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Strategy Dependent Mortality in Life History Games

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Abstract—In games such as the war of attrition and parental care games the length of time spent in a realisation of the game is dependent on the strategy used. Hence, there is a trade off between the mean reward obtained per realisation of the game and the mean number of games played per unit time. Such a game should not be modelled using the standard two-player form, but should be defined as a game against the field (a large population game). In parental care games, such an approach also enables us to define a more consistent model, which takes into account, for example, the obvious fact that each individual has one parent of both sexes and that the ease with which a male deserter can find a new partner depends on the strategy profile used in the population. If the mortality rate is independent of strategy, then each individual should simply maximise the rate of producing offspring. However, if mortality rates depend on strategy, then at equilibrium an individual should maximise the number of offspring produced during their lifetime. This paper considers pure equilibria in a parental care game, in which the mortality rate depends on an individual's strategy.

I. INTRODUCTION

In many classical models in the field of evolutionary game theory (see Maynard Smith [1]) an evolutionarily stable strategy (ESS) is defined as a refinement of a Nash equilibrium in an appropriately defined two-player game. The following are implicit assumptions in such a formulation:

- i) Each individual in the population plays the same number of realisations of the game.
- ii) The opponent in each realisation of the game is chosen at random from the population as a whole.

However, these assumptions may often be unreasonable. For example, in the war of attrition (see Maynard Smith and Price [2]) each player chooses a waiting time. Those who choose longer waiting times will on average spend more time in a realisation of the game. It is expected that such individuals will play the game less frequently than those who choose shorter waiting times. Hence, there will be a tradeoff between the mean reward obtained from a realisation of the game and the rate at which games are played. Also, it may be reasonable to assume that the opponent in a game should be chosen from the set of individuals who are at present not involved in such an interaction. In this case the choice of opponent should be biased towards individuals with shorter waiting times. Canning and Whittaker [3] and Eriksson *et al.* [4] consider models

of the war of attrition in which these effects are taken into account.

Such tradeoffs also arise in parental care games. In simple terms, deserters may be able to breed more often than carers, but the mean number of offspring surviving from each breeding attempt will be less than the mean number of offspring raised per breeding attempt by carers.

Maynard Smith [5] 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 within 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 [6] consider the problems involved in developing a good model for a parental care game. 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 of parental care must take into account the fact that the total number of offspring of males is equal to the total number of offspring of females.

This paper considers a model of a parental care game adapted from Ramsey [7]. The model presented here assumes that there is no breeding season. It is in some ways an extension of Yamamura and Tsuji's [8] model. This model was adapted to the life history of St. Peter's Fish by Balshine-Earn and Earn [9]. In these two models individuals of the rarer sex in the pool of searchers immediately find a mate. However, in the model presented here such individuals find mates at an appropriately faster rate than individuals of the more common sex in the pool of searchers. Similar models have been considered for species that breed seasonally,

but several breeding attempts are possible in a season (see Webb *et al.* [10], McNamara *et al.* [11]).

II. THE MODEL

It is assumed that there is no breeding season and individuals do not form lasting partnerships. Individuals play one of two strategies: care or desert. Carers will produce a greater number of offspring per breeding attempt, but will breed less often than deserters. The rate at which an individual finds mates depends on the proportions of individuals of each sex who care or desert. These proportions are referred to as the strategy profile. A pure strategy profile satisfies the following: all males use the same strategy and all females follow the same strategy.

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. It is assumed that the rate at which juvenile males join the adult population is r_m times the rate at which juvenile females join the adult population. This ratio depends on the sex ratio at birth, the age of maturation and the mortality rates of juveniles and is assumed to be fixed for a given species. It is assumed that on maturing individuals enter the searching or receptive state, as appropriate to sex. An individual inherits the strategy used by the parent of the same sex. 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 q_1 , q_2 and q_3 , respectively. These proportions depend on the strategy profile adopted within the population, but unless we are considering a particular strategy profile, this dependence will not be made apparent by the notation. When we are considering a particular pure strategy profile, the strategy profile will be denoted by a double index. The first and second letters define the strategies used by males and females, respectively. Hence, p_1^{DC} denotes the equilibrium proportion of males that are searching when males desert and females care. The ratio of the number of adult males to the number of adult females is denoted r_0 . This will in general differ from r_m due to the variable mortality rates (see below). Also, r_0 depends on the strategy profile used. Hence, when we consider a specific strategy profile, this will be reflected by adding the appropriate superscript to r_0 .

Males in the searching state find a mate at a rate proportional to the number of receptive females, namely at rate $\lambda_1 q_1$. Similarly, receptive females find a mate at a rate proportional to the number of searching males, namely at rate $\lambda_1 p_1 r_0$. 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 ρ_1 , i.e. the mean length of the receptive period is $\frac{1}{\rho_1}$. Unreceptive females become receptive at rate ρ_2 . It is assumed that the parameters ρ_1 and ρ_2 are fixed according to the physiological processes in a species. Given a female does not mate, she will be receptive for a proportion $\frac{\rho_2}{\rho_1 + \rho_2}$ of the time. By letting $\rho_2 \rightarrow \infty$, we obtain a model in which non-breeding females are always receptive.

The rates at which breeding males rejoin the pool of searching males depends on whether they care for their offspring or not. Deserting males return to the pool of searching males at rate λ_m^D . That is to say that on average the mating process and time to replenish sperm supplies occupies $\frac{1}{\lambda_m^D}$ units of time. Similarly, if females do not care for their young, they return to the pool of receptive females at rate λ_f^D . For example, in mammals λ_m^D tends to be much larger than λ_f^D , i.e. male deserters can return to searching for a new mate much faster than female deserters. When they care for their young, males and females return to the pool of individuals searching for a mate at rates λ_m^C and λ_f^C , respectively. It is assumed that $\lambda_m^C \approx \lambda_f^C$.

The mortality rates of searching males and non-breeding females are assumed to be μ_m and μ_f , respectively. In the breeding state, the mortality rates of male and female deserters are assumed to be μ_m^D and μ_f^D , respectively. The mortality rate of a carer depends on the strategy used by the partner. If the partner also cares, the mortality rates are μ_m^{CC} and μ_f^{CC} , as appropriate. If the partner defects, the corresponding mortality rates are μ_m^{CD} and μ_f^{CD} .

The number of offspring that survive until maturity is measured relative to the number surviving when no parental care is given. It should be noted that a parent may die whilst caring for young. Hence, for simplicity it is assumed that the number of surviving young depends on the number of caring parents alive at the end of the period of care. However, the mortality rates only depend on the strategies adopted by the parents at the beginning of the period of care. Also, it is assumed that if an individual cares then it continues caring when a partner dies. Define the relative numbers of young surviving to maturity when a) just the female cares, b) just the male cares and c) both parents care to be k_{DC} , k_{CD} and k_{CC} , respectively. It is assumed that these values are independent of the strategy profile used within the population. This is a reasonable assumption if the carrying capacity of the environment is independent of the strategy profile used. At equilibrium the rate at which individuals mature must be equal to the rate at which adult individuals die. This rate will be denoted \bar{k} . This rate depends on the strategy profile used and when a specific profile is under consideration this will be specified using the appropriate pair of indices as above. A proportion $\frac{r_m}{r_m+1}$ of these surviving offspring

are male.

We should differentiate between the rates at which individuals pass between states and the relative rates at which transitions occur between states within the population of individuals of a particular sex (the population rate). Such population rates are obtained by multiplying the proportion of individuals of a given sex in a particular starting state by the rate at which such an individual moves to another state. For example, since males are searching for a mate a proportion p_1 of the time and each find mates at rate $\lambda_1 q_1$, the rate at which males breed in the population as a whole is $\lambda_1 p_1 q_1$. Thus, the rate at which males mature in the population as a whole is $\frac{\lambda_1 p_1 q_1 \tilde{k} r_m}{r_m + 1}$. Arguing similarly, the rate at which females mature in the population as a whole is $\frac{\lambda_1 p_1 q_1 r_0 \tilde{k}}{r_m + 1}$. It is assumed that the population is at equilibrium, i.e. infants are born at a steady rate within the population as a whole. Hence, we may assume that the offspring "immediately" mature at a steady rate within the population as a whole.

A. Calculation of the Equilibrium Proportions

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, together with the number of offspring of each sex that survive to maturity per breeding attempt. Let \tilde{k}_{DD} , \tilde{k}_{CD} , \tilde{k}_{DC} and \tilde{k}_{CC} be the expected number of offspring surviving to maturity at equilibrium when there is no parental care, just males care, just females care and both parents care, respectively. Unless a specific strategy profile is under consideration, the index will be omitted. The general form of the model is illustrated in Fig. 1. The rates given are the appropriate population rates.

Given the strategy profile is fixed, at equilibrium the population rate of entering into a state must be equal to the population rate of exiting that state. Considering the two male states, we obtain

$$\begin{aligned} p_1(\lambda_1 q_1 + \mu_m) &= \lambda_m^\bullet (1 - p_1) + \frac{\lambda_1 p_1 q_1 \tilde{k} r_m}{r_m + 1} \quad (1) \\ (1 - p_1)(\lambda_m^\bullet + \mu_m^\star) &= \lambda_1 p_1 q_1, \quad (2) \end{aligned}$$

where \bullet represents C or D according to whether a given sex cares for their offspring or not and \star represents D , CD or CC as appropriate given the strategies used by two parents.

Considering the three female states in turn

$$q_1(\mu_f + \lambda_1 p_1 r_0 + \rho_1) = q_2 \rho_2 + q_3 \lambda_f^\bullet + \frac{\lambda_1 p_1 q_1 r_0 \tilde{k}}{r_m + 1} \quad (3)$$

$$q_2(\rho_2 + \mu_f) = q_1 \rho_1 \quad (4)$$

$$q_3(\mu_f^\star + \lambda_f^\bullet) = \lambda_1 p_1 q_1 r_0. \quad (5)$$

Also, the sex ratio among maturing juveniles must

equal the sex ratio among those dying. This leads to

$$r_m = \frac{r_0 [p_1 \mu_m + (1 - p_1) \mu_m^\star]}{(q_1 + q_2) \mu_f + q_3 \mu_f^\star}. \quad (6)$$

In addition, we must have

$$q_1 + q_2 + q_3 = 1. \quad (7)$$

For a given strategy profile, we need to calculate p_1 , q_1 , q_2 , q_3 , r_0 and \tilde{k} . Since each male entering the breeding state must correspond to a female entering the breeding state, one of the equations given above is redundant. Equations (1)-(7) can be rearranged to give $a q_1^2 + b q_1 + c = 0$, where

$$\begin{aligned} a &= \mu_f + \rho_1 - \frac{\rho_1 \rho_2}{\rho_2 + \mu_f} + \\ &\quad + \frac{\rho_1 + \rho_2 + \mu_f}{r_m (\rho_2 + \mu_f)} \left[(1 - r_m) \mu_f^\star + \lambda_f^\bullet - \frac{\lambda_m^\bullet (\mu_f^\star + \lambda_f^\bullet)}{\lambda_m^\bullet + \mu_m^\star} \right] \\ b &= \mu_f^\star + \frac{\mu_f^\star + \lambda_f^\bullet}{r_m} \left[\frac{\mu_m (\rho_1 + \rho_2 + \mu_f)}{\lambda_1 (\rho_2 + \mu_f)} + \frac{\lambda_m^\bullet}{\lambda_m^\bullet + \mu_m^\star} - 1 \right] \\ c &= - \frac{\mu_m (\mu_f^\star + \lambda_f^\bullet)}{\lambda_1 r_m}. \end{aligned}$$

Once the appropriate value of q_1 has been calculated (when $a > 0$ it is simple to show that there is only one root in $[0, 1]$), we can calculate q_2 , q_3 , p_1 , \tilde{k} and r_0 using

$$\begin{aligned} q_2 &= \frac{\rho_1 q_1}{\rho_2 + \mu_f} \\ q_3 &= 1 - \frac{q_1 (\rho_1 + \rho_2 + \mu_f)}{\rho_2 + \mu_f} \\ p_1 &= \frac{\lambda_m^\bullet + \mu_m^\star}{\lambda_1 q_1 + \lambda_m^\bullet + \mu_m^\star} \\ \tilde{k} &= \frac{(r_m + 1) [p_1 (\lambda_1 q_1 + \mu_m + \lambda_m^\bullet) - \lambda_m^\bullet]}{\lambda_1 p_1 q_1 r_m} \\ r_0 &= \frac{r_m [(q_1 + q_2) \mu_f + q_3 \mu_f^\star]}{p_1 \mu_m + (1 - p_1) \mu_m^\star}. \end{aligned}$$

For example, to calculate the equilibrium proportions, sex ratio r_0 and maturation rate when males desert and females care, we set $\lambda_m^\bullet = \lambda_m^D$, $\lambda_f^\bullet = \lambda_f^C$, $\mu_m^\star = \mu_m^D$ and $\mu_f^\star = \mu_f^{CD}$.

B. Deriving the ESS Conditions

Here, we derive the conditions for biparental care to be an ESS. The derivation of the conditions for the other three possible pure strategy profiles to be an ESS are analogous and hence we just give the conditions.

In order for biparental care to be an ESS, when all the population care for their offspring the expected number of surviving offspring of the same sex produced by a mutant who deserts must be less than one. First, we consider the expected number of surviving male offspring of a male mutant. Let m_i^{CC} be the expected number of future surviving male offspring of a mutant male in state i when both sexes care. From the assumptions of the model, m_1^{CC} is the expected

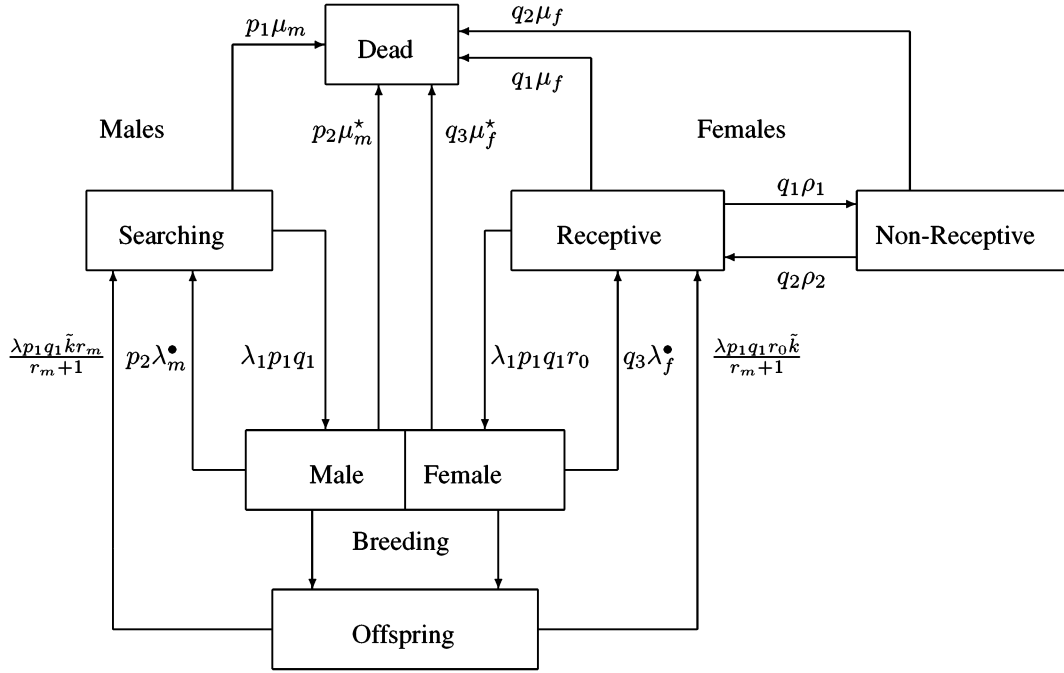


Fig. 1: Transition rates between states.

number of surviving male offspring a mutant male produces during his lifetime. In State 1, no offspring are produced and a male survives to find a mate with probability $\frac{\lambda_1 q_1^{CC}}{\lambda_1 q_1^{CC} + \mu_m}$. Hence,

$$m_1^{CC} = \frac{\lambda_1 q_1^{CC} m_2^{CC}}{\lambda_1 q_1^{CC} + \mu_m}. \quad (8)$$

In order to calculate the relative number of offspring such a male obtains per breeding attempt in comparison to the population as a whole, we must consider the pattern of mortality. First, we consider the population as a whole. When both parents care the probability of a) both parents surviving, s_b^{CC} , b) just the male surviving, s_m^{CC} , c) just the female surviving, s_f^{CC} and d) neither parent surviving, s_n^{CC} are given by

$$\begin{aligned} s_b^{CC} &= \frac{\lambda_m^C \lambda_f^C}{(\lambda_m^C + \mu_m^{CC})(\lambda_f^C + \mu_f^{CC})} \\ s_m^{CC} &= \frac{\lambda_m^C \mu_f^{CC}}{(\lambda_m^C + \mu_m^{CC})(\lambda_f^C + \mu_f^{CC})} \\ s_f^{CC} &= \frac{\lambda_f^C \mu_m^{CC}}{(\lambda_m^C + \mu_m^{CC})(\lambda_f^C + \mu_f^{CC})} \\ s_n^{CC} &= \frac{\mu_f^{CC} \mu_m^{CC}}{(\lambda_m^C + \mu_m^{CC})(\lambda_f^C + \mu_f^{CC})}. \end{aligned}$$

It follows that the relative number of surviving offspring per breeding attempt compared to the situation

where there is no parental care is given by \bar{k}_{CC} , where

$$\bar{k}_{CC} = \frac{\lambda_m^C \lambda_f^C k_{CC} + \mu_m^{CC} \lambda_f^C k_{DC} + \mu_f^{CC} \lambda_m^C k_{CD} + \mu_f^{CC} \mu_m^{CC}}{(\lambda_m^C + \mu_m^{CC})(\lambda_f^C + \mu_f^{CC})}.$$

Now consider a breeding attempt by a male mutant. The number of surviving offspring depends only on whether the mother survives the period of care. Considering the mother's probability of survival, the relative number of surviving offspring compared to the number surviving when no parental care is given by \bar{k}_{DC} , where

$$\bar{k}_{DC} = \frac{\lambda_f^C k_{DC} + \mu_f^{CD}}{\lambda_f^C + \mu_f^{CD}}.$$

Hence, the mean number of surviving offspring per breeding attempt by a male mutant is $\frac{\bar{k}_{DC} \bar{k}_{CC}}{k_{CC}}$.

In state 2, a deserting male survives to return to state 1 with probability $\frac{\lambda_m^D}{\lambda_m^D + \mu_m^D}$. It follows that

$$m_2^{CC} = \frac{\lambda_m^D m_1^{CC}}{\lambda_m^D + \mu_m^D} + \frac{r_m \bar{k}_{DC} \bar{k}_{CC}}{(r_m + 1) \bar{k}_{CC}}. \quad (9)$$

Solving the set of linear equations for m_1^{CC} and m_2^{CC} given by (8) and (9), we obtain

$$m_1^{CC} = \frac{\lambda_1 q_1^{CC} r_m \bar{k}_{DC} \bar{k}_{CC} (\lambda_m^D + \mu_m^D)}{\bar{k}_{CC} (r_m + 1) (\lambda_1 q_1^{CC} \mu_m^D + \mu_m \lambda_m^D + \mu_m \mu_m^D)}. \quad (10)$$

Now we consider a female mutant. Define f_1^{CC} , f_2^{CC} and f_3^{CC} to be the expected number of

future surviving female offspring of a mutant female in states 1, 2 and 3. Considering the probability of transitions from state 1 to states 2 and 3, we obtain

$$f_1^{CC} = \frac{\lambda_1 p_1^{CC} r_0^{CC} f_3^{CC}}{\lambda_1 p_1 r_0^{CC} + \rho_1 + \mu_f} + \frac{\rho_1 f_2^{CC}}{\lambda_1 p_1 r_0^{CC} + \rho_1 + \mu_f}. \quad (11)$$

Similarly, considering the probability of transition from state 2 to state 1, we obtain

$$f_2^{CC} = \frac{\rho_2 f_1^{CC}}{\rho_2 + \mu_f}. \quad (12)$$

In state 3, arguing as in the case of a male mutant, on average $\frac{\bar{k}_{CC} \bar{k}_{CD}}{\bar{k}_{CC}(r_m + 1)}$ females are produced who survive to adulthood, where

$$\bar{k}_{CD} = \frac{\lambda_m^C k_{CD} + \mu_m^{CD}}{\lambda_m^C + \mu_m^{CD}}.$$

The probability that a female deserter survives to return to State 1 is $\frac{\lambda_f^D}{\lambda_f^D + \mu_f^D}$. It follows that

$$f_3^{CC} = \frac{\bar{k}_{CC} \bar{k}_{CD}}{\bar{k}_{CC}(r_m + 1)} + \frac{\lambda_f^D f_1^{CC}}{\lambda_f^D + \mu_f^D}. \quad (13)$$

Equations (11) - (13) can be rearranged to find f_1^{CC} , which from the assumptions is the expected number of surviving female offspring a mutant female produces in her lifetime. We obtain $f_1^{CC} = A_{CC}/B_{CC}$, where

$$\begin{aligned} A_{CC} &= \lambda_1 p_1^{CC} r_0^{CC} \bar{k}_{CC} \bar{k}_{CD} (\lambda_f^D + \mu_f^D) (\rho_2 + \mu_f) \\ B_{CC} &= \bar{k}_{CC} (r_m + 1) [\lambda_1 p_1^{CC} r_0^{CC} \mu_f^D (\rho_2 + \mu_f) + \mu_f (\lambda_f^D + \mu_f^D) (\rho_1 + \rho_2 + \mu_f)]. \end{aligned}$$

Biparental care is an ESS when both $f_1^{CC} < 1$ and $m_1^{CC} < 1$.

The conditions for the other three pure profiles to be an ESS can be derived analogously. Suppose just females care for offspring. The mean number of surviving male offspring of a male mutant is given by

$$m_1^{DC} = \frac{\bar{k}_{CC} \lambda_1 q_1^{DC} r_m \bar{k}_{DC} (\lambda_m^C + \mu_m^{CC})}{\bar{k}_{DC} (r_m + 1) [\lambda_1 q_1^{DC} \mu_m^{CC} + \mu_m \lambda_m^C + \mu_m \mu_m^{CC}]}.$$

The mean number of surviving female offspring of a female mutant is given by $f_1^{DC} = A_{DC}/B_{DC}$, where

$$\begin{aligned} A_{DC} &= \lambda_1 p_1^{DC} r_0^{DC} \bar{k}_{DC} (\lambda_f^D + \mu_f^D) (\rho_2 + \mu_f) \\ B_{DC} &= \bar{k}_{DC} (r_m + 1) [\lambda_1 p_1^{DC} r_0^{DC} \mu_f^D (\rho_2 + \mu_f) + (\lambda_f^D + \mu_f^D) \mu_f (\rho_1 + \rho_2 + \mu_f)]. \end{aligned}$$

Female care is an ESS when both $f_1^{DC} < 1$ and $m_1^{DC} < 1$.

Suppose just males care for offspring. The mean number of surviving male offspring of a male mutant is given by

$$m_1^{CD} = \frac{\lambda_1 q_1^{CD} r_m \bar{k}_{CD} (\lambda_m^D + \mu_m^D)}{\bar{k}_{CD} (r_m + 1) [\lambda_1 q_1^{CD} \mu_m^D + \mu_m \lambda_m^D + \mu_m \mu_m^D]}.$$

The mean number of surviving female offspring of a female mutant is given by $f_1^{CD} = A_{CD}/B_{CD}$, where

$$\begin{aligned} A_{CD} &= \bar{k}_{CC} \lambda_1 p_1^{CD} r_0^{CD} \bar{k}_{CD} (\lambda_f^C + \mu_f^{CC}) (\rho_2 + \mu_f) \\ B_{CD} &= \bar{k}_{CD} (r_m + 1) [\lambda_1 p_1^{CD} r_0^{CD} \mu_f^{CC} (\rho_2 + \mu_f) + \mu_f (\lambda_f^C + \mu_f^{CC}) (\rho_1 + \rho_2 + \mu_f)]. \end{aligned}$$

Male care is an ESS when both $f_1^{CD} < 1$ and $m_1^{CD} < 1$.

Suppose no-one cares for offspring. The mean number of surviving male offspring of a male mutant is given by

$$m_1^{DD} = \frac{\bar{k}_{CD} \lambda_1 q_1^{DD} r_m \bar{k}_{DD} (\lambda_m^C + \mu_m^{CD})}{(r_m + 1) [\lambda_1 q_1^{DD} \mu_m^{CD} + \mu_m \lambda_m^C + \mu_m \mu_m^{CD}]}.$$

The mean number of surviving female offspring of a female mutant is given by $f_1^{DD} = A_{DD}/B_{DD}$, where

$$\begin{aligned} A_{DD} &= \bar{k}_{DC} \lambda_1 p_1^{DD} r_0^{DD} \bar{k}_{DD} (\lambda_f^C + \mu_f^{CD}) (\rho_2 + \mu_f) \\ B_{DD} &= (r_m + 1) [\lambda_1 p_1^{DD} r_0^{DD} \mu_f^{CD} (\rho_2 + \mu_f) + \mu_f (\rho_1 + \rho_2 + \mu_f) (\mu_f^{CD} + \lambda_f^C)]. \end{aligned}$$

No parental care is an ESS when both $f_1^{DD} < 1$ and $m_1^{DD} < 1$.

III. EXAMPLES

These conditions can be used to show how the set of ESSs depends on the benefits of parental care. Assume that $\rho_1 = \rho_2 = 1$, $\lambda_f^C = \lambda_m^C = 0.05$, $\lambda_f^D = 0.2$, $\lambda_m^D = 5$, $\lambda_1 = 20$, $r_m = 1$, $\mu_m = \mu_f = \mu_m^* = \mu_f^* = 0.01$, where $\star \in \{D, CD, CC\}$. The parameters are chosen to reflect the physiological constraints observed in mammals and birds (i.e. deserting males can return to mating much quicker than females). The mortality rate is assumed to be independent of sex, state and strategy. Since the incoming sex ratio is one, the ratio of the number of adult males to the number of adult females will be one.

1. No parental care is an ESS when $k_{CD} < 5.0612$ and $k_{DC} < 3.9360$.
2. Just female care is an ESS when $k_{DC} > 3.9379$ and $k_{DC} > 0.5054 k_{CC} - 0.2202$.
3. Just male care is an ESS when $k_{CD} > 59.3854$ and $k_{CD} > 0.5986 k_{CC} - 0.2239$.
4. Biparental care is an ESS when $k_{CC} > 13.6473 k_{DC} + 2.7695$ and $k_{CC} > 3.8527 k_{CD} + 0.8105$.

The results are qualitatively similar to those obtained for the model presented by Ramsey [7], in which the mortality rate was not taken into account and individuals maximise their reproduction rate. For the parameters considered (based on the physiology of mammals), if uniparental care should evolve, then it is expected that female care will evolve.

Since in the model considered here mortality does not depend on the strategy used, it might be expected that individuals should simply maximise their expected

reproduction rate. However, there are a couple of factors which cause the quantitative results to differ.

1. The model given here assumes that the number of surviving offspring depends on the number of caring parents who survive the period of care. The mortality of parents is likely to discount the value of parental care. It is expected that stronger conditions for parental care will be necessary when the mortality rate is relatively high.
2. Mortality removes individuals from each of the states and offspring enter the adult population via the searching state (males) or receptive state (females). This means that at equilibrium there is a higher proportion of individuals looking for mates. This effect favours those deserting their offspring.

Comparing the results with the original model, as expected from the argument given above greater gains from parental care are required for uniparental or biparental care to be stable. The increase required for female care to occur is relatively small, while a greater increase is required for male care to occur.

Figure 2 illustrates the set of ESSs given the gains from parental care. It is assumed that $k_{CD} = k_{DC}$, i.e. caring ability does not depend on sex. An approximate log scale is used (in particular the diagonal boundaries of the regions should be slightly curved), $\ln(k_b)$ is on the y -axis and $\ln(k_f)$ is on the x -axis.

Table 1 illustrates the effect of mortality on the ESS. Apart from the mortality rate, the parameters used are the same as in the example considered above. It is assumed that the mortality rate μ is independent of the strategy used. It can be seen that greater gains are required for male care to evolve. Mortality does not seem to pay a significant factor in deciding whether female care should evolve. This seems to be due to the following affects of the mortality rate on the availability of prospective mates. As the mortality rate rises, the proportion of females in the receptive state rises due to the, by necessity, influx of young females. The number is large in comparison to the relatively small number of females in the receptive state. However, the large majority of males are in the searching state. Although the faster influx of males will tend to increase this proportion, males can also find mates more easily due to the higher abundance of receptive females. Hence, the proportion of searching males is less affected by the mortality rate. Consideration of the gains required for biparental care to evolve lead to a similar conclusion.

Table 2 illustrates the effect of increased mortality for all single parents. It is assumed that the mortality rate is 0.01 for all other individuals and the remaining parameters are as before. It seems that the conditions required for biparental care to be stable are slightly relaxed, whereas as expected the gains required for

TABLE I
EFFECT OF MORTALITY - GREATEST VALUES OF k_{DC} AND k_{CD} FOR WHICH NO PARENTAL CARE IS AN ESS AND MINIMAL GAINS, k_{CC} , FROM ADDITIONAL MALE CARE REQUIRED FOR BIPARENTAL CARE TO BE AN ESS

μ	k_{CD}	k_{DC}	k_{CC}
0.01	5.0612	3.9360	$13.6473k_{DC} + 2.7695$
0.02	5.2421	3.9332	$14.3038k_{DC} + 5.8815$
0.03	5.4219	3.9305	$14.8823k_{DC} + 9.2894$
0.04	5.6007	3.9277	$15.3974k_{DC} + 12.9580$
0.05	5.7785	3.9250	$15.8601k_{DC} + 16.8601$

uniparental care to be stable increase. It should be noted that the sex ratio differs from one when just one of the sexes care, since the caring sex will be affected by a higher mortality rate.

TABLE II
EFFECT OF DIFFERENTIAL MORTALITY. SINGLE PARENTS HAVE A HIGHER MORTALITY RATE - GREATEST VALUES OF k_{DC} AND k_{CD} FOR WHICH NO PARENTAL CARE IS AN ESS AND MINIMAL GAINS k_{CC} FROM ADDITIONAL MALE CARE REQUIRED FOR BIPARENTAL CARE TO BE AN ESS

μ_{\bullet}^{DC}	k_{CD}	k_{DC}	k_{CC}
0.0105	5.2663	4.1318	$13.5312k_{DC} + 2.8855$
0.011	5.4714	4.3275	$13.4170k_{DC} + 2.9997$
0.012	5.8817	4.7190	$13.1941k_{DC} + 3.2223$
0.013	6.2919	5.1104	$12.9783k_{DC} + 3.4384$
0.015	7.1123	5.8934	$12.5667k_{DC} + 3.8500$

Table 3 shows the effect of increased mortality for all parents. The transition between no parental care and uniparental care is the same as given in the previous case, since this transition is unaffected by the mortality rate of parents when both care. As expected greater gains are required for biparental care to be stable.

TABLE III
EFFECT OF DIFFERENTIAL MORTALITY. ALL PARENTS HAVE A HIGHER MORTALITY RATE - GREATEST VALUES OF k_{DC} AND k_{CD} FOR WHICH NO PARENTAL CARE IS AN ESS AND MINIMAL GAINS k_{CC} FROM ADDITIONAL MALE CARE REQUIRED FOR BIPARENTAL CARE TO BE AN ESS

μ_{\bullet}^*	k_{CD}	k_{DC}	k_{CC}
0.0105	5.2663	4.1318	$14.3330k_{DC} + 3.0540$
0.011	5.4714	4.3275	$15.0230k_{DC} + 3.3535$
0.012	5.8817	4.7190	$16.4156k_{DC} + 3.9974$
0.013	6.2919	5.1104	$17.8248k_{DC} + 4.7021$
0.015	7.1123	5.8934	$20.6919k_{DC} + 6.2976$

IV. CONCLUSIONS

This paper has considered a parental care game in which the operational sex ratio is not only dependent on the ratio between the number of adult males to the number of adult females, but also on the actions of all the members of a population and the physiological differences between the sexes.

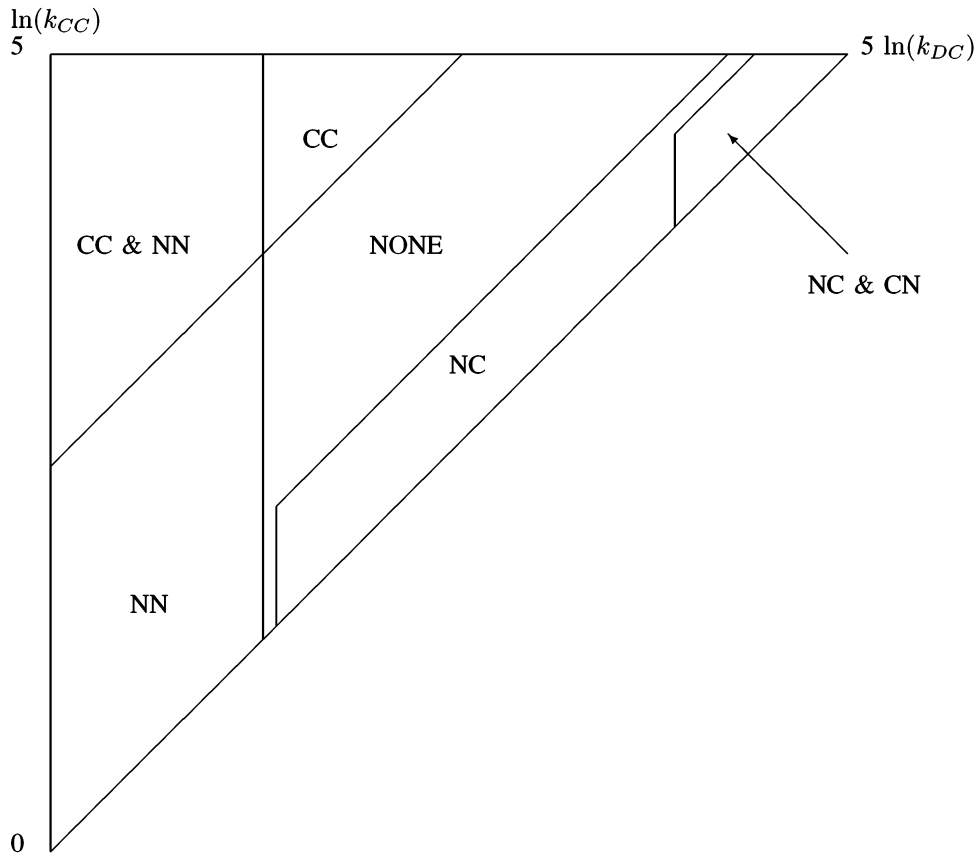


Fig. 2: Set of Pure ESSs according to the values of k_{DC} and k_{CC}

It is argued that in the cases of mammals and birds if uniparental care evolves, it is expected that females will care for their young. It should be noted that in these cases, males will often be able to choose to desert before females can react. In this case, the interaction between mates should be considered as an extended game. A female will be able to gain by reacting to the choice of a male and this will affect the set of ESSs.

Another simplification of the model is the assumption that individuals only have two strategies available to them, either care or desert. However, the basic framework of the game can easily be extended to consider a range of levels of parental care. Although it would be difficult to find analytic results for such a model, it would be relatively easy to simulate the evolution of such systems.

When the gains from both uniparental care and biparental care are moderate, there are no pure equilibria. It is expected in such cases that the population will evolve to a mixed ESS, an evolutionarily stable polymorphism (ESP) or some stable combination of the two (for a definition of an ESP and a discussion of the differences between a mixed ESS and ESP see Ramsey [7]). In simple terms, at an ESP an individual will always choose the same action (care or desert)

on entering the breeding state, but individuals of the same sex take different actions. At a mixed ESS, on entering the breeding state individuals of at least one sex will choose to care with some probability p . Such equilibria will be considered in a forthcoming paper.

Another simplification in the model lies in the fact that there is no variation between individuals of the same sex. It has been noted (see Székely *et al.* [12]) that there is a large degree of feedback between patterns of mate choice and patterns of parental care. It is hoped that these models will be developed to introduce individuals of differing levels of quality and thus introduce the aspect of mate choice into the model. One thing that should be taken into account is that in species with longer life spans pairs are often very stable and will breed repeatedly, especially if successful (see McNamara and Forslund [13]).

Although the model presented has many shortcomings, it provides a general framework that can be built upon to define more realistic, complex models for which numerical results can be obtained. One major problem may be the assumption of a continuous breeding season. It seems difficult to get around this problem using the approach considered here.

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