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# Optimal Joint Allocation of Efforts in Inclusive Fitness by Related Individuals

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## Abstract

Families are places of affection and cooperation, but also of conflict. In his famous paper *Parent-Offspring Conflict*, Robert L. Trivers builds upon W. D. Hamilton's concept of inclusive fitness to argue for genetic conflict in parent-offspring relationships, and to derive numerical predictions on the intensity of the conflict. We propose a mathematical model of game theory that depicts how each member of a family allocates her resource budget to maximize her inclusive fitness; this latter is made of the sum of personal fitness plus the sum of relatives fitnesses weighted by Wright's coefficients of relationship. We define an optimal allocation profile as a Nash equilibrium, and we characterize the solutions in function of resource budgets, coefficients of relationship and derivatives of personal fitnesses.

**Keywords:** parent-offspring conflict, evolutionary biology, inclusive fitness, Nash equilibrium

**AMS classification:** 91A10, 90C46, 92B05

## 1 Introduction

In his famous paper [Trivers(1974)], Robert L. Trivers builds upon W. D. Hamilton's concept of *inclusive fitness* [Hamilton(1964)] to derive numerical predictions on the intensity of the conflict in parent-offspring relationships. In this paper, we propose a mathematical analysis of optimal joint allocation of efforts in inclusive fitness by related individuals in a family.

In Sect. 2, we set up the ingredients of a mathematical model that depicts how each member of a family allocates her resource budget to maximize her inclusive fitness; we define an optimal allocation profile as a Nash equilibrium in game theory. In Sect. 3, we characterize the solutions in function of resource budgets, coefficients of relationship and derivatives of personal fitnesses.

## 2 Problem statement

In §2.1, we set up the mathematical ingredients to formalize investment in personal fitness, relatedness and inclusive fitness. In §2.2, we provide formal definitions of selfish and altruistic individuals. In §2.3, we define an optimal allocation profile as a Nash equilibrium in game theory.

### 2.1 Investment in personal fitness, relatedness, inclusive fitness

Let  $\mathbb{I}$  be a finite set of individuals. One can think of  $\mathbb{I}$  as being relatives, members of a same family.

**Effort/investment.** Each (source) individual  $s \in \mathbb{I}$  has a budget  $\bar{x}_{s \rightarrow} > 0$  of effort/investment that she can allocate between all (target) individuals in  $\mathbb{I}$ , including herself.<sup>1</sup> Let  $x_{st}$  denote the *effort/investment from  $s$  to  $t$* , that is, the quantity that the source individual  $s$  (first index) invests in the target individual  $t$  (second index). Each (source) individual  $s$  decides of an *investment vector*

$$X_s = \{x_{st}\}_{t \in \mathbb{I}} \in \mathbb{R}_+^{\mathbb{I}}, \quad \forall s \in \mathbb{I}, \quad (1a)$$

having the property that its components are nonnegative ( $x_{st} \geq 0$ ), and that the budget constraint is satisfied, that is,

$$\sum_{t \in \mathbb{I}} x_{st} \leq \bar{x}_{s \rightarrow}, \quad \forall s \in \mathbb{I}. \quad (1b)$$

We note the *set of admissible investment vectors for source individual  $s$*  by

$$\mathbb{X}_s = \left\{ \{x_{st}\}_{t \in \mathbb{I}} \in \mathbb{R}_+^{\mathbb{I}} \mid \sum_{t \in \mathbb{I}} x_{st} \leq \bar{x}_{s \rightarrow} \right\} \subset \mathbb{R}_+^{\mathbb{I}}, \quad \forall s \in \mathbb{I}. \quad (1c)$$

An *admissible investment vectors profile* is a collection

$$X = \{X_s\}_{s \in \mathbb{I}} = \{x_{st}\}_{(s,t) \in \mathbb{I}^2} \in \mathbb{X} \quad (1d)$$

where

$$\mathbb{X} = \prod_{s \in \mathbb{I}} \mathbb{X}_s \subset \mathbb{R}_+^{\mathbb{I} \times \mathbb{I}} \quad (1e)$$

is the *set of admissible investment vectors profiles*.

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<sup>1</sup>To avoid using she/he, her/him or herself/himself each time we refer to an individual, we choose to use the feminine for a source individual and the masculine for a target individual.

**Personal fitness.** For any admissible investment vectors profile  $X \in \mathbb{X}$  as in (1d)–(1d), we define the incoming investment profile

$$X_{\rightarrow} = \{x_{\rightarrow t}\}_{t \in \mathbb{I}} \in \mathbb{R}_+^{\mathbb{I}}, \quad (2a)$$

where

$$x_{\rightarrow t} = \sum_{s \in \mathbb{I}} x_{st}, \quad \forall t \in \mathbb{I} \quad (2b)$$

is the *total amount invested in the target individual  $t$  by all source individuals  $s \in \mathbb{I}$ , including herself*. By (1b), we have that

$$X \in \mathbb{X} \implies \sum_{t \in \mathbb{I}} x_{\rightarrow t} \leq \sum_{s \in \mathbb{I}} \bar{x}_{s \rightarrow}. \quad (3)$$

We suppose that there exists a collection  $\{F_t\}_{t \in \mathbb{I}}$  of *personal fitness functions*

$$F_t : \mathbb{R}_+ \rightarrow \mathbb{R}_+, \quad \forall t \in \mathbb{I}, \quad (4)$$

and that the *personal fitness* of any target individual  $t$  is  $F_t(x_{\rightarrow t})$ , that is, personal fitness is a function of the total amount  $x_{\rightarrow t}$  invested in  $t$ .

**Coefficient of relatedness/relationship.** The source individual  $s$  shares with the target individual  $t$  (including herself) a fraction  $r_{st} \in [0, 1]$  of her genetic interests, the *coefficient of relatedness* (Wright's coefficient of relationship). We suppose that

$$0 \leq r_{st} \leq r_{ss} = 1, \quad \forall (s, t) \in \mathbb{I}^2. \quad (5)$$

**Inclusive fitness.** We suppose that the *inclusive fitness*  $W_i$  of the individual  $i$  depends on the whole admissible investment vectors profile  $X = \{x_{st}\}_{(s,t) \in \mathbb{I}^2}$  in (1d)–(1d) in a way that is additive in the personal fitnesses of related individuals, after adjusting by relatedness, giving

$$W_i(X) = \sum_{t \in \mathbb{I}} r_{it} F_t(x_{\rightarrow t}), \quad \forall i \in \mathbb{I}, \quad (6a)$$

where the total amount  $x_{\rightarrow t}$  invested in  $t$  is given in (2b). Thus, we obtain the equivalent, but more explicit, expression of inclusive fitness

$$W_i(\{x_{st}\}_{(s,t) \in \mathbb{I}^2}) = \sum_{t \in \mathbb{I}} r_{it} F_t\left(\sum_{s \in \mathbb{I}} x_{st}\right), \quad \forall i \in \mathbb{I}. \quad (6b)$$

## 2.2 Selfish and altruistic individuals definitions

A (source) individual can have interest to invest in another (target) individual because the source inclusive fitness “includes” the personal fitness of the target individual as in (6). A (target) individual can receive investment from another (source) individual because the target personal fitness is part of the source inclusive fitness as in (6).

For a given admissible investment vectors profile  $X = \{x_{st}\}_{(s,t) \in \mathbb{I}^2} \in \mathbb{X}$  as in (1d)–(1d), we say that

- a (source) individual  $\sigma \in \mathbb{I}$  is *selfish* if  $x_{\sigma t} = 0$  for all  $t \neq \sigma$ , that is,  $\sigma$  does not invest in any other  $t \neq \sigma$ ,
- a (source) individual  $\alpha \in \mathbb{I}$  is *altruistic* if  $x_{\alpha t} > 0$  for at least one other individual  $t \neq \alpha$ ,
- a (source) individual  $\alpha$  is *totally altruistic* if  $x_{\alpha\alpha} = 0$ , that is,  $\alpha$  does not invest in herself,

and we define

- the *beneficiary target individuals* of the source individual  $s \in \mathbb{I}$  by

$$\mathbb{B}_{s \rightarrow}(X) = \{\beta \in \mathbb{I} \mid x_{s\beta} > 0\}, \quad (7a)$$

- the *selfish (source) individuals* as the individuals belonging to the set

$$\mathbb{S}(X) = \{\sigma \in \mathbb{I} \mid \forall t \neq \sigma, x_{\sigma t} = 0\} = \{\sigma \in \mathbb{I} \mid \mathbb{B}_{\sigma \rightarrow}(X) = \{\sigma\}\}, \quad (7b)$$

- the *altruistic (source) individuals* as the nonselfish individuals, that is, those belonging to the set

$$\mathbb{A}(X) = \mathbb{I} \setminus \mathbb{S}(X) = \{\alpha \in \mathbb{I} \mid \exists t \neq \alpha, x_{\alpha t} > 0\}. \quad (7c)$$

## 2.3 Solution as Nash equilibrium

For a given admissible investment vectors profile  $X = \{X_i\}_{i \in \mathbb{I}} \in \mathbb{X}$  as in (1d)–(1d), we denote

$$X_{-i} = \{X_s\}_{s \in \mathbb{I}, s \neq i} \in \prod_{s \neq i} \mathbb{X}_s, \quad \forall i \in \mathbb{I}. \quad (8)$$

A *Nash equilibrium* is an admissible investment vectors profile

$$X^* = \{X_i^*\}_{i \in \mathbb{I}} = \{\{x_{it}^*\}_{t \in \mathbb{I}}\}_{i \in \mathbb{I}} \in \mathbb{X}, \quad (9a)$$

such that

$$\max_{X_i \in \mathbb{X}_i} W_i(X_i, X_{-i}^*) = W_i(X_i^*, X_{-i}^*), \quad \forall i \in \mathbb{I}. \quad (9b)$$

### 3 Optimal allocation of efforts by related individuals

In §3.1, we characterize Nash equilibria. In §3.2, we identify selfish and altruistic individuals at any Nash equilibrium.

#### 3.1 Characterization of Nash equilibria

**Proposition 1** *Suppose that the personal fitness functions  $\{F_t\}_{t \in \mathbb{I}}$  in (4) are twice differentiable nondecreasing concave functions, that is, for all  $t \in \mathbb{I}$ ,*

- $F'_t \geq 0$ , *i.e. personal fitness is nondecreasing with input investment,*
- $F''_t \leq 0$ , *i.e. personal fitness displays nonincreasing returns with input investment.*

*Then, the investment vectors profile  $X^* = \{x_{st}^*\}_{(s,t) \in \mathbb{I}^2} \in \mathbb{X}$  is a Nash equilibrium (that is, a solution of (9b)) if and only if*

$$x_{st}^* \geq 0, \quad \forall (s, t) \in \mathbb{I}^2, \quad (10a)$$

$$\sum_{s \in \mathbb{I}} x_{st}^* = x_{\rightarrow t}^*, \quad \forall t \in \mathbb{I}, \quad (10b)$$

$$\left( \max_{i \in \mathbb{I}} r_{si} F'_i(x_{\rightarrow i}^*) - r_{st} F'_t(x_{\rightarrow t}^*) \right) x_{st}^* = 0, \quad \forall (s, t) \in \mathbb{I}^2, \quad (10c)$$

$$\sum_{t \in \mathbb{I}} x_{st}^* = \bar{x}_{s\rightarrow}, \quad \forall s \in \mathbb{I}. \quad (10d)$$

**Proof.** Each maximization problem (9b) consists of the maximization of the concave function  $X_i \in \mathbb{X}_i \mapsto W_i(X_i, X_{-i}^*)$  in (6) over the convex domain  $\mathbb{X}_i$  defined by (1b), giving

$$(\forall i \in \mathbb{I}) \quad \max_{\{x_{it}\}_{t \in \mathbb{I}}} \sum_{t \in \mathbb{I}} r_{it} F_t \left( x_{it} + \sum_{s \neq i} x_{st}^* \right) \quad (11a)$$

$$0 \leq x_{it}, \quad \forall t \in \mathbb{I}, \quad (11b)$$

$$\sum_{t \in \mathbb{I}} x_{it} \leq \bar{x}_{i\rightarrow}. \quad (11c)$$

This optimization problem consists of the maximization of a concave differentiable function over a convex domain defined by affine inequalities. Therefore, the investment vectors profile  $\{X_i^*\}_{i \in \mathbb{I}} = \{x_{it}^*\}_{(i,t) \in \mathbb{I}^2}$  is a Nash equilibrium (that is, solves (9b)) if and only if the following Karush-Kuhn-Tucker (KKT) conditions hold true

$$0 \leq x_{st}^*, \quad \forall (s, t) \in \mathbb{I}^2, \quad (12a)$$

$$\sum_{t \in \mathbb{I}} x_{st}^* \leq \bar{x}_{s\rightarrow}, \quad \forall s \in \mathbb{I}, \quad (12b)$$

and there exists  $\lambda^* = \{\lambda_s^*\}_{s \in \mathbb{I}} \in \mathbb{R}^{\mathbb{I}}$  and  $\mu^* = \{\mu_{st}^*\}_{(s,t) \in \mathbb{I}^2} \in \mathbb{R}^{\mathbb{I} \times \mathbb{I}}$  which satisfy the following KKT conditions

$$r_{st}F'_t(x_{\rightarrow t}^*) = \lambda_s^* - \mu_{st}^*, \quad \forall (s, t) \in \mathbb{I}^2, \quad (12c)$$

$$\mu_{st}^* \geq 0, \quad \mu_{st}^* x_{st}^* = 0, \quad \forall (s, t) \in \mathbb{I}^2, \quad (12d)$$

$$\lambda_s^* \geq 0, \quad \lambda_s^* \left( \sum_{t \in \mathbb{I}} x_{st}^* - \bar{x}_{s \rightarrow} \right) = 0, \quad \forall s \in \mathbb{I}. \quad (12e)$$

We now show that Equations (12) are equivalent to Equations (10).

Suppose that Equations (12) hold true. Let a (source) individual  $s \in \mathbb{I}$  be fixed. We first show that we necessarily have that

$$\lambda_s^* = \max_{t \in \mathbb{I}} r_{st}F'_t(x_{\rightarrow t}^*). \quad (13)$$

Indeed, from (12c) we deduce that  $\lambda_s^* = r_{st}F'_t(x_{\rightarrow t}^*) + \mu_{st}^*$  and, from (12d), that  $\lambda_s^* = r_{st}F'_t(x_{\rightarrow t}^*) + \mu_{st}^* \geq r_{st}F'_t(x_{\rightarrow t}^*)$ . Therefore  $\lambda_s^* \geq \max_{t \in \mathbb{I}} r_{st}F'_t(x_{\rightarrow t}^*)$ . It is impossible that the inequality be strict. Indeed, else, we would have  $\lambda_s^* > \max_{t \in \mathbb{I}} r_{st}F'_t(x_{\rightarrow t}^*)$  and therefore, by (12c),  $\mu_{st}^* = \lambda_s^* - r_{st}F'_t(x_{\rightarrow t}^*) > 0$  for all  $t \in \mathbb{I}$ . Then, we would obtain that  $x_{st}^* = 0$  for all  $t \in \mathbb{I}$  by (12d). We would also obtain that  $\lambda_s^* > 0$ , as  $\lambda_s^* > \max_{t \in \mathbb{I}} r_{st}F'_t(x_{\rightarrow t}^*) \geq 0$  since  $F'_s \geq 0$  by assumption. But  $\lambda_s^* > 0$  and  $x_{st}^* = 0$  for all  $t \in \mathbb{I}$  would contradict (12e), since we have assumed that  $\bar{x}_{s \rightarrow} > 0$ .

Suppose that Equations (10) hold true. To prove that Equations (12) hold true, we simply define  $\lambda_s^*$  by (13) and  $\mu_{st}^*$  by (12c).  $\square$

## 3.2 Selfish and altruistic individuals at Nash equilibrium

For any vector  $z = \{z_t\}_{t \in \mathbb{I}} \in \mathbb{R}_+^{\mathbb{I}}$  and for any source individual  $s \in \mathbb{I}$ , we introduce the set

$$\mathbb{I}_s^*(z) = \arg \max_{t \in \mathbb{I}} r_{st}F'_t(z_t) \subset \mathbb{I}, \quad \forall s \in \mathbb{I} \quad (14a)$$

of individuals with the *highest adjusted marginal gain in personal fitness*, and the set

$$\mathbb{I}^*(z) = \arg \max_{i \in \mathbb{I}} F'_i(z_t) \subset \mathbb{I} \quad (14b)$$

of individuals with the *highest marginal gain in personal fitness*.

**Proposition 2** *Suppose that the assumptions of Proposition 1 hold true and that the investment vectors profile  $X^* = \{x_{st}^*\}_{(s,t) \in \mathbb{I}^2} \in \mathbb{X}$  as in (1d)–(1d), is a Nash equilibrium (that is, a solution of (9b)).*

*Then any individual  $s \in \mathbb{I}$  will only invest in those related individuals that have the highest adjusted marginal gain in personal fitness, that is,*

$$\mathbb{B}_{s \rightarrow}(X^*) \subset \mathbb{I}_s^*(X_{\rightarrow}^*), \quad (15)$$

*where the beneficiary target individuals  $\mathbb{B}_{s \rightarrow}(X^*)$  have been defined in (7a), individuals  $\mathbb{I}_s^*(X_{\rightarrow}^*)$  with the highest adjusted marginal gain in personal fitness in (14a) and  $X_{\rightarrow}^*$  in (2).*

Moreover, if  $F'_t > 0$  for any  $t \in \mathbb{I}$ , and if any individual is strictly more related to herself/himself than to any other individual, that is, if  $r_{ii} > r_{it}$ , for any  $i \in \mathbb{I}$  and  $t \neq i$ , then any individual  $i \in \mathbb{I}$  that has the highest marginal gain in personal fitness will be selfish, that is,

$$\mathbb{I}^*(X_{\rightarrow}^*) \subset \mathbb{S}(X^*), \quad (16)$$

where individuals  $\mathbb{I}^*(X_{\rightarrow}^*)$  with the highest marginal gain in personal fitness have been defined in (14b),  $X_{\rightarrow}^*$  in (2) and the selfish individuals  $\mathbb{S}(X^*)$  in (7b).

**Proof.** We have

$$\begin{aligned} t \in \mathbb{B}_{s \rightarrow}(X^*) &\iff x_{st}^* > 0 && \text{(by definition (7a) of } \mathbb{B}_{s \rightarrow}(X^*) \text{)} \\ &\implies \max_{i \in \mathbb{I}} r_{si} F'_i(x_{\rightarrow i}^*) - r_{st} F'_t(x_{\rightarrow t}^*) = 0 && \text{(by the KKT condition (10c))} \\ &\implies t \in \mathbb{I}_s^*(X_{\rightarrow}^*). && \text{(by definition (14a) of } \mathbb{I}_s^*(X_{\rightarrow}^*) \text{)} \end{aligned}$$

If  $F'_t > 0$  for any  $t \in \mathbb{I}$  and if  $r_{ii} > r_{it}$ , for any  $i \in \mathbb{I}$  and  $t \neq i$ , we have that

$$\begin{aligned} i \in \mathbb{I}^*(X_{\rightarrow}^*) &\implies F'_i(X_{\rightarrow}^*) \geq F'_t(X_{\rightarrow}^*), \quad \forall t \neq i && \text{(by definition (14b) of } \mathbb{I}^*(X_{\rightarrow}^*) \text{)} \\ &\implies F'_i(X_{\rightarrow}^*) \geq F'_t(X_{\rightarrow}^*) > 0, \quad \forall t \neq i && \text{(by assumption that } F'_t > 0, \forall t \text{)} \\ &\implies r_{ii} F'_i(X_{\rightarrow}^*) > r_{it} F'_t(X_{\rightarrow}^*), \quad \forall t \neq i && \text{(by assumption that } r_{ii} > r_{it}, \forall t \neq i \text{)} \\ &\implies x_{it}^* = 0, \quad \forall t \neq i && \text{(by the KKT condition (10c))} \\ &\implies i \in \mathbb{S}(X_{\rightarrow}^*). && \text{(by definition (7b) of selfish individuals)} \end{aligned}$$

□

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