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SEX RATIO IN THE SOCIAL HYMENOPTERA: A POPULATION-GENETICS STUDY OF LONG-TERM EVOLUTION

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Abstract.—We analyze a two-locus population-genetics model for the queen-workers conflict over the sex ratio in social Hymenoptera. We assume that the total number of reproductives and the proportion of females among them are both functions of a queen's trait α and of a workers' trait β, which are controlled by one locus each. We determine the conditions for a pair $\{\alpha,\beta\}$ to be an evolutionarily stable state (ESS), that is, to be such that no combination of mutations at the two loci is able to invade a population fixed for the pair of genes determining $\{\alpha,\beta\}$. Our results, in some respects, validate the alternative game-theoretic approach, based on maximization of a given pair of queen's and workers' inclusive fitnesses, while showing the limitations of this approach in some other respects. If all mutations are assumed to have a small effect and if linkage between the two loci is not too tight, we show that, indeed, for any ESS $\{\alpha,\beta\}$, α and β maximize the queen's and the workers' payment functions, H and G, respectively, but the ESS predicted by H and G does not always coincide with the ESS predicted by the queen's and workers' inclusive fitness functions. Very strong linkage, however, may destabilize some of the maxima of H and G but preserve as ESSs those among them that maximize a joint, queen-workers payment function, T. We show that ESSs can be of two kinds: (1) isolated points, in which the proportion of females is intermediate between one-half and three-fourths and the colony productivity is less than maximal, because of conflict between queen and workers; (2) a continuum of points, with a corresponding spread of female proportions, usually within $[\frac{1}{2},\frac{3}{4}]$ but also, rarely, beyond this interval. At these points there is full agreement between the two parties, and the colony productivity is accordingly maximal.

The problem of queen-worker conflict over the production of sexual offspring in colonies of Hymenoptera was first raised and discussed by Trivers and Hare (1976). The conflict concerns two aspects: conflict over which party will produce male eggs, and conflict over the ratio of investment in male and reproductive female offspring. As maintained by Trivers and Hare, the first conflict is, in many cases, quite likely to be settled with full queen's dominance, a result that at the time appeared to stand in plausible agreement with empirical data, especially for ants. For recent reviews of contradicting cases, however, see Owen and Plowright (1982) and Bourke (1988).

Assuming that all male eggs are laid by the queen and considering a single-queen nest with single insemination, Trivers and Hare argued further that the workers would maximize their inclusive fitness by investing three times as much

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effort in rearing reproductive females as in rearing male offspring, because, as a result of haplodiploidy, they are three times as related to their sisters as to their brothers. The queen, by contrast, being equally related to male and female offspring, would maximize her own inclusive fitness by equal investment in both. It has been maintained, though, that this conflict is likely to be won by the workers, who can allocate the resources in rearing their preferred sex ratio. Data for ant colonies of various species, presented by Trivers and Hare, were supposed to support their prediction of a 1:3 investment ratio, although there has been some controversy over the interpretation of the data (Alexander and Sherman 1977; MacNair 1978; Forsyth 1981; Taylor 1981). For recent reviews of investment ratios in ants see Nonacs (1986) and Boomsma (1989).

On the theoretical side, the argument of Trivers and Hare has since been questioned on two different levels: one concerns the general validity of the specific measurement of inclusive fitness in this particular case and the assumption of its individual maximization within the conflict; the other concerns the very nature of the conflict, that is, Trivers and Hare's conclusion of full workers' dominance.

Trivers and Hare aimed to combine Hamilton's concept of inclusive fitness (Hamilton 1964, 1970, 1972) with Fisher's approach to the evolution of sex ratio in diploid populations (Fisher 1958, pp. 158–160). In Fisher's argument fitness is determined by the expected number of genes passed on to the grandoffspring's generation. But the validity of this assumption depends heavily on the fact that in diploid organisms each offspring has exactly one male and one female parent. This is obviously not true for a haplodiploid population, because in such populations only females have a mother and a father, while males have only a mother.

The concept of inclusive fitness, as used by Trivers and Hare, instead tacitly takes into consideration the number of genes that a male or a female reproductive is expected to pass on to generations far in the future. These expectations, called "reproductive values," have been extensively studied by Oster et al. (1977) and by later authors (e.g., Benford 1978). The problem of measuring inclusive fitness in sexually asymmetric situations, with the associated notions of reproductive value and relatedness, has been thoroughly treated in general terms by Taylor (1988). All these analyses justify the assumption of Trivers and Hare, as long as mating is random and selection pressure on the sex ratio is weak. With these assumptions, the argument of Trivers and Hare has been restated by Charnov (1978) in terms of an evolutionarily stable state (ESS), in the terminology of Maynard Smith and Price (1973). According to this approach it is assumed that both the queen and the workers seek to increase their own inclusive fitnesses, $R_{Q\to F} f/F + R_{Q\to M} m/M$ and $R_{W\to F} f/F + R_{W\to M} m/M$, respectively, where m and f are the numbers of males and female reproductives in a particular colony, M and F are their relative frequencies in the population, $R_{Q\to F}$, $R_{Q\to M}$, $R_{W\to F}$, and $R_{W\to M}$ are appropriate coefficients of relatedness of queen (Q) and workers (W) to female (F) and male (M) reproductives, respectively. In the general case these values are represented by the "regression" measures of relatedness (Hamilton 1970; Michod and Hamilton 1980; Uyenoyama and Bengtsson 1981; Uyenoyama and Feldman 1981; Taylor 1988). However, with random mating and weak selection these coefficients converge to the usual "consanguinity" measures of relat-

edness (Crozier 1970), $R_{Q\to F} = R_{Q\to M} = 1/2$, $R_{W\to F} = 3/4$, and $R_{W\to M} = 1/4$, and the inclusive fitnesses for workers and queen ($\hat{G}$ and $\hat{H}$, respectively) reduce to

$$\hat{G} = 3f/4F + m/4M \tag{1}$$

and

$$\hat{H} = f/2F + m/2M. \tag{2}$$

A rather different approach was followed by Uyenoyama and Bengtsson (1981), who employed an exact, one-locus, two-allele model to investigate the evolution of the sex ratio in haplodiploids. They analyzed several models involving brood control by various family members, including mothers and sisters (but not multiple control by different family members, with a possible conflict about the sex ratio). They showed that, under certain conditions, inclusive fitness correctly predicts the direction of evolution of the sex ratio, irrespective of the strength of selection, provided that the regression coefficients of relatedness are used. A genetic approach was also followed by Taylor (1981) in the analysis of queen control of the sex ratio in cases in which colonies that are left without a queen rear only males, from eggs laid by one of the workers.

More substantial is the disagreement about Trivers and Hare's conclusion that the workers must have full control over the sex ratio. As it has been argued by Oster et al. (1977) (see also Oster and Wilson 1978) and, more clearly, by MacNair (1978), Bulmer and Taylor (1981), and Bulmer (1981, 1983), the queen must, indeed, have some control over the sex ratio by just deciding the number of fertilized and unfertilized eggs that are laid. The workers, on their part, can destroy a surplus of male eggs and invest the resources in female eggs, as suggested by Trivers and Hare, but this may entail a substantial waste of resources (Oster et al. 1977), especially if the queen, on her part, limits the number of fertilized eggs laid (Bulmer 1981; Bulmer and Taylor 1981). The workers might also decide how many fertilized eggs will be reared as workers and how many will be reared as reproductive females, a decision that can take into consideration not only the welfare of the nest (say, the optimal number of workers) but also their desired sex ratio (Bulmer and Taylor 1981). Workers' manipulation can also precede the queen's decision in cases in which different cell sizes are required for male and female reproductives (e.g., in beehives). In this case, as is assumed in one of the examples studied in this article, it is the queen that can further manipulate the nest sex ratio by laying her eggs in inappropriate cells. In all cases, however, queen-worker disagreement may result in an intermediate sex ratio with some more or less substantial cost to the general productivity of the nest. Thus, the nature of the conflict may be interpreted in terms of a queen-worker game in which each party seeks to maximize a different payment function. Conclusive empirical evidence on the relative powers of the two parties is lacking. It might be observed, however, that the latest statistical analysis of data for monogynous ants' colonies of several species (Boomsma 1989) indicates an average males-to-females investment ratio of about 1:2. This result might be explained as a compromise between the queen and the workers, but other factors, such as multiple inseminations or egg laying by the workers, could also be invoked.

Remaining to be settled, however, are all the questions, mentioned above, concerning the form and, perhaps, the very existence of the relevant payment functions to be maximized by natural selection. While inclusive fitness may be a good candidate, its exact form is not that clear in the context of a family conflict, in which those genes that affect the behavior of one party are also carried and passed on to the next generation by members of the other (cf. Feldman and Eshel 1982; Eshel and Feldman 1991).

In order to resolve these difficulties, we find it worthwhile to analyze a general, exact, two-locus genetic model, in which alleles at one locus determine the queen's behavior (phenotype) while alleles at the other locus determine the workers' behavior (phenotype) concerning the sex ratio. Such an approach was first suggested by Pamilo (1982), who used a computer simulation to check the dynamics of change in genotype frequencies under certain specific assumptions. For other two-locus models of sex determination see Karlin and Lessard (1986). However, we are not studying specific genetic equilibria created by the dynamics of changes in the frequencies of the specific genotypes that are present at a given time in the population, as it is done in the genetic models mentioned above. We try to identify, instead, ESSs for the genetic system of interest, namely, phenotypic configurations that are *stable in the long term*, being determined by genetic equilibria that cannot be invaded by any possible mutation at either of the two loci. These states are equivalent to the "unbeatable strategies" of Hamilton (1967; see also Charlesworth 1978; Eshel and Feldman 1982*a*, 1982*b*, 1984; Karlin and Lessard 1983; Lessard 1984; Eshel 1985; Eshel and Weinshall 1987; Weinshall and Eshel 1987). Thus, in agreement with Hamilton's approach and in contrast to the original game-theoretic approach to the ESS, introduced by Maynard Smith and Price (1973; see also Maynard Smith 1974, 1982), we do not need to specify a particular game structure, nor do we have to postulate that any payment function is individually maximized by natural selection. Indeed, individual maximization of an intuitively well-defined function (e.g., the inclusive fitness) may be a desirable result of the analysis. However, with the genetic approach, criteria for an ESS may depend, in some cases, on the specific genetic structure being assumed, for example, as in our case, on the rate of recombination between the workers' locus and the queen's locus.

We might anticipate, assuming all mutations to have only a small effect on the phenotype, that the criteria for an ESS emerging from our genetic analysis are closely related and in several cases are identical to the corresponding game-theoretic criteria for asymmetric ESSs (see Maynard Smith and Parker 1976; Selten 1980) based on maximization of the inclusive fitnesses of the separate parties, as originally defined by Trivers and Hare (1976). However, this remains true only as long as the maximal quantitative effect of a single mutation is small, relative to the rate of recombination. If linkage between the queen's and workers' loci is tight or mutations of large effect are likely, some of the ESSs of the game may be unstable within the framework of the genetic structure.

Since we are mainly interested in the general method, we confine our model to the biologically simplest situation of a monogynous colony in which workers do not lay male eggs and the queen is inseminated by only one male taken at random

from the population. We hope that the two-locus, external stability method suggested here can be extended to biologically more specific and complex situations.

GENERAL CONDITIONS FOR AN ESS

The Genetic Model

We assume an infinitely large haplodiploid population, divided into social nests, each with a single queen inseminated by a single male. We assume random mating between male and female reproductives emerging from all nests of the previous generation. The sex ratio among reproductive offspring at each nest is determined by both the queen and the workers (which are assumed to be her daughters). Namely, the proportion, F, of females in the reproductive brood is a continuously differentiable function of a parameter α, determined by the genes of the mother at one locus (say, A), and of a parameter β, determined by the distribution of genes carried by the workers at another locus (say, B), that is, $F = F(\alpha,\beta)$. More specifically, we assume that each worker has her own parameter β_i, determined by her own genes, and that the nest parameter β is the average of all individual workers' parameters. Finally, we allow for any rate of recombination, r, such that $0 < r \leq \frac{1}{2}$, between the queen's locus A and the workers' locus B.

With these assumptions, if worker-queen conflict does not affect the success of the entire nest, measured as the number of reproductive offspring, then it can be shown that any mutation of the A locus that initially renders the population sex ratio closer to 1:1, as well as any mutation of the B locus that renders the population sex ratio closer to 1:3, would enter the population (e.g., see Uyenoyama and Bengtsson 1981; Eshel and Feldman 1982*a*, 1982*b*). In this case we see that either one party would get its preferred sex ratio ($F = \frac{3}{4}$ in the case of workers, $F = \frac{1}{2}$ in the case of the queen) or each party would push to its extreme, with the sex ratio being determined by the biological restrictions of the conflict. As it has been argued in previous works, however (Oster et al. 1977; Bulmer 1981; Bulmer and Taylor 1981; see also examples under Normal Representation of the Sex-Ratio Conflict, below), it is most likely that the reproductive success of the nest will be affected by the queen's and the workers' conflicting behavior. This is the case when workers destroy a surplus of male eggs (Trivers and Hare 1976), if workers adjust the proportion of nonreproductive sisters (i.e., workers) not only to the requirement of the nest but also to their preferred sex ratio (Bulmer and Taylor 1981; see also the sections Normal Representation of the Sex-Ratio Conflict and Regular Representations, below), or if the workers disobey queen's pheromones by building more queen cells than the queen would like, and if the queen, in her turn, does not accept the sex ratio dictated by the workers (see Normal Representation). We therefore assume that the relative reproductive success of the nest is also a continuously differentiable function, φ, where $\varphi = \varphi(\alpha,\beta)$, of the queen's and workers' behavior. The numbers of male and female reproductives emerging from a nest of $\{\alpha,\beta\}$ type are, therefore, proportional to $\varphi(\alpha,\beta)[1 - F(\alpha,\beta)]$ and $\varphi(\alpha,\beta)F(\alpha,\beta)$, respectively. We are interested in values α° and β° of the queen's and workers' phenotype, respectively, such that, if they are fixed in the population, no mutant allele or combination of alleles affecting either or both of these traits will successfully enter the population.

Stability of Fixation States

Let the population be fixed on the alleles A and B in the queen's locus and the workers' locus, respectively, with corresponding parameters α and β. Assume an arbitrary mutation A' at the A locus determining the queen's parameter α' as heterozygote and an arbitrary mutation B' at the workers' locus determining the workers' parameter β' as heterozygote.

Denote by ϵ_1 and ϵ_2 the proportion of the genotypes AB/AB' and AB' among adult females and males, respectively. Likewise denote by ϵ_3 and ϵ_4 the corresponding proportions of $AB/A'B$ and $A'B$. By ϵ_5 and ϵ_6 denote the appropriate proportions of the double mutants $AB/A'B'$ and $A'B'$. Assume $\epsilon_i < \epsilon$ ($i = 1, \ldots, 6$) where ϵ is a positive, arbitrarily small constant. Because of random mating, the frequency of the double heterozygote $A'B/AB'$ is kept, each generation anew, at the negligible order of ϵ^2. This is not true for the frequency of the double-mutant chromosome $A'B'$, which, therefore, cannot be ignored. In fact, it is well-known from the general theory of two-locus population genetics that, under tight linkage and/or strong selection, the frequency of this chromosome can even become larger than that of $A'B$ or AB'.

Ignoring terms of the order ϵ^2, we get the frequencies of the six mating types involving mutant parents shown in table 1, together with the composition of their broods. The linear approximation of the transformation $\underline{\epsilon} \to \underline{\epsilon}'$ of the mutants' frequencies from one generation to the next has the form:

$$\epsilon_1' = a_1\epsilon_1 + a_2\epsilon_2 + t_5\epsilon_5,$$
$$\epsilon_2' = a_3\epsilon_1 + t_4\epsilon_5,$$
$$\epsilon_3' = b_1\epsilon_3 + b_2\epsilon_4 + t_5\epsilon_5,$$
$$\epsilon_4' = b_3\epsilon_3 + t_4\epsilon_5,$$
$$\epsilon_5' = t_1\epsilon_5 + t_2\epsilon_6,$$

and

$$\epsilon_6' = t_3\epsilon_5,$$

where

$$a_1 = \frac{1}{2}\frac{\varphi\left(\alpha,\frac{\beta+\beta'}{2}\right)F\left(\alpha,\frac{\beta+\beta'}{2}\right)}{\varphi F}, \quad \text{where } \varphi = \varphi(\alpha,\beta) \text{ and } F = F(\alpha,\beta), \tag{3}$$

$$a_2 = \frac{\varphi(\alpha,\beta')F(\alpha,\beta')}{\varphi F}, \tag{4}$$

$$a_3 = \frac{1}{2}\frac{\varphi\left(\alpha,\frac{\beta+\beta'}{2}\right)\left[1 - F\left(\alpha,\frac{\beta+\beta'}{2}\right)\right]}{\varphi[1-F]}, \tag{5}$$

$$b_1 = \frac{1}{2}\frac{\varphi(\alpha',\beta)F(\alpha',\beta)}{\varphi F}, \tag{6}$$

TABLE 1

TYPES AND FREQUENCIES OF MATINGS INVOLVING A MUTANT PARENT, AND COMPOSITION, BY GENOTYPE AND SEX, AND SIZE OF CORRESPONDING SEXUAL BROODS

Mating	Frequency	Daughters				Sons				Proportion of Daughters	Family Success
		$\frac{AB}{AB}$	$\frac{AB}{AB'}$	$\frac{AB}{A'B}$	$\frac{AB}{A'B'}$	AB	AB'	$A'B$	$A'B'$		
$\frac{AB}{AB'} \times AB$	ϵ_1	$\frac{1}{2}$	$\frac{1}{2}$	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	$F\left(\alpha,\frac{\beta+\beta'}{2}\right)$	$\varphi\left(\alpha,\frac{\beta+\beta'}{2}\right)$
$\frac{AB}{AB} \times AB'$	ϵ_2	0	1	0	0	1	0	0	0	$F(\alpha,\beta')$	$\varphi(\alpha,\beta')$
$\frac{AB}{A'B} \times AB$	ϵ_3	$\frac{1}{2}$	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	$F(\alpha',\beta)$	$\varphi(\alpha',\beta)$
$\frac{AB}{AB} \times A'B$	ϵ_4	0	0	1	0	1	0	0	0	$F(\alpha,\beta)$	$\varphi(\alpha,\beta)$
$\frac{AB}{A'B'} \times AB$	ϵ_5	$\frac{1-r}{2}$	$\frac{r}{2}$	$\frac{r}{2}$	$\frac{1-r}{2}$	$\frac{1-r}{2}$	$\frac{r}{2}$	$\frac{r}{2}$	$\frac{1-r}{2}$	$F\left(\alpha',\frac{\beta+\beta'}{2}\right)$	$\varphi\left(\alpha',\frac{\beta+\beta'}{2}\right)$
$\frac{AB}{AB} \times A'B'$	ϵ_6	0	0	0	1	1	0	0	0	$F(\alpha,\beta')$	$\varphi(\alpha,\beta')$

$$\begin{vmatrix} a_1 & a_2 & 0 & 0 & t_5 & 0 \\ a_3 & 0 & 0 & 0 & t_4 & 0 \\ 0 & 0 & b_1 & b_2 & t_5 & 0 \\ 0 & 0 & b_3 & 0 & t_4 & 0 \\ 0 & 0 & 0 & 0 & t_1 & t_2 \\ 0 & 0 & 0 & 0 & t_3 & 0 \end{vmatrix}$$

FIG. 1.—Matrix of linear approximation

$$b_2 = 1, \tag{7}$$

$$b_3 = \frac{1}{2}\frac{\varphi(\alpha',\beta)[1 - F(\alpha',\beta)]}{\varphi[1 - F]}, \tag{8}$$

$$t_1 = \frac{(1-r)}{2}\frac{\varphi\left(\alpha',\frac{\beta+\beta'}{2}\right)F\left(\alpha',\frac{\beta+\beta'}{2}\right)}{\varphi F}, \tag{9}$$

$$t_2 = a_2, \tag{10}$$

$$t_3 = \frac{(1-r)}{2}\frac{\varphi\left(\alpha',\frac{\beta+\beta'}{2}\right)\left[1 - F\left(\alpha',\frac{\beta+\beta'}{2}\right)\right]}{\varphi[1 - F]}, \tag{11}$$

$$t_4 = \frac{r}{1-r}t_3, \tag{12}$$

$$t_5 = \frac{r}{1-r}t_1. \tag{13}$$

The matrix of the linear approximation (see fig. 1), thus, has a form that is block triangular, with the following three pairs of eigenvalues, corresponding to the three principal minors:

$$\lambda_1 = \frac{1}{2}(a_1 + \sqrt{a_1^2 + 4a_2a_3}),\ \lambda_4 = \frac{1}{2}(a_1 - \sqrt{a_1^2 + 4a_2a_3}),$$

$$\lambda_2 = \frac{1}{2}(b_1 + \sqrt{b_1^2 + 4b_2b_3}),\ \lambda_5 = \frac{1}{2}(b_1 - \sqrt{b_1^2 + 4b_2b_3}),$$

and

$$\lambda_3 = \frac{1}{2}(t_1 + \sqrt{t_1^2 + 4t_2t_3}), \quad \lambda_6 = \frac{1}{2}(t_1 - \sqrt{t_1^2 + 4t_2t_3}).$$

The leading eigenvalue is, indeed, the maximum of λ_1, λ_2, and λ_3. Hence, fixation of AB is stable against the mutant alleles A' and B' if $\lambda_i < 1$ (and only if $\lambda_i \leqq 1$)

for $i = 1,2,3$. But the condition $\lambda_1 < 1$ is equivalent to $a_1 + a_2a_3 < 1$, which, by insertion of equations (3)–(5), becomes

$$1 > \frac{\varphi\left(\alpha,\frac{\beta+\beta'}{2}\right)F\left(\alpha,\frac{\beta+\beta'}{2}\right)}{2\varphi F} + \frac{\varphi(\alpha,\beta')\,\varphi\left(\alpha,\frac{\beta+\beta'}{2}\right)F(\alpha,\beta')\left[1-F\left(\alpha,\frac{\beta+\beta'}{2}\right)\right]}{2\varphi^2F[1-F]} \equiv G(\beta';\alpha,\beta). \tag{14}$$

In the same way, the conditions $\lambda_2 < 1$ and $\lambda_3 < 1$ become, respectively,

$$1 > \frac{\varphi(\alpha',\beta)}{2\varphi}\left[\frac{F(\alpha',\beta)}{F} + \frac{1-F(\alpha',\beta)}{1-F}\right] \equiv H(\alpha';\alpha,\beta), \tag{15}$$

and

$$1 > (1-r)T(\alpha',\beta';\alpha,\beta), \tag{16}$$

where T is defined by

$$T(\alpha',\beta';\alpha,\beta) = \frac{\varphi\left(\alpha',\frac{\beta+\beta'}{2}\right)}{2\varphi F} \times \left\{F\left(\alpha',\frac{\beta+\beta'}{2}\right) + \frac{\varphi(\alpha,\beta')\,F(\alpha,\beta')\left[1-F\left(\alpha',\frac{\beta+\beta'}{2}\right)\right]}{\varphi[1-F]}\right\}. \tag{17}$$

Conditions (14) and (15) stand for stability against invasions by B' and A', respectively. For a discussion of these conditions in relation to Trivers and Hare inclusive fitness functions (eqq. [1]–[2]) the reader is referred to The Game-Theoretic Approach, below. Inequality (16) gives an additional condition for stability against an invasion by the double mutant $A'B'$.

Conditions for an ESS

The fixation of AB with the corresponding pair of strategies $\{\alpha,\beta\}$ is stable with respect to any combination of mutations at each of the two loci, and is therefore an ESS, if conditions (14)–(16) hold for any pair of mutant strategies $\{\alpha',\beta'\}$ for which $\{\alpha',\beta'\} \neq \{\alpha,\beta\}$. Note, however, that

$$G(\beta;\alpha,\beta) \equiv H(\alpha;\alpha,\beta) \equiv T(\alpha,\beta;\alpha,\beta) \equiv 1. \tag{18}$$

Hence, any ESS $\{\alpha^\circ,\beta^\circ\}$ for the phenotypic pair $\{\alpha,\beta\}$ that is determined by genetic fixation at two loci with recombination rate r is a solution of the following (constrained) maximization problem:

$$G(\beta^\circ;\alpha^\circ,\beta^\circ) = \max_{\beta} G(\beta;\alpha^\circ,\beta^\circ), \tag{19}$$

$$H(\alpha^\circ;\alpha^\circ,\beta^\circ) = \max_{\alpha} H(\alpha;\alpha^\circ,\beta^\circ), \tag{20}$$

and

$$T(\alpha^\circ,\beta^\circ;\alpha^\circ,\beta^\circ) > (1-r)T(\alpha,\beta;\alpha^\circ,\beta^\circ) \quad \text{for all } \{\alpha,\beta\} \neq \{\alpha^\circ,\beta^\circ\}. \tag{21}$$

Consider, however, that if the effect of single mutations is not too large, and if linkage is not too tight, it follows from expression (18), by an argument of continuity, that condition (21) is automatically satisfied, irrespective of $\{\alpha^\circ,\beta^\circ\}$. Actually, since T has finite first partial derivatives, we can find some positive constant k such that, for all $\{\alpha^\circ,\beta^\circ\}$, condition (21) is satisfied as long as mutation effects $|\alpha - \alpha^\circ|$ and $|\beta - \beta^\circ|$ are smaller than kr. Thus, if we restrict our attention to smooth evolutionary changes due to mutations of small effect, the conditions for an ESS reduce to conditions (19)–(20) if linkage is not too tight. Note, furthermore, that $H(\alpha';\alpha,\beta)$ and $G(\beta';\alpha,\beta)$ can be interpreted as queen's and workers' payment functions, respectively, each depending on the mutant strategy of the relevant "player" (α' or β', respectively) as well as on the common, population's pair of strategies $\{\alpha,\beta\}$. Thus the population-genetics criterion, described by conditions (19)–(20), for an ESS coincides exactly with the corresponding game-theoretic (strict) criterion for asymmetric games (Maynard Smith and Parker 1976; Selten 1980), namely, the requirement that, by adopting the population strategy, each player (strictly) maximizes his own payment function. Unlike in the game approach, however, the payment functions that happen to be individually maximized are not assumed here, being rather deduced from the population dynamics itself (see also the section The Game-Theoretic Approach).

The foregoing analysis is obviously inadequate if, for a given pair of loci and a given r between them, where $r > 0$, mutations with large effects can occur, simultaneously, in both loci. But, even if mutation effects are limited, there is another situation to be considered that, as we believe, may be of greater evolutionary significance. This is the case in which mutations that affect either the queen's or the workers' behavior may occur, in the long run, at various loci of an ensemble such that the only lower bound for the rate of recombination between a queen's and a workers' locus is zero. If this situation obtains, an ESS $\{\alpha^\circ,\beta^\circ\}$ must then satisfy the additional condition

$$T(\alpha^\circ,\beta^\circ;\alpha^\circ,\beta^\circ) = \max_{\alpha,\beta} T(\alpha,\beta;\alpha^\circ,\beta^\circ). \tag{22}$$

Indeed, if condition (22) is not satisfied, and if r can assume any positive value, as small as one wishes, the inequality $T(\alpha^\circ,\beta^\circ;\alpha^\circ,\beta^\circ) < (1-r)T(\alpha,\beta;\alpha^\circ,\beta^\circ)$ can be satisfied by some pair $\{\alpha,\beta\}$ for which $\{\alpha,\beta\} \neq \{\alpha^\circ,\beta^\circ\}$ and some r such that $r > 0$, which would violate condition (21). Note, furthermore, that

$$T(\alpha^\circ,\beta;\alpha^\circ,\beta^\circ) = G(\beta;\alpha^\circ,\beta^\circ) \text{ and } T(\alpha,\beta^\circ;\alpha^\circ,\beta^\circ) = H(\alpha;\alpha^\circ,\beta^\circ). \tag{23}$$

Thus, any $\{\alpha^\circ,\beta^\circ\}$ that maximizes T with respect to both α and β also maximizes G with respect to β, and H with respect to α. If condition (22) is satisfied, then conditions (19)–(20) are also automatically satisfied. For this reason, condition (22) is also a sufficient (but not necessary) condition for an ESS in the previously mentioned case in which mutations have a large effect.

In view of this analysis, we refer to a pair of strategies, $\{\alpha^\circ,\beta^\circ\}$, satisfying criterion (22) as a *linkage-independent ESS*. Such pairs correspond to maxima of the single two-dimensional function T, thereby also maximizing the individual payment functions, G and H, of the two parties. Only these states are evolutionarily stable, in the long run, if rates of recombination between queen's and workers' genes do not have a positive lower bound. By contrast, a pair of strategies, $\{\alpha^\circ,\beta^\circ\}$, that maximizes separately G and H, according to conditions (19)–(20), will be referred to as a *limited-linkage ESS*. Assuming mutations with small effect, these pairs are evolutionarily stable as long as linkage is not excessively tight.

NORMAL REPRESENTATION OF THE SEX-RATIO CONFLICT

Before we proceed any further in the analysis of evolutionarily stable solutions to the sex-ratio conflict, it is useful to characterize in greater detail the class of functions, $F(\alpha,\beta)$ and $\varphi(\alpha,\beta)$, to which our consideration shall be confined. Any pair $\{F,\varphi\}$ with the properties specific to this class will be called a *normal representation* of the sex-ratio conflict. Let Ω denote the set of possible pairs, $\{\alpha,\beta\}$, of queen's and workers' phenotypes. A normal representation $\{F,\varphi\}$ is identified by the following characteristics.

PROPERTY 1. $F(\alpha,\beta)$, $\varphi(\alpha,\beta) \in [0,1]$ for all $\{\alpha,\beta\} \in \Omega$.

This is justified by the fact that F represents the proportion of females among reproductives, φ represents the reproductive success of the nest, and only relative values of reproductive success are needed.

PROPERTY 2. For all $u \in [0,1]$, there exists $\{\alpha,\beta\} \in \Omega$ such that $F(\alpha,\beta) = u$ and $\varphi(\alpha,\beta) = 1$.

This property expresses the natural requirement that workers and queen can avoid conflict by "agreeing" on any sex ratio. More specifically, it should be genetically possible for a nest to achieve any sex ratio with full reproductive success.

PROPERTY 3. F strictly increases in α and β and has continuous second derivatives anywhere in Ω.

Notice that, if F is monotonically decreasing rather than increasing, it can always be made increasing by an appropriate choice of the positive direction of its arguments.

PROPERTY 4. There is a function $\Delta(\alpha,\beta)$ such that (1) φ depends on α and β only through $\Delta(\alpha,\beta)$, so that, without ambiguity, we shall write $\varphi = \varphi(\Delta(\alpha,\beta))$; (2) $\Delta(\alpha,\beta)$ strictly increases in α and decreases in β and has continuous second derivatives anywhere in Ω; (3) Δ can take both positive and negative values in Ω; (4) $\varphi(\Delta)$ increases for $\Delta < 0$ and decreases for $\Delta > 0$, and $\varphi(0) = 1$.

Among the conditions that define a normal representation, this is the only one that, from a biological point of view, introduces some substantial limitation to possible choices of φ. It means that the dysfunctional effects that may be concomitant of queen's and workers' behaviors, $\{\alpha,\beta\}$, can be represented by a unidimensional measure, $\Delta(\alpha,\beta)$, of (signed) disagreement between the two parties, on which the reproductive success of the nest exclusively depends. The simplest example of such a measure would be, of course, when $\Delta(\alpha,\beta) = \alpha - \beta$, and part 2 of property 4 is nothing but an obvious generalization of this example. Choosing zero to be the value of Δ at which nest success is maximum is, obviously, a mere convention. It can always be satisfied by an appropriate choice of origin for the scale of Δ. Notice that, more generally, Δ needs only to be defined up to a smooth, strictly increasing transformation, because any such transformations can always be absorbed into φ. In combination with parts 3 and 4, part 2 allows for the possibility that a given level of nest distress is caused by "excesses" either on the part of the queen, when $\Delta > 0$, so that it could be ameliorated by a decrease of α, or on the part of the workers, if $\Delta < 0$, with the possibility of improvement by decreasing β. Observe that, by virtue of property 3, it is also possible, by appropriate changes of $\{\alpha,\beta\}$, to improve the nest success and then worsen it again while the sex ratio remains constant.

PROPERTY 5. φ is continuous for all Δ and has continuous second derivatives anywhere, with the possible exclusion of $\Delta = 0$.

In fact, we will consider explicitly two distinct cases. The first, which we call the *smooth punishment* case, obtains when φ has first and second derivatives also at $\Delta = 0$, so that, according to property 4, part 4, $\varphi' = 0$ and $\varphi'' \leq 0$. The second case that we consider is when the left and right derivatives of φ at $\Delta = 0$ are different, so that, according to property 4, part 4, $\varphi'(0-) = c_-$ and $\varphi'(0+) = -c_+$, where c_- and c_+ are positive constants. This will be called the *sharp punishment* case, and we will refer to the constants c_- and c_+ as the *left* and *right marginal punishment for disagreement*, respectively. An example in which a discontinuity of this kind appears in a biologically natural way is provided by the cell-size model discussed below.

PROPERTY 6. $F(\alpha,\alpha) \equiv \alpha$ and $\Delta(\alpha,\alpha) \equiv 0$.

In contrast to what might appear at first sight, this condition adds no further restrictions to previous requirements (properties 1–5). In fact, given properties 2–4, it can always be implemented, without further loss of generality, by an appropriate one-to-one transformation of $\{\alpha,\beta\}$ (see the Appendix). On the other hand, by virtue of this condition, the possibly complicated physiological or behavioral quantities represented by α and β can be objectively and unambiguously replaced by the more natural measure of the proportions of female reproductives that are respectively "preferred" by the queen and by the workers. In fact, according to property 6, arguments and values of F are measured on the same

scale of female proportions and, when maximal agreement is reached between the two parties, that is, when $\Delta = 0$ and therefore $\varphi = 1$, precisely that female proportion is obtained in the nest that the two parties had agreed upon. Property 6 is equivalent to the hypothetical measuring procedure of manipulating the genes of one party, leaving those of the other untouched, until maximal reproductive success of the nest is achieved, and then representing the phenotype of the undisturbed party by the proportion of females that the nest produces. Notice that the part of property 6 that concerns Δ (as well as property 8 below) strengthens the similarity of the general definition of Δ with the special example $\Delta(\alpha,\beta) = \alpha - \beta$. From property 6 and previous properties we can immediately deduce that Ω contains the points $\{0,0\}$ and $\{1,1\}$. We now suppose, for simplicity, that in addition Ω is so large that the following is true.

PROPERTY 7. Ω contains $[0,1] \times [0,1]$.

In other words, any combination of preferred sex ratios is genetically feasible in a nest. The unit square is the only part of Ω to which we will pay attention in the subsequent analyses. Finally, without any further loss of generality and, if necessary, by means of a smooth, strictly increasing transformation of Δ, we can always ensure the following.

PROPERTY 8. $\Delta(1,0) = 1$ and $\Delta(0,1) = -1$.

This will be convenient for purposes of mathematical notation.

When a sex-ratio conflict has a normal representation, there is a simple and natural definition of the "relative power" that is potentially available to each of the two parties, in the given biological and environmental conditions, to change the sex ratio in the colony by a marginal change of its own phenotype. In fact we define the queen's relative power, p, and the workers' relative power, q, as

$$p(\alpha,\beta) = (F_\alpha/\Delta_\alpha)/[(F_\alpha/\Delta_\alpha) - (F_\beta/\Delta_\beta)] \tag{24a}$$

and

$$q(\alpha,\beta) = -(F_\beta/\Delta_\beta)/[(F_\alpha/\Delta_\alpha) - (F_\beta/\Delta_\beta)] = 1 - p(\alpha,\beta), \tag{24b}$$

where, with F_α, F_β, and so forth, we indicate, from here on, first partial derivatives with respect to α and β. According to this definition, in view of property 3 and property 4, part 2, we have that $p \in (0,1)$ and $q \in (0,1)$ for all $\{\alpha,\beta\} \in \Omega$. Obviously p and q represent the relative change of female proportion, per unit size of change of colony disagreement, that the parties can achieve at any given state, $\{\alpha,\beta\}$, of the colony. The greater the marginal increment of female proportion, and the smaller the marginal change of colony disagreement, the greater the relative power of a party. From property 6 we deduce that

$$F_\alpha(\alpha,\beta)|_{\beta=\alpha} + F_\beta(\alpha,\beta)|_{\beta=\alpha} \equiv 1 \text{ and } \Delta_\alpha(\alpha,\beta)|_{\beta=\alpha} + \Delta_\beta(\alpha,\beta)|_{\beta=\alpha} \equiv 0, \tag{25}$$

from which it immediately follows that

$$p(\alpha,\alpha) = F_\alpha(\alpha,\beta)|_{\beta=\alpha} \text{ and } q(\alpha,\alpha) = F_\beta(\alpha,\beta)|_{\beta=\alpha}. \tag{26}$$

These notions will be useful in later analyses.

We now exemplify the class of normal representations by means of two simple but biologically plausible models we already mentioned in the introduction. The same examples will also be used later to illustrate some of the general results that we obtain.

The Workers' Recruitment Model

The following example is a simplified version of a biologically more elaborate model developed by Bulmer and Taylor (1981) and may be applied to species of social Hymenoptera in which diet determines whether female larvae develop into reproductive or worker adults. Since workers perform most of the nest duties, there are many opportunities for them to control how many of the female eggs laid by the queen are going to become reproductives. We assume that the queen, on her part, can determine only the proportion of females and males among the eggs she lays. On the other hand, the survival of larvae that have been chosen as reproductives, and their future vigor as adults, will be influenced by the size of the workers' force. We may suppose that if this size is too small, or too large, with respect to an optimal size, which is determined by prevailing ecological conditions, the reproductive success of the nest will be diminished. Thus, according to these hypotheses, let x be the relative number of female eggs laid by the queen (queen's phenotype); $1 - x$ be the relative number of male eggs laid by the queen; y be the relative number of reproductive females chosen by workers out of x, such that $0 \le y \le x$ (workers' phenotype); w (equal to $x - y$) be the resulting relative size of the workers' force; w^* be the optimal size of workers' force, a fixed parameter, such that $w^* < 1$; Δ be equal to $w - w^*$; and φ (equal to $\varphi(\Delta)$) be the reproductive success of the nest, where $0 \le \varphi \le 1 = \varphi(0)$ and φ decreases in $|\Delta|$. Therefore, the proportion of females among reproductives is $F = [y/(1 - x + y)]$. In this form, however, one can see that property 6 of the normal representation is not fulfilled. If, however, we transform $\{x,y\}$ into a new phenotypic pair $\{\alpha,\beta\}$ according to the equations

$$\alpha = \frac{(x - w^*)}{(1 - w^*)} \text{ and } \beta = \frac{y}{(1 - w^*)},$$

we have the representation

$$\begin{aligned} F(\alpha,\beta) &= \frac{\beta}{(1 - \alpha + \beta)}, \quad \Delta(\alpha,\beta) = (1 - w^*)(\alpha - \beta), \\ F(\alpha,\alpha) &\equiv \alpha, \qquad\qquad \Delta(\alpha,\alpha) \equiv 0, \end{aligned} \tag{27}$$

which agrees with the stipulations of normality. Note, however, that the natural range for $\{\alpha,\beta\}$ is not the unit square but contains the whole region $0 \le \alpha \le \beta \le 1$ in which workers seek to obtain at least as many female reproductives as the queen. In this model, the queen's and workers' power, as defined by equations (24a) and (24b), turn out to depend on $\{\alpha,\beta\}$ only through F, since we find that

$$p = p(F) = F \text{ and } q = q(F) = 1 - F. \tag{28}$$

The Cell-Size Model

This model may be applicable to species, such as honey bees, that raise female and male reproductives in cells of different size, female cells usually being larger. It is up to the workers to build cells for reproductives, and therefore to decide the proportion of large (female) and small (male) cells among them. Let large cells be in proportion β. On the other hand, it is up to the queen to fix the proportion of females among the eggs she lays. Let it be α. Thus, unless $\alpha = \beta$, some larvae will grow up in inappropriate cells, which may cause an excess of mortality to misplaced individuals. It is quite plausible that the number of these deaths is proportional to the number of eggs laid in inappropriate cells. In addition, the inherent asymmetry in the situation of male and female larvae in wrong cells may well be reflected in the mortality rates. Hence, we might have, in this case,

$$\varphi = \varphi(\alpha - \beta) = \begin{cases} 1 - c_+(\alpha - \beta), & \text{for } \alpha - \beta \geq 0,\ 0 < c_+ < 1, \\ 1 - c_-(\beta - \alpha), & \text{for } \alpha - \beta \leq 0,\ 0 < c_- < 1. \end{cases} \tag{29}$$

The proportion of female reproductives is therefore

$$F = F(\alpha,\beta) = \begin{cases} \dfrac{[(1 - c_+)\alpha + c_+\beta]}{[1 - c_+(\alpha - \beta)]}, & \text{for } \alpha - \beta \geq 0, \\ \dfrac{\alpha}{[1 - c_-(\beta - \alpha)]}, & \text{for } \alpha - \beta \leq 0. \end{cases} \tag{30}$$

Hence, this model verifies the requirements of normality, but for the fact that $F(\alpha,\beta)$ has discontinuous derivatives at $\alpha = \beta$. It also provides a natural example of sharp punishment. Of course, misusage of cells may cause additional diseconomies due to waste of cell material, labor, and food, if food is stored in cells in proportion to their size rather than to the needs of their proprietor. If this is the case, the reproductive success of the nest, φ, can be a more general function, decreasing with the number of misplaced eggs, $|\alpha - \beta|$. From expression (30) the queen's power is easily calculated:

$$p(\alpha,\beta) = \begin{cases} c_+F + (1 - c_+), & \text{for } \alpha - \beta > 0, \\ 1 - c_-F, & \text{for } \alpha - \beta < 0. \end{cases} \tag{31}$$

Notice that, in each of the two halves, $\{\alpha,\beta|\alpha - \beta > 0\}$ and $\{\alpha,\beta|\alpha - \beta < 0\}$, of the $\{\alpha,\beta\}$ plane p is a linear function of F alone.

Regular Representations

The two examples just discussed suggest a slight generalization of some convenient features they share. This identifies the class of representations of a sex-ratio conflict that we will call *regular*, characterized by the following properties:

$$F = F(\alpha,\beta) = p(F)\alpha + q(F)\beta,\ q(F) = 1 - p(F), \text{ and } 0 < p(F) < 1; \tag{32}$$

$$p(F) = aF + b(1 - F),\ 0 \leq a \text{ and } 0 \leq b \leq 1 \leq 13; \tag{33}$$

$$\varphi = \varphi(\alpha - \beta) \text{ is a positive decreasing function of } |\alpha - \beta|, \text{ with } \varphi(0) = 1. \tag{34}$$

These representations are obviously normal. As it is easy to verify, the functions $p(F)$ and $q(F)$ correspond to the queen's and workers' powers, respectively. Thus, equation (32) simply indicates that the proportion of females produced by the nest is the average of the proportions preferred by the queen and by the workers, each weighted by the power of its party. Equation (33) simply states that p and q are linear functions of F. This is not implied by equation (32) alone, despite its appearance. Indeed, given α and β, equation (32) is not an identity in F, being true only for the special value $F = F(\alpha,\beta)$. A simple calculation shows that, according to equation (33), a function F with the property of equation (32) is a linear fractional function of $\{\alpha,\beta\}$. Regular representations, with their simpler properties, will permit a more complete analysis of the sex-ratio conflict than is possible for the general class of normal representations.

DISCORD AND CONCORD SOLUTIONS OF SEX-RATIO CONFLICTS

In this section we explore, to some extent, the implications of conditions (19)–(21), which describe evolutionarily stable solutions of a sex-ratio conflict, under the assumption that the representation $\{F,\varphi\}$ of the conflict is normal, as defined in the section Normal Representation of the Sex-Ratio Conflict. In particular, we will identify some phenotypic configurations that should prevail in colonies whenever such equilibria are reached. We begin with the analysis of ESSs in the smooth punishment case (see Normal Representation), which occurs when the maximum, at $\Delta = 0$, of the reproductive mean of the nest, φ, has continuous first and second derivatives, so that φ is distinguished by a "rounded" peak. We then continue with the case of sharp punishment, in which the right and left derivatives of φ at its maximum are different, so that the peak of φ is a sharp corner. We will see that a qualitatively different kind of solution is possible in such a case.

Smooth Punishment

An ESS $\{\alpha^\circ\beta^\circ\}$ can be located either in the interior or on the boundary of the domain Ω of possible phenotypic configurations, $\{\alpha,\beta\}$. In this connection, we assume that Ω coincides with the unit square $[0,1]^2$. Indeed, in any concrete situation, Ω could be different from $[0,1]^2$, but, in the absence of detailed physiological information, this choice seems to be natural and does not seem to pose any serious limitation, nor excessive freedom, to what could be evolutionarily available to a species. We consider first interior ESSs and then, for mathematical completeness, ESSs on the boundary of $[0,1]^2$.

According to conditions (19)–(20), any interior ESS $\{\alpha^\circ,\beta^\circ\}$ coincides with interior maxima of G and H, simultaneously. Hence, since F, φ, and Δ are smooth everywhere in $[0,1]^2$, it must be true that $G_\beta(\beta^\circ;\alpha^\circ,\beta^\circ) = H_\alpha(\alpha^\circ;\alpha^\circ,\beta^\circ) = 0$. Notice that, here and elsewhere, we indicate with G_β, $G_{\beta\beta}$, H_α, $H_{\alpha\alpha}$, $T_{\alpha\alpha}$, $T_{\alpha\beta}$, and so on, the first and second partial derivatives of $G(\beta';\alpha,\beta)$, $H(\alpha';\alpha,\beta)$, and $T(\alpha',\beta';\alpha,\beta)$ with respect to β', α', and so on, calculated at $\alpha' = \alpha$ and $\beta' = \beta$. It follows

from the relations above, and from equations (14)–(15), that all interior ESSs are solutions of the following equations in $\{\alpha,\beta\}$:

$$G_\beta = \frac{3-4F}{4F(1-F)}F_\beta + \frac{\varphi'(\Delta)}{\varphi(\Delta)}\Delta_\beta = 0 \tag{35}$$

and

$$H_\alpha = \frac{1-2F}{2F(1-F)}F_\alpha + \frac{\varphi'(\Delta)}{\varphi(\Delta)}\Delta_\alpha = 0, \tag{36}$$

where $\Delta = \Delta(\alpha,\beta)$ and $F = F(\alpha,\beta)$. Exploiting the definitions of queen's and workers' relative power given in equations (24a) and (24b), we can reduce these equations, with simple algebraic manipulations, to

$$F(\alpha,\beta) = \frac{1}{2}p(\alpha,\beta) + \frac{3}{4}q(\alpha,\beta) \tag{37}$$

and

$$\frac{\varphi'(\Delta)}{\varphi(\Delta)} = \frac{pq}{4F(1-F)}\left[\frac{F_\alpha}{\Delta_\alpha} - \frac{F_\beta}{\Delta_\beta}\right]. \tag{38}$$

Recall that p and q are greater than zero, $p + q = 1$, and, because of normality, the right hand side of equation (38) is positive. Hence, for any solution, $\{\alpha^\circ,\beta^\circ\}$, of these equations we have $\frac{1}{2} < F^\circ = F(\alpha^\circ,\beta^\circ) < \frac{3}{4}$ and $\Delta^\circ = \Delta(\alpha^\circ,\beta^\circ) < 0$, since $\varphi'(\Delta)/\varphi(\Delta)$ is positive only for $\Delta < 0$. Consequently, $0 < \varphi(\Delta^\circ) < 1$. In addition to equations (37)–(38), further conditions must be satisfied for evolutionary stability. Thus, if linkage between queen's and workers' gene pairs is limited (see General Conditions for an ESS, above), any solution of equations (37)–(38) is an ESS if it maximizes $G(\beta';\alpha,\beta)$ with respect to β' and $H(\alpha';\alpha,\beta)$ with respect to α'. Hence, the additional conditions to be satisfied in this case are

$$G_{\beta\beta} < 0 \text{ and } H_{\alpha\alpha} < 0. \tag{39}$$

On the other hand, linkage-independent ESSs maximize $T(\alpha',\beta';\alpha,\beta)$ with respect to α' and β' (see General Conditions). This requires that the matrix of second partial derivatives of T with respect to α' and β' be negative definite, when calculated at a solution of equations (37)–(38). Keeping in mind that, according to equation (23), $T_{\beta\beta} = G_{\beta\beta}$ and $T_{\alpha\alpha} = H_{\alpha\alpha}$, it can be easily verified that this requirement introduces one further condition, in addition to condition (39), namely,

$$G_{\beta\beta}H_{\alpha\alpha} - (T_{\alpha\beta})^2 > 0. \tag{40}$$

These conditions are too complex to be analyzed for general normal representations. Results that can be obtained in the special case of regular representations are discussed in the section Regular Representations, below.

We have to consider now the case in which the limits of physiological possibility are attained in the queen, in the workers, or in both parties, before an evolutionary settlement of the conflict is reached. In this case, an evolutionarily stable state may lie on the boundary of Ω. Assuming that $\Omega = [0,1]^2$, it can be easily

shown that there can be no solution with $\alpha^\circ = 1$ or $\beta^\circ = 0$. Thus, three kinds of boundary solutions have to be examined: (1) $\alpha^\circ = 0$, $\beta^\circ \in (0,1)$; (2) $\alpha^\circ \in (0,1)$, $\beta^\circ = 1$; (3) $\alpha^\circ = 0$, $\beta^\circ = 1$. Since in all cases we have that $\alpha^\circ < \beta^\circ$, it follows immediately from normality that, for all boundary solutions, $\Delta^\circ = \Delta(\alpha^\circ,\beta^\circ) < \Delta(\beta^\circ,\beta^\circ) = 0$. Hence, in all cases $0 < \varphi(\Delta^\circ) < 1$. Boundary solutions of the first kind, in which the queen is trying to force the minimum proportion of females that is physiologically feasible for her, according to equations (19)–(20), must satisfy the following conditions:

$$\alpha^\circ = 0,\ 0 < \beta^\circ < 1,\ H_\alpha \le 0,\ G_\beta = 0, \text{ and } G_{\beta\beta} < 0. \tag{41}$$

Indeed, if condition (41) is satisfied with strict inequality (the case of equality being rather singular), the existence of this boundary solution is guaranteed. In this case, when the fact that $\Delta^\circ < 0$ is considered, it easily follows from the expressions for G_β and H_α given in equations (35)–(36) that $\frac{1}{2}p + \frac{3}{4}q < F^\circ < \frac{3}{4}$. Boundary solutions of the second kind, in which the workers have reached their upper physiological limit, must satisfy, according to equations (19)–(20),

$$0 < \alpha^\circ < 1,\ \beta^\circ = 1,\ H_\alpha = 0,\ G_\beta \ge 0, \text{ and } H_{\alpha\alpha} < 0. \tag{42}$$

If condition (42) is satisfied with strict inequality, the existence of this boundary solution is guaranteed. In this case, it follows from equations (35)–(36) that $\frac{1}{2} < F^\circ < \frac{1}{2}p + \frac{3}{4}q$. Finally, the boundary solution in which both the queen and the workers push to the respective extremes their preferred proportions of females must satisfy, according to equations (19)–(20),

$$\alpha^\circ = 0,\ \beta^\circ = 1,\ H_\alpha \le 0, \text{ and } G_\beta \ge 0, \tag{43}$$

and, if condition (43) is satisfied with strict inequality, the existence of this boundary solution is guaranteed. In view of equations (35)–(36), such a solution is therefore possible only if $\frac{1}{2} < F(0,1) = F^\circ < \frac{3}{4}$. Conditions (41), (42), and (43) each correspond to the requirement of equations (19)–(20) that G and H be maximized at any ESS. But since these maxima lie on the boundary, it follows from the properties of T (eq. [23]) that T is also maximized, in the generic case in which the inequalities in conditions (41)–(43) are satisfied strictly. In other words, the extent of linkage between queen and worker loci has no influence whatsoever on the existence of ESSs on the boundary, for which maximization of the workers' and queen's payment functions is sufficient. As a summary of this analysis we can therefore state the following.

Result 1.—In cases of smooth punishment, any ESS of a sex-ratio conflict is characterized by a female proportion, F°, strictly intermediate between $\frac{1}{2}$ and $\frac{3}{4}$ and by a definite loss of reproductive success of the nest, relative to what would be ecologically possible. If a solution exists in which neither party has reached its physiological limits, the equilibrium F° is exactly balanced between $\frac{1}{2}$ and $\frac{3}{4}$ by weights equal to the queen's and workers' powers, respectively. If the queen, but not the workers, has reached her physiological limit, F° is shifted toward $\frac{3}{4}$ more than the balance of powers would require. A corresponding shift toward $\frac{1}{2}$ obtains if the workers, but not the queen, have reached their physiological limit. Finally, in the generic case, any evolutionarily stable solution on the boundary is linkage-independent.

This result was conjectured, in part, by Trivers and Hare (1976). Perhaps, it would be more difficult to argue, on a purely biological basis, that with smooth punishment a settlement of the sex-ratio conflict is not possible without a loss to the reproductive success of the colony. The loss results from the fact that, with this kind of punishment, there are no ESSs in which the proportion of females, α° and β°, chosen by the queen and by the workers, respectively, coincide. In fact, the relation that prevails among them in any case is $\alpha^\circ < F^\circ < \beta^\circ$. Accordingly, we shall call these solutions *discord ESSs*.

Result 1 merely describes phenotypic properties of ESSs in the smooth punishment case and gives no information on conditions for their existence. The analysis of this problem in general is quite difficult, but the actual existence of discord ESSs can be established in some case, namely, whenever the reproductive success of the nest declines rapidly enough with disagreement between queen and workers. More specifically, we assume that the relative reproductive success of the nest is represented by a function of φ_c, which is a member of a family indexed by the parameter c as follows: $\varphi_c(\Delta) = f(\Delta)^c$ for $c > 0$, where f is any fixed function such that $f(0) = 1$, $0 \le f(\Delta) < 1$ for $|\Delta| < 1$, $f'(0) = 0$, and $f''(0) < 0$, so that f and therefore all φ_c satisfy the requirements of normality and smooth punishment. The parameter c can be taken as a measure of the strength of punishment for disagreement in that, for any fixed Δ such that $\Delta \neq 0$, $\varphi_c(\Delta)$ decreases as c increases, and, as $|\Delta|$ increases from 0 to 1, $\varphi_c(\Delta)$ decreases more rapidly if c has a larger value. Under this parametrization the following can be proved.

Result 2.—Given any sufficiently small, positive ϵ, if the strength of punishment, c, is large enough, there is no ESS $\{\alpha^\circ,\beta^\circ\}$ for which $\Delta^\circ = \Delta(\alpha^\circ,\beta^\circ)$ is outside the interval $(-\epsilon,0)$, and there is at least one ESS for which $-\epsilon < \Delta^\circ < 0$. Each of these ESSs is linkage-independent.

Sharp Punishment

The result that with smooth punishment the sex-ratio conflict can be solved only with discord of the two parties and a loss of reproductive value is remarkable in that, under the normal representation, exactly the same ESS F° would obtain, at no cost for the colony, if only the queen's and workers' phenotypes could be forced to the same value, such that $\alpha = \beta = F^\circ$. It is therefore natural to ask whether there is any condition under which concord in the nest could be maintained, in the sense that *concord ESSs*, of the form $\{\alpha^\circ,\alpha^\circ\}$, would be allowed to exist. Recall that it is a consequence of the normal representation that, for a concord ESS $\{\alpha^\circ,\alpha^\circ\}$, the reproductive success of the colony is maximum, since $\Delta^\circ = \Delta(\alpha^\circ,\alpha^\circ) = 0$, so that $\varphi(\Delta^\circ) = 1$, and the proportion, F°, of female reproductives in the nest is such that $F^\circ = F(\alpha^\circ,\alpha^\circ) = \alpha^\circ$. It turns out that, indeed, the possibility of concord is afforded by sharp punishment.

This is the case, defined in the section Normal Representation, in which the relative reproductive success of the nest, φ, has discontinuous derivatives at its point of maximum, when $\Delta = 0$:

$$\varphi'(0-) = c_- \text{ and } \varphi'(0+) = -c_+ \text{ for } c_- > 0 \text{ and } c_+ > 0. \tag{44}$$

Since condition (44) is the only respect in which this case is distinct from smooth punishment, the previous analysis applies equally well to sharp punishment for

all points $\{\alpha,\beta\}$ where $\alpha \neq \beta$, and thus $\Delta(\alpha,\beta) \neq 0$. Discord ESSs exist in this case under exactly the same conditions as before. However, because of the discontinuity described by condition (44), the conditions for a local maximum of G, H, or T at a point $\{\alpha,\alpha\}$ can no longer be expressed as equations (37)–(40). For example, in this case a local maximum in α' of the function $H(\alpha';\alpha,\beta)$ occurs at a point $\alpha' = \alpha = \beta$ if and only if the left and right derivatives of H satisfy the conditions $H_\alpha(\alpha-;\alpha,\alpha) > 0$ and $H_\alpha(\alpha+;\alpha,\alpha) < 0$. With a straightforward expansion of these and of similar, if slightly more complicated, conditions for local maxima of G and T, and when the properties of the normal representation are used, the conditions for a concord ESS $\{\alpha^\circ,\alpha^\circ\}$ can be expressed in terms of the left and right marginal punishments for disagreement, c_- and c_+, and of the functions, $h(\alpha)$ and $g(\alpha)$, defined by

$$h(\alpha) = \frac{2\alpha - 1}{2\alpha(1-\alpha)} \frac{p(\alpha,\alpha)}{d(\alpha)} \tag{45}$$

and

$$g(\alpha) = \frac{3 - 4\alpha}{4\alpha(1-\alpha)} \frac{q(\alpha,\alpha)}{d(\alpha)}, \tag{46}$$

where $p(\alpha,\alpha) = F_\alpha(\alpha,\beta)|_{\beta=\alpha}$ and $q(\alpha,\alpha) = 1 - p(\alpha,\alpha) = F_\beta(\alpha,\beta)|_{\beta=\alpha}$ are the queen and worker powers, respectively, and $d(\alpha) = \Delta_\alpha(\alpha,\beta)|_{\beta=\alpha} = -\Delta_\beta(\alpha,\beta)|_{\beta=\alpha} > 0$ (see expressions [25]–[26]).

Under limited linkage, any point $\{\alpha^\circ,\alpha^\circ\}$ such that $\{\alpha^\circ,\alpha^\circ\} \in (0,1)^2$ is a concord ESS with $F^\circ = \alpha^\circ$ if α° satisfies the two inequalities

$$c_- > \text{Max}\{h(\alpha^\circ),\, g(\alpha^\circ)\} \equiv m_-(\alpha^\circ) \tag{47}$$

and

$$c_+ > \text{Max}\,\{-h(\alpha^\circ),\, -g(\alpha^\circ)\} \equiv m_+(\alpha^\circ). \tag{48}$$

The conditions for $\{\alpha^\circ,\alpha^\circ\}$ to be a linkage-independent, concord ESS are similarly expressed by a pair of inequalities:

$$c_- > \text{Max}\{h(\alpha^\circ),\, 2g(\alpha^\circ) - h(\alpha^\circ)\} \equiv M_-(\alpha^\circ) \tag{49}$$

and

$$c_+ > \text{Max}\{-h(\alpha^\circ),\, -2g(\alpha^\circ) + h(\alpha^\circ)\} \equiv M_+(\alpha^\circ). \tag{50}$$

These conditions can be easily interpreted when the following properties of $h(\cdot)$ and $g(\cdot)$ are noted:

$$h(\alpha) < 0 \quad \text{in} \quad \left(0, \frac{1}{2}\right), \quad h(0) = -\infty,$$

$$h(\alpha) > 0 \quad \text{in} \quad \left(\frac{1}{2}, 1\right), \quad h(1) = +\infty;$$

$$g(\alpha) > 0 \quad \text{in} \quad \left(0, \frac{3}{4}\right), \quad g(0) = +\infty,$$

$$g(\alpha) < 0 \quad \text{in} \quad \left(\frac{3}{4}, 1\right), \quad g(1) = -\infty;$$

h and g are continuous in (0,1).

It follows from these that the function $m_-(\alpha)$ of inequality (47) is continuous and strictly positive in (0,1) and tends to $+\infty$ as $\alpha \to 0$ or $\alpha \to 1$. It therefore has in the interval (0,1) a positive minimum, at some point α_0, and in the interval [½,¾] a finite maximum and a positive minimum, at some points α_M and α_m, respectively. On the other hand, the function $m_+(\alpha)$ of inequality (48), like $m_-(\alpha)$, is continuous in (0,1) and tends to $+\infty$ as $\alpha \to 0$, 1, but, unlike $m_-(\alpha)$, is negative in (½,¾), zero at $\alpha = ½$ or $\alpha = ¾$, and positive otherwise. Thus, any α in [½,¾] satisfies condition (48).

The corresponding functions $M_-(\alpha)$ and $M_+(\alpha)$, which characterize conditions (49)–(50) for linkage-independent, concord ESSs, have essentially the same qualitative properties of $m_-(\alpha)$ and $m_+(\alpha)$, respectively. This can be inferred easily from the observation that $m_-(\alpha) = h(\alpha) \Rightarrow h(\alpha) \geq g(\alpha) \Rightarrow g(\alpha) \geq 2g(\alpha) - h(\alpha) \Rightarrow h(\alpha) \geq 2g(\alpha) - h(\alpha) \Rightarrow M_-(\alpha) = h(\alpha)$ and, conversely, $m_-(\alpha) = g(\alpha) \Rightarrow g(\alpha) \geq h(\alpha) \Rightarrow 2g(\alpha) - h(\alpha) \geq g(\alpha) \Rightarrow 2g(\alpha) - h(\alpha) \geq h(\alpha) \Rightarrow M_-(\alpha) = 2g(\alpha) - h(\alpha)$. A change of sign produces corresponding inequalities for $-h$, $-g$, and $-2g + h$, which are of relevance for $M_+(\alpha)$. The useful consequence of these inequalities is that $M_-(\alpha) \geq m_-(\alpha)$ and $M_+(\alpha) \geq m_+(\alpha)$ for all $\alpha \in (0,1)$. Furthermore, the set of points over which $M_+(\alpha)$ is negative is smaller than that of $m_+(\alpha)$, since it consists of an interval extending to the right of ½ but not quite up to ¾. Thus, inequality (50), unlike inequality (48), may be violated by some α in [½,¾]. Finally, it is easily shown that $M_+(\alpha) < M_-(\alpha)$ for $\alpha < ¾$, and $M_+(\alpha) > M_-(\alpha)$ for $\alpha > ¾$. In fact, if $\alpha < ¾$, then $g(\alpha) > 0$, which is equivalent to $-h(\alpha) < 2g(\alpha) - h(\alpha) \leq M_-(\alpha)$ and also to $-2g(\alpha) + h(\alpha) < h(\alpha) \leq M_-(\alpha)$. Thus, $M_+(\alpha) < M_-(\alpha)$ for $\alpha < ¾$. If $\alpha > ¾$, these inequalities are reversed. On the basis of this analysis we may therefore state the following.

Result 3.—For limited-linkage ESSs, the following conditions hold. (1) If the left marginal punishment for disagreement, c_-, is smaller than a certain critical value, there is no concord ESS, irrespective of c_+. In fact, one can see that this critical value is $m_-(\alpha_0)$, say, the minimum of $m_-(\cdot)$ in (0,1). (2) For each value of the left marginal punishment, c_-, that is above the critical value $m_-(\alpha_0)$, there is a threshold value, $k(c_-)$, such that, if the right marginal punishment, c_+, exceeds this value, there is a continuity of concord ESS values, α°, in (0,1). The threshold, $k(c_-)$, is either equal to 0 irrespective of c_-, or decreases to 0 as c_- increases. (3) The set of concord ESS values, which consists of a finite number of intervals and, perhaps, isolated points, is nondecreasing with both c_- and c_+ and tends to the whole interval (0,1) as $c_- \to \infty$ and $c_+ \to \infty$. (4) If c_- is larger than $m_-(\alpha_m)$, the minimum of $m_-(\cdot)$ in [½,¾], there is a continuity of concord ESS values in [½,¾], which is nondecreasing with c_-, irrespective of c_+. (5) If c_- is larger than $m_-(\alpha_M)$, the maximum of $m_-(\cdot)$ in [½,¾], every α° in [½,¾] is a concord ESS, irrespective of c_+.

Result 4.—For linkage-independent ESSs, the following conditions hold. (1) Propositions equivalent to points 1–3 above are equally true in this case. (2) Propositions equivalent to points 4–5 above hold true in this case when applied not to the whole of [½,¾] but to an interval [½,a] that is strictly contained in it. (3) The analogues of properties indicated in points 4–5 above may be extended to the interval (0,¾] under the additional sufficient condition that $c_+ \geq c_-$.

In qualitative terms, results 3 and 4 assert that a sex-ratio conflict may be settled at no cost to the colony, provided that the relative reproductive success of the nest, φ, is sufficiently steep on both sides of its maximum at $\Delta = 0$. Whenever such a concord solution is reached, the stable proportion of females, F°, may be anywhere in one or more continuous ranges of values. It is interesting that even values of F° smaller than ½ or larger than ¾ may be achieved in this way. In fact, the spectrum of possible values for F° becomes wider and tends to occupy the entire (0,1) interval as φ becomes steeper and the punishment for breaking concord is accordingly intensified. The left marginal punishment for disagreement, c_-, has a more critical influence than the right marginal punishment, c_+, particularly in relation to the existence of equilibrium values, F°, within the [½,¾] interval. It is also worth recalling that concord ESSs may coexist with discord ESSs, since the presence of concord ESSs depends only on the local properties of the reproductive success of the nest, φ, in the vicinity of its maximum at $\Delta = 0$.

REGULAR REPRESENTATIONS

In this section we analyze the special class of regular representations of a sex-ratio conflict. One reason of particular interest for these representations is that, as seen in the section Normal Representation, both the workers' recruitment and the cell-size models are of this kind. The results illustrate the wide variety of long-term equilibrium configurations that may arise, depending on the properties of the reproductive success of the nest, φ. Recall (expressions [32]–[34]) that regularity is defined by a sex-ratio function, F, and a disagreement function, Δ, with the following properties:

$$F = p(F)\alpha + q(F)\beta; \tag{51}$$

$$p(F) = aF + b(1 - F), \; 0 \leq a \leq 1 \text{ and } 0 \leq b \leq 1; \tag{52}$$

$$\Delta = \alpha - \beta. \tag{53}$$

Thus, each pair of parameters $\{a,b\}$ such that $\{a,b\} \in [0,1]^2$ uniquely identifies F. According to equation (51), the contour lines of $F(\alpha,\beta)$ in the (α,β) plane are straight lines with slope $-p/q$. This slope may vary with the value of F since, according to equation (52), the queen's and workers' powers, p and q, depend linearly on F.

No restrictions are imposed on the relative reproductive success of the nest, φ, where $\varphi = \varphi(\Delta)$, beyond the usual requirements of normality. To simplify the notation we introduce the function η, defined by $\eta(\Delta) = [\varphi'(\Delta)]/[\varphi(\Delta)]$. Accordingly, since $\varphi(0) = 1$, in the case of smooth punishment we have $\eta(0-) = \eta(0+) = 0$, while, in the case of sharp punishment, we have $\eta(0-) = c_-$, $\eta(0+) = -c_+$, where $c_- > 0$ and $c_+ > 0$.

Discord ESSs

It follows from equation (37) that, for any interior, discord ESS, the proportion of females, F°, is obtained by solving for F:

$$F = \frac{1}{2}p(F) + \frac{3}{4}q(F). \tag{54}$$

This equation always has a unique valid solution. In fact, by comparing it with equation (51), we see that $F^\circ = F(\frac{1}{2},\frac{3}{4})$. On the other hand, the associated ESS values, Δ°, of the disagreement between queen and workers, from equation (38), are solutions of

$$\eta(\Delta) = \frac{c^*}{1 - p'\Delta} \equiv s(\Delta), \tag{55}$$

where

$$c^* = \frac{p^\circ q^\circ}{4F^\circ(1 - F^\circ)},\ p^\circ = p(F^\circ),\ q^\circ = q(F^\circ),\ \text{and}\ p' = \frac{dp}{dF} = a - b. \tag{56}$$

Thus, the number of distinct, interior, discord ESSs depends on the number of intersections of $\eta(\Delta)$ with the function $s(\Delta)$ in the interval $[\Delta_m,0)$. Notice that the lower extreme of this interval, at which $\Delta_m = \Delta_m(F^\circ) \geq -1$, corresponds to the value of $\Delta(\alpha,\beta) = \alpha - \beta$ at the point $\{\alpha,\beta\}$ where the contour line $F(\alpha,\beta) = F^\circ$ meets the boundary, $\{\alpha,\beta\colon \alpha = 0,\ 0 < \beta \leq 1\} \cup \{\alpha,\beta\colon 0 < \alpha < 1,\ \beta = 1\}$, of the domain $[0,1]^2$. Since normality, for $\Delta < 0$, requires only that $\eta(\Delta)$ be nonnegative, it is clear that equation (55) can have any number of solutions, given the appropriate reproductive success of the nest, φ.

Any solution $\{F^\circ,\Delta^\circ\}$ of equations (54)–(55) is an ESS, in the case of limited linkage, if it satisfies the conditions of expression (39), which, in this case, if the notation of equation (56) is used, can be written as

$$H_{\alpha\alpha} < 0\colon \frac{\eta'(\Delta^\circ)}{\eta(\Delta^\circ)^2} < 1 + \frac{2p'}{c^*} \equiv A(a,b) \tag{57}$$

and

$$G_{\beta\beta} < 0\colon \frac{3\eta'(\Delta^\circ)}{4\eta(\Delta^\circ)^2} < \frac{3p^\circ - 2q^\circ}{4p^\circ} + \frac{2q^\circ}{c^*p^\circ} + \frac{1 + 3p^\circ}{2c^*p^\circ}p' \equiv B(a,b). \tag{58}$$

However, direct calculations show that, for all $\{a,b\} \in [0,1]^2$,

$$\frac{3}{4}A < B. \tag{59}$$

Hence, condition (58) always holds whenever condition (57) is satisfied. This result is relevant to the comparison of the population-genetics and the game-theoretical approaches to long-term evolution of the sex-ratio conflict that we will discuss under The Game-Theoretic Approach, below.

Any linkage-independent ESS, $\{F^\circ,\Delta^\circ\}$, requires the additional condition (40),

which involves the mixed derivative, $T_{\alpha\beta}$, of the two-party payment function T. In the regular case, at $\{F^\circ,\Delta^\circ\}$, this derivative is $T_{\alpha\beta} = -\frac{1}{2}\eta'(\Delta^\circ) + \eta(\Delta^\circ)^2C(a,b)$, where

$$C(a,b) = \frac{1 + q^\circ}{q^\circ} - \frac{2}{c^*} + \frac{p^\circ - q^\circ}{2c^*p^\circ}p'. \tag{60}$$

If the quadratic, $Q(x)$, is defined as

$$Q(x) = \frac{1}{2}x^2 - \left(\frac{3}{4}A + B - C\right)x + (AB - C^2), \tag{61}$$

condition (40) can be written as

$$Q\left(\frac{\eta'(\Delta^\circ)}{\eta(\Delta^\circ)^2}\right) > 0. \tag{62}$$

It can immediately be verified that $Q(A) = -(\frac{1}{2}A - C)^2 \leq 0$ and that, by virtue of inequality (59), whenever $A = 2C$, so that $Q(A) = 0$, A is in fact the smallest of the two distinct roots of $Q(x)$. Hence, $Q(x)$ has two real and distinct roots in all cases. Let A^*, a function of a and b (i.e., $A^* = A^*(a,b)$) be the smallest root of $Q(x)$. Since condition (62) must be satisfied together with condition (57), we may assert on the basis of these considerations the following.

Result 5.—(1) Any solution $\{F^\circ,\Delta^\circ\}$ of equations (54)–(55) is an ESS only in the case of limited linkage if $A^*(a,b) < [\eta'(\Delta^\circ)]/[\eta(\Delta^\circ)^2] < A(a,b)$. (2) $\{F^\circ,\Delta^\circ\}$ is a linkage-independent ESS if $[\eta'(\Delta^\circ)]/[\eta(\Delta^\circ)^2] < A^*(a,b)$. We note that the only case in which $A(a,b) = A^*(a,b)$ is when $a = 0$, so that $p(F) = b(1 - F)$. In this case linkage is irrelevant for stability. In all other cases the stability conditions are definitely more stringent when linkage is tight than when it is limited.

The conditions of result 5 constrain the slope of $\eta(\cdot)$ (i.e., the curvature of $\varphi(\cdot)$) at a point of intersection with $s(\cdot)$ (see eq. [55]). Hence, to gain some qualitative understanding of these conditions it is helpful to evaluate how they relate to simple properties of $\eta(\cdot)$ such as that of being locally increasing or decreasing and that of intersecting $s(\cdot)$ from above or from below. To evaluate the first aspect we need to consider the signs of $A^*(a,b)$ and of $A(a,b)$. As for the second aspect, we observe that $s'(\Delta^\circ) = s(\Delta^\circ)^2(p'/c^*) = \eta(\Delta^\circ)^2(p'/c^*)$. Hence, $\eta'(\Delta^\circ) \geq s'(\Delta^\circ) \Leftrightarrow [\eta'(\Delta^\circ)]/[\eta(\Delta^\circ)^2] \geq p'/c^*$. Thus, we need to consider the sign of $A^* - p'/c^*$ and of $A - p'/c^*$. The algebraic expressions for A and A^* are complicated, but we can, quite simply, calculate the relevant quantities for a sufficient number of values of the pair of parameters $\{a,b\}$. The results of these numerical evaluations are presented in figure 2, which displays the partition of the parameter space $\{a,b\}$ into six regions where each of the possible orderings of A^*, A, p'/c^*, and 0 obtains. In correspondence with each of these regions, we show the (qualitative) range of spatial relations that $\eta(\cdot)$ must have with $s(\cdot)$, at a point of intersection for conditions 1 and 2 of result 5 to be verified: any $\eta(\cdot)$ that intersects $s(\cdot)$ through a light shaded region meets condition 1; any $\eta(\cdot)$ that intersects $s(\cdot)$ through a dark shaded region meets condition 2. Thus, for example, if b is substantially smaller than a (region 1), any locally decreasing $\eta(\cdot)$ at a point of intersection

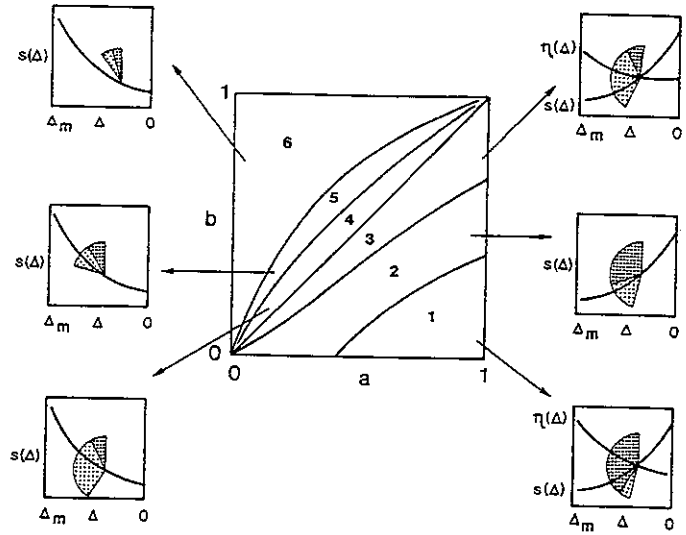

FIG. 2.—Graphic representation of the conditions for a discord ESS, in the regular case. Each point in the $\{a,b\}$ domain (*central picture*) uniquely identifies a particular sex-ratio function, F. This domain is partitioned into regions where different orderings of the quantities (see text) A, A^*, p'/c^*, and 0 obtain. *Region 1*, $0 < p'/c^* < A^* < A$; *region 2*, $0 < A^* < p'/c^* < A$; *region 3*, $A^* < 0 < p'/c^* < A$; *region 4*, $A^* < p'/c^* < 0 < A$; *region 5*, $A^* < p'/c^* < A < 0$; *region 6*, $A^* < A < p'/c^* < 0$. To each ordering there correspond specific bounds to the angle between the functions $\eta(\Delta)$ and $s(\Delta)$ at a point of intersection for such a point to identify an ESS. These bounds are sketched in the pictures at the sides. Any angle within a dark sector (as in the example shown for region 1) indicates a linkage-independent ESS; any angle within a light sector (as in the example shown for region 3) indicates a limited-linkage ESS; angles outside both sectors indicate that there is no ESS there.

produces a linkage-independent ESS; conversely, if b is substantially larger than a (region 6), any intersection where $\eta(\cdot)$ is locally increasing is not an ESS, irrespective of linkage. We see that, roughly, as we proceed in the $\{a,b\}$ domain in the direction of increasing $p'(F)$ (where $p'(F) = a - b$), the conditions of stability become milder. However, a change of $a + b$ appears to have a lesser effect on stability. It seems that long-term stability is more sensitive to the correlation of queen's (workers') power with colony sex ratio than to the actual size of the power.

With respect to discord ESSs on the boundary, a useful result can be proved that excludes their existence in certain cases.

Result 6.—If, in the interior of $[0,1]^2$, there is a pair of nest strategies $\{\alpha^*,\beta^*\}$ that produces the female proportion F°, that is, $F(\alpha^*,\beta^*) = F^\circ$, and a disagreement Δ^*, that is, $\Delta(\alpha^*,\beta^*) = \Delta^*$, such that $\eta(\Delta) > s(\Delta)$ for all $\Delta < \Delta^*$, then there is no ESS on the boundary of $[0,1]^2$.

Concord ESSs

Under regularity, the two functions $h(\cdot)$ and $g(\cdot)$ of equations (45)–(46) that control long-term stability of a concord female proportion F such that $F = F(\alpha,\alpha) = \alpha$, namely, $h(F) = (2F - 1)/[2F(1 - F)]p(F)$ and $g(F) = (3 - 4F)/[4F(1 - F)]q(F)$, are monotone in (0,1), $h(\cdot)$ being increasing and $g(\cdot)$ decreasing. This fact has several useful consequences. The threshold, m_-, for the right marginal punishment c_- (where $c_- = \eta(0-)$), above which F is a concord, limited-linkage ESS, defined by $m_-(F) = \text{Max}\{h(F),g(F)\}$ (see eq. [47]), has a unique extremum, a minimum, at the point where $h(F) = g(F)$. As an equation in F, this reduces exactly to equation (54), which gives the unique female proportion, F°, of $F(\frac{1}{2},\frac{3}{4})$, for any discord ESS. It turns out, in addition, that

$$m_-(F^\circ) = \min_{0<F<1} m_-(F) = c^*,$$

where c^* is the constant defined in equation (56). Obviously, the function $2g - h$ is also decreasing. Hence, M_-, the stability threshold for concord, linkage-independent ESSs (inequality [49]), defined by $M_-(F) = \text{Max}\{h(F),2g(F) - h(F)\}$, has the same properties and is minimized at the same point, $\{F^\circ,c^*\}$, as $m_-(\cdot)$. The functions $m_+(\cdot)$ and $M_+(\cdot)$ of inequalities (48) and (50) that identify corresponding thresholds for the right marginal punishment c_+, where $c_+ = \eta(0+)$, behave similarly. In particular, both are decreasing for $F \in (0,\frac{1}{2}]$ and increasing for $F \in [\frac{3}{4},1)$. In the interval $(\frac{1}{2},\frac{3}{4})$, $m_+(\cdot)$ is negative while $M_+(\cdot)$ is zero at a point larger than F°, negative below this point, and increasing above. Hence, we may assert the following.

Result 7.—If a sex-ratio conflict has a regular representation, the following conditions hold. (1) Irrespective of linkage, concord ESSs exist if and only if the left marginal punishment c_-, where $c_- = \eta(0-)$, exceeds the critical value, c^*, defined by equation (56). (2) The set of female proportions that are concord ESSs consists of an interval that contains the value F°, the unique female proportion of any discord ESS. The concord ESS associated with F° is linkage-independent. (3) The interval of linkage-independent ESSs is strictly contained in the interval of limited-linkage ESSs. Both intervals tend to F° as c_- decreases to c^*, and tend to (0,1) as both c_- and c_+ (where $c_+ = \eta(0+)$) increase to ∞.

Configurations of Long-Term Equilibria

The results obtained above show that, even in the relatively simple cases identified by a regular representation of $\{F,\varphi\}$, the long-term equilibria of a sex-ratio conflict may be arranged in many different patterns, depending mainly on the form of the reproductive success of the nest, φ, as determined by certain properties of the function η, where $\eta = \varphi'/\varphi$. Among the various possibilities, we can easily identify the following.

1. *A unique ESS of the discord type.*—For example, with any sex-ratio function, F, identified by parameters $\{a,b\}$ in regions 1–2 of figure 2, this case occurs if $\eta(\cdot)$ intersects $s(\cdot)$ and is decreasing (i.e., φ is log concave). In fact, this unique

intersection produces an ESS irrespective of linkage. On the other hand, concord ESSs cannot exist, since necessarily $\eta(0) < c^* = s(0)$, and ESSs on the boundary are ruled out by result 6. When this situation prevails, one can observe a number of genetically and ecologically similar species, or geographical races, fixed on the same sex-ratio value, somewhere between 1:1 and 1:3, and with the same nest productivity.

2. *A continuous range of concord ESSs.*—In all regions 1–6 of figure 2, these are the only long-term equilibria if $\eta(\cdot)$ does not intersect $s(\cdot)$ and $\eta(0) > c^* = s(0)$. In fact, boundary ESSs are excluded again by result 6. In this case one can expect a wide, more or less uniform dispersion of sex-ratio values across a group of similar species in which the sex ratio has evolved independently.

3. *A few discrete ESSs of the discord type.*—This configuration can obtain, for example, when the sex-ratio function F belongs to region 1 of figure 2 and $\eta(\cdot)$ has three intersections with $s(\cdot)$ in such a way that $\eta(0) < c^* = s(0)$. When this situation prevails, one can find, in a group of related and ecologically equivalent species, that the sex ratio is constant, while the colony productivities of the different species are clustered around two or three discrete values. In such a case, we could be misled into searching for ecological differences in the respective habitats to account for the observed differences.

4. *One or more discord ESSs and a range of concord ESSs.*—Once more, one could be misled into searching in vain for genetic, behavioral, or ecological causes to account for differences among related species that only exist for historical reasons.

5. *No ESS associated with a monomorphic genetic equilibrium.*—This possibility can arise most easily with sex-ratio functions, F, belonging to region 6 of figure 2. Indeed, in this case, it is enough that $\eta(\cdot)$ intersects $s(\cdot)$ only once and from above, with a sufficiently small angle. Concord ESSs are excluded because $\eta(0) < c^* = s(0)$, and boundary ESSs are ruled out by result 6. However, we cannot infer that there is no state stable in the long term, because the existence of ESSs associated with *polymorphic* genetic equilibria, which we have not analyzed, cannot be precluded.

THE GAME-THEORETIC APPROACH, EVOLUTIONARILY RELEVANT PAYMENT FUNCTIONS, AND THE EFFECT OF LINKAGE

As it appears from the general analysis of the two-locus system, a pair of strategies $\{\alpha,\beta\}$, determining a queen's and a workers' behavior respectively, is stable against any invading mutation if and only if conditions (19)–(21) are satisfied simultaneously. For this, no specific assumption (except for certain smoothness conditions) was required about either the reproductive success of the nest, $\varphi(\alpha,\beta)$, the female proportion function, $F(\alpha,\beta)$, or the rate of recombination, r, between the two relevant loci. It was shown, however, that if linkage is not too tight and if the effect of a single mutation is limited (depending on r) then condition (21) is automatically satisfied and the criterion for evolutionary stability reduces to the generally weaker conditions (19)–(20). More specifically, this is so if the effect of a single mutation on either φ or F is smaller, in magnitude, than a

quantity proportional to r. In this case, the conditions for external genetic stability of the pair $\{\alpha,\beta\}$ are mathematically equivalent to those for evolutionary stability in asymmetric games (Maynard Smith and Parker 1976; Selten 1980), namely, that the value of α', when $\alpha' = \alpha$, will maximize some payment function $H(\alpha';\alpha,\beta)$ of player 1 (the queen) and the value of β', when $\beta' = \beta$, will maximize another payment function $G(\beta';\alpha,\beta)$ of player 2 (the workers), except that in our development of the model the payment functions H and G have not been assumed in advance but, rather, have emerged from the analysis of the exact genetic model.

Not very surprising, but possibly of some interest, is that the queen's payment function shown to be maximized by natural selection,

$$H = \frac{\varphi(\alpha',\beta)\,F(\alpha',\beta)}{2\varphi F} + \frac{\varphi(\alpha',\beta)\,[1 - F(\alpha',\beta)]}{2\varphi(1 - F)},$$

(see eqq. [15], [20]) is identical to her inclusive fitness $\hat{H}$ (eq. [2]), as suggested by Trivers and Hare (1976). However, the payment function that natural selection maximizes for the workers (eqq. [14], [19]),

$$G = \frac{\varphi\left(\alpha,\frac{\beta+\beta'}{2}\right)F\left(\alpha,\frac{\beta+\beta'}{2}\right)}{2\varphi F} + \frac{\varphi(\alpha,\beta')F(\alpha,\beta')\varphi\left(\alpha,\frac{\beta+\beta'}{2}\right)\left[1 - F\left(\alpha,\frac{\beta+\beta'}{2}\right)\right]}{2\varphi^2 F[1 - F]},$$

does not look much like the workers' inclusive fitness, which under the assumption of random mating and weak selection is given by

$$\hat{G} = \frac{3\varphi(\alpha,\beta')F(\alpha,\beta')}{4\varphi F} + \frac{\varphi(\alpha,\beta')[1 - F(\alpha,\beta')]}{4\varphi[1 - F]}, \tag{63}$$

which readily results from a comparison with equation (1).

Note, however, that the functions G and $\hat{G}$ have the same derivatives with respect to β' at $\beta' = \beta$:

$$G_{\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta} = \hat{G}_{\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta} = \frac{\varphi_\beta}{\varphi} + \frac{3 - 4F}{4F(1 - F)}F_\beta. \tag{64}$$

In the terminology of Taylor (1989), this means "first order equivalence" between the exact genetic model and the inclusive fitness approach. Namely, the derivative of the inclusive fitness, $\hat{G}$, as long as it is not zero, correctly indicates the direction of phenotypic changes that are favored by natural selection. This is in agreement with a general result of Taylor (1989) concerning one-locus models.

The relevant implication of this equivalence is that the two approaches agree exactly with respect to m-stability (Taylor 1989; see also Eshel and Motro 1981; Eshel 1983). This is the property of a continuous, unidimensional strategy that, if the population is fixed on any other strategy close to it, only those mutant strategies that are closer to the m-stable one will be favored by selection. How-

ever, m-stability does not generally imply the ESS condition (what Taylor calls δ-stability), according to which, in a population that is fixed on the ESS strategy, selection will operate against any invading mutation. Thus, both ESSs that are not m-stable and m-stable states that are not ESSs may occur. A natural example of the latter kind is provided by Christiansen (1991). While ESSs, particularly m-stable ones, are obviously significant as stable equilibria of long-term evolution, the evolutionary relevance of m-stable states that are not ESSs may be debated, since it is not immediately clear that necessarily, in the long run, the population will remain somehow confined in the vicinity of such a state (I. Eshel, unpublished manuscript).

An immediate consequence of the first-order equivalence between the two payment functions G and $\tilde{G}$, indicated by equation (64) is that the genetic model and the inclusive fitness model completely agree with respect to concord ESSs. Indeed, in the case of sharp punishment, for which the derivative of φ has a point discontinuity, equation (64) remains true for both left and right derivatives.

The situation may be different with respect to discord ESSs, since these depend not only on the equality

$$H_{\alpha'}(\alpha';\alpha,\beta)|_{\alpha'=\alpha} = G_{\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta} = 0, \tag{65}$$

which, when equation (64) is used, becomes equivalent to the equality

$$H_{\alpha'}(\alpha';\alpha,\beta)|_{\alpha'=\alpha} = \tilde{G}_{\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta} = 0, \tag{66}$$

but also on the inequalities

$$H_{\alpha'\alpha'}(\alpha';\alpha,\beta)|_{\alpha'=\alpha} < 0 \text{ and } G_{\beta'\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta} < 0, \tag{67}$$

which, in general, may be different from the inequalities

$$H_{\alpha'\alpha'}(\alpha';\alpha,\beta)|_{\alpha'=\alpha} < 0 \text{ and } \tilde{G}_{\beta'\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta} < 0, \tag{68}$$

which are required for evolutionary stability of the inclusive fitness game, $\{H,\tilde{G}\}$. Moreover, examples can be constructed in which either $G_{\beta'\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta} > \tilde{G}_{\beta'\beta'}(\beta';\alpha,\beta)|_{\beta'=\beta}$, together with equations (65)–(66), or vice versa. This means that in such cases a pure, inevitably discord population state, $\{\alpha,\beta\}$, which is predicted to be evolutionarily stable by the inclusive fitness game, $\{H,\tilde{G}\}$, cannot, in fact, be maintained as a noninvadable monomorphic genetic equilibrium, or that a noninvadable monomorphic genetic equilibrium will not be predicted as stable by the inclusive fitness game $\{H, \tilde{G}\}$.

Yet, it is worth mentioning that this sort of possible inconsistency does not show up in any of the specific biological examples considered in this work or, indeed, in the more general regular case. In fact, as we saw in Regular Representations (expressions [57]–[59]), at any point $\{\alpha,\beta\}$ where equation (65) is satisfied we have that $G_{\beta'\beta'}|_{\beta'=\beta} < 0$ whenever $H_{\alpha'\alpha'}|_{\alpha'=\alpha} < 0$. On the other hand, it can be easily verified that at this point we also have $H_{\alpha'\alpha'}|_{\alpha'=\alpha} = \tilde{G}_{\beta'\beta'}|_{\beta'=\beta}$. Hence, in this case, equation (65) (or, equivalently, eq. [66]) and the condition on the second derivative of H are necessary and sufficient conditions for an *ESS* with either G or $\tilde{G}$ as the workers' payment function, which here become equivalent.

Uyenoyama and Bengtsson (1981) have shown that, under the assumption that

both φF and $\varphi(1 - F)$ are linear functions of β' (so that φ is also linear), stability at the workers' locus is correctly predicted, irrespective of the strength of selection, by the workers' inclusive fitness, as calculated with the appropriate regression coefficients (which under weak selection converge to $\tilde{G}$). As one can easily verify, the linearity assumption of Uyenoyama and Bengtsson, when applied to a normal representation, reduces to a special case of the regularity condition, under which the ESSs of $\{H,G\}$ are identical to those of $\{\tilde{H},\tilde{G}\}$.

In summary, we have found that with loose linkage and mutations of weak effect (1) the externally stable equilibria are always those that guarantee the simultaneous maximization of a pair of individual payment functions for the queen and the workers, thus formally corresponding to the asymmetric ESSs of game theory, (2) the queen's payment function always coincides with her inclusive fitness, (3) the workers' payment function in general is not the same as their inclusive fitness, but, under some conditions, the two functions completely agree with respect to ESSs, and (4) m-stability in the genetic model is always correctly predicted by the inclusive fitness.

The very correspondence of the genetic model with an asymmetric $\{H,G\}$ game is not preserved, however, when linkage between the queen's and workers' loci is tight. In this case, the family setting of the sex-ratio conflict cannot be neglected. As we have seen, the corresponding evolutionarily stable states are more accurately identified by the linkage-independent ESSs (the only stable states if linkage is absolute) where the single, two-party payment function, $T(\alpha',\beta';\alpha,\beta)$, is maximized (eqq. [17], [22]). Since the maximization of T implies that the individual payment functions, H and G, are also maximized, but not vice versa, the effect of extreme linkage is that of destroying the long-term genetic stability of some of the states that a game-theoretic analysis would predict as stable and that would be indeed stable if linkage between the relevant workers' and queen's loci were looser.

DISCUSSION

In this work we have attempted to employ an exact, two-locus genetic model to analyze the problem of queen-worker conflict over the sex ratio in social Hymenoptera, originally raised by Trivers and Hare (1976). We have assumed that the sex ratio among reproductives emerging from the nest is determined by both the phenotype of the queen and the average phenotype of the workers. The queen's phenotype is controlled by one locus, while another locus controls the phenotype of the workers. Any rate of recombination is permitted between the two loci. We have assumed, moreover, that the total success of the nest, in terms of the number of reproductives it releases, depends on the combination of the queen's and workers' phenotypes. More specifically, we were interested in a situation in which both the queen's and the workers' phenotypic traits under investigation could be interpreted as the sex ratio that each of the two parties would respectively "desire." We have assumed that, while the actual sex ratio in the nest would be a general function of the queen's and workers' desires, the total success of the nest would be, instead, a decreasing function of only the amount of disagreement

that of mutations for a single locus or for pairs of more loosely linked queen's and workers' loci, we have here the possibility that a long period of evolutionary stasis, due to persistence of a population in a state, $\{\alpha,\beta\}$, that maximizes H and G but not T, is followed, when the right mutations appear, by a relatively rapid bout of evolution toward a linkage-independent ESS corresponding to a maximum of T.

As we have shown, there are also cases in which no monomorphic ESS, either concord or discord, can possibly exist. Since our study is concerned only with stability of genetically monomorphic equilibria, we cannot say whether in these cases the sex-ratio conflict could be resolved by a genetically polymorphic, evolutionarily stable equilibrium or whether no distribution of workers' and queen's strategies can possibly be stable against all new mutations. In the latter case, a more or less chaotic cycling of long-term evolution is to be expected.

When monomorphic ESSs exist, which in our analysis appears to be the common case, the results indicate that, if the queen and the workers both have some power, the equilibrium sex ratio generally depends on the characteristics of the reproductive success of the nest, φ, which are obviously determined by numerous physiological and ecological factors. Since we expect these factors to vary considerably between taxa, we can see that a part of the large variability between average investment ratios of different ant species (Trivers and Hare 1976; Alexander and Sherman 1977; Nonacs 1986) might be explained by the hypothesis that such ratios reflect a compromise between the queen and the workers. Notice that, as observed by Alexander and Sherman (1977), the hypothesis of full workers' dominance by itself cannot explain interspecific variability. Consider also that, if queen and workers do compromise, some variance can still be expected even when ecological and physiological conditions are absolutely identical, because of the possibility of multiple discord ESSs and of a continuum of concord ESSs.

For the same reason the compromise hypothesis is in a better position than the workers' dominance hypothesis to explain, by itself, the widespread intercolony variability documented by Nonacs (1986) and other authors, if the peculiar character of this variability is taken into account. As reported by Nonacs (1986), the distribution of investment ratios appears to be bimodal, with concentrations of colonies towards extreme male and female biases, and, in addition, investment ratios seem to correlate with ecological conditions to which colonies are exposed. Suppose that, in agreement with one of the arguments proposed by Nonacs (1986), we admit that preferred investment ratios (sex ratios, in our model) can respond in a plastic (nongenetic) fashion to varying external conditions, as they are reflected in changes of the reproductive success of the nest. We can, then, easily extrapolate from our results the conjecture that the ESS investment ratios, when resulting from a compromise solution of the queen-workers conflict, will be correspondingly variable with the environment in a way that could be made to approximate the observed bimodality if appropriate patterns of environmental variability and physiological response were assumed.

We hope the method suggested here can be extended to deal with other components of the sex-ratio conflict in social Hymenoptera (e.g., polygyny, laying workers, multiple insemination), which are necessary for a satisfactory interpretation of the complex natural history of this phenomenon.

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APPENDIX

Transformations of Queen's and Workers' Phenotypes to Achieve Normality

We have to show that, if a representation of the sex-ratio conflict already satisfies the conditions of normality defined by properties 2, 3, and 4, then it can always be made to satisfy the additional property 6 by a suitable transformation of the queen's and workers' phenotypes.

Let us then denote by $\{\alpha^*,\beta^*\}$ the queen-worker phenotypic pair in the original scale of measurement, by Ω^* the set of genetically feasible phenotypic pairs, and by $\{F^*,\Delta^*\}$ the two functions defined in Ω^* to represent female proportion and nest disagreement, respectively. To show what we need, it is in fact sufficient to suppose that the following is true about $\{F^*,\Delta^*\}$:

Property A1. $F^* \uparrow$ in α^*,β^* strictly, continuous in Ω^*.
Property A2. $\Delta^* \uparrow$ in α^*, $\downarrow$ in β^* strictly, continuous in Ω^*.
Property A3. For every $v \in [0,1]$, there exists $\{\alpha^*,\beta^*\} \in \Omega^*$ such that $F^*(\alpha^*,\beta^*) = v$ and $\Delta^*(\alpha^*,\beta^*) = 0$.

Because of properties A1 and A2, the solution $\{\alpha^*,\beta^*\}$ of

$$F^*(\alpha^*,\beta^*) = v \text{ and } \Delta^*(\alpha^*,\beta^*) = 0 \tag{A1}$$

that, according to property A3, exists in Ω^* for any $v \in [0,1]$ must be unique for any given v. Thus, for any such v, let $\{\alpha^*(v),\beta^*(v)\}$ denote the corresponding solution of equation (A1). Furthermore, both $\alpha^*(v)$ and $\beta^*(v)$ must be continuous and strictly increasing in $v \in [0,1]$. Thus, the relation of $\{\alpha^*(v),\beta^*(v)\}$ to $v \in [0,1]$ defines, parametrically in v, a continuous, strictly increasing function $\delta(\cdot):[\alpha^*(0),\alpha^*(1)] \rightarrow [\beta^*(0),\beta^*(1)]$. Notice that, by definition of $\delta(\cdot)$, we have

$$\Delta(\alpha^*,\delta(\alpha^*)) = 0, \text{ for every } \alpha^* \in [\alpha^*(0),\alpha^*(1)]. \tag{A2}$$

Having defined $\delta(\cdot)$, we can define one more function, $f(\cdot):[\alpha^*(0),\alpha^*(1)] \rightarrow [0,1]$, by means of the relation

$$f(\alpha^*) = F(\alpha^*,\delta(\alpha^*)). \tag{A3}$$

By virtue of property A1 and of the properties of $\delta(\cdot)$, $f(\cdot)$ is also continuous and strictly increasing. The two functions, obviously, have continuous and strictly increasing inverses, δ^{-1} and f^{-1}. Observe that, since $\delta^{-1}(\cdot):[\beta^*(0),\beta^*(1)] \rightarrow [\alpha^*(0),\alpha^*(1)]$, the composite function $f(\delta^{-1}(\cdot))$ is also well defined, and $f(\delta^{-1}(\cdot)):[\beta^*(0),\beta^*(1)] \rightarrow [0,1]$. Thus, we now have a continuous, strictly increasing, and therefore one-to-one transformation, from points

$\{\alpha^*,\beta^*\} \in \Omega^*$ to points $\{\alpha,\beta\} \in [0,1]^2$, defined by

$$\begin{aligned} \alpha &= f(\alpha^*) \\ \beta &= f(\delta^{-1}(\beta^*)) \end{aligned} \quad \Leftrightarrow \quad \begin{aligned} \alpha^* &= f^{-1}(\alpha), \\ \beta^* &= \delta(f^{-1}(\beta)). \end{aligned} \tag{A4}$$

Obviously, this transformation is defined only for all points $\{\alpha^*,\beta^*\}$ that belong to the intersection of Ω^* and R^*, where $R^* = [\alpha^*(0),\alpha^*(1)] \times [\beta^*(0),\beta^*(1)]$. For simplicity, we make, therefore, the further assumption that

$$\Omega^* \supseteq R^* = [\alpha^*(0),\alpha^*(1)] \times [\beta^*(0),\beta^*(1)]. \tag{A5}$$

Under this hypothesis, equation A4 transforms R^* to $[0,1]^2$, and vice versa. Hence, equation A5 corresponds to property 7 of normal representations. With respect to the transformed phenotypic pair $\{\alpha,\beta\}$, the representation of the sex-ratio conflict $\{F,\Delta\}$ induced by $\{F^*,\Delta^*\}$ is

$$\begin{aligned} F(\alpha,\beta) &= F^*(f^{-1}(\alpha),\delta(f^{-1}(\beta))) \\ \text{and} \\ \Delta(\alpha,\beta) &= \Delta^*(f^{-1}(\alpha),\delta(f^{-1}(\beta))). \end{aligned} \tag{A6}$$

The representation $\{F,\Delta\}$ is defined for all $\{\alpha,\beta\} \in [0,1]^2$, because of equation A5, and shares with $\{F^*,\Delta^*\}$ the continuity and monotonicity implied by properties A1 and A2. In addition, it immediately follows from equations A2, A3, and A6 that, for every $\alpha \in [0,1]$,

$$\begin{aligned} \Delta(\alpha,\alpha) &= \Delta^*(f^{-1}(\alpha),\delta(f^{-1}(\alpha))) = 0 \\ \text{and} \\ F(\alpha,\alpha) &= F^*(f^{-1}(\alpha),\delta(f^{-1}(\alpha))) = f(f^{-1}(\alpha)) = \alpha. \end{aligned} \tag{A7}$$

Q.E.D.

LITERATURE CITED

Alexander, R. D., and P. W. Sherman. 1977. Local mate competition and parental investment in social insects. Science (Washington, D.C.) 196:494–500.

Benford, F. A. 1978. Fisher's theory of the sex ratio applied to the social Hymenoptera. Journal of Theoretical Biology 72:701–727.

Boomsma, J. J. 1989. Sex-investment ratios in ants: has female bias been systematically overestimated? American Naturalist 133:517–532.

Bourke, A. F. G. 1988. Worker reproduction in the higher eusocial Hymenoptera. Quarterly Review of Biology 63:291–311.

Bulmer, M. G. 1981. Worker-queen conflict in annual social Hymenoptera. Journal of Theoretical Biology 93:239–251.

———. 1983. The significance of protandry in social Hymenoptera. American Naturalist 121:540–551.

Bulmer, M. G., and P. D. Taylor. 1981. Worker-queen conflict and sex ratio theory in social Hymenoptera. Heredity 47:197–207.

Charlesworth, B. 1978. Some models of the evolution of altruistic behaviour between siblings. Journal of Theoretical Biology 72:297–319.

Charnov, E. L. 1978. Sex ratio selection in eusocial Hymenoptera. American Naturalist 112:317–326.

Christiansen, F. B. 1991. On conditions for evolutionary stability for a continuously varying character. American Naturalist 138:37–50.

Crozier, R. H. 1970. Coefficients of relationship and the identity of genes by descent in the Hymenoptera. American Naturalist 104:216–217.

Eshel, I. 1983. Evolutionary and continuous stability. Journal of Theoretical Biology 103:99–111.

———. 1985. Evolutionary genetic stability of Mendelian segregation and the role of free recombination in the chromosomal system. American Naturalist 125:412–420.

Eshel, I., and M. W. Feldman. 1982*a*. On evolutionary genetic stability of the sex ratio. Theoretical Population Biology 21:430–439.

———. 1982*b*. On the evolution of sex determination and the sex ratio in haplodiploid populations. Theoretical Population Biology 21:440–450.

———. 1984. Initial increase of new mutants and some continuity properties of ESS in two-locus systems. American Naturalist 124:631–640.

———. 1991. The handicap principle in parent-offspring conflict: comparison of optimality and population-genetic analyses. American Naturalist 137:167–185.

Eshel, I., and U. Motro. 1981. Kin selection and strong evolutionary stability of mutual help. Theoretical Population Biology 19:420–433.

Eshel, I., and D. Weinshall. 1987. Sexual reproduction and viability of future offspring. American Naturalist 130:775–787.

Feldman, M. W., and I. Eshel. 1982. On the theory of parent-offspring conflict: a two-locus genetic model. American Naturalist 119:285–292.

Fisher, R. A. 1958. The genetical theory of natural selection. 2d ed. Dover, New York.

Forsyth, A. 1981. Sex ratio and parental investment in an ant population. Evolution 35:1252–1253.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. Journal of Theoretical Biology 7:1–52.

———. 1967. Extraordinary sex ratios. Science (Washington, D.C.) 156:477–488.

———. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature (London) 228: 1218–1220.

———. 1972. Altruism and related phenomena, mainly in social insects. Annual Review of Ecology and Systematics 3:193–232.

Karlin, S., and S. Lessard. 1983. On the optimal sex ratio. Proceedings of the National Academy of Sciences of the USA 80:5931–5935.

———. 1986. Theoretical studies on sex ratio evolution. Princeton University Press, Princeton, N.J.

Lessard, S. 1984. Evolutionary dynamics in frequency-dependent two-phenotype models. Theoretical Population Biology 25:210–234.

MacNair, M. R. 1978. An ESS for the sex ratio in animals with particular reference to the social Hymenoptera. Journal of Theoretical Biology 70:449–459.

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. Journal of Theoretical Biology 47:209–221.

———. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.

Maynard Smith, J., and G. A. Parker. 1976. The logic of asymmetric contests. Animal Behaviour 24:159–175.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature (London) 246:15–18.

Michod, R. E., and W. D. Hamilton. 1980. Coefficients of relatedness in sociobiology. Nature (London) 288:694–697.

Nonacs, P. 1986. Ant reproductive strategies and sex allocation theory. Quarterly Review of Biology 61:1–21.

Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in social insects. Princeton University Press, Princeton, N.J.

Oster, G., I. Eshel, and D. Cohen. 1977. Worker-queen conflict and the evolution of social insects. Theoretical Population Biology 12:49–85.

Owen, R. E., and R. C. Plowright. 1982. Worker-queen conflict and male parentage in bumble bees. Behavioral Ecology and Sociobiology 7:287–291.

Pamilo, P. 1982. Genetic evolution of sex ratios in eusocial Hymenoptera: allele frequency simulations. American Naturalist 119:638–656.

Selten, R. 1980. A note on evolutionarily stable strategies in asymmetric animal conflicts. Journal of Theoretical Biology 84:93–102.

Taylor, P. D. 1981. Sex ratio compensation in ant populations. Evolution 35:1250–1251.

———. 1988. Inclusive fitness models with two sexes. Theoretical Population Biology 34:145–168.

———. 1989. Evolutionary stability in one-parameter models under weak selection. Theoretical Population Biology 36:125–143.

Trivers, R. L., and H. Hare. 1976. Haplodiploidy and the evolution of social insects. Science (Washington, D.C.) 191:249–263.

Uyenoyama, M. K., and B. O. Bengtsson. 1981. Towards a genetic theory for the evolution of the sex ratio. II. Haplodiploid and diploid models with sibling and parental control of the brood sex ratio and brood size. Theoretical Population Biology 20:57–79.

Uyenoyama, M. K., and M. W. Feldman. 1981. On relatedness and adaptive topography in kin selection. Theoretical Population Biology 19:87–123.

Weinshall, D., and I. Eshel. 1987. On the evolution of an optimal rate of sexual reproduction. American Naturalist 130:758–774.

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