

Laws of Adaptation

A course on biological evolution in eight lectures
by Carlo Matessi

Lecture 6

about (numerical) equality of the sexes, or evolution of the sex-ratio

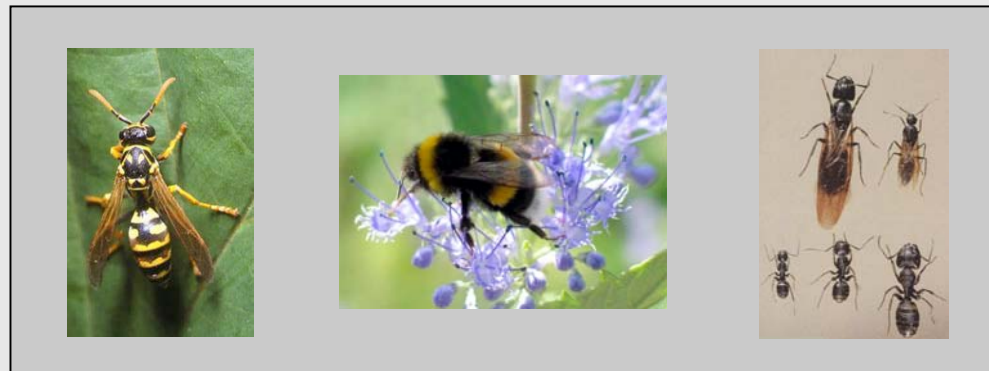
Monday October 16, 13:00-14:00

Adaptive value of the sex-ratio

- ❖ The sex-ratio is perhaps the most heavily studied topic in the mathematical theory of evolution. The first and most pressing question, raised already by Darwin and unanswered till Fisher (1930), is why most organisms with sexual reproduction, both animal and plants, have equal proportions of adult females and males in their natural populations?



- ❖ Once a satisfactory answer to this question was identified, the issue of sex-ratio has become a sharp probe by which the theory of evolution through natural selection could be subjected to critical tests, the new questions posed being whether the same method and type of argument could equally well explain a few odd deviations from a 1:1 sex-ratio that occur in special ecological conditions (Hamilton, 1967), and even whether certain as yet unobserved deviations, that could be predicted by the theory under certain conditions, were indeed identifiable in nature (Trivers and Hare, 1976)



Why a 1:1 sex-ratio?

- ❖ Consider a population where all newborn of a given sex have the same chance, however small, to enter the group of adults of that sex that will mate and give birth to the offspring of next generation (*outbreeding population*)
- ❖ Suppose now that in the population there are more males than females, and consider a parent that has the opportunity to choose the sex of her next offspring
- ❖ Clearly, if her intent is to have as many grandchildren as possible, she should choose a female, because any particular individual of this sex has a greater chance than any specific male to become one of the mating adults of her generation, given that she should be chosen at random from among a smaller cohort of individuals
- ❖ As a consequence of this choice this particular parent is likely to have, in future generations, more descendants than other members of the population that stick to the population habit of preferring males. In other terms, this parent has a greater fitness, as measured, not by the number of children, which is the same for all, but by the number of grandchildren
- ❖ But if selection, by this argument, favours this behaviour, it follows that as a result the proportion of females will increase until the advantage due to being the minority sex disappears at a sex-ratio of 1:1. Of course the same argument, turned in favour of males, would hold in a population where the females were the majority

- ❖ The literature on the mathematical theory of the evolution of sex-ratio in outbreeding populations is impressive. Besides a very large number of papers, it includes two monographs: Charnov (1982), “The Theory of Sex Allocation”, centered on the ESS approach and addressing a variety of organisms and life cycles; Karlin and Lessard (1986), “Sex Ratio Evolution”, characterized by a thorough and rigorous analysis of a broad spectrum of one-gene and multi-gene models, following mostly a short term dynamic approach but with several openings on the long term approach

An elementary ESS analysis (Shaw and Mohler, 1953; Maynard Smith, 1982)

- ❖ ϵ : proportion of mutant parents
- ❖ m, f : mean number of males, females in the brood of mutant parents; $m+f=N$; $\sigma' = \frac{m}{N}$
- ❖ M, F : mean no of males, females in the brood of resident (majority) parent; $M+F=N$; $\sigma = \frac{M}{N}$
- ❖ mean proportion of males in brood of average parent: $\bar{\sigma} = \epsilon\sigma' + (1 - \epsilon)\sigma$
- ❖ Fitness of mutants (probability that a random member of the grandchildren generation descends from mutant):

$$W(\sigma', \bar{\sigma}) \propto \frac{m}{\epsilon m + (1 - \epsilon)M} + \frac{f}{\epsilon f + (1 - \epsilon)F} = \frac{\sigma'}{\bar{\sigma}} + \frac{1 - \sigma'}{1 - \bar{\sigma}}$$

- ❖ Therefore

$$W(\sigma', \bar{\sigma}) > W(\bar{\sigma}, \bar{\sigma}) \quad \text{iff} \quad \frac{\sigma'}{\bar{\sigma}} + \frac{1 - \sigma'}{1 - \bar{\sigma}} > 2 \quad \text{or} \quad (\sigma' - \bar{\sigma})(1 - 2\bar{\sigma}) > 0 \quad \Rightarrow \quad \sigma' \text{ invades if}$$

$\bar{\sigma} < \frac{1}{2}$ and $\sigma' > \bar{\sigma}$

or

$\bar{\sigma} > \frac{1}{2}$ and $\sigma' < \bar{\sigma}$

- ❖ moreover

$$\left. \frac{\partial W(\sigma', \bar{\sigma})}{\partial \sigma'} \right|_{\sigma'=\sigma} = \left. \frac{\partial W(x, y)}{\partial x} \right|_{x=y=\sigma} + \left. \frac{\partial W(x, y)}{\partial y} \right|_{x=y=\sigma} \frac{\partial \bar{\sigma}}{\partial \sigma'} = \frac{1 - 2\sigma}{\sigma(1 - \sigma)} + O(\epsilon)$$

$$\therefore \text{ as } \epsilon \rightarrow 0, \quad \left. \frac{\partial W(\sigma', \bar{\sigma})}{\partial \sigma'} \right|_{\sigma'=\sigma} = 0 \quad \text{iff} \quad \sigma = \sigma^\circ = \frac{1}{2}$$

- ❖ and σ° cannot be invaded because if $\bar{\sigma} = \epsilon\sigma' + (1 - \epsilon)\sigma^\circ = \epsilon\sigma' + (1 - \epsilon)\frac{1}{2}$ then $W(\sigma', \bar{\sigma}) < W(\bar{\sigma}, \bar{\sigma}) \quad \forall \sigma' \neq \sigma^\circ$

so that σ' is unable to invade. Conclude that σ° is a continuously stable ESS

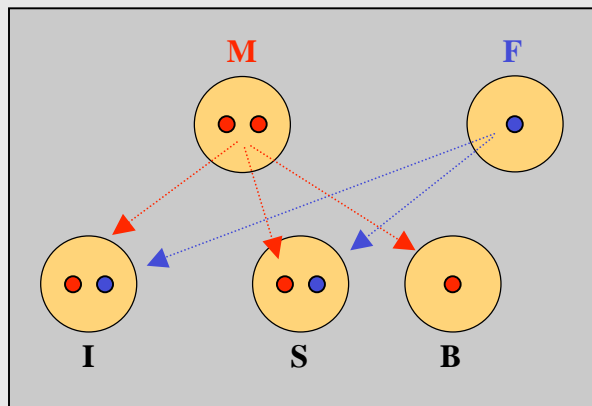
Extremely biased sex-ratios in parasitoid wasps (Hamilton, 1967)

- ❖ Parasitoid wasps inject eggs in larvae or pupae of other insects. The offspring of one, or few female wasps grow at the expenses of the parasitized individual
- ❖ Once they emerge as adults, they mate among themselves before the females disperse to found new “colonies”
- ❖ In these wasps, and other insects with a similar life cycle where matings occur within small groups formed by the offspring of one or few females, the sex-ratio is very biased in favour of females
- ❖ As demonstrated by Hamilton, by a numerical analysis that anticipates the long term point of view and introduces for the first time the notion of LTE (and ESS) under the name of “*Unbeatable Strategy*”, under these ecological conditions, to maximize the number of her grandchildren a female wasp should maximize the number of fertilized daughters, which requires to reduce the number of sons to the minimum (e.g., *one*) necessary to fertilize all newborn females in the colony (possibly even those born to the few other wasps that might have joined the founder)
- ❖ Several papers, adopting a long-term approach (Bulmer, 1986; Courteau and Lessard, 2000) have refined this analysis and identified exact LTE and their stability properties in a variety of situations (e.g., as a function of the number of cofoundresses and of the dispersal and mating patterns of newborn)



Female biased sex-ratios in social Hymenoptera (Trivers and Hare, 1976)

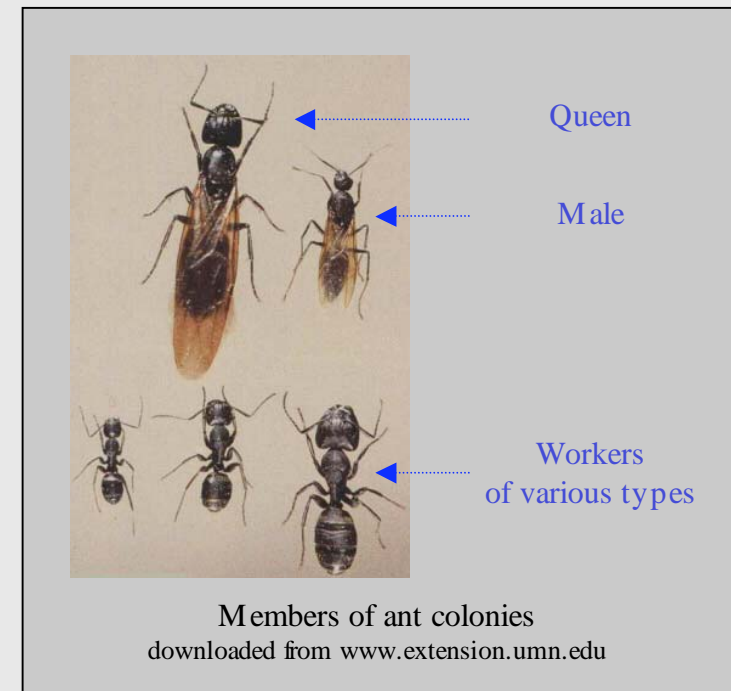
- ❖ Hymenoptera have a peculiar mode of sex determination (*haplodiploidy*): while females are born from regularly fertilized eggs and therefore carry genes from mother and father in equal proportions, males instead are born from unfertilized eggs and carry only genes from the mother



- ❖ As a consequence, females are more genetically related (higher degree of consanguinity) to sisters than to brothers
- ❖ In fact the relatedness of females to sisters stands in the ratio of 3:1 to the relatedness to brothers
- ❖ *Relatedness*: $R_{AB} = \Pr\{\text{random gene of A is identical by descent to a gene of B}\}$

$$R_{IS} = \frac{1}{2} \times \frac{1}{2} + \frac{1}{2} \times 1 = \frac{3}{4} \quad ; \quad R_{IB} = \frac{1}{2} \times \frac{1}{2} + \frac{1}{2} \times 0 = \frac{1}{4} \quad ; \quad R_{MS} = R_{MB} = \frac{1}{2}$$

- ❖ Sex-ratio distortion: worker females, that can affect sex-ratio of reproductives through differential care of larvae, can foster the multiplication of genes identical by descent to their owns, by favouring the production of sisters and brothers in the same ratio as their relatedness to them



An elementary ESS analysis

- ❖ Payoff functions for mutants of sex-ratio control:

$$\text{Queen : } W_Q(\sigma', \bar{\sigma}) \propto \frac{1}{2} \frac{\sigma'}{\bar{\sigma}} + \frac{1}{2} \frac{1-\sigma'}{1-\bar{\sigma}} \Rightarrow W_Q(\sigma', \bar{\sigma}) > W_Q(\bar{\sigma}, \bar{\sigma}) \text{ iff } (\sigma' - \bar{\sigma})(1 - 2\bar{\sigma}) > 0$$

$$\text{Worker : } W_W(\sigma', \bar{\sigma}) \propto \frac{1}{4} \frac{\sigma'}{\bar{\sigma}} + \frac{3}{4} \frac{1-\sigma'}{1-\bar{\sigma}} \Rightarrow W_W(\sigma', \bar{\sigma}) > W_W(\bar{\sigma}, \bar{\sigma}) \text{ iff } (\sigma' - \bar{\sigma})(1 - 4\bar{\sigma}) > 0$$

- ❖ Hence the sex-ratio should evolve to different ESS, depending on whether its control is of the queen or of the workers

$$\text{Queen control: } \sigma_Q^o = \frac{1}{2}$$

$$\text{Workers control: } \sigma_W^o = \frac{1}{4}$$

Long-term evolution of the queen-worker sex-ratio conflict

(Matessi and Eshel, 1992)

General form of haplodiploid (short-term) selection dynamics

- ❖ $\{X_1(t), \dots, X_m(t)\}$, $\{Y_1(t), \dots, Y_m(t)\}$: adult, newborn frequencies of female types $\{1, \dots, m\}$ at generation $t=0, 1, \dots$
- ❖ $\{U_1(t), \dots, U_n(t)\}$, $\{V_1(t), \dots, V_n(t)\}$: adult, newborn frequencies of male types $\{1, \dots, n\}$ at generation $t=0, 1, \dots$
- ❖ $f_{ij}(k)$: mean number of females type k born to mother type i and father type j
- ❖ $h_{ij}(k)$: mean number of males type k born to mother type i and father type j
- ❖ w_i , s_i : probability that newborn female, male type i survives to reproduce

	newborn	→	adults	mean fitness
females	$Y_i(t+1) = \frac{\sum_j \sum_k X_j(t) U_k(t) f_{jk}(i)}{\sum_1 \sum_j \sum_k X_j(t) U_k(t) f_{jk}(1)}$		$X_i(t+1) = \frac{w_i Y_i(t+1)}{\sum_j w_j Y_j(t+1)}$	$\bar{w}(t) = \sum_i \sum_j \sum_k w_i X_j(t) U_k(t) f_{jk}(i)$
males	$V_i(t+1) = \frac{\sum_j \sum_k X_j(t) U_k(t) h_{jk}(i)}{\sum_1 \sum_j \sum_k X_j(t) U_k(t) h_{jk}(1)}$		$U_i(t+1) = \frac{s_i V_i(t+1)}{\sum_j s_j V_j(t+1)}$	$\bar{s}(t) = \sum_i \sum_j \sum_k s_i X_j(t) U_k(t) h_{jk}(i)$

A genetic model of sex-ratio control by queens and workers

- ❖ $\alpha \in [0,1]$: queen control effort; a continuous trait that affects sex-ratio, expressed by the queen
- ❖ $\beta \in [0,1]$: worker control effort; a continuous trait that affects sex-ratio, expressed by each worker
- ❖ $F(\alpha,\beta) \in [0,1]$: proportion of females in a colony where the queen effort is α and the *mean* worker effort is β ;
 $F(\alpha,\beta) \uparrow$ in α,β
- ❖ $\varphi(\alpha,\beta) \in [0,1]$: relative reproductive success of a colony where the queen effort is α and the *mean* worker effort is β
- ❖ $\forall u \in [0,1]$ there is a pair (α,β) such that $F(\alpha,\beta)=u$ and $\varphi(\alpha,\beta)=1$
- ❖ There is a function $\Delta(\alpha,\beta) \in (-\infty,\infty)$ such that: (i) $\varphi(\alpha,\beta) = \varphi(\Delta(\alpha,\beta))$; (ii) $\Delta(\alpha,\beta) \uparrow$ in α , \downarrow in β ; (iii) $\varphi(\Delta) \downarrow$ in $|\Delta|$ and $\varphi(0)=1$; in other words, $\Delta(\alpha,\beta)$ is a measure of the contrast between workers and queen with respect to colony sex-ratio, as a consequence of which colony productivity is reduced
- ❖ Consider a population monomorphic for the pair $\{\alpha,\beta\}$ and suppose that a mutation event occurs that simultaneously introduces, in a small minority of individuals, a mutant allele **a** of a gene for queen control, of which the resident allele is A, and a mutant allele **b** of a gene for worker control, of which the resident allele is B. Let r be the recombination rate between the two genes
- ❖ After this mutation occurs we have to consider the following new genotypes in the population

genotype	females			males		
	a B AB	A b AB	a b AB	a B	A b	a b
Q phenotype	α'	α	α'			
W phenotype	β	β'	β'			
frequency	$\varepsilon_1(t)$	$\varepsilon_2(t)$	$\varepsilon_3(t)$	$\delta_1(t)$	$\delta_2(t)$	$\delta_3(t)$

where : $\sum_i \varepsilon_i(t) = \varepsilon(t) \cong 0$; $\sum_i \delta_i(t) = \delta(t) \cong 0$

Mating pairs and their offspring

mating	frequency	females				males				proportion of females	productivity
		$\frac{AB}{AB}$	$\frac{Ab}{AB}$	$\frac{aB}{AB}$	$\frac{ab}{AB}$	AB	Ab	aB	ab		
$\frac{Ab}{AB} \times AB$	$\varepsilon_1(t) + O(\varepsilon(t)\delta(t))$	$\frac{1}{2}$	$\frac{1}{2}$	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	$F\left(\alpha, \frac{\beta + \beta'}{2}\right)$	$\varphi\left(\alpha, \frac{\beta + \beta'}{2}\right)$
$\frac{AB}{AB} \times Ab$	$\delta_1(t) + O(\varepsilon(t)\delta(t))$	0	1	0	0	1	0	0	0	$F(\alpha, \beta')$	$\varphi(\alpha, \beta')$
$\frac{aB}{AB} \times AB$	$\varepsilon_2(t) + O(\varepsilon(t)\delta(t))$	$\frac{1}{2}$	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	$F(\alpha', \beta)$	$\varphi(\alpha', \beta)$
$\frac{AB}{AB} \times aB$	$\delta_2(t) + O(\varepsilon(t)\delta(t))$	0	0	1	0	1	0	0	0	$F(\alpha, \beta)$	$\varphi(\alpha, \beta)$
$\frac{ab}{AB} \times AB$	$\varepsilon_3(t) + O(\varepsilon(t)\delta(t))$	$\frac{1-r}{2}$	$\frac{r}{2}$	$\frac{r}{2}$	$\frac{1-r}{2}$	$\frac{1-r}{2}$	$\frac{r}{2}$	$\frac{r}{2}$	$\frac{1-r}{2}$	$F\left(\alpha', \frac{\beta + \beta'}{2}\right)$	$\varphi\left(\alpha', \frac{\beta + \beta'}{2}\right)$
$\frac{AB}{AB} \times ab$	$\delta_3(t) + O(\varepsilon(t)\delta(t))$	0	0	0	1	1	0	0	0	$F(\alpha, \beta')$	$\varphi(\alpha, \beta')$
$\frac{AB}{AB} \times AB$	$1 - \varepsilon(t) - \delta(t) + O(\varepsilon(t)\delta(t))$	1	0	0	0	1	0	0	0	$F(\alpha, \beta)$	$\varphi(\alpha, \beta)$
other	$O(\varepsilon(t)\delta(t))$										

female mean fitness: $\bar{w}(t) = F(\alpha, \beta)\varphi(\alpha, \beta) + O(\varepsilon(t) + \delta(t))$

male mean fitness: $\bar{s}(t) = [1 - F(\alpha, \beta)]\varphi(\alpha, \beta) + O(\varepsilon(t) + \delta(t))$

❖ Consequently, the linearized system of recurrence equations, has the following form

$$\boldsymbol{\omega}(t+1) = \begin{pmatrix} \varepsilon_1(t+1) \\ \delta_1(t+1) \\ \varepsilon_2(t+1) \\ \delta_2(t+1) \\ \varepsilon_3(t+1) \\ \delta_3(t+1) \end{pmatrix} = \begin{pmatrix} a_1 & a_2 & 0 & 0 & d_1 & 0 \\ a_3 & 0 & 0 & 0 & d_2 & 0 \\ 0 & 0 & b_1 & b_2 & t_1 & 0 \\ 0 & 0 & b_3 & 0 & d_2 & 0 \\ 0 & 0 & 0 & 0 & c_1 & c_2 \\ 0 & 0 & 0 & 0 & c_3 & 0 \end{pmatrix} \begin{pmatrix} \varepsilon_1(t) \\ \delta_1(t) \\ \varepsilon_2(t) \\ \delta_2(t) \\ \varepsilon_3(t) \\ \delta_3(t) \end{pmatrix} = \mathbf{A}\boldsymbol{\omega}(t)$$

where :

$$a_1 = \frac{1}{2} \frac{\varphi\left(\alpha, \frac{\beta+\beta'}{2}\right) F\left(\alpha, \frac{\beta+\beta'}{2}\right)}{\varphi(\alpha, \beta) F(\alpha, \beta)}$$

$$a_2 = \dots$$

$$\dots$$

- ❖ The resident sex-ratio control policy, $\{\alpha, \beta\}$, is a LTE if the *dominant* eigenvalue, $\lambda > 0$, of the transition matrix \mathbf{A} is less than 1 (and only if $\lambda \leq 1$), because in this case $\boldsymbol{\omega}(t) \rightarrow 0$ as $t \rightarrow \infty$, for all possible mutant policies $\{\alpha', \beta'\} \neq \{\alpha, \beta\}$
- ❖ Due to the block triangular form of \mathbf{A} , its eigenvalues coincide with those of the three diagonal 2×2 submatrices. Thus, if $\lambda_1, \lambda_2, \lambda_3$ denote the *dominant* eigenvalues of these submatrices, we see that $\{\alpha, \beta\}$ is a LTE if $\lambda_i < 1$ for $i=1,2,3$, for all mutant policies $\{\alpha', \beta'\} \neq \{\alpha, \beta\}$. Straightforward calculations show that these three conditions can be expressed as

$$(i) G(\beta'; \alpha, \beta) < 1 \quad , \quad (ii) H(\alpha'; \alpha, \beta) < 1 \quad , \quad (iii) (1-r)T(\alpha', \beta'; \alpha, \beta) < 1 \quad , \quad \forall \{\alpha', \beta'\} \neq \{\alpha, \beta\}$$

where

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

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

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

$$(i) G(\beta'; \alpha, \beta) < 1 \quad , \quad (ii) H(\alpha'; \alpha, \beta) < 1 \quad , \quad (iii) (1-r)T(\alpha', \beta'; \alpha, \beta) < 1 \quad , \quad \forall \{\alpha', \beta'\} \neq \{\alpha, \beta\}$$

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

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

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

❖ Notice that $G(\beta; \alpha, \beta) = H(\alpha; \alpha, \beta) = T(\alpha, \beta; \alpha, \beta) = 1$

❖ Hence the conditions for $\{\alpha, \beta\}$ to be a LTE can be written as

$$(i) G(\beta; \alpha, \beta) = \max_{\beta'} G(\beta'; \alpha, \beta) \quad ,$$

$$(ii) H(\alpha; \alpha, \beta) = \max_{\alpha'} H(\alpha'; \alpha, \beta) \quad ,$$

$$(iii) T(\alpha, \beta; \alpha, \beta) > (1 - r)T(\alpha', \beta'; \alpha, \beta) \quad , \quad \forall \{\alpha', \beta'\} \neq \{\alpha, \beta\}$$

❖ However, if we assume that mutations always have a small effect, so that $\{\alpha', \beta'\} \approx \{\alpha, \beta\}$, the third condition is always satisfied, unless recombination is too small ($r \approx 0$), or there are genes that simultaneously affect both the queen and the worker sex-ratio control activities ($r=0$)

❖ In the latter case the third condition obviously reduces to

$$(iv) T(\alpha, \beta; \alpha, \beta) = \max_{\alpha', \beta'} T(\alpha', \beta'; \alpha, \beta)$$

❖ But observe that $T(\alpha, \beta'; \alpha, \beta) \equiv G(\beta'; \alpha, \beta)$ and $T(\alpha', \beta; \alpha, \beta) \equiv H(\alpha'; \alpha, \beta)$, so that if (iv) is satisfied, (i) and (ii) are also satisfied

❖ Hence, for $r=0$, the only condition of LTE is maximization of T with respect to α' and β' simultaneously

Queen and worker power of sex-ratio control

- Assume that the functions F , φ and Δ are smooth. For any control policy $\{\alpha, \beta\}$ adopted by a colony, we can reasonably define the queen and worker “relative power” as follows

$$\text{Queen power: } p(\alpha, \beta) = \frac{\frac{F_\alpha}{\Delta_\alpha}}{\frac{F_\alpha}{\Delta_\alpha} - \frac{F_\beta}{\Delta_\beta}} \quad ; \quad \text{Worker power: } q(\alpha, \beta) = \frac{-\frac{F_\beta}{\Delta_\beta}}{\frac{F_\alpha}{\Delta_\alpha} - \frac{F_\beta}{\Delta_\beta}} = 1 - p(\alpha, \beta)$$

where $F_\alpha \equiv \frac{\partial F(\alpha, \beta)}{\partial \alpha}$, $\Delta_\alpha \equiv \frac{\partial \Delta(\alpha, \beta)}{\partial \alpha}$, ...

- By the assumptions on F and Δ , we see that $0 \leq p(\alpha, \beta) \leq 1$ and $0 \leq q(\alpha, \beta) \leq 1$ for all policies $\{\alpha, \beta\}$

Characterization of LTE of the queen-worker sex-ratio conflict

- Suppose that $\{\alpha, \beta\}$ is a LTE strictly internal to $[0, 1]^2$. Then, irrespective of the recombination rate, it must satisfy

$$G_\beta = \frac{3 - 4F}{4F(1 - F)} F_\beta + \frac{\varphi'(\Delta)}{\varphi(\Delta)} \Delta_\beta = 0 \quad , \quad H_\alpha = \frac{1 - 2F}{2F(1 - F)} F_\alpha + \frac{\varphi'(\Delta)}{\varphi(\Delta)} \Delta_\alpha = 0$$

where $H_\alpha \equiv \frac{\partial H(\alpha'; \alpha, \beta)}{\partial \alpha'} \Big|_{\alpha'=\alpha}$, $G_\beta \equiv \frac{\partial G(\beta'; \alpha, \beta)}{\partial \beta'} \Big|_{\beta'=\beta}$, ...

all functions being evaluated at (α, β) . These equations by simple manipulations are reduced to

$$F(\alpha, \beta) = \frac{1}{2} p(\alpha, \beta) + \frac{3}{4} q(\alpha, \beta) \quad , \quad \frac{\varphi'(\Delta)}{\varphi(\Delta)} = \frac{pq}{4F(1 - F)} \left[\frac{F_\alpha}{\Delta_\alpha} - \frac{F_\beta}{\Delta_\beta} \right]$$

- Recalling the properties of F , p , q , Δ and φ , we can conclude that at an internal LTE:

- (i) the proportion of females may vary anywhere between 1/2 and 3/4, depending on the relative power of queen and workers;
- (ii) this result is achieved necessarily with a cost to the colony, because the maximum colony productivity obtains only at $\Delta=0$, where $\varphi'(\Delta)=0$, although there exist a different policy $\{\alpha', \beta'\}$ where the same sex-ratio would be realized

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

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

Comparison with the ESS analysis

- ❖ Taking into account the fact that not all policies have the same number of offspring emerging from the colony, due to the contrast between queen and workers, the payoff functions proposed in the ESS approach for queen and workers are

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

$$W_W(\beta'; \alpha, \beta) = \frac{\varphi(\alpha, \beta')}{\varphi(\alpha, \beta)} \left[\frac{3}{4} \frac{F(\alpha, \beta')}{F(\alpha, \beta)} + \frac{1}{4} \frac{1 - F(\alpha, \beta')}{1 - F(\alpha, \beta)} \right] \neq G(\beta'; \alpha, \beta)$$

- ❖ However, although G and W_W are quite different, they agree entirely in their derivatives (evaluated at $\beta' = \beta$), so that the ESS payoff function can produce correctly the direction of evolutionary change and the possible locations of internal LTE
- ❖ What the ESS analysis, in general, cannot identify correctly is whether a stationary point of G is indeed a LTE, because this requires a consideration of second derivatives
- ❖ In addition, no attempt has ever been made to deal, from the point of view of ESS analysis, with the case of double mutation with small recombination, or of genes influencing simultaneously both partners of the conflict. It is not clear even if a meaningful fitness function, corresponding to our $T(\alpha', \beta', \alpha, \beta)$, could be proposed in such case