Q level contours. If the worker strategy, v, is held constant, then by adjusting her strategy, u, the queen can only improve her fitness up to the U_Q contour tangent to the v = constant line. The locus of such points is shown by the curve C_Q

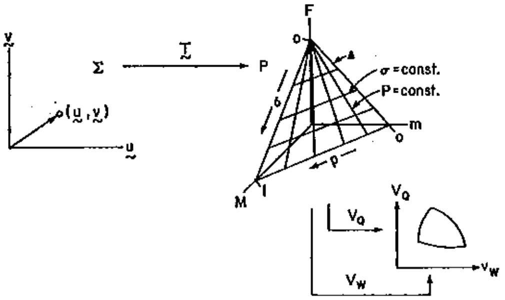

FIG. 5. The demographic equations $\mathbf{T}$ map strategy, pairs $(\mathbf{u}, \mathbf{v}) \in \Sigma$ to population vectors $\mathbf{N} \in P$. On the population simplex, Δ, p, and σ may be used as coordinates. The inclusive fitnesses V_Q and V_W are real-valued functions on Δ.

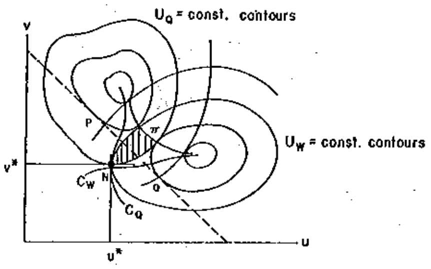

FIG. 6. $N = (u^*, v^*)$ is the (strong) Nash competitive equilibrium: Neither party can improve her fitness by changing strategy if the other holds her strategy constant.

in Fig. 6. Similarly, the line C_W is the locus of points where the V_W contours are tangent to $u =$ constant lines. If the lines C_Q and C_W intersect at, say, (u^*, v^*)—point N in the figure—that point has the following property: Neither party can improve her fitness by changing strategies, provided that her opponent keeps her strategy constant. That is, at N,

$$\left.\frac{\partial V_Q}{\partial u}\right|_{v^*} = \left.\frac{\partial V_W}{\partial v}\right|_{v^*} = 0. \tag{4.4}$$

As we have drawn it in Fig. 6, N is a strong Nash equilibrium since each party strictly loses by a unilateral strategy change.

The Nash point is stable to unilateral "cheating," and thus constitutes a reasonable candidate for an evolutionary equilibrium. Indeed, Maynard Smith, in an entirely different context, has proposed a similar criterion as an "evolutionarily stable strategy" (ESS). We follow historical precedent, however, and call a strategy set $(\mathbf{u}^*, \mathbf{v}^*)$ satisfying Eqs. (4.3) (or 4.4) a Nash equilibrium.

4.6. Before taking the above notion of a competitive equilibrium too seriously, several caveats are in order. First, the Nash point in Fig. 6 is stable against "local" cheating only: Small deviations from N are punished by fitness loss. However, a larger strategy shift may well produce a fitness increase if the fitness contours are not convex, as we have drawn them in Fig. 6. (Large phenotypic changes can easily be brought about by regulatory gene alterations (King and Wilson, 1975). Second, it is clear from Fig. 6 that if both parties can "cooperate" both can improve their fitnesses. In particular, moving $(\mathbf{u}, \mathbf{v})$ into the shaded cone improves both parties fitness until the line π is reached, whereupon improvements in one party's fitness must be at the expense of the other's. The locus of such points is called the Pareto set, or "cooperative" equilibrium. (π is the locus of points where the fitness contours are tangent: $\nabla U_Q = k \nabla U_w$, $k < 0$.) While it is not clear how drastic a genetic reorganization would be required to effect such cooperation, the possibility cannot be discounted. Finally, there is the question of whether the system could have evolved to the Nash point in the first place. We must always bear in mind that underlying the phenotypic–behavioral strategy variables **u** and **v** are a complex ensemble of genes whose evolution is constrained by the laws of Mendelian inheritance. It can be demonstrated that the following two possibilities can arise: (a) The equilibrium point of the equations of motion governing the genetic dynamics may not correspond to the Nash equilibrium (Rocklin and Oster, 1976), or (b) the genetic dynamics may be so complicated that they admit of no stable equilibrium points. The dynamically stable sets may be periodic or chaotic orbits (Oster, Ipaktchi, and Rocklin, 1976; Auslander, Guckenheimer, and Oster, 1976). In either case, the system cannot evolve to the Nash equilibrium. Having said this, however, it does appear that the social insects have evolved to some sort of behavioral equilibrium. Moreover, our analysis using the Nash concept of equilibrium does have the attraction of subsuming several evolutionary criteria for social insects suggested by other authors (Trivers and Hare, 1976; Benford, 1976), and so its properties are of more than academic interest.

In the next section, we compute the Nash equilibrium for a few simple choices for the demographic dynamics, **T**.

4.7. Depending on the choice of strategies available to each party there may or may not exist a Nash point in the region of conflict. Indeed, if the demographic equations **T** are one-to-one (i.e., $\det[D\mathbf{T}] \neq 0$ anywhere), then the only Nash equilibria are on the boundary of the conflict triangle. This is because there is no optimum for either queen or workers in the interior of the constraint set, as we have shown earlier. Moreover, any model for investment allocation during rearing which is 1:1 will yield Nash equilibria along all of *A–B*. The fitness optimization theory developed so far cannot distinguish between these points; the actual equilibrium point on *A–B* must be determined by either the relative power of the queen or workers to *impose* their preference on the other. This is a question of dominance by one or the other party. In a sense, therefore, the kin-selection theory of Hamilton and the maternal control hypothesis of Alexander may not really be in conflict. Rather the former sets the stage for the latter.

A second possibility is that colony-level selection may be the final arbiter between queens and workers. Regarding the colony as the unit of selection is equivalent to assuming that the fitness is

$$V_c = S_F[X_1 + SX_2]. \tag{4.5}$$

Thus, when $p = 1$, the gradient of the queen's inclusive fitness is colinear with that of the colony. Therefore, the queen's sex ratio preference is reinforced by colony-level selection. When $p = 1$ this would tend to favor the queen's 1:1 sex ratio. If workers control investment, the only way they can raise the colony fitness to the level it would have if $R = 1$ and yet retain their $R = \frac{1}{3}$ preference is to increase their ergonomic efficiency and thus increase the energy constraint, E. This suggests that one effect of colony-level selection is to ease the way to the evolution of specialized castes. Such castes greatly enhance the ability of the colony to exploit its environment and defend the nest (Oster and Wilson, 1978), and thus, provide an advantageous tradeoff in return for a worker-biased R. In any event, we see that kin selection alone may be not sufficient to determine the equilibrium ratio of investment and recourse to other factors (queen domination, colony-level selection) may be necessary to establish a unique, stable R^*.

4.8. First, let us assume that the workers can discriminate between all brood types and can allocate their rearing efforts according to their fitness preferences. Once again we can take advantage of the facts that (i) the fitness equilibria must lie on the boundary of the strategy set if $\mathbf{T}$ is 1:1, and (ii) the equilibria lie on the edge $M = 0$ or $m = 0$, depending on whether γ is less than or greater than $4\bar{r}\beta$, respectively. Consider first the case when $m = 0$. The queen will certainly lay male and female eggs in her preferred ratio $\sigma = 1/c$ since otherwise she will lose fitness. Denote by $e = e_F + e_m$ the total number of eggs she lays. In Fig. 7a we show the queen's strategy set (e_M, e_F). On it we superimposed the ergonomic constraint Δ (actually, $E \circ \mathbf{T}$, where E is $\sum \alpha_i N_i = 1$), and the optimal fitness contours $V_W{}^* \circ \mathbf{T}$ and $V_Q{}^* \circ \mathbf{T}$. If the queen lays $e' = e_M{}' + e_F{}'$ less than the available energy (i.e., $\alpha e_F{}' + \beta e_M{}' < 1$), then the workers in trying to raise females in their preferred ratio of $\sigma = 1/3c$ have no choice but to rear young in the proportion along the ray $0Q$ in Fig. 7. When the queen lays just the right amount of eggs to exhaust the resources $(\alpha e_F'' + \beta e_M'' = 1)$, she achieves her maximum fitness at Q. If she lays eggs in excess of this—presumably at $\sigma = 1/c$—the workers can gain fitness by rearing females preferentially $(\sigma = 1/3\sigma)$. That is, the sex ratio will move along the ergonomic frontier Q–W until the workers' maximum fitness is achieved at W. Eggs of either sex in excess of $e''' = e_F''' + e_M'''$ add to neither party's fitness.

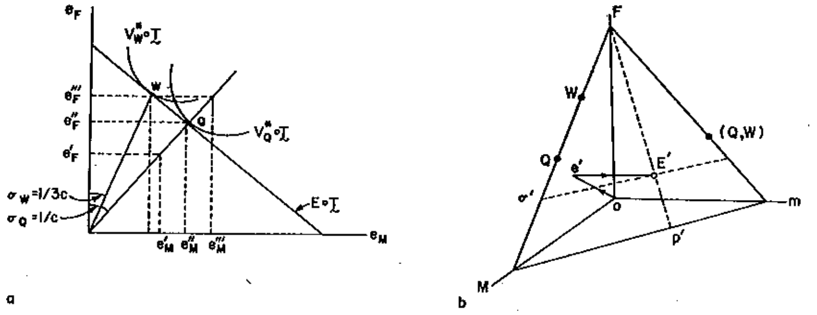

FIGURE 7

Indeed, we see that the queen generally loses fitness if she lays eggs in excess of $e''_M + e''_F = e''$. Therefore, we expect that the queen will be selected to lay eggs in amounts that just keep pace with the worker's ergonomic capacities. Then, if $\gamma > 4\bar{r}\beta$, the colony investment will be $R = 1$. In order for workers to increase their fitness, they must increase their collective ergonomic efficiency to outstrip the queen's reproductive capacity. As we mentioned above, this suggests at least one selective force favoring the evolution of worker castes (Oster and Wilson, 1978). If the queen for some reason (e.g., senescence or death) fails to lay enough eggs, $e < e''$, and providing some workers can lay eggs themselves, then the adult composition lies near the point E' shown in Fig. 7b, corresponding to an *average* colony investment of

$$\bar{R} = \sigma' \frac{p'\beta + (1 - p')\gamma}{\alpha}.$$

If $\gamma < 4\bar{r}\beta$, so that m's are cheaper to produce than M's, then, as we have shown, the workers and queen agree on the investment ratio at $(Q\text{–}W)$ in Fig. 7b, providing the queen does not, or cannot, lay eggs. However, if both lay eggs, then the fitness optimization alone cannot determine the investment ratio and one must add additional hypotheses concerning the relative power of the queen and workers to preferentially eliminate the other's male offspring. Since this may be a complex business, any model of this process would be dubious. Therefore, we do not pursue this direction further, but rather make the much simpler assumption that the workers can lay eggs, but cannot discriminate between any of the brood types.

Let us begin with the simplest set of demographic equations for this situation. We assume that a total of e eggs are laid by the queen and workers and that the available energy is aportioned uniformly among the larva. Let e_i, $i = F, M, m$ be the number of eggs of type i, and $e = \sum e_i$ be the total number of eggs. Then out of a total of E available calories, a fraction $E \cdot e_i/e$ is rationed to the ith type larva. Since an adult of type i costs C_i calories to raise, the number of adults of each type is

$$N_i = \frac{Ee_i}{c_i e} = \frac{e_i}{\alpha e}. \tag{4.6}$$

Thus, the demographic equations $\mathbf{T}$ are

$$\begin{pmatrix} e_F \\ e_M \\ e_m \end{pmatrix} \xrightarrow{\mathbf{T}} \begin{pmatrix} e_F/\alpha e \\ e_M/\beta e \\ e_m/\gamma e \end{pmatrix} = \begin{pmatrix} F \\ M \\ m \end{pmatrix}. \tag{4.7}$$

The ergonomic constraint $E(\mathbf{N}) \equiv \sum \alpha_i N_i = 1$ on the adult population corresponds to the constraint $E \circ \mathbf{T}$ or $\sum e_i = e$ on the maximum number of eggs reared to adulthood. Therefore, we can eliminate say, e_F, and regard the queen's control parameter as e_M and the workers' as e_m. A Nash equilibrium in the interior of the (preimage of the) conflict triangle—if it exists—can be found by solving

$$\frac{\partial}{\partial e_m}(V_W \circ \mathbf{T}) = 0, \qquad \frac{\partial}{\partial e_M}(V_Q \circ \mathbf{T}) = 0.$$

However, the map **T** defined above is continuous and 1:1 and so we know that the competitive equilibria are on the boundary.

In this case, it is easy to see that the colony investment ratio is always $R = 1$. If $\gamma > 4\bar{r}\beta$ so that $m = 0$, then regardless of how many eggs the queen lays in excess of the workers' capacity, they are raised in her preferred ratio of $\sigma = 1/c$ (since the workers attend to each larval type equally). If $M = 0$, then, as we have shown, $R_Q = R_W = 1$, which will be achieved by an equitable allocation of rearing effort between F's and m's. Only if the queen's egg-laying falls short of the constraint will the male ratio $0 < p < 1$ and therefore the investment ratio, R, differ from unity.

According to the kin-selection theory developed herein there are only two mechanisms for obtaining an investment ratio intermediate between $\frac{1}{3}$ and 1: (a) There is a switch in male production so that $0 < p < 1$. The only reason for this which appears plausible to us is due to the senescence or death of the queen, or the loss of queen dominance due to increasing colony size. In either case, the observed $\bar{R}$ is intermediate between the optima for the queen and workers. (b) The demographic equations **T** are not 1:1. This would require some sort of extreme density dependence on colony growth during one season, so that increased egg-laying actually *decreased* the resulting adult population. Without a much more elaborate model for the colony life cycle we can make no predictions in this direction.

5. A Microscopic Model

5.1. The competitive equilibria computed in Sections 3 and 4 were obtained by applying optimization procedures. Although optimization arguments are common in ecological thinking, they have recently been called into question in several contexts. It is not difficult to construct models at the gene frequency, or "microscopic," level for which it is not possible to define a "fitness" which is optimized along trajectories (cf. Slatkin, 1976; Auslander, Guckenheimer, and Oster, 1976). Therefore, it behooves us to see if the "macroscopic" arguments we have presented are consistent with the microscopic laws of genetics. That is, do the constraints of Mendelian inheritance and haplodiploidy permit the realization of the strategic optima inferred from maximizing the macroscopic quantity "inclusive fitness"?

In order to address this question, we investigate a highly simplified model wherein the trait governing the workers' brood-rearing behavior is controlled by a single autosomal locus with two alleles (A, a). Alternatively, one could view this locus as a modifier allele for the behavioral trait which is surely polygenic.

To begin, we examine the composition of colonies at the nuptial flight time. The population of females is of three types (AA, Aa, aa) whose frequencies in the population are (x_1, x_2, x_3). The males, being haploid, come in two genotypes: (A, a) with frequencies (y_1, y_2). Thus, after mating, the fertilized queens found six possible colony types: ($A_iA_j \times A_k$), $i, j, k = A$ or a, as shown in column 1 of Table II. We assume that mating is random in the community so that the frequency of each colony type is proportional to x_iy_j, as shown in column 2 of the table.

TABLE II

A Summary of Colony Types and Offspring Types Produced by Them

Colony type $Q \times K$	Frequency of matings proportional to	Offspring produced (units of maximum colony fertility)				
		AA	Aa	aa	A	a
1. $AA \times A$	x_1y_1	w_1	0	0	$v_1 + \theta u_1$	0
2. $AA \times a$	x_1y_1	0	w_1	0	$v_1 + \frac{\theta}{2} u_1$	$\theta u_1 v$
3. $Aa \times A$	x_2y_1	$\frac{w_1}{2}$	$\frac{w_1}{2}$	0	$\frac{v_1}{2} + \frac{3\theta u_1}{4}$	$\frac{v_1}{2} + \frac{\theta u_1}{4}$
4. $Aa \times a$	x_2y_2	0	$\frac{w_1+w_2}{4}$	$\frac{w_1+w_2}{4}$	$\frac{v_1+v_2}{4} + \frac{\theta u_1}{4}$	$\frac{v_1+v_2}{4} + \theta\left(\frac{u_1}{4} + \frac{u_2}{2}\right)$
5. $aa \times A$	x_3y_1	0	w_1	0	$\frac{\theta u_1}{2}$	$v_1 + \frac{\theta u_1}{2}$
6. $aa \times a$	x_3y_2	0	0	w_2	0	$v_1 + \theta u_2$

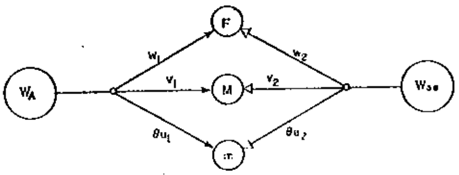

FIG. 8. Allocation of effort by the worker phenotypes to the three brood types. (F, M, m).

Next, we must model how rearing effort is allocated among the three brood types (F, M, m) in each colony type. To do this, we assume that A is dominant over a and that the rearing costs (α, β, γ) are in the ratio $(1, 1, \gamma)$, with $\gamma \geqslant 1$. Thus, there are two worker phenotypes $(A, \cdot)$ and (a, a). Workers of type $(A, \cdot)$ allocate their rearing efforts to (F, M, m) in the proportions $(w_1, v_1, \theta u_1)$ where $\theta \equiv 1/\gamma \leqslant 1$, while workers of type (a, a) rear in proportion to $(w_2, v_2, \theta u_2)$, as shown in Fig. 8.

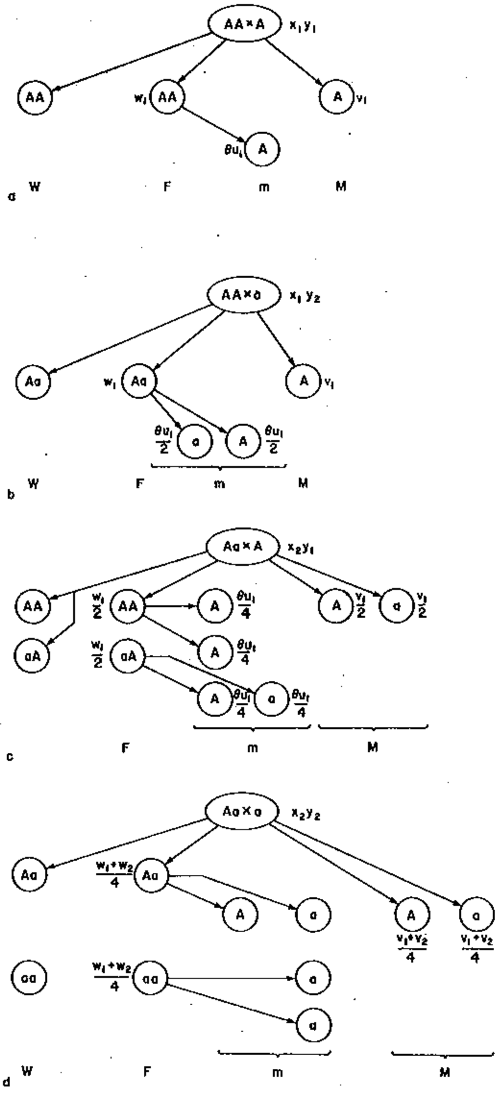

FIGURE 9

Using this scheme we can determine the composition of each colony type at the time of the next nuptial flight as follows.

1. Colonies of type $(AA \times A)$ will produce workers and reproductive females of type (AA) only and males of type A only. The W_{AA} workers will raise type F_{AA} females in proportion to the effort v_1. The queen males, M_A, are allocated v_1 and the worker males, m_A, are allocated θu_1. This is shown schematically in Fig. 9a. Thus, at the next nuptial flight the frequency of each reproductive type will be $(F_{AA}, M_A, m_A) \sim (w_1, v_1, \theta u_1)$. With regard to mating we can disregard the distinction between M_A and m_A, so that the frequency of A-type males in the population at nuptial flight time is proportional to $v_1 + \theta u_1$. These frequencies are recorded in the first row of Table II.

2. The reproductive scheme of $(AA \times a)$-type colonies is shown in Fig. 9b. In such colonies all females are Aa, queen males are A, while half of the worker males are a and half are A. Thus, $F_{Aa} \sim w_1$, $(M + m)_A \sim v_1 + (\theta u_1/2)$, and $(M + m)_a \sim \theta u_1/2$; cf. Table II, row 2.

3. Colonies of type $(Aa \times A)$ will produce reproductives as shown in Fig. 9c. Half of the females and workers are Aa and half are AA, while half of the queen males are A, as are three-fourths of the worker males. The frequencies of reproductive types is given in row 3 of Table II. Note that we are assuming that during rearing workers cannot distinguish between the various genotypes of each sex, and so effort is apportioned equally.

4. In colonies of type $(Aa \times a)$ workers of both phenotypes are produced, as shown in Fig. 9d. We assume that each worker type dispenses half of the colony effort to each genotype in proportion to its abundance. Thus the frequency of F_{Aa}'s is proportional to $\frac{1}{2}((w_1/2) + (w_1/2))$. There are two hypotheses we could make regarding allocation to males. Assuming all males are equivalent to a worker, the allocation to M_A's is $\frac{1}{2}((v_1/2) + (v_1/2))$ and to m_A's is $\frac{1}{2}(\theta u_1/2)$. Of the allocation to a-type males, $\frac{1}{2}((v_1/2) + (v_1/2))$ goes to M_a's and $\frac{1}{2}[(\theta u_1/4) + (\theta u_2/2)] = \frac{3}{8}\theta(u_1 + u_2)$ goes to m_a's. On the other hand, if laying workers can discriminate their own progeny, one would have for the frequency of A-type males

$$\frac{v_1 + v_2}{4} + \frac{\theta}{4}\left(\frac{u_1 + u_2}{2}\right)$$

and for a-type males

$$\frac{v_1 + v_2}{4} + \frac{3\theta}{4}\left(\frac{u_1 + u_2}{2}\right).$$

In what follows we consider the former case.

The remaining cases follow by identical reasoning, and the entire model is summarized in Table II.

Finally, we obtain the equations for the genotype composition of the population at the next nuptial flight by summing over all the colony types (columns)

$$x_1' = \frac{1}{\underline{W}} \left[x_1 + \frac{x_2}{2} \right] y_1 w_1 \tag{5.1}$$

$$x_2' = \frac{1}{\underline{W}} \left[\left(x_1 + \frac{x_2}{4} \right) y_2 w_1 + \left(x_3 + \frac{x_2}{2} \right) y_1 w_1 + \frac{x_2 y_2}{4} w_2 \right] \tag{5.2}$$

$$x_3' = \frac{1}{\underline{W}} \left[\frac{x_2}{4} (w_1 + w_2) + x_3 w_2 \right] y_2 \tag{5.3}$$

$$\begin{aligned} y_1' = \frac{1}{\underline{W}} \Bigg[& \left(x_1 y_1 + x_1 y_2 + \frac{x_2 y_1}{2} + \frac{x_2 y_2}{4} \right) v_1 + \frac{x_2 y_2}{4} v_2 \\ & + \left(x_1 y_1 + \frac{x_1 y_2}{2} + \frac{3}{4} x_2 y_1 + \frac{1}{4} x_2 y_2 + \frac{x_3 y_1}{2} \right) \theta u_1 \Bigg] \end{aligned} \tag{5.4}$$

$$\begin{aligned} y_2' = \frac{1}{\underline{W}} \Bigg[& \left(\frac{x_2 y_1}{2} + \frac{x_2 y_2}{4} + x_3 y_1 \right) v_1 + \left(x_3 + \frac{x_2}{4} \right) y_2 v_2 + \left(x_1 + \frac{x_2}{2} \right) \frac{y_2}{2} \theta u_1 \\ & + \left(x_3 + \frac{x_2}{2} \right) \frac{y_1}{2} \theta u_1 + \left(x_3 + \frac{x_2}{2} \right) y_2 \theta u_2 \Bigg] \end{aligned} \tag{5.5}$$

where $u_1 + v_1 + w_1 = 1$, $u_2 + v_2 + w_2 = 1$ and the normalizing factor $\underline{W}$ is given by

$$\begin{aligned} \underline{W} = {} & (x_1 + x_2 + x_3)(y_1 + y_2) \\ & + (\theta - 1) \left[u_1 \left(x_1 y_1 + x_1 y_1 + x_2 y_1 + \frac{x_2 y_2}{2} + x_3 y_1 \right) + u_2 \left(x_3 y_2 + \frac{x_2 y_2}{2} \right) \right] \end{aligned} \tag{5.6}$$

Or, in vector form, the equations of motion may be summarized

$$\mathbf{X}' = \mathbf{F}(\mathbf{X}, \mathbf{U}_1, \mathbf{U}_1), \tag{5.7}$$

where $\mathbf{X} = (x_1, x_2, x_3, y_1, y_2)$, $\mathbf{U}_1 = (u_1, v_1, w_1)$, $\mathbf{U}_2 = (u_2, v_2, w_2)$, and where the map $\mathbf{F}: \mathbb{R}_+^5 \to \mathbb{R}_+^5$ is given by Eqs. (5.1)–(5.6).

5.2. Equations (5.1)–(5.5) are clearly too formidable to solve analytically; however, we can ask a simpler question. Suppose the population is initially monomorphic for the *a* allele, so that from Eqs. (5.3) and (5.5), the equations for this monomorphic equilibrium are

$$\bar{x}_3 = \frac{w_2}{1 - (1 - \theta) u_2}, \tag{5.8}$$

$$\bar{y}_2 = \frac{v_2 + \theta u_2}{1 - (1 - \theta) u_2} = 1 - \bar{x}_3, \tag{5.9}$$

$$\underline{\overline{W}}(x_3, y_2) = \frac{(u_2 + v_2)(\theta u_2 + v_2)}{1 - (1 - \theta) u_2}. \tag{5.10}$$

We can inquire whether this equilibrium is stable against a mutation corresponding to a change in brood-rearing strategy. Since the A allele will initially appear at very low frequencies, we need only check the local stability of $(\bar{x}_3, \bar{y}_2)$. To do this we first compute the Jacobian of $\mathbf{F}$ at $(\bar{x}_3, \bar{y}_2)$: $D\mathbf{F}(\bar{\mathbf{X}})$. A straightforward calculation shows that the eigenvalues of $D\mathbf{F}(\bar{X})$ coincide with those of the reduced matrix

$$\mathbf{J} \triangleq \begin{pmatrix} \dfrac{\partial x_2'}{\partial x_2} & \dfrac{\partial x_2'}{\partial y_1} \\ \dfrac{\partial y_1'}{\partial x_2} & \dfrac{\partial y_1'}{\partial y_1} \end{pmatrix} = \begin{pmatrix} \dfrac{w_1 + w_2}{4w_2} & \dfrac{w_1}{v_2 + \theta u_2} \\ \dfrac{v_1 + v_2 + u_1}{4w_2} & \dfrac{\theta u_1}{2(v_2 + \theta u_2)} \end{pmatrix}. \tag{5.11}$$

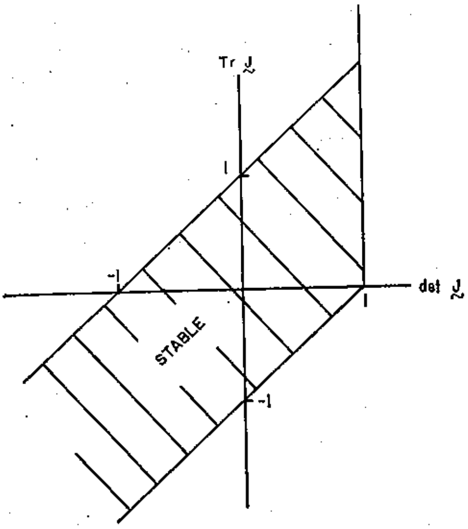

FIG. 10. Stability region for the matrix J.

Since the entries in $\mathbf{J}$ are all positive, the Frobenius theorem (Pease, 1965) ensures that the eigenvalue of largest modulus is real and positive. The condition for the eigenvalues of $\mathbf{J}$ to lie inside the unit circle is (Marden, 1966); cf. Fig. 10

$$\begin{aligned} \det \mathbf{J} &< 1 \\ \det \mathbf{J} - 1 < \operatorname{Trace} \mathbf{J} &< \det \mathbf{J} + 1 \end{aligned} \tag{5.12}$$

or, in terms of the system parameters,

$$\begin{aligned} 2w_1(v_1 + v_2 + \theta u_1) &< (3w_2 - w_1)(2v_2 + 2\theta u_2 - \theta u_1) \\ &> (w_1 + w_2)\,\theta u_1 - 8w_2(v_2 + \theta u_2). \end{aligned} \tag{5.13}$$

If we assume that both phenotypes allocate the same fraction of effort to females, $w_1 = w_2 = w$, the stability condition reduces to

$$(2\theta - 1)(u_1 - u_2) < 0. \tag{5.14}$$

From this equation we see that if $u_1 > u_2$, that is, the mutant allocates more energy to her own sons, then the resident (a) allele is stable providing $\theta < \frac{1}{2}$. This corresponds to a value of $\gamma > 2$, or, recalling that we have normalized $\beta \equiv 1$, the stability condition is

$$\gamma/\beta > 2. \tag{5.15}$$

Thus, we conclude that a mutation $a \to A$ favoring an increased allocation of effort to the workers' own sons will be selected for at low frequencies only if $\gamma/\beta < 2$, which is just the conclusion we reached in Eq. (5.10) on the basis of inclusive fitness arguments.

Next, we examine the sex ratio which is stable against mutational perturbation. From Eq. (5.14) we see that when $\theta < \frac{1}{2}$ (i.e., $\gamma/\beta > 2$), a mutant A such that $u_1 < u_2$ is favored. That is, a subpopulation of workers who allocate less effort to their own sons can be established. The only way the resident a allele can be stable against this strategy is to adhere to a strategy of $\mathbf{U}_1 = (w_1, v_1, 0) = (w, 1 - w, 0)$. When $u_1 \equiv 0$ the stability condition (5.13) reduces to

$$w_1(2 - w_1 - w_2) \leqslant (1 - w_2)(3w_2 - w_1)$$

or

$$P(w_1, w_2) = w_1^2 + w_1(2w_2 - 3) + 3w_2(1 - w_2) \geqslant 0. \tag{5.16}$$

The equation $P(w_1, w_2) = 0$ divides the unit square $0 \leqslant w_1, w_2 \leqslant 1$ into four regions as shown in Fig. 11 corresponding to values of resource allocation ratios $w_1 : w_2$ where one or the other allele is favored at low frequencies. We see that if the resident allele maintains a allocation of $w_2 = \frac{3}{4}$, then it is immune from invasion by w_1. Any deviation from this strategy, however, admits a region of w_1 wherein A is favored at low frequencies. Thus, we conclude that the sex ratio $\sigma = M/F = 1/3$ is indeed a competitive equilibrium for the a-type workers and is in agreement with the macroscopic arguments presented earlier.

It is apparent from Fig. 11 that when $w_2 \neq \frac{3}{4}$, there may only be a restricted range of values of w, which will allow A to invade. This result is unexpected and is different from the results of genetic models for the evolution of modifiers of the sex ratio in diploid organisms (Eshel, 1972).

In panmictic diploid organisms, if the population sex ratio deviates from the stable equilibrium point, there is a selective advantage for any modifier mutants which change the sex ratio in the opposite direction *without limit*.

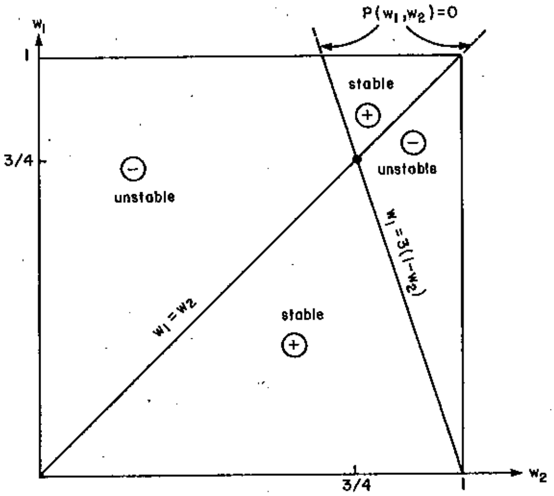

FIG. 11. The zeros of $P(w_1, w_2) = w^2 + w_1(2w_2 - 3) + 3w_2(1 - w_2)$ are plotted on the (w_1, w_2) strategy square. The stable root is located at $w_1 = w_3 = \frac{3}{4}$, corresponding to a stable sex ratio of $\sigma = \frac{1}{3}$ when $\theta < \frac{1}{2}$, $u = 0$, $v = 1 - w$.

It is easy to show by an extreme example how the haplodiploid genetic system modifies the selective advantage of sex-ratio modifiers. If $w_2 > \frac{3}{4}$ to a small extent, then mutant workers with $w_1 = 0$ will cause the queen to produce only males. But the mutant gene will not be transmitted to the next generation, because these males will have mutant workers which will cause the queen to produce only males, which will not have the mutant gene, since they develop from unfertilized eggs.

The same argument can be applied, in a weaker sense, to cases of $w_2 < \frac{3}{4}$ and the advantage of mutants which produce an excess of females.

It is apparent from Fig. 11 that the restriction on the advantage of mutants producing an excess of females extends only over the range $6 < w_2 < \frac{3}{4}$.

The optimal allocation $w = \frac{3}{4}$, $v = \frac{1}{4}$, $u = 0$ is not always stable against mutants which change u and w simultaneously, despite the fact that $u = 0$ is stable for any value of w, and $w = \frac{3}{4}$ is stable when $u = 0$.

Inserting the optimal allocation $(w_2, v_2, u_2) = (\frac{3}{4}, \frac{1}{4}, 0)$ into (5.16), and setting $v_1 = 1 - w_1 - u_1$ gives as the condition for stability

$$u_1[(2 - \theta)\, w_1 - \tfrac{9}{4}\theta] > -2(w_1 - \tfrac{3}{4})^2. \tag{5.17}$$

In addition, there is always the constraint

$$u_1 \leqslant 1 - w_1 .$$

Thus, at the point $w_2 = \frac{3}{4}$, $u_2 = 0$, stability against invasion by a mutant which changes both u_1 and w_1 is maintained under the following conditions:

A. When the multiplier of u_1 in (5.17) is positive, i.e., if $w_1 > 9\theta/4(2-\theta)$, which holds for $w_1 > \frac{3}{4}$ when θ is at its highest value, $\theta = \frac{1}{2}$, and holds for smaller w_1 when θ is smaller.

B. If $w_1 < 9\theta/(4(2-\theta))$, then a sufficiently small u_1 is always stable.

Instability may arise for large enough u_1.

Substituting $u_1 = 1 - w_1$ in (5.17) gives

$$\theta w_1{}^2 + w_1[\tfrac{5}{4}\theta - 1] - \tfrac{9}{4}\theta + \tfrac{9}{8} > 0. \tag{5.18}$$

For $\theta = \frac{1}{2}$ and for θ close to $\frac{1}{2}$ there is a region of instability of u_1, w_1 which can invade.

The critical value of θ which still allows such instability is given by the solution to the discriminant equation of (5.18), i.e., the solution to the quadratic equation

$$\frac{169}{16}\theta^2 - 7\theta + 1 = 0,$$

the roots of which are

$$\theta_{11} = \frac{89}{169}, \frac{20}{169}.$$

When $\theta < 2\theta/169$, no mutant with different u_1, w_1 can invade the optimal allocation of $w_2 = \frac{3}{4}$, $u_2 = 0$, $v_2 = \frac{1}{4}$.

With larger θ, a mutant may invade the "optimal" population over a range of u_1 and w_1. The population will, however, return to $w = \frac{3}{4}$, $v = \frac{1}{4}$, because $u = 0$ will always increase its frequency at any w, and when $u = 0$, $w = \frac{3}{4}$ will dominate.

Nest let us examine the case where $\theta > \frac{1}{2}$. Selection favors the tendency of the workers to prefer their own sons over the queen's sons. With a complete monopoly of the workers on the production of males $(w, v, u) = (w_2, 0, 1 - w_2)$ the condition for stability against invasion by an alternative allocation $(w_1, 0, 1 - w_1)$ now becomes

$$2w_1(1 - w_1) > (3w_2 - w_1)(1 - w_1 - 2w_2), \tag{5.19}$$

from which we get the quadratic

$$w_1{}^2 + w_1(5w_2 - 3) + 3w_2 - 6w_2{}^2 < 0. \tag{5.20}$$

The roots of (24) are

$$\begin{aligned} w_1 &= w_2, \\ w_1 &= 3 - 6w_2. \end{aligned}$$

$w_2 = \frac{3}{7}$ is the stable point at which invasion by $w_1 \neq w_2$ is not possible.

The stable allocation is $(w, v, u) = (\frac{3}{7}, 0, \frac{4}{7})$ and the stable sex ratio $m/F = 4\theta/3$.

As in the case of $\theta < \frac{1}{2}$, if w_2 is slightly different from the stable value of $\frac{3}{7}$, i.e., within the range $\frac{1}{3} < w_2 < \frac{1}{2}$, there is a selective advantage for mutants which change the sex ratio in the opposite direction, up to some limit. Outside this range, the selective advantage extends to the extreme mutants in the opposite direction.

The optimal allocation $(w, v, u) = (\frac{3}{7}, 0, \frac{4}{7})$ is not always stable against mutants which change both w and v at the same time. Substituting the optimal allocation in (5.16) and setting $u_1 = 1 - v_1 - w_1$, we get as the condition for stability

$$v_1 \left[\frac{9}{7} - w_1 \left(\frac{2}{\theta} - 1\right)\right] > -\left(w_1 - \frac{3}{7}\right)^2 \qquad (5.21)$$

with the additional constraint $v_1 \leqslant 1 - w_1$.

Inequality (5.21) is always satisfied when the multiplier of u_1 is positive, i.e., if $w_1 < \frac{9}{7}((2/\theta) - 1)$, which always holds at $\theta > \frac{7}{8}$. When $w_1 > \frac{9}{7}((2/\theta) - 1)$, the inequality will not hold for large v_1, so that there are mutants which can invade if u_1 and w_1 are changed at the same time. But the optimal policy of $(w, v, u) = (\frac{3}{7}, 0, \frac{4}{7})$ will tend to dominate, because $v = 0$ will always invade at any level of w, and $w = \frac{3}{7}$ will invade when $v = 0$. By substituting in (5.21), $v_1 = 1 - w_1$, we finally find that a double mutant cannot invade if $\theta > \frac{5}{8}$.

5.3. The results of the genetic analysis agree with the optimization model in predicting the critical level of $\theta = \frac{1}{2}$, i.e., $\gamma/\beta \leqslant 2$ for a changeover from production of queen's males to worker's males. The sex ratios of $M/F = \frac{1}{3}$ when $\theta < \frac{1}{2}$ are also as predicted by the optimization model when $\alpha = \beta = 1$, and with $r_{wm} = \frac{1}{2}$, since we had assumed that a worker is rearing her own sons.

It should be noted, however, that the genetic model is different in some details from the optimization model and also gives some additional information. Of special interest is the finding that when the population deviates from the stable sex ratio, there is selective advantage for mutants which change the sex ratio in the opposite direction, up to some limit. This limit is more pronounced when $\theta < \frac{1}{2}$ and the queen is producing the males and, in that case, the limit is much stronger when there is selection for mutants which produce an excess of males.

Another interesting finding is that the allocation which is stable against deviations in each one of the factors separately is not always stable against mutant genes which change both factors at the same time. Each such double-factor mutants will be displaced by other mutants which are closer to the stable point only in u or v, and when u or v are at the stable value, a gene with w at the stable value will displace all other genes, so that eventually the stable point will be restored, and these are the values of the variables expected under natural selection.

The empirical data available so far do not include cases where the workers produce *all* the males.

Some production of males by laying workers is widespread although the genetic basis for this phenomenon is still unknown. Our genetic model in its present form does not allow polymorphism in this locus.

Modifications allowing the possibility of polymorphism are: (1) some degree of heterozygote advantage; (2) frequency of dependence of θ such that it decreases when laying workers become more common in the colony. Both modifications are probably important. In an extreme case, the frequency dependence of θ will be the result of an excess of workers over the capacity of the queen to lay eggs. Such an excess capacity was indicated as a possible factor which may account for the production of queen's males and workers' males at the same time, according to the optimization model.

In a recent paper, Charnov (1976) analyzed the genetics of the sex ratio in Hymenoptera using a somewhat different approach. He considers the fraction of resources spent on workers' males out of the resources spent on all males as given. He finds the same stable points as we do, i.e., $w = \frac{3}{4}$ when no worker's males are produced, and $w = \frac{3}{7}$ when only workers' males are produced (he assumed $\theta = 1$). His model shows, however, that if the population deviates from the stable point, mutants which deviate in the opposite direction without any limit are selected for.

His analysis of the model is not presented in sufficient detail to enable us to find the reasons for this discrepancy with our model.

6. DISCUSSION

In eusocial haplodiploids the genetic interests of the mother queen differs from that of her worker daughters. Therefore, there is "disagreement" over colony "policy" on two points: (1) the laying of male (haploid) eggs, measured by the male ratio parameter $p = M/(m + m)$, and (2) the proportion of colony resources invested in rearing (diploid) females measured by the sex ratio $\sigma = (M + m)/F$. Trivers and Hare (1976) used this conflict of interest to test which party controlled the colony's investment ratio in a number of species, both social and asocial. Their data for ants suggested a 3:1 investment in favor of females, indicating that workers do indeed control the colony investment. Although there is some disagreement concerning their data for other species (cf. Alexander and Sherman, 1977),[3] this has been viewed by many as confirming

---

[3] Alexander and Sherman argue that "local mate competition" (Hamilton, 1967) can also yield female-biased investment ratios, although no particular ratio is predicted.

Hamilton's inclusive fitness theory for the evolution of altruism and eusociality in social insects.

We have attempted to construct a mathematical model of the worker–queen conflict situation for the case of an equilibrium community. Our definition of inclusive fitness given in Section 2 has the form:

$$\begin{bmatrix}\text{Inclusive fitness}\\ \text{of agent } l\end{bmatrix} = \sum_{k=1}^{\text{all relatives}} \begin{bmatrix}\text{Genetic relatedness}\\ \text{of relative } k \text{ to } l\end{bmatrix} \begin{bmatrix}\text{Expected number}\\ \text{of relative}\\ \text{of type } k\end{bmatrix} \begin{bmatrix}\text{Expected}\\ \text{reproductive}\\ \text{success of}\\ \text{relative } k\end{bmatrix}$$

A central feature of this formula is the expression for reproductive success, i.e., the expected number of genes in generation t identical to a particular gene in generation 0. This expression shows how inclusive fitness of each individual depends on the sex ratio and male ratio of the community as a whole.

By computing the optimum inclusive fitness of both queen and workers, subject to the constraint of finite resources, we obtain the ratio of investment preferred by each party. These are summarized in Table I and correspond in most cases to those calculated by Trivers and Hare by other means not clear to us. These calculations assume that either the queen or the workers control the situation, and so while there is "disagreement," there is not "conflict." In this case a "mixed" male brood is never preferred by either party (i.e., $p = 0$ or 1).[4]

In order to model the true conflict situation wherein each party has some control over egg-laying and/or investment we viewed the model as a continuous game and sought Nash equilibria (or, in Maynard Smith's terminology, "evolutionarily stable strategies"). The conflict situation is quite complicated and we investigated only a few of the very simplest cases. However, we trust that the conceptual framework we developed can be generalized to model conflict situations in other ecological contexts.

Finally, we attempted to relate the inclusive fitness optimization arguments to more conventional population genetic models. We constructed a grossly simplified model wherein the workers' investment policy was controlled by one locus with two alleles. Even this model proved intractable, but we were able to show that the conditions for local stability corresponded to those deduced from inclusive fitness optimization. This is encouraging, but not convincing, evidence that inclusive fitness reasoning may be a reliable way of inferring evolutionary trends.

---

[4] If some randomness were introduced into the model parameters than, as is characteristic of stochastic programming models, one could expect intermediate solutions, $0 < p < 1$. We shall treat the stochastic problem in a future publication.

ACKNOWLEDGMENTS

We would like to thank Ed Wilson and Dick Lewontin for the hospitality we found in their laboratories and their generosity with their time during our stay at Harvard, where this paper was written. Many other colleagues gave us invaluable suggestions and engaged us in stimulating and productive conversations which aided the paper immeasureably. In this connection, we would especially like to thank Russ Lande, John Seger, Frank Benford, Bob Trivers, Carla Lipow, Sol Rocklin, and Jon Roughgarden.

One of us (G.F.O.) would like to acknowledge the National Science Foundation (BMS-21240) and the John Simon Guggenheim Foundation for their financial support during this period.

REFERENCES

ALEXANDER, R., AND SHERMAN, P. 1977. Local mate competition and parental investment patterns in social insects, *Science* **196**, 494–500.

AUSLANDER, D., GUCKENHEIMER, J., AND OSTER, G. 1976. Chaotic evolutionarily stable strategies, *Theor. Popul. Biol.*, to appear.

BENFORD, F. 1976. Fisher's theory of the sex ratio applied to the social Hymenoptera, *J. Theor. Biol.*, to appear.

BODMER, W., AND EDWARDS, A. 1960. Natural selection and the sex ratio, *Ann. Human Genet.* **24**, 239–244.

CAVALLI-SFORZA, L., AND FELDMAN, M. 1976. Evolution of continuous variation: Direct approach through joint distribution of genotypes and phenotypes, *Proc. Nat. Acad. Sci. USA* **73**, 1689–1692.

CHARNOV, E. L. 1976. Sex ratio selection in eusocial Hymenoptera, to appear.

COCKERHAM, C. C. 1971. Higher order probability functions of identity of alleles by descent, *Genetics* **69**, 235–246.

COHEN, D., AND ESHEL, I. 1976. On the founder effect and the evolution of altruistic traits, *Theor. Popul. Biol.* **10**, 276–302.

CROZIER, R. 1970. Coefficients of relationship and the identity of genes by descent in the Hymenoptera, *Amer. Natur.* **104**, 216–217.

ESHEL, I. 1972. On the neighbor effect and the evolution of altruistic traits, *Theor. Popul. Biol.* **3**, 258–277.

FISHER, R. A. 1958. "The Genetical Theory of Natural Selection," 2nd revised ed., Dover, New York.

HAMILTON, W. D. 1964. The genetical theory of social behavior, I, II, *J. Theor. Biol.* 1–16, 17–52.

HAMILTON, W. D. 1967. Extraordinary sex ratios, *Science*, **156**, 477–488.

HAMILTON, W. D. 1972. Altruism and related phenomena, mainly in the social insects, *Ann. Rev. Ecol. Syste.* **3**, 193–232.

KING, M. C., AND WILSON, A. 1975. Evolution at two levels in humans and chimpanzees, *Science* **188**, 107–116.

LANDE, R. 1976. The maintenance of genetic variability by mutation in a polygenetic character with linked loci, *Genet. Res.* **26**, 221–235.

LIPOW, C. 1977. Reproductive success in Hymenoptera, to appear.

LI, C. C. 1955. "Population Genetics," Univ. of Chicago Press, Chicago.

MARDEN, M. 1966. "Geometry of Polynomials," American Math. Soc., Providence, R.I.

OSTER, G., IPAKTCHI, A., AND ROCKLIN, S. 1976. Phenotype structure and bifurcation behavior of population models, *Theor. Popul. Biol.*, **10**, 365–382.

OSTER, G., AND WILSON, E. O. 1978. "Caste and the Ecology in the Social Insects," Princeton Univ. Press, Princeton, N.J..

PEASE, M. 1965. "Methods of Matrix Algebra," Academic Press, New York.

RÖSSLER, O. 1976. Chaotic behavior in simple reaction systems, *Z. Naturforsch*, **31a**, 259–264.

ROCKLIN, S., AND OSTER, G. 1976. Competition between phenotypes, *J. Math. Biol.* **3**, 225–761.

ROUGHGARDEN, J. 1976. Resource partitioning among competing species—a coevolutionary approach, *Theor. Popul. Biol.* **9**, 388–424.

ROUGHGARDEN, J. 1978. "Theory of Population Genetics and Evolutionary Ecology," Macmillan, New York.

SEGER, J. 1976. Adaptive responses to homozygosity.

SHASHAHANI, S. 1976. A new mathematical framework for the study of linkage and selection, to appear.

SLATKIN, M. 1976. On the equilibrium of fitnesses by natural selection, to appear.

SLATKIN, M., AND LANDE, R. 1976. Niche width in a fluctuating environment-density independent model, *Amer. Natur.* **110**, 31–55.

SPIETH, P. 1974. Theoretical considerations of unequal sex ratios, *Amer. Natur.* **108**, 837–849.

TRIVERS, R., AND HARE, H. 1976. Haplodiploidy and the evolution of the social insects, *Science* **191**, 249–263.

WILSON, D. S. 1975. A theory of group selection, *Proc. Nat. Acad. Sci. USA* **72**, 143–146.

WILSON, E. O. 1963. Social modification related to rareness in ant species, *Evolution* **17**(2), 249–253.

Printed by the St Catherine Press Ltd., Tempelhof 37, Bruges, Belgium.