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LARGE POPULATION EVOLUTIONARY GAMES PLAYED WITHIN A LIFE HISTORY FRAMEWORK

In many evolutionary games, such as parental care games, the length of time spent playing a realisation of the game is dependent on the strategy of an individual. Also, the payoff of a deserting male cannot be defined in isolation from the strategies used in the population as a whole. Such games should be defined as games against the field (large population games) rather than two-player games. Several examples are presented to illustrate the theory of such games against the field.

Keywords: *evolutionary game theory, game against the field, phase, evolutionarily stable strategy, neighbourhood invasion strategy, polymorphism*

1. Introduction

In the classical two-player symmetric war of attrition (see Maynard Smith and Price [13]), two players decide the time they are prepared to wait, in order to obtain a resource of value V. The player who chooses the longest waiting time obtains a net reward of $V-ct$, where t is the time the opponent was willing to wait and c is a positive constant. The other player obtains a net reward of $-ct$. The evolutionarily stable strategy (ESS) in this game is to choose one's waiting time from the exponential distribution with expected value V/c. The expected length of the game is $V/2c$ and the mean net reward gained is 0.

Cannings and Whittaker [5] argued that individuals who wait for shorter lengths of time are able to play the game more often and thus there is a trade off between the mean reward obtained per game and the mean number of games played per unit time. They defined the following game against the field (referred to as the supergame). Time is discrete and there is a finite time horizon k. Each individual uses a determi-

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nistic waiting time that is an integer number of units. Initially an individual is paired with an opponent chosen at random from the population to play the war of attrition game (referred to as the subgame). On finishing a subgame an individual is then paired with an opponent who has also just finished playing a subgame. A subgame is won by the individual with the longest waiting time, who receives a payoff of 1. If both players in a subgame use the same waiting time, then they both receive a payoff of 0.5. The total payoff of an individual in the supergame is the sum of the payoffs obtained in the subgames. The set of ESSs in such a game is heavily dependent on k and its derivation becomes increasingly complex as k increases.

Eriksson et al. [8] consider a model which is very similar to the one presented here. In their model individuals can be in one of two states: playing a war of attrition subgame or not playing a war of attrition subgame. Individuals who are not playing a war of attrition game enter such subgames at rate λ and the opponent is picked at random from the population of individuals who are not presently involved in a war of attrition subgame. An individual uses the same deterministic waiting time (a positive real number) in each subgame and the length of a subgame is the shortest waiting times of the two players involved. The winner (the one choosing the longer time) obtains a reward of 1 and the loser receives a reward of c, where $0 \leq c < 1$. They use replicator dynamics to observe the evolution of the population when the fitness of a strategy in the present generation is taken to be the mean rate at which rewards are obtained. Depending on the parameters of the game, limit cycles may be observed.

Another situation in which there are tradeoffs between the mean rate at which games are played and the mean reward gained in each game arises in parental care games. In simple terms, deserters will breed more often than carers, but carers will have more surviving offspring per breeding attempt. Maynard Smith [14] considered three different models of parental care. The first two models were defined as standard two-player games. However, he was aware that such models are inappropriate as the payoff of e.g. a deserting male depends on the availability of females, which in turn depends on the strategies used by the population as a whole. Hence, he proposed a third model in which the payoffs of an individual are dependent on the strategies used within the population as a whole. He could not however find an analytic solution to such a game.

Houston and McNamara [12] consider the problems involved in developing good models of parental care. They state that although it is necessary when defining a model to consider some aspects in isolation from others, this leads to a distorted picture when there is clear feedback between two factors. For example, the operational sex ratio (OSR, the ratio of the number of males searching for a mate to the number of females searching for a mate) is a key factor in such models. However, the OSR is obviously dependent on the strategies employed. The more females care for their young, the higher the OSR. Hence, a model cannot define a value for the OSR without referring to the strategies used within the population. Also, to be self-

consistent a model must take into account the fact that the total number of offspring of males is equal to the total number of offspring of females.

The model presented here assumes that there is no breeding season. It is in some ways an extension of Yamamura and Tsuji's model [26]. This model was adapted to the life history of St. Peter's Fish by Balshine-Earn and Earn [3]. In the models mentioned above, individuals of the rarer sex in the pool of searchers immediately find a mate, while in the model presented here such individuals find mates at an appropriately faster rate than individuals of the more common sex. Similar models have been considered for species that breed seasonally, but several breeding attempts are possible in a season (see Webb et al. [25], McNamara et al. [17]).

2. The general concepts used

2.1. Phases

The models presented here are based on the concept of phases, which were introduced by Erlang in the first half of the 20th century and developed by himself and others. Erlang considered the distribution of the number of active calls in a telephone exchange. The simplest case occurs when calls come in as a Poisson process of rate λ and the length of calls has an exponential distribution with mean length $\mu = 1/r$, where r is termed the rate at which calls are concluded. The phase (state) of the telephone exchange can be understood as the number of active calls. The phase changes each time an event occurs, where an event is understood as an incoming call or the conclusion of a call. Given that there are i active calls, the time until the next change of state has an exponential distribution with mean $1/(\lambda + ir)$. With probability $\lambda/(\lambda + ir)$, this event is an incoming call and hence the number of active calls increases to $i + 1$. Otherwise, the event is the conclusion of a call. In this case, the number of active calls decreases to $i - 1$. Suppose there are n lines available in the exchange and denote the equilibrium (long run) proportion of time for which i calls are active by p_i. We can derive these proportions using the fact that the total rate at which the phase changes from i to $i + 1$, p_i times the rate at which the phase changes from i to $i + 1$ (here λ), must be equal to the total rate at which the phase changes from $i + 1$ to i, calculated analogously. This leads to the following system of equations:

$$\lambda p_i = (i+1)rp_{i+1}, \qquad r = 0, 1, ..., n-1,$$

$$\sum_{i=0}^{n} p_i = 1.$$

Cox [6] extended this theory to include a wider range of distributions for the time between events of a given type. The concept of phases was applied to foraging theory in the middle of the 1970s (see Beddington [4] and DeAngelis et al. [7]). Foragers are either searching for food or feeding. While feeding, they may be interrupted by other individuals. Van der Meer and Smallegange [24] apply these ideas to small populations. Similar methods have also been used to model the passage of patients through hospital and aid the management of hospitals (see McClean and Millard [16], Shaw et al. [21]). These ideas are also applied in the field of actuarial science (see e.g. Haberman and Pitacco [11]).

The concept of phase will be used in this paper to describe the state of an animal. For example, in the parental care model considered here a female may be in one of three states: receptive, non-receptive or breeding. In the receptive state a female finds a mate at some defined rate and hence enters the breeding phase. The rate of passing between phases and the payoff gained in a given phase may be dependent on the strategy used by an individual and the strategy used by any other player that the individual interacts with. In particular, a female who cares for her young will spend longer on average in the breeding phase than a female who deserts, but will rear more young per breeding attempt. In order to illustrate the concept of such "life history" games and obtain analytic results, we assume that the set of available pure strategies is small and the rates of transition between phases are constant. The long run proportion of individuals in each phase can be calculated using a method analogous to the one described above (see the three examples given later). It is also assumed that mortality does not depend on the strategy used and so individuals aim to maximise the rate at which they obtain (appropriately defined) payoffs. However, such models can be easily extended to consider larger strategy sets and differential mortality. Although it might be difficult to obtain analytic results for such models, it would be relatively easy to obtain interesting numerical results.

2.2. Concepts of evolutionary stability

There are several concepts of stability used in evolutionary game theory. The most commonly used one is the concept of an evolutionarily stable strategy (ESS, see Maynard Smith [15]). In the context of this paper, each individual wishes to maximise his/her payoff rate. Hence, a strategy is an ESS if the following condition holds:

Definition 1. *Whenever all the population use an ESS, then an individual mutant cannot obtain a greater payoff rate by using a different strategy and if an individual mutant can obtain the same payoff rate, then whenever the proportion of mutants in a population is sufficiently small* (*but non-zero*), *they obtain a strictly lower payoff rate than the incumbents.*

It should be noted that this definition assumes that the population is large (essentially infinite). In the case of a finite population of size N: 1) mutants using strategies that are selected against fixate with a non-zero probability, 2) a strategy that is an ESS according to Definition 1 may be selected against when there is just one mutant (i.e. the proportion of mutants in the population is $1/N$, see Schaffer [19]).

When we consider games against the field, it is often difficult to derive the payoff of individuals when there is a small proportion of mutants in the population. Hence, another useful criterion for stability is given by the concept of a neighbourhood invader strategy (NIS) introduced by Apaloo (see [1], [2]). Let $f(a; b)$ be the expected payoff of an individual using a strategy a when all the population use the strategy b.

Definition 2. *An NIS, denoted π^N, is a strategy that satisfies $f(\pi^N; \pi) > f(\pi; \pi)$ for all π in some suitably defined neighbourhood of π^N such that $\pi \neq \pi^N$.*

This states that if all the population uses a strategy π which is similar to π^N, then a group of individuals using the strategy π^N will obtain a higher payoff rate. In [1], Apaloo shows that an ESS is not necessarily an NIS and vice versa. In the second paper, he notes that a strategy which is both an ESS and an NIS (a so called ESNIS) has strong stability properties in a wide range of games. That is to say, using replicator dynamics the population evolves to a population using an ESNIS if at the beginning of the simulation they all used similar strategies, but this is not the case if a strategy is just an ESS or just an NIS. Ramsey [18] describes a large population mate choice game, in which there may exist an ESS that cannot invade a population using any similar strategy.

Example 1 is based on the war of attrition game and is used to illustrate these two concepts of stability. For the purposes of this example, we assume that the only admissible mixed strategies involve choosing a waiting time from an exponential distribution. In this case a mixed strategy can be denoted by the parameter of this distribution (taken to be the reciprocal of the mean waiting time). A neighbourhood of such a mixed strategy is defined to be the set of mixed strategies corresponding to an exponential distribution with a sufficiently similar parameter value.

A global invading strategy, denoted π^G, satisfies $f(\pi^G; \pi) > f(\pi; \pi)$, $\forall \pi \in S$, where S is the set of admissible strategies. It is clear that if π^G is a GIS, then no other strategy can be an ESS.

It is assumed that all the mutants use the same strategy (i.e. we do not consider simultaneous invasions by mutants using various strategies).

Example 2 is used to illustrate the concept of an evolutionarily stable polymorphism (ESP). In terms of evolutionary game theory, a polymorphism can be characterised as follows: 1) each individual in the population uses a pure strategy, 2) there is variation in the population. In addition, at an ESP: a) selection does not favour any pure strategy that is present in the population (i.e. in the support of the strategies used) and acts against any pure strategy that is not present, b) when the distribution of the strategies used is sufficiently similar to an ESP, then selection will act towards the

ESP. Example 2 considers a Hawk–Dove type game in which there are only two pure strategies available. In this context, the following definition of an ESP will be used.

Definition 3. *Suppose there are only two pure strategies available, A and B, and mixed strategies cannot be used. A polymorphism in which a proportion q of the population play A is an ESP if the following two conditions are satisfied*: 1) *all individuals obtain the same payoff rate*, 2) $\exists\ q_1$ *and* q_2 *with* $q_1 < q < q_2$, *such that selection favours individuals using A when the proportion of A players is in* (q_1, q), *but favours individuals using B when the proportion of A players is in* (q, q_2).

One question addressed by Maynard Smith [15] concerns the stability properties of polymorphisms in two-player games. Suppose the set of available pure strategies is finite. If such a polymorphism is stable, then the proportions of individuals playing each pure strategy must correspond to the probabilities of choosing the relevant action under a mixed ESS. It is shown that this is not true for the class of games considered here.

Example 3 introduces a parental care game that will be investigated in more detail in a forthcoming paper. The population is split into two types, males and females. Define $g_m(\pi;\ \pi_m,\ \pi_f)$ and $g_f(\pi;\ \pi_m,\ \pi_f)$ to be the payoff rates (reproduction rates) obtained by an individual male and female, respectively, when the individual uses π, the population of males use π_m and the population of females use π_f. Suppose the sets of strategies available to males and females are S_m and S_f, respectively. A sufficient set of conditions for a profile of pure strategies $(\pi_m^{\ddagger}, \pi_f^{\ddagger})$ to be an ESS profile is given by the following two inequalities

$$g_m(\pi_m^{\ddagger};\pi_m^{\ddagger},\pi_f^{\ddagger}) > g_m(\pi_m;\pi_m^{\ddagger},\pi_f^{\ddagger})$$
$$g_f(\pi_f^{\ddagger};\pi_m^{\ddagger},\pi_f^{\ddagger}) > g_f(\pi_f;\pi_m^{\ddagger},\pi_f^{\ddagger})$$

for all $\pi_m \in S_m$, $\pi_f \in S_f$, $\pi_m \neq \pi_m^{\ddagger}$, $\pi_f \neq \pi_f^{\ddagger}$. We will not consider mixed ESSs or ESPs for such asymmetric games in this paper.

3. Example 1 – A war of attrition type game

Suppose individuals can be in one of two states: A – playing a war of attrition game and B – not playing a war of attrition game. It is assumed that when in state B individuals gain rewards at rate c per unit time. The rate at which an individual enters war of attrition games is assumed to be λ independently of the strategy used in the war of attrition game. In the war of attrition game the two players choose waiting times t_1 and t_2. The player who chooses the larger waiting time obtains a resource assumed

to be of value *V*. If the players choose the same waiting time, the winner is chosen at random (i.e. each has an expected payoff of *V*/2).

Arguing as in the case of the standard war of attrition, no pure strategy can define an ESS. Suppose each individual is prepared to wait a time *t*. Each individual gains an average reward of *V*/2 in a war of attrition game and each war of attrition lasts *t* units. Hence, the mean reward rate is $c[1–p]+pV/2t$, where *p* is the equilibrium proportion of time spent playing war of attrition games. It should be stressed that the term "equilibrium proportion" will be used strictly to describe the proportion of time an individual is in a particular state given that the strategies used by the population do not change over time. One important aspect to note is the feedback between selection and these equilibrium proportions. Selection changes the frequencies of the strategies used, which in turn affects the equilibrium proportions. Unless a specific strategy profile is being considered, simplified notation will be used, which does not reflect the dependency of the equilibrium proportions on the strategies used.

By choosing a waiting time of $t + \delta$ units, where $\delta > 0$, a mutant obtains a reward rate of $c[1 - p] + pV/t$. This is due to the following facts: 1) since each game lasts *t* units, a mutant spends the same proportion of time playing war of attrition games as the rest of the population. 2) The mutant will always win the war of attrition, thus obtaining a reward rate of *V/t* in such games. Hence, a mutant who is prepared to wait slightly longer than the rest of the population will always be able to invade the population.

Now assume that each member of the population chooses a waiting time from an exponential distribution. Hence, the strategy used by an individual may be denoted by the parameter of the exponential distribution from which the waiting time is chosen (defined to be the reciprocal of the expected waiting time). When all the population use the strategy μ, each individual wins a war of attrition with probability ½ and the distribution of the length of the game is exponential with parameter 2μ. It follows that the reward rate gained in the war of attrition games is $V\mu$. Given the population follow such a strategy, the equilibrium proportion of time spent playing war of attrition games, $p(\mu)$ satisfies

$$2\mu p(\mu) = \lambda[1 - p(\mu)].$$

Here, the left hand side gives the relative rate of exiting from a war of attrition game in the population as a whole and the right hand side gives the relative rate of entering into a war of attrition game. It follows that $p(\mu) = \lambda/(2\mu + \lambda)$.

Let $f(\alpha; \mu)$ be the reward rate obtained by an individual using strategy α when the rest of the population use μ. The reward rate obtained by each member of the population is given by

$$f(\mu; \mu) = V\mu p(\mu) + c[1 - p(\mu)] = \frac{\mu(V\lambda + 2c)}{2\mu + \lambda}.$$

Now consider the payoff rate of an individual using strategy α. This mutant wins a war of attrition with probability $\mu/(\mu + \alpha)$ and on average a game lasts $1/(\mu + \alpha)$

units of time. Hence, the reward rate of the mutant in war of attrition games is $V\mu$. The proportion of time the mutant spends playing war of attrition games can be calculated as the mean length of the games it plays divided by the mean cycle length (the mean length of a game plus the mean time between games). Since the rate at which an individual enters into war of attrition games is λ, the mean cycle length for the mutant is

$$\frac{1}{\mu+\alpha}+\frac{1}{\lambda}.$$

It follows that the proportion of time the mutant spends in war of attrition games is given by

$$p_m = \frac{\lambda}{\lambda+\mu+\alpha}.$$

Hence,

$$f(\alpha;\mu) = p_m V\mu + (1-p_m)c = \frac{\lambda V\mu + c(\mu+\alpha)}{\lambda+\mu+\alpha}.$$

The mutant can invade the population if $g(\alpha;\mu) = f(\alpha;\mu) - f(\mu;\mu) > 0$. Note $g(\mu;\mu) = 0$ and

$$\frac{\partial g}{\partial \alpha} = \frac{\lambda(\lambda+2\mu)(c-V\mu)}{(\lambda+\mu+\alpha)^2}.$$

Note that this partial derivative is positive if and only if $\mu < c/V$, i.e. when the population wait on average more than V/c units of time, then any mutant can invade by choosing any shorter mean waiting time. Similarly, when the population wait on average less than V/c units of time, a mutant can invade by choosing any longer mean waiting time. It follows that the strategy $\mu = c/V$ is a GIS. It should be noted that such a strategy is not a continuously stable strategy (CSS, see Eshel [9], Eshel and Motro [10]). A CSS, denoted π^C, satisfies the condition that a strategy π which is sufficiently close to π^C can only be invaded by a strategy that is closer to π^C.

We now give a sketch proof of the fact that the strategy $\mu = c/V$ is an ESS in the sense that a uniform group of mutants making up a proportion ε of the population will be selected against when the remaining individuals use the strategy μ. Suppose the mutants use the strategy α, where $\alpha > \mu$, i.e. mutants give up at a faster rate than the incumbents. Let p_m and p_i be the proportion of time spent in war of attrition subgames by mutants and incumbents, respectively. Intuitively, mutants spend a smaller proportion of their time in war of attrition games than incumbents. Let q be the probability of being matched with a mutant in a war of attrition game. Since an opponent is chosen at random from those not presently playing a war of attrition game, it follows that $q > \varepsilon$. Using a similar argument as the one used to find the payoff rate of a mutant

against an incumbent in war of attrition games, it follows that both mutants and incumbents gain rewards at rate $V\alpha$ when playing against mutants. Hence, the payoff rates obtained by mutants and incumbents, R_m and R_i respectively, are given by

$$R_m = [1 - p_m]c + p_m[qV\alpha + (1 - q)V\mu]$$
$$R_i = [1 - p_i]c + p_i[qV\alpha + (1 - q)V\mu].$$

It follows that both groups obtain rewards at the same rate as each other in war of attrition games and since $V\alpha > V\mu = c$, this rate is faster than the rate achieved outside of war of attrition games. Since incumbents spend a higher proportion of time in war of attrition games, they obtain a higher payoff rate. It can be shown analogously that mutants who are prepared to wait longer will be selected against. Hence, when individuals can choose a waiting time according to an exponential distribution, μ describes an ESNIS in the sense considered.

It should be noted that this model can be adapted by assuming that the rate of entering war of attrition games depends on the proportion of individuals not involved in such games. For example, this rate may be proportional to the fraction of individuals not involved in a war of attrition game, i.e. $\lambda(1 - p)$. Assume all the population choose a waiting time from the exponential distribution with parameter μ. In this case, the equilibrium condition for $p(\mu)$ is given by

$$2\mu p(\mu) = \lambda[1 - p(\mu)]^2 .$$

Suppose a mutant chooses a waiting time from the exponential distribution with parameter α. Arguing as above, the proportion of time a mutant spends playing war of attrition games is given by

$$p_m = \frac{1}{\mu + \alpha}\left[\frac{1}{\mu + \alpha} + \frac{1}{\lambda[1 - p(\mu)]}\right]^{-1} = \frac{\lambda[1 - p(\mu)]}{\lambda[1 - p(\mu)] + \mu + \alpha} .$$

The expected payoff of such a mutant is $f(\alpha; \mu) = p_m V\mu + (1 - p_m)c$, hence

$$\frac{\partial f(\alpha; \mu)}{\partial \alpha} = [V\mu - c]\frac{\partial p_m}{\partial \alpha} .$$

It is relatively simple to check that $\partial p_m/\partial \alpha < 0$, $\forall \alpha > 0$. Hence, for $\mu > c/V$, i.e. the population are prepared to wait for a relatively short time, we have $\partial f(\alpha; \mu)/\partial \alpha < 0$ and so any mutant waiting a longer time on average can invade. Similarly, for $\mu < c/V$, any mutant waiting a shorter time on average can invade. Arguing as above, $\mu = c/V$ is the unique ESNIS.

It is interesting to compare this result with the classical war of attrition game. The assumption made in the model considered here is that outside of the war of attrition game, the reward gained in time t by an individual is c_t. This is analogous to assuming

in the classical game that the costs of waiting for time t are c_t. It is interesting that the ESS derived here is identical to the ESS in the classical game and is robust to assumptions regarding the rate at which individuals enter into war of attrition games. In accordance with foraging theory (see Stephens and Krebs [22]), the payoff rate in the war of attrition is equalised with the payoff rate outside of such games.

Finally, it seems that this ESS does not correspond to the ESP of such a problem, i.e. if individuals each choose their own deterministic waiting time, then the distribution of the waiting times used at an ESP is not exponential. This is due to the fact that individuals who choose short waiting times will spend a smaller proportion of time in subgames. Hence, the distribution of the waiting time conditional on the event that an individual is not playing a subgame (i.e. the distribution of the waiting time of a randomly chosen opponent) will be biased towards lower waiting times. Eriksson et al. [8] consider such a problem, but their framework is somewhat different to the one presented here, so it is difficult to directly compare the results. The next example considers an example based on the Hawk–Dove game, which highlights the difference between an ESS and an ESP.

4. Example 2 – A simple Hawk–Dove type game

We now consider a game in which individuals can take one of two actions, Hawk or Dove, denoted H and D, respectively. Individuals that are not presently playing a Hawk–Dove game enter into such games at a rate of λ. When a Hawk meets a Dove, the Hawk obtains a resource of value V and returns to the population of non-players at rate μ_{HD}. This rate reflects the time it takes to chase off the Dove and consume the resource. The Dove does not obtain any reward and returns to the population of non-players at rate μ_{DH}. It is assumed that $\mu_{DH} > \mu_{HD}$. When two individuals play Hawk, each wins the resource with probability ½. In this case they return to the population of non-players at rate μ_{HH}. The mean time spent in such an interaction reflects the expected time spent fighting, consuming resources and recovering from any wounds incurred. It is assumed that $\mu_{HH} < \mu_{HD}$. When two Doves meet, both players obtain a reward of $V/2$ and return to the population of non-players at rate μ_{DD}. In the case where the resource can be shared and individuals can react quickly to the action taken by an opponent, it seems reasonable to assume that $\mu_{DD} = 2\mu_{HD}$. In the case where the resource cannot be shared, the individuals may some type of war of attrition game (not considered here), but in this case we may assume that $\mu_{DD} < 2\mu_{HD}$. In general, we assume that $\mu_{DD} \leq 2\mu_{HD}$. Outside of these interactions, individuals accrue rewards at a rate of c per unit time. It is assumed that $V\mu_{HD} > c$, i.e. the rate of reward from consuming the resource is greater than the mean reward rate gained outside the interactions.

We first consider the conditions necessary for a pure ESS to exist. Suppose that all the population are using the strategy D. The expected reward gained per cycle (from the end of one Hawk–Dove game to the end of the next) is $V/2 + c/\lambda$. The expected length of such a cycle is

$$\frac{1}{\lambda} + \frac{1}{\mu_{DD}} = \frac{\lambda + \mu_{DD}}{\lambda \mu_{DD}}.$$

It follows that the reward rate gained by the population is

$$\frac{\left(\frac{V}{2} + \frac{c}{\lambda}\right) \lambda \mu_{DD}}{\mu_{DD} + \lambda} = \frac{\mu_{DD}(V\lambda + 2c)}{2(\lambda + \mu_{DD})}.$$

Now consider a mutant playing Hawk. The expected reward of this mutant per cycle is $V + c/\lambda$. The expected length of a cycle is

$$\frac{1}{\lambda} + \frac{1}{\mu_{HD}} = \frac{\lambda + \mu_{HD}}{\lambda \mu_{HD}}.$$

Hence, the reward rate gained by this mutant is

$$\frac{\mu_{HD}[V\lambda + c]}{\lambda + \mu_{HD}}.$$

It is relatively easy to show that under the assumptions made above, such a mutant will invade. Hence, D can never be an ESS in such a game, as in the standard Hawk–Dove game.

Now we consider the conditions under which H is an ESS. Suppose all the population are playing H. Considering the expected reward gained per cycle and the expected length of a cycle as above, the reward rate gained by the population is

$$\frac{\left(\frac{V}{2} + \frac{c}{\lambda}\right) \lambda \mu_{HH}}{\lambda + \mu_{HH}} = \frac{\mu_{HH}(V\lambda + 2c)}{2(\lambda + \mu_{HH})}.$$

Similarly, the reward rate gained by a single Dove mutant is $c\mu_{DH}/(\lambda + \mu_{DH})$. Comparing the reward rate of the Dove mutant with the reward rate of the population as a whole, it follows that H is an ESS if

$$V > \frac{2c}{\lambda} \left[\frac{\mu_{DH}(\lambda + \mu_{HH})}{\mu_{HH}(\lambda + \mu_{DH})} \right]. \tag{1}$$

In particular, when $\mu_{DH} \rightarrow \infty$, i.e. Doves do not lose any time when interacting with Hawks, this condition simplifies to $V/2 > c/\mu_{HH}$. The left-hand side in this ine-

quality is the expected reward from the contest, whereas the right-hand side is the expected cost of the contest in terms of time lost. This condition is completely analogous to the condition that H is an ESS in the standard Hawk–Dove game.

Now assume that Inequality (1) does not hold and individuals can only play pure strategies. It is expected that there will be an ESP. Suppose at such an ESP a proportion q_H of the population play H and a proportion $q_D = 1 - q_H$ play D. Since the mean length of time an individual spends in an interaction depends on the strategy used, the equilibrium proportion of Hawk players in the population of individuals not interacting at a given moment will differ from q_H. Let $p_{1,H}$ and $p_{1,D}$ be the equilibrium proportions of time for which Hawks and Doves, respectively, do not interact. Let p_1 be the equilibrium proportion of the total population that are not interacting. Using Bayes laws, we have $p_1 = p_{1,H} q_H + p_{1,D} q_D$. A proportion $p_{1,H} q_H / p_1$ of players enter into games with Hawks and a proportion $p_{1,D} q_D / p_1$ enter into games with Doves. It follows that the mean time a Hawk spends playing a game is

$$\frac{p_{1,H} q_H}{p_1} \frac{1}{\mu_{HH}} + \frac{p_{1,D} q_D}{p_1} \frac{1}{\mu_{HD}} = \frac{p_{1,H} q_H \mu_{HD} + p_{1,D} q_D \mu_{HH}}{p_1 \mu_{HH} \mu_{HD}}.$$

Hence, the equilibrium condition for the proportion of non-interacting Hawks is given by

$$\lambda p_{1,H} = \frac{p_1 \mu_{HH} \mu_{HD} (1 - p_{1,H})}{p_{1,H} q_H \mu_{HD} + p_{1,D} q_D \mu_{HH}}. \tag{2}$$

Arguing similarly, the equilibrium condition for the proportion of non-interacting Doves is given by

$$\lambda p_{1,D} = \frac{p_1 \mu_{DD} \mu_{DH} (1 - p_{1,D})}{p_{1,H} q_H \mu_{DD} + p_{1,D} q_D \mu_{DH}}. \tag{3}$$

In addition, at an ESP the mean reward rate of Hawks and Doves must be equal. The mean cycle length for a Hawk is given by

$$\frac{1}{\lambda} + \frac{p_{1,H} q_H \mu_{HD} + p_{1,D} q_D \mu_{HH}}{p_1 \mu_{HH} \mu_{DD}}.$$

When not playing, a Hawk obtains rewards at rate c. In the Hawk-Dove game a Hawk obtains V when playing against a Dove and $V/2$ on average when playing against a Hawk. It follows that the expected reward of a Hawk per cycle is

$$\frac{c}{\lambda} + V \left[1 - \frac{p_{1,H} q_H}{2 p_i} \right].$$

Hence, the reward rate obtained by Hawks, R_H is

$$R_H = \frac{\mu_{HH}\mu_{HD}[2(p_{1,H}q_H + p_{1,D}q_D)(c+V\lambda) - Vp_{1,H}q_H\lambda]}{2[(p_{1,H}q_H + p_{1,D}q_D)\mu_{HH}\mu_{HD} + \lambda(p_{1,H}q_H\mu_{HD} + p_{1,D}q_D\mu_{HH})]}.$$

Similarly, it can be shown that the reward rate obtained by Doves is

$$R_D = \frac{\mu_{DD}\mu_{DH}[2c(p_{1,H}q_H + p_{1,D}q_D) + Vp_{1,D}q_D\lambda]}{2[(p_{1,H}q_H + p_{1,D}q_D)\mu_{DH}\mu_{DD} + \lambda(p_{1,H}q_H\mu_{DD} + p_{1,D}q_D\mu_{DH})]}.$$

Equations (2)–(3), together with the equation $R_H = R_D$ gives a system of three equations for three unknowns, $p_{1,H}$, $p_{1,D}$ and q_H. Intuitively, the relative advantage of Hawks increases as the proportion playing Dove increases. Given this is true and no pure ESS exists, there will be only one valid solution of this system of equations. Also, whenever the proportion of Hawks is greater (less) than the q_H corresponding to this solution, then selection acts so as to reduce (increase) the proportion of Hawks. Thus this solution is an ESP. It should be noted that Hawks gain a greater expected reward from each interaction than Doves (regardless of the proportion of individuals playing H). Hence, at an ESP, Hawks must spend on average a longer time in each interaction. It follows that at the ESP, the probability that a randomly chosen opponent plays H is less than q_H.

Now we consider the mixed ESS for this game. Suppose this is given by the strategy "Play H with probability $q^{\ddagger}$". Consider what happens when all the population use the mixed strategy "Play H with probability q_H", then the probability that a randomly picked opponent plays H is simply q_H (i.e. greater than at the ESP). When there is no pure ESS, the larger the probability of playing against a Hawk, the more selection will favour Doves. Thus it is expected that $q^{\ddagger} < q_H$.

Suppose the population all use the mixed strategy: "Play H with probability q". The expected length of a game played by a mutant using the strategy "Play H with probability r" is given by $T(r; q)$ where

$$T(r;q) = \frac{rq}{\mu_{HH}} + \frac{r(1-q)}{\mu_{HD}} + \frac{(1-r)q}{\mu_{DH}} + \frac{(1-r)(1-q)}{\mu_{DD}}.$$

The expected reward gained by such a mutant in a Hawk–Dove game is

$$\frac{rqV}{2} + r(1-q)V + \frac{(1-r)(1-q)V}{2} = \frac{V(1+r-q)}{2}.$$

The reward rate obtained by such a mutant, $f(r; q)$, is given by the mean reward per cycle divided by the mean cycle time, i.e.

$$f(r;q) = \frac{V(1+r-q) + 2cT_0}{2[T_0 + T(r;q)]},$$

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where $T_0 = \lambda^{-1}$ is the mean time between interactions. An ESS must satisfy

$$\frac{\partial f(r;q^{\updownarrow})}{\partial r}\bigg|_{r=q^{\updownarrow}} = 0$$

This leads to the quadratic equation $a[q^{\ddagger}]^2 + bq^{\ddagger} + c = 0$, where (the form of the solution is given for completeness)

$$a = V\left[\frac{1}{\mu_{HH}} + \frac{1}{\mu_{DD}} - \frac{1}{\mu_{HD}} - \frac{1}{\mu_{DH}}\right],$$

$$b = V\left[\frac{2}{\mu_{DH}} + \frac{2}{\mu_{HD}} - \frac{1}{\mu_{HH}} - \frac{3}{\mu_{DD}}\right] - 2cT_0\left[\frac{1}{\mu_{HH}} + \frac{1}{\mu_{DD}} - \frac{1}{\mu_{HD}} - \frac{1}{\mu_{DH}}\right],$$

$$c = V\left[T_0 + \frac{2}{\mu_{DD}} - \frac{1}{\mu_{HD}}\right] - 2cT_0\left[\frac{1}{\mu_{HD}} - \frac{1}{\mu_{DD}}\right].$$

From the assumptions made, $a, c > 0$, $b < 0$. It can be shown that whenever H is not an ESS, there is one solution to this equation in the interval $(0, 1)$. This is given by

$$g^{\ddagger} = \frac{-b - \sqrt{b^2 - 4ac}}{2a}.$$

Numerical solutions for various sets of parameters are given in Table 1.

Table 1

Evolutionary Stable Strategies and Polymorphisms in the Hawk-Dove type game. It is assumed $\mu_{DD} = 2\mu_{HD}$, $V = 2$, $c = 1$. q^c gives the probability of playing Hawk at the ESS of the classical Hawk–Dove game, which is obtained by letting $\lambda \to 0$, $\mu_{HD}, \mu_{DD}, \mu_{DH} \to \infty$, while leaving μ_{HH} unchanged

Case	λ	μ_{HH}	μ_{HD}	μ_{DH}	$p_{1,H}$	$P_{1,D}$	q_H	$q^{\ddagger}$	q^c
1	0.001	0.25	1000	10^6	0.9990	$1-4\times10^{-7}$	0.2499	0.2497	0.25
2	0.1	0.25	10	10^6	0.9115	0.9961	0.2389	0.2232	0.25
3	0.01	0.25	10	10^6	0.9899	0.9996	0.2405	0.2387	0.25
4	1	0.25	10	10^6	0.6245	0.9582	0.1845	0.1285	0.25
5	0.1	0.25	100	10^6	0.9147	0.9996	0.2474	0.2313	0.25
6	0.1	0.25	1	10^6	0.8776	0.9584	0.1418	0.1314	0.25
7	0.1	0.5	10	10^6	0.9109	0.9973	0.4849	0.4623	0.5
8	0.1	0.125	10	10^6	0.9118	0.9956	0.1186	0.1097	0.125
9	0.1	0.25	10	10^3	0.9115	0.9961	0.2390	0.2232	0.25
10	0.1	0.25	10	10^2	0.9113	0.9959	0.2396	0.2238	0.25
11	0.1	0.25	10	10	0.9094	0.9939	0.2457	0.2297	0.25

Case 1 illustrates the relation between the asymptotic properties of the game considered here and the standard Hawk–Dove game. In the case where interactions are rare ($\lambda \to 0$), the resource can be consumed immediately (μ_{HD}, $\mu_{DD} \to \infty$) and Hawks do not disturb/harm Doves ($\mu_{DH} \to \infty$), individuals should simply maximise their expected reward from an interaction, understood to last the mean time spent by two Hawks in an interaction. In Case 1, Hawks will fight on average for 4 units of time. Each Hawk has an expected reward of 1 from the fight. If a Hawk met a Dove, in 4 units of time the Hawk would instantly consume the resource (payoff of 2) and obtains further rewards at rate 1. Thus a Hawk obtains a total payoff of 6 in this period. In this case the Dove obtains a payoff of 4. When two Doves meet, they share the resource and obtain further rewards at rate 1, giving a total reward of 5. Subtracting 4 from each payoff to obtain the standard form of the Hawk–Dave game, we obtain the following matrix game

	H	D
H	(−3, −3)	(2, 0)
D	(0, 2)	(1, 1)

The ESS in this game is to play *H* with probability 1/4.

The effect of the interaction rate, λ, is illustrated by Cases 1–4. It can be seen that as the interaction rate increases the probability of playing *H* decreases. However, we should not conclude that as the population density increases, then in general the level of aggression decreases. The examples considered assume that individuals obtain rewards at a fixed rate outside the interactions. This may be interpreted as assuming that in each realisation individuals have the same level of access to resources. However, as the population density increases, we would expect access to resources to decrease. Hence, a more complex model would be required to study the interaction between the level of aggression, population density and the availability of resources.

In order to see why this model predicts that the level of aggression falls as the interaction rate increases, suppose all the population use a pure strategy. As the interaction rate increases, the probability that an individual plays *D* given that he/she is not involved in a game increases. There are two opposing effects:

1. Since an opponent in a game is chosen at random from the individuals not involved in Hawk–Dove games, an individual is more likely to be paired with a Dove than if the opponent was chosen at random from the population as a whole. This effect acts to increase the proportion of Hawks in the population.

2. Since Doves spend less time on average in each interaction, they play the Hawk–Dove game more frequently than Hawks. This effect acts to increase the proportion of Doves in the population.

For the parameter sets investigated, the second effect is stronger and as the interaction rate increases, the proportion of Hawks in the population decreases. When each

individual plays a mixed strategy, the first effect is no longer present and so $q^{\ddagger}$ falls more rapidly than q_H as the interaction rate increases.

Cases 2, 5, 6 illustrate the effect of μ_{HD}. This parameter may be interpreted as the rate at which the resource can be consumed. As μ_{HD} increases, the resource gives a higher rate of reward and thus becomes more valuable. As expected, the level of aggression is increasing in μ_{HD}.

Cases 2, 7, 8 illustrate the effect of μ_{HH}. This parameter may be interpreted as a measure of the expected costs of fighting (the expected costs are $1/\mu_{HH}$). This parameter has a very clear effect on the level of aggression. As μ_{HH} increases (the costs of fighting decrease), the level of aggression rises.

Cases 2, 9, 10, 11 illustrate the effect of μ_{DH}. This parameter may be interpreted as a measure of the harm Hawks inflict on Doves before Doves escape (the expected damage is $1/\mu_{DH}$). As expected the more harm that Hawks can inflict on Doves without retaliation, the higher the level of aggression.

It should be noted that as in the standard Hawk–Dove game, we can extend the set of available strategies to include other types of behaviour such as retaliation.

5. Example 3 – A parental care game

We present a simple model of this kind for which we can give analytical results. It is assumed that there is no breeding season and individuals do not form lasting partnerships. Males may be in one of two states: searching or breeding. Females may be in one of three states: receptive, non-receptive or breeding. For simplicity, it is assumed that when individuals are in the breeding state they do not attempt to breed with other partners. The sex ratio is assumed to be one. Denote the equilibrium proportions of males in the two states, searching and breeding, as p_1 and p_2, respectively. The proportions of females in the three female states, receptive, non-receptive and breeding, are denoted by q_1, q_2 and q_3, respectively. These proportions depend on the strategies adopted by the population, but unless we are considering a particular strategy profile, this dependence will not be made apparent by the notation.

Males in the searching state find a mate at a rate proportional to the number of receptive females, namely at rate $\lambda_1 q_1$. That is to say that in a small interval of time of length δ units, a proportion $\lambda_1 q_1 \delta$ of the searching males will find a mate. Similarly, receptive females find a mate at a rate proportional to the number of searching males, i.e. at rate $\lambda_1 p_1$. It should be noted that these assumptions satisfy the condition that the number of males entering the breeding state equals the number of females entering the breeding state. Receptive females become unreceptive at rate μ_1, i.e. the mean length of their receptive period is $1/\mu_1$. Unreceptive females become receptive at rate μ_2.

Given a female does not mate, she will be receptive for a proportion $\mu_2/(\mu_1 + \mu_2)$ of the time. It is assumed that the parameters μ_1 and μ_2 are fixed according to the physiological processes in a species. By letting $\mu_2 \rightarrow \infty$, we obtain a model in which non-breeding females are always receptive.

The rates at which breeding males rejoin the pool of searching males and breeding females return to the pool of receptive females depend on whether they care for their young or not. Deserting males return to the pool of searching males at rate $\lambda_{2,N}$, that is to say that on average the mating process and time to replenish sperm supplies occupies $1/\lambda_{2,N}$ units of time. Similarly, if females do not care for their young, they return to the pool of receptive females at rate $\mu_{3,N}$. For example, in mammals and birds $\lambda_{2,N}$ tends to be much larger than $\mu_{3,N}$, i.e. male deserters can return to searching for a new mate much faster than female deserters. When they care for their offspring, males and females return to the pool of individuals searching for a mate at rates $\lambda_{2,C}$ and $\mu_{3,C}$, respectively. It is assumed that $\lambda_{2,C} \approx \mu_{3,C}$. The transition between states is illustrated in Fig. 1.
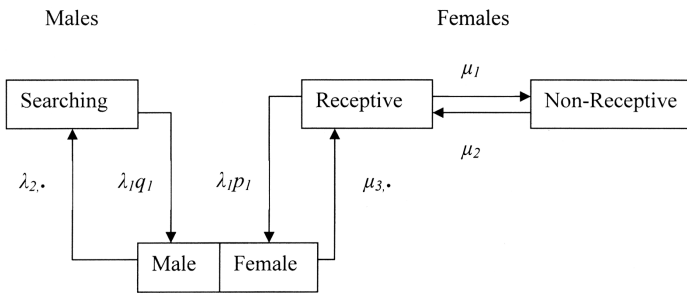
Fig. 1. Transition rates between states
• represents *C* or *N* according to whether a given sex cares for their offspring or not

The number of young surviving to maturity is measured in relation to the number surviving when no parental care is given. Suppose the relative number of young surviving to maturity when a) just the female cares, b) just the male cares and c) both parents care are k_f, k_m and k_b, respectively. It is assumed that the goal of each individual is to maximise the rate of producing offspring that survive until maturity. For simplicity, this will be referred to as the reproduction rate.

In order to investigate pure ESSs of such a game, we must first derive the equilibrium proportions of individuals in each state when each member of the population follows a given strategy appropriate to its sex. Considering the transition of females from receptive to non-receptive, the relative number of females becoming non-receptive per unit time is the proportion of receptive females times the rate of transition from being receptive to being non-receptive, i.e. $\mu_1 q_1$. Similarly, the relative number of females becoming receptive per unit time is $\mu_2 q_2$. Hence, at equilibrium we have

$$\mu_1 q_1 = \mu_2 q_2. \tag{4}$$

Considering firstly the transition of receptive females to/from mating females and then the rate of transition of searching males to/from mating males, since $p_2 = 1 - p_1$ we obtain

$$\lambda_1 p_1 q_1 = \mu_{3,\bullet} q_3, \tag{5}$$

$$\lambda_1 p_1 q_1 = \lambda_{2,\bullet}(1 - p_1), \tag{6}$$

where each $\bullet$ corresponds to N or C according to the strategy adopted by the appropriate sex. In addition, we have

$$q_1 + q_2 + q_3 = 1. \tag{7}$$

Rearranging Equations (4)–(7), we obtain $a_1 q_1^2 + bq_1 + c = 0$, where (the appropriate form of the solution is given just for completeness)

$$a = \frac{\mu_{3,\bullet}\lambda_1[\mu_1 + \mu_2]}{\mu_2},$$

$$b = \mu_{3,\bullet}\lambda_{2,\bullet} + \frac{\mu_{3,\bullet}\lambda_{2,\bullet}\mu_1}{\mu_2} + \lambda_1\lambda_{2,\bullet} - \mu_{3,\bullet}\lambda_1,$$

$$c = -\mu_{3,\bullet}\lambda_{2,\bullet}.$$

The unique solution to this equation between zero and one is

$$q_1 = \frac{-b + \sqrt{b^2 - 4ac}}{2a}.$$

The remaining equilibrium proportions may be calculated from the following relations

$$q_2 = \frac{\mu_1 q_1}{\mu_2},$$

$$q_3 = 1 - q_1 - q_2,$$

$$p_1 = \frac{\mu_{3,\bullet} q_3}{\lambda_1 q_1}.$$

Since these equilibrium proportions depend on the strategies adopted, they will be denoted using subscripts indicating firstly the strategy used by males and secondly the strategy used by females. For example, $p_{1,CN}$ denotes the equilibrium proportion of males searching when males care for their offspring, but females do not.

First, we consider the conditions for no parental care to be an ESS. To find the equilibrium frequencies when neither sex cares for offspring, we set $\mu_{3,\bullet} = \mu_{3,N}$ in Equations (5)–(6). It is clear that the mean reproduction rate of both sexes must be

equal. Hence, we calculate the reproductive rate of males, since this is the simpler calculation. The reproduction rate of males is given by the relative number of offspring surviving from breeding divided by the mean cycle time, which is the mean time required to move from the searching state to the breeding state and back again. Assume neither parent cares for the offspring. Define this mean cycle time to be T_{NN}. We have

$$T_{NN} = \frac{1}{\lambda_1 q_{1,NN}} + \frac{1}{\lambda_{2,N}} = \frac{\lambda_{2,N} + \lambda_1 q_{1,NN}}{\lambda_{2,N} \lambda_1 q_{1,NN}}.$$

Note that from Equation (6), we obtain

$$p_{1,NN} = \frac{\lambda_{2,N}}{\lambda_{2,N} + \lambda_1 q_{1,NN}}.$$

Hence, the reproduction rate is $1/T_{NN} = \lambda_1 q_{1,NN} p_{1,NN}$. This is intuitively clear, since the mean reproduction rate of the population must be the rate at which mating occurs, here $\lambda_1 q_{1,NN} p_{1,NN}$, time the relative number of surviving offspring, here 1.

In order for no parental care to be an ESS, this rate must be greater than the reproduction rate of a mutant of either sex who cares for their offspring. Calculating as above, the expected cycle time of a male mutant, denoted $T_{m,NN}$ who cares for his offspring is

$$T_{m,NN} = \frac{1}{\lambda_1 q_{1,NN}} + \frac{1}{\lambda_{2,C}} = \frac{\lambda_{2,C} + \lambda_1 q_{1,NN}}{\lambda_{2,C} \lambda_1 q_{1,NN}}.$$

Since the relative number of offspring surviving to maturity is k_m, it follows that a male mutant cannot invade if

$$\lambda_1 p_{1,NN} q_{1,NN} > \frac{k_m \lambda_{2,C} \lambda_1 q_{1,NN}}{\lambda_{2,C} + \lambda_1 q_{1,NN}}. \tag{8}$$

The mean cycle time for a female is the mean time required to go from the responsive state to the breeding state and back. Denote the mean cycle time of a mutant female who cares for her offspring when no-one else cares by $T_{f,NN}$. The rate at which the state of a responsive female changes, denoted $\mu_{R,NN}$, is the sum of the rate of finding a mate and the rate at which she becomes unresponsive, i.e. $\mu_{R,NN} = \lambda_1 p_{1,NN} + \mu_1$. The mean time to the first change of state is $1/\mu_{R,NN}$. The probability that she finds a mate before becoming non-receptive is $\lambda_1 p_{1,NN}/\mu_{R,NN}$. Given she first finds a mate, then the mean time for a mutant female who cares for young to return to the receptive state is $1/\mu_{3,C}$. Given she first becomes non-receptive, she must then return to the receptive state (after an expected period of $1/\mu_2$ units) and then the additional length of time expected to complete the cycle is $T_{f,NN}$, as she has simply returned to her starting point. Hence, conditioning on the type of the first change of state, we have

$$T_{f,NN} = \frac{1}{\mu_{R,NN}} + \frac{\lambda_1 p_{1,NN}}{\mu_{R,NN}\mu_{3,C}} + \frac{\mu_1}{\mu_{R,NN}}\left[\frac{1}{\mu_2} + T_{f,NN}\right].$$

This equation leads to

$$T_{f,NN} = \frac{\mu_2\mu_{3,C} + \mu_2\lambda_1 p_{1,NN} + \mu_1\mu_{3,C}}{\lambda_1\mu_2\mu_{3,C} p_{1,NN}}.$$

It follows that a female mutant cannot invade the population if

$$\lambda_1 q_{1,NN} p_{1,NN} > \frac{k_f \mu_{3,C}\mu_2\lambda_1 p_{1,NN}}{\mu_2\mu_{3,C} + \mu_2\lambda_1 p_{1,NN} + \mu_1\mu_{3,C}}. \tag{9}$$

The derivations of the stability conditions for the remaining three possible pure equilibria are analogous. Therefore, we present just the conditions themselves. In each case the left hand side of the inequality is the reproduction rate of the population, the first entry on the right hand side is the reproduction rate of a mutant male and the second entry is the reproduction rate of a mutant female.

To find the equilibrium frequencies when only males care for offspring, we set $\mu_{3,\bullet} = \mu_{3,N}$ and $\lambda_{2,\bullet} = \lambda_{2,C}$ in Equations (4)–(7). Only male parental care is an ESS if

$$k_m\lambda_1 q_{1,CN} p_{1,CN} > \max\left\{\frac{\lambda_1 q_{1,CN}\lambda_{2,N}}{\lambda_{2,N} + \lambda_1 q_{1,CN}}, \frac{k_b\mu_2\lambda_1\mu_{3,C} p_{1,CN}}{\mu_2\mu_{3,C} + \mu_2\lambda_1 p_{1,CN} + \mu_1\mu_{3,C}}\right\}. \tag{10}$$

To find the equilibrium frequencies when only females care for offspring, we set $\mu_{3,\bullet} = \mu_{3,C}$ and $\lambda_{2,\bullet} = \lambda_{2,N}$ in Equations (4)–(7). Only female parental care is an ESS if

$$k_f\lambda_1 q_{1,NC} p_{1,NC} > \max\left\{\frac{k_b\lambda_1 q_{1,NC}\lambda_{2,N}}{\lambda_{2,C} + \lambda_1 q_{1,NC}}, \frac{\mu_2\lambda_1\mu_{3,N} p_{1,NC}}{\mu_2\mu_{3,N} + \mu_2\lambda_1 p_{1,NC} + \mu_1\mu_{3,N}}\right\}. \tag{11}$$

To find the equilibrium frequencies when both parents care for offspring, we set $\mu_{3,\bullet} = \mu_{3,C}$ and $\lambda_{2,\bullet} = \lambda_{2,C}$ in Equations (4)–(7). Biparental care is an ESS if

$$k_b\lambda_1 q_{1,CC} p_{1,CC} > \max\left\{\frac{k_f\lambda_1 q_{1,CC}\lambda_{2,N}}{\lambda_{2,N} + \lambda_1 q_{1,CC}}, \frac{k_m\mu_2\lambda_1\mu_{3,N} p_{1,CC}}{\mu_2\mu_{3,N} + \mu_2\lambda_1 p_{1,CC} + \mu_1\mu_{3,N}}\right\}. \tag{12}$$

Inequalities (8)–(12) can be used to show how the set of ESSs depends on the benefits of parental care. Assume that $\mu_1 = \mu_2 = 1$, $\mu_{3,C} = \lambda_{2,C} = 0.05$, $\mu_{3,N} = 0.2$, $\lambda_{2,N} = 5$, $\lambda_1 = 20$.

1. No parental care is an ESS when $k_m < 4.57572$ and $k_f < 3.8754$.
2. Just female care is an ESS when $k_f > 3.8824$ and $k_b < 1.9701 k_f$.
3. Just male care is an ESS when $k_m > 30.4512$ and $k_b < 1.7402 k_m$.
4. Biparental care is an ESS when $k_b > 8.8322\, k_f$ and $k_b > 3.1119 k_m$.

The set of pure ESSs for the case $k_m = k_f$ is illustrated in Figure 2. An approximate log scale is used, $\ln(k_b)$ is on the y-axis and $\ln(k_f)$ is on the x-axis.
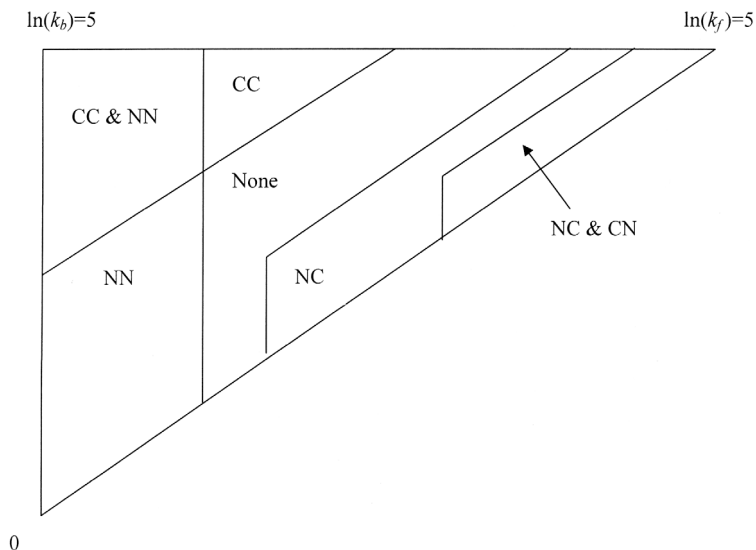
Fig. 2. Set of Pure ESSs in the parental care game

Two pure ESSs exist for some sets of parameters. Both biparental care and no parental care can be ESSs when there is little gain from uniparental care, but biparental care gives significant benefits. What system evolves in this case would depend on the initial set of strategies used within a population.

Uniparental care will evolve if there is a significant gain when one parent cares compared to no parental care, but care by a second parent gives very little benefit. In the case of mammals, it would be expected that female care would evolve, as males have the opportunity of defecting before offspring are born. One possible adaptation of this model would be to take into account the order in which decisions are made and allow females to react to the strategy used by their partner.

For many sets of parameters there is no pure ESS. In such cases a mixed ESS will exist. There are two types of such ESSs possible:

1. A totally mixed ESS, in which some individuals of both sexes care and some defect.

2. A mixed ESS in which members of one sex always care or always defect and some of the members of the other sex care and some defect.

In many such cases, a female will be able to gain by reacting to the choice of a male and this will affect the set of ESSs. Mixed ESSs and the adaptation of the model so that females react to the choice of their partner will be considered in a forthcoming paper.

6. Conclusion

This article has considered the necessity of considering certain evolutionary games, such as the war of attrition and parental games, as games against the field rather than two-player matrix games. This results from two factors:

1. The strategies used in a game may involve choosing a "waiting time", in this case players who choose a shorter mean waiting time may be able to play the game more often. Hence, there is a trade off between the number of games played per unit time and the mean reward obtained in each game.

2. The expected reward from a given strategy cannot be defined in a consistent manner without taking into account the strategies used in the population as a whole.

Three simple examples were considered based on the concept of phases. Individuals move between phases (states) at rates that depend on their strategy and the strategies used by the population as a whole. In certain phases an individual interacts with another and plays a subgame. The goal of each individual is to maximise the rate at which he/she obtains rewards.

Three examples were given. The first example was based on the war of attrition. Strategies that are both evolutionarily stable and neighbourhood invader strategies within a class of mixed strategies were derived. By appropriately interpreting the rewards gained in the game against the field, the solution given here corresponds to the solution of the classical war of attrition game. The second example was based on the Hawk-Dove game and was used to show how an evolutionarily stable polymorphism differs from a mixed ESS in such games against the field.

The third example gives an introductory analysis of a parental care game. It seems that such an approach can be adapted to give more insight into the factors determining the system of parental care that has evolved in various species. The model should also be extended to take mate choice into account, as there is a large amount of feedback between patterns of mate choice and patterns of parental care (see Székely et al. [23]). This could be done by introducing individuals of differing levels of quality.

As Selten [20] notes, there cannot be a mixed ESS in an asymmetric two-player game. However, this does not apply to games against the field in which there are two classes of players. There are mixed equilibria in the parental game considered above, where e.g. all females care but only some males care. Such equilibria will be considered in detail in a forthcoming paper.

Although the models presented here are very simple, they present a framework that can easily be generalised to more complex models. For example, strategy dependant mortality rates could be introduced. The assumption that states change at given rates is a simplification. If there are no seasons, it seems reasonable that at the population level the rate of switching between states is constant. At an individual level this

assumption (i.e. the time spent in a given state is exponentially distributed) is more problematic. However, this assumption should not affect the qualitative interpretation of the results. A more major problem in the applicability of this model to various scenarios is the assumption of a lack of seasons. Using such a phase type approach, it does not seem easy to get round this problem. Although it would be difficult to obtain analytic results for more complex models of this form, numerical results may give us more insight into such systems.

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Wieloosobowe gry ewolucyjne typu „cyklu życiowego"

W dziedzinie gier ewolucyjnych zwykle zakłada się, że każda jednostka gra wiele razy w dany rodzaj gry dwuosobowej, z tym że za każdym razem jej przeciwnik zmienia się. W przypadku gier ewolucyjnych, takich jak „wojna na wyczerpanie" czy „opieka rodzicielska", czas wykorzystany na realizację gry zależy od strategii wybranej przez jednostkę. W takich przypadkach należy brać pod uwagę nie tylko średnią wypłatę z każdej realizacji gry, ale też średni czas potrzebny na jej realizację. W tej sytuacji model standardowej gry dwuosobowej powinien być zastąpiony grą wieloosobową. Dodatkowo, w grach typu „opieka rodzicielska" wypłata samca, który nie opiekuje się swoimi dziećmi, zależy od możliwości uzyskania dodatkowych partnerek, co z kolei zależy od strategii używanych w całej populacji. W pracy rozważono kilka przykładów gier wieloosobowych, które są wygenerowane przez grę dwuosobową.

Słowa kluczowe: *gry ewolucyjne, gry wieloosobowe, faza, strategia ewolucyjnie stabilna, strategia lokalnie wypierająca, polimorfizm*