



ELSEVIER

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

A large population parental care game: Polymorphisms and feedback between patterns of care and the operational sex ratio

David M. Ramsey *

Department of Mathematics and Statistics, University of Limerick, Limerick, Ireland

ARTICLE INFO

Article history:

Received 21 December 2009

Received in revised form

9 June 2010

Accepted 21 July 2010

Available online 3 August 2010

Keywords:

Evolutionarily stable strategy

Cycle time

Fisher condition

Polymorphism

Mixed strategy

ABSTRACT

This article presents a game theoretic model of parental care which models the feedback between patterns of care and the operational sex ratio. It is assumed here that males can be in one of two states: searching for a mate or breeding (including caring for their offspring). Females can be in one of three states: receptive (searching), non-receptive or breeding. However, these sets of states can be adapted to the physiology of a particular species. The length of time that an individual remains in the breeding state depends on the level of care an individual gives. When in the searching state, individuals find partners at a rate dependent on the proportion of members of the opposite sex searching. These rates are defined to satisfy the Fisher condition that the total number of offspring of males equals the total number of offspring of females. The operational sex ratio is not defined exogenously, but can be derived from the adult sex ratio and the pattern of parental care. Pure strategy profiles and so-called single sex stable polymorphisms, in which behaviour is varied within one sex, are derived analytically. The difference between mixed evolutionarily stable strategies and stable polymorphisms within this framework is highlighted. The effects of various physiological and demographic parameters on patterns of care are considered.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Research on the evolution of patterns of parental care has indicated the complex nature of this process. Trivers (1972) gave an in depth exposition of the then current state of research into patterns of parental care. By definition females invest more in gametes. He argues that females have more to lose than males if the offspring die and should thus invest more in caring for their offspring. Males can potentially reproduce at a much higher rate than females. However, due to the physiological constraints of breeding, the ratio of the number of males searching for a mate to the number of such females (the operational sex ratio, OSR) will tend to be much greater than one, i.e. males may face strong competition from other males when looking for a mate. It is argued that due to these factors, males should attempt to maximise the number of females they breed with by being attractive to females and/or outcompeting other males, rather than investing in parental care.

Emlen and Oring (1977) carried out an excellent review on the evolution of mating systems. They define the concept of the OSR and its relation with sexual selection. They note the feedback between patterns of parental care and the mating system

(e.g. clear mutual mate choice is normally associated with biparental care). In addition, they note that parental care in the form of egg incubation among birds will affect the OSR (the more males care, the less male biased the OSR is). Kokko and Jennions (2008) argue that if males desert then it is difficult for them to find a partner (since the OSR is male biased). It follows that if the level of male desertion increases, paternal care may well become a relatively more successful strategy, i.e. parental care is subject to frequency dependent selection.

Dawkins and Carlisle (1976) argue that Trivers' argument is a type of "Concorde fallacy", i.e. if one has invested heavily in a project, then one should continue even if losses are expected. The decision of a female on whether to care for her present brood should, in evolutionary terms, be based on a comparison of her future gains from care with the gains she could achieve by following another strategy. Maynard Smith (1977) defends Trivers' approach to some degree by stating that in calculating the expected number of future offspring one needs to take into account the investment that has to be made. In this paper Maynard Smith describes three models of parental care. The first two are matrix games in which deserting males find another partner with probability p . He recognized that this probability depends on the behaviour of the population as a whole, i.e. treating p as fixed is a weak point of the model. The third model is more realistic, since it takes into account the Fisher condition that the total number of offspring of males equals the total number of

* Tel.: +353 61 234225; fax: +353 61 334927.

E-mail address: david.ramsey@ul.ie

offspring of females (see Houston and McNamara, 2002, 2005; Kokko and Jennions, 2003). This third model is a so-called “time in/time out” model in which individuals spend part of the time breeding and caring for their young and part of their time searching for a partner (between breeding attempts). The cycle time of an individual is the mean time he/she spends between breeding attempts. If the adult sex ratio is r , then the mean cycle time of males must be r times the mean cycle time of females. It is assumed that individuals maximise the rate of producing offspring that survive to adulthood. Grafen and Sibly (1978) develop this approach. However, these models assume that there is a pure equilibrium and so do not enable investigating the possibility of stable polymorphisms or mixed strategies. One other problem lies in the assumption that members of the least common sex in the mating pool immediately find a mate. As Székely et al. (2000) argue, the problems of mate choice and parental care are strongly interlinked and such time in/time out models cannot be adapted in a simple way to take such feedback into account. Using Maynard Smith’s approach the OSR is undefined, since members of one of the sexes do not spend any time in the mating pool.

Clutton-Brock and Parker (1992) consider a similar time in/time out model to derive the OSR given the adult sex ratio, patterns of parental investment (including both gamete production and parental care). They include a parameter describing the level of interaction between the sexes in a population, which in turn defines the mean time individuals spend looking for a partner. However, they assume that the amount of parental care given is fixed, since their goal is to derive the OSR and in this way predict which of the sexes will compete most strongly for mates (assumed to be the most common sex in the pool of searchers). As such, this model does not give us any insight into why a particular pattern of parental care evolves. As well as giving an excellent review of the development of research on patterns of mate choice and parental care, Kokko and Jennions (2008) extend this model by allowing the level of parental care given to evolve. Offspring survival is increasing in the level of care from a parent given the level of care from the other parent. At the time of fertilisation, parents simultaneously choose the amount of time for which they will care from a continuous range. The minimum time females can choose is assumed to be larger than the minimum time a male can choose to reflect the fact that males can replenish their gametes more quickly than females. Sexual selection is incorporated into the model by assuming that only a fraction of the members of a particular sex mate. Due to the complexity of the model, they assume that the level of sexual selection is fixed, although they admit that in reality it would evolve along with the parental care strategies.

The model of Yamamura and Tsuji (1993) is in many ways the most similar to the one presented here. Just as in Maynard Smith (1977) and Grafen and Sibly (1978) they assume that the members of the less common sex in the mating pool immediately find a mate. It is assumed that parents can only make one of two possible decisions: care or desert. Their model was adapted to the life cycle of the St. Peter’s Fish, *Sarotherodon galilaeus* by Balshine-Earn and Earn (1997).

As in Yamamura and Tsuji, in the model presented here individuals can make only one of two possible decisions. This is done partly for simplicity, but mainly for clarity in classifying the types of evolutionarily stable strategies (ESS) found and to illustrate the differences between a stable polymorphism and a mixed ESS within the framework of a large population game. The model can be relatively easily adapted to allow individuals to choose the level of parental care they give from some range. As in Kokko and Jennions (2008), members of the less common sex in the mating pool find mates at a faster rate than members of the more common sex in such a way that ensures each female mating

corresponds to a male mating. Hence, the ASR is fixed, but the present OSR is derived as a resultant of the ASR and the observed pattern of parental care, rather than being given as an exogenous parameter. In this way, the OSR and the pattern of parental-care co-evolve as argued in Jennions and Kokko (2010). The rate at which mates are found depends on an exogenously defined underlying interaction rate, λ_1 . This parameter can be thought of as a measure of the density and mobility of the population. As Kokko and Rankin (2006) argue, density effects may be very important in the evolution of behaviour. By defining λ_1 and the rate of transition of females from the non-receptive state to the receptive state to be arbitrarily large, we essentially obtain the model of Yamamura and Tsuji (1993). The model can be adapted to take into account the particular nature of physiological processes involved in reproduction (the assumption used here that females can be receptive or non-receptive is used to model oestrus cycles in mammals). It should be noted that these processes are assumed to be given (i.e. the model cannot explain why these processes evolved in the first place).

Székely et al. (2000) argue that there is strong feedback between patterns of mate choice and patterns of parental care. Owens and Thompson (1994), Kokko and Johnstone (2002) and Härdling and Kokko (2005) use a similar approach to the one used here to investigate the relationships between sexual selection, patterns of mate choice and the sex ratios. Jennions and Kokko (2010) give a clear exposition of the nature of feedback between various factors in the reproductive cycle and the interaction between mate choice and parental care.

One major advantage of the approach used here (in comparison to the one used by Yamamura and Tsuji) is that the model can be directly extended to incorporate the evolution of mate choice, which is a goal of future research. The expected length of time that an individual spends in the mating pool and type of mate obtained would depend on his/her choosiness and his/her attractiveness as a mate. The model can also be adapted to take into account differing mortality rates according to the sex and state of an individual (see Ramsey, 2009b, also Kokko and Jennions, 2008). Also, the analytical results obtained regarding polymorphisms and mixed ESSes are an advance on the numerical results obtained by Yamamura and Tsuji and give some insight into intraspecific variation in patterns of parental care.

All the models described above assume that breeding is non-seasonal and the population size is large. In such a case, at equilibrium the OSR will be constant over time. In the case of seasonal breeders, the strategies used by individuals will change over the breeding season and this is associated with temporal fluctuations in the OSR (see Webb et al., 1999; McNamara et al., 2000).

As argued above, the evolution of mating systems depends on many interacting factors. Verbal explanations of such evolution cannot realistically take these interactions into account. The continued development of mathematical models that take such interactions into account will prove useful in explaining observed behaviour and predicting the long term reaction of mating systems to changes in the environment.

Section 2 presents the model and the derivation of so-called pure equilibrium profiles in which all the members of a particular sex always use the same action. Four pure equilibrium profiles are possible: no parental care, maternal care, paternal care and biparental care. Since there may be intraspecific variation in the level of parental care and/or female care (see e.g. Booth and Dabbs, 1993), Section 3 considers stable polymorphisms and mixed equilibrium profiles. At a stable polymorphism, each individual always uses the same action, but variations in behaviour are observed within a particular sex. At a mixed equilibrium, the variation in behaviour results from individuals

choosing the action to be used in each breeding attempt at random. Section 4 considers an example and derives the set of pure equilibrium profiles according to the gains from parental care. Section 5 investigates the relationship between some of the physiological and demographic parameters and the set of pure equilibrium profiles. This is used to investigate how the patterns of parental care we expect to see depend on these parameters. Section 6 gives examples of stable polymorphisms and considers the relation between stable polymorphisms and mixed equilibria. These results are used to investigate the conditions under which we might expect variable care patterns within one sex of a particular species and whether one of the sexes is more likely to exhibit such patterns. Section 7 includes a discussion of the results and directions for future research.

2. The model

A basic formulation of this model can be found in Ramsey (2009a). Consider a large population in which there is no variation in the quality of mates and individuals only decide whether to care for their young or desert. The model can be adapted to allow individuals to choose the level of care they give from a continuous interval. However, allowing only two discrete actions will enable us to highlight how the range of possible ESSes in large population games with two types of player can fundamentally differ from the ESSes in asymmetric 2-player versions of such a game.

It is assumed that there is no breeding season. Males may be in one of two states: searching or breeding. Females may be in one of three states: receptive, non-receptive or breeding. These assumptions reflect the reproductive cycle of most mammals, where females have oestrus cycles (see Bronson, 1989). However, this model can be adapted to other reproductive cycles. For example, female rabbits come into oestrus after having sex. In this case, the model may be simplified so that females are in one of two states: searching or breeding. The general approach to such a problem would be the same. Within the class of time in/time out models, the adaptability of this model to the physiological processes observed in a species seems to be novel.

For simplicity, it is assumed that when individuals are in the breeding state that they do not attempt to (or cannot) breed with other partners. The ratio of the number of males to the number of females (the ASR) is denoted as r . Denote the proportions of males in the two male 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 as q_1 , q_2 and q_3 , respectively.

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 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 $\lambda_1 p_1 r$. It should be noted that these assumptions satisfy the condition that a male entering the breeding state corresponds to a female going into the breeding state. Also, it is assumed that the population is freely mixing.

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 . Hence, 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.

The rate at which breeding males rejoin the pool of searching males and females return to the pool of receptive females depends on whether they care for their young or not. If they do not care for their young, males return to the pool of searching males at rate λ_2^D ,

that is to say that on average the mating process and time to replenish sperm supplies together occupy on average $1/\lambda_2^D$ units of time. Similarly, if females do not care for their young they return to the pool of receptive females at rate μ_3^D . It is assumed that λ_2^D is larger than μ_3^D , i.e. male deserters can return to searching for a new mate 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 λ_2^C and μ_3^C , respectively. It is assumed that $\lambda_2^C \approx \mu_3^C$. The transition between states is illustrated in Fig. 1. A summary of the notation used is given in Tables 1–3.

The number of young surviving to maturity per brood 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 $1 < k_f < k_b$ and $1 < k_m < k_b$, i.e. the greater the number of caring parents, the greater the average number of surviving offspring per brood. See Gubernick and Teferi (2000) and Wright (2006) for examples of parental care increasing offspring survival. It is assumed that the goal of each individual is to maximise the rate of producing offspring that survive until maturity. For simplicity this is referred to as the reproduction rate.

For other game theoretic models of large population games with state transitions see Broom and Ruxton (1998) and Eriksson et al. (2004).

2.1. Derivation of pure evolutionarily stable strategies

In order to investigate the pure ESSes of such a system, it is necessary to first derive the “steady-state” proportions of individuals in each state given the strategy profile used in the population. The strategy profile is defined by a description of both the strategies used by the males and the strategies used by the females. In this section, it is assumed that all individuals of a particular sex use the same strategy. It should be stressed that the term “steady-state” will only be used to describe the values q_1 , q_2 , q_3 , p_1 and p_2 would tend to, given that the strategy profile used by the population does not change over time. One important aspect to note is the feedback between selection and the frequencies of individuals in each state. Selection will change the proportions of males and females who care for their offspring, which in turn will change these steady-state proportions.

At the steady-state proportions the number of individuals moving from state A to state B per unit time must equal to the number of individuals moving from state B to state A. 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 females who are receptive times the rate of transition from being receptive to being non-receptive, i.e. $q_1 \mu_1$. This rate will be called the population rate of transition from

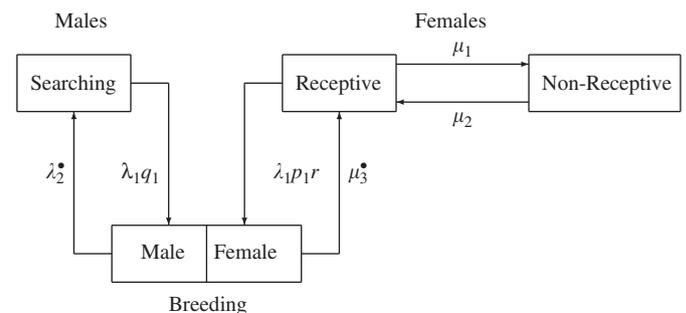


Fig. 1. Transition rates between states. • represents C or D according to whether a given sex cares for their offspring or not.

Table 1
Glossary of the notation used (ratios).

r	Adult sex ratio	k_m	Relative no. of offspring with male care
k_f	Relative no. of offspring with female care	k_b	Relative no. of offspring with biparental care

Table 2
Glossary of the notation used (proportions).

p_1	Prop. of all males searching	$p_{1,C}$	Prop. of caring males searching
$p_{1,D}$	Prop. of deserting males searching	p_2	Prop. of all males breeding
$p_{2,C}$	Prop. of caring males breeding	$p_{2,D}$	Prop. of deserting males breeding
q_1	Prop. of all females who are receptive	$q_{1,C}$	Prop. of caring females who are receptive
$q_{1,D}$	Prop. of deserting females who are receptive	q_2	Prop. of all females who are non-receptive
$q_{2,C}$	Prop. of caring females who are non-receptive	$q_{2,D}$	Prop. of deserting females who are non-receptive
q_3	Prop. of all females breeding	$q_{3,C}$	Prop. of caring females breeding
$q_{3,D}$	Prop. of deserting females breeding	s_m	Prop. of males who care
s_f	Prop. of females who care		

Table 3
Glossary of the notation used (rates).

μ_1	Rate at which females become non-receptive	μ_2	Females become receptive
λ_2^D	Deserting males return to searching	λ_2^C	Caring males return to searching
μ_3^D	Deserting females return to searching	μ_3^C	Caring females return to searching
λ_1	Interaction rate		

receptive to non-receptive. In general, a population transition rate from state *A* to state *B* is obtained by multiplying the proportion of individuals in state *A* by the rate at which an individual in state *A* moves to state *B*. Thus the population rate of females becoming receptive per unit time is $q_2\mu_2$. Hence, at the steady-state proportions

$$q_1\mu_1 = q_2\mu_2. \tag{1}$$

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

$$\lambda_1 p_1 q_1 r = \mu_3^* q_3, \tag{2}$$

$$\lambda_1 p_1 q_1 = \lambda_2^* (1 - p_1), \tag{3}$$

where each \bullet corresponds to *D* or *C* according to the strategy adopted by the appropriate sex. In addition,

$$q_1 + q_2 + q_3 = 1. \tag{4}$$

Rearranging Eqs. (1)–(4), it follows that $aq_1^2 + bq_1 + c = 0$, where

$$a = \mu_3^* \lambda_1 [\mu_1 + \mu_2],$$

$$b = \lambda_2^* \mu_2 \lambda_1 r + \lambda_2 \mu_3^* (\mu_1 + \mu_2) - \lambda_1 \mu_2 \mu_3^*,$$

$$c = -\mu_2 \mu_3^* \lambda_2^*.$$

The unique solution to this equation between 0 and 1 is

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

The remaining equilibrium proportions may be calculated from the following relations:

$$q_2 = \frac{\mu_1 q_1}{\mu_2}, \quad q_3 = 1 - q_1 - q_2, \quad p_1 = \frac{\mu_3^* q_3}{\lambda_1 q_1}.$$

Since these steady-state proportions depend on the strategy profiles adopted, the strategy profile will be denoted using superscripts indicating firstly the strategy used by males and secondly the strategy used by females. For example, p_1^{CD} denotes the equilibrium proportion of males searching when males care for their offspring, but females do not.

First, consider the conditions for no parental care to be an ESS. To find the equilibrium frequencies when neither sex cares for offspring, set $\mu_3^* = \mu_3^D$ and $\lambda_2^* = \lambda_2^D$ in Eqs. (2)–(3).

From the Fisher condition, the average reproduction rate of females must be r times the average reproduction rate of males. There are two ways of calculating the reproduction rate of males. Firstly, it can be calculated as the relative number of offspring surviving from a breeding attempt 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^{DD} . It follows that

$$T^{DD} = \frac{1}{\lambda_1 q_1^{DD}} + \frac{1}{\lambda_2^D} = \frac{\lambda_2^D + \lambda_1 q_1^{DD}}{\lambda_2^D \lambda_1 q_1^{DD}}.$$

Since the relative number of offspring surviving per breeding attempt is 1, the mean reproduction rate of males is given by R^{DD} , where

$$R^{DD} = \frac{1}{T^{DD}} = \frac{\lambda_2^D \lambda_1 q_1^{DD}}{\lambda_2^D + \lambda_1 q_1^{DD}}. \tag{5}$$

The second way of calculating the reproduction rate of males is by noting that it must be the population rate of males entering the breeding state multiplied by the relative number of surviving offspring per breeding attempt. Hence, the mean reproduction rate of males is given by

$$R^{DD} = \lambda_1 q_1^{DD} p_1^{DD}. \tag{6}$$

Note that from Eq. (3),

$$p_1^{DD} = \frac{\lambda_2^D}{\lambda_2^D + \lambda_1 q_1^{DD}}.$$

Hence, Eqs. (5) and (6) are equivalent.

In order for no parental care to be an ESS, this rate must be greater than the reproduction rate of a male mutant who cares for his offspring. Since this is a large population game, such a mutant does not affect the steady-state frequencies or the reproduction rate of the population as a whole. The reproduction rates of mutants are calculated by considering their average cycle time.

The expected cycle time of a male mutant who cares for his offspring when the rest of the population desert, denoted as T_m^{DD} , is

$$T_m^{DD} = \frac{1}{\lambda_1 q_1^{DD}} + \frac{1}{\lambda_2^C} = \frac{\lambda_2^C + \lambda_1 q_1^{DD}}{\lambda_2^C \lambda_1 q_1^{DD}}.$$

Since the relative number of surviving offspring of such a male per brood is k_m , it follows that a male mutant cannot invade if

$$\lambda_1 p_1^{DD} q_1^{DD} > \frac{k_m \lambda_2^C \lambda_1 q_1^{DD}}{\lambda_2^C + \lambda_1 q_1^{DD}}. \tag{7}$$

The mean cycle time of 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 and the rate at which the state of any responsive female changes by T_f^{DD} and μ_R^{DD} , respectively. It follows that $\mu_R^{DD} = \lambda_1 p_1^{DD} r + \mu_1$. The mean length of time to the first change of state is $1/\mu_R^{DD}$. The probability that she finds a mate before becoming non-receptive is $\lambda_1 p_1^{DD} r / \mu_R^{DD}$. Given she first finds a mate, then the mean time for such a mutant female 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^{DD} , as she has simply returned to her starting point. Hence, conditioning on the type of the first change of state,

$$T_f^{DD} = \frac{1}{\mu_R^{DD}} + \frac{\lambda_1 p_1^{DD} r}{\mu_R^{DD} \mu_3^C} + \frac{\mu_1}{\mu_R^{DD}} \left[\frac{1}{\mu_2} + T_f^{DD} \right].$$

This equation leads to

$$T_f^{DD} = \frac{\mu_2 \mu_3^C + \mu_2 \lambda_1 p_1^{DD} r + \mu_1 \mu_3^C}{\mu_3^C \mu_2 \lambda_1 p_1^{DD} r}.$$

It follows that a female mutant cannot invade the population if

$$\lambda_1 q_1^{DD} p_1^{DD} r > \frac{k_f \mu_3^C \mu_2 \lambda_1 p_1^{DD} r}{\mu_2 \mu_3^C + \mu_2 \lambda_1 p_1^{DD} r + \mu_1 \mu_3^C}. \tag{8}$$

It should be noted that the OSR at such an equilibrium, denoted as S^{DD} , is given by

$$S^{DD} = \frac{r p_1^{DD}}{q_1^{DD}}.$$

The OSR at other equilibria can be calculated in an analogous way.

The derivation of the stability conditions for the remaining three possible pure equilibria is analogous. Therefore, just the equilibrium conditions are presented. In each case the left hand side of the inequality is the reproduction rate of males (which according to the Fisher condition must be the reproduction rate of the females divided by the ASR), 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 divided by the ASR.

To find the equilibrium frequencies when only males care for offspring, set $\mu_3^* = \mu_3^D$ and $\lambda_2^* = \lambda_2^C$ in Eqs. (1)–(4). Only male parental care is an ESS if

$$k_m \lambda_1 q_1^{CD} p_1^{CD} > \max \left\{ \frac{\lambda_1 q_1^{CD} \lambda_2^D}{\lambda_2^D + \lambda_1 q_1^{CD}}, \frac{k_b \mu_3^D \mu_2 \lambda_1 p_1^{CD}}{\mu_2 \mu_3^D + \mu_2 \lambda_1 p_1^{CD} r + \mu_1 \mu_3^D} \right\}. \tag{9}$$

To find the equilibrium frequencies when only females care for offspring, set $\mu_3^* = \mu_3^C$ and $\lambda_2^* = \lambda_2^D$ in Eqs. (1)–(4). Only female parental care is an ESS if

$$k_f \lambda_1 q_1^{DC} p_1^{DC} > \max \left\{ \frac{k_b \lambda_1 \lambda_2^C q_1^{DC}}{\lambda_2^C + \lambda_1 q_1^{DC}}, \frac{\mu_3^D \mu_2 \lambda_1 p_1^{DC}}{\mu_2 \mu_3^D + \mu_2 \lambda_1 p_1^{DC} r + \mu_1 \mu_3^D} \right\}. \tag{10}$$

To find the equilibrium frequencies when both parents care for offspring, set $\mu_3^* = \mu_3^C$ and $\lambda_2^* = \lambda_2^C$ in Eqs. (1)–(4). Parental care by

both sexes is an ESS if

$$k_b \lambda_1 q_1^{CC} p_1^{CC} > \max \left\{ \frac{k_f \lambda_1 \lambda_2^D q_1^{CC}}{\lambda_2^D + \lambda_1 q_1^{CC}}, \frac{k_m \mu_3^D \mu_2 \lambda_1 p_1^{CC}}{\mu_2 \mu_3^D + \mu_2 \lambda_1 p_1^{CC} r + \mu_1 \mu_3^D} \right\}. \tag{11}$$

3. Stable polymorphisms and mixed evolutionarily stable strategies

Such equilibria may well be of interest with regard to variation in patterns of maternal or paternal care within a single species. [Hammock and Young \(2005\)](#) report that the length of the *avpr1a* microsatellite is associated with the patterns of paternal care in prairie voles, but not with patterns of maternal care. According to [Booth and Dabbs \(1993\)](#), human males with higher levels of testosterone are less likely to marry and when married are more likely to divorce. The results obtained in this section may be helpful in explaining which sex is more likely to show such variable patterns and under what circumstances such variation might be observed, even when there is no observable difference between individuals of a particular sex.

One important question in evolutionary game theory relates to whether a mixed ESS (at which each individual uses the appropriate randomized strategy) corresponds to a stable polymorphism (at which each individual uses a pure strategy) such that the proportion of individuals using a given action at the polymorphism equals the probability of that action being used at the mixed ESS. See [Maynard Smith \(1982\)](#) for an overview of this question. For the model considered, if there is a stable polymorphism, the probability of using a particular action at the mixed ESS will differ from the proportion of individuals using that action at the stable polymorphism. This occurs for the following reason: Suppose all males use the same mixed strategy “care with probability p , otherwise desert”. The probability that a searcher will care is clearly p . Now suppose a proportion p of males care. Since carers spend a greater proportion of time in the breeding state, the probability that a male in the searching state is a carer will be less than p . Hence, the expected number of surviving offspring of a female from mating differs in the two considered scenarios. For further illustration of this issue, see [Ramsey \(2009a\)](#).

The following types of polymorphisms and mixed ESSes are among the possible equilibria:

- (1) *A complete polymorphism*: In both sexes, a certain proportion of individuals always care, while the remainder always desert. An individual's reproduction rate is independent of the strategy used.
- (2) *A male polymorphism*: At such an equilibrium all females use the same pure strategy. A mutant female using the other pure strategy will obtain a lower reward. Some males always care and the remainder always desert. A male's reproduction rate is independent of the strategy used.
- (3) *A female polymorphism*: As above, but females, rather than males, show variation in observed behaviour.
- (4) *A completely mixed ESS*: At such an equilibrium all individuals follow the mixed strategy appropriate to their sex.
- (5) *A male mixed ESS*: At such an equilibrium all females use the same pure strategy. All males use the same mixed strategy.
- (6) *A female mixed ESS*: As above, but females, rather than males, use a mixed strategy.

The following criterion for the stability of a polymorphism is also required: Suppose at a polymorphism a proportion s of the members of one sex cares, $0 < s < 1$. If this proportion rises above s (falls below s), then selection must favour deserting

(favour caring, respectively). This condition ensures that if the frequency of carers is slightly different from the equilibrium frequency s , then selection acts in such a way that this proportion tends towards s . An analogous condition, where s is interpreted as the probability of caring, is required for the stability of a mixed ESS.

It is possible that a population could be at equilibrium in a multitude of ways. For example, all males could follow the same randomized strategy, while some females always care while the other females always desert. It is also possible that in both sexes some individuals follow pure strategies while others follow mixed strategies. The focus in this paper will be on single sex polymorphisms. One type of single sex mixed ESS will be derived for comparative purposes. To keep the paper of reasonable length, other types of equilibria are not considered here.

3.1. Stable male polymorphisms with female carers

The equilibrium proportions at such a polymorphism will be denoted using the superscript PC . Suppose there exists a stable polymorphism in which females always care and a proportion s_m^{PC} of males care. Define $p_{1,C}^{PC}$ and $p_{1,D}^{PC}$ to be the proportion of male carers and deserters who are searching, respectively. At equilibrium, the population rate at which male carers move from the searching state must equal the rate at which they move in the opposite direction. Hence,

$$\lambda_2^C(1-p_{1,C}^{PC}) = \lambda_1 q_1^{PC} p_{1,C}^{PC} \tag{12}$$

Similarly, considering the male deserters,

$$\lambda_2^D(1-p_{1,D}^{PC}) = \lambda_1 q_1^{PC} p_{1,D}^{PC} \tag{13}$$

As before,

$$\mu_1 q_1^{PC} = \mu_2 q_2^{PC} \tag{14}$$

$$q_1^{PC} + q_2^{PC} + q_3^{PC} = 1. \tag{15}$$

The rate at which male carers find mates is $\lambda_1 p_{1,C}^{PC} q_1^{PC}$ and the relative number of surviving offspring from such matings is k_b . Hence, the reproduction rate of male carers is $k_b \lambda_1 p_{1,C}^{PC} q_1^{PC}$. Similarly, the reproduction rate of male deserters is $k_f \lambda_1 p_{1,D}^{PC} q_1^{PC}$. At such an equilibrium the reproduction rates of male deserters and male carers must be equal. Hence,

$$k_b p_{1,C}^{PC} = k_f p_{1,D}^{PC} \tag{16}$$

Solving Eqs. (12)–(16),

$$q_1^{PC} = \frac{\lambda_2^D \lambda_2^C (k_b - k_f)}{\lambda_1 (\lambda_2^D k_f - \lambda_2^C k_b)},$$

$$q_2^{PC} = \frac{\mu_1 \lambda_2^D \lambda_2^C (k_b - k_f)}{\mu_2 \lambda_1 (\lambda_2^D k_f - \lambda_2^C k_b)},$$

$$q_3^{PC} = 1 - \frac{\lambda_2^D \lambda_2^C (k_b - k_f) (\mu_1 + \mu_2)}{\mu_2 \lambda_1 (\lambda_2^D k_f - \lambda_2^C k_b)},$$

$$p_{1,C}^{PC} = \frac{\lambda_2^D k_f - \lambda_2^C k_b}{k_b (\lambda_2^D - \lambda_2^C)},$$

$$p_{1,D}^{PC} = \frac{\lambda_2^D k_f - \lambda_2^C k_b}{k_f (\lambda_2^D - \lambda_2^C)}.$$

The total proportion of males searching is p_1^{PC} , where

$$p_1^{PC} = s_m^{PC} p_{1,C}^{PC} + (1 - s_m^{PC}) p_{1,D}^{PC}.$$

Considering the population rate of transition of females between the breeding and receptive states,

$$\lambda_1 q_1^{PC} r [s_m^{PC} p_{1,C}^{PC} + (1 - s_m^{PC}) p_{1,D}^{PC}] = \mu_3^C q_3^{PC}.$$

Together with Eq. (16), this leads to

$$s_m^{PC} = \frac{k_b}{k_b - k_f} \left[1 - \frac{\mu_3^C q_3^{PC}}{\lambda_1 q_1^{PC} p_{1,D}^{PC} r} \right].$$

For such a stable polymorphism to exist, the following conditions must be satisfied: $0 < q_i^{PC} < 1$, $i=1,2,3$, $0 < p_{1,\bullet}^{PC} < 1$, $\bullet \in \{N,C\}$ and $0 < s_m^{PC} < 1$. These conditions lead to

$$\frac{k_b}{k_f} < \frac{\lambda_2^D [\lambda_1 \mu_2 + \lambda_2^C (\mu_1 + \mu_2)]}{\lambda_2^C [\lambda_1 \mu_2 + \lambda_2^D (\mu_1 + \mu_2)]}, \tag{17}$$

$$\frac{k_f}{k_b} < \frac{\mu_3^C q_3^{PC}}{\lambda_1 q_1^{PC} p_{1,C}^{PC} r} < 1. \tag{18}$$

In addition, a female carer must have a higher reproduction rate than a mutant female deserter. The mean reproduction rate of a female carer is r times the mean reproduction rate of a male, i.e. $k_b \lambda_1 p_{1,C}^{PC} q_1^{PC} r$. Arguing as in the case of a pure ESS, the mean cycle length of a mutant female deserter is

$$T_f^{PC} = \frac{\mu_2 \mu_3^D + \mu_2 \lambda_1 p_{1,C}^{PC} r + \mu_1 \mu_3^D}{\mu_3^D \mu_2 \lambda_1 p_{1,C}^{PC} r}.$$

The probability that a female mates a male carer is given by $\frac{s_m^{PC} p_{1,C}^{PC} / p_1^{PC}}$. It follows that the following is a necessary condition for such a stable polymorphism:

$$k_b \lambda_1 p_{1,C}^{PC} q_1^{PC} > \frac{\mu_3^D \mu_2 \lambda_1 [k_m s_m^{PC} p_{1,C}^{PC} + (1 - s_m^{PC}) p_{1,D}^{PC}]}{\mu_2 \mu_3^D + \mu_2 \lambda_1 p_{1,C}^{PC} r + \mu_1 \mu_3^D}. \tag{19}$$

As stated earlier, selection must act in such a way that the proportion of males caring tends towards s_m^{PC} . Consider a population in which all females care and a proportion s_m of males care. As s_m increases, intuitively the proportion of males searching for a mate decreases. It follows that females take longer to find a mate and hence the proportion of females searching for a mate is increasing in s_m . The ratio of the reproductive rate of a male carer to the reproductive rate of a male deserter is given by

$$\frac{k_b \lambda_2^C (\lambda_2^D + \lambda_1 q_1)}{k_f \lambda_2^D (\lambda_2^C + \lambda_1 q_1)}.$$

Since k_b, k_m, λ_2^D and λ_2^C are fixed, this ratio is determined by the ratio between $\lambda_2^D + \lambda_1 q_1$ and $\lambda_2^C + \lambda_1 q_1$. Since $\lambda_2^D > \lambda_2^C$, this ratio is decreasing in q_1 . Hence, as the proportion of male carers increases, selection increasingly favours male deserters. It follows that there can be at most one such stable polymorphism and the conditions given by Inequalities (17), (18) and (19) are sufficient.

The derivations of the form of the remaining types of single sex stable polymorphism are analogous. They are given in the appendix for completeness. It should be noted that, apart from the specific case $k_f = k_m = \sqrt{k_b}$, the set of equations defining a stable complete polymorphism are difficult to solve analytically and only numeric solutions have been found. Due to the lack of space, complete polymorphisms are omitted.

3.2. A male mixed ESS with female carers

Now suppose that a male mixed ESS exists in which all the females care and all the males play the same mixed strategy: care with probability s_m^{MC} and desert with probability $1 - s_m^{MC}$. Analogously, the steady-state proportions are denoted using the superscript MC . The expected length of time a male spends in

the breeding state is $1/\lambda_2^M$, where

$$\frac{1}{\lambda_2^M} = \frac{s_m^{MC}}{\lambda_2^C} + \frac{1-s_m^{MC}}{\lambda_2^D}$$

It follows that the rate at which males go from the breeding state to the searching state is

$$\lambda_2^M = \frac{\lambda_2^C \lambda_2^D}{s_m^{MC} \lambda_2^D + (1-s_m^{MC}) \lambda_2^C}$$

Hence, the equations for the steady-state proportions are

$$q_1^{MC} \mu_1 = q_2^{MC} \mu_2, \tag{20}$$

$$\lambda_1 p_1^{MC} r q_1^{MC} = \mu_3^C q_3^{MC}, \tag{21}$$

$$q_1^{MC} + q_2^{MC} + q_3^{MC} = 1, \tag{22}$$

$$\lambda_1 q_1^{MC} p_1^{MC} = \frac{\lambda_2^C \lambda_2^D (1-p_1^{MC})}{s_m^{MC} \lambda_2^D + (1-s_m^{MC}) \lambda_2^C}. \tag{23}$$

At such an ESS, the reproduction rate of a male is independent of his strategy. In particular, the reproduction rate of a male mutant who always cares must be equal to the reproduction rate of a male mutant who always deserts. The expected cycle length of a mutant male carer and a mutant male deserter are given by T_C^{MC} and T_D^{MC} , where

$$T_C^{MC} = \frac{1}{\lambda_1 q_1^{MC}} + \frac{1}{\lambda_2^C} = \frac{\lambda_2^C + \lambda_1 q_1^{MC}}{\lambda_1 q_1^{MC} \lambda_2^C},$$

$$T_D^{MC} = \frac{1}{\lambda_1 q_1^{MC}} + \frac{1}{\lambda_2^D} = \frac{\lambda_2^D + \lambda_1 q_1^{MC}}{\lambda_1 q_1^{MC} \lambda_2^D}.$$

Equating the reproduction rates of such mutants,

$$\frac{k_b}{T_C^{MC}} = \frac{k_f}{T_D^{MC}} \Rightarrow \frac{k_b \lambda_2^C}{\lambda_2^C + \lambda_1 q_1^{MC}} = \frac{k_f \lambda_2^D}{\lambda_2^D + \lambda_1 q_1^{MC}}.$$

It follows that

$$q_1^{MC} = \frac{\lambda_2^C \lambda_2^D (k_b - k_f)}{\lambda_1 (\lambda_2^D k_f - k_b \lambda_2^C)}.$$

Hence, $q_1^{MC} = q_1^{PC}$. From Eqs. (20) and (22), it can be seen that the proportion of females in each of the three states at this mixed equilibrium must be the same as at the stable male polymorphism where females care. From Eq. (21), it follows that the proportion of males in the searching state at the mixed equilibrium must equal the proportion of all males searching at the corresponding male polymorphism. It follows that

$$p_1^{MC} = \frac{\mu_3^C (\lambda_2^D k_f - \lambda_2^C k_b)}{\lambda_2^D \lambda_2^C r (k_b - k_f)} - \frac{\mu_3^C (\mu_1 + \mu_2)}{\mu_2 \lambda_1 r}.$$

From Eq. (23),

$$s_m^{MC} = \frac{\lambda_2^C \lambda_2^D (1-p_1^{MC})}{\lambda_1 q_1^{MC} p_1^{MC} (\lambda_2^D - \lambda_2^C)} - \frac{\lambda_2^C}{\lambda_2^D - \lambda_2^C}.$$

At such an equilibrium, the reproduction rate of female carers must be greater than the reproduction rate of a mutant female deserter. The expected number of surviving offspring of a caring female per breeding attempt is $s_m^{MC} k_b + (1-s_m^{MC}) k_f$. Hence, considering the expected cycle length of a mutant female deserter,

$$[s_m^{MC} k_b + (1-s_m^{MC}) k_f] \lambda_1 p_1^{MC} q_1^{MC} > \frac{\mu_3^D \mu_2 \lambda_1 [k_m s_m^{MC} + (1-s_m^{MC})] p_1^{MC}}{\mu_2 \mu_3^D + \mu_2 \lambda_1 p_1^{MC} r + \mu_1 \mu_3^D}.$$

4. Numerical results—pure evolutionarily stable strategy profiles

Suppose $\mu_1 = \mu_2 = 1$, $\mu_3^D = 0.2$, $\lambda_2^D = 5$, $\lambda_2^C = \mu_3^C = 0.05$, $\lambda_1 = 20$, $r = 1$. These parameters reflect the natural constraint that a deserting male can return to the pool of searchers more quickly than a deserting female. For example, males of the cichlid fish species *Aequidens portalegrensis* can spawn daily, whereas females can only spawn once every five days (see Polder, 1970). The relative difference between these rates is generally much more pronounced in mammal species (see Bronson, 1989). The adult sex ratio is 1.

First consider how the set of pure ESS profiles depend on the gains from uniparental and biparental care, i.e. on k_f , k_m and k_b . The procedure is to first find the steady-state proportions for a given strategy profile and then check the equilibrium conditions [see Conditions (7)–(11)]. These calculations give

1. No parental care is an ESS profile when $k_m < 4.8793$, $k_f < 3.9388$.
2. Just female parental care is an ESS profile when $k_f > 3.9406$, $k_b/k_f < 1.9850$.
3. Just male parental care is an ESS profile when $k_m > 60.4523$, $k_b/k_m < 1.7450$.
4. Biparental care is an ESS profile $k_b/k_m > 3.3202$, $k_b/k_f > 12.8912$.

Assume now that males are equally good at caring as females, i.e. $k_m = k_f$. Fig. 2 illustrates the set of pure ESS profiles (an approximate log scale is used). The benefits of uniparental care increase from left to right. Along the diagonal there are no benefits from biparental care compared to uniparental care. The gains from biparental care increase in the vertical direction.

The results obtained are qualitatively similar to those obtained by Balshine-Earn and Earn (1997). Just male care is an ESS profile only when the gains from uniparental care are very large and the gains from biparental care relatively small. However, in such cases just female care is also an ESS profile and the results suggest that just female care will have a much larger basin of attraction and so is likely to evolve.

5. Effect of the parameters on the set of pure ESSes

The analysis below is not intended to be exhaustive, but to give an indication of the effect of parameters on stable patterns of

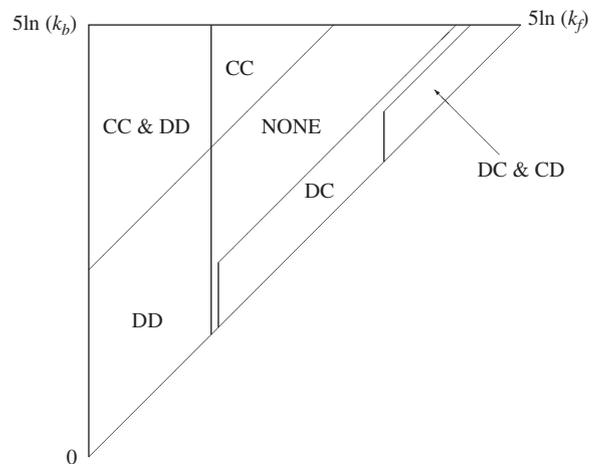


Fig. 2. Set of pure ESSes in the parental care game.

parental care. In general, just one or two parameters are changed at a time, while the remaining parameters take the same values as in the original problem. The results presented here concentrate on factors that are not considered in either Kokko and Jennions (2008) or Yamamura and Tsuji (1993) (e.g. the proportion of time for which females are receptive) or conclusions that seem to deviate from the conclusions they make.

The results indicate that biparental care will only ever be observed if the number of surviving offspring is around twice the number from uniparental care or greater. These results are similar to those obtained by Yamamura and Tsuji, as well as McNamara et al. (2000).

5.1. Effect of the proportion of time for which females are receptive

To observe the effect of the proportion of time for which females are fertile, the values of μ_1 and μ_2 are changed in such a way that the mean time between female's fertile periods (given she does not mate) remains constant (i.e. $1/\mu_1 + 1/\mu_2$ is fixed), but the proportion of time for which female is fertile varies. As μ_1 decreases, the proportion of time for which a female is fertile increases. The results are presented in Table 4. The first line gives the minimum value of k_f for just female care to be an ESS profile. The second line gives the minimum value of k_m for which just male care is an ESS. The third line gives the minimum value of k_b/k_m for which biparental care is an ESS profile (this is the gain from biparental care compared to female care required for males to care in addition to females). In virtually all of the scenarios considered, this ratio determined the situations in which biparental care is evolutionarily stable.

It can be seen from the first row (at least for the values of the other parameters considered) that the proportion of time a female spends fertile has very little effect on her decision to care or desert. The smaller the proportion of time females are fertile, the more likely males are to give care as a second carer. This does not appear to agree with classical theory based on parental investment. It seems logical that as females spend a smaller proportion of time fertile, they invest more in producing eggs. Hence, the relative parental investment of males at the time of fertilisation falls and so males should be less likely to care. However, this argument ignores the fact that such increased female parental investment makes the OSR more male biased. Thus it will be harder for males to find mates and so paternal care becomes a relatively better option. Hence, these results seem consistent with the results of Queller (1997) and Kokko and Jennions (2008), who take into account such feedback between patterns of parental care and the OSR.

It should be noted that changing the length of time between female's fertile periods while leaving the proportion of time she remains fertile constant leaves the set of ESS profiles unchanged.

5.2. Effect of the level of anisogamy

To observe the effect of the level of anisogamy, the value of λ_2^D (the rate at which deserting males can return to the pool of

searchers) was changed. As λ_2^D increases the level of anisogamy increases.

The results are presented in Table 5. Decreasing the level of anisogamy increases the likelihood of male care to some degree. However, male care is only expected when females also care. These conclusions are similar to the ones made by Yamamura and Tsuji (1993), but seem to differ from the conclusions of Kokko and Jennions (2008), who conclude that given parental care is just as valuable as maternal care and the ASR is one that males should give a similar level of care to females. One possible explanation for this difference is the type of decision that is made. Yamamura and Tsuji and the model presented here assume that the choice is either to care or not to care, while Kokko and Jennions allow individuals to choose the time for which they care from some range. The lowest level of anisogamy considered here (male deserters return to the pool of searchers about 6 times as quickly as female deserters) is of a similar level to that observed in cichlid fishes (see Polder, 1970). It is not entirely clear what levels of anisogamy were considered by Kokko and Jennions.

5.3. Effect of the interaction rate

The parameter λ_1 can be interpreted as a measure of the interaction rate between members of the opposite sex.

It should be noted that the model assumes that the population is large and free moving, hence it seems natural to assume that the interaction rate should not be small in comparison to the rate at which female deserters return to the pool of searchers. Given this assumption, the interaction rate has very little effect on female behaviour (see Table 6). Males are more likely to care (as a second parent) at low interaction rates. This seems intuitive, since the lower the interaction rate the harder it is to find a partner.

5.4. Effect of the adult sex ratio

The results are presented in Table 7. For large values of r ($r > 1.32$), the gain from biparental care compared to just paternal care, k_b/k_m , determines whether biparental care is stable. Thus, this table also gives the critical value of this ratio.

The gains from care required for maternal care to be stable are almost independent of the adult sex ratio. The results indicate that just paternal care is very unlikely to evolve even when the sex ratio is very biased towards males. For low values of r , the pattern of parental care will be for females to care if the gains from care are large enough and males will care in addition if the gains from biparental care are large enough. The situation for large values of r seems somewhat more complex. If uniparental care evolves, then it seems that females will care. However, there are situations in which males may be more "willing" to be a second parent than females are to care given that males care. In such a situation there will be "conflict" over parental roles and within the framework of the model presented here, we might expect varied patterns of parental care. These results seem to be in line with those of Yamamura and Tsuji (1993), but discordant with the results of Kokko and Jennions (2008), who predict a greater level of balance between the level of care given by males

Table 4
Effect of proportion of time for which females are fertile on pure ESS profiles.

	$\mu_1 = 3, \mu_2 = 0.6$	$\mu_1 = 4/3, \mu_2 = 0.8$	$\mu_1 = \mu_2 = 1$	$\mu_1 = 0.8, \mu_2 = 4/3$	$\mu_1 = 0.6, \mu_2 = 3$
k_f required for DC	3.8283	3.9213	3.9406	3.9523	3.9641
k_m required for CD	34.1426	53.48319	60.4523	65.6048	71.7411
k_b/k_f required for CC	8.0611	11.4155	12.8912	14.1514	15.9338

Proportion of time spent fertile increases from left to right.

Table 5
Effect of length of time out for males on ESS profiles.

	$\lambda_2^D = 20$	$\lambda_2^D = 10$	$\lambda_2^D = 5$	$\lambda_2^D = 2.5$	$\lambda_2^D = 1.25$
k_f required for DC	3.9410	3.9409	3.9406	3.9400	3.9388
k_m required for CD	109.9924	86.3930	60.4523	37.7702	21.5779
k_b/k_f required for CC	14.1675	13.7149	12.8912	11.5088	9.4765

Length of time out increases from left to right.

Table 6
Effect of interaction rate on ESS profiles.

	$\lambda_1 = 80$	$\lambda_1 = 40$	$\lambda_1 = 20$	$\lambda_1 = 10$	$\lambda_1 = 5$
k_f required for DC	3.9849	3.9700	3.9406	3.8835	3.7757
k_m required for CD	85.8639	75.2705	60.4523	43.5343	28.1682
k_b/k_f required for CC	22.5284	17.1591	12.8912	9.5994	7.1196

Table 7
Effect of adult sex ratio on ESS profiles.

	$r=2$	$r=1.5$	$r=1.32$	$r=1$	$r=\frac{2}{3}$	$r=0.5$
k_f required for DC	3.9750	3.9603	3.9549	3.9406	3.9113	3.8824
k_m required for CD	50.7415	56.1156	57.7802	60.4523	62.9026	64.0186
k_b/k_f required for CC	1.9706	2.8867	3.8309	12.8912	41.2752	50.7415
k_b/k_m required for CC	3.9415	3.8867	3.8309	3.3202	1.9717	1.5906

and females. It is likely that this difference results from the types of decision allowed (here either care or desert, but in Kokko and Jennions the time a parent cares for is chosen from some interval).

6. Numerical results—stable single sex polymorphisms

The existence of stable polymorphisms according to the values of k_b and k_f was investigated for the set of problems given by the parameters for the original problem ($\mu_1 = \mu_2 = 1, \mu_3^D = 0.2, \lambda_2^D = 5, \lambda_2^C = \mu_3^C = 0.05, \lambda_1 = 20, r=1$). It was assumed that $k_m = k_f$. The calculations involved are relatively straightforward, but time consuming and so the details are left out.

6.1. A female polymorphism when males desert

The two conditions for a putative stable polymorphism to be valid are given by Inequalities (24) and (25) (see Appendix A), which lead to $3.9388 < k_f < 3.9406$. It should be noted that this corresponds exactly to the range of k_f for which neither no parental care nor just maternal care are ever stable.

Secondly, a male deserter must have a higher reproduction rate than a male carer. This corresponds to Inequality (26), which gives

$$k_b < k_f^2 + \frac{(k_f - 1)^2 [40\,198 - 10\,598k_f + 100k_f^2]}{8150k_f - 100k_f^2 - 30\,550}$$

If k_f is just above 3.9388, then essentially k_b can take any value. As k_f tends to the upper boundary (approx. 3.9406), the maximum value of k_b possible for such a polymorphism tends to $1.9850k_f$.

Comparing these results with the results on pure equilibria (see Fig. 2), it can be seen that the range of values of k_b and k_f for which such a stable polymorphism can exist is given by a narrow strip in the horizontal direction (i.e. a narrow range of k_f). The left hand boundary of this region is the vertical boundary of the

region in which no parental care is an ESS. The right hand side of the boundary is made up of the left hand boundary of the region in which female care is an ESS and a curve starting from the top left hand corner of this region. As gains from biparental care increase (moving upwards in Fig. 2), this strip becomes narrower.

When the gains from biparental care are small, there is no pure equilibrium. Hence, it seems that such a polymorphism could evolve. However, the narrow range of parameters suitable for such a polymorphism to be stable suggests that we would not observe such patterns of parental care.

6.2. A female polymorphism when males care

The two conditions for a putative stable polymorphism to be valid are given by Inequalities (27) and (28) (see Appendix B), which lead to $1.7450 < k_b/k_m < 3.3202$. It should be noted that this corresponds exactly to the range of values of this ratio for which not all females should care given that males care, but just paternal care cannot be an ESS.

Secondly, a male carer must have a higher reproduction rate than a male deserter. This corresponds to Inequality (29), which gives for $1.7450 < c = k_b/k_m < 1.7544$

$$k_m > \frac{1175c^2 - 9925c + 20\,000}{49c^3 + 5003c^2 - 28\,978c + 35\,176}$$

For $1.7544 < c < 3.3202$, the direction of this inequality is reversed. It can be shown that for $1.7544 < c < 3.3202$ the right hand side of the inequality above is negative. Hence, there can be no such stable polymorphism for this range of values of c .

Now consider the range $1.7450 < c < 1.7544$. As c tends to the lower boundary of this interval, the minimum value of k_f for which the above inequality is satisfied is 60.4523. As c tends to the upper boundary of this interval, the minimum value of k_f required tends to infinity. It follows that the region in which there is a stable female polymorphism with male care is a very thin strip above the region in which just paternal care is an ESS (see Fig. 2). Since just maternal care is an ESS in this region, it seems unlikely that a stable female polymorphism with males caring would evolve.

6.3. A male polymorphism when females desert

The two conditions for a putative stable polymorphism to be valid are given by Inequalities (30) and (31) (see Appendix C), which lead to $4.8793 < k_m (= k_f) < 60.4523$. It should be noted that this corresponds exactly to the range of k_m for which paternal care cannot be an ESS, but not all males should desert given that females desert.

Secondly, a female deserter must have a higher reproduction rate than a female carer. This corresponds to Inequality (32), which gives

$$k_b < k_m^2 + \frac{(k_m - 1)^2 [40\,150 - 10\,550k_m + 100k_m^2]}{10\,694k_m - 100k_m^2 - 49\,798}$$

As k_m tends to the upper limit the region given above (approx. 60.4523), the maximum value of k_b for which such a stable polymorphism exists tends to $1.7450k_m$. Hence, the right hand border of the region in which such a polymorphism may occur coincides with the left hand border of the region in which just male care is an ESS.

As k_m tends to the lower limit of this region (approx. 4.8793), the right hand side of the inequality above tends to $-\infty$. Hence, the minimum value of k_m required for such a stable polymorphism to occur must be greater than 4.8793. Since $k_b \geq k_m$, in order to find the minimum required value of k_m , it is necessary to

solve

$$k_m = k_m^2 + \frac{(k_m - 1)^2 [40\,150 - 10\,550k_m + 100k_m^2]}{10\,694k_m - 100k_m^2 - 49\,798}$$

This leads to $k_m \approx 21.6493$. It can be shown that for $k_m > 21.6493$ that the right hand side of the equation above is greater than k_m . It follows that the region in which there is a stable male polymorphism with deserting females is bounded above by a curve from the point on the diagonal line corresponding to $k_m = k_f = 21.6493$ to the top left hand corner of the region in which just paternal care is an ESS. Since just maternal care is also an ESS in this region, it seems likely that a male polymorphism in which females desert would never evolve.

6.4. A male polymorphism when females care

The two conditions for a putative stable polymorphism to be valid are given by Inequalities (17) and (18), which lead to $1.9850 < c = k_b/k_f < 12.8912$. This is precisely the range of values for which neither maternal care nor biparental care can be an ESS.

Condition (19) states that a female carer must have a higher reproduction rate than a female deserter. This leads to

$$k_f > \frac{20\,000 - 301c - 97c^2}{25c^3 + 5075c^2 - 30\,322c + 44\,824}$$

This is illustrated in Fig. 3. Fixing k_f , the set of values of k_b for which a male polymorphism with female care is stable can be derived from the graph. This is done by finding the values of $c = k_b/k_f$ for which the horizontal line $y = k_f$ lies above the curve on the interval $1.9850 < c < 12.8912$.

For example, for $k_f = 20$, the line lies above the curve for $1.9850 < k_b/k_f < 2.5468$ and $3.2927 < k_b/k_f < 12.8912$. It follows that for $k_f = 20$ there is a stable male polymorphism if $39.700 < k_b < 50.936$ or $65.854 < k_b < 257.824$.

The height of the curve when k_b/k_f is 1.9850 is approximately 3.9406. From the form of the graph when $k_f < 3.9406$ there is only a stable polymorphism for large enough values of k_b/k_f . Table 8 gives the minimum value of k_b/k_f for a stable male polymorphism

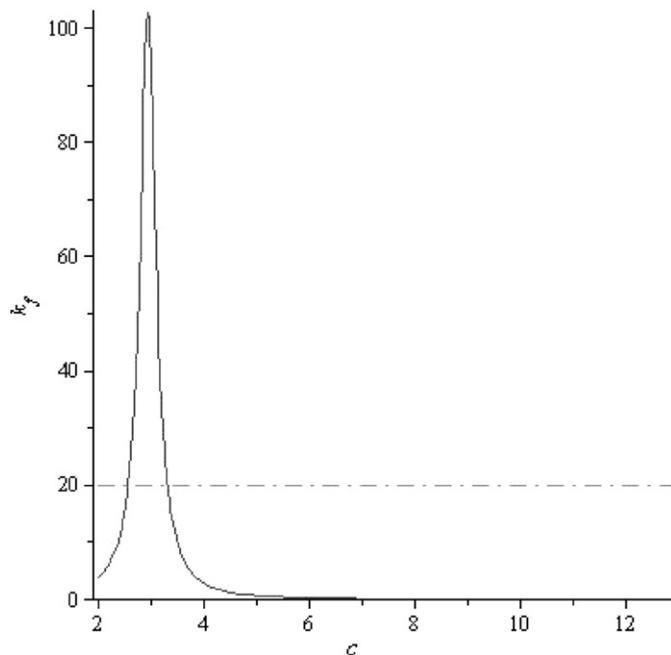


Fig. 3. Illustration of the region in which a stable male polymorphism with female care exists. For a given value of k_f such a stable polymorphism exists when the horizontal line $y = k_f$ lies above the curve.

of this type to exist when k_f is between 1 and 3.9406. This is given by the one value of c where the line $y = k_f$ intersects the curve. The maximum value in each case is 12.8912. Some numerical results are given in Table 8.

For intermediate values of k_f , from $k_f = 3.9406$ to the maximum height attained by the curve $k_f = 103.0036$, there are two ranges of k_b/k_f for which there is a stable male polymorphism. The first region is from 1.9850 to the value of c where the curve first intersects $y = k_f$. The second region is from the value of c at the second intersection of the curve with $y = k_f$ up to 12.8912. For values of k_b/k_f between these intersection points there is no stable male polymorphism. Some numerical results are given in Table 9.

For values of k_f greater than 103.0036, a stable male polymorphism exists for all values of k_b/k_f between 1.9850 and 12.8912.

It can be seen that the set of values of k_f and k_b for which there exists such a stable polymorphism covers a wide range of the values for which there is no pure equilibrium, as well as some of the region in which no parental care is an ESS profile. Hence, within the framework of the model presented, in many scenarios a system could evolve in which females cared, but males showed variation in their behaviour.

The set of values of k_f and k_b for which no stable profile has been described in this paper is made up of intermediate values of k_f (approximately between 5 and 100 for the problem considered) and intermediate values of k_b/k_f (approximately between 2 and 4). Initial calculations indicate that there are stable complete polymorphisms in this region (they also exist in other regions). The analytical results show that there can be only one stable single sex polymorphism of a given type, but numerical results indicate that there may be multiple stable complete polymorphisms for given values of k_f and k_b .

In order to gain more insight into the patterns of parental care that evolve in various scenarios, consider the stable proportion of male carers for three values of k_f , allowing k_b/k_f to vary between 1.9850 and 12.8912. The values of k_f considered are 2, 20 and 120. These three values correspond to the set of values of k_f for which: (a) there is a stable male polymorphism only for relatively large values of k_b/k_f , (b) there are two intervals of values of k_b/k_f for which there is a stable male polymorphism, (c) for all values of

Table 8
Region of stability of male polymorphism for small values of k_f .

k_f	k_b/k_f required	k_f	k_b/k_f required
1.0	4.6716	2.0	4.1762
1.2	4.5266	2.2	4.1191
1.4	4.4126	2.4	4.0690
1.6	4.3197	3.0	3.9490
1.8	4.2422	3.9406	3.8180

Table 9
Regions of stability of male polymorphisms for intermediate values of k_f .

k_f	Region 1 for k_b/k_f	Region 2 for k_b/k_f
5	(1.9850, 1.9924)	(3.8113, 12.8912)
10	(1.9850, 2.3572)	(3.4734, 12.8912)
20	(1.9850, 2.5468)	(3.2927, 12.8912)
30	(1.9850, 2.6357)	(3.2069, 12.8912)
50	(1.9850, 2.7339)	(3.1110, 12.8912)
75	(1.9850, 2.8112)	(3.0350, 12.8912)
100	(1.9850, 2.8916)	(2.9551, 12.8912)

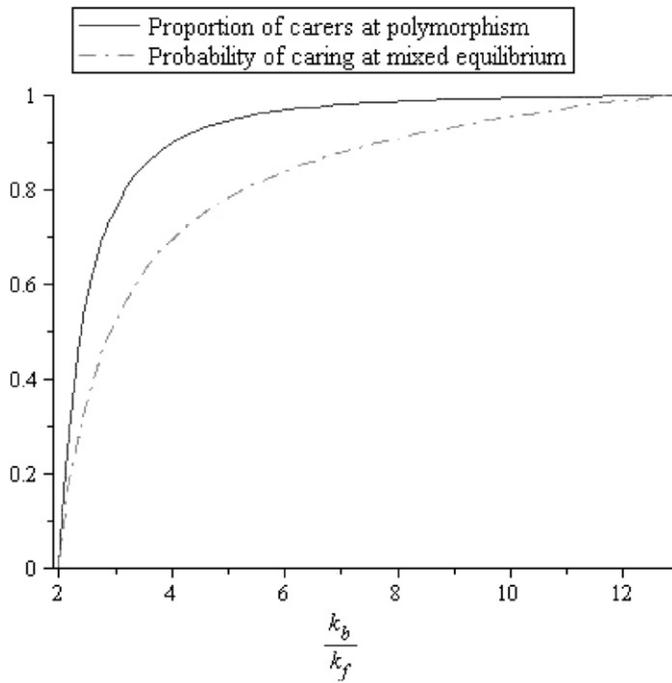


Fig. 4. Proportion of male carers at the stable polymorphism and probability of caring at the mixed ESS for $k_f=200$.

k_b/k_f between 1.9850 and 12.8912 there is a stable male polymorphism.

Fig. 4 illustrates how the proportion of carers at a stable polymorphism and the probability of caring at a mixed equilibrium change according to k_b/k_f . The forms of these graphs are very similar for all values of k_f . The proportion of carers at a stable polymorphism is greater than the probability of caring at a mixed equilibrium. However, numerical calculations indicate that the probability of an individual in the pool of searchers caring is independent of the equilibrium.

Figs. 5–7 illustrate the reproduction rates of female carers and of a mutant female deserter. In order for the polymorphism to be stable, female carers must reproduce at a faster rate than the mutant.

Fig. 5 shows that for $k_f=2$, there is only a stable polymorphism for relatively large values of k_b/k_f (between 4.1762 and 12.8912). Fig. 4 indicates that at any such equilibrium the proportion of male carers will always be high. That is to say for $k_f=2$ and $k_b < 8.3524$ there will only be one ESS (no parental care). For values of k_b between 8.3524 and 25.7824, there is also a stable polymorphism where all females and a large proportion of males care.

Fig. 6 shows that for $k_f=20$ there is no stable polymorphism for intermediate values of k_b/k_f . In fact, there is a stable polymorphism when $1.9850 < k_b/k_f < 2.5468$ and $3.2927 < k_b/k_f < 12.8912$. As k_b/k_f increases from 1.9850, the proportion of male carers at such a polymorphism increases very rapidly. This means that there are less males in the pool of searchers (i.e. males face less competition when looking for a mate), which favours deserters. This factor seems to initially outweigh the gains from parental care and so the polymorphism becomes unstable. For larger values of k_b/k_f the proportion of male carers at such a, now putative, polymorphism rises more slowly and so in turn the gains from parental care begin to outweigh the advantages gained by deserters due to reduced competition for females. Hence, for larger values of k_b/k_f the polymorphism again becomes stable.

Fig. 7 shows that for $k_f=200$ the polymorphism is stable for $1.9850 < k_b/k_f < 12.8912$. There is a range of values of k_b/k_f for

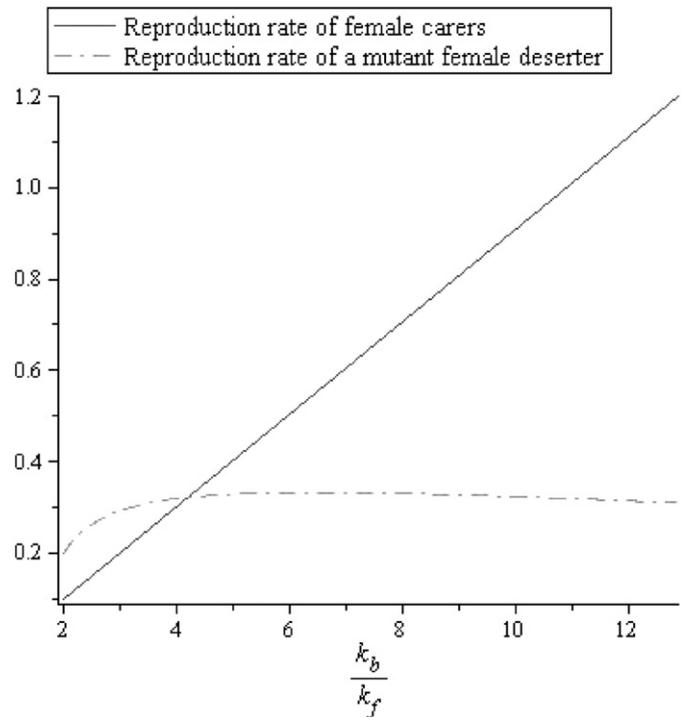


Fig. 5. Reproduction rates of female carers and a mutant female deserter at a putative stable polymorphism with $k_f=2$. The polymorphism is stable if the reproduction rate of carers is greater than the reproduction rate of a deserter (i.e. for large values of k_b/k_f).

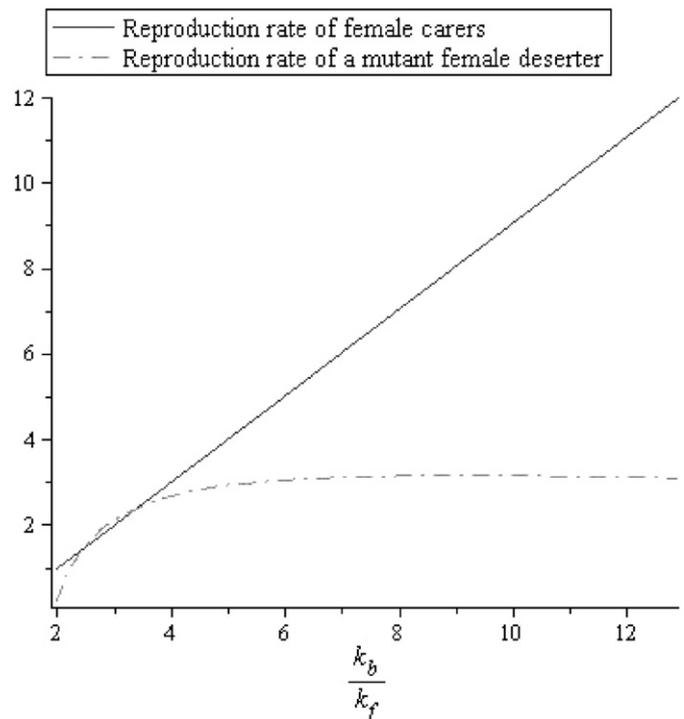


Fig. 6. Reproduction rates of female carers and a mutant female deserter at a putative stable polymorphism with $k_f=20$. The polymorphism is stable if the reproduction rate of carers is greater than the reproduction rate of a deserter (i.e. not for intermediate values of k_b/k_f).

which a mutant female deserter reproduces at virtually the same rate as a female carer (this is true for all large values of k_f when $k_b/k_f \approx 3$ in the problem considered). This may indicate a large

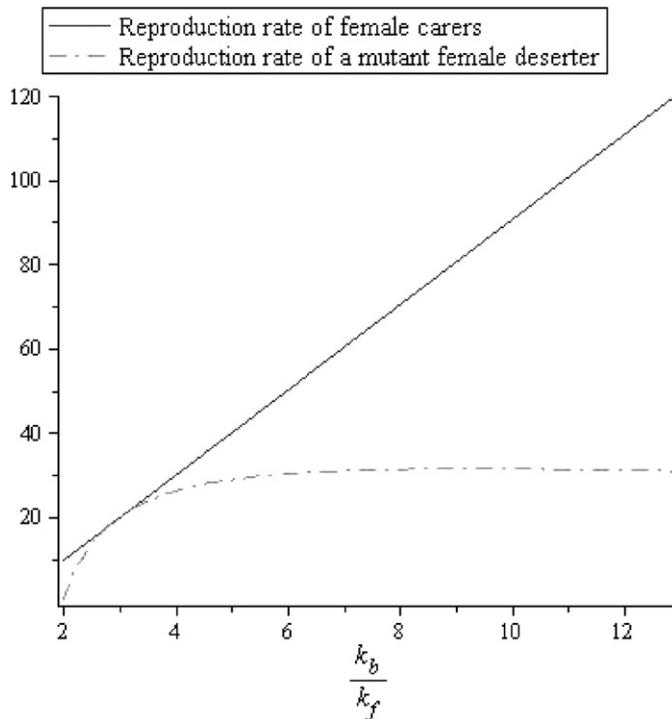


Fig. 7. Reproduction rates of female carers and a mutant female deserter at a putative stable polymorphism with $k_f=200$. The polymorphism is stable for all values of k_b/k_f in the range considered.

degree of conflict over which parent(s) should care in such situations.

7. Conclusion

This article has presented a model of a parental care game which is an adaptation of the model of Yamamura and Tsuji (1993). Unlike their model, individuals of the rarer sex in the mating pool do not find a mate immediately on becoming receptive. This approach allows us to model the interaction between the patterns of parental care and the OSR. In this way, the model presented shows similarities to the model presented by Kokko and Jennions (2008).

The model can be thought of as representing a primeval situation in which the only difference between the sexes is the gametes they produce. By definition, females produce larger gametes and hence their minimum time out is greater than the minimum time out of males. Given such a scenario, it is generally expected that if uniparental care occurs, then females care. Males care if the gains from biparental care are sufficient. The major exception to this seems to occur when the ASR is male biased. In this case, if uniparental care is evolutionarily stable, then again females care. However, the outcome is somewhat unclear when there are moderate gains from biparental care. In this case, males should care given females care, but females should not care given that males care (this is never the case for an even or female biased ASR). One possible area for future research is to investigate what patterns of parental care would evolve in such situations.

While Kokko and Jennions assume that both parents choose the time for which they care from some range, the model here assumes that the decision is dichotomous: i.e. a parent either cares or deserts. In the case of St. Peter's fish (see Balshine-Earn and Earn, 1997), if a parent decides to brood after fertilization, then he/she broods until the eggs hatch otherwise the offspring will not survive. Hence, in this scenario it seems reasonable to

restrict the set of available actions in this way. In other cases, it may well be realistic to allow parents to case the level of care they give from a range of values. Comparing the results obtained here and in Yamamura and Tsuji (1993) with the results obtained by Kokko and Jennions (2008), it seems that situations in which the decision is dichotomous make it more likely that female only care evolves, even when the ASR is heavily male biased (Kokko and Jennions predict a more even distribution of parental care between males and females if the only difference between the sexes is the anisogamy of gametes). The model presented here can be easily adapted to allow parents to choose the level of care they give from a range. It would be interesting to see whether the predominance of female care found here is an artifact of the assumptions made regarding the set of actions available to the parents. Also, the models compared here all assume that the decisions made regarding parental care are made simultaneously, whereas in reality one parent may be able to desert before the other has an opportunity to desert, who can react to such a desertion (this is discussed more fully below in comparing the parental care patterns of mammals, birds and fish). Dawkins (1976) argues that if uniparental care is evolutionarily stable, the sex which can desert earlier will be the one which deserts. It would be relatively easy to adapt the model to take this asymmetry into account and in this way explain what effect this asynchronicity of decisions effects the evolution of patterns of parental care.

In practice, individuals may well balance the level of parental care they give with other types of behaviour on a day-to-day basis and may well be able to react to the level of care provided by their partner (see e.g. McNamara et al., 1999; Houston et al., 2005). However, adapting the model presented here to such adaptive behaviour is likely to lead to an overly complex model.

Analytical results have been obtained describing so-called single sex polymorphisms, at which variation in behaviour is observed within a particular sex. The results suggest that variable patterns of parental care within a species are more likely to be observed among males than among females. Such equilibria may evolve for intermediate gains from biparental care. In such cases, males exhibiting a relatively rare behaviour will be selected for. Those models considered here in which parents choose the time they care for from a range (Maynard Smith, 1977; Grafen and Sibly, 1978; Kokko and Jennions, 2008) assume that the ESS profile is pure. However, it may be that for a given level of care by e.g. the female, for low levels of care from the male the marginal gains from an increase in the level of care he gives may be increasing. Hence, it seems possible that for such models stable polymorphisms exist in which some males “desert” (i.e. give the least possible amount of care) and some males “care” (i.e. give some higher level of care).

One particular advantage of this model compared to the model of Yamamura and Tsuji (1993) is that it could be extended to include variation between individuals and take mate choice into account. Although it would seem that such a model would be too complex to obtain analytical results, numerical results could be obtained using simulations. As Székely et al. (2000) note there is strong feedback between mate choice and patterns of parental care. Seki et al. (2007) use a genetic model to simulate the coevolution of patterns of polyandry and parental care. It has been noted that many species in which only females care there is sexual dimorphism. In such species males often invest in “weaponry” or “ornaments”, in order to mate with as many females as possible while avoiding the costs of parental care (see Weckerly, 1998; Duckworth et al., 2003; Bro-Jørgensen, 2007; Mitchell et al., 2007). However, the relation between attractiveness and parental care is not entirely clear. Møller and Jennions (2001) observe that males who give parental care can be

interpreted as attractive. Balshine-Earn (1995) also argues there may well be a correlation between the attractiveness of a partner and the level of care they can give. Females prefer larger males as mates, who are more able to give parental care than small males (as the same level of parental care from a large male would cost him less than it would cost a smaller male). Sargent and Gross (1993) argue that in teleost fish the costs to females of caring are greater than the costs to males of caring, since females invest more in reproduction and thus have lower reserves than males.

The model presented here assumes that the only difference between individuals is sex, whereas obviously individuals vary according to other traits. In this case, individuals should not only care about the number of offspring surviving to adulthood, but also the quality of such offspring. Field and Brace (2004) note some of the benefits extended parental care gives to offspring apart from increased survival. One goal of future research should be to develop models to investigate under what conditions dimorphism may evolve from a non-dimorphic species in which there is some initial variation between the members of the population. Future research should also include a dynamic analysis of how the population evolves in various scenarios, rather than the static equilibrium analysis carried out here. This would be particularly useful in cases where there are multiple equilibria and/or complete stable polymorphisms.

One question that is not addressed here is the difference between patterns of care in various classes of species. As Clutton-Brock (2007) observes, once sex differences have evolved, selection can become sex specific and the various reproductive processes in different classes may lead to e.g. dimorphism or a variety of patterns of parental care. For example, female care is present in virtually all mammal species, with males caring in less than 10% of species (see Alcock, 2009; Clutton-Brock, 1991). In bird species, female care is much more common than male care and biparental care is more common than in mammals (see Cockburn, 2006). These differences are somewhat predictable considering the results given above and the physiological constraints of reproduction in these classes. The gains from biparental care with respect to uniparental care in birds are likely to be relatively large. This is due to the fact that one parent can incubate the eggs while their partner forages. In mammalian species, females have evolved to specialise in caring for offspring (e.g. supplying milk) and the benefits of biparental care seem less clear. Hence, it is expected that the tendency for just female care to be evolutionarily stable is stronger in mammals than in the “primeval” species considered by the model. The patterns of parental care in fishes are much more varied. Male only care is observed in many fish species (see Goodwin et al., 1998; Reynolds et al., 2002). Various reasons have been put forward for this difference. Hale and St. Mary (2007) note that males who are already caring for offspring are preferred by females. The model presented here is inappropriate in this case, as it is assumed that males either care for young or attempt to gain extra matings. Also, it seems reasonable to assume that the length of male time outs in relation to the length of female time outs is longer in fish than in mammals or birds (see Levitan and Petersen, 1995). Another possible reason is that due to external fertilisation, in fish species females are able to desert before males have the opportunity of deserting, while in mammal and bird species it is the opposite way round.

One major drawback of the model is that it does not take into account the certainty of parentage. Queller (1997) argues that one reason for males providing less parental care is that they are less certain of their paternity. In socially monogamous mammal and bird species, the fact that males attempt to gain extra-pair copulations means that males will be on average less related to the offspring than their partners are. Dawson (1996) describes a so-called trade off between paternal care and attempting to gain

extra matings. Magrath and Komdeur (2003) argue that male care does not always compromise the search for additional partners. Møller and Birkhead (1993) observe that there is a correlation between the level of male care and certainty of parentage. Møller and Thornhill (1998) argue that males adjust their level of care according to their expected future rewards, i.e. if they expect that their latest brood is more highly related to them than average they will care more. Westneat and Sherman (1993) come to a similar conclusion and furthermore argue that given the expected relationship of two males to their partner's present brood is equal to their average relationship, then those two males should give the same level of paternal care, even if one male is on average more related to the offspring of his partner than the other. Houston and McNamara (2002) argue that the model of Westneat and Sherman is inconsistent and that the level of male care must depend on the average level of relationship of a male to his partner's brood. They look at how levels of care should vary from season to season, within a population, in different populations of the same species and across species. Kokko and Morrell (2005) note that by caring for their offspring, males also tend to guard themselves against lower levels of paternity. They show that the relationship between guarding and paternity levels is complex. The traditional argument is that low levels of paternity lead to males trying to mate with more females and caring less, which leads to lower levels of paternity, etc. However, this circle can be broken by mate guarding. It is clear that the problem of the uncertainty of parentage is a great challenge to modellers.

Another problem with the model presented here is that it does not consider the mortality of individuals. Ramsey (2009b) derives pure ESSes for a similar problem in which the mortality rate may depend on the state and/or strategy of an individual. In this case one should consider three sex ratios. The incoming sex ratio, ISR, is the ratio of the rate at which males join the adult population to the rate at which females join the adult population. This parameter is defined exogenously. The OSR and ASR depend on the strategy profile used and can be calculated using the fact that in a steady state the rates at which males and females mature must equal the rates at which adult males and females die.

Roff (2002) notes that present investment lowers expected future reproductive success. Such a relationship would be difficult to capture using a model of the form considered here. One way of doing this would be to allow individuals to age at different rates according to the strategy they use. Clutton-Brock et al. (1985) and Clutton-Brock and Isvaran (2007) note that in dimorphic mammalian species there is a very female biased ASR, due to the fact that males take longer to mature and male–male competition leads to a higher rate of mortality among adult males than among adult females. Liker and Székely (2005) and Donald (2007) observe that in most bird species there tends to be a more balanced ASR than in mammalian species. Also, in avian species where just female care is observed the ASR tends to be female biased. Kokko and Monaghan (2001) note that the relationship between mortality and patterns of parental care may be complex. For example, suppose in a species where only female care is observed, the mortality rate of males increases due to increased male–male competition (this may be due to density dependent effects). The increased cost of male–male competition would lead to a more female biased ASR, i.e. greater gains for the males who outcompete others. It is not clear whether these gains outweigh the increased costs of male–male competition.

Acknowledgements

The author is grateful for the support of Science Foundation Ireland under the BIO-SI project (no. 07MI012) and the comments

of three anonymous referees which helped improve the original manuscript.

Appendix A. Female polymorphism when males desert

Let $q_{i,\bullet}^{DP}$ denote the proportion of females using strategy \bullet in state i , $\bullet \in \{C,D\}$, $j \in \{1,2,3\}$ and s_f^{DP} be the proportion of female carers at such a stable polymorphism. From the equilibrium conditions for the proportions of individuals in each state,

$$q_{1,\bullet}^{DP} \mu_1 = q_{2,\bullet}^{DP} \mu_2,$$

$$\lambda_1 q_{1,\bullet}^{DP} p_1^{DP} r = \mu_3^D q_{3,\bullet}^{DP},$$

$$q_{1,\bullet}^{DP} + q_{2,\bullet}^{DP} + q_{3,\bullet}^{DP} = 1,$$

$$\lambda_1 p_1^{DP} [s_f^{DP} q_{1,C}^{DP} + (1-s_f^{DP}) q_{1,D}^{DP}] = \lambda_2^D (1-p_1^{DP}),$$

where $\bullet \in \{C,D\}$. Since female deserters must have the same reproduction rate as female carers,

$$q_{1,D}^{DP} = q_{1,C}^{DP} k_f.$$

Solving this system of eight equations,

$$q_{1,D}^{DP} = \frac{\mu_2(\mu_3^D - k_f \mu_3^C)}{(\mu_3^D - \mu_3^C)(\mu_1 + \mu_2)},$$

$$q_{1,C}^{DP} = \frac{\mu_2(\mu_3^D - k_f \mu_3^C)}{k_f(\mu_3^D - \mu_3^C)(\mu_1 + \mu_2)},$$

$$q_{2,D}^{DP} = \frac{\mu_1(\mu_3^D - k_f \mu_3^C)}{(\mu_3^D - \mu_3^C)(\mu_1 + \mu_2)},$$

$$q_{2,C}^{DP} = \frac{\mu_1(\mu_3^D - k_f \mu_3^C)}{k_f(\mu_3^D - \mu_3^C)(\mu_1 + \mu_2)},$$

$$q_{3,D}^{DP} = \frac{(k_f - 1)\mu_3^C}{\mu_3^D - \mu_3^C},$$

$$q_{3,C}^{DP} = \frac{(k_f - 1)\mu_3^D}{k_f(\mu_3^D - \mu_3^C)},$$

$$p_1^{DP} = \frac{\mu_3^D \mu_3^C (\mu_1 + \mu_2) (k_f - 1)}{\mu_2 \lambda_1 r (\mu_3^D - \mu_3^C k_f)},$$

$$s_f^{DP} = \frac{k_f}{k_f - 1} \left[1 - \frac{\lambda_2^D (1 - p_1^{DP})}{\lambda_1 p_1^{DP} q_{1,D}^{DP}} \right].$$

For this solution to be valid, the following must hold:

$$k_f < \frac{\mu_3^D [\mu_2 \lambda_1 r + (\mu_1 + \mu_2) \mu_3^C]}{\mu_3^C [\mu_2 \lambda_1 r + (\mu_1 + \mu_2) \mu_3^D]} \tag{24}$$

$$\frac{1}{k_f} < \frac{\lambda_2^D (1 - p_1^{DP})}{\lambda_1 p_1^{DP} q_{1,D}^{DP}} < 1. \tag{25}$$

In addition, a male carer must have a lower reproduction rate than a male deserter. This gives

$$\lambda_1 p_1^{DP} q_{1,D}^{DP} > \frac{\lambda_2^C \lambda_1 [s_f^{DP} q_{1,C}^{DP} k_b + (1 - s_f^{DP}) q_{1,D}^{DP} k_m]}{\lambda_2^C + \lambda_1 [s_f^{DP} q_{1,C}^{DP} + (1 - s_f^{DP}) q_{1,D}^{DP}]} \tag{26}$$

Appendix B. Female polymorphism when males care

Let $q_{i,\bullet}^{CP}$ denote the proportion of females using strategy \bullet in state i , $\bullet \in \{C,D\}$, $j \in \{1,2,3\}$ and s_f^{CP} be the proportion of female

carers at such a stable polymorphism. From the equilibrium conditions for the proportions of individuals in each state,

$$q_{1,\bullet}^{CP} \mu_1 = q_{2,\bullet}^{CP} \mu_2,$$

$$\lambda_1 q_{1,\bullet}^{CP} p_1^{CP} r = \mu_3^C q_{3,\bullet}^{CP},$$

$$q_{1,\bullet}^{CP} + q_{2,\bullet}^{CP} + q_{3,\bullet}^{CP} = 1,$$

$$\lambda_1 p_1^{CP} [s_f^{CP} q_{1,C}^{CP} + (1 - s_f^{CP}) q_{1,D}^{CP}] = \lambda_2^C (1 - p_1^{CP}),$$

where $\bullet \in \{C,D\}$. Since female deserters must have the same reproduction rate as female carers,

$$q_{1,D}^{CP} k_m = q_{1,C}^{CP} k_b.$$

Solving this system of eight equations,

$$q_{1,D}^{CP} = \frac{\mu_2 (k_m \mu_3^D - k_b \mu_3^C)}{k_m (\mu_3^D - \mu_3^C) (\mu_1 + \mu_2)},$$

$$q_{1,C}^{CP} = \frac{\mu_2 (k_m \mu_3^D - k_b \mu_3^C)}{k_b (\mu_3^D - \mu_3^C) (\mu_1 + \mu_2)},$$

$$q_{2,D}^{CP} = \frac{\mu_1 (k_m \mu_3^D - k_b \mu_3^C)}{k_m (\mu_3^D - \mu_3^C) (\mu_1 + \mu_2)},$$

$$q_{2,C}^{CP} = \frac{\mu_1 (k_m \mu_3^D - k_b \mu_3^C)}{k_b (\mu_3^D - \mu_3^C) (\mu_1 + \mu_2)},$$

$$q_{3,D}^{CP} = \frac{(k_b - k_m) \mu_3^C}{k_m (\mu_3^D - \mu_3^C)},$$

$$q_{3,C}^{CP} = \frac{(k_b - k_m) \mu_3^D}{k_b (\mu_3^D - \mu_3^C)},$$

$$p_1^{CP} = \frac{\mu_3^D \mu_3^C (\mu_1 + \mu_2) (k_b - k_m)}{\mu_2 \lambda_1 r (k_m \mu_3^D - k_b \mu_3^C)},$$

$$s_f^{CP} = \frac{k_b}{k_b - k_m} \left[1 - \frac{\lambda_2^C (1 - p_1^{CP})}{\lambda_1 p_1^{CP} q_{1,D}^{CP}} \right].$$

For this solution to be valid, the following must hold:

$$\frac{k_b}{k_m} < \frac{\mu_3^D [\mu_2 \lambda_1 r + (\mu_1 + \mu_2) \mu_3^C]}{\mu_3^C [\mu_2 \lambda_1 r + (\mu_1 + \mu_2) \mu_3^D]} \tag{27}$$

$$\frac{k_m}{k_b} < \frac{\lambda_2^C (1 - p_1^{CP})}{\lambda_1 p_1^{CP} q_{1,D}^{CP}} < 1. \tag{28}$$

In addition, a male deserter must have a lower reproduction rate than a male carer. This gives

$$\lambda_1 p_1^{CP} q_{1,D}^{CP} k_m > \frac{\lambda_2^D \lambda_1 [s_f^{CP} q_{1,C}^{CP} k_f + (1 - s_f^{CP}) q_{1,D}^{CP}]}{\lambda_2^D + \lambda_1 [s_f^{CP} q_{1,C}^{CP} + (1 - s_f^{CP}) q_{1,D}^{CP}]} \tag{29}$$

Appendix C. Male polymorphism when females desert

Let $p_{1,\bullet}^{PD}$ denote the proportion of males using strategy \bullet in the searching state, $\bullet \in \{C,D\}$, and s_m^{PD} be the proportion of male carers at such a stable polymorphism. From the equilibrium conditions for the proportions of individuals in each state,

$$\lambda_1 p_{1,D}^{PD} q_1^{PD} = \lambda_2^D (1 - p_{1,D}^{PD}),$$

$$\lambda_1 p_{1,C}^{PD} q_1^{PD} = \lambda_2^C (1 - p_{1,C}^{PD}),$$

$$q_1^{PD} \mu_1 = q_2^{PD} \mu_2,$$

$$q_1^{PD} + q_2^{PD} + q_3^{PD} = 1,$$

$$\lambda_1 q_1^{PD} [s_m^{PD} p_{1,c}^{PD} + (1 - s_m^{PD}) p_{1,d}^{PD}] r = \mu_3^D q_3^{PD}.$$

Since male deserters and male carers must have the same reproduction rate, $p_{1,D}^{PD} = k_m p_{1,C}^{PD}$.

Solving this system of six equations,

$$q_1^{PD} = \frac{\lambda_2^C \lambda_2^D (k_m - 1)}{\lambda_1 [\lambda_2^D - \lambda_2^C k_m]},$$

$$q_2^{PD} = \frac{\mu_1 \lambda_2^C \lambda_2^D (k_m - 1)}{\mu_2 \lambda_1 [\lambda_2^D - \lambda_2^C k_m]},$$

$$q_3^{PD} = 1 - \frac{(\mu_1 + \mu_2) \lambda_2^C \lambda_2^D [k_m - 1]}{\mu_2 \lambda_1 [\lambda_2^D - \lambda_2^C k_m]},$$

$$p_{1,D}^{PD} = \frac{\lambda_2^D - \lambda_2^C k_m}{\lambda_2^D - \lambda_2^C},$$

$$p_{1,C}^{PD} = \frac{\lambda_2^D - \lambda_2^C k_m}{k_m (\lambda_2^D - \lambda_2^C)},$$

$$s_m^{PD} = \frac{k_m}{k_m - 1} \left[1 - \frac{\mu_3^D q_3^{PD}}{\lambda_1 q_1^{PD} r p_{1,D}^{PD}} \right].$$

For this solution to be valid, the following must hold:

$$k_m < \frac{\lambda_2^D [\lambda_2^C (\mu_1 + \mu_2) + \lambda_1 \mu_2]}{\lambda_2^C [\lambda_2^D (\mu_1 + \mu_2) + \lambda_1 \mu_2]}, \tag{30}$$

$$\frac{1}{k_m} < \frac{\mu_3^D q_3^{PD}}{\lambda_1 q_1^{PD} r p_{1,D}^{PD}}. \tag{31}$$

In addition the reproduction rate of a female carer must be lower than the reproduction rate of a female deserter. It follows that

$$\lambda_1 q_1^{PD} p_{1,D}^{PD} r > \frac{\mu_2 \mu_3^C \lambda_1 r [s_m^{PD} p_{1,c}^{PD} k_b + (1 - s_m^{PD}) p_{1,d}^{PD} k_f]}{\mu_2 \mu_3^C + \mu_1 \mu_3^C + \lambda_1 \mu_2 r [s_m^{PD} p_{1,c}^{PD} + (1 - s_m^{PD}) p_{1,d}^{PD}]}. \tag{32}$$

References

Alcock, J., 2009. *Animal Behavior: An Evolutionary Approach*, ninth ed. Sinauer Associates, Sunderland, MA.

Balshine-Earn, S., 1995. The costs of parental care in Galilee St. Peters fish, *Sarotherodon galilaeus*. *Anim. Behav.* 50, 1–7.

Balshine-Earn, S., Earn, D.J.D., 1997. An evolutionary model of parental care in St. Peter's fish. *J. Theor. Biol.* 184, 423–431.

Booth, A.G., Dabbs, J.M., 1993. Testosterone and men's marriages. *Social Forces* 72, 463–477.

Bro-Jørgensen, J., 2007. The intensity of sexual selection predicts weapon size in male bovinds. *Evolution* 61, 1316–1326.

Bronson, F.H., 1989. *Mammalian Reproductive Biology*. University of Chicago Press.

Broom, M., Ruxton, G.D., 1998. Evolutionarily stable stealing: game theory applied to kleptoparasitism. *Behav. Ecol.* 9 (4), 397–403.

Clutton-Brock, T.H., 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.

Clutton-Brock, T.H., 2007. Sexual selection in males and females. *Science* 318, 1882–1885.

Clutton-Brock, T.H., Albon, S.D., Guinness, F.E., 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313, 131–133.

Clutton-Brock, T.H., Isvaran, K., 2007. Sex differences in ageing in natural populations of vertebrates. *Proc. R. Soc. London B, Biol. Sci.* 274, 3097–3104.

Clutton-Brock, T.H., Parker, G.A., 1992. Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.* 67, 437–456.

Cockburn, A., 2006. Prevalence of different modes of parental care in birds. *Proc. R. Soc. London B* 273, 1375–1383.

Dawkins, R., 1976. *The Selfish Gene*. Oxford University Press.

Dawkins, R., Carlisle, T.R., 1976. Parental investment and mate desertion: a fallacy. *Nature* 262, 131–133.

Dawson, K.J., 1996. Evolutionary consequences of a trade-off between parental effort and mating effort. *J. Theor. Biol.* 183, 139–158.

Donald, P.F., 2007. Adult sex ratios in wild bird populations. *Ibis* 149, 671–692.

Duckworth, R.A., Baddyayev, A.V., Parlow, A.F., 2003. Elaborately ornamented males avoid costly parental care in the house finch (*Carpodacus mexicanus*): a proximate perspective. *Behav. Ecol. Sociobiol.* 55, 176–183.

Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215–223.

Eriksson, A., Lindgren, K., Lundh, T., 2004. War of attrition with implicit time costs. *J. Theor. Biol.* 203, 319–332.

Field, J., Brace, S., 2004. Pre-social benefits of extended parental care. *Nature* 428, 650–652.

Goodwin, N.B., Balshine-Earn, S., Reynolds, J.D., 1998. Evolutionary transitions in parental care in cichlid fish. *Proc. R. Soc. London B* 265, 2265–2272.

Grafen, A., Sibily, R., 1978. A model of mate desertion. *Anim. Behav.* 26, 645–652.

Gubernick, D.J., Teferi, T., 2000. Adaptive significance of male parental care in a monogamous mammal. *Proc. R. Soc. London B* 267, 147–150.

Hale, R.E., St. Mary, C.M., 2007. Nest tending increases reproductive success, sometimes: environmental effects of paternal care and mate choice in flag fish. *Anim. Behav.* 74, 577–588.

Hårdling, R., Kokko, H., 2005. The evolution of prudent choice. *Evol. Ecol. Res.* 7, 697–715.

Hammock, E.A.D., Young, L.J., 2005. Microsatellite instability generates diversity in brain and sociobehavioral traits. *Science* 308, 1630–1634.

Houston, A.I., McNamara, J.M., 2002. A self-consistent approach to paternity and parental effort. *Philos. Trans. R. Soc. London B* 357, 351–362.

Houston, A.I., McNamara, J.M., 2005. John Maynard Smith and the importance of consistency in evolutionary game theory. *Biol. Philos.* 20, 933–950.

Houston, A.I., Székely, T., McNamara, J.M., 2005. Conflict between parents over care. *Trends Ecol. Evol.* 20, 33–38.

Jennions, M.D., Kokko, H., 2010. Sexual selection. In: Westneat, D.F., Fox, C.W. (Eds.), *Evolutionary Behavioral Ecology*. Oxford University Press.

Kokko, H., Jennions, M., 2003. It takes two to tango. *Trends Ecol. Evol.* 18, 103–104.

Kokko, H., Jennions, M.D., 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* 21, 919–948.

Kokko, H., Johnstone, R.A., 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos. Trans. R. Soc. London B* 357, 319–330.

Kokko, H., Monaghan, P., 2001. Predicting the direction of sexual selection. *Ecol. Lett.* 4, 159–165.

Kokko, H., Morrell, L.J., 2005. Mate guarding, male attractiveness and paternity under monogamy. *Behav. Ecol.* 16, 724–731.

Kokko, H., Rankin, D.J., 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philos. Trans. R. Soc. B* 361, 319–334.

Levitan, D.R., Petersen, C., 1995. Sperm limitation in the sea. *Trends Ecol. Evol.* 10, 228–231.

Liker, A., Székely, T., 2005. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* 59, 890–897.

Magrath, M.J.L., Komdeur, J., 2003. Is mare care compromised by additional mating opportunity? *Trends Ecol. Evol.* 18, 424–430.

Maynard Smith, J., 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25, 1–9.

Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press.

McNamara, J.M., Gasson, C.E., Houston, A.I., 1999. Incorporating rules for responding into evolutionary games. *Nature* 401, 368–371.

McNamara, J.M., Székely, T., Webb, J.N., Houston, A.I., 2000. A dynamic game-theoretic model of parental care. *J. Theor. Biol.* 205, 605–623.

Mitchell, D.P., Dunn, P.O., Whittingham, L.A., Freeman-Gallant, C.R., 2007. Attractive males provide less parental care in two populations of the common yellowthroat. *Anim. Behav.* 73, 165–170.

Møller, A.P., Birkhead, T.R., 1993. Certainty of paternity covaries with paternal care in birds. *Behav. Ecol. Sociobiol.* 33, 261–268.

Møller, A.P., Jennions, M.D., 2001. How important are direct fitness benefits of sexual selection? *Naturwissenschaften* 88, 401–415.

Møller, A.P., Thornhill, R., 1998. Male parental care, differential parental investment by females and sexual selection. *Anim. Behav.* 55, 1507–1515.

Owens, I.P.F., Thompson, D.B.A., 1994. Sex differences, sex ratios and sex roles. *Proc. R. Soc. London B* 258, 93–99.

Polder, J., 1970. On gonads and reproductive behavior in the cichlid fish *Aequidens portalegensis* (Hensel). *Neth. J. Zool.* 21, 265–365.

Queller, D.C., 1997. Why do females care more than males? *Proc. R. Soc. London B* 264, 1555–1557.

Ramsey, D.M., 2009a. Large population evolutionary games played within a life history framework. *Oper. Res. Decisions* 7 (2), 51–74.

Ramsey, D.M., 2009b. Strategy dependent mortality in life history games. In: *Proceedings of 2009 International Conference on Game Theory for Networks*, 13–15 May, 2009, Boğaziçi University, Istanbul, pp. 339–346. Doi: 10.1109/GAMENETS.2009.5137419.

Reynolds, J.D., Goodwin, N.B., Freckleton, R.P., 2002. Evolutionary transitions in parental care and live bearing in vertebrates. *Philos. Trans. R. Soc. London B, Biol. Sci.* 357, 269–281.

Roff, D.A., 2002. *Life History Evolution*. Sinauer Associates, Sunderland, MA.

Sargent, R.C., Gross, M.R., 1993. William's principle: an explanation of parental care in teleost fishes. In: Pitcher, T.J. (Ed.), *Behaviour of Teleost Fishes*. Chapman Hall, London, pp. 333–361.

- Seki, M., Wakano, J.Y., Ihara, Y., 2007. A theoretical study on the evolution of male parental care and female multiple mating: effects of female mate choice and male care bias. *J. Theor. Biol.* 247, 281–296.
- Székely, T., Webb, J.N., Cuthill, I.C., 2000. Mating patterns sexual selection and parental care: an integrative approach. In: Apollonio, M., Festa-Bianchet, M., Mainardi, D. (Eds.), *Vertebrate Mating Systems*. World Science Publishing, Singapore, pp. 194–223.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), *Sexual Selection and the Descent of Man 1871–1971*. Aldine Press, Chicago, pp. 139–179.
- Webb, J.N., Houston, A.I., McNamara, J.M., Székely, T., 1999. Multiple patterns of parental care. *Anim. Behav.* 58, 983–993.
- Weckerly, F.W., 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* 79, 33–52.
- Westneat, D.F., Sherman, P.W., 1993. Parentage and the evolution of parental behavior. *Behav. Ecol.* 4, 66–77.
- Wright, H.W.Y., 2006. Paternal den attendance is the best predictor of offspring survival in the socially monogamous bat-eared fox. *Anim. Behav.* 71, 503–510.
- Yamamura, N., Tsuji, N., 1993. Parental care as a game. *J. Evol. Biol.* 6, 103–127.