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Time-dependent animal conflicts: 2. The asymmetric case

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Abstract

This paper presents an asymmetric game-theoretical model to the following type of animal conflicts: a member of a group 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, time-dependent rate of dying. Assisting the individual which is at risk accrues a cost, but losing it decreases each member's inclusive fitness. A potential helper's interval between the moment a group member gets into trouble and the moment it assists is a random variable, hence its strategy is to choose the distribution of this random variable. In the asymmetric conflict all the potential helpers have identical strategy sets, but each plays a different role. For example, male or female and young or old. We consider both payoff-irrelevant asymmetry and payoff-relevant asymmetry and characterize each role's stable replies. The evolutionarily stable strategies (ESS) are computed, and the model is applied to the n brothers' problem. According to our results immediate assistance and no assistance are possible ESS both under payoff-relevant asymmetry and under payoff-relevant asymmetry.

Keywords: ESS; Asymmetric conflict; Time-dependent strategy sets

1. Introduction

In asymmetric animal conflicts each of the players is randomly chosen to play a different role during a certain contest (Maynard Smith and Parker, 1976; Selten, 1980; Hammerstein, 1981). For example, owner or intruder in the war of attrition (Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982), male or female 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; McNamara et al., 2000; Barta et al., 2002; McNamara et al., 2003; Yaniv and Motro, 2004a), and older brother and younger brother in the three brothers' problem (Eshel and Motro, 1988; Motro and Eshel, 1988).

It has been shown, that any asymmetry between the players affects their evolutoinarily stable strategies (ESS) (Maynard Smith and Parker, 1976; Selten, 1980). For example, in the symmetric war of attrition mixed ESS exist (Bishop and Cannings, 1978; Bishop et al., 1978), while in the asymmetric war of attrition there may exist no ESS (Maynard Smith and Parker, 1976; Selten, 1980; Hammerstein and Parker, 1982).

We consider the following type of animal conflicts: a member of $n \geqslant 3$ 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, time-dependent rate of dying. Each of the other group members is a potential helper. Assisting this individual accrues a cost, but losing it 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. Thus, a potential helper's strategy is to choose the probability distribution function of this random variable. Note that in such conflicts the death process of the individual which is at risk motivates the potential helpers to make their decisions.

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In our previous paper (Yaniv and Motro, 2004b), we have presented a symmetric game-theoretical model for this type of animal conflicts, and characterized the ESS given two information structures. In this paper, we develop an asymmetric game-theoretical model for this type of animal conflicts considering a full information structure, each of the players knows all the strategies and is able to observe their realizations. It is assumed that all the potential helpers have identical strategy sets but each plays a different role. First we describe each role's stable replies, and then we compute the ESS. We apply the model to the n brothers' problem and the ESS are characterized both under payoff-irrelevant asymmetry and under payoff-relevant asymmetry.

According to our results, ESS always exist both under payoff-irrelevant and under payoff-relevant asymmetry. No assistance and immediate assistance are possible ESS. Fixation depends on each role's payoff from each possible outcome of the game.

2. The model

A member of a group, sized $n \geqslant 3$, is at risk and needs the help of another member to be saved. Assisting the individual which is at risk 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 time-dependent rate of dying, $0 < \mu(t) < \infty$ for all $t \geqslant 0$. This rate function defines a continuous probability distribution function with the nonnegative half line as its support.

A potential helper's interval between the beginning of the game and the moment it "enters" the game and assists is a continuous random variable. Hence, its strategy is to a priori choose the probability distribution function of this random variable.

We make the following assumptions:

(1) At the beginning of the game, each of the potential helpers is randomly chosen to play one of $K = n - 1$ different roles.
(2) Two or more potential helpers never play the same role simultaneously.
(3) A single gene determines a single decision of a certain role.
(4) Each of the potential helpers carries a gene for each decision of each role.
(5) The genes are independent (unlinked).
(6) A mutation can only appear in one gene at a time.
(7) The behavior of each group member is described by a non-homogeneous Poisson process, thus a potential helper's strategy is the same as to choose its "entering" rate function.

The moment a group member finds himself at risk, $t = 0$, n non-homogeneous Poisson processes occur simultaneously. If at time t the individual which is at risk has not been saved yet and is still alive, then one of the following events can happen during $(t, t + \Delta t)$: the individual dies with probability $\mu(t)\Delta t + o(\Delta t)$, a potential helper playing role k saves the individual with probability $\lambda_k(t)\Delta t + o(\Delta t)$. None of these events happens with probability $1 - [\mu(t) + \sum_{k \in K} \lambda_k(t)]\Delta t + o(\Delta t)$ during $(t, t + \Delta t)$.

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

- The individual which is at risk was saved by him.
- The individual which is at risk was saved by another potential helper (playing another role).
- The individual which is at risk has died.

Let P_1^k, P_2^k and P_3^k be the probabilities of each of the described outcomes for a player playing role k, and let U_1^k, U_2^k and U_3^k be the respective payoffs.

A potential helper's expected payoff from playing role k is

$$E_k = U_1^k P_1^k + U_2^k P_2^k + U_3^k P_3^k. \tag{1}$$

A pure strategy determines the exact "entering" point in time, a degenerated random variable. A mixed strategy is defined by a continuous probability distribution function. Since a potential helper is randomly chosen to play a role in a certain situation, we denote its strategy by $M = (m_1, m_2, \ldots, m_K)$: "play m_1 in role 1, play m_2 in role 2" and so on, where m_k is either pure, or mixed. A potential helper's behavior in a certain situation is determined by the role it plays, thus its behavioral strategy is a component in its strategy vector.

To compute the ESS in the game, we find each role's stable reply function. The stable reply function returns a role's stable strategy given the other roles' strategies. The ESS are represented by some of the intersection points between the different roles' stable reply functions.

Role k's stable reply is computed as follows:

- Assume that almost all the individuals in the population adopt the mixed strategy, M, which defines a continuous probability distribution function for each of the roles, and denote by m_k role k's strategy.
- Assume that a mutant player playing role k adopts the strategy "assist at t", where the strategies of the other roles are the common strategies.
- Study the properties of a potential helper's expected payoff from playing role k and adopting the mutant's strategy.

Note that if M is an ESS, then player k's expected payoff is constant, regardless of the strategy it adopts (Bishop et al., 1978). According to our assumptions, a single gene determines the strategy of a certain role and a mutation can only appear in one gene at a time. Therefore, if a mutation occurs in the gene which determines the behavioral strategy of role k, then it only affects the potential helper's expected payoff from playing role k, as in all the other roles the potential helper adopts the common strategies.

2.1. A potential helper's stable replies

Each of the potential helpers knows the others' strategies: the rate of dying and the entering rates of all roles, and is able to observe each of the realizations.

If a player playing role k adopts the strategy $\tilde{m}_k$: "assist at t", then its expected payoff from playing role k is

$$E_k(\tilde{m}_k, M) = U_1^k \bar{Q}(t)\left(\prod_{i\neq k}\bar{F}_i(t)\right) + U_2^k \sum_{j\neq k}\int_{s=0}^{t}\bar{Q}(s)\left(\prod_{i\neq j,k}\bar{F}_i(s)\right)\mathrm{d}F_j(s) + U_3^k\int_{s=0}^{t}\left(\prod_{i\neq k}\bar{F}_i(s)\right)\mathrm{d}Q(s), \quad (2)$$

where $Q(t)$ is the probability that the individual which is at risk died before t, and $F_i(t)$ is the probability that a player playing role i assisted the before t. In addition, $\bar{Q}(t) = 1 - Q(t)$ and $\bar{F}(t) = 1 - F(t)$.

Differentiating the last equation with respect to t we get:

$$\begin{aligned}\frac{\partial E_k(\tilde{m}_k, M)}{\partial t} &= U_2^k\bar{Q}(t)\sum_{j\neq k}\left(\prod_{i\neq j,k}\bar{F}_i(t)\right)\mathrm{d}F_j(t) + U_3^k\left(\prod_{i\neq k}\bar{F}_i(t)\right)\mathrm{d}Q(t) \\ &\quad - U_1^k\left\{\left(\prod_{i\neq k}\bar{F}_i(t)\right)\mathrm{d}Q(t) + \bar{Q}(t)\sum_{j\neq k}\left(\prod_{i\neq j,k}\bar{F}_i(t)\right)\mathrm{d}F_j(t)\right\} \\ &= (U_2^k - U_1^k)\bar{Q}(t)\sum_{j\neq k}\left(\prod_{i\neq j,k}\bar{F}_i(t)\right)\mathrm{d}F_j(t) - (U_1^k - U_3^k)\left(\prod_{i\neq k}\bar{F}_i(t)\right)\mathrm{d}Q(t).\end{aligned}$$

Proposition 2.1. *If $U_1^k \geqslant \max(U_2^k, U_3^k)$, then role k's stable reply is to immediately assist.*

Proof. If $U_1^k \geqslant \max(U_2^k, U_3^k)$, then $\partial E_k(\tilde{m}_k, M)/\partial t < 0$ for all $t \geqslant 0$ and the player's stable reply is to immediately assist. □

Proposition 2.2. *If $U_1^k \leqslant \min(U_2^k, U_3^k)$, then role k's stable reply is to never assist.*

Proof. If $U_1^k \leqslant \min(U_2^k, U_3^k)$, then $\partial E_k(\tilde{m}_k, M)/\partial t > 0$ for all $t \geqslant 0$ and the player's stable reply is to never assist. □

To find the mutant's stable replies in the other cases, $U_2^k > U_1^k > U_3^k$ and $U_3^k > U_1^k > U_2^k$, we study the properties of role k's instantaneous expected payoff from entering the game during $(t, t+\Delta t)$. We denote role k's instantaneous expected payoff by $\Delta E_k(\tilde{m}_k, M)$ and compute it by dividing $\partial E_k(\tilde{m}_k, M)/\partial t$ by $(\Pi_{j\neq k}\bar{F}_j(t))\bar{Q}(t)$,

$$\Delta E_k(\tilde{m}_k, M) = (U_2^k - U_1^k)\sum_{j\neq k}\frac{\mathrm{d}F_j(t)}{\bar{F}_j(t)} - (U_1^k - U_3^k)\frac{\mathrm{d}Q(t)}{\bar{Q}(t)}.$$

Let $\mathrm{d}F_j(t)/\bar{F}_j(t) = \lambda_j(t)$ and note that $\mathrm{d}Q(t)/\bar{Q}(t) = \mu(t)$, role k's instantaneous expected payoff can be written as

$$\Delta E_k(\tilde{m}_k, M) = (U_2^k - U_1^k)\sum_{j\neq k}\lambda_j(t) - (U_1^k - U_3^k)\mu(t). \quad (3)$$

According to Selten (1980), the ESS of the game are necessarily pure, therefore we only present role k's stable replies with respect to possible situations resulting from the others adopting pure strategies.

Proposition 2.3. *Given $U_2^k > U_1^k > U_3^k$, role k's stable reply depends on the other roles' strategies*:

- *If at least one of the other potential helpers immediately assists, then role k's stable reply is to never assist.*
- *If all the other potential helpers never assist, then role k's stable reply is to immediately assist.*
- *Denote by T_c the point in time which satisfies*:

  $$\bar{Q}(T_c) = \frac{U_1^k - U_3^k}{U_2^k - U_3^k}.$$

  If none of the other potential helpers immediately assists and there exists a positive and finite point in time, T, at which the assistance is given by one of the other potential helpers, then role k's stable reply is
  (1) *Immediately assist where $T > T_c$.*
  (2) *Never assist where $T < T_c$.*

Proof. See Appendix A. □

Proposition 2.4. *Given $U_3^k > U_1^k > U_2^k$, role k's stable reply depends on the other roles' strategies*:

- *If at least one of the other potential helpers immediately assists, then role k's stable reply is to immediately assist.*
- *If none of the other potential helpers immediately assists, then role k's stable reply is to never assist.*

Proof. See Appendix A. □

2.2. Equilibrium

The following proposition describes the ESS considering a payoff-irrelevant asymmetry, all roles have identical payoff from the same outcome, $U_1^k = U_1$, $U_2^k = U_2$ and $U_3^k = U_3$ for all $k \in K$.

Proposition 2.5. *The ESS are determined by the payoffs from the different outcomes*:

- *If* $U_1 \leqslant \min\{U_2, U_3\}$, *then the ESS is no assistance.*
- *If* $U_1 \geqslant \max\{U_2, U_3\}$, *then the ESS is*: *all roles immediately enter the game and a random role assists.*
- *If* $U_2 > U_1 > U_3$, *then the ESS is*: *a random role immediately assist*, *while the others never assist.*
- *If* $U_3 > U_1 > U_2$ *then the ESS are either all roles immediately enter the game and a random role assists*, *or no assistance.*

Proof. See Appendix A. □

In cases where the ESS is no assistance, a potential helper's payoff is U_3. In cases where the ESS is immediate assistance by a random role, a potential helper's expected payoff is

$$E = \frac{U_1 + (n-2)U_2}{n-1}.$$

Considering a payoff-relevant asymmetry: each role has a different payoff from the same outcome, each role's stable reply is influenced both by the ratio between its own payoffs, and by the behavior of the other roles. In the general case, ESS cannot be computed explicitly, as they are represented by some of the intersection points between all roles' stable reply functions. In the next section we characterize the ESS in the n brothers' problem under payoff-relevant asymmetry and under payoff-irrelevant asymmetry.

3. The *n* brothers' problem

A member of $n \geqslant 3$ related individuals is at risk and needs the help of another member to be saved. Assisting this individual accrues a cost. We denote by $0 < r < 1$ the degree of relatedness between two members. First, we present the ESS assuming that assisting the individual which is at risk accrues a different cost for each role. Later, we present the ESS assuming that assisting the individual which is at risk accrues identical costs for all roles.

3.1. Equilibrium considering payoff-relevant asymmetry

Assisting the individual which is at risk accrues a different cost for each role, a payoff-relevant asymmetry. We denote by $0 < c_k < 1$ role k's probability for losing its life while assisting.

The expected payoff from playing role k and adopting the strategy $\tilde{m}_k$: "assist at t" is

$$\begin{aligned} E_k(\tilde{m}_k, M) = {} & (1-c_k)\bar{Q}(s)\left(\prod_{i \neq k} \bar{F}_i(s)\right) \\ & + \sum_{j \neq k} (1 - rc_j) \\ & \times \int_{s=0}^{t} \bar{Q}(s)\left(\prod_{i \neq j,k} \bar{F}_i(s)\right) \mathrm{d}F_j(s) \\ & + (1-r)\int_{s=0}^{t}\left(\prod_{i \neq k} \bar{F}_i(s)\right) \mathrm{d}Q(s). \end{aligned} \tag{4}$$

The following propositions describe role k's stable replies.

Proposition 3.1. *If* $c_k/\min_{j \neq k}\{c_j\} < r$, *then role k's stable reply is to immediately assist.*

Proof. We explicitly compute U_1^k, U_2^k and U_3^k. In the payoff-relevant asymmetric model:

$$\begin{aligned} U_2^k = {} & \frac{\sum_{j \neq k}(1-rc_j)\int_{s=0}^{t}\bar{Q}(s)(\prod_{i \neq j,k}\bar{F}_i(s))\,\mathrm{d}F_j(s)}{\sum_{j \neq k}\int_{s=0}^{t}\bar{Q}(s)(\prod_{i \neq j,k}\bar{F}_i(s))\,\mathrm{d}F_j(s)} \\ & \leqslant \max_{j \neq k}\{1 - rc_j\} = 1 - r\min_{j \neq k}\{c_j\}, \end{aligned}$$

$U_1^k = 1 - c_k$ and $U_3^k = 1 - r$. Since $c_k/\min_{j \neq k}\{c_j\} < r$, we get $U_1^k > 1 - r\min_{j \neq k}\{c_j\} \geqslant U_2^k > U_3^k$ and following from Proposition 2.1 player k's stable reply is to immediately assist. □

Proposition 3.2. *If* $r < c_k$, *then role k's stable reply is to never assist.*

Proof. We explicitly compute U_1^k, U_2^k and U_3^k. In the payoff-relevant asymmetric model:

$$\begin{aligned} U_2^k = {} & \frac{\sum_{j \neq k}(1-rc_j)\int_{s=0}^{t}\bar{Q}(s)\prod_{i \neq j,k}\bar{F}_i(s)\,\mathrm{d}F_j(s)}{\sum_{j \neq k}\int_{s=0}^{t}\bar{Q}(s)\prod_{i \neq j,k}\bar{F}_i(s)\,\mathrm{d}F_j(s)} \\ & \geqslant \min_{j \neq k}\{1 - rc_j\} = 1 - r\max_{j \neq k}\{c_j\}, \end{aligned}$$

$U_1^k = 1 - c_k$ and $U_3^k = 1 - r$. Since $r < c_k$, we get $U_2^k \geqslant 1 - r\max_{j \neq k}\{c_j\} > U_3^k > U_1^k$ and following from Proposition 2.2 player k's stable reply is to never assist. □

Proposition 3.3. *If* $c_k < r < c_k/\max_{j \neq k}\{c_j\}$, *then role k's stable replies are*:

- *If at least one of the other potential helpers immediately assists*, *then role k's stable reply is to never assist.*
- *If all the other potential helpers never assist*, *then role k's stable reply is to immediately assist.*

- *Denote by T_c the point in time which satisfies*

  $$\bar{Q}(T_c) = \frac{U_1^k - U_3^k}{U_2^k - U_3^k}.$$

  If there exists a positive and finite point in time, T, at which the assistance is given by one of the other potential helpers, then role k's stable reply is
  (1) *Immediately assist where $T > T_c$.*
  (2) *Never assist where $T < T_c$.*

Proof. If $c_k < r < c_k / \max_{j \neq k}\{c_j\}$, then using the same technique as in the proof of Proposition 3.2 it can be shown that $U_2^k \geqslant 1 - r\max_{j \neq k}\{c_j\} > U_1^k > U_3^k$, hence role k's stable replies are as described in Proposition 2.3. □

The following proposition describes the ESS.

Proposition 3.4. *The ESS in the game are determined by the ratio between the degree of relatedness, r, and lowest cost accrued from assisting, $\min_{k \in K}\{c_k\}$.*

- *If $r < \min_{k \in K}\{c_k\}$, then the ESS is no assistance.*
- *If $r > \min_{k \in K}\{c_k\}$, then the ESS is: the role accruing the lowest cost immediately assists and the other roles never assist.*

Proof. If $r < \min_{k \in K}\{c_k\}$, then following from Proposition 3.2 all roles' stable replies are to never assist, and the ESS is no assistance. In this case, all the roles have identical payoffs, $(1 - r)$.

Let $c_{(1)} = \min_{k \in K}\{c_k\}$. If $r > c_{(1)}$, then $r > c_{(1)} / \min_{j > (1)}\{c_j\}$ and it follows from Proposition 3.1 that the stable reply of the role accruing the lowest cost is to immediately assist. In this case, it follows from Propositions 3.2 and 3.3 that the other roles' stable replies are to never assist. In equilibrium, the expected payoff of the role accruing the lowest cost is $(1 - c_{(1)})$, while each of the other roles' expected payoff is $(1 - rc_{(1)})$. □

3.2. Equilibrium considering payoff-irrelevant asymmetry

Assisting the individual which is at risk accrues identical costs for all the roles, each of the roles has the same probability of losing its life while assisting, $0 < c < 1$. Hence, each of the roles has the same payoff from a certain outcome: $U_1 = 1 - c$ where the individual which is at risk was saved by him, $U_2 = 1 - rc$ where the individual which is at risk was saved by another potential helper and $U_3 = 1 - r$ where the individual which is at risk has died. Substituting $U_1^k = 1 - c$, $U_2^k = 1 - rc$ and $U_3^k = 1 - r$ in Eq. (2), the expected payoff from playing role k and adopting the pure strategy $\tilde{m}_k$: "assist at t" is

$$E_k(\tilde{m}_k, M) = (1 - c)\bar{Q}(t)\left(\prod_{i \neq k} \bar{F}_i(t)\right) + (1 - rc)\sum_{j \neq k}\int_{s=0}^{t} \bar{Q}(s)\left(\prod_{i \neq j,k} \bar{F}_i(s)\right) \mathrm{d}F_j(s) + (1 - r)\int_{s=0}^{t}\left(\prod_{i \neq k} \bar{F}_i(s)\right) \mathrm{d}Q(s). \quad (5)$$

Note that if $K = 2$, i.e. there are only two potential helpers, then this equation is similar to a potential helper's expected payoff adopting the strategy "assist at t" in the symmetric model with full information.

The following proposition describes the possible ESS.

Proposition 3.5. *The ESS in the game are determined by the ratio between the degree of relatedness, r, and cost accrued from assisting, c.*

- *If the cost accrued from assisting is greater than the degree of relatedness, $c > r$, then the ESS is no assistance.*
- *If the cost accrued from assisting is lower than the degree of relatedness, $c < r$, then the ESS is: a random role immediately assists while the others never assist.*

Proof. If $c > r$, then $U_1 < \min\{U_2, U_3\}$ and following from Proposition 2.5 the ESS is no assistance. In this case a potential helper's payoff is $(1 - r)$.

If $c < r$, then $U_2 > U_1 > U_3$ and the ESS follows from Proposition 2.5. In this case a potential helper's expected payoff is

$$E = \frac{(1 - c) + (n - 2)(1 - rc)}{n - 1}. \qquad \square$$

4. Discussion

This paper presented an asymmetric game-theoretical model to the following type of animal conflicts: a member of a group sized $n \geqslant 3$ 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.

Considering an asymmetric model, we have distinguished between two possible situations, payoff-irrelevant asymmetry and payoff-relevant asymmetry. Under the payoff-irrelevant asymmetry, all roles have identical payoff from a certain outcome. Under the payoff-relevant asymmetry, each of the roles has a different payoff from a certain outcome (Maynard Smith and Parker, 1976). We have assumed that under the payoff-irrelevant asymmetry, the cost accrued from assisting is identical for all roles. Under the payoff-relevant asymmetry each role accrues a different cost. According to our results the ESS is either immediate assistance, or no assistance in both cases.

Comparing the payoff-irrelevant asymmetric model to the symmetric model with full information (Yaniv and Motro, 2004b) we see that the ESS are identical except for the case where $U_2 > U_1 > U_3$. In this case, a potential helper's payoff from assisting the individual which is at risk is lower than its payoff if the individual is saved by another helper, but is greater than its payoff if the individual dies. Considering such payoffs, the ESS is delayed assistance (a mixed strategy) in the symmetric model with full information. In the asymmetric model mixed strategies cannot be ESS (Selten, 1980), and the ESS is either immediate assistance or no assistance. To compute the ESS in the asymmetric model we first compute each role's stable replies. In this particular case, we found these replies by comparing the other roles instantaneous total entering rate to a critical total entering rate. This critical entering rate is similar to the stable entering rate in the symmetric model with full information.

Applying both asymmetric models to the *n* brothers' problem, we show that the ESS depend on the ratio between the degree of relatedness, and the cost accrued from assisting. Under the payoff-irrelevant asymmetry, if the degree of relatedness is greater than the cost, then the ESS is immediate assistance by a random role, otherwise the ESS is no assistance. Under the payoff-relevant asymmetric model, if the degree of relatedness is greater than the lowest cost, then the ESS is immediate assistance by the role that accrued the lowest cost, otherwise the ESS is no assistance.

A known animal conflict whose ESS are characterized both under role symmetry and role asymmetry is the war of attrition. In the war of attrition at least two players compete for the same resource. Instead of fighting, each of the players persists and the winner is the one who persists longer. This conflict was first described in (Maynard Smith and Price, 1973), who claimed that unique ESS in the symmetric conflict is mixed. It was later widely discussed by Bishop and Cannings (1978) and by Bishop et al. (1978) which characterized the ESS in the generalized war of attrition. Haigh and Cannings (1989) have generalized the existing models and characterized the ESS in the *n*-person war of attrition. In the asymmetric conflict, various ESS were characterized under different information structures regarding roles and strategies. It has been shown, that in the complete asymmetric conflict there exist no ESS (Maynard Smith and Parker, 1976; Selten, 1980), but where there is a possibility of errors in role identification a unique mixed ESS may exist (Hammerstein and Parker, 1982). Additional asymmetric ESS, considering mistakes in role identification or in decision making, were characterized in Hammerstein (1981), Yang-Gwan (1993), McNamara et al. (1997) and in Haccou and Glaizot (2002).

Comparing our model to the asymmetric war of attrition we see that these models differ in a player's payoff function. In the war of attrition a player's payoff function is affected by the strategies of the decision makers. In the conflicts we considered, a player's payoff function is not only affected by the strategies of the decision makers, but also by the death process. The death process enables the existence of ESS in our complete asymmetric model, while in the complete asymmetric war of attrition there exist no ESS.

A possible extension of our asymmetric model is allowing the existence of mistakes. As in other conflicts, the existence of mistakes may change the characteristics of the ESS in the game. We suggest to consider both mistakes in role identification and in strategy choice. It has been shown (Silk, 2002a, b), that sometimes it is not so simple for a group member to estimate and define the asymmetry. In her work, Silk (2002b) presents examples of random acts of aggression and senseless acts of intimidation among female baboons. Silk claims that when fighting is costly, it is profitable for individuals to exchange information about asymmetries in their payoffs. These signals allow each individual to assess its opponents' payoffs and compare them to their own. Individuals are willing to pay a cost in order to identify their exact role among group members. Based on the results of Harsanyi (1973) and Selten (1980), Binmore and Samuelson (2001) have shown that uncertainty regarding role identification and payoff perturbations enables mixed ESS under ceratin conditions. Applying this idea to our conflicts, even where asymmetry exists, may allow delayed assistance to be an ESS.

Appendix A

Proof of Proposition 2.3. Let $U_2^k > U_1^k > U_3^k$. Considering the first case, there is at least one role, for example role i, which immediately assists: $\lambda_i(0) = \infty$ and $\lambda_i(t) = 0$ for all $t > 0$. The individual has been immediately saved, thus $\mu(t) = 0\ \forall t > 0$. This implies that $\Delta E_k(\tilde{m}_k, M) > 0\ \forall t \geqslant 0$ and role k's stable reply is to never assist.

Considering the second case, all the other roles never assist. That is, $\lambda_j(t) = 0$ for all $j \neq k$ and for all $t \geqslant 0$.

Since $U_1^k > U_3^k$, $\Delta E_k(\tilde{m}_k, M) < 0\ \forall t \geq 0$ and player k's stable reply is to immediately assist.

Assume that there exists a positive and finite point in time, T, at which assistance is given by one of the other roles, for example role i. In this case, $\sum_{j\neq k}\lambda_j(t)$ a priori equals:

$$\sum_{j\neq k}\lambda_j(t) = \begin{cases} 0 & \text{for } 0 \leq t < T, \\ \infty & \text{for } t = T, \\ \sum_{j\neq i,k}\lambda_j(t) & \text{for } t > T. \end{cases}$$

Since $U_1^k > U_3^k$ and since $\mu(t) = 0\ \forall t > T$, $\Delta E_k(\tilde{m}_k, M) < 0\ \forall 0 < t < T$ and $\Delta E_k(\tilde{m}_k, M) \geq 0\ \forall t > T$. Hence, role k's stable reply will be either to immediately assist, or to never assist. We find the stable reply by comparing the expected payoff from each of the suggested strategies. If role k's strategy is $\tilde{m}_k$: "immediately assist", then its expected payoff is

$$E_k(\tilde{m}_k, M) = U_1^k.$$

If its strategy is $\tilde{m}_k$: "never assist", then role k's expected payoff is

$$E_k(\tilde{m}_k, M) = U_2^k \bar{Q}(T) + U_3^k Q(T).$$

There exists a critical finite point in time, T_c, such that,

$$\bar{Q}(T_c) = \frac{U_1^k - U_3^k}{U_2^k - U_3^k}.$$

Note that $U_1^k > U_2^k \bar{Q}(T) + U_3^k Q(T)$ for all $T > T_c$, and $U_1^k < U_2^k \bar{Q}(T) + U_3^k Q(T)$ for all $T < T_c$. Therefore, if $T > T_c$ then role k's stable reply is to immediately assist, and if $T < T_c$ then role k's stable reply is to never assist. □

Proof of Proposition 2.4. Let $U_3^k > U_1^k > U_2^k$. Role k's instantaneous revenue is

$$\Delta E_k(\tilde{m}_k, M) = -(U_1^k - U_2^k)\sum_{j\neq k}\lambda_j(t) + (U_3^k - U_1^k)\mu(t), \quad (6)$$

where $\sum_{j\neq k}\lambda_j(t)$ is the instantaneous total entering rate of the other roles.

Considering the first case, there is at least one role, for example role i, which immediately assists: $\lambda_i(0) = \infty$ and $\lambda_i(t) = 0\ \forall t > 0$. That is, the individual is immediately saved, thus $\mu(t) = 0\ \forall t > 0$. Since $U_1^k > U_2^k$, $\Delta E_k(\tilde{m}_k, M) < 0\ \forall t \geq 0$ and role k's stable reply is to immediately assist.

If none of the other potential helpers immediately assists then either all of them never assist, or one of them assists at a positive and finite point in time. Assume that all the other roles never assist, thus $\lambda_j(t) = 0$ for all $j \neq k$ and for all $t \geq 0$. Since $U_1^k < U_3^k$, $\Delta E_k(\tilde{m}_k, M) > 0\ \forall t \geq 0$ and player k's stable reply is to never assist.

Assume that there exists a positive and finite point in time, T, at which assistance is given by one of the other roles, for example by role i. In this case, $\sum_{j\neq k}\lambda_j(t)$ a priori equals:

$$\sum_{j\neq k}\lambda_j(t) = \begin{cases} 0 & \text{for } 0 \leq t < T, \\ \infty & \text{for } t = T, \\ \sum_{j\neq i,k}\lambda_j(t) & \text{for } t > T. \end{cases}$$

Since $\mu(t) = 0\ \forall t > T$ and since $U_1^k < U_3^k$, $\Delta E_k(\tilde{m}_k, M) > 0\ \forall t \geq 0$ and role k's stable reply is to never assist. □

Proof of Proposition 2.5. If $U_1 \leq \min\{U_2, U_3\}$, then it follows from Proposition 2.1 that all roles' stable replies are to never assist, and the unique ESS is no assistance.

If $U_1 \geq \max\{U_2, U_3\}$, then according to Proposition 2.2 all roles' stable reply are to immediately assist. In equilibrium, all roles immediately enter the game and a random role assists.

If $U_2 > U_1 > U_3$, then according to Proposition 2.3 the unique possible ESS is that a random role immediately assists while the others never assist.

If $U_3 > U_1 > U_2$, then according to Proposition 2.4 both immediate assistance and no assistance are ESS candidates. We show that both strategies are indeed ESS of the game.

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

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

Since $U_3 > U_1 > U_2$, adopting any different strategy decreases the expected payoff. Thus, immediate assistance is a possible ESS.

If most of the individuals in the population adopt the strategy M: "never assist", then a potential helper's expected payoff equals

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

Since $U_3 > U_1 > U_2$, adopting any different strategy decreases the expected payoff. Thus, immediate assistance is a possible ESS. □

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