

An introduction to the evolutionary modelling of conflict

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Purpose :

- Offer "how-to" approach to analysis of conflict
- Explain
 - Steve Frank's methods
(*'The Foundations of Social Evolution'*)
 - how it combines concepts from game and IF theory
 - why IF theory (Hamilton's rule) sometimes fails
 - what we can do about this
 - the distinction between direct and IF problems
 - 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)
- Give brief intro in computer algebra systems (*Mathematica*)

Two-player games

- e.g. 2 males that compete for females
queens that may fight or cooperate during nest founding
parasitoid larvae that may kill or tolerate each other
- ‘**strategies**’: e.g. fight or cooperate
- ‘**players**’: the actual strategists
genes – chromosomes – individuals – groups – nations
- ‘**payoffs**’: consequences for reproductive success
- ‘**equilibrium**’: evolutionary stable strategy or ESS
 - **mixed ESS**: players adaptively adjust probability of cooperating. ESS when it cannot be invaded by players that cooperate with slightly different probability. (infinite allele model)
 - **pure ESS**: each player is of one of two types, and the equilibrium consists of a stable mix between the two. (2 allele model)
- **symmetrical games**: when the role of each player is interchangeable and when they have the same strategies available
i.e. payoffs to player 1 when fighting player 2 =
payoffs to player 2 when fighting player 1
- **asymmetrical games**
e.g. interspecific interactions – two species have not the same strategies available, e.g. parasite can be virulent or avirulent, host can be susceptible or resistant

Two-player games

Mixed strategy case

Consider the following game (Prisoner's dilemma) :

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

(payoffs are to player 1)

with C = personal cost of cooperating
 B = personal benefit of other player's altruism

The **direct fitness of player 1** w_1 can be written as

$$w_1 = -C.y_1 + B.y_2 \quad (+ \text{ a constant})$$

'neighbour modulated fitness'

(y_1 and y_2 = probabilities with which player 1 & 2 cooperate)

- Game assumes costs and benefits are additive over interactions,
 i.e. cost of cooperating independent of what other player does
 benefit of the other player's altruism independent of what
 player 1 does

Hamilton's rule assumes such additive fitness effects.

- **Can cooperation invade?** NO, risk of being a sucker.

$$E(\text{defect,defect}) > E(\text{cooperate,defect})$$

- But what if player 1 tends to be matched with an opponent of like type, say a clone? A cooperative player would then tend to be matched with a cooperative opponent.

COOPERATION CAN THEN INVAD E provided that

$$E(\text{cooperate,cooperate}) > E(\text{defect,defect}), \text{ i.e. when } B-C > 0$$

Relatedness in direct fitness models

Under what circumstances do players tend to interact with their own kind?

Possible causes:

- **kinship (most common)**
e.g. identical twins tend to behave the same way
- common environment
e.g. individuals raised in same environment tend to behave the same way
- direct recognition of partners of like type
e.g. green beard recognition
learning from previous encounters
- prior information about how partner tends to behave (e.g. based on reputation)

In the rest of this handout we will assume that correlated behaviour arises as a result of shared genes at common genetic loci, but it is important to realise there may be other causes.

Two-player games

Mixed strategy case

Above we assumed that the correlation r was one. How generalise to any r ?

Steve Frank's 3-step **direct fitness method** :

1. Write an individual's fitness w as a function of own and partner behaviour ('*neighbour modulated fitness*')

2. Calculate when gene for playing particular strategy increases ones reproduction.

- Done by checking when regression of fitness w on individual genotype g is positive.

- Correlated behaviour arises as an association between player 1's genotype and player 2's phenotype ($= r$).

- Rationale of method: Price equation.

3. Obtained equation says when a strategy is favoured; setting it to zero allows the derivation of the ESS.

Two-player games

Mixed strategy case

Example.

1. direct fitness player 1 $w_1 = -C.y_1 + B.y_2$ (+ a constant)
2. statistical regression of player 1's fitness on its genotype > 0

Awkward to calculate, but easily approximated using analytical equivalent – total derivative :

$$\begin{aligned} \beta_{w_1 g_1} = dw_1 / dg_1 &= \frac{\partial w_1}{\partial y_1} \cdot \frac{dy_1}{dg_1} + \frac{\partial w_1}{\partial y_2} \cdot \frac{dy_2}{dg_1} && \text{(chain rule)} \\ &= -C \cdot \frac{dy_1}{dg_1} + B \cdot \frac{dy_2}{dg_1} \\ &= -C \cdot 1 + B \cdot r > 0 \end{aligned}$$

Often used as proof of Hamilton's rule, but meaning is different:

- B = benefit to player 1 of opponent's altruism
not benefit to player 2 of player 1's altruism
 (are the same only for symmetrical games)
- r measures correlated behaviour.
 $r \neq$ kinship, but = information about opponent's behaviour
- ESS strategy MAXIMISES DIRECT FITNESS on part of each player GIVEN INFORMATION (r) ABOUT OPPONENT'S BEHAVIOUR.

In game theory: 'correlated equilibrium' \neq 'Nash equilibrium', reached when player's strategies are uncorrelated (no information about opponent's behaviour)

Direct vs. inclusive fitness

All this may appear a bit weird. This is because we are assuming a *direct fitness perspective*, whereas we have always learnt to look at social phenomena from an *inclusive fitness* angle. Although often described as equivalent, they are not:

Direct fitness point of view

Appropriate when all individuals express the social trait and when one's direct fitness is a function of own and partner behaviour. Relatedness in this context measures **correlated behaviour** between the social interactants. Not kin selection, but '**correlated selection**' (Frank 1997). Cf. correlated equilibrium in game theory.

e.g. 2-player games, evolution of worker reproduction, tragedies of the commons, evolution of dispersal, sex ratios under local mate competition

Inclusive fitness point of view

Appropriate when an active class of individuals affects a passive class of relatives. Relatedness does refer to kinship; we now have true '**kin selection**'. Has no equivalent in game theory. Kinship = extended notion of heritability (Frank 1997).

e.g. worker fratricide

worker policing

workers eat nephews to the benefit of brothers

workers express trait, nephews and brothers are affected, but do not themselves have a phenotype.

Passive class does not express the gene under study but may transmit copies of it to future generations.

Two-player games

Mixed strategy case

But even if we call our previously derived condition $B.r > C$ a Hamilton's rule, we are often left with a problem: costs & benefits usually are not constant !

Consider the 'hawk-dove game' :

'Hawk' = fight to gain a greater share of the resource,

'Dove' = peacefully share the resource

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

with C = the cost of fighting
 B = the value of the resource

Fitness of player 1

$$w_1 = -C.y_1.y_2 + B.y_1.(1-y_2) - B.(1-y_1).y_2 = B.y_1 - B.y_2 - C.y_1.y_2$$

if y_1 and y_2 are probabilities with which player 1 & 2 play hawk

But unlike in previous game, consequences of playing hawk or dove now depend on what opponent does.

Central idea in all of game theory!

Benefit of playing hawk = $\partial w_1 / \partial y_1 = B - C.y_2$. Not constant!

Cost of having a hawk partner = $\partial w_1 / \partial y_2 = B - C.y_1$.

Frequency dependence cause the population to evolve towards a **mixed ESS**.

With $r = 0$ ESS = play hawk with prob. B/C
 $r = 1$ ESS = always play dove

Two-player games

Mixed strategy case

The ESS as a function of r can be calculated using Frank's method:

Playing hawk with higher probability favoured when

$$dw_1 / dg_1 = \partial w_1 / \partial y_1 \cdot 1 + \partial w_1 / \partial y_2 \cdot r > 0,$$

i.e. when

$$(\text{Benefit of playing hawk}) - (\text{Cost of having hawk partner}) \cdot r > 0$$

$$\text{which is when } (B - C \cdot y_2) \cdot 1 - (B + C \cdot y_1) \cdot r > 0$$

Generalised Hamilton's rule : allow costs & benefits to be dependent on opponent's behaviour.

Near ESS y_1 and y_2 will evolve towards same value y .

ESS reached when $(B - C \cdot y) \cdot 1 - (B + C \cdot y) \cdot r = 0$ which is when a player plays hawk with a probability $y^* = (B/C) \cdot (1-r)/(1+r)$.

Derivation of invasion criteria :

- spread of hawk behaviour in all-dove population: set $y=0$
 $B - B \cdot r > 0$, hawk always invades
- spread of dove behaviour in all-hawk population: set $y=1$
 $C(1+r) > B \cdot (1-r)$; for $r=0$ this is when $C > B$

Summary of method

1. Write an individual's fitness w as a function of own and partner behaviour

$$w_1 = B.y_1 - B.y_2 - C.y_1.y_2$$

2. When is an increase in y favoured?

$$dw_1 / dg_1 = \partial w_1 / \partial y_1 \cdot 1 + \partial w_1 / \partial y_2 \cdot r > 0$$

$$(B - C.y_2) \cdot 1 - (B + C.y_1) \cdot r > 0$$

$$(\text{Benefit of playing hawk}) - (\text{Cost of having hawk partner}) \cdot r > 0$$

3. Near the ESS, $y_1 = y_2 = y$, and setting the selection equation to zero yields the mixed ESS.

$$(B - C.y) \cdot 1 - (B + C.y) \cdot r = 0 \quad \text{for} \quad y^* = (B/C) \cdot (1 - r) / (1 + r)$$

Two-player games

Pure strategy case

The equilibrium for **pure strategy games** can be calculated in a similar way, except that we now have to assume that players are constrained to play one strategy or another, and can not play anything in between.

Predicted equilibrium \neq mixed ESS!

Confusing because most optimisation models assume mixed strategies, but most genetic models pure strategies.

For now, we won't worry too much about pure strategies because if enough alleles are played out against each other over the course of evolution, the **final endpoint** will correspond to the **mixed ESS** (Eshel 1996).

The handout also gives an example of how to analyse **asymmetrical games**.

What have we learnt so far?

- How to analyse **direct fitness problems**

i.e. what is the optimal strategy when the consequences of what I do depend on what others do? **cf. Game Theory**

- That Frank's method allows **costs & benefits** to be determined in an easy way

- Derive the optimum in cases where the behaviour of social interactants tends to be correlated (**'correlated selection'**)

- That relatedness in direct fitness models measures **correlation** or **information** about the social interactant's behaviour (cf. Correlated game theory)

- Distinction between **direct** and **inclusive fitness** problems

- We will now analyse an **example** of a direct fitness problem: the evolution of worker reproduction in social insects

Application 1: The evolution of worker reproduction

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

Biological question :

- How many workers should reproduce within a colony?
- **Tragedy of the commons :**
lone laying worker has reproductive advantage, but if all would do so the colony would perish
- To simplify the problem let us analyse how reproduction should be partitioned in queenless colonies

Application 1: The evolution of worker reproduction

Let y and z be the individual and average probability with which workers breed within the colony

- Step 1 : write eqn. of reproductive success of worker

proportional to own breeding level (y)

inversely proportional to others' breeding level (z)
(compete for reproduction)

directly proportional to number of foragers ($1-z$)
(assuming linear cost function and optimum with few reproductive workers)

So we get $w = (y/z).(1-z)$
 $y/z =$ relative individual success
 $1-z =$ colony productivity

- Step 2 : calculate costs & benefits

Benefit of reproducing = $\partial w / \partial y = (1-z) / z$

Cost of having other workers reproducing = $\partial w / \partial z = -y/z^2$
(quotient rule)

- Step 3 : calculate selection equation & solve for ESS

$\partial w / \partial y + \partial w / \partial z . r = 0$ for $y = z$

$(1-z)/z - (1/z).r = 0$

$(1-z) - 1.r = 0$

$(1-z) = r$

$z^* = 1-r$

Application 1: The evolution of worker reproduction

Conclusion :

When a social insect colony loses its queen, a fraction $1-r$ of the workers should become reproductive.

When relatedness is caused by kinship this means
25% of all workers under single mating
50% under double mating, etc...

Excessive from a colony level perspective.
Usually far less workers reproduce. Why?
Social policing.

Reproductive success of a worker not only depends on own and colony mates' reproduction, but also on whether or not they police your reproduction.

Two-locus direct fitness model. Handout shows how to deal with this.

Conclusion is that when $c < 1-r$ social policing is favoured.
(cost of policing < cost of excessive breeding)

Application 2: Conflict over caste fate in social insects

Wenseleers, T., Ratnieks, F.L.W. & Billen, J. Conflict over caste fate in social insects: a tragedy of the commons examined. Submitted.

Bourke & Ratnieks (1999): social insect female more related to own than to a sister's offspring
→ benefits from becoming a queen
→ conflict over caste fate

Has also the structure of a tragedy of the commons: single female that becomes a queen has an advantage, but colony would perish if all would do so.

Only difference relative to worker reproduction problem: individual selfishness also affects a passive class of relatives – males. ('kin selection' component)
Solution: calculate cost to males and weigh by relatedness

Specific aim: make a model for swarming social insects, and derive with what optimal probability any larva would like to become a queen.

Application 2: Conflict over caste fate in social insects

Let y and z be the individual and average probability with which larvae become queens in the colony

- Step 1 : write eqns. for reproductive success

Success through female function :

- . proportional to own prob. of developing as a queen (y)
- . inversely proportional to average prob. with which larvae become queens (z) (compete for heading daughter swarm)
- . directly proportional to number of workers ($1-z$) (assuming linear cost function and optimum = little queen production)

So we get $W_f = (y/z) \cdot (1-z)$
 y/z = relative individual success
 $1-z$ = success of colony or swarm

Success through male function : $W_m = 1-z$

- Step 2 : calculate costs & benefits

Benefit of becoming a queen = $\partial W_f / \partial y = (1-z) / z$

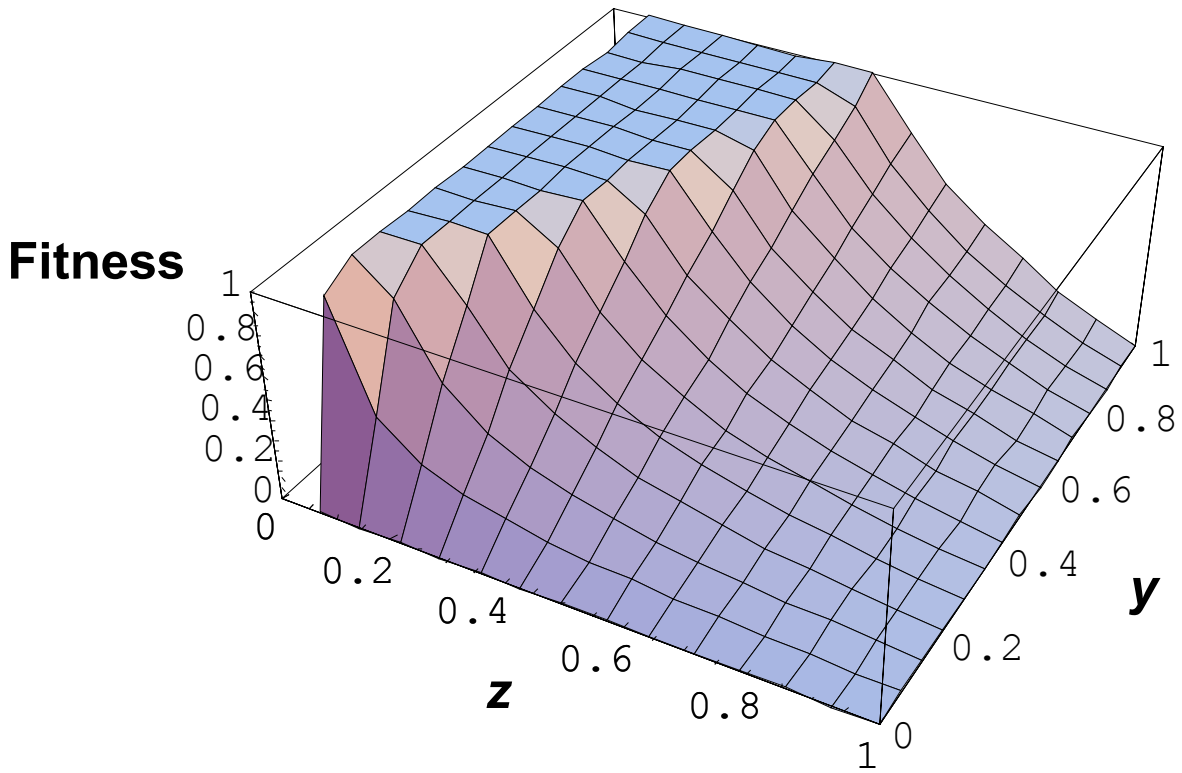
Cost of having other larvae become queens = $\partial W_f / \partial z = -y/z^2$

Cost to male production = $\partial W_m / \partial z = -1$

- Step 3 : calculate selection equation & solve for ESS

$\partial W_f / \partial y + \partial W_f / \partial z \cdot R_f + \partial W_m / \partial z \cdot R_m = 0$ for $y = z$

$(1-z)/z - (1/z) \cdot R_f - 1 \cdot R_m = 0$ $z^* = (1-R_f)/(1+R_m)$



Application 2: Conflict over caste fate in social insects

Conclusion:

A female would prefer to develop as a queen with a probability of $(1-R_f)/(1+R_m)$, with R_f = relatedness among sisters and R_m = (life-for-life) relatedness to males.

e.g. $(1-0.75)/(1+0.25) = 20\%$ single mating, no W reproduction
 $(1-0.75)/(1+0.5) = 14\%$ single mating, all males W produced
Excessive from colony-level perspective !

But model assumes that larvae have individual control over their caste fate. Is this ever the case? Unusual, but probably the case in *Melipona* stingless bees.

- Q & W morphologically distinct, but same size
- reared in mass provisioned cells

Supporting evidence:

- Excess queen production, killed by adult workers upon eclosion
- 20% queen production in *M. beecheii* (no W reproduction)
- 14% queen production in *M. favosa* (most males W produced)

What about other swarming social insects such as *Apis* honey bees or army ants? Their typically low levels of queen production are caused by a transition from individual to social control over caste development.

Application 2: Conflict over caste fate in social insects

When is social control over caste fate favoured?

Write fitness of affected parties (females and males) as a function of

- individual (y) and average (z) level of queen production
- individual (p) and average (P) level of 'caste policing'

Male fitness $W_m = G = 1 - z \cdot (1 - P) - c \cdot P$

Female fitness $W_f = G \cdot I = (1 - z \cdot (1 - P) - c \cdot P) \cdot (P + (1 - P) \cdot (y/z))$

We now get two equations, one specifying selection for becoming a queen, the other for caste policing (2-locus model)

Selection for becoming a queen

$$\partial W_f / \partial y + \partial W_f / \partial z \cdot R_f + \partial W_m / \partial z \cdot R_m > 0$$

Same eqn. as before, except that costs & benefits will now depend on whether or not there is caste policing.

Selection for 'caste policing'

$$\partial W_f / \partial P \cdot R_f + \partial W_m / \partial P \cdot R_m > 0$$

$$(z - c) \cdot R_f + (z - c) \cdot R_m > 0$$

Assume we start out from a situation where females become queens according to their individual optimum

$$z = (1 - R_f) / (1 + R_m).$$

Caste policing will then invade when $c < (1 - R_f) / (1 + R_m)$

Application 2: Conflict over caste fate in social insects

Conclusion:

Caste policing favoured when

cost of policing $<$

the cost of excess queen production $(1-R_f)/(1+R_m)$

Reason why *Apis* produces few queens:

- queens larger than workers
- workers can control caste allocation process
- need to be reared in special cells & given special food (royal jelly)

Adult workers force individual females to become workers against their own interests! (their optimum is to become a queen with a probability of 70%)

Coevolution of behaviour of females and workers can also be illustrated graphically :

