The parental investment conflict in continuous time: St. Peter's fish as an example

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Abstract

The parental investment conflict considers the question of how much each sex should invest in each brood, thereby characterizing different animal species. Each species usually adopts a certain parental care pattern: female-care only, male-care only, biparental care, or even no parental care at all. The differences in care patterns are usually explained by the different costs and benefits arising from caring for the offspring in each animal species. This paper proposes a game-theoretical model to the parental investment conflict based on the parental behavior of St. Peter's fish. St. Peter's fish exhibit different parental care patterns, allowing the examination of the factors which determine the particular behavior in each mating. We present a continuous time, two-stage, asymmetric game, with two types of players: male and female. According to the model's results, three parental care patterns: male-only care, female-only care and biparental care, are possible evolutionarily stable strategies. The evolutionarily stable parental care pattern in a certain mating depends on a parent's increase in mortality due to parental care, and on its advantage from biparental care. These results may explain the different parental care patterns observed in a variety of animal species, including those found in the St. Peter's fish.
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Keywords: Parental investment conflict; Asymmetric games; ESS; St. Peter's fish; *Sarotherodon galilaeus*

1. Introduction

The parental investment conflict considers the question of how much each sex should invest in its own brood, and is widely discussed in many papers (Maynard Smith, 1977; Grafen and Sibly, 1978; Taylor, 1979; Yamamura and Tsuji, 1993; Motro, 1994; Balshine-Earn and Earn, 1997, 1998; McNamara et al., 2000, 2003; Balshine et al., 2002; Barta et al., 2002; Royle et al., 2002; Webb et al., 2002).

In nature, different species are characterized by different parental care patterns, where each species usually adopts a certain care pattern. Female-only care is the most common parental pattern among mammals. Most birds exhibit biparental care, while fish often adopt a uniparental care pattern. The conflict between sexes over parental efforts can only be viewed in biparental caring species, but it may influence the evolution of various caring patterns.

A possible way for explaining these observed different parental care patterns is using game-theoretical techniques, and characterizing the evolutionarily stable strategies (ESS). According to several existing game-theoretical models (Maynard Smith, 1977; Grafen and Sibly, 1978; Taylor, 1979; Yamamura and Tsuji, 1993; Motro, 1994; Balshine-Earn and Earn, 1997; McNamara et al., 2000, 2003; Barta et al., 2002; Royle et al., 2002), the ESS in the parental investment conflict are influenced by the differences in the costs and benefits for each sex: the fitness benefits from biparental care relative to uniparental care, the probability of a deserting male mating a second female and the cost accrued from parental investment. Since measuring these parameters is difficult, investigating a population which is characterized by more than one parental pattern can be useful.

Galilee St. Peter's fish, *Sarotherodon galilaeus*, is a mouth-brooding cichlid fish whose parental care may be

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provided by either sex alone, or by both parents. This unusual flexibility in caring patterns provides an opportunity to examine the factors that influence the parental pattern following each mating (Balshine-Earn, 1995; Balshine-Earn and Earn, 1997).

St. Peter's fish mate monogamously: the female lays eggs into a shallow depression in the substrate, which both parents dig together, and the male fertilizes the eggs as they are deposited (Goldstein, 1973). The fertilized eggs should be picked up for mouth incubation by one of the parents or both; otherwise they may be destroyed by predatory adults, conspecifics or from other species (Balshine-Earn, 1995). During the incubation period the parents do not feed (Fryer and Iles, 1972). Each such mating can end in one of the four different caring patterns: male-only care, female-only care, biparental care and no parental care (Balshine-Earn and Earn, 1997).

In Balshine-Earn (1995) and Balshine-Earn and Earn (1997), a game-theoretical model of the parental investment conflict in St. Peter's fish is presented. This model tries to explain the observed frequencies of each of the four caring patterns in the wild. According to the model, the stable parental strategies are sensitive to two factors: the operational sex ratio (OSR) and the number of offspring produced under biparental care relative to uniparental care.

The work presented here suggests a different game-theoretical model based on the behavior observed in St. Peter's fish. We consider a continuous time, two-stage game. It is assumed, that the time until a player starts to pick up eggs is a random variable, having an exponential distribution. Hence, in the first stage each of the parents makes two decisions: choosing the expected value of the time distribution until it starts picking up eggs, and choosing the proportion of eggs picked up, once it enters the game. In the second stage of the game, after eggs were picked up by one of the parents, the other parent decides whether it picks up the remaining eggs or deserts. We assume that a cost is accrued during the incubation period as a result of the inability to eat, and as a result of a possible reduction of future mating opportunities. A main assumption of the model is that biparental care pattern increases the number of surviving offspring, an assumption based on observations in fish (Balshine-Earn, 1995; Itskowitz et al., 2001), as well as in other species (Fetherston et al., 1994; Markman et al., 1996).

This paper is organized as follows. In Section 2, a description of the game-theoretical model is presented. Section 3 describes the stable reply function for a player, that is, the stable strategy of a player as a function of the strategy of the other player. In Section 4, some general properties of the stable strategies are presented. Section 5 describes the stable strategies for each sex in each stage of the game. The resulting mutual ESS of the game are presented in Section 6.

2. The model

The game begins at time $t = 0$, when the eggs are laid by the female and are immediately fertilized by the male. Both parents circle over the fertilized eggs before one or the other starts picking up eggs (Balshine-Earn, 1995). In particular, neither parent is willing to pick up eggs until the other has committed itself, although both parents "know" that as long as the eggs are on the ground they can be destroyed by predators. Therefore, we can consider a three-player game: two players, the male and the female, are the decision makers, and their fertilized eggs are a passive player, who motivates the active players to make their decisions (Motro and Eshel, 1988).

We assume that three independent, time homogeneous, Poisson processes occur at the same time. We denote by μ the rate of dying of the fertilized eggs, by λ_1 the male's rate of entering the game, and by λ_2 the female's rate of entering the game. During the time interval $(t, t + \Delta t)$, if the eggs are still viable and are not yet picked up by any of the parents, one of the following events can happen: the eggs are destroyed by predators with probability $\mu\Delta t + o(\Delta t)$ (where $\lim_{\Delta t \to 0} o(\Delta t)/\Delta t = 0$), the eggs are picked up by the male with probability $\lambda_1\Delta t + o(\Delta t)$, or the eggs are picked up by the female with probability $\lambda_2\Delta t + o(\Delta t)$. Notice that none of the above events happens with probability $1 - (\mu + \lambda_1 + \lambda_2)\Delta t + o(\Delta t)$ during the time interval $(t, t + \Delta t)$.

It is assumed that the expected number of surviving offspring depends on the proportion of eggs which is picked up by each of the parents. It is also assumed, that biparental care increases the number of surviving offspring. This assumption is based on observations in different species (Fetherston et al., 1994; Balshine-Earn, 1995; Markman et al., 1996), where in St. Peter's fish biparental care approximately doubles the reproductive success of uniparental care (Balshine-Earn, 1995). Denoting by $\alpha \in (0, 1]$ the proportion of eggs picked up in the first stage, we consider the following mathematical function for computing the expected progeny number (EPN): $1 - e^{-f(\alpha)}$, where $f(\alpha) = 1 + \alpha(1 - \alpha)$ for biparental caring and $f(\alpha) = \alpha$ for uniparental caring. Note that $(1 - e^{-[1+\alpha(1-\alpha)]})/(1 - e^{-1}) > 1$ for all $0 < \alpha < 1$, and that $1 - e^{-f(\alpha)}$ is a concave function which increases in the total proportion of incubated eggs, and indicates diminishing returns from the proportion of incubated eggs. That is, the EPN increases in the total parental effort, but each extra unit of effort is worth less.

A player that picks up eggs for mouth incubation pays a cost accrued by the inability to eat during the incubation, and by the reduce in future mating opportunities. We assume this cost to be equal and constant for both sexes, and denote it by $0 < c < 1$.

We consider an asymmetric model in which each sex has a different role. Each sex carries both male's and female's genes for each decision, but the behavior of a player in a certain situation (its phenotype) is determined according to the role it plays, male or female. Assuming that one gene determines one decision, we denote by $(\lambda_1, \alpha_1, q_1)$ a male's strategy. λ_1 is the male's rate of entering the game, α_1 is the proportion of eggs a male picks up if it plays first and q_1 is the male's probability of picking up the remaining eggs in the second stage. Similarly, we denote by $(\lambda_2, \alpha_2, q_2)$ a female's strategy.

To find the stable strategies for each decision in the game, we consider two mathematical functions: the expectation of the number of surviving offspring and the stable reply function. The first function computes a player's EPN weighted by the probability of each situation in the game. A player's stable reply function returns its stable strategy against any possible mutation, considering the other player's strategy.

We denote by $w(I, M)$ the male's (by the appropriate probabilities) EPN if it plays first, by $w(II, M)$ the male's EPN if it plays second. Similarly, we denote by $w(I, F)$ and $w(II, F)$ the female's EPN in each of the stages. Hence, the males EPN are:

$$w(I, M) = q_2(1 - e^{-[1+\alpha_1(1-\alpha_1)]}) + (1 - q_2)(1 - e^{-\alpha_1})$$
$$= 1 - e^{-\alpha_1} + q_2(e^{-\alpha_1} - e^{-[1+\alpha_1(1-\alpha_1)]}),$$

$$w(II, M) = q_1(1 - e^{-[1+\alpha_2(1-\alpha_2)]}) + (1 - q_1)(1 - e^{-\alpha_2})$$
$$= 1 - e^{-\alpha_2} + q_1(e^{-\alpha_2} - e^{-[1+\alpha_2(1-\alpha_2)]}).$$

Likewise, the female's EPN are $w(I, F) = w(II, M)$ and $w(II, F) = w(I, M)$.

To compute the ESS in the game, we assume that a mutation can only appear in one gene at a time and that the genes are independent. We first present a female's stable reply function against any possible mutation, considering changes on the mutation's frequency over time (Motro, 1994). The male's stable reply is symmetric with respect to the female's strategy, and has the same mathematical properties. We then present some general properties of the ESS in the game. Later we find the male's and the female's stable strategies in each stage of the game. Finally, we present the ESS in the game, these strategies are represented by some of the intersection points between the male's and the female's stable reply functions.

3. The stable reply functions

A player's stable reply function returns its stable strategy against any possible mutation in a certain gene, considering its mate's strategy (Motro, 1994). To compute a female's stable reply function, we introduce a mutation in one of the female's genes and consider the change in the frequency of the mutants in succeeding generations. The distribution of mutants in the next breeding season is affected by the distribution of mutants in the present breeding season, the distribution of mutants among the surviving offspring, and the fraction of the adult mutants which survived to the next breeding season (Motro, 1994). For simplicity, we assume a haploid population model, and let ε_1 be the frequency of mutants among males in this breeding population and ε_2 be the frequency of mutants among females. There are four mating combinations among the breeding population:

(1) A *"wild-type" male and a "wild-type" female*. The frequency of the mating is $(1 - \varepsilon_1)(1 - \varepsilon_2) = 1 - \varepsilon_1 - \varepsilon_2 + o(\varepsilon)$, where $\varepsilon = \max\{\varepsilon_1, \varepsilon_2\}$ and $o(\varepsilon)$ satisfies $\lim_{\varepsilon \to 0} o(\varepsilon)/\varepsilon = 0$. We denote by U the expected number of surviving offspring of this type of mating.

(2) A *"wild-type" male and a "mutant" female*. The frequency of the mating is $(1 - \varepsilon_1)\varepsilon_2 = \varepsilon_2 + o(\varepsilon)$. We denote by $\tilde{U}$ the expected number of surviving offspring of this type of mating.

(3) A *"mutant" male and a "wild-type" female*. The frequency of the mating is $\varepsilon_1(1 - \varepsilon_2) + o(\varepsilon)$. Since a mutant male's strategy is the same as a wild-type male's strategy, the expected number of surviving offspring of this mating equals U.

(4) A *"mutant" male and a "mutant" female*. The frequency of the mating is $\varepsilon_1\varepsilon_2 = o(\varepsilon)$. Thus, this mating rarely appears.

Note that both males and females can carry the mutation in one of their female's genes. Since the behavior of a player is determined according to its sex, the mutation is expressed only in females. Hence, the behavior of a mutant male is the same as a wild-type male, as well as its number of surviving offspring.

Let D be the frequency of offspring from matings in which one of the parents is a mutant, then:

$$D = \frac{\varepsilon_1 U + \varepsilon_2 \tilde{U}}{(1 - \varepsilon_1 - \varepsilon_2)U + \varepsilon_1 U + \varepsilon_2 \tilde{U}} + o(\varepsilon).$$

Considering a haploid model, the frequency of mutants among offspring equals $\frac{1}{2}D$.

We denote by A the fraction of males that survived to the next breeding season, by B the fraction of wild-type females that survived to the next breeding season and by $\tilde{B}$ the fraction of mutant females that survived to the next breeding season. Assuming a constant population size, the fraction of adults which did not survive to the next breeding season is randomly replaced by offspring of the appropriate sex. Therefore, assuming a 1:1 sex ratio among offspring, the frequency of mutants in the

next generation is

$$\varepsilon_1' = \varepsilon_1 A + 0.5(1-A)D + o(\varepsilon),$$
$$\varepsilon_2' = \varepsilon_2 \tilde{B} + 0.5(1-B)D + o(\varepsilon).$$

Let $R = \tilde{U}/U$, then ε_1' and ε_2' can be written as

$$\varepsilon_1' = \varepsilon_1 A + 0.5(1-A)(\varepsilon_1 + \varepsilon_2 R) + o(\varepsilon),$$
$$\varepsilon_2' = \varepsilon_2 \tilde{B} + 0.5(1-B)(\varepsilon_1 + \varepsilon_2 R) + o(\varepsilon).$$

To compute the stable reply function, we examine the stability of the point $(\varepsilon_1, \varepsilon_2) = (0,0)$. This is the case of no mutant in the population. The linear approximation matrix of the last equations is

$$\Phi = \begin{bmatrix} \dfrac{\partial \varepsilon_1'}{\partial \varepsilon_1} & \dfrac{\partial \varepsilon_1'}{\partial \varepsilon_2} \\[2mm] \dfrac{\partial \varepsilon_2'}{\partial \varepsilon_1} & \dfrac{\partial \varepsilon_2'}{\partial \varepsilon_2} \end{bmatrix},$$

where the derivatives are calculated at $(\varepsilon_1, \varepsilon_2) = (0,0)$. The point $(\varepsilon_1, \varepsilon_2) = (0,0)$ is stable only if the absolute values of the eigenvalues of Φ are smaller than 1. It can be shown, that since all four derivatives are positive the leading eigenvalue is real and positive. Thus, the stability of $(\varepsilon_1, \varepsilon_2) = (0,0)$ can be determined by examining the sign of $\Gamma = -\det(\Phi - \mathbf{I})$. Substituting the relevant equations we get

$$\Gamma = 0.5(1-A) \times [R(1-B) - (1-\tilde{B})]. \tag{1}$$

A necessary condition for stability is $\Gamma \leqslant 0$, and a sufficient condition is $\Gamma < 0$.

It can be shown, that in evolutionary stability Γ has the same properties as a mutant female's fitness function: it is negative for every mutant's strategy which is different from the wild-type female's strategy and it becomes zero if the mutant adopts a wild-type female's strategy. Thus, the female's stable reply function is determined according to the behavior of the following function:

$$\begin{aligned} W_F &= R(1-B) - (1-\tilde{B}) \\ &= \frac{\tilde{U}}{U}(1-B) - (1-\tilde{B}) \\ &= \frac{1}{U}[\tilde{U}(1-B) - U(1-\tilde{B})], \end{aligned} \tag{2}$$

where U is a wild-type female's expected number of surviving offspring, and $1 - B$ is the fraction of wild-type females that did not survive to the next breeding season. These females are randomly replaced by their offspring. Similarly, $\tilde{U}$ is a mutant female's expected number of surviving offspring, and $1 - \tilde{B}$ is the fraction of mutant females that did not survive to the next breeding season.

We define $U/(1-B)$ to be the wild-type females' rate of replacement and $\tilde{U}/(1-\tilde{B})$ to be the mutant females rate of replacement. In equilibrium, the mutant females rate of replacement cannot exceed the wild-type females' rate of replacement, $\tilde{U}/(1-\tilde{B}) \leqslant U/(1-B)$.

4. General properties of the stable strategies

To find the ESS of the game, we first compute the stable reply function of each sex in each stage of the game. The following propositions present two general properties of the stable strategies of both sexes. The first proposition proves that the stable behavior in the second stage of the game is either to pick up the remaining eggs ($q = 1$), or to desert ($q = 0$), depending on the other parameters of the game. Therefore, in equilibrium, the stable probability distribution in the second stage is a discrete distribution. The second proposition concerns the stable behavior of a player in the first stage of the game, considering the suggested behavior in the second stage. The model assumes that a player that enters the game picks up a proportion $0 < \alpha \leqslant 1$ of the eggs; hence, it chooses a probability distribution with $(0, 1]$ as its support. The second proposition proves that the stable behavior of a player that enters the game is to pick up half or all of the fertilized eggs in the first stage. Thus, in equilibrium, the stable distribution of the proportion of eggs a player picks up in the first stage is a discrete distribution with $\alpha = 0.5$ or 1, depending on the behavior of the other player in the second stage on the game.

Proposition 4.1. *The stable behavior in the second stage of the game is either to pick up the remaining eggs ($q = 1$), or to desert ($q = 0$).*

Proof. See Appendix A.

Proposition 4.2. *The stable behavior of a player that enters the game is to pick up half ($\alpha = 0.5$) or all of the fertilized eggs ($\alpha = 1$), depending on the other player's behavior in the second stage on the game.*

Proof. See Appendix A.

According to these propositions, we consider a modified two stage, asymmetric game. In the first stage, each sex decides whether it enters the game, and if so, it picks up half ($\alpha = 0.5$) or all ($\alpha = 1$) of the fertilized eggs. In the second stage, the other sex decides whether it picks up the remaining eggs, or deserts. A male's strategy in the game is (λ_1, p_1, q_1). λ_1 is the male's rate of entering the game, p_1 is the male's probability of picking up half ($\alpha_1 = 0.5$) of the eggs in the first stage and q_1 is the male's probability of picking up the remaining eggs in the second stage, in case the female was the first to enter the game. Similarly, a female's strategy is (λ_2, p_2, q_2).

For simplicity, we rescale the computed EPN values. We denote by $0 < \delta < 0.5$ the advantage from cooperation, and assume that the EPN resulting from biparental caring (each of the parents picks up half of the eggs) is 1.

If all the eggs are picked up by a single parent, then the EPN is $1 - \delta$. If only half of the eggs are picked up by a single parent (while the other deserts) then the EPN is 0.5.

Therefore, the male's weighted EPN playing in each of the stages are

$$w(I, M) = (1 - p_1)(1 - \delta) + p_1[(1 - q_2)0.5 + q_2]$$
$$= (1 - \delta) + p_1(\delta + 0.5q_2 - 0.5),$$

$$w(II, M) = (1 - p_2)(1 - \delta) + p_2[(1 - q_1)0.5 + q_1]$$
$$= (1 - \delta) + p_2(\delta + 0.5q_1 - 0.5).$$

Likewise, the female's weighted EPN are $w(I, F) = w(II, M)$ and $w(II, F) = w(I, M)$.

5. Stable strategies at each decision

This section presents a female's stable strategies considering a possible mutation in each of the genes. The male's stable strategies are symmetric with respect to the female's behavior, thus can be immediately computed using the females stable strategies.

5.1. Stable entering rates

Let λ_2 be the common entering rate in the population, and denote by $\tilde{\lambda}_2$ a mutant female's strategy.

Denote by $0 < \beta < 1$ the survival probability of a player that does not pick up eggs, and let $0 < c < 1$ be the cost of picking up eggs. The fractions of wild-type females and mutant females that survived to the next breeding season are

$$B = \frac{\lambda_1 \beta(1 - cq_2) + \lambda_2 \beta(1 - c) + \mu\beta}{\lambda_1 + \lambda_2 + \mu},$$

$$\tilde{B} = \frac{\lambda_1 \beta(1 - cq_2) + \tilde{\lambda}_2 \beta(1 - c) + \mu\beta}{\lambda_1 + \tilde{\lambda}_2 + \mu}$$

and the expected numbers of surviving offspring for each mating are

$$U = \frac{\lambda_1 w(II, F) + \lambda_2 w(I, F)}{\lambda_1 + \lambda_2 + \mu},$$

$$\tilde{U} = \frac{\lambda_1 w(II, F) + \tilde{\lambda}_2 w(I, F)}{\lambda_1 + \tilde{\lambda}_2 + \mu}.$$

Substituting U, $\tilde{U}$, B and $\tilde{B}$ in W_F we get

$$W_F = \left[\frac{1}{\lambda_1 w(II, F) + \lambda_2 w(I, F)} \right] \left[\frac{\tilde{\lambda}_2 - \lambda_2}{\lambda_1 + \tilde{\lambda}_2 + \mu} \right]$$
$$\times \{ \lambda_1 \{ w(I, F)[1 - \beta(1 - cq_2)] - w(II, F)$$
$$\times [1 - \beta(1 - c)] \} + w(I, F)\mu(1 - \beta) \}.$$

To find the female's stable reply function, we compute the derivative of W_F with respect to $\tilde{\lambda}_2$ at $\tilde{\lambda}_2 = \lambda_2$.

$$\left. \frac{\partial W_F}{\partial \tilde{\lambda}_2} \right|_{\tilde{\lambda}_2 = \lambda_2}$$
$$= \frac{\lambda_1 \{ w(I, F)[1 - \beta(1 - cq_2)] - w(II, F)[1 - \beta(1 - c)] \}}{[\lambda_1 w(II, F) + \lambda_2 w(I, F)][\lambda_1 + \lambda_2 + \mu]}$$
$$+ \frac{w(I, F)\mu(1 - \beta)}{[\lambda_1 w(II, F) + \lambda_2 w(I, F)][\lambda_1 + \lambda_2 + \mu]}.$$

We consider the following cases:

(1) If $w(I, F)/[1 - \beta(1 - c)] \geqslant w(II, F)/[1 - \beta(1 - cq_2)]$, then the female's stable reply function is $\lambda_2(\lambda_1) = \infty$. In this case, the female immediately enters the game and picks up a portion of the eggs.

(2) If $w(I, F)/[1 - \beta(1 - c)] < w(II, F)/[1 - \beta(1 - cq_2)]$, then there exist two possible stable strategies considering the male's strategy. Let

$$\lambda^* = \frac{w(I, F)\mu(1 - \beta)}{w(II, F)[1 - \beta(1 - c)] - w(I, F)[1 - \beta(1 - cq_2)]}$$

then,

$$\lambda_2(\lambda_1) = \begin{cases} \infty & \text{if } \lambda_1 < \lambda^*, \\ 0 & \text{if } \lambda_1 > \lambda^*. \end{cases}$$

That is, the female immediately enters the game ($\lambda_2 = \infty$), or hesitates entering the game ($\lambda_2 = 0$), depending on the male's behavior.

Symmetrically, for the male,

(1) If $w(I, M)/[1 - \beta(1 - c)] \geqslant w(II, M)/[1 - \beta(1 - cq_1)]$, then the male's stable reply function is $\lambda_1(\lambda_2) = \infty$.

(2) If $w(I, M)/[1 - \beta(1 - c)] < w(II, M)/[1 - \beta(1 - cq_1)]$, then there exist two possible stable strategies considering the female's strategy. Let

$$\lambda^* = \frac{w(I, M)\mu(1 - \beta)}{w(II, M)[1 - \beta(1 - c)] - w(I, M)[1 - \beta(1 - cq_1)]}$$

then,

$$\lambda_1(\lambda_2) = \begin{cases} \infty & \text{if } \lambda_2 < \lambda^*, \\ 0 & \text{if } \lambda_2 > \lambda^*. \end{cases}$$

5.2. Stable proportions of first picking

Let p_2 be the common proportion in the population, and denote by $\tilde{p}_2$ a mutant female's strategy.

Since the cost of picking up half of the eggs equals the cost of picking up all the eggs, the fractions of wild-type females and mutant females that survived to the next breeding season are equal, $B = \tilde{B}$. The expected number of surviving offspring for each mating are

$$U = \frac{\lambda_1 w(II, F) + \lambda_2(1 - \delta) + \lambda_2 p_2(\delta + 0.5q_1 - 0.5)}{\lambda_1 + \lambda_2 + \mu},$$

$$\tilde{U} = \frac{\lambda_1 w(II, F) + \lambda_2(1 - \delta) + \lambda_2 \tilde{p}_2(\delta + 0.5q_1 - 0.5)}{\lambda_1 + \lambda_2 + \mu}.$$

Therefore,

$$W_F = \frac{(1 - B)}{U}(\tilde{U} - U)$$
$$= \frac{(1 - B)}{U}[\lambda_2(\tilde{p}_2 - p_2)(\delta + 0.5q_1 - 0.5)].$$

For $\lambda_2 > 0$, the function W_F is linear in $\tilde{p}_2$, therefore it attains its maximum at $\tilde{\rho}_2 = 0$ or at $\tilde{\rho}_2 = 1$, depending on the male's behavior in the second stage of the game (q_1). If the male deserts, $q_1 = 0$, then the female's stable strategy is to pick up all of the eggs in the first stage, $p_2 = 0$. If the male picks up the remaining eggs, $q_1 = 1$, then the female's stable strategy is to pick up half of the eggs in the first stage of the game, $p_2 = 1$.

Symmetrically, the male's stable strategy is determined according to the female's behavior in the second stage of the game.

5.3. Stable probability of second picking

Let q_2 be the common probability in the population, and denote by $\tilde{q}_2$ a mutant female's strategy. The fractions of wild-type females and mutant females that survived to the next breeding season are

$$B = \frac{\lambda_1 \beta(1 - cq_2) + \lambda_2 \beta(1 - c) + \mu\beta}{\lambda_1 + \lambda_2 + \mu},$$
$$\tilde{B} = \frac{\lambda_1 \beta(1 - c\tilde{q}_2) + \lambda_2 \beta(1 - c) + \mu\beta}{\lambda_1 + \lambda_2 + \mu}$$

and the expected number of surviving offspring for each mating satisfy

$$\frac{\tilde{U}}{U} = \frac{\lambda_1(1 - \delta) + \lambda_1 p_1(\delta + 0.5\tilde{q}_2 - 0.5) + \lambda_2 w(I, F)}{\lambda_1(1 - \delta) + \lambda_1 p_1(\delta + 0.5q_2 - 0.5) + \lambda_2 w(I, F)}.$$

Let

$$R = \lambda_1 p_1(\delta - 0.5) + \lambda_1(1 - \delta) + \lambda_2 w(I, F),$$
$$S = (\lambda_1 + \lambda_2 + \mu)(1 - \beta) + \lambda_2 \beta c.$$

Then,

$$\frac{\tilde{U}}{U} = \frac{0.5\lambda_1 p_1 \tilde{q}_2 + R}{0.5\lambda_1 p_1 q_2 + R},$$
$$1 - B = \frac{\lambda_1 \beta cq_2 + S}{\lambda_1 + \lambda_2 + \mu},$$
$$1 - \tilde{B} = \frac{\lambda_1 \beta c\tilde{q}_2 + S}{\lambda_1 + \lambda_2 + \mu}.$$

Substituting U, $\tilde{U}$, B and $\tilde{B}$ in W_F we get

$$W_F = \frac{\lambda_1 T(\tilde{q}_2 - q_2)}{U(\lambda_1 + \lambda_2 + \mu)^2} \tag{3}$$

where $T = 0.5p_1 S - R\beta c$. The function W_F is linear in $\tilde{q}_2$, hence the female's stable strategy depends on the sign of T. If the male picks up all the eggs in the first stage, $p_1 = 0$, then $T < 0$ and the female's stable strategy is to

desert in the second stage, $q_1 = 0$. But, if the male picks up half of the eggs in the first stage, $p_1 = 1$, then there exist two possible stable strategies depending on the other parameters of the game.

Substituting $p_1 = 1$ in R, S and T we get

$$T|_{p_1=1} = 0.5(1 - \beta)(\lambda_1 + \lambda_2 + \mu) + 0.5\beta c(\lambda_2 - \lambda_1) - \lambda_2 \beta cw(I, F). \tag{4}$$

We define

$$T^* = \frac{T|_{p_1=1}}{(\lambda_1 + \lambda_2 + \mu)(1 - \beta)}$$
$$= 0.5 + 0.5m^* \left(\frac{\lambda_2}{\lambda_1 + \lambda_2 + \mu} - \frac{\lambda_1}{\lambda_1 + \lambda_2 + \mu} \right)$$
$$- m^* w(I, F) \frac{\lambda_2}{\lambda_1 + \lambda_2 + \mu}, \tag{5}$$

where $m^* = \beta c/(1 - \beta)$ is the increase in mortality due to parental care (i.e. picking up eggs), compared with the mortality without any parental care (Motro, 1994). In this case the female's stable strategy is to pick up the remaining eggs ($q_2 = 1$) only if $T^* > 0$.

6. Evolutionary stable strategies of the game

A strategy of a player in the game is a three-component vector, where each component represents one decision. The presented model assumes that each sex carries both a male and a female gene for each decision. Thus, ESS in the game are represented by a six-component matrix (a male and a female gene for each decision) in which each of the components satisfies all the equilibrium conditions.

The four following propositions present the possible ESSs in the game.

Proposition 6.1. *If the increase in mortality due to parental care is smaller than the mortality without parental care (i.e. $0 < m^* < 1$), then a possible ESS is: both sexes immediately enter the game, and each picks up half of the eggs,*

$$\begin{pmatrix} \lambda_1 = \infty & \lambda_2 = \infty \\ p_1 = 1 & p_2 = 1 \\ q_1 = 1 & q_2 = 1 \end{pmatrix}.$$

Proof. See Appendix B.

This is the case of full cooperation between the parents. In this case, both parents are willing to take part in caring for their offspring. Moreover, both parents immediately enter the game where one sex is randomly chosen to be the first that picks up half of the eggs, while its mate picks up the remaining half right after it.

Proposition 6.2. *If the increase in mortality due to parental care is smaller than the mortality without parental care (i.e. $0 < m^* < 1$), then a possible ESS is: one sex immediately enters the game and picks up half of the eggs, while its mate hesitates at the beginning, but picks up the remaining eggs in the second stage of the game,*

$$\begin{pmatrix} \lambda_1 = \infty & \lambda_2 = 0 \\ p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{pmatrix} \quad or \quad \begin{pmatrix} \lambda_1 = 0 & \lambda_2 = \infty \\ p_1 = 0 & p_2 = 1 \\ q_1 = 1 & q_2 = 0 \end{pmatrix}.$$

Proof. See Appendix B.

This is the case of "forced" cooperation. By hesitating to enter the game, a player "forces" its mate to pick up eggs. A player that enters the game picks up only half of the eggs, while its "hesitating" mate picks up the remaining half right after it.

Consider the strategy in which one sex enters immediately the game and picks up all of the eggs, while its mate hesitates but intends to pick up half of the eggs at the beginning of the game, and deserts in the second stage,

$$\begin{pmatrix} \lambda_1 = 0 & \lambda_2 = \infty \\ p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{pmatrix} \quad or \quad \begin{pmatrix} \lambda_1 = \infty & \lambda_2 = 0 \\ p_1 = 0 & p_2 = 1 \\ q_1 = 1 & q_2 = 0 \end{pmatrix}.$$

Proposition 6.3. *The described strategy is an ESS only if one of the two following conditions is satisfied:*

(1) *The increase in mortality due to parental care is higher than the mortality without parental care (i.e. $m^* > 1$), and the advantage from cooperation is high (i.e. $0.5(1 - 1/m^*) < \delta < 0.5$).*

(2) *The increase in mortality due to parental care is smaller than the increase in mortality without parental care (i.e. $0 < m^* < 1$), and the advantage from cooperation is not high (i.e. $0 < \delta < 1 - 1/(1 + m^*)$).*

Proof. See Appendix B.

This is the case of "hesitative" uniparental care. Each sex prefers that its mate will care for the offspring. By hesitating at the beginning and deserting in the second stage, a player "forces" its mate to pick up all the eggs.

Proposition 6.4. *If the increase in mortality due to parental care is higher than the mortality without parental care (i.e. $m^* > 1$), then where the advantage from cooperation is low (i.e. $0 < \delta < 0.5(1 - 1/m^*)$) a possible*

ESS is: *one sex immediately picks up all the eggs, while the other sex hesitates and stays out of the game,*

$$\begin{pmatrix} \lambda_1 = \infty & \lambda_2 = 0 \\ p_1 = 0 & p_2 = 0 \\ q_1 = 0 & q_2 = 0 \end{pmatrix} \quad or \quad \begin{pmatrix} \lambda_1 = 0 & \lambda_2 = \infty \\ p_1 = 0 & p_2 = 0 \\ q_1 = 0 & q_2 = 0 \end{pmatrix}.$$

Proof. See Appendix B.

This is the case of a uniparental care. In this situation, caring for the offspring significantly reduces a player's chances of survival. Therefore, each player prefers that its mate will care for the offspring. By hesitating to enter the game, a player forces its mate to pick up eggs, and by deserting in the second stage, it forces its mate to pick up all the eggs.

7. Discussion

We presented a game-theoretical model of the parental investment conflict, based on the behavior observed in St. Peter's fish. In St. Peter's fish, the fertilized eggs should be picked up for mouth incubation either by one of the parents, or by both (Balshine-Earn, 1995).

We considered an asymmetric, continuous time, two-stage game. In the first stage, each of the parents makes two decisions: choosing the expected value of the time distribution until it starts picking up eggs, and choosing the proportion of eggs picked up once it enters the game. In the second stage, after eggs were picked up by one of the parents, the other parent decides whether it picks up the remaining eggs, or deserts.

It turns that male-only care, female-only care and biparental care are possible ESS. Fixation depends on the advantage from biparental caring, and on a parent's increase in mortality due to parental care relative to the mortality without parental care.

An earlier model (Balshine-Earn, 1995; Balshine-Earn and Earn, 1997) studies the evolutionary stability of care frequencies observed in St. Peter's fish in Lake Kinneret. Their model also considers two types of players, male and female, where a player's strategy is the probability for caring in each of the roles. The model presents the evolutionarily stable parental care patterns (male care, female care, biparental care and no care) as a function of two main parameters: the operational sex ratio and the number of surviving offspring produced under biparental care relative to uniparental care. For the observed values of these parameters in Lake Kinneret, the Balsine-Earn and Earn's model (1997) predicts a male care pattern only. However, in Lake Kinneret males sometimes desert and females care. To explain these

sporadic observations of male desertion, Balshine-Earn and Earn (1997) point out the possibility that the parents caring decisions are probably not made independently, as their model assumes. After laying and fertilizing the eggs, both male and female circle over the fertilized eggs before one or the other starts to pick up eggs (Balshine-Earn, 1995). In particular, neither parent is willing to pick up eggs until the other has committed itself, although both parents "know" that as long as the eggs are on the ground they can be devoured. Thus, each fish's decisions are likely to be influenced by its partner's decisions.

This observed hesitative behavior has motivated us to suggest an asymmetric, two-stage game-theoretical model. In a two-stage game, a parent can adjust its behavior in the second stage to its mate's behavior in the first stage. It is assumed, that as long as the eggs are on the ground they have a positive and constant rate of dying. Hence, at the beginning of the game three homogenous Poisson processes occur simultaneously, each describes the behavior of a player: male, female and their fertilized eggs, which motivate the parents to make their decisions. This can mathematically present the observed period of time the parents circle over the vulnerable eggs.

The assumption that biparental care increases the number of surviving offspring conforms with many observations on various animals (Fetherston et al., 1994; Balshine-Earn, 1995; Markman et al., 1996; Itskowitz et al., 2001). In the game-theoretical model suggested by Balshine-Earn and Earn (1997), the OSR is a main parameter, hence different OSR may yield different care patterns. We have computed the ESS considering a constant 1:1 sex ratio.

Two recent works present game-theoretical models to the parental investment conflict, assuming a finite breeding season at which each individual can produce and raise several batches of offspring (McNamara et al., 2000; Barta et al., 2002). Both models assume that one of the players (for example, the male) makes its decision first, while the other player (the female) makes its decision on the basis of its mate's decision. In McNamara et al. (2000) a biparental care occurs at the end of the breeding season, when the chances of raising another brood are zero. In Barta et al. (2002), a state-dependent dynamic game of parental care is presented, considering the influence of the parents' reserves on their strategies. According to the model, if the male is the first to make a decision, it can, by deserting, force the female to care. However, if reserves are taken into consideration, then if the difference between the cost of uni- and biparental care is small, the female forces the male to care by keeping her reserves low. When the difference between the costs is large, each sex avoids being exploited by keeping its reserves between the level required for biparental care and the level required for uniparental care.

Another approach is presented by Webb et al. (2002), where a dynamic programming model is used to explore how changes in the level of energetic reserves, time in the breeding season and the possibility for re-mating determine changes in parental care. According to the model, there may be several fluctuations in the average duration of care during the breeding season. It has also been shown, that changing some of the costs of care influences differently a parent's duration of care, in different times of the breeding season.

The game-theoretical model we propose does not include a re-mating probability, but it considers the genes distribution and a player's survival chances to the next breeding season. According to the model's results, if picking up eggs does not significantly reduce a player's chances of surviving, then a biparental care is an ESS. Assuming an asymmetric, two-stage game, allows both players to investigate simultaneously their mate's behavior. There exist some situations in the game in which a "hesitant" player forces its mate to enter the game and pick up eggs, while the proportion of the eggs this player picks up is determined by its mate's behavior in the second stage of the game.

According to our model, immediate biparental care, "forced" biparental care and "forced" uniparental care are possible ESS. As in other existing game-theoretical models (Maynard Smith, 1977; Grafen and Sibly, 1978; Taylor, 1979; Yamamura and Tsuji, 1993; Motro, 1994; Balshine-Earn and Earn, 1997, 1998; McNamara et al., 2000, 2003; Barta et al., 2002), the evolutionarily stable parental care pattern in a certain mating depends on several biological parameters. In our model, these parameters are a parent's increase in mortality due to parental care relative its mortality without parental care, and its advantage from cooperation.

In equilibrium, either both parents, or one of the parents immediately "enter" the game and pick up eggs; delayed biparental care or delayed uniparental care (which are defined by mixed strategies) are not ESS. Hence, the observed delayed parental care (Balshine-Earn, 1995) is not explained by the model. However, if uncertainty regarding the roles or strategies exists, it can sometimes establish mixed strategies as ESS (Harsanyi, 1973; Hammerstein and Parker, 1982; Binmore and Samuelson, 2001).

Finally, we propose to extend the presented model in several different directions. We first propose to extend the players strategy sets, considering a general, time dependent, rate of dying and allowing also the parents to choose a time-dependent entering rate. In this case each player's behavior is described by a non-homogeneous Poisson process. An additional direction is to consider different information structures. In the parental investment conflict in St. Peter's fish, each of the parents is able to investigate its mate behavior, as well as the condition of the fertilized eggs. That is, each of the

players knows the other players' strategies and is able to observe their realizations. One can think of a different situation, in which each of the parents cannot investigate its mate's behavior. In this case, a player knows the other players' strategies, but it cannot observe their realizations. Considering different information structures can lead to different ESS. Our last proposed extension concerns the cost accrued from parental care. The presented model assumes a constant and equal incubation cost for both sexes, hence the asymmetry is payoff irrelevant. It is more likely to assume that incubating eggs, or caring for offspring, accrues a different cost for each sex. Therefore, a more elaborate game-theoretical model should consider not only role asymmetry, but also payoff asymmetry.

Appendix A

Proof of Proposition 4.1. We compute the female's stable strategy in the second stage of the game. The male's stable strategy is symmetric with respect to female's behavior.

Let q_2 be the common strategy in the population, and denote by $\tilde{q}_2$ a female's mutant strategy. To find the female's stable strategy, we investigate the behavior of the function W_F. Denote by $0 < \beta < 1$ the survival probability of a player that does not pick up eggs, and let $0 < c < 1$ be the incubation cost. The fractions of wild-type and mutant females that survived to the next breeding season are

$$B = \frac{\lambda_1\beta(1 - cq_2) + \lambda_2\beta(1 - c) + \mu\beta}{\lambda_1 + \lambda_2 + \mu},$$
$$\tilde{B} = \frac{\lambda_1\beta(1 - c\tilde{q}_2) + \lambda_2\beta(1 - c) + \mu\beta}{\lambda_1 + \lambda_2 + \mu}.$$

The expected number of surviving offspring for each mating satisfy

$$\frac{\tilde{U}}{U} = \frac{\lambda_1[1 - e^{-\alpha_1} + \tilde{q}_2(e^{-\alpha_1} - e^{-[1+\alpha_1(1-\alpha)]})] + \lambda_2 w(I, F)}{\lambda_1[1 - e^{-\alpha_1} + q_2(e^{-\alpha_1} - e^{-[1+\alpha_1(1-\alpha_1)]})] + \lambda_2 w(I, F)}.$$

Let

$$R = \lambda_1(1 - e^{-\alpha_1}) + \lambda_2 w(I, F),$$
$$S = (\lambda_1 + \lambda_2 + \mu)(1 - \beta) + \lambda_2\beta c.$$

Then,

$$\frac{\tilde{U}}{U} = \frac{\lambda_1\tilde{q}_2[e^{-\alpha_1} - e^{-(1+\alpha_1(1-\alpha_1))}] + R}{\lambda_1 q_2[e^{-\alpha_1} - e^{-(1+\alpha_1(1-\alpha_1))}] + R},$$
$$1 - B = \frac{\lambda_1\beta c q_2 + S}{\lambda_1 + \lambda_2 + \mu},$$
$$1 - \tilde{B} = \frac{\lambda_1\beta c \tilde{q}_2 + S}{\lambda_1 + \lambda_2 + \mu}$$

and

$$W_F = \frac{1}{U}\left[\frac{\tilde{q}_2 - q_2}{(\lambda_1 + \lambda_2 + \mu)^2}\right]$$
$$\times \lambda_1[S(e^{-\alpha_1} - e^{-(1+\alpha_1(1-\alpha_1))}) - R\beta c]. \tag{A.1}$$

Let

$$f(q_1) = S(e^{-\alpha_1} - e^{-[1+\alpha_1(1-\alpha_1)]}) - R\beta c.$$

Since W_F is linear in $\tilde{q}_2$, the female's stable strategy depends on the male's behavior in the second stage, q_1, and is determined by the sign of $f(q_1)$. The female's stable reply is to pick up the remaining eggs, $q_2 = 1$, for all $0 \leqslant q_1 \leqslant 1$ that satisfy $f(q_1) > 0$. The female's stable strategy is to desert, $q_2 = 0$, for all $0 \leqslant q_1 \leqslant 1$ that satisfy $f(q_1) < 0$. If there exists q_1^* such that $f(q_1^*) = 0$, the female is indifferent for all $0 \leqslant q_2 \leqslant 1$.

The male's stable reply is symmetric with respect to the female's behavior in the second stage of the game. According to Selten (1980), the ESS in an asymmetric game with linear payoffs are necessarily pure strategies. Therefore, the only possible stable replies for the female are $q_2 = 0$ and 1. Similarly, for the male, $q_1 = 0$ and 1.   □

Proof of Proposition 4.2. Let α_2 be the common proportion in the population, and denote by $\tilde{\alpha}_2$ a female's mutant strategy. Since we assume a constant incubation cost, the fractions of wild-type females and mutant females that survived to the next breeding season are equal, $B = \tilde{B}$. Therefore,

$$W_F = \frac{(1 - B)}{U}(\tilde{U} - U), \tag{A.2}$$

where

$$U = \frac{\lambda_1 w(II, F) + \lambda_2\{(1 - e^{-\alpha_2}) + q_1[e^{-\alpha_2} - e^{-(1+\alpha_2(1-\alpha_2))}]\}}{\lambda_1 + \lambda_2 + \mu},$$
$$\tilde{U} = \frac{\lambda_1 w(II, F) + \lambda_2\{(1 - e^{-\tilde{\alpha}_2}) + q_1[e^{-\tilde{\alpha}_2} - e^{-(1+\tilde{\alpha}_2(1-\tilde{\alpha}_2))}]\}}{\lambda_1 + \lambda_2 + \mu}.$$

The female's stable reply is determined according to the behavior of $(\tilde{U} - U)$ hence,

$$\left.\frac{\partial(\tilde{U} - U)}{\partial\tilde{\alpha}_2}\right|_{\tilde{\alpha}_2 = \alpha_2}$$
$$= \frac{\lambda_2\{e^{-\alpha_2} + q_1[(1 - 2\alpha_2)e^{-(1+\alpha_2(1-\alpha_2))} - e^{-\alpha_2}]\}}{\lambda_1 + \lambda_2 + \mu}. \tag{A.3}$$

The female's stable strategy depends on the male's behavior in the second stage of the game: if the male

deserts, $q_1 = 0$ then the female's stable strategy is to pick up all of the eggs in the first stage, $\alpha_2 = 1$. If the male picks up the remaining eggs, $q_1 = 1$, then the female's stable strategy is to pick up half of the eggs in the first stage of the game, $\alpha_2 = 0.5$, and symmetrically for the male. $\square$

Appendix B

The following Lemma proves that the suggested strategies are the only candidates for ESS.

Lemma. *There are four possible stable strategies considering a mutation in one of the genes which determine the probability of picking up eggs, for each of the sexes, in each of the stages.*

(1) *Each of the sexes picks up half of the eggs in each stage of the game,*

$$\begin{pmatrix} p_1 = 1 & p_2 = 1 \\ q_1 = 1 & q_2 = 1 \end{pmatrix}.$$

(2) *Each of the sexes picks up all of the eggs in the first stage and deserts in the second stage,*

$$\begin{pmatrix} p_1 = 0 & p_2 = 0 \\ q_1 = 0 & q_2 = 0 \end{pmatrix}.$$

(3) *The female picks up half of the eggs in the first stage and deserts in the second stage, while the male picks up all the eggs in the first stage and picks up the remaining eggs in the second stage,*

$$\begin{pmatrix} p_1 = 0 & p_2 = 1 \\ q_1 = 1 & q_2 = 0 \end{pmatrix}.$$

(4) *The male picks up half of the eggs in the first stage and deserts in the second stage, while the female picks up all the eggs in the first stage and picks up the remaining eggs in the second stage,*

$$\begin{pmatrix} p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{pmatrix}.$$

Proof. It follows from Section 5.2 that the stable strategy for each of the sexes in the first stage is determined uniquely by the behavior of the other sex in the second stage. If one sex deserts in the second stage, then the other sex's stable strategy is to pick up all the eggs in the first stage. If one sex picks up the remaining eggs in the second stage, then the other sex's stable strategy is to pick up half of the eggs in the first stage. $\square$

Proof of proposition 6.1. If each sex picks up half of the eggs in each of the stages, then

$$\frac{w(I,F)}{1-\beta(1-c)} = \frac{w(II,F)}{1-\beta(1-cq_2)} = \frac{w(I,M)}{1-\beta(1-c)}$$
$$= \frac{w(II,M)}{1-\beta(1-cq_1)} = \frac{1}{1-\beta(1-c)}$$

and the stable entering rates are $\lambda_2 = \lambda_1 = \infty$. That is, both sexes are willing to enter immediately the game and pick up eggs. In this case, the player that plays first is randomly chosen, and the suitable probabilities are

$$\frac{\lambda_1}{\lambda_1 + \lambda_2 + \mu} = \frac{\lambda_2}{\lambda_1 + \lambda_2 + \mu} = 0.5.$$

Assuming the suggested strategies, the female's stable strategy is to pick up the remaining eggs only if $T^* > 0$. Substituting in Eq. (5), we get

$$T^* = 0.5(1 - m^*).$$

Therefore, $T^* > 0$ only if $0 < m^* < 1$. $\square$

Proof of Proposition 6.2. Since the stable strategy of each sex is symmetric with respect to the behavior of the other sex, it is sufficient to prove that only one of the suggested strategies is an ESS.

We prove that the following strategy is an ESS: the male enters immediately to the game and picks up half of the eggs, while the female hesitates at the beginning, but picks up the remaining eggs in the second stage,

$$\begin{pmatrix} \lambda_1 = \infty & \lambda_2 = 0 \\ p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{pmatrix}.$$

In this case,

$$w(I,F) = w(II,M) = 1 - \delta,$$
$$w(II,F) = w(I,M) = 1.$$

Assuming that the male's entering rate is the suggested one, $\lambda_1 = \infty$, a necessary condition under which the female's stable entering rate, λ_2, equals zero is

$$\frac{w(I,F)}{1-\beta(1-c)} < \frac{w(II,F)}{1-\beta(1-cq_2)}.$$

But $q_2 = 1$ and $w(I,F) = 1 - \delta < 1 = w(II,F)$, therefore this condition is satisfied.

Assuming that the female's entering rate is $\lambda_2 = 0$, the male's stable entering rate is $\lambda_1 = \infty$. Hence, the suggested entering rates are stable and the suitable probabilities are

$$\frac{\lambda_1}{\lambda_1 + \lambda_2 + \mu} = 1 \quad \text{and} \quad \frac{\lambda_2}{\lambda_1 + \lambda_2 + \mu} = 0.$$

To make sure that the suggested strategy is an ESS, we have to find the conditions under which the female's stable strategy is to pick up the remaining eggs in the second stage, assuming the male picks up half of the

eggs in the first stage. Substituting in Eq. (5), we get

$$T^* = 0.5(1 - m^*). \tag{B.1}$$

The female's stable strategy is $q_2 = 1$ only if $T^* > 0$, that is, $0 < m^* < 1$. ☐

Proof of Proposition 6.3. Since the stable strategy of each sex is symmetric with respect to the behavior of the other sex, it is sufficient to prove that only one of the suggested strategies is an ESS.

We prove that the following strategy is an ESS: the female enters immediately to the game and picks up all of the eggs, while the male hesitates but intend to pick up half of the eggs at the beginning, and leaves in the second stage,

$$\begin{pmatrix} \lambda_1 = 0 & \lambda_2 = \infty \\ p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{pmatrix}.$$

In this case,

$$w(I, F) = w(II, M) = 1 - \delta,$$
$$w(II, F) = w(I, M) = 1.$$

Assuming that the male's entering rate is $\lambda_1 = 0$, then the female's stable entering rate is $\lambda_2 = \infty$.

Assuming that the female's entering rate is $\lambda_2 = \infty$, a necessary condition under which the male's stable strategy equals $\lambda_1 = 0$ is

$$\frac{w(I, M)}{1 - \beta(1 - c)} < \frac{w(II, M)}{1 - \beta(1 - cq_1)}.$$

Since $m^* = \beta c/(1 - \beta)$, the last inequality can be written as follows:

$$\frac{w(I, M)}{(1 + m^*)} < \frac{w(II, M)}{(1 + m^* q_1)}.$$

Considering the suggested strategy, this inequality is satisfied only if either $m^* < 1$, or $m^* > 1$ and $0 < \delta < 1 - 1/(1 + m^*)$. Thus, where $\lambda_1 = 0$ and $\lambda_2 = \infty$ the suitable probabilities are

$$\frac{\lambda_1}{\lambda_1 + \lambda_2 + \mu} = 0 \quad \text{and} \quad \frac{\lambda_2}{\lambda_1 + \lambda_2 + \mu} = 1.$$

We now find the conditions under which the female's stable strategy is to pick up the remaining eggs in the second stage. Substituting in Eq. (5), we get

$$T^* = 0.5(1 - m^*) + m^* \delta. \tag{B.2}$$

$T^* > 0$ for all $0 < m^* < 1$. If $m^* > 1$, then $T^* > 0$ only for $0.5(1 - 1/m^*) < \delta < 0.5$. To conclude, the suggested strategy is an ESS only if one of the two following conditions is satisfied:

(1) The increase in mortality due to parental care is higher than the mortality without parental care

(i.e. $m^* > 1$), and the advantage from cooperation is high (i.e. $0.5(1 - 1/m^*) < \delta < 0.5$).

(2) The increase in mortality due to parental care is smaller than the mortality without parental care (i.e. $0 < m^* < 1$), and the advantage from cooperation is not high (i.e. $0 < \delta < 1 - 1/(1 + m^*)$). ☐

Proof of Proposition 6.4. It follows immediately from the proof of Proposition 6.3.

Consider the strategy in which one sex picks up immediately all of the eggs, while its mate hesitates but intends to pick up half of the eggs in the first stage, and deserts in the second stage

$$\left(\text{for example} \quad \begin{pmatrix} \lambda_1 = 0 & \lambda_2 = \infty \\ p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{pmatrix} \right).$$

We already proved that if $m^* > 1$, then the female's stable strategy is to pick up the remaining eggs only if the advantage from cooperation is high (i.e. $0.5(1 - 1/m^*) < \delta < 0.5$). Thus, if the advantage from cooperation is low (i.e. $0 < \delta < 0.5(1 - 1/m^*)$), then the female's stable strategy is to desert in the second stage. This causes the male to change its strategy in the first stage; its stable strategy is now to pick up all of the eggs in the first stage ($p_1 = 0$).

It can be shown, that under these new strategies the suggested entering rates are still stable. Therefore, if the increase in mortality due to parental care is higher than the mortality without parental care, and the advantage from cooperation is low, then a possible ESS is that one sex enters immediately to the game and picks up all of the eggs, while its mate deserts. ☐

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