Evolutionary games, strategy-dependent interactions and non-linearity

Mark Broom

City University

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Outline

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Classical games

- Evolutionary games often involve pairwise contests between individuals randomly chosen from a well-mixed population.
- This leads to payoff functions that are linear both in the strategy of the focal individual, and in the mean population strategy.
- There are a number of types of situation in which such linearity does not occur, for example
    - playing the field games which are non-linear in the mean population strategy,
    - spatial games where the population is not well-mixed.
- One situation which has received little direct attention, although it has often been implicitly built into models, is the case where there is dependence between the strategy of an individual and which opponent it must face (or whether it faces an opponent at all).

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The owner-intruder game

- Consider the classical owner intruder game introduced by Maynard Smith, J. & Parker, G.A. (1976). The logic of asymmetric contests *Animal Behaviour* **24** 159-75.
- In this game an intruding individual challenges an owning individual for a resource of value V to the owner and v to the intruder, with two choices of play (Hawk and Dove) in each of the owner and intruder positions.
- this yielded four pure strategies;
  - Hawk: play Hawk as owner and intruder,
  - Dove: play Dove as owner and intruder,
  - Bourgeois: play Hawk as owner and Dove as intruder,
  - X: play Dove as owner and Hawk as intruder.
- It was assumed that each individual was in the role of owner and intruder with equal probabilities.

The owner-intruder game with strategy-dependent interactions

- One consequence of the assumption of the independence of roles and strategy is that there can never be a mixed ESS in such asymmetric games, due to the classical result from
  Selten,R. (1980) A note on evolutionarily stable strategies in asymmetric animal conflicts *Journal of Theoretical Biology* **84** 93-101.
- Suppose that the population follows a random process where they move between owner and intruder states only after a contest.
- In any mixture of Hawk and Bourgeois for instance, either all Hawks would end up as owners (if the Bourgeois were in the majority), or all Bourgeois would end up as intruders.
- Thus Bourgeois could not be an ESS as in the classical game.

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What is kleptoparasitism?

- Kleptoparasitism is the stealing by one animal of food that has been caught by another.
- Interspecific and intraspecific kleptoparasitism are widespread among vertebrates, and commonly observed amongst birds, especially seabirds.
- Frigate birds and skuas obtain much of their food by stealing from other species e.g. puffins.
- Gulls,terns and even sparrows are documented to steal off their own species.
- The model described below is based upon
  Broom,M., Luther,R.M., Ruxton,G.D. & Rychtar,J. (2008) A game-theoretic model of kleptoparasitic behavior in polymorphic populations *Journal of Theoretical Biology* **255** 81-91,

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The Broom-Ruxton model

Broom,M. & Ruxton,G.D. (1998) Evolutionarily Stable Stealing: Game Theory applied to Kleptoparasitism *Behavioral Ecology* **9** 397-403.
modelled a population such that;

- all individuals search for food and birds which are handling food (handlers),
- the time for a bird to successfully handle a food item follows an exponential distribution,
- if a bird spots another bird handling a food item then it may or may not initiate a contest, but the handler always resists,
- the length of a contest follows an exponential distribution, the winner obtains the food item (becomes a handler), the loser resumes searching,
- searching for handlers does not affect a bird's ability to search for food and vice versa.

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The strategies

- In the 2008 paper individuals either challenge always or never, and resist challenges always or never. There are thus four pure strategies in the game, with all individuals pure strategists. The strategies are:
  - Hawk: always attack, always resist when attacked,
  - Dove: never attack, never resist when attacked,
  - Retaliator: never attack, always resist when attacked,
  - Marauder: always attack, never resist when attacked.
- These strategies are associated with different searching behaviours.
  - Doves and Retaliators find food at rate $\nu_f f$.
  - Hawks and Marauders find food at rate $\nu_g f$.
  - Hawks and Marauders search for handlers as well, at rate ν_h.
  - Hawks and Marauders may thus have to divide their attention between the two searches and it is possible that because of this that $\nu_g < \nu_f$.

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The behavioural states

Parameter	meaning
P	density of the population
P_s, P_h, P_a, P_r	density of searchers, handlers, attackers and resisters
D_e, R_e, H_e, M_e	density of Doves, Retaliators, Hawks and Marauders
D_s, R_s, H_s, M_s	density of searching Doves, Retaliators, Hawks and Marauders
D_h, R_h, H_h, M_h	density of handling Doves, Retaliators, Hawks and Marauders
H_a, M_a	density of attacking Hawks and Marauders
R_r, H_r	density of resisting Retaliators and Hawks
h_r	handling ratio H_h/P in a population of Hawks only
$\nu_f f$	rate that Doves and Retaliators find food
$\nu_g f$	rate that Hawks and Marauders find food
ν_h	area Hawks and Marauders can search for handlers per unit time
t_h	expected time to consume a food item (if undisturbed)
$t_a/2$	expected duration of a contest over food
α	probability that the attacker wins the contest

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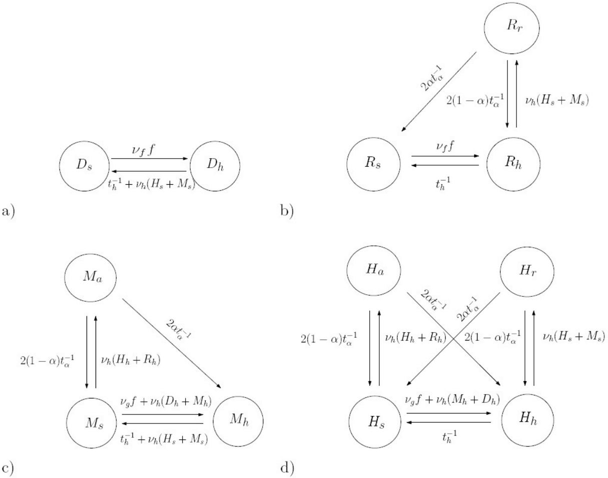
State transitions



The payoff to Dove

Doves can go through searching and handling stages only.

$$\frac{dD_s}{dt} = t_h^{-1} D_h + \nu_h (H_s + M_s) D_h - \nu_f D_s \qquad (1)$$

$$\frac{dD_h}{dt} = -t_h^{-1} D_h - \nu_h (H_s + M_s) D_h + \nu_f D_s \qquad (2)$$

$$D_e = D_s + D_h \qquad (3)$$

In the equilibrium, the right hand terms of the equations (1) and (2) equal 0 which together with (3) provides

$$\frac{D_e}{D_h} = 1 + \frac{1}{t_h \nu_f f} + \frac{\nu_h (H_s + M_s)}{\nu_f f} \qquad (4)$$

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The payoff to Retaliator

Retaliators can go through searching, handling and resisting stages.

$$0 = \frac{dR_s}{dt} = -\nu_f f R_s + t_h^{-1} R_h + 2\alpha t_a^{-1} R_r \tag{5}$$

$$0 = \frac{dR_h}{dt} = -t_h^{-1} R_h - \nu_h (H_s + M_s) R_h + \nu_f f R_s + 2(1-\alpha) t_a^{-1} R_r \tag{6}$$

$$0 = \frac{dR_r}{dt} = -2 t_a^{-1} R_r + \nu_h (H_s + M_s) R_h \tag{7}$$

$$R_e = R_s + R_h + R_r \tag{8}$$

By (5), (6), (7) and (8)

$$\frac{R_e}{R_h} = 1 + \frac{1}{\nu_f f} \left(t_h^{-1} + \alpha \nu_h (H_s + M_s) \right) + \nu_h (H_s + M_s) \frac{t_a}{2} \tag{9}$$

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The payoff to Marauder

Marauders can go through searching, handling and attacking stages.

$$0=\frac{dM_s}{dt}=-\nu_h P_h M_s - \nu_g f M_s + \left(t_h^{-1}+\nu_h(H_s+M_s)\right)M_h 2(1-\alpha)t_a^{-1}M_a \qquad (10)$$

$$0=\frac{dM_h}{dt}=-(t_h^{-1}+\nu_h(H_s+M_s))M_h+(\nu_g f+\nu_h(D_h+M_h))\,M_s+2\alpha t_a^{-1}M_a \qquad (11)$$

$$0=\frac{dM_a}{dt}=-2t_a^{-1}M_a+\nu_h(H_h+R_h)M_s \qquad (12)$$

$$M_e=M_s+M_h+M_a \qquad (13)$$

By (10), (11), (12) and (13) we obtain

$$\frac{M_e}{M_h}=1+\frac{t_h^{-1}+\nu_h(H_s+M_s)}{\nu_h P_h+\nu_g f-(1-\alpha)\nu_h(H_h+R_h)}\left(1+\nu_h(H_h+R_h)\frac{t_a}{2}\right) \qquad (14)$$

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The payoff to Hawk I

Hawks can go through four different stages - searching, handling, attacking, and resisting.

$$0 = \frac{dH_s}{dt} = -\nu_h P_h H_s - \nu_g f H_s + t_h^{-1} H_h + 2(1-\alpha) t_a^{-1} H_a 2\alpha t_a^{-1} H_r \qquad (15)$$

$$0 = \frac{dH_h}{dt} = -\nu_h (H_s + M_s) H_h - t_h^{-1} H_h + \left(\nu_g f + \nu_h (M_h + D_h)\right) H_s + 2\alpha t_a^{-1} H_a$$
$$+2(1-\alpha) t_a^{-1} H_r \qquad (16)$$

$$0 = \frac{dH_a}{dt} = -2 t_a^{-1} H_a + \nu_h (H_h + R_h) H_s \qquad (17)$$

$$0 = \frac{dH_r}{dt} = -2 t_a^{-1} H_r + \nu_h (H_s + M_s) H_h \qquad (18)$$

The payoff to Hawk II

We also have

$$H_e = H_s + H_h + H_a + H_r \qquad (19)$$

Using equations (15), (16), (17), (18) and (19) we obtain

$$\frac{H_e}{H_h} = 1 + \frac{t_h^{-1} + \alpha\nu_h(H_s + M_s)}{\nu_g f + \nu_h(D_h + M_h) + \alpha\nu_h(H_h + R_h)} \left(1 + \nu_h(H_h + R_h)\frac{t_a}{2}\right)$$

$$+\nu_h(H_s + M_s)\frac{t_a}{2} \qquad (20)$$

Finding ESSs

- We search for evolutionarily stable strategies (ESSs).
- A strategy **p** is an ESS if, for any other strategy **q**, and for sufficiently small ϵ;
  in a population comprising a fraction $1-\epsilon$ of **p** individuals and ϵ **q** individuals, **p** has a higher handling fraction (equivalent to the payoff) than **q**.
- For pure strategies we have shown that we only need to consider invasion by strategies that differ in one of their components e.g. for Dove to be an ESS it must resist Retaliator and Marauder, and if it resists these it will also resist Hawk.
- Thus Dove is an ESS if in a population almost entirely consisting of Doves

$$\frac{D_h}{D_e} > \max\left(\frac{R_h}{R_e}, \frac{M_h}{M_e}\right)$$

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Pure ESSs I: Dove

We consider Dove as an example.

- To resist invasion by Retaliator (by drift), we must allow a constant presence of a small amount of Hawks and/or Marauders (a trembling hand).
- Then Retaliator cannot invade Dove as long as

$$1 - \alpha < \frac{t_a}{2}\nu_f f \tag{21}$$

- Since $D_e \approx P$, from (8) we get that Dove cannot be invaded by Marauder if

$$D_h < \frac{\nu_f f - \nu_g f}{\nu_h} \Rightarrow P < \frac{\nu_f f - \nu_g f}{\nu_h}\frac{t_h \nu_f f + 1}{t_h \nu_f f} \tag{22}$$

- Dove is an ESS if the two conditions (21) and (22) hold.

Pure ESSs II: Hawk

When Hawk is the only type in the population, we obtain $H_h = Ph_r$, where h_r is the positive root of $h_r^2 t_a \nu_h P + h_r(1 + \nu_g f t_h) - \nu_g f t_h = 0$.
Retaliator cannot invade Hawk if

$$\begin{aligned} &\frac{t_a}{2}\nu_f f < \alpha \quad \text{and} \quad Ph_r > \frac{\nu_f f - \nu_g f}{\nu_h}\frac{1}{\alpha - \frac{t_a}{2}\nu_f f} \\ &\qquad\text{or} \\ &\frac{t_a}{2}\nu_f f > \alpha \quad \text{and} \quad Ph_r < \frac{\nu_g f - \nu_f f}{\nu_h}\frac{1}{\frac{t_a}{2}\nu_f f - \alpha} \end{aligned} \tag{23}$$

Similarly Hawk cannot be invaded by Marauder if

$$\begin{aligned} &2\alpha < 1 \quad \text{and} \quad Ph_r > \frac{\nu_g f - 2(1-\alpha)/t_a}{\nu_h}\frac{1}{1-2\alpha} \\ &\qquad\text{or} \\ &2\alpha > 1 \quad \text{and} \quad Ph_r < \frac{\nu_g f - 2(1-\alpha)/t_a}{\nu_h}\frac{1}{1-2\alpha} \end{aligned} \tag{24}$$

Hawk is an ESS if the above conditions (23) and (24) hold.

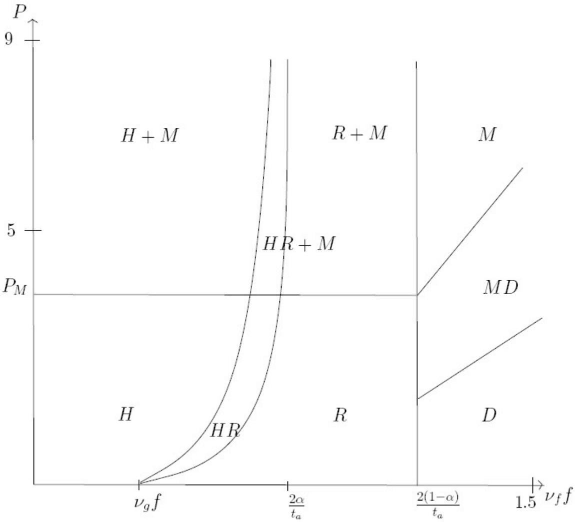
Mixed ESSs

We consider a mixture of Dove and Marauder as an example.
A mixture of Marauders and Doves occurs if Doves can invade Marauders, Marauders can invade Doves and neither Hawks nor Retaliators can invade. This gives the following conditions, the first resisting invasion, the second necessary for a Dove-Marauder equilibrium

$$\nu_f f \frac{t_a}{2} > 1 - \alpha, \frac{(\nu_f f - \nu_g f)(\nu_f f t_h + 1)}{\nu_f f t_h \nu_h} < P < \frac{(\nu_f f - \nu_g f)(\nu_g f t_h + 1)}{\nu_g f t_h \nu_h}$$

Notice that this is possible only if $\nu_f f > \nu_g f$, i.e. if kleptoparasites have a lower foraging rate.

Possible ESS combinations



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Results summary

- Hawk occurs when the food gathering ability of foragers that also attack, or general food availability, is poor and population density is not large.
- Marauders generally thrive when the population density is large and food availability is also large.
- Retaliators do better when food levels are intermediate and the population density is not large.
- Doves do better when food is plentiful and the population density is not too large.
- Cases where kleptoparasites have the higher foraging rate (including when Marauder, Retaliator and Hawk are all ESSs) are perhaps unrealistic.
- The "paradoxical" Marauder might not occur in conditions when it is not the only ESS.

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Outline

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The basic model

- Webb J.N., Houston,A.I.& McNamara, J.M. (1999) Multiple patterns of parental care *Animal Behaviour* **58** 983-993
  considers a two-stage game of brood care and desertion which reduces to a bimatrix game.
- At the start of a breeding season all individuals have found a mate. After their first breeding attempt there is the opportunity for a second, but to take this they will have to desert their offspring.
- If both parents desert, then the offspring will die and so they receive reward 0 from that mating.
- If both stay they receive reward V_2.
- If one deserts and one stays, they both receive $V_1 < V_2$, and the deserter has the chance to mate again.

The payoffs

- If the male deserts, the probability that he can mate again is r_m, and if the female deserts the probability that she can mate again is r_f.
- Since $V_2 > V_1$ and there is no opportunity for a third mating, it is clear that the best strategy in any second mating for both individuals is not to desert, so gaining reward V_2 for that mating.
- The game thus reduces to whether to "Desert" or "Care" at the first mating. With the male in role 1 and the female in role 2, this gives us the bimatrix of payoffs as

Male/Female	*Care*	*Desert*
Care	V_2, V_2	$V_1, V_1 + r_f V_2$
Desert	$V_1 + r_m V_2, V_1$	$r_m V_2, r_f V_2$

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ESSs

As described above, from Selten (1980) there cannot be any mixed ESSs for this game. Any of the pure strategy pairs can be ESSs for this game.

- There can be biparental care (male chooses Care, female chooses Care) if

$$r_m < \frac{V_2 - V_1}{V_2}, r_f < \frac{V_2 - V_1}{V_2}.$$

- There can be male uniparental care (male Cares, female Deserts) if

$$r_m < \frac{V_1}{V_2}, r_f > \frac{V_2 - V_1}{V_2}.$$

- There can be female uniparental care (male Deserts, female Cares) if

$$r_m > \frac{V_2 - V_1}{V_2}, r_f < \frac{V_1}{V_2}.$$

- There can be biparental desertion (male Deserts, female Deserts) if

$$r_m > \frac{V_1}{V_2}, r_f > \frac{V_1}{V_2}.$$

The variable remating model

- Webb et al (1999) also extended their model to consider variable remating possibilities.
- After desertion the potential number of available partners will depend upon whether other males or females desert, i.e. they will depend upon the strategies of the players in the current game.
- They use the payoffs

$$r_f(x,y) = k\frac{x}{\sqrt{x+y}}, r_m(x,y) = k\frac{y}{\sqrt{x+y}}$$

where r_f and r_m are the payoffs to males and females as before, this time being functions of x and y, the proportion of males and females respectively which desert their first broods.

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Non-linearity and a mixed ESS

- An interesting consequence of this non-linearity, is that the result of Selten (1980) no longer holds.
- It was shown that a mixed ESS occurred for sufficiently large V_1/V_2.
- If $3/4 \leq V_1/V_2$ then $x^* = y^* = 1/2$ is the ESS, and if $1/\sqrt{2} < V_1/V_2 < 3/4$ then the ESS is

$$x^* = y^* = \frac{2(V_2 - V_1)^2}{(2V_1 - V_2)^2}.$$

- Otherwise for $V_1/V_2 \leq 1/\sqrt{2}$ biparental care is an ESS (as implausibly is biparental desertion, although this is removed by the inclusion of any mating cost).

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Outline

The game

- The simplest non-trivial scenario to consider where interaction rates are not constant is a two player contest with two pure strategies A and B, with payoffs given by a standard payoff matrix

	A	B
A	a	b
B	c	d

  but where the three types of interaction happen with probabilities not simply proportional to their frequencies.
- This is the scenario in
  Taylor,C. & Nowak,M.A. (2006) Evolutionary game dynamics with non-uniform interaction rates *Theoretical Population Biology* **69** 243-252,
  where it is assumed that each pair of A individuals meet at rate r_1, each pair of A and B individuals meet at rate r_2 and each pair of B individuals meet at rate r_3.

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Payoffs

- Thus the frequency of interactions of a type A individual with other type A individuals is $r_1 p$ and the frequency with type B individuals is $r_2(1-p)$, where p is the proportion of As in the population.
- This yields the following non-linear payoff function

$$E[A, \mathbf{p}] = \frac{ar_1 p + br_2(1-p)}{r_1 p + r_2(1-p)}.$$

- Similarly for B individuals we have

$$E[B, \mathbf{p}] = \frac{cr_2 p + dr_3(1-p)}{r_2 p + r_3(1-p)}.$$

- This reduces to the standard payoffs for a matrix game when $r_1 = r_2 = r_3$, but otherwise does not.

ESSs

- How do these non-uniform interaction rates affect the game?
- In particular, when are there differences between this case and the simple two player matrix game?
- Taylor and Nowak (2006) consider replicator dynamics rather than ESSs. However, a strategy **p** is an ESS of this game (with two strategies) if and only if it is a stable rest point of the replicator dynamics.
- In the simple game if $a < c$ and $b > d$ there is a mixed ESS, and this is not altered by the use of non-uniform interaction rates, although the ESS proportions of the strategies do change.
- If $a > c$ and $b < d$ then there are two ESSs in the simple case, and this is also always true for non-uniform interactions, although the location of the unstable equilibrium between the pure strategies changes, which affects the dynamics.

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A mixed ESS

- In the game with constant interaction rates, if $a < c$ and $b < d$, then B is a unique ESS. This is the most interesting case here.
- Under some circumstances there is not a unique solution in this case for the non-uniform situation, and it is possible that there can be two ESSs, a pure B ESS, but also a mixed ESS.
- Setting $r_2 = 1$ without loss of generality, this occurs if either $c > a > d > b$ and

$$r_1 r_3 > \left(\frac{\sqrt{(a-b)(c-d)} + \sqrt{(a-c)(b-d)}}{d-a} \right)^2$$

- or $d > b > c > a$ and

$$r_1 r_3 < \left(\frac{\sqrt{(a-b)(c-d)} - \sqrt{(a-c)(b-d)}}{d-a} \right)^2$$

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The prisoner's dilemma

- The prisoner's dilemma is an example of the final case above, and cooperation is possible if interaction rates are non-uniform.
- There is a mixed ESS if

$$r_1 r_3 > \frac{1}{(R-P)^2}\left(\sqrt{(T-R)(P-S)} + \sqrt{(R-S)(T-P)}\right)^2 .$$

- In particular setting $r_1 = r_3 (= r)$ with payoffs from Axelrod and Hamilton (1981) $T = 5, R = 3, P = 1, S = 0$ there is a mixed ESS of cooperators and defectors when $r > 2.44$.
- As $r \to \infty$ the proportion of cooperators in the mixture tends to 1, and the basin of attraction of the mixed ESS in the proportion of cooperators p increases, tending to $p \in (0, 1]$.

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Existing models of strategy-dependent interactions

- There are a number of different game models which involve strategy-dependent interactions.
- In general they are models of specific biological situations.
- The exception is the model of Nowak and Taylor (2006). This is a symmetric game with no “roles”, and interactions are instantaneous and sequentially independent.
- In the brood care game of Webb et al (1999), the game is asymmetric with fixed roles, and interactions are effectively sequentially independent.
- In the kleptoparasitism game of Broom et al (2008), the game is asymmetric and interactions depend upon the game history, following a Markov process.

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What do we know about games with strategy-dependent interactions?

- It is possible to have mixed ESSs in asymmetric contests with strategy-dependent interactions.
- In general these models show that a wide range of behaviour is possible which cannot be predicted by independent interactions.
- It is possible to have very complex structures of dependence. Broom,M., Cannings,C., & Vickers,G.T. (2000) Evolution in Knockout Contests: the Variable Strategy Case. *Selection* **1** 5-21 considered multi-player games comprised of pairwise interactions in a structure where selection of opponents depends on previous results.
- With two strategies, there could be 2^n ESSs in an n round game.
- Thus with no restrictions on the ways interactions can be dependent on strategy there are likely to be few rules which govern what behaviours can occur.

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Where do we go from here?

- Different models have been developed for various specific reasons, and so currently there is no consistent framework for games with strategy-dependent interactions.
- We need to limit the kind of strategy-dependence in some way to a restricted set of useful concepts.
- Games can be symmetric or asymmetric.
- Strategy may affect the probability of occupying a given role, as well as the rate of interaction.
- The history of the sequence of interactions may affect the probability of certain interactions as well as the probability of occupying a given role.
- Ideas are welcome!

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