

An introduction to the evolutionary modelling of conflict

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Purpose :

- Offer a "how-to" approach to the evolutionary analysis of conflict.
- Make you understand
 - why the methods introduced by Steve Frank are more powerful than both game theory and inclusive fitness theory
 - why the use of classical inclusive fitness theory (i.e. Hamilton's rule) requires much caution and why some of its assumptions are often violated; you will see that Frank's methods can solve problems where Hamilton's rule fails
 - why the concept of relatedness may have several meanings
- Illustrate Frank's approach using several real-life problems :
 - social interactions between two players (e.g. siblicide in parasitoid wasps, Section 1)
 - worker reproduction (Section 2)
 - conflict over caste fate in social insects (Section 3)
- Each section of this handout is accompanied by a *Mathematica* sheet that offers easy analysis of each problem. These are available at <http://www.shef.ac.uk/uni/projects/taplab/twpub.html#courses>

Section 1. Two-player games

In this first section we will use the simple two-player game as a basis to introduce Frank's methods. This allows us to demonstrate how his approach is related to game theory and kin selection. A relevant paper that you could read beforehand is Wenseleers & Ratnieks (submitted) "*Towards a general theory of conflict: the sociobiology of mendelian segregation*".

Biological examples :

As biological examples of two-player games you can think of two males that may either fight (play "hawk") or cooperate (play "dove") when they compete for mates, of two ant queens that may either cooperate or fight during nest founding or of 2 parasitoid larvae that may either kill or tolerate each other within their host (Godfray 1987). Note that the players can be of any kind, e.g. it could also be two groups or nations, or two homologous chromosomes at a locus that compete for gamete production (Wenseleers & Ratnieks, submitted). That is, concepts of cooperation and conflict apply at any level.

Below we will use two simple games to introduce the method; in the Questions & Answers section you can find applications to related problems (e.g. reciprocal altruism and siblicide in parasitoid wasps).

Assumptions :

We first assume that any individual (or group, or cell, or chromosome) can adaptively adjust its probability of cooperating. This model derives what is referred to as a *mixed ESS*. In genetic terms, it assumes that there are an infinite number of alleles each specifying a particular probability of cooperating, and that the allele that fixates near the ESS cannot be invaded by any

other allele that specifies a slightly different probability of cooperating. The mixed ESS therefore corresponds to a situation with *weak selection* (population geneticists often use the term '*low penetrance*', i.e. a situation in which any invading allele has very small selective effects). In a second model we assume that any player is either of the cooperative or the defecting type and that the equilibrium will then consist of a stable mix between the two. This situation is referred to as a *pure or discrete ESS* model. Population geneticists call this a '*high penetrance*' model, because alleles in this case have large effects, and selection can no longer be assumed to be weak. It is also for this case that Hamilton's rule has been shown to fail (Bulmer 1994, p. 193-194).

In both models we assume that both players are members of the same species and that payoffs are symmetrical. That is, that the payoffs to player 1 when it fights player 2 are the same as the payoffs to player 2 when it fights player 1.

In a third model it is shown how asymmetrical payoffs can be accommodated for and how the method can be extended to illuminate interactions between different species.

1.1 Mixed ESS model

Parameters:

w_1 = direct fitness of player 1

w_2 = direct fitness of player 2

y_1 = phenotype of player 1 (probability of cooperating)

y_2 = phenotype of player 2 (probability of cooperating)

g_1 = genotype or breeding value (predictor of phenotype) of player 1

g_2 = genotype/breeding value of player 2

B = benefit of having a cooperative partner

C = cost of cooperating

r = relatedness between the two players

Let us consider the following payoff matrix:

		PLAYER 2	
		Defect	Cooperate
PLAYER 1	Defect	0	B
	Cooperate	-C	B-C

(payoffs are to player 1)

As we will see, it is this payoff matrix that is implicit in Hamilton's rule. A specific property of this matrix is that the behaviour of each player is taken to have additive effects on the focal player's reproduction. This assumption, as we will see, is often violated.

Frank's approach for calculating when a particular behaviour is favoured has 3 steps:

1. Write an individual's direct fitness w as a function of its own behaviour and the behaviour of social interactants. Direct fitness is what Hamilton (1964) called 'neighbour modulated fitness'.
2. Calculate when having the gene for the behaviour has positive effects on your own reproduction. Formally, this is done by checking when the regression (or the analytical equivalent – the total derivative) of individual fitness w on individual genotype g (or breeding value, as in quantitative genetics) is positive. If phenotypes of social interactants influence the focal player's fitness, then these will enter the equation as indirect effects. The rationale for this method stems from the Price equation (Frank 1997a, b; 1998).
3. The obtained equation says when a particular behaviour is favoured; setting the equation to zero allows the derivation of the equilibrium, i.e. the ESS.

A note on direct and inclusive fitness

For now, we will assume that all individuals express the altruistic (or other) trait under study. The type of social selection that then occurs is sometimes referred to as 'correlated selection' (Frank 1997a, 1998) because the relatedness coefficient that arises in this context measures phenotypic correlation in behaviour between social interactants (also see Queller 1984). Problems of this type are most intuitively looked at from a neighbour modulated or direct fitness angle. In Section 3 we will look at a problem where the class of individuals that expresses the trait influences the direct fitness of a passive class of relatives. In that case, an inclusive fitness perspective is more appropriate - it is genuine 'kin selection' (Frank 1997a, 1998). In fact, most of the classical problems in social evolution are of this type, e.g. worker policing where workers eat nephews to the benefit of brothers; workers express the trait, and nephews and brothers are affected, but do not themselves have any phenotype. The passive class does not express the gene under study but may transmit copies of the actor's genes.

Step 1: write the individual reproductive success of both players as a function of the behaviour of each :

From the matrix above, the direct fitness of player 1 is given by $w_1 = -C.y_1 + B.y_2$ (+ a constant, but can be left out). And similarly, because we assume symmetrical payoffs, the direct fitness of player 2 is $w_2 = -C.y_2 + B.y_1$.

Step 2: analyse when regression of player 1's fitness on its genotype is positive

The statistical regression $\beta_{w_1 g_1}$ of player 1's fitness (w_1) on its genotype g_1 is a bit awkward to calculate, but can more easily be approximated by its analytical equivalent – the total derivative (Frank 1998). This is exact when the genetic variants that occur in the population have almost identical phenotypes, and is therefore correct for the mixed and continuous strategy case (Frank 1998, Wenseleers & Ratnieks submitted). This works as follows :

$$\begin{aligned}
 \beta_{w_1 g_1} &= \frac{dw_1(y_1, y_2)}{dg_1} = \frac{\partial w_1}{\partial y_1} \cdot \frac{dy_1}{dg_1} + \frac{\partial w_1}{\partial y_2} \cdot \frac{dy_2}{dg_1} && \text{(chain rule)} \\
 &= -C \cdot \frac{dy_1}{dg_1} + B \cdot \frac{dy_2}{dg_1} \\
 &= -C \cdot 1 + B \cdot r
 \end{aligned}
 \tag{1.1}$$

In this derivation, $\partial w_1 / \partial y_1$ is the partial effect of your own behaviour (altruism) on your own reproduction, i.e. the personal cost of altruism, and $\partial w_1 / \partial y_2$ is the benefit of the other player's altruism (because of the symmetrical payoffs, it also equals $\partial w_2 / \partial y_1$, the benefit of player 1 to player 2). The other terms in the equation are the slope of individual phenotype on individual genotype, dy_1 / dg_1 , which is by definition 1, and the slope of partner phenotype on individual genotype, dy_2 / dg_1 , a common measure of the relatedness coefficient (Orlove & Wood 1978). Note, however, that dy_2 / dg_1 may be positive either due to common descent ($\partial g_2 / \partial g_1 > 0$) or due to a purely phenotypic correlation ($\partial y_2 / \partial y_1 > 0$), arising e.g. from common environment, or prior knowledge of how player 2 tends to behave. Relatedness in this case measures information about the behavior of social interactants. For this reason, this type of selection is sometimes thought of as being distinct from kin selection. Frank (1997, 1998) calls it 'correlated selection', and in concept it has close parallels to the idea of correlated equilibrium and Bayesian rationality in economic game theory (Aumann 1987; Skyrms 1994, 1996; their conclusion is that the Prisoner's dilemma may be overcome if social interactants have better than random information about what each will do, e.g. based on reputation, Nowak *et al.* 2000).

Step 3: solve to yield the ESS

The equation above means that when $B.r > C$, altruism is selected for – a simple rederivation of Hamilton's rule (Hamilton 1964, 1975). In this case, once this rule is fulfilled, it will favour ever greater degrees of altruism, until all players in the population will cooperate with probability 1. In many other cases, however, the population will tend towards an ESS with each individual being favoured to be cooperative with a particular probability.

A good example is the *hawk-dove game*, characterised by the following payoff matrix :

		PLAYER 2	
		Dove	Hawk
PLAYER 1	Dove	B/2	0
	Hawk	B	(B-C)/2

which can be renormalised (x 2 -B) to

		PLAYER 2	
		Dove	Hawk
PLAYER 1	Dove	0	-B
	Hawk	B	-C

The idea of this game is that when two individuals compete for a limited resource (e.g. food, a nesting site, etc...), they may either fight over it (play 'hawk') to gain a greater than average share, or behave peacefully (play 'dove'), and take no more than their fair share (Maynard Smith 1982). Hawk has an advantage in a population of all-doves (benefit= B) but in a population of all-hawks, it will cause resources to be wasted on fighting (fighting cost= C).

The fitness of player 1 is now given as $w_1 = -C.y_1.y_2 + B.y_1.(1-y_2) - B.(1-y_1).y_2 = B.y_1 - B.y_2 - C.y_1.y_2$ if y_1 and y_2 are the probabilities with which player 1 and player 2 play hawk. However, unlike in the previous game, the consequences of playing hawk or dove now depend on what the opponent does—the central idea in all of game theory. Formally, the personal benefit of playing hawk, $\partial w_1 / \partial y_1$, is now $B - C.y_2$. That is, unlike in Hamilton's rule it is no longer a constant. Similarly, the effect of the opponent's behaviour on player 1 is $\partial w_1 / \partial y_2 = -B - C.y_1$. Unlike in the previous game, the effects of the behaviour of each player no longer adds up. Or looked at in a different way, in the previous game, the cost of behaving altruistically was independent of the behaviour

of the opponent – this is no longer true here. Non-additivity or non-constancy of costs and benefits will in this case cause the population to evolve towards a mixed ESS. This ESS can be calculated as follows :

Playing hawk with a higher probability is favoured when

$dw_1 / dg_1 = \partial w_1 / \partial y_1 \cdot 1 + \partial w_1 / \partial y_2 \cdot r > 0$ which is when $(B-C \cdot y_2) \cdot 1 - (B+C \cdot y_1) \cdot r > 0$. When hawk behaviour in both players is controlled by a gene at the same locus, y_1 and y_2 will evolve towards the same value y . Thus the ESS is reached when $(B-C \cdot y) \cdot 1 - (B+C \cdot y) \cdot r = 0$ which is for $y^* = (B/C) \cdot (1-r) / (1+r)$.

Setting y to zero (all-dove=ancestral situation), it can also be checked that hawk will always spread in an all-dove population (since $B-B \cdot r$ is always >0). Setting y to 1 (all-hawk=ancestral situation), it can be checked that dove is favoured in an all-hawk population when $C(1+r) > B \cdot (1-r)$; when relatedness is absent this is when $C > B$, i.e. when the fighting cost exceeds the benefit of sole use of a resource.

1.2 Pure ESS model

The mixed strategy assumes that a player can adopt a probabilistic phenotype, randomly expressing one strategy or another. Alternatively, the genotype may fix a player's strategy, but different genotypes may express different strategies. In the mixed strategy case, individuals are mixed, but the population is pure (near the ESS); in the pure strategy case, individuals are pure, but the population is mixed. Pure strategy games do not generally predict the same invasion criteria and equilibrium conditions as their mixed strategy counterparts. This is a major source of confusion, because most population genetic models analyse the pure strategy case, whereas most inclusive fitness/optimisation models analyse the mixed strategy case. In any case, one should always specify which of the two that is modelled.

Analysis of the pure strategy case is more difficult than analysis of the mixed strategy case because the assumption of little genetic variance no longer holds. The consequence is that the regression of fitness on genotype can no longer be approximated using a total derivative. One way around this is to calculate regressions directly—below it is shown how to do this using the equilibration method of Frank (1998, p. 91-92). Wenseleers & Ratnieks (submitted) show how this regression can be partitioned into social components to yield a Hamilton's rule that is correct for both the mixed and pure strategy case (Wenseleers & Ratnieks submitted).

The method again consists of three steps; the hawk-dove game is used as an example.

Step 1: write the individual reproductive success of both players as a function of the behaviour of each

Direct fitness of player 1 = $w_1 = B \cdot y_1 - B \cdot y_2 - C \cdot y_1 \cdot y_2$

Direct fitness of player 2 = $w_2 = B \cdot y_2 - B \cdot y_1 - C \cdot y_1 \cdot y_2$

Step 2: analyse when regression of player 1's fitness on its genotype is positive

This regression now needs to be calculated explicitly as the difference in expected fitness between a player that is of the hawk (w_H) and one that is of the dove type (w_D), i.e.

$$\beta_{w_1 g_1} = w_H - w_D = E(w_1 | g_1 = 1) - E(w_1 | g_1 = 0) \quad (1.2)$$

The expected fitness of player 1 when it is of the hawk or dove type can be calculated as follows.

Relatedness, as before, is the regression of partner phenotype on actor genotype. That is, relatedness predicts to what extent a change in actor genotype is associated with a change in partner phenotype, i.e. $r = \beta_{y_2 g_1} = \Delta y_2 / \Delta g_1 = (y_2 - \bar{y}_2) / (g_1 - \bar{g}_1)$. (Grafen 1985's genetic measure of relatedness $(g_2 - \bar{g}) / (g_1 - \bar{g})$ closely resembles this equation)

Therefore, the expected value of player 2's strategy, y_2 , given player 1's genotype g_1 is $E(y_2 | g_1) = \bar{y}_2 + r.(g_1 - \bar{g}_1)$. If we take genotypes as equivalent to phenotypes (so that $y = g$, which is appropriate because all players express their genotypes), and if we assume that both players come from the same population (so that $\bar{y}_1 = \bar{y}_2 = p$), we get

$$E(y_2 | y_1) = p + r.(y_1 - p).$$

By consequence, the expected behaviour of player 2 y_2 is $p - r.p$ when player 1 is of the dove type ($g_1=y_1=0$), but $p + r.(1 - p)$ when it is of the hawk type ($g_1=y_1=1$). This means that with positive relatedness ($r > 0$), player 1 will not just play against the population at random, but will more likely play against its own type (i.e. it will play with a probability less than p against hawks if it is itself a dove, and with a probability higher than p against hawks if it is itself a hawk).

With these identities we can now calculate the expected fitness of player 1 given that it is of the hawk or the dove type :

$$w_H = w_1 |_{y_1 \rightarrow 1, y_2 \rightarrow p+r.(1-p)} = B.1 - B.(p + r.(1 - p)) - C.1.(p + r.(1 - p)) \quad (1.3)$$

$$w_D = w_1 |_{y_1 \rightarrow 0, y_2 \rightarrow p-r.p} = B.0 - B.(p - r.p) - C.0.(p - r.p) = -B.(p - r.p) \quad (1.4)$$

Fow hawk to be favoured over dove, $w_H > w_D$ (eqn. 1.2).

Step 3: solve to yield the ESS

A pure ESS is reached when $w_H = w_D$, which is for $p^* = (B/C) - r/(1-r)$. As one can see, for non-zero relatedness, the predicted equilibrium is different from, and tends to be less hawkish, than the corresponding mixed ESS ($y^* = (B/C).(1-r)/(1+r)$, see section 1.1). The reasons for this are discussed more fully in Grafen (1979), Queller (1984) and Wenseleers & Ratnieks (submitted). Setting p to zero (ancestral all-dove population), it can also be checked that hawk will spread in an all-dove population when $B(1-r) > C.r$ (this is more stringent than for the mixed strategy case, where hawk would always spread). Setting p to 1 (ancestral all-hawk population), it can be checked that dove is favoured in an all-hawk population when $C > B(1-r)$.

Note, however, that at the pure ESS, individual fitnesses are not at a local maximum with respect to variations in the probability that a particular individual will play hawk or dove. This suggests that if we release the constraint that individuals express only pure strategies, and allow individuals to express mixed strategies, the population will evolve from the pure to the mixed equilibrium (Frank 1998, p. 42 and 92). Therefore, if only enough alleles are played out against each other over the course of evolution, the final endpoint will correspond to the mixed ESS of optimisation models (Eshel 1996). Thus the short-term outcome of selection may be a pure ESS, but in the long term it seems likely that the population will tend towards the mixed strategy equilibrium, which is independent of detailed genetics (e.g. dominance assumptions etc...). One could also consider the mixed strategy analysis a first order approximation of the pure strategy case.

1.3 Mixed ESS model with asymmetrical payoffs, also applicable to interspecific interactions

Above we assumed that payoffs are symmetrical. In many cases, however, the two interactants do not have the same behavioural options. Think e.g. about hosts and parasites where the parasite can have one of two virulence genes and the host one of two resistance genes. In that case, payoffs will be asymmetrical.

Or in case of *Polistes* wasps, a resident wasp might either accept or reject a joining wasp, and the joining wasp might either cooperate in nest building or fight to obtain a greater share of the reproduction. Here, owner/intruder asymmetries will also cause asymmetrical payoffs.

Below it is shown how to analyse such problems. We will use the '*battle of the sexes*' game introduced by Dawkins (1976) to illustrate the method (cf. Maynard Smith 1982, p. 130).

The "battle of the sexes" game. The idea is as follows. Suppose that the successful raising of an offspring is worth +15 to each parent. The cost of raising an offspring is -20, which can be borne by one parent only, or shared equally between the two. The cost of a long courtship is -3 to both participants. Females can be 'coy' or 'fast'; males can be 'faithful' or 'philanderer'. Coy females insist on a long courtship, whereas fast females do not; all females care for the offspring they produce. Faithful males are willing, if necessary, to engage in a long courtship, and also care for the offspring. Philanderers are not prepared to engage in a long courtship, and do not care for their offspring. With these assumptions, we get the following payoff matrix :

		FEMALE	
		Coy	Fast
MALE	Faithful	(2,2)	(5,5)
	Philanderer	(0,0)	(15,-5)

(the first number is the payoff to the male, the second is the payoff to the female)

This game illustrates quite neatly that the best strategy from either player's perspective will depend on what the other player does. In this case, we see that this will likely lead to cyclical dynamics, because if

females are coy, it pays males to be faithful

males are faithful, it pays females to be fast

females are fast, it pays males to philander

males philander, it pays females to be coy

Parameters:

w_1 = direct fitness of player 1 (the male)

w_2 = direct fitness of player 2 (the female)

y_1 = phenotype of player 1 (probability of philandering)

y_2 = phenotype of player 2 (probability that female is fast)

r = 'relatedness' between male and female (see below for an important qualification)

Step 1: write individual reproductive success of both players as a function of the behaviour of each :

Player 1's (the male) direct fitness :

$$w_1 = 2 \cdot (1 - y_1) \cdot (1 - y_2) + 5 \cdot (1 - y_1) \cdot y_2 + 0 \cdot y_1 \cdot (1 - y_1) + 15 \cdot y_1 \cdot y_2;$$

Player 2's (the female) direct fitness :

$$w_2 = 2 \cdot (1 - y_1) \cdot (1 - y_2) + 5 \cdot (1 - y_1) \cdot y_2 + 0 \cdot y_1 \cdot (1 - y_1) - 5 \cdot y_1 \cdot y_2;$$

Step 2: analyse when regression of each player's fitness on their genotype is positive

We now have 2 equations: one specifying when an increase in male philandery is favoured, the other specifying when females are selected to be less coy. But since each of these is dependent on what the opposite sex does, they will need to be simultaneously maximised to provide the joint ESS.

Selection for philander males :

$$\begin{aligned} dw_1 / dg_1 &= \partial w_1 / \partial y_1 \cdot dy_1 / dg_1 + \partial w_1 / \partial y_2 \cdot dy_2 / dg_1 \\ &= \partial w_1 / \partial y_1 \cdot 1 + \partial w_1 / \partial y_2 \cdot r_1 \\ &= (-2 \cdot (1 - y_2) + 10 \cdot y_2) \cdot 1 + (3 \cdot (1 - y_1) + 15 \cdot y_1) \cdot r_1 \end{aligned} \quad (1.5)$$

Selection for fast females :

$$\begin{aligned} dw_2 / dg_2 &= \partial w_2 / \partial y_2 \cdot dy_2 / dg_2 + \partial w_2 / \partial y_1 \cdot dy_1 / dg_2 \\ &= \partial w_2 / \partial y_2 \cdot 1 + \partial w_2 / \partial y_1 \cdot r_2 \\ &= (3 \cdot (1 - y_1) - 5 \cdot y_1) \cdot 1 + (-2 \cdot (1 - y_2) - 10 \cdot y_2) \cdot r_2 \end{aligned} \quad (1.6)$$

Note that, while in the previous examples r could still be taken to be a measure of kinship this is no longer true in this case. What, for example, does $r_1 = dy_2 / dg_1$ measure? To understand what it means, expand r_1 as

$dy_2 / dg_1 = \partial y_2 / \partial y_1 \cdot dy_1 / dg_1 + \partial y_2 / \partial g_2 \cdot dg_2 / dg_1 = \partial y_2 / \partial y_1 \cdot 1 + 1 \cdot dg_2 / dg_1$, where $\partial y_2 / \partial y_1$ measures phenotypic association, i.e. to what extent player 1 (males) can predict the behaviour of player 2 (females) and dg_2 / dg_1 measures the genetic association between actor and partner genotype. But while the latter coefficient would equal kinship relatedness for the symmetrical games considered above, in this case it seems likely that male philandery and female coyness are not under control of the same locus. Therefore, dg_2 / dg_1 can be positive only due to linkage disequilibrium (when the female coyness and male philandery locus are closely linked) or pleiotropy (when the female coyness gene also influences male philandery) (Frank 1998, p. 102-103). For interactions between different species, genetic correlations are usually absent ($dg_2 / dg_1 = 0$, but see Frank 1994), and the sole type of relatedness that can arise is due to phenotypic correlation ($\partial y_2 / \partial y_1 > 0$), which may arise when one species has better than average information about how an interspecific partner tends to behave (Frank 1998, p. 93). Thus it is important to realize that relatedness can sometimes be taken to mean different things, and that care should be taken to interpret it correctly. Below, I will take $r_1 = r_2 = r$.

Step 3: Joint maximisation to provide the joint equilibrium

Setting eqn. (1.2) & (1.3) to zero, and solving the system of equations yields the equilibrium behaviour of both players (male and female).

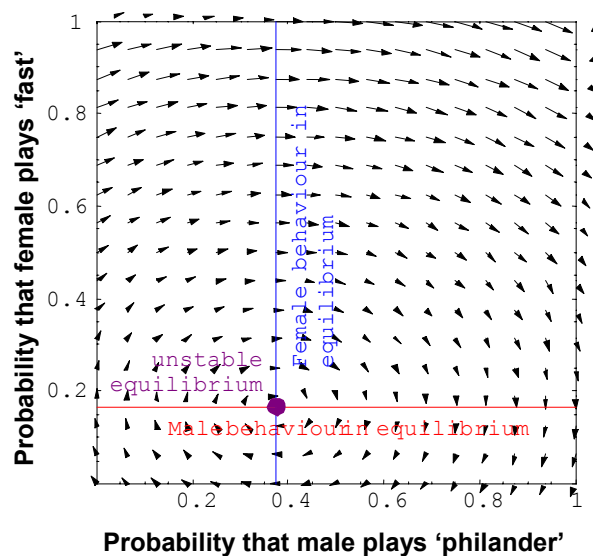
The easiest way to do this is to use the Solve function in *Mathematica*, which yields the equilibrium (see enclosed notebook)

$$\text{equilibrium} = \left\{ y_1 = \frac{9 - 10 \cdot r + 6 \cdot r^2}{24 \cdot (1 - r^2)}, y_2 = \frac{4 - 15 \cdot r + 6 \cdot r^2}{24 \cdot (1 - r^2)} \right\}$$

Evaluating this equilibrium for $r=0$ gives $y_1=3/8$ and $y_2=1/6$, i.e. males should philander with a probability of 3/8 and females should be fast with a probability of 1/6 (cf. Dawkins 1976).

The dynamics of this system can also be investigated graphically using a field plot, since for each pair of y_1 and y_2 we get a direction of selection.

A field plot reveals that there is indeed an equilibrium, and that there are cyclical dynamics, as predicted. Less clearly visible is whether the equilibrium is stable (globally attracting), or whether the dynamics of this system are characterised by limit cycles (ever-lasting cyclical dynamics). The enclosed *Mathematica* notebook shows that in this case the system is characterised by limit cycles, i.e. an ever-lasting arms race. In sum – as Dawkins (1989, p. 303) put it – ‘The behaviour of lovers is oscillating like the moon, and unpredictable as the weather.’. In other words, although there is an equilibrium, it is not strictly speaking an ESS (note that Dawkins (1976) got this wrong in the first edition of *The Selfish Gene*). For other payoffs one can sometimes get a globally attracting equilibrium – a true ESS. Other arms-races (e.g. host-parasite dynamics) are often characterised by similar dynamics.



1.4 Questions & Answers

1. Investigate the evolution of reciprocal altruism. For this, replace the ‘Cooperate’ strategy in the 2-player mixed strategy game by ‘TIT-FOR-TAT’ (TFT, cooperate on the first move and then do what your opponent did on the previous move); let defect stand for unconditional defection (‘always defect’, AD). Assume that the game is played an unknown number of times, and that after each play of Prisoner’s dilemma, the next play will occur with probability p , with $0 < p < 1$ (this game is known as the iterated Prisoner’s dilemma). Calculate the payoffs $E(AD,AD)$, $E(AD,TFT)$, $E(TFT, AD)$ and $E(TFT, TFT)$, and check (1) when TFT can invade an all-defecting population and (2) when AD can invade an all-TFT population. Assume for simplicity that the players are unrelated to each other.

The payoff of TFT playing against itself ($E(TFT, TFT)$) is

$$(b-c) + p(b-c) + p^2(b-c) + p^3(b-c) + \dots = (b-c)/(1-p) \quad (\text{see proof below})$$

The other payoffs remain unaffected: $E(AD,AD)=0$, $E(TFT,AD)=-c$ and $E(AD,TFT)=b$.

With these payoffs it is easy to check that (1) TFT can never invade an all-defecting population (because it takes two TFT individuals to gain any advantage) and (2) that AD invades an all-TFT population when $b.p < c$. Note the similarity of the latter condition to Hamilton’s rule, with p taking over the role of relatedness [in fact p is a nongenetic type of relatedness (Skyrms 1996); as Hamilton (1971, p. 65) put it: “Rather than continue in the jangling partnership, the disillu-

sioned cooperator can part quietly from the selfish companion at the first clear sign of unfairness and try his luck in another union. The result would be some degree of assortative pairing.”]. Putting (genetic) relatedness into the equation one would find (1) that TFT can only invade an all-defecting population when $b.r > c$ and (2) that AD invades an all-TFT population when $b.(p+r)/(1+p.r) < c$. All this means that if noncooperation is the primitive condition, it is difficult to see how reciprocal altruism could evolve from it. Axelrod & Hamilton (1981) suggest that cooperative behaviour might originate as altruism between relatives selected by kin selection and then spread to encompass nonrelatives, or it might spread from a small cluster of cooperative individuals. But clearly, the transition from noncooperation to reciprocal altruism is a difficult one.

proof:

for any $p \neq 1$, $1+p+p^2+\dots+p^{m-1}=(1-p^m)/(1-p)$ since $(1-p)(1+p+p^2+\dots+p^{m-1})=1-p^m$
 now, as m goes to infinity, p^m goes to zero so that $1+p+p^2+p^3+\dots=1/(1-p)$

Or you can have Mathematica do all the work:

$$(b-c) \cdot \sum_{i=0}^{\infty} p^i$$

$$\frac{b-c}{1-p}$$

2a. Godfray (1987) uses an explicit genetic model to derive when parasitoid wasp larvae should either tolerate or eat each other within their host. Show that Godfray’s results can be derived in a much easier way using Steve Frank’s methods. For simplicity, model only the case with a clutch size c of 2. To parallel Godfray’s notation, assume the following payoffs to larva 1:

$E(\text{fighter}, \text{fighter})=1/2$ (it survives half of the time), $E(\text{fighter}, \text{tolerant})=1$ (the fighter larva gets the host for itself), $E(\text{tolerant}, \text{fighter})=0$ (the tolerant larva gets killed) and $E(\text{tolerant}, \text{tolerant})=f$ where f is the ratio of the reproduction as a pair over the reproduction alone. Furthermore, assume that competing larvae are of a random sex and that their mother is singly mated so that the average relatedness among them is $1/2$. Calculate (1) when tolerance can invade in an all-fighter population and (2) when fighting will invade in an all-tolerant population assuming either discrete or mixed strategies. Also calculate the mixed and pure strategy ESSs, not calculated in Godfray’s paper.

2b. Assume the parasitoid wasp mother mates twice. How would this affect the likely evolution of tolerance? If the level of siblicide among larvae were conditional on relatedness structure, how would this affect the optimal mating strategy of the mother?

2c. In parasitoid wasps, after egg deposition, larvae are left on their own, i.e. there is no parental care. How could parental care affect the possible outcome?

2a.

Bulmer (1994, p. 193) mentions that this problem represents “an extreme example of a situation in which inclusive-fitness arguments cannot be used, because the costs and benefits of altruism are not constant”. But let’s see how we can tackle it using the methods above.

First, write the fitness of larva 1 as a function of its own (y_1) and its partner (y_2) phenotype (whether or not to behave tolerant), as in $w_1 = (1-y_1).(1-y_2).1/2 + (1-y_1).y_2.1 + y_1.y_2.f$

MIXED STRATEGY CASE :

Under 'relaxing assumptions', point 7 'Incomplete penetrance' (p. 229) Godfray mentions this case.

An increase in the probability of playing 'tolerant' is favoured when :

$$dw_1 / dg_1 = \partial w_1 / \partial y_1 \cdot 1 + \partial w_1 / \partial y_2 \cdot r > 0 \quad (\text{generalised Ham. 's rule, eqn. 1.1})$$

Where the cost of playing tolerant = $\partial w_1 / \partial y_1 = -(1/2) \cdot (1 - y_2) - (1 - f) \cdot y_2$ and the benefit of having a tolerant partner = $\partial w_1 / \partial y_2 = (1/2) \cdot (1 - y_1) + f \cdot y_1$. Again, as in the hawk-dove game, one can see that the costs and benefit depend on what the opponent does so that Hamilton's assumption of constant costs & benefits is violated. But a Hamilton's rule defined as above is always valid for the mixed or continuous strategy case (for a derivation of a Hamilton's rule that is also correct for the discontinuous strategy case, see Wenseleers & Ratnieks submitted).

Near the ESS, $y_1 = y_2 = y$, so that the equation above can be solved to yield the ESS probability with which any larva should behave tolerantly $y^* = (1 - r) / [(2 \cdot f - 1) \cdot (1 + r)]$.

Tolerance will invade in an all-fighting population when $dw_1 / dg_1|_{y \rightarrow 0} > 0$ which is when $-(1/2) + (1/2) \cdot r > 0$. This is never possible, even not when the two larvae would be identical twins ! (cf. Bulmer 1994, p. 194 and Godfray 1987 p. 229 1st paragraph with penetrance z approaching zero)

Fighting will invade in an all-tolerant population when $dw_1 / dg_1|_{y \rightarrow 1} < 0$ which is when $(1 - f) - f \cdot r > 0$, i.e. when $f < 1 / (1 + r) < 2 / 3$ for $r = 1/2$. (cf. Godfray 1987 p. 229 eqn. 12 with clutch size $c=2$)

DISCRETE (PURE) STRATEGY CASE :

Tolerance is favoured over fighting when the expected reproduction of larva 1 is higher as a tolerant than as a fighter (eqn. 1.2).

$$\text{The fitness of larva 1 when it is of the tolerant type is } w_{\text{tolerant}} = w_1|_{y_1 \rightarrow 1, y_2 \rightarrow p+r \cdot (1-p)} = f \cdot (r \cdot (1-p) + p)$$

The fitness of larva 1 when it is of the fighter type is

$$w_{\text{fighter type}} = w_1|_{y_1 \rightarrow 0, y_2 \rightarrow p+r \cdot (0-p)} = p \cdot (1-r) + (1-p+r \cdot p) / 2$$

Tolerance will invade in an all-fighting population when $(w_{\text{tolerant}} - w_{\text{fighter type}})|_{p \rightarrow 0} > 0$ (p has been set to zero because all-fighting is the ancestral state), i.e. when $f \cdot r - 1/2 > 0$, or for $r = 1/2$ when $f > 1$. This requires that an individual should have a higher fitness as one of a pair than when alone (implying some unlikely Allee effect). This result is identical to the population genetic result of Godfray 1987 (eqn. 2 p. 223), and shows how difficult it is to evolve tolerance once fighting has evolved. Bull & Charnov (1985) call this irreversible evolution.

Fighting will invade in an all-tolerant population when $(w_{\text{fighter type}} - w_{\text{tolerant}})|_{y \rightarrow 1} = 1 - f - r/2 > 0$ (p has been set to 1 because all-tolerance is the ancestral state). For $r = 1/2$ this is when $f < 3/4$. By setting $c=2$ in eqn. 5 of Godfray 1987, it can again be checked that this is identical to the population genetic result.

A pure strategy ESS is reached when the fitness of a fighting larva equals the fitness of a tolerant larva, which is when $p = (2 \cdot f \cdot r - 1) / [(1 - 2 \cdot f) \cdot (1 - r)]$.

Overall it can be seen that this method is much easier, and vastly more economical and general than the corresponding population genetic model, e.g. you don't need to compile massive mating tables, it does not require any complex matrix algebra, is valid under any relatedness structure, etc...

2b. The average relatedness among the mother's offspring of random sex is given by $r =$

$1/4 \cdot r_{MM} + 1/4 \cdot r_{MF} + 1/4 \cdot r_{FM} + 1/4 \cdot r_{FF}$ where r_{MM} , r_{MF} , r_{FM} and r_{FF} stand for relatedness between 2 male offspring, between a male and a female offspring, between a female and a male offspring and between 2 female offspring (we assume a 1:1 sex ratio in the brood). Under single mating $r_{MM} = 1/2$, $r_{MF} = 1/2$, $r_{FM} = 1/4$ and $r_{FF} = 3/4$, giving $r = 1/2$. But under double mating, r_{FF} drops from $3/4$ to $1/2$ so that $r = 7/16$, which is lower than $1/2$. This lower relatedness will make it harder for tolerance to evolve (substitute in the above equations).

If larvae adjust their probability of being siblicidal based on the average relatedness within the brood, it might pay for mothers not to mate twice (or not to superparasitise a host, which may be another cause of low relatedness).

2c. If the parent rears her offspring to adulthood he/she might prevent offspring from behaving aggressively, or punish them if they behave aggressively. Punishment, in turn, may make it unprofitable for any offspring to even try to behave aggressively. This may be why so many parasitoid wasps have larvae with huge mandibles, adapted for fighting, something that is never seen in species with parental care. Hamilton (1964) suggested that bees and wasps might have evolved combs to prevent larvae from eating each other.

Section 2. Application 1. The evolution of worker reproduction

Accompanying paper:

Frank, S.A. 1995a. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* 377: 520-522.

Purpose :

Many papers in the social insect literature have pointed out that since workers are related more to sons than to nephews, any worker should gain from producing male offspring. But how many workers should breed within a colony? Clearly, a rare laying worker within a colony would be at an advantage relative to a nonlaying one, but what if all workers took on a reproductive role? In that case, the colony would perish as a result of a dearth of foragers. Here we will derive the ESS probability for a worker to switch to a reproductive role, using the model of Frank (1995, 1996) as a basis. To simplify the matter we will only model the evolution of worker reproduction under queenless condition and see what level of worker reproduction is evolutionary stable, i.e. how male production should be partitioned within a queenless colony.

Frank's model (1995, 1996) was not specifically formulated to solve the worker reproduction problem (in fact worker reproduction is not even mentioned in the paper), instead it is framed around the more general concept of a *tragedy of the commons*. The reasoning is as follows. Any individual in the group will maximise its success relative to others by reproducing more (or with higher probability) than average. But since all individuals are selected to do this, it will eventually cause all individuals in the group to reproduce at a higher rate than can be sustained, hence the *"tragedy of the commons"*. Frank then analyses two situations. The first (*"self restraint model"*, Ratnieks sometimes uses the terms *"self policing"*) is where individuals can control their own probability to breed but can not control the behaviour of others. The second (*"policing model"*) is where individuals also have the possibility to prevent others from breeding.

In terms of our worker reproduction problem, this corresponds to the situations where workers can either (1) control their own probability to become a reproductive worker, but not influence the fate of others, or (2) also inhibit others from becoming reproductive workers.

Assumptions :

Throughout Frank assumes that the optimum for the group is to have very few reproductive individuals, and that group efficiency is a linear decreasing function of the proportion of selfish (i.e. breeding) individuals in the group. This may be quite reasonable for the worker reproduction problem, since a few workers are enough to produce all the male eggs and mainly foragers are needed to rear these into adults.

2.1 Self-restraint model

Parameters:

y = probability with which a focal individual takes on a breeding role

z = average probability with which individuals start to breed within the colony

g = genotype of a focal individual

Step 1: Write individual reproductive success w as a function of your own breeding probability (y) and the average probability with which individuals breed in the colony (z)

Frank (1995) uses the equation $w = (y/z).(1-z)$, because the chance that any reared egg is yours is y/z , but the chance that it will be reared into adulthood is $1-z$ (with $z=1$ there are no foragers, so that no eggs can be reared). If you find this equation hard to understand you could think of the absolute fitness of a worker w as being the product of the relative individual success of a worker and colony productivity, with relative individual success given by y/z , and colony productivity given by $1-z$ (i.e. the total number of males reared over the colony's lifetime).

Step 2: Analyse when the regression of fitness on genotype is positive

$$\beta_{wg} = \frac{dw(y,z)}{dg} = \frac{\partial w}{\partial y} \cdot \frac{dy}{dg} + \frac{\partial w}{\partial z} \cdot \frac{dz}{dg} \quad (\text{chain rule}) \quad (2.1)$$
$$= \frac{(1-z)}{z} \cdot 1 - \frac{y}{z^2} \cdot r > 0$$

Note that, as in the hawk-dove game, the costs and benefits of becoming a reproductive worker again depend on what everyone else does in the colony. E.g., the personal benefit of becoming a reproductive worker ($\partial w / \partial y$) is very large if everyone else decides not to reproduce ($(1-z)/z$ then approaches plus infinity), but tends towards zero as more workers become reproductive. Similarly, the personal cost of a high average level of worker reproduction ($\partial w / \partial z$) depends on the reproductive decisions of all other workers in the colony. However, while in the hawk-dove game it would still have been possible to write down costs and benefits straight away, this would have been a bit challenging in this case.

The derivative dz/dg , mentioned by Frank (1995) to equal relatedness, deserves some explanation. Before we had relatedness to be the slope of partner phenotype on actor genotype, but in this case z is the average phenotype of any worker in the colony, including the actor itself. That is, suppose you would have a colony with only worker. In that case z would be equal to y , and dz/dg would equal 1. Therefore, dz/dg is not just pairwise genetic relatedness, but average relatedness to any individual in the group, including self (Frank 1996). Formally, with group size N , $r = (1/N) + r' \cdot (N-1)/N$, where r' is pairwise genetic relatedness (see also Q&A question 6).

Step 3: Solve to yield the ESS

Near the ESS, eqn. 2.1 should equal 0, and the behaviour of all workers will tend towards the same probabilistic optimum, so that we can set $y=z=z^*$. So near the ESS, we have $(1-z)/z - (1+(1-z)/z).r = 0$, and solving for z yields the mixed ESS $z^* = 1-r$.

Conclusion:

The ESS probability with which workers should become reproductives = $1-r$

E.g., 25% of all workers should start laying male eggs when their mother queen is singly mated, 50% when she is doubly mated, etc...

(assuming a linear cost function)

If you find it hard to understand why 25% reproductive workers is the ESS with single mating, then it is also possible to look at the problem from a classical inclusive fitness angle :

At the ESS the

$$\begin{aligned} &\text{Selfish direct fitness benefits due to own male production } (r = 0.5) = \\ &0.25 \quad \quad \quad (\text{chance of becoming a reproductive worker}) \\ &* (1-0.25) \quad \quad (\text{chance that any egg laid can be reared into an adult}) \\ &* 0.5 \quad \quad \quad (\text{relatedness to sons}) \\ &= 3/32 \end{aligned}$$

$$\begin{aligned} &\text{Inclusive fitness costs due to reduced production of nephews } (r = 0.375) = \\ &0.25 \quad \quad \quad (25\% \text{ fewer nephews are reared into adults}) \\ &* 0.375 \quad \quad \quad (\text{relatedness to nephews}) \\ &= 3/32 \end{aligned}$$

Therefore, at the ESS the selfish benefits of worker laying exactly balance with the inclusive fitness costs due to reduced nephew production, which is what had to be shown. Note, however, that one can no longer take an inclusive fitness angle for asymmetrical games – in that case a direct fitness perspective is the only correct way to handle the problem.

2.2 Social policing model

2.2.1 ANALYTICAL SOLUTION

Parameters:

y = probability with which a focal individual takes on a breeding role

z = average probability with which individuals start breeding within the colony

p = individual investment in a policing trait that inhibits others to breed

P = average individual investment in policing within the group

b = focal individual's genotype at the breeding locus

π = focal individual's genotype at the policing locus

c = individual cost of policing

Step 1: Write individual reproductive success w as a function of individual (y) and average (z) breeding probability and the individual (p) and average (P) investment in policing.

Many different equations are possible, depending on assumptions, but this is the equation that Frank used:

$$w = I.G$$

with $I = \text{individual success (relative to group members)} = P - c.p + (1-P).y/z$
 $G = \text{group success (total number of sexuals reared over the colony's lifetime)} = 1 - (1-P).z$

Step 2: Analyse when the regression of fitness on genotype is positive

We now have 2 equations: one specifying selection for breeding (becoming a reproductive worker), the other specifying selection for policing, i.e. we are analysing a 2-locus model. But since each of the selection equations is dependent on each other, they will need to be simultaneously maximised to provide the joint ESS. The equations themselves are messy (see the enclosed *Mathematica* sheet), so I will just explain the rationale of how to derive them.

A higher probability of becoming a reproductive worker is favoured when

$$\frac{dw(y, z, p, P)}{db} = \frac{\partial w}{\partial y} \cdot \frac{dy}{db} + \frac{\partial w}{\partial z} \cdot \frac{dz}{db} + \frac{\partial w}{\partial p} \cdot \frac{dp}{db} + \frac{\partial w}{\partial P} \cdot \frac{dP}{db} > 0 \quad (\text{chain rule})$$

where we can set $dy/db = 1$, $dz/db = r$, and, assuming that the breeding and policing locus are not linked, $dp/db = 0$, $dP/db = 0$. In addition, we can evaluate for $y = z = z^*$ and for $p = P = p^*$ because we are evaluating the equation near the ESS (z^* and p^*).

Similarly, an increase in the investment in policing is favoured when

$$\frac{dw(y, z, p, P)}{d\pi} = \frac{\partial w}{\partial p} \cdot \frac{dp}{d\pi} + \frac{\partial w}{\partial P} \cdot \frac{dP}{d\pi} + \frac{\partial w}{\partial y} \cdot \frac{dy}{d\pi} + \frac{\partial w}{\partial z} \cdot \frac{dz}{d\pi} > 0 \quad (\text{chain rule})$$

where we can set $dp/d\pi = 1$, $dz_p/d\pi = r$, and, assuming that the breeding and policing locus are not linked, $dy/d\pi = 0$, $dz/d\pi = 0$. Again, we should evaluate this equation for $y = z = z^*$ and $p = P = p^*$.

Step 3: Joint maximisation to provide the joint ESS

Joint maximisation of these 2 equations is difficult, but as a first start let us check when a policing trait can invade from a situation where all individuals are reproducing with optimum probability (breeding probability $z^* = 1-r$, see Section 2.1 above). For this, set the probability of breeding (z^*) to $1-r$ and the level of policing p^* to 0 in the selection equation for policing, and see when an increase in policing is favoured.

As it turns out, this is when $(z-c).r > 0$ with $z = 1-r$, i.e. when $c < 1-r$.

Conclusion :

When the cost of policing $c < 1-r$, policing is favoured. Otherwise, the self restraint and no policing optimum will be reached (Section 2.1). Below it is checked graphically that whenever policing invades it will also tend to be maximally favoured. This can best be done using field plots.

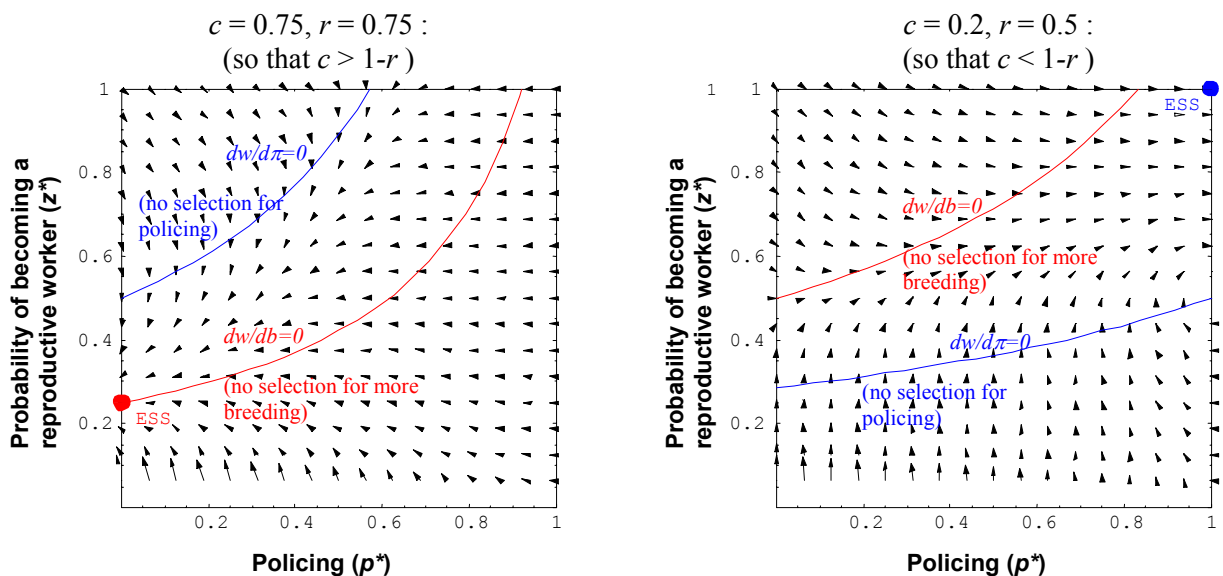
The intuitive explanation for this result is that unrestrained breeding will reduce the net group output by a fraction $1-r$, whereas policing can restore group output at a cost c (the cost of polic-

ing). If policing can restore group efficiency (i.e. resolve the *tragedy of the commons*) at a lesser cost, it will be favoured. Low relatedness will cause large costs due to limited restraint, and is therefore conducive to the evolution of social policing (Frank 1995a).

With respect to worker reproduction this means that if policing occurs in queenless condition (e.g. workers that force other workers to work rather than to reproduce) it will cause fewer workers to reproduce than is predicted by the self restraint model (Section 2.1). For example, less than 25% of the workers for single mating or less than 50% for double mating, perhaps just a few (which is the colony optimum).

2.2.2. GRAPHICAL SOLUTION

As in the battle of the sexes game, the way the ESS is reached can also be illustrated graphically using a field plot.



2.3 Questions & Answers

1. Whenever policing is favoured, will this necessarily lead to a more efficient running of a society than if it is not?

Yes, it should, although animals would also waste a lot of energy on mutual inhibition of each other's selfishness (e.g. on aggression, see the c parameter in the model).

2. When a social insect colony loses its queen it seems likely that not all workers are totipotent and can switch to a reproductive role (this should be true especially for foragers with regressed ovaries). Also, the workers that do become reproductive may be able to both lay eggs and do some foraging. How could this be accommodated in the model?

If t is the fraction of totipotent workers then a fraction $(1-t)$ might keep foraging. This tends to reduce the costs to colony function, making a higher level of breeding favourable from the perspective of the totipotent workers. To take this into account in Model 1, let colony success be $(1-z)(1-t)$ instead of just $(1-z)$. By the same methods as above, this yields an ESS probability of becoming a reproductive worker of $(1-r)/(1-t)$. For example, if half of the workers are totipotent at the time the queen is lost ($t=0.5$), then 50% of them should become reproductives instead of just 25% if all are totipotent (this assumes single mating). Try to check this result.

If reproductive workers can spend a fraction f of their time foraging, then, again costs to colony function would not be as severe. Formally, colony success would become $(1-z)(1-f)$ rather than just $(1-z)$. So this affects the ESS in the same way as above.

3. Above we assumed that workers become reproductives with some ESS probability in the event the queen is lost. In other words, the ESS is what is often called a *mixed ESS*. Alternatively, it could be that the ESS reflects how each worker will divide its time between reproduction and foraging over its entire lifetime. In that case, the ESS reflects a *continuous ESS*. Does the model apply to both situations? And how does this relate to the level of skew predicted by Model 1? How does policing interact with the predicted level of reproductive skew? What are the more general implications for skew theory?

The continuous and mixed ESS situation are very similar, and it seems reasonable to assume that the fitness function for each case is identical. Therefore, the model adequately predicts the right ESS for each situation. In terms of reproductive skew, the probabilistic (mixed ESS) model predicts high skew in high relatedness groups (just a few workers should lay eggs), but low skew in low relatedness groups (many workers should lay eggs). But the continuous ESS model would cause each worker to contribute equally to male production irrespective of relatedness, i.e. it predicts low skew under all circumstances. So even though these two situations are theoretically almost identical they lead to very different skew predictions.

Policing will tend to increase skew since it should cause fewer individuals in the group to reproduce than is dictated by their own inclusive fitness preferences. But since policing is favoured especially at low relatedness, it makes the opposite prediction as above: it should favour high skew at low relatedness (due to policing) and low skew at high relatedness (due to the absence of policing and limited self-restraint).

All this means that any attempt to simply relate skew to relatedness patterns is probably in vain - any pattern is possible depending on the specific biology. We already know this from the long series of theoretical papers on skew theory, but it is also easy to see from the simple models above. Message: don't worry about skew theory but construct a specific model for the problem at hand. And if necessary, provide intuitive explanations in terms of Hamilton's rule - the only truly fundamental principle in social evolution theory.

4. Suppose that group success is not a decreasing linear but a decreasing concave or a convex function of the proportion of selfish individuals within the group. How would this affect the predictions of the model?

With a concave colony productivity function unrestrained breeding would reduce group output more than with a linear cost function. The consequence would be that in Model 1, the ESS probability of breeding would be lower than with a linear cost function. The inverse is true for a convex productivity function. To formalise this, let group success be $1 - z^k$ instead of just $(1-z)$ in Model 1 ($k=1$, >1 and <1 then correspond to a linear, a concave and a convex cost function). By the same methods as above, this yields an ESS probability of breeding $= (1-r)/(1+r(k-1))$. Try to check this result.

5. Frank discusses his model in rather broad terms, arguing that it might be relevant to explain cooperation among slime mould cells, among homologous chromosomes within diploid cells (Mendelism), etc... But do you think the assumptions of the model really warrant such a broad discussion? E.g. think about the slime mould case. What fraction of slug cells should develop into spore rather than stalk cells according to Model 1? But how realistic is it that an average cells' success is a linear decreasing function of the proportion of spore forming cells? And what about meiotic drive?

Slime moulds: Frank assumes that the group optimum is near zero allocation to reproduction. This is probably an OK assumption for the worker reproduction problem and for the level of queen production in swarming social insects (see section 3). But for slime moulds it seems likely that some intermediate allocation to spores is the group optimum. A case in point is that even when slime moulds are composed of single clones (so that cell-cell relatedness is 1), 20% of all cells become stalk cells and 80% become spores.

Mendelism/Meiotic drive: driving and cooperative genes typically reach a pure strategy equilibrium; Frank models a mixed/continuous ESS. Wenseleers & Ratnieks (submitted) analyses meiotic drive as a social interaction using a generalised version of Hamilton's rule; alternatively, the 2-player pure strategy analysis of Section 1.2 could be used.

6. Hammerstein (1995) commented on Frank's study, saying that the policing model wasn't quite convincing at explaining cooperation in low relatedness groups, because at least in genetically unrelated groups no individual should care about the reproduction of others in the group (since there could be no inclusive fitness gains). What did Hammerstein overlook?

Policing increases overall group productivity, and since the policing individual makes up a fraction $1/N$ of the total group (if N is group size), policing will have a $1/N$ selfish benefit (cf. $r = (1/N) + r' \cdot (N-1)/N$ with r' = pairwise genetic relatedness). Even in genetically unrelated groups, therefore, policing is selected for, even though the motive is then ultimately selfish. For the same reason, a slight degree of restraint is favoured in unrelated groups. In D.S. Wilson's terminology (Wilson 1990), the $1/N$ selfish component of restrained breeding causes weak altruism within social groups (Pepper 2000 discusses the matter more fully). Although the $1/N$ component can probably be neglected for the worker reproduction problem (colony sizes are typically large), it may be important in other contexts. For example, no parent-offspring conflict over the exploitation rate of parental resources is expected if parents have only one offspring ($N=1$, it will then only compete with itself).

7. In what sense does the type of policing assumed in Frank's model differ from Ratnieks' (1988) concept of "worker policing" (mutual inhibition of worker laying under queenright condition)? What are the commonalities?

In Frank's model, policing is favoured because it increases group output. This has inclusive fitness benefits in case group members are related (e.g. increased production of nephews) or a $1/N$ selfish benefit in case group members are unrelated (if N is group size). Worker policing as envisaged by Ratnieks (1988) is selected for when workers are related more to the males they kill (nephews) than to the males they spare (brothers). Here policing can have no direct selfish benefits. Common to all policing models is that they address the question of when individuals are selected to inhibit each other's selfish tendencies (i.e. when is what I do not OK for others to do).

8. How could the model be extended so that it also applies to the evolution of worker laying under queenright condition (hint: first take a look at Section 3 on caste conflict)? Should the predicted proportion of reproductive workers be higher or lower? And if worker policing is allowed for, could it be that it is favoured at any queen mating frequency, rather than just at queen mating frequencies higher than two, as predicted by Ratnieks (1988)?

Haven't done this yet, but the predicted level of worker laying should be lower than under queenless condition, because worker reproduction would also reduce the number of queens reared, i.e. it would have additional inclusive fitness costs. The idea that worker reproduction would reduce colony productivity would still apply, and therefore it seems quite likely that if po-

licing can be performed at low cost, it would be favoured at any queen mating frequency (although for a different reason than envisaged by Ratnieks (1988), see Question 7).

9. Tragedies of the commons have been extensively discussed in economics (e.g. livestock owners that overexploit common grazing land to increase revenues relative to others using the same piece of land, see e.g. Hardin 1968). What are the formal differences between calculating the best rational strategy in economics and calculating an ESS in biology? Have concepts such as relatedness any meaning in economics?

George Price was perhaps among the first evolutionary biologists to see the strong similarities between tragedies of the commons in economics and some problems of group selection in biology (Frank 1995b p. 386). The differences mainly pertain to what is assumed to be maximised: net income (or more generally utility) in economics, fitness in biology. Economic models are also purely phenotypic models, i.e. instead of gene frequency change they investigate phenotypic strategy change. Much more could probably be learned by explicit carry over of concepts between both fields. For example, phenotypic versions of relatedness (e.g. Queller 1984) have sometimes been described as measuring "better than average information about a social interactant's behaviour/strategy" (Frank 1997a). Such a relatedness coefficient does have a meaning in economics: if anyone has better than average information about the likely behaviour of others (i.e. $r > 0$), then that would tend to favour strategies that benefit the global economy (i.e. a Pareto optimal outcome) (for more on this, see Aumann 198; Skyrms 1994, 1996). Currently, economists often use evolutionary rather than classical game theory on the premise that even though strategies may not necessarily be heritable, the successful ones are copied (imitated) more often by others.

Section 3. Application 2.

Conflict over caste fate in social insects

Accompanying paper:

Wenseleers, T., Ratnieks, F.L.W. & Billen, J. 2001. Chapter 10. Conflict over caste fate in social insects: a tragedy of the commons examined. In: T. Wenseleers, "Conflict from Cell to Colony", PhD thesis, p. 174-195, Katholieke Universiteit Leuven, Belgium, 205 pp.

Biological question :

Bourke & Ratnieks (1999) pointed out that in social insects any female is related more to own offspring than to a sister's offspring, so that a female should benefit from becoming a queen rather than a worker. The predicted consequence of selfish manipulation of caste fate would be excess queen production. But how excessive should queen production be? Clearly, if all females would become queens the colony would perish as a result of a dearth of workers. So what is the best thing for a female to do? And what are the interests of the adult workers and the mother queen?

I remember that upon first reading of Bourke & Ratnieks' paper it occurred to me that there were striking similarities between caste fate conflict and Frank's tragedy of the commons model (1995, 1996), the commons in this case being a common workforce. But it was only when Francis showed me an unpublished manuscript (now published: Ratnieks 2001 and Ratnieks *et al.* 2001) where he derived the ESS probability for females to become queens using a genetic

model, that I took renewed interest in this problem and arrived at a more general solution using Frank's methods. This model (Wenseleers et al. submitted) is explained below. Overall, the model can explain why *Melipona* stingless bees rear very many queens (most of which are killed upon eclosion by the workers), whereas *Trigona* stingless bees and honey bees produce very few queens. The reason, as we will see, is connected to individual control of caste fate in *Melipona*, and social control of caste development in nearly all other social insects.

Assumptions :

We model caste fate conflict for swarming social insects, because here the colony optimum is known: just a few queens need to be reared since mainly workers are needed for swarming. This matches Frank's assumption (1995, 1996) that the optimum for the group is to have very few reproductive (queen destined) individuals. As in Frank (1995, 1996), we also assume that colony productivity is a linear decreasing function of the proportion of selfish (queen destined) individuals in the group. Below we model two cases. The first model derives the optimum probability for a female to develop as a queen assuming caste development is under individual control. This scenario is shown to cause excess queen production (i.e. production of more queens than needed for swarming). The second model derives the adult worker's interests, and shows when they are selected to gain social control over the caste allocation process.

3.1 Individual control of caste development

Parameters:

y = probability with which a focal female larva develops as a queen

z = average probability with which females develop as queens in the colony

g_f = genotype of a focal female (which does express the caste development gene)

g_m = genotype of males (males do not express the caste development gene, but their survival is affected by the caste allocation decisions of females)

c_f = relative reproductive value of females

c_m = relative reproductive value of males

r_f and r_m = regression relatedness to females and males

R_f and R_m = life-for-life relatedness to females and males

The main difference compared to the basic tragedy of the commons model of section 2 is that we now have a passive class of relatives, namely males, that are affected by the caste allocation decisions of female larvae. Males do not themselves express the caste development gene but may transmit copies of it to subsequent generations. Therefore, we need to keep track both of the effects of correlated behaviour within the active class (female larvae; "correlated selection", Frank 1997a), and the effects of the active class on a passive class of relatives (males; "kin selection", Frank 1997a). Frank's (1997a, 1998) direct fitness method, that allows to analyse such complex problems, is described below.

Step 1: Write individual reproductive success W of a random recipient as a function of the behaviour of the active class

The first step is to write the direct fitness of members of the active (females) and passive (males) class as a function of the behaviour of members of the active class.

As before, we assume that the colony's total productivity G , measured over the colony's lifetime, is given as $(1-z)$, where z is the average probability with which larvae become queens.

Thus the direct fitness through male function $W_m = 1-z$.

The direct fitness of female larvae can, as before, be written as $W_f = (1-z).(y/z)$, where y/z measures the individual success of any larvae relative to others (I), and $1-z$ measures the success of

any daughter swarm or colony (G , proportional to the number of workers available, and thus equal to $1-z$). I can be thought of as an above-average probability of becoming a queen, i.e. the relative chance of inheriting a swarm or colony. The equation of W_f illustrated the *tragedy of the commons*: the fitness of a female increases in proportion to its probability of becoming a queen (W_f increases as a function of y), but decreases as more females would opt to do the same (W_f decreases as a function of z).

Step 2: Analyse when the slope of a recipient's fitness on its genotype is positive

The second step is to analyse when the slope of a random recipient's fitness on its genotype is positive. The only difference compared to the models of Section 1 and 2 are that a random recipient is now taken to be either a female (a member of the active class) or a male (a member of the passive class). Therefore, a gene causing a larva to develop as a queen with slightly higher probability is selected for when

$$\beta_{W_g} = \frac{dW(y, z)}{dg} = c_f \cdot \frac{dW_f}{dg_f} + c_m \cdot \frac{dW_m}{dg_m} > 0 \quad (3.1)$$

where W_f and W_m are the direct fitnesses of females and males and g_f and g_m are their genotypes. Note that the two components of selection have been weighted by class (sex)-specific reproductive values c_f and c_m . This is necessary because in haplodiploids twice as many genes are present in females than in males (if there is no worker reproduction), so that effects on female fitness change gene frequency twice as much as effects on male fitness. (in cases where interactions occur between different age classes, the c 's stand for age class specific reproductive value)

As before, the regressions of eqn. (3.1) can be expanded using the chain rule :

$$\frac{dW_f(y, z)}{dg_f} = \frac{\partial W_f}{\partial y} \cdot \frac{dy}{dg_f} + \frac{\partial W_f}{\partial z} \cdot \frac{dz}{dg_f} = \frac{\partial W_f}{\partial y} \cdot 1 + \frac{\partial W_f}{\partial z} \cdot r'_f = \frac{1-z}{z} - \frac{y}{z^2} \cdot r'_f \quad (3.2)$$

and

$$\frac{dW_m(z)}{dg_m} = \frac{\partial W_m}{\partial z} \cdot \frac{dz}{dg_m} = \frac{\partial W_m}{\partial z} \cdot r_m = -r_m \quad (3.3)$$

As in the basic tragedy of the commons model, dz/dg_f is not just pairwise sister-sister relatedness, but the relatedness to an average female, including self (Frank 1996, Wenseleers et al. submitted). Formally, if N larvae compete to become queens, then $dz/dg_f = r_f = (1/N) + r'_f \cdot (N-1)/N$, where r'_f is pairwise relatedness among female larvae (i.e. sister-sister relatedness). Also note that in the derivation of eqn. (3.3) we use the direct fitness interpretation of regression relatedness, which are slopes of actor phenotype on recipient genotype (dz/dg_m , the slope of average female behaviour on male genotype), rather than the more usual inclusive fitness coefficients, which are slopes of recipient genotype on actor genotype (dg_m/dg_f). Frank (1997) shows that relatedness among members of the active class (females, i.e. r_f) measures correlated behaviour, whereas relatedness to a passive class (in this case r_m), i.e. the classical inclusive fitness coefficients, are an extended notion of heritability.

Step 3: Solve to yield the ESS

Near the ESS, eqn. 3.1 should equal 0, and the behaviour of all female larvae will tend towards the same probabilistic optimum, so that we can set $y=z=z^*$. Consequently, we have

$$\frac{(1-z^*)}{z^*} \cdot 1 - \frac{1}{z^*} \cdot R_f - 1 \cdot R_m = 0 \quad (3.4)$$

where $R_f = c_f \cdot r_f$ is the life-for-life relatedness to a sister and $R_m = c_m \cdot r_m$ is the life-for-life relatedness to males.

This condition can be interpreted as a Hamilton's rule with three affected parties: (1) self, $r=1$, (2) sisters ($r=R_f$) and (3) males (brothers or nephews, $r=R_m$), although the costs and benefits again depend on the behaviour of all larvae within the colony. That is, costs and benefits are not constant.

Solving eqn. 3.4 for z yields the optimal probability with which larvae should develop into queens :

$$z^* = (1-R_f)/(1+R_m) \quad (3.5)$$

In the case where the colony is headed by a single singly-mated queen, and with all males produced by the queen, expression (3.5) predicts that larvae should develop as queens with a probability of $(1-0.75)/(1+0.25)=20\%$, which matches the allele frequency model prediction of Ratnieks (2001). When all males are produced by the workers, R_m is higher (0.75), and the ESS probability of developing as a queen is lower (14%).

Conclusion:

The ESS probability with which larvae should become queens in a swarming social insect = $(1-R_f)/(1+R_m)$

But do larvae ever have control over their own caste fate? Although certainly unusual, individual control of caste development is thought to be present in *Melipona* stingless bees (Bourke & Ratnieks 1999, Ratnieks 2001), because *Melipona* queens and workers are of the same size, yet are morphologically distinct, and are reared in mass provisioned cells that are all of the same type. Empirical evidence also provides good support for the predictions of the caste conflict model: under optimal conditions, levels of queen production range from around 14% in *Melipona favosa*, where most of the males are produced by the workers, to 20% in *M. beecheii*, where all males are produced by the queen (Wenseleers et al. submitted). In addition, most of the virgin queens are killed by the workers soon after eclosure, which shows that individual control of caste fate causes excess queen production from the perspective of the adult workers.

But what about other swarming social insects such as *Apis* honey bees or army ants? Below it is shown that their typically low level of queen production is caused by a transition from individual to social control over caste development.

3.2 Social control of caste development

3.2.1 ANALYTICAL SOLUTION

Parameters:

y = probability with which a focal female larva develops as a queen

z = average probability with which female larvae develop as queens in the colony

P = average worker investment in caste policing

b = genotype at the breeding locus (b_f and b_m =genotypes of females and males)

p = genotype at the caste policing locus (p_f and p_m =genotypes of females and males)

c = colony level cost of policing

c_f = relative reproductive value of females

c_m = relative reproductive value of males

r_f and r_m = regression relatedness to females and males

R_f and R_m = life-for-life relatedness to females and males

We model a transition from individual to social control by assuming that the ancestral condition is one where each larva may decide over its own caste fate, and then checking when adult workers are selected to take over the caste allocation process. Thus we must study the joint evolution of two traits, one controlling the individual probability of becoming a queen, and the other controlling whether workers should prevent larvae from becoming queens (worker caste policing).

Step 1: Write individual reproductive success W of a random recipient as a function of the behaviour of the active classes

We now have to write male and female fitness as a function of the behaviour of two active classes: (1) females, who may adjust their probability of becoming a queen, and (2) workers, who may or may not inhibit immature females from developing as a queen. An adequate equation for the average success of a colony or swarm would be $G = 1-z.(1-P)-c.P$, because this is $1-z$ in the absence of caste policing ($P=0$), but $1-c$ when workers can prevent ($P=1$) any excess queen production (where such prevention is assumed to come at a colony level cost c). Similarly, we can write the relative individual success of a female larva as $I = P + (1-P).(y/z)$, because in the absence of worker policing ($P=0$) the relative success of any female larva is given as y/z (an above-average probability of developing as a queen), whereas with worker policing ($P=1$), it becomes impossible for any female to gain an advantage over any other ($I=1$).

Consequently,

The fitness through male function $W_m = G = 1-z.(1-P)-c.P$

The direct fitness of a female $W_f = G.I = (1-z.(1-P)-c.P).(P + (1-P).(y/z))$

Step 2: Analyse when the slope of a recipient's fitness on its genotype is positive

We now have 2 equations: one specifying selection for female larvae to become queens, the other specifying selection for worker caste policing, i.e. we are again analysing a 2-locus kin selection problem. As before, these two selection equations need to be simultaneously maximised to provide the joint ESS. The equations themselves are messy (see the enclosed *Mathematica* sheet), so I will just explain the rationale of how to derive them.

For a female larva, a higher probability of developing as a queen is favoured when

$$\begin{aligned} \frac{dW(y, z, P)}{db} &= c_f \cdot \frac{dW_f(y, z, P)}{db_f} + c_m \cdot \frac{dW_m(z, P)}{db_m} \\ &= c_f \cdot \frac{\partial W_f}{\partial y} \cdot \frac{dy}{db_f} + c_f \cdot \frac{\partial W_f}{\partial z} \cdot \frac{dz}{db_f} + c_m \cdot \frac{\partial W_m}{\partial z} \cdot \frac{dz}{db_m} \\ &= \frac{\partial W_f}{\partial y} \cdot 1 + \frac{\partial W_f}{\partial z} \cdot R_f + \frac{\partial W_m}{\partial z} \cdot R_m > 0 \quad (\text{chain rule}) \end{aligned}$$

where derivatives can be evaluated near the point where $y = z = z^*$ and $P = P^*$ and terms involving dP/db_f or dP/db_m are left out, because we assume that the caste determining locus of female larvae is not linked to the worker caste policing locus. The other substitutions are as in eqns. (3.3) and (3.4).

Similarly, an increase in the investment in worker caste policing is favoured when

$$\begin{aligned}
\frac{dW(y, z, P)}{dp} &= c_f \cdot \frac{dW_f(y, z, P)}{dp_f} + c_m \cdot \frac{dW_m(z, P)}{dp_m} \\
&= c_f \cdot \frac{\partial W_f}{\partial P} \cdot \frac{dP}{dp_f} + c_m \cdot \frac{\partial W_m}{\partial P} \cdot \frac{dP}{dp_m} \\
&= \frac{\partial W_f}{\partial P} \cdot R_f + \frac{\partial W_m}{\partial P} \cdot R_m = (z_Q - c) \cdot R_f + (z_Q - c) \cdot R_m > 0 \quad (\text{chain rule})
\end{aligned}$$

where derivatives are also evaluated near the point where $y = z = z^*$ and $P = P^*$, and terms involving dy/dp_f , dz/dp_f or dy/dp_m are left out, because we assume that the caste determining locus of female larvae is not linked to the worker caste policing locus.

Step 3: Joint maximisation to provide the joint ESS

Joint maximisation of these 2 equations is difficult, but as a first start let us check when worker caste policing can invade in a situation where all larvae are becoming queens with their own optimum probability ($z^* = (1 - R_f) / (1 + R_m)$, see Section 3.1 above). For this, set the probability of developing as a queen (z^*) to $(1 - R_f) / (1 + R_m)$ and the level of worker caste policing P to 0 in the selection equation for policing, and see when an increase in policing is favoured.

As it turns out, this is when $c < (1 - R_f) / (1 + R_m)$.

Conclusion :

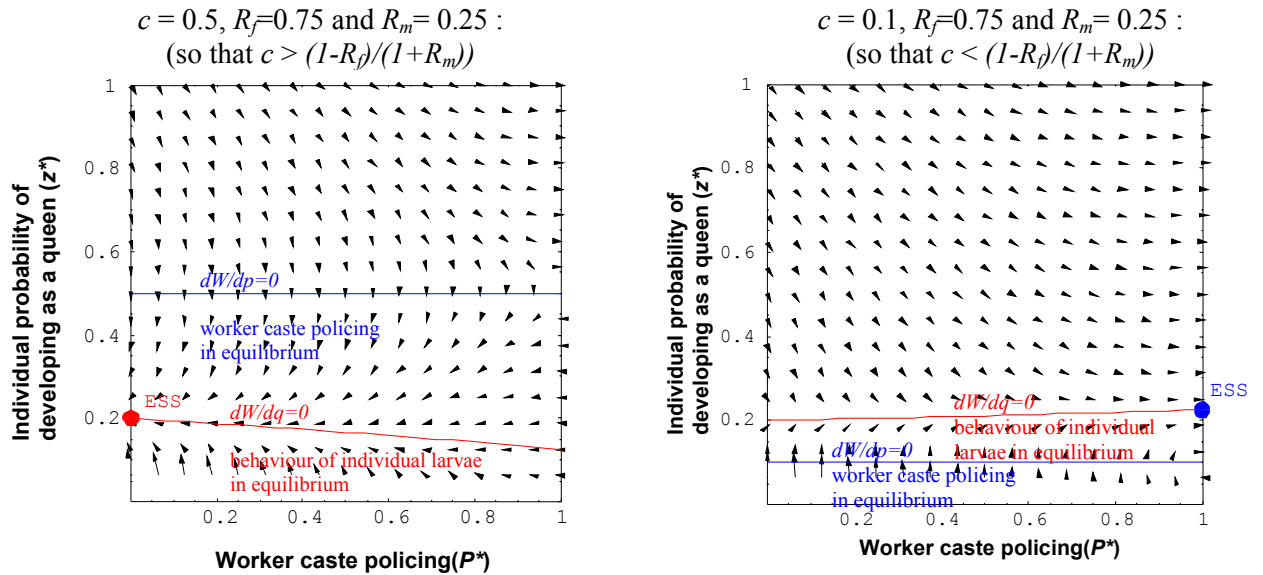
When the cost of policing $c < (1 - R_f) / (1 + R_m)$, worker caste policing, i.e. social control over caste development, is favoured. Below it is checked graphically that whenever worker caste policing invades it will also tend to be maximally favoured. This can best be done using field plots.

The intuitive explanation for this result is that excess queen production will reduce colony productivity by a fraction $(1 - R_f) / (1 + R_m)$, and that worker caste policing can prevent this to happen at a productivity cost c (the cost of policing). Thus caste policing is favoured when the cost of policing $<$ the cost of having a colony with excess queen production.

Social control over caste development is the reason why *Apis* produces few queens, in keeping with colony needs: queens are larger than workers, and if females are to become queens, they need to be reared in specially built cells and given special food (royal jelly). Note, however, that adult workers constantly force individual females to become workers, even when this is not in the inclusive fitness interests of any single female (check from eqn. 3.5 what their optimum is). This means that the increased efficiency of a honeybee relative to a *Melipona* colony also comes at a cost: a complete loss of individual freedom.

3.2.2. GRAPHICAL SOLUTION

As in section 2.2.2, the way the ESS is reached can also be illustrated graphically using field plots.



3.3 Questions & Answers

1. With what probability would a female larva in an *Apis* honeybee colony like to develop as a queen? Why is the observed level of queen production lower?

*In honeybee colonies, $R_f=0.15$ due to multiple mating and $R_m=0.25$. Therefore, any larva is selected to become a queen with a probability of $(1-0.15)/(1+0.25)=68\%$. Of course, *Apis* colonies produce far fewer queens than this, usually just a few over a whole season. This is because caste is under complete social control in honeybees. Note that caste is often said to be non-genetically determined, i.e. set purely by the feeding regime imposed on by the workers. But could the way workers feed larvae not be heritable?*

2. In an unpublished study, Strassmann *et al.* have produced a caste conflict model using Hamilton's constant cost/benefit rule. What is the problem with such an approach?

The assumption of constant costs and benefits is inappropriate. E.g., the benefit of becoming a queen depends on what other larvae do within the colony (the benefit becomes less as more larvae develop as queens). With frequency dependent costs and benefits (as derived above) one can calculate the ESS probability for a larva to develop as a queen, but with a constant cost/benefit rule this is not possible.

3. In *Melipona* nearly all virgin queens are killed by the workers soon after eclosion. What is there to gain then from becoming a queen? That is, why develop as a queen with a probability of 20% if no one is going to survive anyway? Should the ESS not be a function of the proportion of queens that get executed?

No, queen execution by workers does not affect the optimum probability for female larvae to develop as queens. The reason is that if, say, half of all queens get executed, the remaining queens' fitness will be twice as high, since they compete with half as few queens for heading a daughter swarm. Probability one half of twice as much yields the same payoff. The same argument has

been used to show that if many males die before mating, this has no influence on optimal sex allocation.

4. A slight artificiality of the model is that it assumes that zero allocation to queens is the colony optimum. Actually, it may be that colonies that produce 5 queens do better than queens that produce only 1 queen (and certainly better than colonies that produce no queens), because they can split in more daughter colonies. How could this problem be alleviated?

One way around this would be to assume that the optimum allocation to queens from a colony level perspective is k , and to use a colony success function G that has a maximum at k and then decreases as more larvae become queens. One such possible function is $G = z^k \cdot (1 - z)^{1-k}$. By the same methods as before, it is easy to show that the ESS is then $z^ = (1 - Rf + k \cdot (Rf + Rm)) / (1 + Rm)$. For example, for $k = 0.05$, $z^* = 24\%$ rather than 20% when $k = 0$. But more realistically, k is probably in the range of 0.1% , in which case the deviation from the simple model becomes negligibly small.*

Section 4. Assignments

The associated *Mathematica* file is available at <http://www.shef.ac.uk/uni/projects/taplab/twpub.html#courses>.

Purpose :

- Over the next few days you will be given a chance to carefully go through the enclosed *Mathematica* sheets and the *Questions & Answers* sections to better understand all this. Enthusiasts can even attempt to solve some problems for themselves - below are some suggestions.
- Each problem below has an associated difficulty score ranging from * (easy), over ** (intermediate) to *** (difficult) and **** (masterful).
- There is also a section of '*Sociobiology Classics*' – classical problems that have featured prominently in the social evolution literature: Trivers & Hare's (1976) sex ratio theory, sex ratios under local mate competition (Hamilton 1967, 1979), split sex ratio theory (Boomsma & Grafen 1991), Hamilton & May's (1977) dispersal model and skew theory (e.g. Reeve & Ratnieks 1993). The enclosed *Mathematica* notebook contains model solutions to each of these problems (and some of the other problems too).
- Finally, I have prepared a list of discussion topics. These are more general thoughts about where our field might be heading. Ideal to discuss over beer.

4.1 Problems related to Section 1 on 2 Player Games

1. (*) Derive the mixed ESS level of cooperation for the 2-player game with general payoffs $E(C,C)$, $E(C,D)$, $E(D,C)$ and $E(D,D)$ using the method outlined in section 1.1.
2. (*) Check the equilibrium frequency of driving genes in a population as derived by Wensleers & Ratnieks (submitted) using the method as outlined in section 1.2.
3. (**) Q&A 1.4 question 1
4. (***) Q&A 1.4 question 2

4.2 Problems related to Sections 2 and 3 on Tragedies of the Commons

1. (*) Q&A 2.3 question 2
2. (*) Q&A 2.3 question 4
3. (***) Calculate the ESS probability with which a slime mould slug cell should become a spore rather than a stalk cell as a function of the number of constituent clones (assume that the different clones are drawn randomly from the population, and hence unrelated to each other). Assume that the global optimum, i.e. the one that yields the most successful spores, is 20% stalk cells, and that when fewer than 20% stalk cells are formed, total net spore production will be reduced. Initially assume that there are no benefits of being larger when composed of 2 or several clones, then relax this assumption. If it were found that the ratio of spore to stalk cells is independent of the number of constituent clones, how could this be explained? What would be the result if cell fate were under social rather than individual cellular control?
4. (****) Q&A 2.3 question 8
5. (****) Tragedies of the commons often result from an excessive breeding or exploitation *rate*. How could one make a more detailed model that derives the optimal breeding or exploitation *rate* as a function of relatedness?
No idea. If you know how to do this, let me know.

4.3 Sociobiology Classics

1a. (*) *SKEW THEORY*

Consider the basic reproductive skew model of Reeve & Ratnieks (1993; for an accessible review see Keller & Reeve 1994). Two paper wasps may either nest on their own, or share their reproduction on a single nest. Using Frank's approach (terminology cf. section 3), derive when (1) a subordinate wasp is selected to join a dominant? and (2) how much reproduction the subordinate should be able to obtain to make staying worthwhile ('the staying incentive')? Let r be the relatedness between two foundresses, p the fraction of a nest's direct reproduction that is the subordinate's, k the total reproductive output of a group with two females, relative to a value of 1 for an already established nest with one female (k will usually be >1) and x the expected reproductive success of a subordinate if she nests elsewhere, relative to a value of 1 for an already established nest (usually x will be <1). Let y_s stand for the probability with which a subordinate stays. To make things easy I have already calculated the payoffs to subordinate and dominant as a function of these parameters

(first payoff is to subordinate, second to dominant):

	DOMINANT
SUBORDINATE (prob. $1-y_s$)	$(x,1)$
(prob. y_s)	$(p.k,(1-p).k)$

1b. (**) In 1a we derived what fraction of the reproduction the subordinate would like to obtain to make staying worthwhile ('staying incentive'). Usually the staying incentive is interpreted a bit differently as the fraction of the reproduction that the dominant would like to allow to the subordinate to make her stay. But is the dominant really selected to share any reproduction with the

subordinate? To investigate this, try to derive what fraction of the reproduction that the dominant is selected to give. To do this, substitute p in the previous fitness equations by a continuous character y_D (the fraction of the reproduction that the dominant allows the subordinate to have), and make a few field plots of the joint evolution of subordinate and dominant behaviour.

2a. (**) *BASIC SEX RATIO THEORY*

Rederive using Frank's approach the classical result of Trivers & Hare (1976) that social hymenopteran workers are selected to allocate 3 times more to sisters than to brothers (assuming single mating) (use the terminology of section 3). First assume an infinite population size then try to derive the ESS for a population of size N . Let y and z stand for the allocation to queens in a focal colony and the population at large (focal colony included).

2b. (***) *SPLIT SEX RATIOS*

Assume we have variation in mating structure with a proportion p of all queens doubly mated and a proportion $1-p$ singly mated. Derive the joint sex allocation optimum of workers in single and double mated colonies. Derive this graphically, using a field plot.

2c. (***) *SEX RATIOS UNDER LOCAL MATE COMPETITION*

Consider the local mate competition scenario as envisaged by Hamilton (1967, 1979) with a life cycle as in fig wasps: (1) N foundresses lay eggs within a fig, (2) sexuals emerge, (3) males compete locally for mating with undispersed females, (4) mated females disperse, What optimal sex ratio should a foundress produce? Use the following parameters: N = foundress number, y = a single focal foundresses' allocation to males, z = the average allocation to males within a fig (average of all foundresses; the population average sex allocation is not needed, since mating is independent of this; mating occurs locally), r_m and r_f = the relatedness to a son and daughter and R_m = the relatedness between a foundress and an average male within a fig (includes sons with probability $1/N$ and sons of other foundresses with a probability of $(N-1)/N$).

(hint: allocating more resources to sons is a tragedy of the commons: it increases your competitiveness relative to other foundresses (more of your own sons will succeed in finding a mate), but if all foundresses do this there will be no females left to mate with, hence the tragedy).

3. (****) *EVOLUTION OF DISPERSAL*

Consider a population of dandelions (*Taraxacum*) that has completely taken in its habitat. Assume that the population is divided into patches and that each patch can support only one plant. The plant is annual, i.e. dies at the end of the year, and is replaced the next spring. What proportion of dispersing seeds should the plant produce at the end of the season ('winged' seeds; in proper terminology seeds with a 'pappus', i.e. 'parachute' seeds)? Assume that a dispersing seed is equally likely to arrive at any patch; let the relative chances of survival of dispersing vs. stay at home seeds be $1-c$, where c is the cost of dispersal. Calculate the optimum both from the mother plant's and an individual seed's perspective and check that (1) the optimal dispersal rate is very high even when the chances of surviving are very low (high c) (Hamilton & May 1977) and (2) that the mother plant favours higher dispersal than any individual seed (Motro 1983). If flowers are pollinated by pollen from many different plants, would this influence the optimal dispersal rate?

4.4 Discussion Topics

1. Price recognized that his equation was a step towards a more general theory of selection. Here is the opening paragraph of Price's manuscript "*The Nature of Selection*" (Price 1995) :

Selection has been studied mainly in genetics but of course there is much more to selection than just genetical selection. In psychology for example trial-and-error learning is simply learning by selection. In chemistry selection operates in a recrystallisation under equilibrium conditions, with impure and irregular

crystals dissolving, and pure, well-formed crystals growing. In paleontology and archaeology selection especially favours stones, pottery, and teeth, and greatly increases the frequency of mandibles among the bones of hominid skeletons. In linguistics, selection unceasingly shapes and reshapes phonetics, grammar, and vocabulary. In history we see political selection in the rise of Macedonia, Rome, and Muscovy. Similarly, economic selection in private enterprise systems causes the rise and fall of firms and products. And science itself is shaped in part by selection, with experimental tests and other criteria selecting among rival hypotheses.

Price then remarks that he “hopes that the concept of selection ... will contribute to the future development of “selection theory” as helpfully as Hartley’s concept of information contributed to Shannon’s communication theory.” Indeed, the Price equation is already providing deeper insight into cultural evolution (e.g. Frank 1998, p. 55), trial-and-error learning (Frank 1997c), developmental selection and self-organization (Frank 1997d).

Read Price (1995) and Frank (1995) and reflect on the potential of such a “general theory of selection”.

2. Currently, self-organisation models are quite successful at making predictions of dynamic aspects of social organisation, but entirely neglect the possibility of conflict (e.g. Bonabeau *et al.* 1996, 1999 consider the dynamics of dominance hierarchy formation, but don’t seem to be aware of the conflicts that arise in this context). Kin selection models on the other hand make useful predictions on the evolution of conflict, but are poor at making dynamic predictions, and the methods available for studying dynamic kin selection problems still need further development (McNamara *et al.* 1994; Day & Taylor 1997, 2000; Iwasa 2000). For an example of a dynamic problem think about how a social insect colony should allocate resources to reproduction vs. growth at any given time. Macevicz & Oster (1976) showed that for annual social insects the colony optimum is to produce workers early on in the colony lifecycle, and switch to sexual production only towards the very end of the season (also see Bulmer 1994, p. 83-84). But suppose that workers can lay eggs, would this not favour an earlier onset of the sexual (male) production phase? Or if females could manipulate their caste fate and become queens would this not favour an earlier onset of the queen production phase?

Discuss the relative merits of complexity/self-organisation models and evolutionary models.

E.g., can both make testable predictions? In what ways do their predictions differ? Is there a different emphasis on proximate vs. ultimate aspects of social organisation, etc... Hardcore modellers could discuss possible means by which dynamic aspects of conflict evolution might be studied.

3. In biology we take as a dogma that all behaviour is genetically determined. In the social sciences there is an almost exclusive focus on cultural inheritance and learning. The study of how genetic and cultural evolution might interact is remarkably slow-going, but there seems to be a prospect that the Price equation might bring some formalism to it all.

Read the rebellious child model of Frank (1998, p. 55), a model of the cultural evolution of an altruistic trait. Think about the following: (1) could nurture ever go against nature? (i.e. could a culturally inherited trait that harms one’s biological fitness ever spread through a population?), (2) are gene-culture arms-races ever expected?, (3) if so, which type of evolution will tend to be ahead?, (3) what are the fundamental differences in the inheritance laws and the way phenotypic variance is created? (e.g. mutation rate etc...). Take self-sacrifice propagated by some religious sect as an example of a culturally inherited trait.

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Appendix 1. Differentiation Calculus

No mathematical skills beyond simple differentiation calculus are needed to solve any of the problems in this handout. For those who can't quite remember how this works, this section will fresh up your mind.

The derivative of a function tells us something about the rate at which the function changes. Given a function $y = f(x)$, the derivative is denoted as dy/dx or $f'(x)$ and is defined as

$$\frac{dy}{dx} = \lim_{\Delta x \rightarrow 0} \frac{\Delta y}{\Delta x} = \lim_{\Delta x \rightarrow 0} \frac{f(x + \Delta x) - f(x)}{\Delta x}$$

The geometrical meaning of the derivative is the slope of the line tangent to a function at a specific point. The terms Δy and Δx are called differentials and the ratio of differentials when $\Delta x \rightarrow 0$ is the derivative.

The derivatives of most common functions have been worked out and can be calculated according to the following rules:

Constant function:	$y = a$	$dy/dx = 0$
Linear function	$y = ax$	$dy/dx = a$
Power function	$y = x^n$	$dy/dx = nx^{n-1}$
Sum or differences of functions	$y = g(x) \pm h(x)$	$dy/dx = dg/dx \pm dh/dx$
Product rule	$y = uv$ where $u = f(x)$ and $v = g(x)$	$dy/dx = u.dv/dx + v.du/dx$
Quotient rule	$y = u/v$ where $u = f(x)$ and $v = g(x)$	$dy/dx = [v.du/dx - u.dv/dx]/v^2$
Chain rule	If we have a function $y=f(z)$ and z is also a function such as $f(x)$ then	$dy/dx = dy/dz.dz/dx$
Logarithmic function	$y = \ln(x)$	$dy/dx = 1/x$
Exponential function	$y = e^x$	$dy/dx = e^x$
Sine function	$y = \sin(ax)$	$dy/dx = a \cos(ax)$
Cosine function	$y = \cos(ax)$	$dy/dx = -a \sin(ax)$

If we have a function of more than one independent variable then we need to distinguish between the *partial* and *total derivative*. The *partial derivative* says what happens to a function when only one variable changes. For example if w is a function of two independent variables y and z , then the partial derivative $\partial w / \partial x$ says how w changes with x , holding constant y . Similarly, $\partial w / \partial y$ says how w changes with y , holding constant x . The *total derivative* says what happens to a function when a variable changes, but without the constraint that the other variables remain constant.

For a function w dependent on two variables y and z , the total derivative of w with respect to y is given as

$$\frac{dw(y, z)}{dy} = \frac{\partial w}{\partial y} + \frac{\partial w}{\partial z} \cdot \frac{dz}{dy}$$

This shows that a change in y may cause a change in w both as a result of a direct effect of y on w ($\partial w / \partial y$), or as a result of an indirect effect of y on z (dz / dy), with z in turn influencing w

$(\partial w / \partial z)$. For people more familiar with multiple regression, one can think of partial and total derivatives as approximations of partial and total regressions in a given point.

Example. In the text we often encounter situations where actor fitness w depends on own and partner behaviour, y and z , with y and z in turn being correlated with actor genotype g (y by l and z by r). If we are then interested in how fitness w changes with actor genotype, we need to calculate the total derivative dw/dg :

$$\frac{dw(y, z)}{dg} = \frac{dw}{dy} \cdot \frac{dy}{dg} = \left(\frac{\partial w}{\partial y} + \frac{\partial w}{\partial z} \cdot \frac{dz}{dy} \right) \frac{dy}{dg} = \frac{\partial w}{\partial y} \cdot \frac{dy}{dg} + \frac{\partial w}{\partial z} \cdot \frac{dz}{dg}$$

where the first identity applies the chain rule given above. Note that $dy/dg = 1$ and dz/dg equals relatedness.

Appendix 2. Computer Algebra Systems

Computer algebra systems (CAS) are computer programs that allow manipulation of symbolic equations. CAS can make the life of modellers considerably easier, since it allows one to focus more on problem solving as such, without having to waste any time on doing basic algebra. Some of the most powerful commercial systems are *Mathematica* and *Maple*, but there are also a few freeware programs with more limited capabilities, such as *Maxima*, *HartMath* and *Yacas*. Below I give a brief summary of the commands you may need to solve the problems of this handout. I focus my attention on *Mathematica* because it is one of the most powerful and widely used systems available — it can do anything from the symbolic calculation of derivatives, integrals and differential equations to matrix algebra or simulating numerical problems using its in-built computer language (that resembles C++). It also has Mac, PC and UNIX/LINUX versions, the in and output of which are all compatible.

Mathematica

You need to press SHIFT+ENTER to evaluate each line of input.

Define a function	<code>funcname [y_, z_] = (1-z) * (y/z)</code>
Calculate a (partial) derivative	<code>D[eqn, var]</code>
Replace something in the output by something else	<code>/. e.g. if you want to replace y by z in the output: /. {y->z}</code>
Solve an equation	<code>Solve[eqn==0, var]</code>
Solve a system of equations	<code>Solve[{eqn1==0, eqn2==0}, {var1, var2}]</code>
Simplify an equation	<code>Simplify[eqn] or FullSimplify[eqn]</code>
Plot a 2D function	<code>Plot[func[x], {x, min, max}]</code>
Plot a 3D function	<code>Plot3D[func[x, y], {x, xmin, xmax}, {y, ymin, ymax}]</code>
Make a field plot	<code><< Graphics`PlotField` (load the required package) PlotVectorField[{fx, fy}, {x, xmin, xmax}, {y, ymin, ymax}]</code>
Make an implicit plot (a plot of a curve that is given implicitly, as the solution to an equation)	<code><< Graphics`ImplicitPlot` (load the required package) ImplicitPlot[eqn==0, {x, xmin, xmax}]</code>

A typical solution to a problem of this handout would be :

```
In:   Wf = (1-z) * (y/z);
      Wm = 1-z;
      selection = (D[Wf, y] * 1 + D[Wf, z] * Rf + D[Wm, z] * Rm) /. {y->z};
      Solve[selection == 0, z];
      Plot3D[(1-Rf) / (1+Rm), {Rf, 0.1, 0.75}, {Rm, 0.25, 0.75}]

Out:  {z->(1-Rf) / (1+Rm)} plus a 3D graph of the ESS
```