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ESS IN SYMMETRIC ANIMAL CONFLICTS WITH TIME DEPENDENT STRATEGY SETS

by

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ESS in Symmetric Animal Conflicts with Time Dependent Strategy Sets

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Abstract

Animal conflicts are often characterized by time dependent strategy sets. This paper considers the following type of animal conflicts: a member of a group is at risk and needs the assistance of another member to be saved. As long as assistance is not provided, the individual which is at risk has a positive, time dependent rate of dying. Each of the other group members is a potential helper. Assisting this individual accrues a cost, but losing him decreases the inclusive fitness of each group member. A potential helper's interval between the moment an individual finds itself at risk and the moment it assists is a random variable, hence its strategy is to choose the probability distribution for this random variable. Assuming that each of the potential helpers knows the others' strategies, we show that the ability to observe their realizations influences the Evolutionarily Stable Strategies (ESS) of the game. According to our results, where the realizations can be observed ESS always exist: immediate assistance, no assistance and delayed assistance. Where the realizations cannot be observed ESS do not always exist, immediate assistance and no assistance are possible ESS, while delayed assistance cannot be an ESS. We apply our model to the n brothers' problem and to the parental investment conflict.

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1 Introduction

Time is a crucial parameter in many animal conflicts. A common situation in which time affects an individual's fitness is where it should choose the length of the interval up to making a certain decision: assisting, mating, caring, fighting, deserting. Three well known such animal conflicts are the war of attrition, the parental investment conflict, and the n brothers' problem.

In the war of attrition at least two individuals compete for the same resource. Instead of fighting, each of the individuals persists and the winner is the one who persists longer. Persisting accrues a cost, for example, delaying the start of breeding. Applying a game-theoretical approach to the conflict, the individuals are modelled as players, and each strategy is to choose the probability distribution function of the interval between the beginning of the game and the time of desertion. Existing game-theoretical models consider both a symmetric conflict (Maynard Smith and Price, 1973; Bishop and Cannings, 1978; Bishop et al., 1978; Haigh and Cannings, 1989) and an asymmetric conflict (Maynard Smith and Parker, 1976; Hammerstein, 1981; Hammerstein and Parker, 1982; Haigh and Cannings, 1989; Yang-Gwan, 1993; Mcnamara et al., 1997; Haccou and Glaizot, 2002).

In the parental investment conflict (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; Balshine et al., 2002; Barta et al., 2002; Royle et al., 2002; Webb et al. , 2002; McNamara et al., 2003; Yaniv and Motro, 2004), each sex should decide how much it invests in its own brood. Observations of animal behavior (Clutton-Brock, 1991; Balshine-Earn, 1995; Balshine-Earn and Earn, 1997) have shown, that there are cases where after mating each sex studies its mate's behavior and only then chooses its amount of parental investment. During this time interval of mutual study, the offspring are at risk. Thus, the offspring death process affects each sex's decision process.

In the n brothers' problem (Eshel and Motro, 1988; Motro and Eshel, 1988), a member of $n \geq 3$ related individuals is at risk and needs the help of another member to be saved. As long as assistance is not provided, this individual has a positive rate of dying. Each of the other group members is a potential helper. Assisting accrues a cost, but losing the individual which is at risk decreases the inclusive fitness of each group member. The interval between the moment an individual finds itself at risk, and the moment a potential helper assists is a random variable. A potential helper's strategy is to choose the probability distribution function of this variable.

In all these conflicts time may have direct and indirect effects on a player's decision. In the war of attrition, time only has a direct effect on the players' decisions. In the parental investment conflict and in the n brothers problem, time has both direct and indirect effect on the players' decisions.

In the war of attrition, a player's strategy is to choose the time of desertion. All the players are decision makers, and the winner is the one who persists longer. A player's expected payoff depends on all players' times of desertion.

In the parental investment conflict and in the n brothers problem, a potential helper's strategy is to choose the distribution function of the interval between the beginning of the game and the moment it "enters" the game to assist. In addition, there is an external time dependent process which influences the strategies of all the decision makers: as long as assistance is not provided, the individual which is at risk (offspring, brother) has a positive rate of dying. Since losing this individual decreases a potential helper's inclusive fitness, the death process motivates the potential helpers to make their decisions. In both conflicts a potential helper's expected payoff is influenced by the strategies of the decision makers, and by the death process.

We consider the following type of animal conflicts: a member of a group sized $n \geq 3$ is at risk and needs the help of another member to be saved. As long as assistance is not provided, this individual has a positive rate of dying. Assisting the individual accrues

a cost, but losing it decreases the inclusive fitness of each group member. Each of the other group members is a potential helper, and its strategy is to choose the distribution function of the interval between the beginning of the game, and the moment it "enters" the game and assists.

Existing game-theoretical models for this type of animal conflicts (Motro and Eshel, 1988; Yaniv and Motro, 2004) assume, that the individual which is at risk has a positive and constant rate of dying; its lifetime is an exponentially distributed random variable. In addition, a potential helper is only allowed to choose an exponential distribution for the interval between the beginning of the game and the moment it "enters" the game and assists. These game-theoretical models are characterized by time independent strategy sets: both the individual's rate of dying, and the potential helpers "entering" rates are constant.

We generalize these models by extending the strategy sets. Both the individual's rate of dying and the potential helpers "entering" rates are assumed to be time dependent. Thus, the lifetime of the individual which is at risk, and the interval between the beginning of the game and the moment a potential helper "enters" the game to assist can a-priori have any continuous probability distribution function.

This paper considers a symmetric conflict, all the potential helpers have the same strategy sets and they all play the same role. A general game theoretical model is developed under two information structures: full information and partial information. Under the full information each of the players knows the others' strategies and is able to observe their realizations. Under the partial information structure each of the players knows the others' strategies, but it cannot observe their realizations.

According to our results the information structure influences the ESS. Under the full information structure ESS always exist. No assistance, immediate assistance and delayed assistance are possible ESS. Fixation depends on a potential helpers payoffs from each of the possible outcomes of the game. Under the partial information structure

ESS do not always exist. No assistance and immediate assistance are possible ESS, while delayed assistance cannot be an ESS.

This paper is organized as follows. In section 2 a general symmetric model is presented. In section 3 the ESS are characterized under the full information structure. In section 4 the ESS are characterized under the partial information structure. In section 5 the model is applied to the n brothers' problem and the ESS are computed under both information structures. In section 6 the model is applied to the parental investment conflict and the ESS are computed under the full information structure.

2 The Model

Consider a group of $n \geq 3$ individuals. The game begins at time $t = 0$ where one of the individuals finds itself at risk and needs the help of another individual to be saved. As long as assistance is not provided, the individual which is at risk has a positive and time dependent rate of dying. Each of the other group members is a potential helper. Assisting the individual accrues a cost, but losing it decreases each group member's inclusive fitness. The interval between the beginning of the game and the time a potential helper "enters" the game to assists is a random variable. Therefore, a potential helper's strategy is to a-priori choose the distribution function of this random variable.

We consider a continuous time conflict. A pure strategy is an exact "entering" point in time, a degenerated random variable. A mixed strategy is defined by a continuous probability distribution function. Let F be a continuous probability distribution function for a potential helper's "entering" point in time. The rate function, $r(t)dt$, is the probability that the potential helper will "enter" the game during the infinitesimal time interval $(t, t + \Delta t)$, given that it has not entered the game before t,

$$r(t)dt = \frac{dF(t)}{1 - F(t)}.$$

It is assumed that at the beginning of the game, n non-homogeneous Poisson processes occur simultaneously, each describes the behavior of a player: the individual which is at risk and $(n-1)$ potential helpers. Thus, a potential helper's strategy is to choose its "entering" rate function. We denote by $\mu(t)$ the rate of dying of the individual which is at risk during $(t, t+\Delta t)$, and by $\lambda(t)$ a potential helpers rate of "entering" the game during $(t, t+\Delta t)$. If at time t assistance has not been provided yet and the individual which is at risk is still alive, then one of the following events can happen during $(t, t+\Delta t)$: the individual which is at risk dies with probability $\mu(t)\Delta t + o(\Delta t)$, one of the $(n-1)$ potential helpers saves the individual which is at risk with probability $(n-1)\lambda(t)\Delta t + o(\Delta t)$. None of these events happens with probability $1 - [\mu(t) + (n-1)\lambda(t)]\Delta t + o(\Delta t)$ during $(t, t+\Delta t)$.

To compute its expected payoff, a potential helper considers three outcomes:

1. The individual which is at risk was saved by him.

2. The individual which is at risk was saved by another potential helper.

3. The individual which is at risk has died.

We denote by P_1, P_2 and P_3 the probability for each of the described outcomes and by U_1, U_2 and U_3 the respective payoffs, where U_1, U_2, $U_3 \geq 0$.

A potential helper's expected payoff is:

$$E = U_1 P_1 + U_2 P_2 + U_3 P_3. \tag{1}$$

3 ESS Under the Full Information Structure

Under the full information structure each of the potential helpers knows all the strategies: the rate of dying and the potential helpers' entering rates, and is able to their realizations.

We assume that almost all the individuals in the population adopt the strategy I, defined by a continuous probability distribution function F. If a mutant player adopts the strategy J: "assist at t", then its expected payoff is:

$$
\begin{aligned}
E(J, I) &= U_1 \bar{Q}(t) \bar{F}(t)^{(n-2)} + U_2(n-2) \int_{s=0}^{t} \bar{Q}(s) \bar{F}(s)^{(n-3)} dF(s) \\
&+ U_3 \int_{s=0}^{t} \bar{F}(s)^{(n-2)} dQ(s)
\end{aligned}
\tag{2}
$$

where $Q(t)$ is the probability that the individual which is at risk died before t, $\bar{Q}(t) = 1 - Q(t)$ and $\bar{F}(t) = 1 - F(t)$.

To characterize the ESS of the game we study the properties of the mutant's expected payoff, using the result of Bishop et al. (1978) : if I is a mixed ESS, then a player's expected payoff is constant adopting any pure strategy which belongs to the support of I.

Differentiating equation (2) with respect to t we get:

$$
\frac{\partial E(J, I)}{\partial t} = [(U_2 - U_1)(n-2)]\bar{Q}(t)\bar{F}(t)^{(n-3)}dF(t) - [U_1 - U_3]\bar{F}(t)^{(n-2)}dQ(t)
\tag{3}
$$

The following propositions describe the ESS.

Proposition 3.1 *If $U_1 \geq \max\{U_2, U_3\}$, then the ESS is immediate assistance.*

Proof If $U_1 \geq \max\{U_2, U_3\}$, then $\frac{\partial E(J,I)}{\partial t} < 0 \ \forall t \geq 0$ and a potential helper's stable reply is to immediately assist. In equilibrium, all the potential helpers immediately enter the game and a random helper assists the individual which is at risk.

Proposition 3.2 *If $U_1 \leq \min\{U_2, U_3\}$, then the ESS is no assistance.*

Proof If $U_1 \leq \min\{U_2, U_3\}$, then $\frac{\partial E(J,I)}{\partial t} > 0 \ \forall t \geq 0$ and a potential helper's stable reply is to never assist. In equilibrium, none of the potential helpers assists the individual which is at risk and the ESS is no assistance.

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Proposition 3.3 *If $U_3 > U_1 > U_2$, then the possible ESS are no assistance and immediate assistance.*

Proof If $U_3 > U_1 > U_2$, then adopting the strategy "never assist" by all the potential helpers ensures the highest expected payoff, U_3. Adopting any different strategy decreases a potential helper's expected payoff, thus no assistance is a possible ESS.

If most of the individuals in the population adopt the strategy I: "immediately assist", then a potential helper's expected payoff is:

$$E(I, I) = U_1 \left[\frac{1}{n-1} \right] + U_2 \left[\frac{n-2}{n-1} \right].$$

Since $U_1 > U_2$, adopting any different strategy decreases a potential helper's expected payoff. Therefore, immediate assistance is a possible ESS.

If most of the individuals in the population adopt the strategy I: "assist at t, $0 < t < \infty$", then a potential helper's expected payoff is:

$$E(I, I) = \left[U_1 \frac{1}{n-1} + U_2 \frac{n-2}{n-1} \right] \bar{Q}(t) + U_3 Q(t). \tag{4}$$

Since $U_1 > U_2$, a mutant player can increase its expected payoff by assisting at $s = t - \Delta t$, and I cannot be an ESS.

Finally, we show that a strategy I, defined by a continuous probability distribution function cannot be an ESS. Let I be the common strategy in the population. If I is an ESS, then a potential helper is indifferent between adopting any different strategy. In addition, I should satisfy $E(J, J) < E(I, J) \ \forall J \in \text{supp}(F)$, where F is the probability distribution function defining I. If J is the strategy "never assist", then $E(J, J) = U_3$ and $E(J, I) = PU_2 + (1 - P)U_3$, where P is the probability that the individual which is at risk will be saved by another potential helper before it will die, $0 < P \leq 1$. Since $U_3 > U_2$, $E(J, J) > E(I, J)$ for all $0 < P \leq 1$ and I cannot be an ESS.

Proposition 3.4 *Let $U_2 > U_1 > U_3$. The probability distribution function defining a mixed ESS has the following properties:*

- *It is a strictly increasing continuous function.*

- *It has the non-negative half line as its support.*

Proof See Appendix A.

If I is a mixed ESS and if I is the common strategy in the population, then a potential helper's expected payoff is constant adopting any strategy. It follows from the last proposition that the probability distribution function defining a mixed ESS has the non-negative half line as its support. Thus, if I is a mixed ESS and J is the strategy "assist at t", then $E(J, I)$ satisfies:

$$\frac{\partial E(J, I)}{\partial t} = 0 \ \forall t \geq 0.$$

We find the mixed ESS candidates by solving $\frac{\partial E(J,I)}{\partial t} = 0$. Following from equation 3, solving $\frac{\partial E(J,I)}{\partial t} = 0$ yields,

$$\frac{dF(t)}{\bar{F}(t)} = \frac{dQ(t)}{\bar{Q}(t)} \left[\frac{U_1 - U_3}{(U_2 - U_1)(n - 2)} \right].$$

Let $\lambda(t) = \frac{dF(t)}{\bar{F}(t)}$ and note that $\mu(t) = \frac{dQ(t)}{\bar{Q}(t)}$, the equation $\frac{\partial E(J,I)}{\partial t} = 0$ has a unique solution which satisfies the requirements of proposition 3.4:

$$\lambda(t) = \mu(t) \left[\frac{U_1 - U_3}{(U_2 - U_1)(n - 2)} \right] \ \forall t \geq 0, \tag{5}$$

$\lambda(t)$ is the unique mixed ESS candidate.

Proposition 3.5 *If $U_2 > U_1 > U_3$, then the unique ESS of the game is delayed assistance defined by the following rate function:*

$$\lambda^*(t) = \mu(t) \left[\frac{U_1 - U_3}{(U_2 - U_1)(n - 2)} \right] \ \forall t \geq 0 \tag{6}$$

Proof See Appendix A.

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4 ESS Under the Partial Information Structure

Under the partial information structure each of the potential helpers knows all the strategies: the rate of dying and the potential helpers' entering rates, but it cannot observe their realizations.

We assume that almost all the individuals in the population adopt the strategy I, defined by a continuous probability distribution function G. Both "entering" the game and assisting accrue a cost. We denote the total cost by $c = \gamma c + (1 - \gamma)c$, $0 < \gamma < 1$, where γc is the cost accrued from entering the game and $(1 - \gamma)c$ is the cost accrued from assisting the individual which is at risk.

If a mutant player adopts the strategy J: "enter at t", then its expected payoff is:

$$
\begin{aligned}
E(J, I) &= [U_1 - (n-2)\gamma c]\bar{Q}(t)\bar{G}(t)^{(n-2)} + [U_2 - (n-2)\gamma c](n-2)\int_{s=0}^{t} \bar{Q}(s)\bar{G}(s)^{(n-3)}dG(s) \\
&+ [U_3 - (n-1)\gamma c]\int_{s=0}^{t} \bar{G}(s)^{(n-2)}dQ(s) \\
&= (U_1 + \gamma c)\bar{Q}(t)\bar{G}(t)^{(n-2)} + (U_2 + \gamma c)(n-2)\int_{s=0}^{t} \bar{Q}(s)\bar{G}(s)^{(n-3)}dG(s) \\
&+ U_3 \int_{s=0}^{t} \bar{G}(s)^{(n-2)}dQ(s) - (n-1)\gamma c.
\end{aligned}
$$

Let $\tilde{U}_1 = U_1 + \gamma c$ and let $\tilde{U}_2 = U_2 + \gamma c$, the mutant's expected payoff can be written as follows:

$$
\begin{aligned}
E(J, I) &= \tilde{U}_1 \bar{Q}(t)\bar{G}(t)^{(n-2)} + \tilde{U}_2(n-2)\int_{s=0}^{t} \bar{Q}(s)\bar{G}(s)^{(n-3)}dG(s) \\
&+ U_3 \int_{s=0}^{t} \bar{G}(s)^{(n-2)}dQ(s) - (n-1)\gamma c. \tag{7}
\end{aligned}
$$

If a mutant player adopts the strategy $\tilde{J}$: "never enter", then its expected payoff is:

$$
\begin{aligned}
E(\tilde{J}, I) &= [U_2 - (n-3)\gamma c]\int_{s=0}^{\infty} \bar{Q}(s)\bar{G}(t)^{(n-3)}dG(s) + [U_3 - (n-2)\gamma c]\int_{s=0}^{\infty} \bar{G}(t)^{(n-2)}dQ(s) \\
&= \tilde{U}_2 \int_{s=0}^{\infty} \bar{Q}(s)\bar{G}(s)^{(n-3)}dG(t) + U_3 \int_{s=0}^{\infty} \bar{G}(t)^{(n-2)}dQ(s) - (n-2)\gamma c. \tag{8}
\end{aligned}
$$

Proposition 4.1 *Under the partial information structure, the pure strategy "enter at t, $0 < t < \infty$" cannot be an ESS.*

Proof Assume that most of the individuals in the population adopt the strategy I, "enter at t, $0 < t < \infty$". A potential helper's expected payoff is:

$$E(I, I) = \left[\tilde{U}_1 \frac{1}{n-1} + \tilde{U}_2 \frac{n-2}{n-1} \right] \bar{Q}(t) + U_3 Q(t) - (n-1)\gamma c. \tag{9}$$

We show that a mutant player can increase its expected payoff by adopting a different strategy, considering each of the following cases:

- $\tilde{U}_1 > \max\{\tilde{U}_2, U_3\}$. If a mutant player adopts the pure strategy J: "immediately enter", then its expected payoff is:

$$E(J, I) = \tilde{U}_1 - (n-1)\gamma c$$

  hence, $E(J, I) > E(I, I)$ and I cannot be an ESS.

- $\tilde{U}_1 < \min\{\tilde{U}_2, U_3\}$. If a mutant player adopts the pure strategy J: "never enter", than its expected payoff is:

$$E(J, I) = \tilde{U}_2 \bar{Q}(t) + U_3 Q(t) - (n-1)\gamma c$$

  hence, $E(J, I) > E(I, I)$ and I cannot be an ESS.

- $\tilde{U}_2 > \tilde{U}_1 > U_3$. If a mutant player adopts the pure strategy J: "never enter", then its expected payoff is:

$$E(J, I) = \tilde{U}_2 \bar{Q}(t) + U_3 Q(t) - (n-1)\gamma c$$

  hence, $E(J, I) > E(I, I)$ and I cannot be an ESS.

- $U_3 > \tilde{U}_1 > \tilde{U}_2$. If a mutant player enters the game at $s = t - \Delta t$, then it increases its expected payoff and I cannot be an ESS.

Therefore, the only ESS candidates are "immediately enter" and "never enter".

We now find the ESS in each of the possible cases.

Proposition 4.2 *If $\tilde{U}_1 > \max\{\tilde{U}_2, U_3\}$, then:*

- *Where $\tilde{U}_2 + (n-1)\gamma c < \tilde{U}_1 < U_3 + \gamma c$, both immediate assistance and no assistance are possible ESS .*

- *Where $\tilde{U}_1 > \max\{\tilde{U}_2 + (n-1)\gamma c, U_3 + \gamma c\}$, immediate assistance is the unique ESS.*

- *Where $\tilde{U}_1 < \min\{\tilde{U}_2 + (n-1)\gamma c, U_3 + \gamma c\}$, no assistance is the unique ESS.*

- *Where $U_3 + \gamma c < \tilde{U}_1 < \tilde{U}_2 + (n-1)\gamma c$, there exist no ESS in the game.*

Proof We prove that $\tilde{U}_1 > \tilde{U}_2 + (n-1)\gamma c$ is a necessary condition for the strategy "immediately enter" to be an ESS, and that $\tilde{U}_1 < U_3 + \gamma c$ is a necessary condition for the strategy "never enter" to be an ESS. The proof of the proposition follows immediately.

If most of the individuals in the population adopt the strategy I: "immediately enter", then a potential helper's expected payoff is:

$$E(I, I) = \tilde{U}_1 \left[\frac{1}{n-1}\right] + \tilde{U}_2 \left[\frac{n-2}{n-1}\right] - (n-1)\gamma c. \tag{10}$$

If a mutant player adopts a different strategy, J, then its expected payoff is:

$$E(J, I) = \tilde{U}_2 - (n-2)\gamma c. \tag{11}$$

Following from equations 10 and 11, $E(I, I) > E(J, I) \; \forall J \neq I$ if and only if $\tilde{U}_1 > \tilde{U}_2 + (n-1)\gamma c$.

If most of the individuals in the population adopt the strategy I: "never enter", then a potential helper's expected payoff is:

$$E(I, I) = U_3. \tag{12}$$

If I is an ESS, then adopting any different strategy decreases the expected payoff. Since $\tilde{U}_1 > \max\{\tilde{U}_2, U_3\}$, the strategy that should yield the highest payoff is the pure strategy

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J: "immediately enter". If a mutant player adopts strategy J, then its expected payoff is:

$$E(J, I) = \tilde{U}_1 - \gamma c. \tag{13}$$

Following from equations 12 and 13, $E(I, I) > E(J, I)$ if and only if $\tilde{U}_1 < U_3 + \gamma c$.

Proposition 4.3 *If $\tilde{U}_1 < \min\{\tilde{U}_2, U_3\}$, then the unique ESS is no assistance.*

Proof If most of the individuals in the population adopt the strategy "never enter", then a potential helper's expected payoff equals U_3, and adopting any different strategy decreases a potential helper's expected payoff. In addition, the strategy "immediately enter" cannot be an ESS. Thus, no assistance is the unique ESS of the game.

Proposition 4.4 *If $\tilde{U}_2 > \tilde{U}_1 > U_3$, then if in addition $\tilde{U}_1 < U_3 + \gamma c$ then no assistance is an ESS, otherwise there exists no ESS in the game.*

Proof We first prove that "immediately enter" cannot be an ESS, and then prove that $\tilde{U}_1 < U_3 + \gamma c$ is a necessary condition for the strategy "never enter" to be an ESS. If most of the individuals in the population adopt the strategy I: "immediately enter", then a potential helper's expected payoff is:

$$E(I, I) = \tilde{U}_1 \left[\frac{1}{n-1}\right] + \tilde{U}_2 \left[\frac{n-2}{n-1}\right] - (n-1)\gamma c.$$

If a mutant player adopts a different strategy J, then its expected payoff is:

$$E(J, I) = \tilde{U}_2 - (n-2)\gamma c,$$

and $\tilde{U}_1 > \tilde{U}_2 + (n-1)\gamma c$ is a necessary condition for the strategy I to be an ESS. Since $\tilde{U}_1 < \tilde{U}_2$, this necessary condition cannot be satisfied, hence I cannot be an ESS.

If most of the individuals in the population adopt the strategy J: "never enter", then a potential helper's expected payoff is

$$E(J, J) = U_3.$$

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If a mutant player adopts the strategy I:"immediately enter", then its expected payoff is:

$$E(I, J) = \tilde{U}_1 - \gamma c.$$

Hence, a necessary condition for J to be an ESS is $\tilde{U}_1 < U_3 + \gamma c$.

Proposition 4.5 *If $U_3 > \tilde{U}_1 > \tilde{U}_2$, then no assistance is a possible ESS. If in addition, $\tilde{U}_1 > \tilde{U}_2 + (n-1)\gamma c$, then both no assistance and immediate assistance are possible ESS.*

Proof If most of the individuals in the population adopt strategy I: "never enter", a potential helper's expected payoff equals U_3, and adopting any different strategy decreases a players expected payoff. Thus, no assistance is a possible ESS in the game.

If most of the individuals in the population adopt the strategy I: "immediately enter", then a potential helper's expected payoff is as given by equation 10. If a mutant player adopts a different strategy J, then its expected payoff is:

$$E(J, I) = \tilde{U}_2 - (n-2)\gamma c.$$

Therefore, where $\tilde{U}_1 > \tilde{U}_2 + (n-1)\gamma c$, $E(I,I) > E(J,I)$ for all $J \neq I$ and I is a possible ESS.

4.1   Influence of Information Structure on the ESS

The cost accrued from a certain decision is different under each of the information structures, therefore a potential helper may behave differently under each of the information structures. We have assumed that both "entering" the game and assisting the individual which is at risk accrue a cost. Under the full information structure, each of the potential helpers can observe all the realizations, thus it enters the game only if the individual has not been saved yet and is still alive. Under the partial information structure, a potential helper cannot observe either of the realizations. Therefore, it

may enter the game and pay a cost, while the individual has already been saved or died.

We have shown, that under the full information structure no assistance, immediate assistance and delayed assistance are possible ESS. Under the partial information structure, delayed assistance cannot be an ESS. There are cases where immediate assistance is an ESS, but in most cases either there exist no ESS, or the ESS is no assistance. According to propositions 4.4 and 4.5, a necessary condition for "immediate assistance" to be an ESS is:

$$\tilde{U}_1 > \tilde{U}_2 + (n-1)\gamma c. \tag{14}$$

Since $\tilde{U}_1 = U_1 + \gamma c$ and $\tilde{U}_2 = U_2 + \gamma c$, this condition can be written as:

$$U_1 > U_2 + (n-1)\gamma c,$$

hence it is satisfied for $n < \frac{U_1 - U_2}{\gamma c} - 1$. The following proposition summarizes this result.

Proposition 4.6 *Under the partial information structure, if the number of group members, n, satisfies $n > \frac{U_1 - U_2}{\gamma c} - 1$, then immediate assistance cannot be an ESS of the game.*

Under the partial information structure, for a sufficiently large group either no assistance is the ESS, or there exists no ESS in the game.

In situations where ESS do not exist, one can think of a different type of strategy as an ESS candidate, a strategy which chooses with probability $0 < p < 1$ "immediately enter" and with the complement probability, $1 - p$, "never enter". Such a strategy is an ESS in the known Hawk-Dove game (Maynard Smith, 1982), it chooses "Hawk" with a certain probability and "Dove" with the complement probability. In the Hawk-Dove game, the evolutionary stability of such a strategy implies the stability of a genetic polymorphism with the suitable frequencies of pure "Hawk" and pure "Doves".

We show that in our game-theoretical model this type of strategy cannot be an ESS, thus there are situations where an ESS do not exist.

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Proposition 4.7 *Under the partial information structure, a strategy which chooses with probability $0 < p < 1$ "immediately enter" and with probability $1 - p$ "never enter" cannot be an ESS.*

Proof See Appendix B.

Under the full information structure, where delayed assistance is the ESS, a potential helper's stable entering rate is a decreasing function of the group size, and so is the total rate of entering. We show that where the group size tends to infinity, a potential helper's stable entering rate tends to zero, but the total entering rate tends to a positive and finite time dependent rate.

$$
\begin{aligned}
\lim_{n \to \infty} \lambda^*(t) &= \lim_{n \to \infty} \mu(t) \left[\frac{U_1 - U_3}{(n-2)(U_2 - U_1)} \right] = 0 \ \forall t \geq 0 \\
\lim_{n \to \infty} (n-1)\lambda^*(t) &= \lim_{n \to \infty} \mu(t) \left[\frac{(n-1)(U_1 - U_3)}{(n-2)(U_2 - U_1)} \right] = \lim_{n \to \infty} \mu(t) \left[1 - \frac{1}{n-2} \right] \left[\frac{U_1 - U_3}{U_2 - U_3} \right] \\
&= \mu(t) \left[\frac{U_1 - U_3}{U_2 - U_3} \right] \ \forall t \geq 0,
\end{aligned}
$$

where $0 < \mu(t) < \infty \ \forall t \geq 0$.

5 The n Brothers' Problem

In the n brothers' problem a member of n related individuals is at risk and needs the help of another member to be saved (Eshel and Motro, 1988; Motro and Eshel, 1988). It is assumed that all the group members have the same degree of relatedness. Let be $0 < r < 1$ the degree of relatedness between any two members. As long as assistance is not provided, the individual which is at risk has positive rate of dying, $0 < \mu(t) < \infty$ for all $t \geq 0$. A potential helper has a positive probability, $0 < c < 1$, for losing its life while "entering" the game and assisting this individual.

5.1 Equilibrium Under the Full Information Structure

Assume that almost all the individuals in the population adopt the strategy I, defined by a continuous probability distribution function F.

If a mutant player adopts the pure strategy J: "assist at t", then its immediate payoffs are: $1 - c$ if the individual which is at risk has been saved by him in t, $1 - rc$ if the individual which is at risk has been saved by another member before t, and $1 - r$ if the individual which is at risk has died before t. Therefore, substituting $U_1 = 1 - c$, $U_2 = 1 - rc$ and $U_3 = 1 - r$ in equation 2, the mutant's expected payoff is:

$$
\begin{aligned}
E(J, I) \quad = \quad & (1 - c)\bar{Q}(t)\bar{F}(t)^{(n-2)} + (1 - rc)(n - 2) \int_{s=0}^{t} \bar{Q}(s)\bar{F}(s)^{(n-3)} dF(s) \\
+ \quad & (1 - r) \int_{s=0}^{t} \bar{F}(s)^{(n-2)} dQ(s) \quad \quad (15)
\end{aligned}
$$

The following proposition describes the ESS.

Proposition 5.1 *Under the full information structure there exist two possible ESS:*

- *If the degree of relatedness is lower than the probability for losing one's life while entering the game and assisting, $r < c$, then the ESS is no assistance.*

- *If the degree of relatedness is greater than the probability for losing one's life while entering the game and assisting, $r > c$, then the ESS is delayed assistance and the stable entering rate is:*

$$
\lambda^*(t) = \mu(t) \left[\frac{r - c}{c(1 - r)(n - 2)} \right] \quad \forall t \geq 0.
$$

Proof If $c > r$, then $U_1 = (1 - c) < \min \{U_2 = (1 - rc), U_3 = (1 - r)\}$ and it follows from proposition 3.2 that the unique ESS is no assistance.

If $c < r$, then $U_2 = (1 - rc) > U_1 = (1 - c) > U_3 = (1 - r)$ and it follows from propositions 3.4 and 3.5, that the ESS is delayed assistance. Substituting $U_1 = (1 - c)$, $U_2 = (1 - rc)$ and $U_3 = (1 - r)$ in equation 6, the stable entering rate is:

$$
\lambda^*(t) = \mu(t) \left[\frac{r - c}{c(1 - r)(n - 2)} \right] \quad \forall t \geq 0. \quad \quad (16)
$$

5.2 Equilibrium Under the Partial Information Structure

Under the partial information structure a potential helper may enter the game and pay the accrued cost, while its assistance is not required, the individual which is at risk has been saved or died.

We denote by $0 < r < 1$ the degree of relatedness between two group members, by γc the cost accrued from "entering" the game and by $(1 - \gamma)c$ the cost accrued from assisting. The total cost is $c = \gamma c + (1 - \gamma)c$, $0 < \gamma < 1$ and $0 < c < 1$.

Assume that most of the individuals in the population adopt the strategy I defined by a continuous probability distribution function G, and that a mutant player adopts a pure strategy J: "enter at t". In this case each of the potential helpers will eventually enter the game and pay the accrued cost. The mutant's payoff from each of the possible outcomes are: $[1 - c - (n - 2)r\gamma c]$ if the individual which is at risk has been saved by him, $[1 - rc - \gamma c - (n - 3)r\gamma c]$ if the individual which is at risk has been saved by another helper, and $[1 - r - \gamma c - (n - 2)r\gamma c]$ if the individual which is at risk has died. Substituting these payoffs in equation 7, the mutant's expected payoff is,

$$
\begin{aligned}
E(J, I) &= \tilde{U}_1 \bar{Q}(t) \bar{G}(t)^{(n-2)} + \tilde{U}_2 (n - 2) \int_{s=0}^{t} \bar{Q}(s) \bar{G}(s)^{(n-3)} dG(s) \\
&+ U_3 \int_{s=0}^{t} \bar{G}(s)^{(n-2)} dQ(s) - \gamma c[1 + (n - 2)r],
\end{aligned}
\tag{17}
$$

where $\tilde{U}_1 = 1 - (1 - \gamma)c$, $\tilde{U}_2 = 1 - (1 - \gamma)rc$ and $U_3 = 1 - r$.

If a mutant adopts the pure strategy $\tilde{J}$: "never enter", then its expected payoff is:

$$
E(\tilde{J}, I) = \tilde{U}_2 (n-2) \int_{s_0}^{\infty} \bar{Q}(s) \bar{G}(s)^{(n-3)} dG(s) + U_3 \int_{s=0}^{\infty} \bar{G}(s)^{(n-2)} dQ(s) - (n-2)r\gamma c. \tag{18}
$$

The following proposition describes the ESS of the game.

Proposition 5.2 *Under the partial information structure, the ESS are characterized under each of the following situations:*

- *If the degree of relatedness is lower than the probability for losing one's life while entering the game and assisting, $r < c$, then the ESS is no assistance.*

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- *If the degree of relatedness is greater than the probability for losing one's life while entering the game and assisting, $r > c$, then there exists no ESS in the game.*

Proof If $r < (1-\gamma)c$, then $\tilde{U}_1 < \min\{\tilde{U}_2, U_3\}$ and it follows from proposition 4.3 that the unique ESS is no assistance.

If $r > (1-\gamma)c$, then $\tilde{U}_2 > \tilde{U}_1 > U_3$. If in addition $\tilde{U}_1 < U_3 + \gamma c$, then according to proposition 4.4 the ESS is no assistance, otherwise there exist no ESS.

In our case, $\tilde{U}_1 = 1 - (1-\gamma)c$ and $U_3 = 1 - r$, therefore if $(1-\gamma)c < r < c$, then the ESS is no assistance, and if $r > c$ then there exists no ESS in the game.

6   The Parental Investment Conflict

The parental investment conflict considers the question of how much each sex should invest in its own brood. We consider a symmetric two-stage game, based on the behavior observed in St. Peter's fish (Balshine-Earn, 1995; Balshine-Earn and Earn, 1997; Yaniv and Motro, 2004). During the game, each of the parents makes three decisions, two decisions in the first stage:

- Choosing the rate of entering the game, $\lambda(t)$.

- Choosing the amount of parental investment, $\alpha \in (0, 1]$,

and one decision in the second stage:

- Choosing the probability for cooperating, $0 \leq q \leq 1$.

Therefore, a parent's strategy is a three component vector, $(\lambda(t), \alpha, q)$.

It is assumed, that as long as none of the parents cares for the offspring the offspring have a positive rate of dying, $0 < \mu(t) < \infty$ for all $t \geq 0$, and that caring for the offspring accrues a constant cost. In addition, it assumed that each of the parents

is able to observed its mate's behavior, thus the ESS are computed under the full information structure.

To compute the ESS, we find a parent's stable decisions in each of the stages. The parent's stable entering rate is computed using the results from section 3. The ESS are the decisions that satisfy all the equilibrium conditions.

6.1   Stable Entering Rates

Let the second and the third decisions be known and given, and let W_1 be the expected payoff for a player that plays in the first stage, and let W_2 be the expected payoff for a player that plays in the second stage. It is assumed, that if the offspring have not survived then a parent's revenue equals zero.

Assume that most individuals of a population adopt the strategy I, defined by a continuous probability distribution function F, and that a mutant player adopts the pure strategy J: "assist at t". Substituting $U_1 = W_1$, $U_2 = W_2$ and $U_3 = 0$ in equation 2, the mutant's expected payoff is:

$$E(J, I) = W_1 \bar{Q}(t) \bar{F}(t) + W_2 \int_{s=0}^{t} \bar{Q}(s) dF(s), \tag{19}$$

where $Q(t)$ is the probability that the offspring died before t.

Proposition 6.1 *A parent's stable entering rate depends on the expected payoff from playing in the first stage, W_1, and on the expected payoff from playing in the second stage, W_2.*

- *If $W_1 \geq W_2$, then the stable strategy is to immediately assist.*

- *If $W_1 < W_2$, then the stable strategy is delayed assistance defined by the following rate function:*
$$\lambda^*(t) = \mu(t) \left[\frac{W_1}{W_2 - W_1} \right] \quad \forall t \geq 0.$$

Proof $W_1 \geq W_2$ implies $U_1 \geq U_2$ in the general model, and it follows from proposition 3.1 that immediate assistance is the stable strategy.

If $W_1 < W_2$, then according to proposition 3.5 delayed care is the stable strategy. Substituting $U_1 = W_1$, $U_2 = W_2$, $U_3 = 0$ and $n = 3$ in equation 6, the stable rate is:

$$\lambda^*(t) = \mu(t) \left[\frac{W_1}{W_2 - W_1} \right] \quad \forall t \geq 0. \tag{20}$$

6.2 Stable Amounts of Parental Investment

It is assumed that cooperation between the parents, biparental care, increases the number of surviving offspring (Fetherston et al., 1994; Balshine-Earn, 1995; Markman et al., 1996; Itzkowitz et al., 2001). It has been proven (Yaniv and Motro, 2004) that if biparental care increases the number of surviving offspring, then the possible stable strategy is either to choose $\alpha = 0.5$, or to choose $\alpha = 1$ in the first stage, and is either to fully cooperate, $q = 1$, or to desert, $q = 0$, in the second stage. Hence, a parent's strategy is: $(\lambda(t), p, q)$. $\lambda(t)$ is the rate of entering the game, p is the probability for choosing $\alpha = 0.5$ in the first stage, and q is the probability for cooperating.

Let $0 < \delta < 0.5$ be the advantage from cooperation. We assume that given biparental care the expected number of surviving offspring is 1. Given a full uniparental care, one of the parents chooses $\alpha = 1$, the expected number of surviving offspring is $1 - \delta$. Given a partial uniparental care, one of the parents chooses $\alpha = 0.5$ and the other deserts, the expected number of surviving offspring is 0.5

Denote by $0 < c < 1$ the cost accrued from parental caring, a parent's expected payoff in each of the stages is:

$$
\begin{aligned}
W_1 &= (1-p)(1-\delta-c) + p[q(1-c) + (1-q)(0.5-c)] \\
&= (1-\delta-c) + p[\delta - 0.5(1-q)], \tag{21} \\
W_2 &= (1-p)(1-\delta) + p[q(1-c) + (1-q)0.5] \\
&= (1-\delta) + p[\delta - 0.5 - q(c-0.5)]. \tag{22}
\end{aligned}
$$

The total expected payoff is:

$$E = W_1 P_1 + W_2 P_2, \tag{23}$$

where P_1 is the probability to play in the first stage, and P_2 is the probability to play in the second stage.

Stable Probability for Investing $\alpha = 0.5$

Let p be the common probability for choosing $\alpha = 0.5$ in the first stage, and denote by $\tilde{p} \neq p$ a mutant's probability. A mutant's expected payoff is:

$$E(\tilde{p}, p) = P_1\{(1 - c - \delta) + \tilde{p}[\delta - 0.5(1 - q)]\} + P_2 W_2. \tag{24}$$

The mutant's expected payoff, $E(\tilde{p}, p)$, is linear in $\tilde{p}$. Considering $P_1 > 0$, the stable probabilities are:

- If $\delta > 0.5(1 - q)$, then $p = 1$ (choose $\alpha = 0.5$).

- If $\delta < 0.5(1 - q)$, then $p = 0$ (choose $\alpha = 1$).

If $P_1 = 0$, then a player is indifferent between choosing $\alpha = 0.5$, or $\alpha = 1$.

Stable Probability for Cooperating

Let q be the common probability for cooperating, and denote by $\tilde{q} \neq q$ a mutant's probability. A mutant's expected payoff is:

$$E(\tilde{q}, q) = P_1 W_1 + P_2\{(1 - \delta) + p[\delta - 0.5 - \tilde{q}(c - 0.5)]\}. \tag{25}$$

The mutant's expected payoff, $E(\tilde{q}, q)$, is linear in $\tilde{q}$. Considering $P_2 > 0$ and $p > 0$, the stable probabilities are:

- If $c < 0.5$, then $q = 1$ (cooperate).

- If $c > 0.5$, then $q = 0$ (desert).

If $P_2 = 0$, or if $p = 0$, then a player is indifferent between cooperating, or deserting.

6.3 Equilibrium Under the Full Information Structure

The two following propositions describe the ESS.

Proposition 6.2 *If the cost accrued from parental care is low, $0 < c < 0.5$, then the ESS is immediate biparental care.*

Proof It follows from the last subsection that if $0 < c < 0.5$, then $q = 1$, which implies $p = 1$. In this case $W_1 = W_2 = 1 - c$ and according to proposition 3.1, the unique stable strategy is to immediately assist. The ESS in the game is immediate full cooperation and a parent's strategy vector is:

$$(\lambda^*(0) = \infty, p = 1, q = 1).$$

Both parents immediately "enter" the game and the amount of parental investment is equally divided between them.

Proposition 6.3 *If the cost accrued from parental care is high, $0.5 < c < 1$, and the advantage from cooperation is low, $0 < \delta < 1 - c$, then the ESS is delayed full uniparental care.*

Proof It follows from the last subsection that if $0.5 < c < 1$, then $q = 0$, which implies $p = 0$. In this case, $W_1 = 1 - \delta - c < W_2 = 1 - \delta$ and following from proposition 6.1 delayed care is the stable strategy. The stable rate function is:

$$\lambda^*(t) = \mu(t) \left[\frac{W_1}{W_2 - W_1} \right] = \mu(t) \left[\frac{1 - \delta - c}{c} \right] \quad \forall t \geq 0. \qquad (26)$$

A parent's stable strategy vector is:

$$(\lambda^*(t), p = 0, q = 0) \ \forall t \in (0, \infty).$$

7 Discussion

This paper considers the following type of animal conflicts: a member of a group sized $n \geq 3$ is at risk and needs the help of another individual to be saved. Assisting this individual accrues a cost, but losing it decreases the inclusive fitness of each group member. As long as assistance is not provided, the individual which is at risk has a positive and time dependent rate of dying. Each of the other group members is a potential helper. A potential helper's interval between the moment a group member finds itself at risk, and the moment it assists is a continuous random variable. Therefore, a potential helper's strategy is to a-priori choose the probability distribution function of this random variable.

We have developed a symmetric game-theoretical model, all the potential helpers have identical strategy sets and they all play the same role. We have assumed that each of the potential helpers knows all the strategies, and distinguished between two information structures, full information and partial information. Under the full information structure, each of the potential helpers can observe all the realizations. Under the partial information structure, a potential helper cannot observe the others' realizations. Our results show, that the information structure influences the ESS. If each of the players is able to observe all the realizations, then there always exists an ESS: immediate assistance, no assistance and delayed assistance. Fixation depends on a potential helper's payoff from each of the possible outcomes of the game. One of our results shows, that the "entering" rate function defining the mixed ESS is a linear function of the rate of dying. This result justifies limiting the potential helpers' strategy sets to time independent strategy sets, under the assumption of a constant rate of death (Motro and Eshel, 1988; Yaniv and Motro, 2004).

If the realizations cannot be observed, then there may not exist an ESS. Moreover, in most cases the only possible ESS is no assistance, immediate assistance is never an ESS in large groups.

The reason for these differences is the cost accrued from "entering" the game. If the realizations can be observed, then a potential helper "enters" the game and pays the accrued cost only if its assistance is required. If the realizations cannot be observed, then a potential helper may "enter" the game and pay the accrued cost, while its assistance is not required: the individual has already been saved or died. An important result is that the inability to observe the realizations decreases the chances of survival for the individual which is at risk.

The inability to observe the realizations significantly influences the ESS in the n brothers' problem. If the degree of relatedness is greater than the accrued cost and the realizations are observed, then the ESS is delayed assistance. If the realizations cannot be observed, then there exist no ESS. If the degree of relatedness is smaller than the accrued cost, then the ESS is no assistance regardless of the information structure.

In many situations the realizations are observed by each of the group members. In these situations each of the potential helpers can study the behavior of the others before making its own decision (Balshine-Earn and Earn, 1997; Silk, 2002a,b, 2003). In such cases, we expect the common behavior to be delayed assistance, however this is rarely observed. The observed behavior is usually immediate assistance (Silk, 2003). A possible explanation for such behavior is that the benefits arising from assisting exceed the payoffs arising from any other possible situation. For example, the benefits of a protector male arise not only from saving its own kin, but also from becoming more popular thereby increasing its mating opportunities.

In the parental investment conflict we have computed the ESS under the full information structure. Our results show that the possible ESS are immediate biparental care and delayed uniparental care. The ESS are influenced by the cost accrued from parental care and by the revenue arising from cooperation. St. Peter's fish exhibit an unusual example of delayed parental care (Balshine-Earn, 1995; Balshine-Earn and Earn, 1997). After mating both parents circle over the fertilized eggs before one of them starts picking up eggs for mouth incubation. In particular, neither parent is will-

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ing to pick up eggs until the other has committed itself, although both parents know that as long as the fertilized eggs are on the ground they can be destroyed.

The models that have been presented in this paper, have been applied to conflicts between related individuals. In the n brothers' problem, the degree of relatedness between two individual has been defined and affected each group member's inclusive fitness. In the parental investment conflict the parents are assumed to be non-related, but their offspring carry their genes. Thus losing the offspring decreases each parent's inclusive fitness. In both conflicts, the motivation for assisting arises from a genetic relatedness between the individual which is at risk and its potential helpers. One can think of similar situations, in which a genetic relatedness cannot be defined. If the group consists of non-related individuals, then assisting an individual which is at risk may ensure the helper a future assistance if it will find itself in the same situation. The death process may motivate the others to assist despite risking their own lives. Such a payoff function is presented in the repeated prisoner's dilemma, where strategies like Tit For Tat (TFT) are considered (Axelrod and Hamilton, 1981; Maynard Smith, 1984; Selten and Stoecker, 1986; Boyd and Lorberbaum, 1987; May, 1987; Farrell and Ware, 1989; Boyd, 1989; Lorberbaum, 1994). A similar situation is presented in Eshel and Shaked (2001), where partnership sometimes motivates mutual assistance between non-related individuals.

Appendix A

Proof of proposition 3.4

We first prove that the probability distribution function defining a mixed ESS is a strictly increasing function, and then we prove that its support contains no atoms of probability.

Assume that most of the individuals in the population adopt the mixed strategy I, defined by the probability distribution function F_1. Denote by $\mathcal{A}_1$ the support of F_1, $\mathcal{A}_1 = \{s : s \in \{(0, T_1) \cup (T_2, \infty]\}, T_1 < T_2\}$, where $F_1(T_1 < s < T_2) = 0$.

We show that a mutant player that adopts the strategy $\tilde{I}$, defined by probability distribution function, F_2, can improve its expected payoff if F_2 has the following properties:

- The support of F_2 is $\mathcal{A}_2 = \{s : s \in \{(0, T_1) \cup (T_2 + \delta, \infty)\}, \delta > 0\}$, where $F_2(T_1 < s < T_2 + \delta) = 0$.

- The Radon-Nikodym derivative of F_2 with respect to F_1 is:

$$\frac{dF_2}{dF_1} = \begin{cases} 1 & s \in (0, T_1) \\ C & s \in (T_2 + \delta, \infty], \end{cases}$$

  where $C > 1$.

Note that $\mathcal{A}_2 \subset \mathcal{A}_1$, and that F_2 stochastically dominates F_1. Let $\lambda(s)$ be the rate function defining F_1. For a sufficiently small δ ($0 < \delta < \frac{1}{\lambda(T_2 + \Delta t)}$), C is explicitly computed by solving the following equation:

$$\int_{s \in \mathcal{A}_2} dF_2(s) = \int_{s=0}^{T_1} dF_1(s) + C \int_{s=T_2+\delta}^{\infty} dF_1(s) = 1. \tag{27}$$

That is,

$$C = \frac{F_1(\bar{T}_1)}{F_2(\bar{T}_2 + \delta)} \cong \frac{F_1(\bar{T}_1)}{F_1(\bar{T}_2)(1 - \delta\lambda(T_2 + \Delta t))} = \frac{1}{1 - \delta\lambda(T_2 + \Delta t)}, \tag{28}$$

where $0 < \Delta t << \delta$. If most of the individuals in the population adopt the strategy I, then a potential helper's expected payoff is:

$$E(I, I) = [U_1 + U_2(n-2)] \int_{s \in \mathcal{A}_1} \bar{Q}(s)\bar{F}_1(s)^{n-2} dF_1(s) + U_3 \int_{s=0}^{\infty} \bar{F}_1(s)^{n-1} dQ(s). \tag{29}$$

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The mutant's expected payoff is:

$$E(\tilde{I}, I) = U_1 \int_{s \in \mathcal{A}_2} \bar{Q}(s) \bar{F}_1(s)^{n-2} dF_2(s) \tag{30}$$

$$+ U_2(n-2) \int_{s \in \mathcal{A}_1} \bar{Q}(s) \bar{F}_1(s)^{n-3} \bar{F}_2(s) dF_1(s) + U_3 \int_0^\infty \bar{F}_1(s)^{n-2} \bar{F}_2(s) dQ(s).$$

Therefore,

$$E(\tilde{I}, I) - E(I, I) = U_1 \{ C \int_{s=T_2+\delta}^\infty \bar{Q}(s) \bar{F}_1(s)^{(n-2)} dF_1(s) - \int_{s=T_2}^\infty \bar{Q}(s) \bar{F}_1(s)^{(n-2)} dF_1(s) \}$$

$$+ U_2(n-2) \int_{s=T_2}^\infty \bar{Q}(s) \bar{F}_1(s)^{(n-3)} [\bar{F}_2(s) - \bar{F}_1(s)] dF_1(s)$$

$$+ U_3 \int_{s=T_2}^\infty \bar{F}_1(s)^{(n-2)} [\bar{F}_2(s) - \bar{F}_1(s)] dQ(s).$$

Since F_2 stochastically dominates F_1 and since $U_1, U_2 > 0$, a sufficient condition for $E(\tilde{I}, I) - E(I, I) > 0$ is:

$$U_2(n-2) \int_{s=T_2}^\infty \bar{Q}(s) \bar{F}_1(s)^{(n-3)} [\bar{F}_2(s) - \bar{F}_1(s)] dF_1(s) - U_1 \int_{s=T_2}^\infty \bar{Q}(s) \bar{F}_1(s)^{(n-2)} dF_1(s) = 0. \tag{31}$$

For all $s \geq T_2$

$$\bar{F}_2(s) - \bar{F}_1(s) \doteq \frac{\lambda(T_2 + \Delta t)\delta}{1 - \lambda(T_2 + \Delta t)\delta} \bar{F}_1(s),$$

and the sufficient condition can be written as follows:

$$U_2(n-2) \frac{\lambda(T_2 + \Delta t)\delta}{1 - \lambda(T_2 + \Delta t)\delta} = U_1$$

or,

$$0 < \delta = \frac{U_1}{\lambda(T_2 + \Delta t)[U_1 + U_2(n-2)]} < \frac{1}{\lambda(T_2 + \Delta t)}.$$

If I is a mixed ESS, then the suitable probability distribution function is a strictly increasing function (its support contains no "gaps").

Let I be the common mixed strategy, defined by the probability distribution function F. Assume that there is a non-zero probability, P, for choosing a point t, $t \in \text{supp}(F)$. Let $E(J, I)$ be the expected payoff of a player that adopts the strategy J: "assist at t", and let $E(\tilde{J}, I)$ be the expected payoff of a player that adopts the strategy $\tilde{J}$ "assist at $t + \delta$".

If I is an ESS then, $E(J, I) = E(\tilde{J}, I) = \text{const}$ for all $\{\delta : t + \delta \in \text{supp}(F)\}$, and $E(J, I) > E(\tilde{J}, I)$ for all $\{\delta : t + \delta \notin \text{supp}(F)\}$. Considering the first case,

$$
\begin{aligned}
E(J, I) &= U_1 \bar{Q}(t) \bar{F}(t)^{(n-2)} + U_2(n-2)\{\int_{s=0}^{t} \bar{Q}(s) \bar{F}(s)^{(n-3)} dF(s) - \bar{Q}(t) P[\bar{F}(t) + P]^{(n-3)}\} \\
&\quad + U_3\{\int_{s=0}^{t} \bar{F}(s)^{(n-2)} dQ(s) - \bar{Q}(t)[\bar{F}(t) + P]^{(n-2)}\mu(t)\},
\end{aligned}
\tag{32}
$$

and

$$
\begin{aligned}
E(\tilde{J}, I) &= U_2(n-2)\int_{s=0}^{t+\delta} \bar{Q}(s) \bar{F}(s)^{(n-3)} dF(s) + U_1 \bar{Q}(t+\delta) \bar{F}(t+\delta)^{(n-2)} \\
&\quad + U_3 \int_{s=0}^{t+\delta} \bar{F}(s)^{(n-2)} dQ(s).
\end{aligned}
$$

Hence,

$$
\begin{aligned}
E(\tilde{J}, I) &> U_1 \bar{Q}(t+\delta) \bar{F}(t+\delta)^{(n-2)} + U_2(n-2)\int_{s=0}^{t} \bar{Q}(s) \bar{F}(s)^{(n-3)} dF(s) \\
&\quad + U_3 \int_{s=0}^{t} \bar{F}(s)^{(n-2)} dQ(s).
\end{aligned}
\tag{33}
$$

For a sufficiently small δ,

$$
\begin{aligned}
\bar{Q}(t+\delta) &= \bar{Q}(t)(1 - \delta\mu(t)). \\
\bar{F}(t+\delta)^{n-2} &= (\bar{F}(t) - \delta P)^{n-2} = \sum_{i=0}^{n-2} \binom{n-2}{i} (-\delta P)^i \bar{F}(t)^{n-2-i} \\
&= \bar{F}(t)^{n-2} - (n-2)\delta P \bar{F}(t)^{n-3} + o(\delta),
\end{aligned}
$$

where $o(\delta)$ satisfies $\lim_{\delta \to o} \frac{o(\delta)}{\delta} = 0$. Thus,

$$
\begin{aligned}
\bar{Q}(t+\delta) \bar{F}(t+\delta)^{n-2} &= \bar{Q}(t) \bar{F}(t)^{n-2} \\
&\quad - \delta \bar{Q}(t) \bar{F}(t)^{n-3}[P(n-2) + \mu(t)\bar{F}(t)] + o(\delta).
\end{aligned}
\tag{34}
$$

It follows from equations 32, 33 and 34 that a sufficient condition for $E(\tilde{J}, I) - E(J, I) > 0$ is

$$
\bar{Q}(t) \bar{F}(t)^{n-2} - \delta \bar{Q}(t) \bar{F}(t)^{n-3}[P(n-2) + \mu(t)\bar{F}(t)] \geq 0
$$

or,

$$
0 < \delta \leq \frac{\bar{F}(t)}{[P(n-2) + \mu(t)\bar{F}(t)]}
$$

There exist pure strategies that ensure a greater payoff, thus I cannot be an ESS.

We now prove that if I is a mixed ESS it cannot have an atom of probability in the right boundary of its support. Assuming that $t \in \text{supp}(F)$ and that for all $\delta > 0$, $t + \delta \notin \text{supp}(F)$. Let J be the strategy "assist at t" and let $\tilde{J}$ be the strategy "assist at $t + \delta$, the expected payoffs are:

$$
\begin{aligned}
E(J, I) &= U_2(n-2)\{\int_{s=0}^{t} \bar{Q}(s)\bar{F}(s)^{(n-3)}dF(s) - \bar{Q}(t)P^{(n-2)}\} + U_1\bar{Q}(t)P^{(n-2)} \\
&+ U_3\{\int_{s=0}^{t} \bar{F}(s)^{(n-2)}dQ(s) - \bar{Q}(t)\mu(t)P^{(n-2)}\}. \\
E(\tilde{J}, I) &= U_2(n-2)\int_{s=0}^{t} \bar{Q}(s)\bar{F}(s)^{(n-3)}dF(s) + U_3\int_{s=0}^{t} \bar{F}(s)^{(n-2)}dQ(s).
\end{aligned}
$$

Therefore,

$$
E(\tilde{J}, I) - E(J, I) = \bar{Q}(t)P^{(n-2)}[U_2(n-2) - U_1 + U_3\mu(t)]. \tag{35}
$$

Since $U_2 > U_1$, $E(\tilde{J}, I) - E(J, I) > 0$ for all $\delta > 0$ and I is not an ESS.

Proof of proposition 3.5 We first prove that if $U_2 > U_1 > U_3$, then no pure strategy can be an ESS.

If most of the individuals in the population adopt the pure strategy I: "immediately assist", then a potential helper's expected payoff is:

$$
E(I, I) = U_1\left[\frac{1}{n-1}\right] + U_2\left[\frac{n-2}{n-1}\right].
$$

Since $U_2 > U_1$, a mutant player can increase its expected payoff by adopting any different strategy, thus I cannot be an ESS.

If most of the individuals in the population adopt the pure strategy, I, "never assist", then a potential helper's expected payoff is

$$
E(I, I) = U_3,
$$

and a mutant player can increase its expected payoff by adopting any different strategy, thus I cannot be an ESS .

If most of the individuals in the population adopt the pure strategy I: "assist at t, $0 < t < \infty$, then a potential helper's expected payoff is

$$E(I, I) = \left[U_1 \frac{1}{(n-1)} + U_2 \frac{(n-2)}{(n-1)} \right] \bar{Q}(t) + U_3 Q(t),$$

and a mutant player can increase its expected payoff by adopting the pure strategy "never assist", thus I cannot be an ESS.

Finally, we prove that delayed assistance defined by $\lambda^*(t)$ is an ESS of the game. Let I be the mixed strategy defined by $\lambda^*(t)$. We have already shown that I satisfies $E(J, I) = \text{const}$, where J is "enter at t". Therefore, if I is an ESS it should satisfy:

$$E(I, J) > E(J, J).$$

We have already shown that if the common strategy J is "immediately assist" then adopting any different strategy, including I, increases the expected payoff. The same happens where the common strategy is "never assist". Therefore, we only have to prove that $E(I, J) > E(J, J)$, if J is the strategy "assist at t, $0 < t < \infty$".

We assume that the common strategy in the population is J, "assist at t, $0 < t < \infty$. Denoting by F the probability distribution function defined by $\lambda^*(t)$, the expected payoffs are:

$$E(I, J) = U_1 \int_{s=0}^{t} \bar{Q}(s) dF(s) + U_2 \bar{F}(s) \bar{Q}(s) + U_3 \int_{s=0}^{t} \bar{F}(s) dQ(s),$$

$$E(J, J) = \left[U_1 \frac{1}{(n-1)} + U_2 \frac{(n-2)}{(n-1)} \right] \bar{Q}(t) + U_3 Q(t).$$

Differentiating each of the payoffs with respect to t yields,

$$\frac{\partial t E(I, J)}{\partial t} = -(U_2 - U_1) \bar{Q}(t) dF(t) - (U_2 - U_3) \bar{F}(t) dQ(t),$$

$$\frac{\partial t E(J, J)}{\partial t} = -\left[(U_1 - U_3) \frac{1}{n-1} + (U_2 - U_3) \frac{n-2}{n-1} \right] dQ(t).$$

Since $U_2 > U_1 > U_3$, both payoffs decrease in t. In addition, $E(I, J) > E(J, J)$ if J is "immediately assist", or if J is "never assist".

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We now assume that the required inequality is not satisfied, that is, there exists a non-zero measure set of times $\{T\} = \{t : t_1 \leq t \leq t_2, t_1 < t_2\}$ such that for all $t \in \{T\}$, $E(J, J) \geq E(I, J)$ where J is "assist at t". Since both payoff functions are continuous in t, $E(J, J) = E(I, J)$ where J is "assist at t_1" or "assist at t_2". Therefore, the differentiations with respect to t of both payoffs are equal in t_1 and in t_2.

We show that these terms are equal only at one point in time, thus the required inequality is satisfied. Solving $\frac{\partial t E(I,J)}{\partial t} = \frac{\partial t E(J,J)}{\partial t}$ yields,

$$(U_2 - U_1)\bar{Q}(t)dF(t) + (U_2 - U_3)\bar{F}(t)dQ(t) = \left[(U_1 - U_3)\frac{1}{n-1} + (U_2 - U_3)\frac{n-2}{n-1} \right] dQ(t).$$

Since $\lambda^*(t) = \mu(t)\frac{U_1 - U_3}{(U_2 - U_1)(n-2)}$, we get $dF(t) = \mu(t)\frac{U_1 - U_3}{(U_2 - U_1)(n-2)}\bar{F}(t)$. Dividing both sides of the last equation by $\bar{Q}(t)$, and substituting $dF(t)$, if both payoffs are equal in time t, then t necessarily satisfies,

$$\bar{F}(t) = \frac{n-2}{n-1}. \tag{36}$$

Since $\bar{F}(t)$ is continuous and a decreasing function of t, there exists exactly one point in time that solves equation 36. Therefore, there exists no non-zero measure set of times, $\{T\}$, such that $E(J, J) > E(I, J) \; \forall t \in \{T\}$. Strategy I satisfies the required inequality, and it is the unique ESS of the game.

Appendix B

Proof of proposition 4.7

We first find the ESS candidates and then show that these candidates cannot be an ESS.

Assume that most of the individuals in the population adopt the strategy I, which chooses with probability $0 < p < 1$ "immediately enter" and with probability $1 - p$ "never enter". If a mutant player adopts a different strategy J, which chooses with probability $\tilde{p} \neq p$ "immediately enter" and with $1 - \tilde{p}$ "never enter", then its expected payoff is:

$$E(J, I) = \tilde{p}p\left[\tilde{U}_1\frac{1}{n-1} + \tilde{U}_2\frac{n-2}{n-1} - (n-1)\gamma c \right] + \tilde{p}(1-p)[\tilde{U}_1 - \gamma c]$$

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$$+ \quad (1 - \tilde{p})p[\tilde{U}_2 - (n - 2)\gamma c] + (1 - \tilde{p})(1 - p)U_3,$$

where $\tilde{U}_1 = U_1 + \gamma c$ and $\tilde{U}_2 = U_2 + \gamma c$. Differentiating the mutant's expected payoff with respect to $\tilde{p}$ yields,

$$\frac{\partial E(J, I)}{\partial \tilde{p}} = p\left[\frac{\tilde{U}_1 - \tilde{U}_2}{n - 1} - \gamma c\right] + (1 - p)[\tilde{U}_1 - \gamma c - U_3] \tag{37}$$

Therefore, there exists an ESS candidate only if $\tilde{U}_2 + (n - 1)\gamma c < \tilde{U}_1 < U_3 + \gamma c$ or if $U_3 + \gamma c < \tilde{U}_1 < \tilde{U}_2 + (n - 1)\gamma c$. The ESS candidate chooses "immediately enter" with probability

$$p^* = \frac{U_3 - \tilde{U}_1 + \gamma c}{\frac{\tilde{U}_1 - \tilde{U}_2}{n - 1} + U_3 - \tilde{U}_1}. \tag{38}$$

Let $\tilde{U}_2 + (n - 1)\gamma c < \tilde{U}_1 < U_3 + \gamma c$, and denote by I the ESS candidate defined by p^*. If I is an ESS and if I is the common strategy in the population, then a potential helper is indifferent between choosing "immediately enter" and "never enter". In addition, I should satisfy the stability condition $E(I, J) > E(J, J)$, where J is either "immediately enter", or "never enter".

If J is "never enter", then

$$E(J, J) = U_3$$

and,

$$E(I, J) = p^*(\tilde{U}_1 - \gamma c) + (1 - p^*)U_3.$$

Since $\tilde{U}_1 < U_3 + \gamma c$, $E(J, J) > E(I, J)$ the stability condition is not satisfied, and I cannot be an ESS.

Let $U_3 + \gamma c < \tilde{U}_1 < \tilde{U}_2 + (n - 1)\gamma c$. If I is an ESS and if I is the common strategy in the population, then a potential helper's expected payoff is:

$$E(I, I) = E(J, I) = p^*[\tilde{U}_2 - (n - 2)\gamma c] + (1 - p^*)U_3,$$

where J is "never enter". If a mutant player adopts the strategy $\tilde{J}$, "enter at t, $0 < t < \infty$", then its expected payoff is:

$$E(\tilde{J}, I) \quad = \quad p^*[\tilde{U}_2 - (n - 2)\gamma c] + (1 - p^*)[\bar{Q}(t)\tilde{U}_1 + Q(t)U_3] - \gamma c,$$

$$= p^*[\tilde{U}_2 - (n-2)\gamma c] + (1-p^*)\bar{Q}(t)(\tilde{U}_1 - U_3) + (1-p^*)U_3 - \gamma c.$$

We show that $E(\tilde{J}, I) > E(I, I)$ for all $t > 0$ that satisfies:

$$\bar{Q}(t) > \frac{\gamma c}{(1-p^*)(\tilde{U}_1 - U_3)}.$$

Since

$$1 - p^* = \frac{\frac{\tilde{U}_1 - \tilde{U}_2}{n-1} - \gamma c}{\frac{\tilde{U}_1 - \tilde{U}_2}{n-1} + U_3 - \tilde{U}_1},$$

and since $\tilde{U}_1 > U_3 + \gamma c$ we get,

$$0 < \frac{\gamma c}{(1-p^*)(\tilde{U}_1 - U_3)} < 1.$$

Let t^* satisfy

$$\bar{Q}(t^*) = \frac{\gamma c}{(1-p^*)(\tilde{U}_1 - U_3)}$$

Adopting the strategy "enter at t^*" ensures the same payoff as adopting the strategy strategy I. Since $\bar{Q}(t)$ decreases in t, adopting the strategy "enter at t" , $0 < t < t^*$ ensures a greater payoff than adopting strategy I. Therefore, I cannot be an ESS.

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