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**THE PARENTAL INVESTMENT CONFLICT
IN CONTINUOUS TIME: ST. PETER'S FISH
AS AN EXAMPLE**

by

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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 groups. Each such group 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 group. This paper proposes a game-theoretical model to the parental investment conflict based on the parental behavior in Cichlid fish. Cichlid 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. Fixation depends on the investment costs and benefits, and on the initial conditions of the game. These results may explain the different parental care patterns observed in different animal groups as well as in Cichlid fish.

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1 Introduction

The parental investment conflict is raised between sexes in different groups of animals, where each group is usually characterized by a certain parental 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. A possible explanation for these different parental patterns are the differences in the costs and benefits of care for each sex (Maynard Smith, 1977). The general parental investment conflict is widely described in Maynard Smith (1977), Grafen and Sibly (1978) and Taylor (1979). These papers propose game-theoretical models for the parental investment conflict and present some possible Evolutionarily Stable Strategies (ESS), depending on biological parameters such as the fitness benefits from biparental care relative to uniparental care, the probability of a deserting male mating a second female and a cost which is accrued from parental investment. Since measuring these parameters is very complicated, 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 whose parental care may be provided by either sex alone, male-only or female-only, or by both parents. This unusual liability in caring patterns provides an opportunity to examine the factors that influence the parental pattern in each mating (Balshin-Earn, 1994; Balshin-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 are destroyed. During the incubation period, the parents do not feed (Fryer and Iles, 1972). Each such mating can end in one of four different caring patterns: male-only care, female-only care, biparental care and no parental care.

In Balshine-Earn (1994) and Balshine-Earn and Earn (1997, 1998), a game-theoretical model of the parental investment conflict in Cichlid fish is presented. This model is based on observed frequencies of each of the four caring patterns in the wild and on empirically measured costs and benefits for each sex. The model investigates the evolutionary stability of the care frequencies observed and claims that the stable parental strategies are sensitive to two factors: the operational sex ratio and the fitness benefit of biparental care in relation to uniparental care.

The work presented here suggests a different game-theoretical model. We consider a continuous time, two-stage game. During the first stage, each of the parents decides whether it enters the game and if so, which proportion of the fertilized eggs it picks up. In the second stage, the other parent decides whether it picks up the remaining eggs. We assume that a cost is accrued during the incubation period as a result of the inability to eat. We also assume that the benefit of each parent depends on the proportion of the eggs both parents pick up and on the advantage arising from biparental care.

This paper is organized as follows. In section 2 a description of the game theoretical model is presented. Section 3 presents the general form of the stable reply function for each decision. In section 4 some general properties of the evolutionarily stable strategies are presented. Section 5 describes the stable strategies for each sex in each stage of the game. The ESSs are presented in section 6.

2 The Model

The game begins at time $t = 0$, when the eggs are laid by the female and immediately fertilized by the male. Both parents circle over the fertilized eggs before one or the other starts picking up eggs. 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. 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 vital and are not yet picked up by any of the parents, one of the following events can happen: the eggs are destroyed with probability $\mu\Delta t + o(\Delta t)$ (where $\lim_{\Delta t \rightarrow 0} \frac{o(\Delta t)}{\Delta t} = 0$), the eggs are picked up by 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 $(t, t + \Delta t)$.

In the presented game, each player's amount of parental investment equals the proportion of eggs it picks up for mouth incubation. The expected number of surviving young per brood (ESP, the expected progeny size), depends on the proportion of eggs which is picked up by each of the players. In Cichlid fish, parent cooperation is super-additive, increasing the number of surviving offspring. There exist other groups of animals in which such cooperation is sub-additive, as shown in Royle *et al.*, (2002).

Let $0 < \alpha \leq 1$ be the proportion of eggs a player picks up in the first stage. We consider the following EPS function:

$$\text{EPS} = \begin{cases} 1 - e^{-[1+\alpha(1-\alpha)]} & \text{if a player picks up a proportion } \alpha \\ & \text{of the eggs, and its mate picks up the} \\ & \text{remaining eggs} \\ 1 - e^{-\alpha} & \text{if a player picks up a proportion } \alpha \\ & \text{of the eggs, and its mate deserts} \end{cases}$$

A player that picks up eggs for mouth incubation pays a cost which is caused by the inability to eat during the incubation period. We assume this cost to be constant 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 expected number of surviving offspring 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 weighted EPS if it plays first, by $w(II, M)$ the male's weighted EPS if it plays second, by $w(I, F)$ the female's weighted EPS if it plays first and by $w(II, F)$ the female's weighted EPS if it plays second. The players weighted EPS are:

$$\begin{aligned} w(I, M) = w(II, F) &= q_2(1 - e^{-[1+\alpha_1(1-\alpha_1)]}) + (1 - q_2)(1 - e^{-\alpha_1}) \\ &= 1 - e^{-\alpha_1} + q_2(e^{-\alpha_1} - e^{-[1+\alpha_1(1-\alpha_1)]}) \end{aligned} \quad (1)$$

$$\begin{aligned} w(II, M) = w(I, F) &= q_1(1 - e^{-[1+\alpha_2(1-\alpha_2)]}) + (1 - q_1)(1 - e^{-\alpha_2}) \\ &= 1 - e^{-\alpha_2} + q_1(e^{-\alpha_2} - e^{-[1+\alpha_2(1-\alpha_2)]}). \end{aligned} \quad (2)$$

To compute the ESSs 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 the stable reply function against any possible mutation for each sex, considering changes on the mutation's frequency over time (Motro, 1994). 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. 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. 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 possible mates among the breeding population:

1. **A "wild type" male and a "wild type" female.** The frequency of the mating is $(1 - \epsilon_1)(1 - \epsilon_2) = 1 - \epsilon_1 - \epsilon_2 + o(\epsilon_1) + o(\epsilon_2)$, where $o(\epsilon)$ satisfies $\lim_{\epsilon \rightarrow 0} \frac{o(\epsilon)}{\epsilon} = 0$. 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 $(1 - \epsilon_1)\epsilon_2 = \epsilon_2 + o(\epsilon_2)$. 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 $(1 - \epsilon_2)\epsilon_1 = \epsilon_1 + o(\epsilon_1)$. 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.** This mating rarely appears.

Let D be the frequency of the mutants among the offspring, half of them males and the other half females, then:

$$D = \frac{\epsilon_1 U + \epsilon_2 \tilde{U}}{(1 - \epsilon_1 - \epsilon_2)U + \epsilon_1 U + \epsilon_2 \tilde{U}} \quad (3)$$

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, the frequency of mutants in the next generation is:

$$\begin{aligned} \epsilon_1' &= \epsilon_1 A + 0.5(1 - A)D + o(\epsilon_1) + o(\epsilon_2) \\ \epsilon_2' &= \epsilon_2 \tilde{B} + 0.5(1 - B)D + o(\epsilon_1) + o(\epsilon_2) \end{aligned} \quad (4)$$

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

$$\begin{aligned} \epsilon_1' &= \epsilon_1 A + 0.5(1 - A)(\epsilon_1 + \epsilon_2 R) + o(\epsilon_1) + o(\epsilon_2) \\ \epsilon_2' &= \epsilon_2 \tilde{B} + 0.5(1 - B)(\epsilon_1 + \epsilon_2 R) + o(\epsilon_1) + o(\epsilon_2) \end{aligned} \quad (5)$$

To compute the stable reply function, we examine the stability of the point $(\epsilon_1, \epsilon_2) = (0, 0)$. This is the case of no mutant in the population. The linear approximation matrix of the above equations is:

$$\Phi = \begin{bmatrix} \frac{\partial \epsilon_1'}{\partial \epsilon_1} & \frac{\partial \epsilon_1'}{\partial \epsilon_2} \\ \frac{\partial \epsilon_2'}{\partial \epsilon_1} & \frac{\partial \epsilon_2'}{\partial \epsilon_2} \end{bmatrix},$$

where the derivatives are calculated at $(\epsilon_1, \epsilon_2) = (0, 0)$. The point $(\epsilon_1, \epsilon_2) = (0, 0)$ is stable only if the absolute values of the eigenvalues of Φ are smaller than 1. Since all four derivatives are positive, Perron's theorem for positive matrices guarantees that

the leading eigenvalue is real and positive. Thus, the stability of $(\epsilon_1, \epsilon_2) = (0, 0)$ can be determined by examining the sign of $\Gamma = -\det(\Phi - \mathbf{I})$. Substituting the relevant equations we get,

$$\Gamma = 0.5(1 - A) \times [R(1 - B) - (1 - \tilde{B})] \quad (6)$$

A necessary condition for stability is $\Gamma \leq 0$, 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:

$$\begin{aligned} W_F &= R(1 - B) - (1 - \tilde{B}) \\ &= \frac{\tilde{U}}{U}(1 - B) - (1 - \tilde{B}) \\ &= \frac{1}{U}[\tilde{U}(1 - B) - U(1 - \tilde{B})], \end{aligned} \quad (7)$$

where U is a wild type female's expected number of surviving offspring, and $1 - B$ is the fraction of wild type females that 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 $\frac{U}{1-B}$ to be the wild type females' rate of replacement and $\frac{\tilde{U}}{1-\tilde{B}}$ 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, $\frac{\tilde{U}}{1-\tilde{B}} \leq \frac{U}{1-B}$.

4 General Properties of the ESS

To find the ESSs in 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 $0 < \alpha \leq 1$ 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 $\alpha = 1$, 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 EPS values considering the super-additivity property of the EPS function. We denote by $0 < \delta < 0.5$ the advantage from cooperation, and from here on we use the following EPS function:

$$\text{EPS} = \begin{cases} 1 & \text{if each player picks up half of the eggs} \\ 1 - \delta & \text{if all of the eggs are picked up by one of the players} \\ 0.5 & \text{if only half of the eggs are picked up by one of the players} \end{cases}$$

Therefore, each sex's weighted EPS are now:

$$\begin{aligned} w(I, M) = w(II, F) &= (1 - p_1)(1 - \delta) + p_1[(1 - q_2)0.5 + q_2] \\ &= (1 - \delta) + p_1(\delta + 0.5q_2 - 0.5) \end{aligned} \tag{8}$$

$$\begin{aligned} w(II, M) = w(I, F) &= (1 - p_2)(1 - \delta) + p_2[(1 - q_1)0.5 + q_1] \\ &= (1 - \delta) + p_2(\delta + 0.5q_1 - 0.5). \end{aligned} \tag{9}$$

5 Stable Strategies at Each Decision

This section presents both sexes stable strategies considering a possible mutation in each of the genes.

5.1 Stable Entering Rates

Let λ_2 be the common 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:

$$W_F = \left[\frac{1}{\lambda_1 w(II, F) + \lambda_2 w(I, F)} \right] \left[\frac{\tilde{\lambda}_2 - \lambda_2}{\lambda_1 + \tilde{\lambda}_2 + \mu} \right] \quad (10)$$

$$\times \{ \lambda_1 \{ w(I, F) [1 - \beta(1 - cq_2)] - w(II, F) [1 - \beta(1 - c)] \} + w(I, F) \mu (1 - \beta) \}$$

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

$$\frac{\partial W_F}{\partial \tilde{\lambda}_2} \Big|_{\tilde{\lambda}_2 = \lambda_2} = \frac{\lambda_1 \{ w(I, F) [1 - \beta(1 - cq_2)] - w(II, F) [1 - \beta(1 - c)] \} + w(I, F) \mu (1 - \beta)}{[\lambda_1 w(II, F) + \lambda_2 w(I, F)] [\lambda_1 + \lambda_2 + \mu]} \quad (11)$$

We consider the following cases:

1. If $\frac{w(I, F)}{1 - \beta(1 - c)} \geq \frac{w(II, F)}{1 - \beta(1 - cq_2)}$, then the female's stable reply function is $\lambda_2(\lambda_1) = \infty$. In this case, the female enters immediately the game and picks up a portion of the eggs.
2. If $\frac{w(I, F)}{1 - \beta(1 - c)} < \frac{w(II, F)}{1 - \beta(1 - cq_2)}$, 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 enters immediately 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 $\frac{w(I,M)}{1-\beta(1-c)} \geq \frac{w(II,M)}{1-\beta(1-cq_1)}$, then the male's stable reply function is $\lambda_1(\lambda_2) = \infty$.
2. If $\frac{w(I,M)}{1-\beta(1-c)} < \frac{w(II,M)}{1-\beta(1-cq_1)}$, 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 to 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

$$\begin{aligned} U &= \frac{\lambda_1 w(II, F) + \lambda_2(1 - \delta) + \lambda_2 p_2(\delta + 0.5q_1 - 0.5)}{\lambda_1 + \lambda_2 + \mu} \\ \tilde{U} &= \frac{\lambda_1 w(II, F) + \lambda_2(1 - \delta) + \lambda_2 \tilde{p}_2(\delta + 0.5q_1 - 0.5)}{\lambda_1 + \lambda_2 + \mu}. \end{aligned}$$

Therefore,

$$W_F = \frac{(1 - B)}{U}(\tilde{U} - U) = \frac{(1 - B)}{U}[(\tilde{p}_2 - p_2)(\delta + 0.5q_1 - 0.5)] \quad (12)$$

The function W_F is linear in \tilde{p}_2 , therefore it attains its maximum at $p_2 = 0$ or at $p_2 = 1$, 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 are:

$$\frac{\tilde{U}}{U} = \frac{\lambda_1(1 - \delta) + \lambda_1p_1(\delta + 0.5\tilde{q}_2 - 0.5) + \lambda_2w(I, F)}{\lambda_1(1 - \delta) + \lambda_1p_1(\delta + 0.5q_2 - 0.5) + \lambda_2w(I, F)}$$

Let

$$R = \lambda_1p_1(\delta - 0.5) + \lambda_1(1 - \delta) + \lambda_2w(I, F)$$

$$S = (\lambda_1 + \lambda_2 + \mu)(1 - \beta) + \lambda_2\beta c$$

Then,

$$\frac{\tilde{U}}{U} = \frac{\lambda_1p_1\tilde{q}_2 + R}{\lambda_1p_1q_2 + R}$$

$$1 - B = \frac{\lambda_1\beta cq_2 + S}{\lambda_1 + \lambda_2 + \mu}$$

$$1 - \tilde{B} = \frac{\lambda_1\beta c\tilde{q}_2 + S}{\lambda_1 + \lambda_2 + \mu}$$

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

$$W_F = \frac{\lambda_1T(\tilde{q}_2 - q_2)}{U(\lambda_1 + \lambda_2 + \mu)} \quad (13)$$

where $T = 0.5p_1S - R\beta c$. 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:

$$T |_{p_1=1} = 0.5(1 - \beta)(\lambda_1 + \lambda_2 + \mu) + 0.5\beta c(\lambda_2 - \lambda_1) - \lambda_2\beta cw(I, F) \quad (14)$$

We define

$$T^* = \frac{T |_{p_1=1}}{(\lambda_1 + \lambda_2 + \mu)(1 - \beta)} = 0.5 + 0.5m^* \left(\frac{\lambda_2}{\lambda_1 + \lambda_2 + \mu} - \frac{\lambda_1}{\lambda_1 + \lambda_2 + \mu} \right) - m^* w(I, F) \frac{\lambda_2}{\lambda_1 + \lambda_2 + \mu} \quad (15)$$

where $m^* = \frac{\beta c}{1 - \beta}$ 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. Therefore, the decisions of one sex influence the decisions of the other sex during the game. Thus, evolutionarily stable strategies 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 enter immediately 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 enter immediately 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 enters immediately 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,*

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

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,

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

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 increase in mortality without parental care (i.e., $m^* > 1$), and the advantage from cooperation is high (i.e., $0.5(1 - \frac{1}{m^*}) < \delta < 0.5$).*
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., $0 < \delta < 1 - \frac{1}{1+m^*}$).*

Proof See Appendix B.

This is the case of "hesitative" uni-parental 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 of the eggs.

Proposition 6.4 *If the increase in mortality due to parental care is higher than the increase in mortality without parental care (i.e., $m^* > 1$), then where the advantage from cooperation is low (i.e., $0 < \delta < 0.5(1 - \frac{1}{m^*})$) a possible ESS is: one sex picks up immediately all the eggs, while the other sex hesitates and stays out of the game,*

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

Proof See Appendix B.

This is the case of a uni-parental 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 of the eggs.

7 Discussion

The parental investment conflict is widely discussed in many papers. Several papers present game-theoretical models and compute the ESS considering some biological parameters. Maynard-Smith's model (1977) is the first and the most basic one. It assumes that the strategy of each sex is the time it spends caring for offspring, while the payoff ('fitness') equals the rate at which an individual produces offspring which survive to enter into the adult breeding population. The model presents ESS with pure strategies: all the members of each sex play the same strategy.

Taylor's game-theoretical model (1979) is based on Grafen and Sibly's mate desertion model (1978). This model assumes a more complicated payoff function and presents an additional ESS with a mixed strategy: the players of one sex all play the same strategy while the other sex divides its players in some proportion between two strategies, one of which is an immediate desertion strategy.

Motro's model (1994) considers an asymmetric game with continuous strategy sets. The model assumes that each sex carries both male and female genes that are passed on to their offspring. Thus, the payoff function is affected by both the sex strategies and the distribution of these strategies in the next generation. The model proves that in an asymmetric game, two types of ESS, continuously stable and non-continuously stable ESS, can exist simultaneously. An ESS is called a continuously stable ESS (CSS) if a population that is fixed at any strategy in the neighborhood of the ESS can be invaded by mutants with strategies that are 'closer' to the ESS (Eshel and Motro, 1981; Eshel, 1983). It also proves that the presented parental investment conflict always has a continuously stable ESS.

An additional model is an evolutionary model of parental care in St. Peter's fish (Balshine-Earn and Earn, 1997; 1998). In St. Peter's fish, each mating can end in one of four care states: biparental care, female only care, male only care, or no care. The strategy of a player in this game is its probability of providing care after spawning. The

model predicts the stable parental care strategies based on nine measured biological parameters. The model shows that the predictions are sensitive to two factors: the operational sex ratio and the fitness benefits of biparental care relative to uniparental care. Where the operational sex ratio is strongly biased toward one sex, then parental care by that sex is most likely. Where biparental care leads to much greater reproductive success than uniparental care (for example, where the egg clutches are large), then biparental care is expected. For intermediate operational sex ratio and fitness benefits, mixed strategies are expected.

We suggest a more elaborate game theoretical model to the parental investment conflict, based on the parental behavior in Cichlid fish. We assume a two stage game with two type of players, male and female. In the first stage, each player decides whether it enters the game and if so, it chooses whether to pick up half or all of the eggs. In the second stage, each player decides whether it picks up the remaining eggs. We assume a continuous time model and present the ESS considering a 1:1 sex ratio.

We also consider some general parameters which influence each player's decision. The first parameter is the fertilized eggs' rate of dying. Each of the parents knows, that as long as the eggs are on the ground, they can be destroyed; therefore, these eggs are considered as a third, passive, player who motivates the parents to "pick them up" (Motro and Eshel, 1988). The presented model assumes a constant rate of dying, while the active players, the male and female, are allowed to choose a stable constant entering rate. This behavior is described by a three independent, time homogeneous, Poisson processes. An interesting extension is to consider some general rate of dying and allow the active players to choose a general rate of entering. In this case, the behavior of each player is determined due to a non-time homogeneous Poisson process.

The second parameter is a constant cost which is accrued during the incubation period. This cost is caused by the inability to eat during the incubation period and it reduces a parent's chances of surviving to the next breeding season. An additional parameter is the advantage from cooperation. The model assumes a super-additive payoff func-

tion; therefore, this parameter measures the benefits of biparental care relatively to uniparental care.

According to the model's results, both biparental and uniparental care patterns are possible ESSs. Fixation depends on the increase in mortality due to parental care compared with mortality without any parental care, the advantage from cooperation and the behavior of the other sex.

Two recent works consider 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 of the 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.

The first model (McNamara et al., 2000) presents a dynamic game-theoretic model. The model shows that each parent's decision depends on its mating opportunities, while mating opportunities, in turn, influence the parent's decision. One of the model's results is that a biparental care occurs at the end of the breeding season, when the chances of raising another brood are zero.

The second work (Barta et al., 2002) presents a state depended dynamic game of parental care, considering the influence of the parents' reserves on their strategies. According to the model, if the male makes its decision first, then when reserves are not included, it forces the female to care by deserting. In contrast, when the reserves have effect and 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 to uniparental care.

The game theoretical model we propose does not define 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.

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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 the female's behavior.

Let q_2 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,

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

The expected number of surviving offspring for each mating are,

$$\frac{\tilde{U}}{U} = \frac{\lambda_1[1 - e^{-\alpha_1} + \tilde{q}_2(e^{-\alpha_1} - e^{-[1+\alpha_1(1-\alpha)]})] + \lambda_2w(I, F)}{\lambda_1[1 - e^{-\alpha_1} + q_2(e^{-\alpha_1} - e^{-[1+\alpha_1(1-\alpha)]})] + \lambda_2w(I, F)}$$

Let

$$\begin{aligned} R &= \lambda_1(1 - e^{-\alpha_1}) + \lambda_2w(I, F) \\ S &= (\lambda_1 + \lambda_2 + \mu)(1 - \beta) + \lambda_2\beta c \end{aligned}$$

Then,

$$\begin{aligned} \frac{\tilde{U}}{U} &= \frac{\lambda_1\tilde{q}_2[e^{-\alpha_1} - e^{-(1+\alpha_1(1-\alpha))}] + R}{\lambda_1q_2[e^{-\alpha_1} - e^{-(1+\alpha_1(1-\alpha))}] + R} \\ 1 - B &= \frac{\lambda_1\beta cq_2 + S}{\lambda_1 + \lambda_2 + \mu} \\ 1 - \tilde{B} &= \frac{\lambda_1\beta c\tilde{q}_2 + S}{\lambda_1 + \lambda_2 + \mu} \end{aligned}$$

and

$$W_F = \frac{1}{U} \left[\frac{\tilde{q}_2 - q_2}{\lambda_1 + \lambda_2 + \mu} \right] \times \lambda_1 [S(e^{-\alpha_1} - e^{-(1+\alpha_1(1-\alpha))}) - R\beta c] \quad (16)$$

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 $0 \leq q_1 \leq 1$ that satisfy $f(q_1) > 0$. The female's stable strategy is to desert, $p_2 = 0$, for all $0 \leq q_1 \leq 1$ that satisfy $f(q_1) < 0$. If there exists q_1^* such that $f(q_1^*) = 0$, the female is indifferent for all $0 \leq q_2 \leq 1$.

The male's stable reply is symmetric with respect to the female's behavior in the second stage of the game. It follows from Seletn's theorem (1980) that an ESS in an asymmetric game with linear payoffs is necessarily a pure strategy. Therefore, the only possible stable replies for the female are $q_2 = 0$ and $q_2 = 1$. Similarly, for the male, $q_1 = 0$ and $q_1 = 1$.

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,

$$W_F = \frac{(1-B)}{U}(\tilde{U} - U), \quad (17)$$

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,

$$\frac{\partial(\tilde{U} - U)}{\partial \tilde{\alpha}_2} \Big|_{\tilde{\alpha}_2 = \alpha_2} = e^{-\alpha_2} + q_1 [(1 - 2\alpha_2)e^{-(1+\alpha_2(1-\alpha_2))} - e^{\alpha_2}] \quad (18)$$

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.

Appendix B

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

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.

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 equation 15, we get:

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

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

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,

$$\begin{aligned} w(I, F) &= w(II, M) = 1 - \delta \\ w(II, F) &= w(I, M) = 1 \end{aligned}$$

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 equals $\lambda_2 = 0$ 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 rate rates are stable and the suitable probabilities are:

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

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 equation 15, we get:

$$T^* = 0.5(1 - m^*) \tag{19}$$

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, $\left(\begin{array}{cc} \lambda_1 = 0 & \lambda_2 = \infty \\ p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{array} \right)$.

In this case,

$$\begin{aligned} w(I, F) &= w(II, M) = 1 - \delta \\ w(II, F) &= w(I, M) = 1 \end{aligned}$$

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

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

Denote by $m^* = \frac{\beta c}{1 - \beta}$, then 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 $0 < \delta < 1 - \frac{1}{(1+m^*)}$. Thus, where $\lambda_1 = 0$ and $\lambda_2 = \infty$ the suitable probabilities are:

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

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 equation 15, we get:

$$T^* = 0.5(1 - m^*) + m^* \delta \tag{20}$$

$T^* > 0$ for all $0 < m^* < 1$. If $m^* > 1$, then $T^* > 0$ only for $0.5(1 - \frac{1}{m^*}) < \delta < 0.5$. 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 increase in mortality without parental care (i.e., $m^* > 1$), and the advantage from cooperation is high (i.e., $0.5(1 - \frac{1}{m^*}) < \delta < 0.5$).
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., $0 < \delta < 1 - \frac{1}{1+m^*}$).

Proof of proposition 6.4 It follows immediately from the prove 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 (for example, $\begin{pmatrix} \lambda_1 = 0 & \lambda_2 = \infty \\ p_1 = 1 & p_2 = 0 \\ q_1 = 0 & q_2 = 1 \end{pmatrix}$). 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.*, $0.5(1 - \frac{1}{m^*}) < \delta < 0.5$). Thus, if the advantage from cooperation is low (*i.e.*, $0 < \delta < 0.5(1 - \frac{1}{m^*})$), 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 increase in 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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