

# Evolution of Behavior in Family Games

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# 1 Does Hamilton’s Rule Govern Kin-Selection?

## Hamilton’s Rule

William Hamilton [9] proposed that evolutionary selection would result in a population of individuals in which each acts to maximize its *inclusive fitness*. Hamilton defined an individual’s inclusive fitness to be a weighted average of its own survival probability and the survival probabilities of its kin, with the weights applied to relatives being proportional to their *degree of relationship*.<sup>1</sup> He stated the following proposition, which has come to be known as *Hamilton’s Rule*:

“The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbors’ fitness against his own according to the coefficients of relationship appropriate to that situation.” [9], p 19.

Hamilton takes *individual fitness* as an undefined primitive of his theory, without dwelling in detail on how it is determined. For the purposes of this paper, we will interpret *individual fitness* of an organism as the probability that it survives to maturity. In so doing, we are implicitly assuming that all individuals who survive to adulthood have the same expected fertility.<sup>2</sup>

Hamilton’s papers were written almost 10 years before G. R. Price and John Maynard Smith [12] introduced game theory to biologists. It is therefore not surprising that he did not model familial interactions as a game. Hamilton studied interactions where players can benefit each other at a cost to themselves, and where a player’s payoff is the sum of benefits received from others, minus costs incurred in helping others. When Hamilton’s analysis is restated in game-theoretic language, it is apparent that the kind of interactions he studied belong to a special class of games, which we will call *additive games between relatives*. Informally stated, an additive game between relatives is a game in which individuals can at some “cost” to themselves confer “benefits” on their relatives and where the survival probability of an individual is equal to a constant plus the sum of benefits received from relatives, minus the sum of costs incurred in helping relatives.<sup>3</sup>

## Hamilton Dethroned?

Many interesting economic and social interactions lack the additive structure assumed by Hamilton. In an additive game, the benefit one gets from actions of

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<sup>1</sup>The degree of relationship between two individuals is defined as the probability that they share the gene at any particular locus by inheritance through a common ancestor. In families where there is no inbreeding, the degree of relationship between full siblings is 1/2, between half siblings it is 1/4, between (full) cousins it is 1/8, between parent and offspring it is 1/2 and between grandparent and grandchild it is 1/4.

<sup>2</sup>In caste systems or hierarchical societies in which adults in different social roles have different fertilities, a more elaborate measure of fitness is required. Bergstrom [2] discusses this problem for the institution of male primogeniture.

<sup>3</sup>A more formal description of additive games is found in the Appendix.

a relative can not depend on one's own action, nor can the effect of one relative's actions on an individual's well-being depend on the actions of other relatives.

John Maynard Smith [11] proposed that the concept of inclusive fitness could be extended to games with general payoff functions. He conjectured that, whether or not the game is additive, equilibrium populations would consist of players who use strategies that are ESS (evolutionary stable strategies) in the game with inclusive fitness payoff functions.

Alan Grafen [8] showed with a simple example that, for games between relatives, the ESS of a game with inclusive fitness payoffs is not in general the rest point of a reasonable evolutionary dynamic model. Grafen's example is a symmetric, two-player game (the hawk-dove game) in which the players must choose one of two discrete pure strategies. He argues that the reason that ESS under inclusive fitness does not accurately predict evolutionary equilibrium is that "an individual is more likely to play against his own strategy than he would if he played the population at random."

Grafen does not offer a genetic analysis of a sexual diploid species. His dynamic model can be interpreted as a model of asexually reproducing clones, who produce more copies, the higher the payoff they receive. Marcus Feldman and Luigi Cavalli-Sforza [5], [7] develop explicit genetic models of the evolutionary dynamics of games between sexual diploid relatives. In these models, players can play one of two discrete strategies. Feldman and Cavalli-Sforza show that ESS with inclusive fitness payoffs does not coincide with stable monomorphic equilibrium of games with multiplicative payoffs, although these solutions do coincide in the case of additive games.<sup>4</sup>

W. G. S. Hines and Maynard Smith [10] accepted Grafen's argument and agreed that for non-additive games between relatives, Hamilton's inclusive fitness should be replaced by the measure of fitness introduced by Grafen. Hines and Maynard Smith formalize this measure, which they call "personal fitness," for the case of symmetric two-player games between asexually-reproducing relatives.

This paper explores the relation between stable monomorphic populations of sexual diploids and Nash equilibrium (or ESS) for games in which the payoff functions are respectively, inclusive fitness and personal fitness. It will show when the equilibria for the two distinct payoff functions coincide and how they differ when they do not coincide. Explicit genetic models of sexual diploid reproduction will be used to show the correspondence between stable monomorphic equilibria and Nash equilibrium for games with these payoff functions.

## Individual Fitness, Inclusive Fitness, and Personal Fitness Functions

In a symmetric two person game, *individual fitness* (own survival probability) is determined as follows. If one player plays  $x$  and the other plays  $y$ , the individual

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<sup>4</sup>They also show that, even with additive payoffs, inclusive fitness analysis does not correctly identify polymorphic equilibria.

fitness of the  $x$ -player is  $\Pi(x, y)$  and the individual fitness of the  $y$ -player is  $\Pi(y, x)$ .

When this game is played between two relatives with coefficient of relatedness  $r$ , the *inclusive fitness payoff* of a player who plays  $x$  while its relative plays  $y$  is defined to be

$$H(x, y) = \Pi(x, y) + r\Pi(y, x). \quad (1)$$

The *personal fitness payoff* is defined by Hines and Maynard Smith as follows:

$$V(x, y) = r\Pi(x, x) + (1 - r)\Pi(x, y). \quad (2)$$

Hines and Maynard Smith explain the difference between personal fitness and inclusive fitness in the following way.

“Personal fitness modifies classical fitness by allowing for the effects that an individual’s relatives will have on the number of his own offspring to survive, whereas inclusive fitness modifies classical fitness by allowing for the effects that an individual will have on the number of his relative’s offspring that survive.” [10], p 20.

Stated another way, one’s *inclusive fitness* counts the help that one *gives* to relatives, one’s *personal fitness* counts the help that one *receives from* relatives. To decide which, if either of these measures is appropriate for finding evolutionary equilibrium, it seems necessary to specify a dynamic model with explicit assumptions about the genetics of transmission of behavior.

The personal fitness payoff can be expressed as a probabilistic variant of Kant’s *categorical imperative*:<sup>5</sup>

“Act as you would act to maximize your individual fitness *if you believed that with probability  $r$ , your relative’s actions would mimic your own.*”<sup>6</sup>

In contrast, the inclusive fitness payoff function can be expressed as the maxim:

“Act as if you valued your relative’s individual fitness  $r$  times as much as you value your own.”

It is quite easy to construct examples in which for given individual payoffs (own survival probabilities), the set of Nash equilibrium outcomes with inclusive fitness payoffs is not the same as the set of Nash equilibrium outcomes with personal fitness payoffs. Consider the following case: suppose that two siblings play a *prisoners’ dilemma* game in which the payoffs to the two strategies  $C$  (cooperate) and  $D$  (defect) are given by the game matrix in table 1.

<sup>5</sup>Bergstrom [4] refers to the personal fitness function as the *semi-Kantian utility function*.

<sup>6</sup>While not all Kantian philosophers would agree, it seems to me that this rule where  $r = 1$  is the most plausible interpretation of Kant’s *categorical imperative*.

Table 1: Individual Fitness payoffs,  $\Pi(x, y)$

	C	D
C	.75,.75	0,1
D	1,0	.6,.6

Using Equation 1 and the individual fitnesses found in Table 1, we can calculate the payoff matrix for the game with inclusive fitness payments, which is shown in Table 2.

Table 2: Inclusive Fitness  $H(x, y) = \Pi(x, y) + \frac{1}{2}\Pi(y, x)$

	C	D
C	1.125,1.125	.5,1.0
D	1.0,.5	.9,.9

Similarly, we can use Equation 2 to calculate the payoff matrix for the game with inclusive fitness payments, which is shown in Table 3.

Table 3: Personal Fitness  $V(x, y) = \frac{1}{2}\Pi(x, x) + \frac{1}{2}\Pi(x, y)$

	C	D
C	.75,.75	.375,.8
D	.8,.375	.6,.6

The game with inclusive fitness payoffs has two Nash equilibria, one in which both players cooperate and one in which both defect.<sup>7</sup> In contrast, the game with personal fitness payoffs has only one pure strategy Nash equilibrium, the outcome where both players defect.<sup>8</sup> In this example, as in many others that can be constructed, we find different predictions resulting from the alternative conjectures that stable outcomes are: (i) those where individuals use Nash equilibrium strategies in the game in which players' payoff functions are given by Hamilton's inclusive fitness or (ii) Nash equilibrium strategies in the game in which payoff functions are the inclusive fitness payoffs. In order to determine which, if either, of these conjectures is correct, we need to explore the underlying genetic situation.

<sup>7</sup>In this game, if the other player cooperates, then the best response is cooperate, with a payoff of 1.125, while defection yields a payoff of 1.0. Thus cooperate is the best response to cooperate and the outcome where both cooperate is a Nash equilibrium. If the other player defects, then cooperation yields a payoff of .5, while defection yields a payoff of .9. Therefore defect is the best response to defect and defect is also a Nash equilibrium

<sup>8</sup>One sees from Table 3 that a player gets a higher payoff by defecting than by cooperating, regardless of whether the other player cooperates or defects.

## Monomorphic Populations of Sexual Diploids

Sexual diploids have two genes in each genetic locus, one inherited from each parent. We assume that in the game it plays with siblings, each player's strategy is determined by the pair of genes found at a single locus. For the purpose of our discussion, the *genotype* of an individual is specified by the gene pair in the locus that determines that individual's strategy. We further assume that mating among surviving adults is random with respect to genotype.

A genotype is said to be *homozygous* if the two genes in that locus are identical and *heterozygous* if they are different. A diploid population is said to be *monomorphic* if almost all members of the population are of the same, homozygous genotype. Let  $A$  and  $a$  be two different genes such that  $aa$  genotypes take action  $x$  and  $AA$  genotypes take action  $y$ . The gene  $A$  is said to be *dominant* (over gene  $a$ ) if  $Aa$  genotypes take the same action  $y$  as  $AA$  genotypes. The gene  $A$  is said to be *recessive* (to gene  $a$ ) if  $Aa$  genotypes take the same action  $x$  as  $aa$  genotypes.

A mutant gene  $A$  is able to *invade* the original population, if while it is rare, the  $A$  gene reproduces more rapidly than normal  $a$  genes.<sup>9</sup> In this paper, we explore necessary conditions and sufficient conditions for a monomorphic population to be resistant against invasion by dominant mutant genes.

## 2 Two-Sibling Symmetric Games

A two-player symmetric game is defined by a single payoff function  $\Pi(\cdot, \cdot)$ . If one player takes action  $x$  and the other takes action  $y$ , the payoff to the  $x$ -player is  $\Pi(x, y)$  and the payoff to the  $y$ -player is  $\Pi(y, x)$ . For the purposes of this discussion, "siblings" are individuals who have the same mother and who, with a given probability  $s$  also have the same father.<sup>10</sup>

Consider a monomorphic population of  $aa$  genotypes, who all play strategy  $\bar{x}$ . Let  $A$  be a dominant mutant gene such that  $Aa$  heterozygotes play the strategy  $x$ . If mating is random and  $A$  genes are rare, almost all of the  $A$  genes in the population will be carried by  $Aa$  heterozygotes (rather than by  $AA$  homozygotes). Moreover, almost all  $Aa$  genotypes will mate with normal  $aa$  genotypes and each of their offspring will either be an  $Aa$  genotype or  $aa$  genotype. The mutant  $A$  gene will be able to invade the population if in this environment, the  $A$  genes reproduce more rapidly than the normal  $a$  genes. It turns out that for the case of two-player symmetric games between siblings

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<sup>9</sup>The fact that a mutant gene can enter the population while rare does *not* imply that it will eventually become fixed in a monomorphic equilibrium. It may be that the advantage enjoyed by  $x$  of a rare mutant disappears as the gene becomes more common.

<sup>10</sup>Of course a sexual species in which each pair of parents produced only two offspring would be doomed to extinction unless the offspring were all certain to survive. But a model of two-player symmetric interaction would apply reasonably well to a species in which mothers have a litter of two offspring each season and where siblings born in different seasons do not interact. The model of two-sibling games also applies in cases where parents may have more than two offspring, but the only interactions between offspring take the form of two-player games between each pair of individuals.

in a monomorphic equilibrium it must be that the strategy played by each individual is a strategy  $\bar{x}$  that is a symmetric Nash equilibria for the game with personal fitness function  $V(\cdot, \cdot)$ . This result, which we state here as Proposition 1 is discussed in detail by Bergstrom . A proof can be found in the Appendix of this paper.

**Proposition 1** *For siblings playing a symmetric two-player game, a necessary condition for a monomorphic population of  $\bar{x}$ -strategists to resist invasion by dominant mutants is that  $\bar{x}$  is a symmetric Nash equilibrium for the two-player game with the semi-Kantian (personal fitness) payoff function  $V(\cdot, \cdot)$ . A sufficient condition is that  $\bar{x}$  is a strict symmetric Nash equilibrium<sup>11</sup> for the game with payoff function  $V(\cdot, \cdot)$ .*

### 3 N-Sibling Symmetric Games

An  $n$ -player game is defined to be *symmetric* if (i) the payoff to any player is invariant to permutations in the actions of other players. (ii) players all have identical payoff functions defined on their own actions and the actions of other players.

In a symmetric game in which only two strategies  $x$  and  $\bar{x}$  are being used, the payoff to any player is determined by the player's own strategy and the number of other players who use each of the two strategies  $x$  and  $\bar{x}$ . We define the function  $\Phi(x, \bar{x}, k)$  to be the payoff to an individual who takes action  $x$  while  $k$  of its siblings take action  $x$  and the remaining  $N - k$  of its siblings take action  $\bar{x}$ . Thus

$$\Phi(x, \bar{x}, k) = \Pi^1(\overbrace{x, x, \dots, x}^{k \text{ times}}, \overbrace{\bar{x}, \dots, \bar{x}}^{N-k-1 \text{ times}}) \quad (3)$$

Canonical examples of N-sibling symmetric games are the following:

#### Example: Joint labor with shared output

A group of human siblings work together, either as hunter-gatherers, or as peasant farmers and divide their joint output equally among themselves. Let the total amount of output depend on the work effort of each sibling, and assume that work-effort is costly to perform.

This sibling interaction can be modelled as an  $N$ -player symmetric game. Where  $x_i$  if the amount of work done by player  $i$ , total output is given by a

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<sup>11</sup>A symmetric Nash equilibrium for a two-player symmetric game with payoff function  $F$  is defined to be a strategy  $\bar{x}$  such that for all  $x \in S$ ,  $F(x, \bar{x}) \leq F(\bar{x}, \bar{x})$ . A *strict* symmetric Nash equilibrium for this game is a strategy  $\bar{x}$  such that for all  $x \in S$ , if  $x \neq \bar{x}$  then  $F(x, \bar{x}) < F(\bar{x}, \bar{x})$ . Maynard Smith's notion of ESS refines the notion of symmetric Nash equilibrium by adding an additional restriction that applies "in case of ties". According to Maynard Smith, an ESS for the payoff function  $V$  is a symmetric Nash equilibrium  $\bar{x}$  for  $V$  with the additional property that if  $V(x, \bar{x}) = V(\bar{x}, \bar{x})$  for  $x \neq \bar{x}$ , then  $V(x, x) < V(\bar{x}, x)$ . Simple examples demonstrate that for symmetric games: (i) Every ESS is a symmetric Nash equilibrium, but not every symmetric Nash equilibrium is an ESS. (ii) Every strict symmetric Nash equilibrium is an ESS, but not every ESS is a strict symmetric Nash equilibrium.

“production function”  $f(\sum_{i=1}^N x_i)$  and the cost to player  $i$  of  $x_i$  units of work effort is  $c(x_i)$ . Since output is shared equally among the players, the payoff to the  $i$ th player is

$$\Pi^i(x_1, \dots, x_N) = \frac{1}{N} f\left(\sum_{i=1}^N x_i\right) - c(x_i). \quad (4)$$

For this game,

$$\Phi(x, \bar{x}, k) = \frac{1}{N} f((k+1)x + (N-k-1)\bar{x}) - c(x). \quad (5)$$

### Example: Depleting a common resource

A litter of baby mammals compete for their mother’s milk, or a batch of caterpillar siblings all chew on the same plant. In these examples, there is a fixed amount of resource to be divided. Exercising claims on this food requires costly effort. The fraction of the total resource that is obtained by any one of the siblings depends on its own effort relative to the amount of effort expended by its siblings.

Let  $x_i$  be the cost of exerting  $x_i$  units of effort in food-claiming, and let the share of the available resources received by player  $i$  be given by  $f(x_i)/\sum_{j=1}^n f(x_j)$ , where  $f(\cdot)$  is a positive-valued, monotone increasing function. When the strategies of the  $n$  siblings are given by  $(x_1, \dots, x_N)$ , the payoff to sibling  $i$  is

$$\Pi^i(x_1, \dots, x_N) = \frac{f(x_i)}{\sum_{j=1}^N f(x_j)} - x_i. \quad (6)$$

For this game,

$$\Phi(x, \bar{x}, k) = \frac{f(x)}{kf(x) + (N-k-1)f(\bar{x})} - x \quad (7)$$

### Stable Population as a Nash Equilibrium

We have seen that in two-player symmetric games, individuals in a stable monomorphic population must be playing Nash-equilibrium strategies for a two-player game with the semi-Kantian payoff function. Perhaps surprisingly, even where the game between siblings involves *more than two players*, a stable monomorphic equilibrium must can be shown to be a Nash equilibrium for a symmetric *two*-player game. This result becomes less surprising when we realize that the two “players” in the game two types of genes—the normal gene  $a$  and a rival dominant mutant gene  $A$ .<sup>12</sup>

Consider a monomorphic population of  $aa$  genotypes, all of whom use strategy  $\bar{x}$ . Let  $A$  be a dominant mutant gene such that  $Aa$  heterozygotes play the strategy  $x$ . As in the case of two-player games, if mating is random and  $A$

<sup>12</sup>The notion of evolutionary equilibrium as the equilibrium of a game in which the players are genes seems to bein the spirit of Richard Dawkins’ [6] focus on genes as replicating agents.

genes are rare, almost all of the  $A$  genes in the population will be carried by  $Aa$  heterozygotes rather than by  $AA$  homozygotes, and almost all  $Aa$  genotypes will mate with normal  $aa$  genotypes. The offspring of an  $aa$  and an  $Aa$  will either be of genotype  $Aa$  and use strategy  $x$  or of genotype  $aa$  siblings and use strategy  $\bar{x}$ . The survival probability of an  $Aa$  genotype depends on the number of its siblings who are of each of these two genotypes.

Let us define  $p(k)$  to be the probability that an  $Aa$  genotype offspring has exactly  $k$  siblings of genotype  $Aa$ . The probability distribution  $p(k)$  is a binomial random variable such that  $p(k)$  is the probability of  $k$  successes in  $n$  binomial trials where  $r$  (the degree of relationship between siblings) is the probability of success on a single trial.

Recall that  $\Phi(x, \bar{x}, k)$  is the payoff to an individual who takes action  $x$  while  $k$  of its siblings also take action  $x$  and the remaining siblings take action  $\bar{x}$ . The survival probability of a randomly selected offspring of genotype  $Aa$  is then given by:

$$V(x, \bar{x}) = \sum_{k=1}^{k=N-1} p(k)\Phi(x, \bar{x}, k). \quad (8)$$

In the special case where  $n = 2$ , the function  $V(\cdot, \cdot)$  reduces to the function that Bergstrom calls the semi-Kantian payoff function and Hines and Maynard Smith's call the personal fitness payoff function for symmetric two-sibling games. The same argument that is used to prove Proposition 1 establishes a generalization for symmetric  $n$ -sibling games.

**Proposition 2** *For siblings playing a symmetric  $n$ -player game, a necessary condition for a monomorphic population of  $\bar{x}$ -strategists to resist invasion by dominant mutants is that  $\bar{x}$  is a symmetric Nash equilibrium for the two-player game with the payoff function  $V(\cdot, \cdot)$  defined in Equation 8. A sufficient condition is that  $\bar{x}$  is a strict symmetric Nash equilibrium for this game.*

## 4 A Partial Restoration of Hamilton's Rule

Cavalli-Sforza and Feldman [5], Grafen [8], and Bergstrom and Oded Stark [3] have shown examples of games with a finite number of discrete strategies for which Nash equilibria with personal fitness payoffs do not coincide with Nash equilibria for the corresponding inclusive fitness payoffs. These authors find other examples in which the Nash equilibria for the two different payoff functions are the same. Grafen examined a hawk-dove game in which individuals are genetically instructed to use specific mixed strategies. In this case, the strategy space becomes a simplex, and payoff functions are differentiable (in fact, bilinear) functions of individual strategies. Grafen found that in this case, the inclusive fitness approach "amazingly happens to give the correct answer." Hines and Maynard Smith extended Grafen's treatment to the general class of symmetric two-relative games, in which there is a finite set of possible pure

strategies and where individual strategy sets are the simplex of all possible mixed strategies.<sup>13</sup> They discovered that for such games, a Nash equilibrium with inclusive fitness payoffs must also be a Nash equilibrium with personal fitness payoffs, but the converse is not true.

Given these tantalizing hints, it seems useful to explore the general relation between Nash equilibrium for games with inclusive fitness functions and Nash equilibrium for games with personal fitness payoff functions.

The inclusive fitness function for symmetric two-player games is usefully generalized to symmetric  $n$ -player games by defining  $H(x, y)$  which measures the inclusive fitness of an individual that plays strategy  $x$ , while all of its siblings play strategy  $y$ . Because the game played between siblings is assumed to be symmetric, no generality is lost if we let player 1 play  $x$  and the other players play  $y$ . Thus we have:

$$H(x, y) = \Pi^1(x, y, \dots, y) + r \sum_{j \neq i} \Pi^j(x, y, \dots, y) \quad (9)$$

$$= \Pi^1(x, y, \dots, y) + r(n-1)\Pi^1(y, x, y, \dots, y) \quad (10)$$

where the step from Equation 9 to Equation 10 follows from the symmetry of the game.

## The Case of Differentiable Payoff Functions

If the individual payoff functions  $\Pi^i(x_1, \dots, x_n)$  are differentiable, then the personal fitness function  $V(x, y)$  and the inclusive fitness function  $H(x, y)$  are also differentiable. For a game with payoff function  $F(x, y)$  a necessary condition for  $\bar{x}$  to be an interior symmetric Nash equilibrium is that  $F_1(\bar{x}, \bar{x}) = 0$ , where  $F_1(x, y)$  is defined the gradient of  $F$  with respect to  $x$ .

For the differentiable case, the association between Nash equilibria of games with payoff functions  $V$  and  $H$  is revealed by the fact that the first-order calculus condition for an interior symmetric Nash equilibrium for a game with payoff function  $V$  is precisely the same as the corresponding condition for a game with payoff function  $H$ . However, as we will show, the second-order conditions are not identical, and it is in general possible to have an  $\bar{x}$  that is a symmetric Nash equilibrium for  $V$  but not for  $H$  and *vice versa*.

For any function  $F(x_1, \dots, x_n)$ , let  $F_i(x_1, \dots, x_n)$  denote the gradient of  $F$  with respect to its  $i$ th argument and let  $F_{ij}(x_1, \dots, x_n)$  denote the ‘‘Hessian’’ matrix of second-order partials. In the Appendix, we prove the following result.

**Lemma 1** *For a symmetric  $n$ -sibling game, if the individual payoff functions  $\Pi^i$  are differentiable, then  $V_1(\bar{x}, \bar{x}) = 0$  if and only if  $H_1(\bar{x}, \bar{x}) = 0$ .*

A function  $F(\cdot)$  is said to be a concave function if for all  $x$  and  $x'$  in the domain of  $F$ , and for all  $\lambda \in [0, 1]$ ,  $F(\lambda x + (1 - \lambda)x') \geq \lambda F(x) + (1 - \lambda)F(x')$ .

<sup>13</sup>They also study the case where individuals can choose only pure strategies. They refer to this as the case where ‘‘only pure strategies breed true.’’

Using a well-known result from game theory on the existence of Nash equilibrium and a standard result from calculus on maxima of concave functions, we can claim the following.

**Lemma 2** *If the personal fitness function  $V(x, y)$  is a concave function of  $x$ , then there exists a symmetric Nash equilibrium strategy  $\bar{x}$  for the game with payoff function  $V(x, y)$ . A point  $\bar{x}$  in the interior of the strategy space is a symmetric Nash equilibrium if and only if  $V_1(\bar{x}, \bar{x}) = 0$ . A parallel statement applies to the inclusive fitness function  $H(x, y)$ .*

Lemmas 1 and 2 enable us to prove the following.

**Proposition 3** *For a symmetric  $n$ -sibling game with differentiable payoff functions,*

- i.) if the semi-Kantian payoff function  $V(x, y)$  is a concave function of  $x$ , then an interior symmetric Nash equilibrium for the game with inclusive fitness payoffs  $H(x, y)$  is also a Nash equilibrium for a game with semi-Kantian payoffs  $V(x, y)$ .*
- ii.) if the inclusive fitness payoff function  $H(x, y)$  is a concave function of  $x$ , then an interior symmetric Nash equilibrium for the game with semi-Kantian fitness payoffs  $V(x, y)$  is also a Nash equilibrium for a game with inclusive fitness payoffs,  $H(x, y)$ .*

*Proof:*

If  $(x, x)$  is an interior symmetric Nash equilibrium for  $H(\cdot, \cdot)$ , then  $H_1(x, x) = 0$ . By Lemma 1, this implies that  $V_1(x, x) = 0$ . Since  $V(\cdot, \cdot)$  is assumed to be a concave function, it follows that  $(x, x)$  satisfies both the first and second-order sufficiency conditions for a Nash equilibrium. This proves assertion (i). A parallel argument establishes assertion (ii). ■

**Corollary 1** *(Hines and Maynard Smith) For a symmetric game in which there are a finite number of pure strategies and where the strategy space consists of the simplex of mixed strategies, an interior symmetric Nash equilibrium for the game with semi-Kantian (personal) fitness payoffs  $V(\cdot, \cdot)$  is a Nash equilibrium for the game with inclusive fitness payoffs  $H(\cdot, \cdot)$ , but not conversely.*

*Proof:*

In the case where the strategy space is the simplex of mixed strategies over a finite set of pure strategies, the payoff function for a two player game is a bilinear function  $\Pi(p, q) = p'Aq$  for some matrix  $A$ . Inclusive fitness is given by  $H(p, q) = p'Aq + r q'Ap$ , which is a linear function of  $p$  and hence also a concave function of  $p$ . It follows from Proposition 2(ii) that a Nash equilibrium for the game with personal fitness payoffs is also a Nash equilibrium for the game with inclusive fitness payoffs. The function  $V(p, q) = r p'Ap + (1 - r)q'Ap$ , however,

is not linear in  $p$  and is a concave function only if the matrix  $A$  is negative semi-definite (on the simplex). Thus examples can be found of Nash equilibria for personal fitness payoffs that are not Nash equilibria for inclusive fitness payoffs. ■

A differentiable function is concave if and only if its Hessian matrix of second-order partial derivatives is negative semi-definite. Examining these second-order partials enables us to see how it can happen that the Nash equilibria for personal fitness and inclusive fitness payoffs are different.

Direct calculation gives us the following expressions for the second-order cross partials of  $V$  and  $H$  :

**Lemma 3** *For a symmetric  $n$ -sibling game, with twice-differentiable individual payoff functions,*

$$H_{11}(\bar{x}, \bar{x}) = \Pi_{11}(\bar{x} \dots, \bar{x}) + r\Pi_{22}(\bar{x} \dots, \bar{x}) \quad (11)$$

$$\begin{aligned} V_{11}(\bar{x}, \bar{x}) &= \sum_{k=0}^{n-1} p(k) (\Pi_{11}(\bar{x}, \dots, \bar{x}) + 2k\Pi_{12}(\bar{x}, \dots, \bar{x}) \\ &\quad + k^2\Pi_{22}(\bar{x}, \dots, \bar{x})) \end{aligned} \quad (12)$$

For two-player games, these expressions take a particularly simple form:

**Lemma 4** *For a symmetric 2-sibling game, with twice-differentiable individual payoff functions,*

$$H_{11}(\bar{x}, \bar{x}) = \Pi_{11}(\bar{x}, \bar{x}) + r\Pi_{22}(\bar{x}, \bar{x}) \quad (13)$$

$$V_{11}(\bar{x}, \bar{x}) = \Pi_{11}(\bar{x}, \bar{x}) + 2r\Pi_{12}(\bar{x}, \bar{x}) + r\Pi_{22}(\bar{x}, \bar{x}) \quad (14)$$

$$= H_{11}(\bar{x}, \bar{x}) + 2r\Pi_{12}(\bar{x}, \bar{x}) \quad (15)$$

From Lemma 4, we see that the following is true:

**Proposition 4** *For a symmetric 2-sibling game, if for all  $x$ ,  $\Pi_{12}(x, x)$  is negative semi-definite, then every inclusive-fitness Nash equilibrium is a personal-fitness Nash equilibrium and if for all  $x$ ,  $\Pi_{12}(x, x)$  is positive semi-definite, then every personal-fitness Nash equilibrium is an inclusive fitness Nash equilibrium.*

### Possibly Useful Additional Results

For completeness, we note the following results which may turn out to be useful.

If the functions  $\Pi^i(x_1, \dots, x_n)$  are concave functions not only of  $i$ 's own strategy  $x_i$ , but concave over the Cartesian product of all players' strategies, then both  $V$  and  $H$  will also be concave functions. Accordingly we have the following:

**Lemma 5** *For a symmetric  $n$ -sibling game, if the individual payoff functions  $\Pi^i(x_1, \dots, x_n)$  are concave functions, then the personal fitness function  $V(x, y)$  and the inclusive fitness function  $H(x, y)$  are both concave functions.*

**Proposition 5** *For a symmetric  $n$ -sibling game, if the individual payoff functions  $\Pi^i(x_1, \dots, x_n)$  are concave functions for each  $i$ , then the Nash equilibria for the game with personal fitness payoffs are the same as Nash equilibria for the game with personal fitness payoffs.*

## 5 Two-Sibling Asymmetric Games

Games between relatives of different ages or different sexes often have a strongly asymmetric payoff function. For example, older siblings may be able to bully their younger siblings and deprive them of resources, or they may help their parents with the upbringing of their juniors. In species where siblings are born in different years and never interact directly, the amount of resources that an older child takes from its mother may affect her health and the survival probability of later-born children, while the actions taken by later-born siblings have no effects on their older siblings.

The asymmetry in games between kin is typically determined by the familial role in which an individual is cast. An individual's genetic code may contain a set of contingent instructions, telling it how it should behave in each role in which it might be cast. For example, an individual may be genetically programmed to act aggressively if it finds itself as the older sibling and passively if it finds itself to be the younger. . For the offspring of some bird species, such as the black eagle, the asymmetry is particularly stark. The parent usually lays two eggs. The first chick to hatch will almost always peck its younger sibling to death. In other species, elder siblings practice *facultative aggression* in which the rate of aggression by older siblings toward younger depends on environmental conditions; brood size in the case of cattle egrets, prey size in the case of blue herons, and various indicators of food supply in the case of skuas, kittiwakes, and medium sized raptors. <sup>14</sup>

O'Connor [13] proposed an elegant model of the circumstances under which a senior sibling, guided by Hamilton's rule, would find it worthwhile to oust a younger nestmate from the nest

Given that individual behavior may be contingent on its familial role, it will matter whether the instructions that inform it how to behave in different familial roles are determined by the alleles in different (unlinked) genetic loci or whether the contents of a single genetic locus determines the individual's actions in each possible role that it might play. Intermediate between these two polar models are genetic models of *linkage disequilibrium*. For example in interactions between older and younger siblings, it could be that "behavior if younger" and "behavior if older" are controlled by two distinct genetic loci, but the contents of these loci are correlated, rather than statistically independent.

We find that the extent of linkage disequilibrium (fix this) determines whether Hamilton or semi-Kantian payoff functions are appropriate. that if behavior in different familial roles is determined by separate, unlinked genetic loci, then

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<sup>14</sup>See [1], Chapter 12 for a detailed review of the literature on sibling aggression in birds.

the Nash equilibrium for games with inclusive fitness payoffs coincide with stable monomorphic equilibria. However, if the function that maps familial roles into actions is determined by a single genetic locus, then stable monomorphic equilibrium, in general, coincides with Nash equilibrium for a generalization of personal fitness payoffs rather than inclusive fitness payoffs.

## Payoff Functions for Asymmetric Games

For a two-player asymmetric game, let  $x_1$  be the action taken by the relative cast in role 1 and  $x_2$  be the strategy taken by the relative cast in role 2. Let  $\Pi^1(x_1, x_2)$  denote the individual fitness of relative 1 and  $\Pi^2(x_1, x_2)$  denote the individual fitness of relative 2. A *strategy* for an asymmetric game is a vector  $x = (x_1, x_2)$  specifying the action  $x_1$  that will be taken if the individual is cast in role 1 and the action  $x_2$  that will be taken if an individual is cast in role 2.

Inclusive fitness of relative 1 is defined to be

$$H^1(x_1, x_2) = \Pi^1(x_1, x_2) + r\Pi^2(x_1, x_2) \quad (16)$$

and inclusive fitness of relative 2 is

$$H^2(x_1, x_2) = r\Pi^1(x_1, x_2) + \Pi^2(x_1, x_2). \quad (17)$$

It is useful to define a symmetric inclusive fitness function that can be viewed as the payoff function for a symmetric game between genes, whose strategies specify what an individual will do if cast in each of the two familial roles. For any two strategies,  $x = (x_1, x_2)$  and  $y = (y_1, y_2)$ , define

$$\tilde{H}(x, y) = H^1(x_1, y_2) + H^2(y_1, x_2). \quad (18)$$

Hines and Maynard Smith defined personal fitness only for two-player *symmetric* games. We propose an extension of this definition to the case of two-player asymmetric games. Let  $x = (x_1, x_2)$  and  $y = (y_1, y_2)$  denote strategies for an asymmetric game. Define the function  $\tilde{V}(x, y)$  as follows:

$$\tilde{V}(x, y) = r(\Pi^1(x_1, x_2) + \Pi^2(x_1, x_2)) + (1 - r)(\Pi^1(x_1, y_2) + \Pi^2(y_1, x_2)) \quad (19)$$

“Personal fitness” seems an awkward term for this payoff function, since  $\tilde{V}(x, y)$  is better thought of as a payoff to a *gene*, rather than to a person. Therefore I have chosen to call  $\tilde{V}(\cdot, \cdot)$  function, the *semi-Kantian* payoff function.

## Strategy Controlled by a Single Genetic Locus

Suppose that the genes in a single genetic locus determine an individual’s actions in each of two familial roles. Consider a monomorphic population of genotype  $aa$ . An  $aa$  genotype will take the action  $\bar{x}_1$  if it happens to be an older sibling and the action  $\bar{x}_2$  if it happens to be a younger sibling. Suppose that there is a dominant mutant gene  $A$ , such that an  $Aa$  heterozygote takes the action  $x_1$  if it

happens to be an older sibling and the action  $x_2$  if it happens to be a younger sibling. If the mutant gene is rare, almost all  $Aa$  genotypes will have one parent of genotype  $Aa$  and one parent of genotype  $aa$ . The  $A$  gene will be able to invade the population if the survival probability of an  $Aa$  genotype born to one normal and one heterozygote parent is greater than the survival probability of a normal  $aa$  genotype.

On average, half of the  $Aa$  genotypes are born as older members of a sibling pair and half are born as younger members. An  $Aa$  genotype cast as the older sibling will take action  $x_1$ . With probability  $r$ , its younger sibling will also be an  $Aa$  genotype and take action  $x_2$ . With probability  $1 - r$ , its younger sibling will be an  $aa$  genotype and take action  $\bar{x}_2$ . Therefore the survival probability of an older sibling of genotype  $Aa$  is  $r\Pi^1(x_1, x_2) + (1 - r)\Pi^1(x_1, \bar{x}_2)$ . An  $Aa$  genotype cast as the younger sibling will take action  $x_2$ . With probability  $r$ , its older sibling will also be an  $Aa$  genotype and take action  $x_1$ . With probability  $1 - r$ , its older sibling will be an  $aa$  genotype and take action  $\bar{x}_1$ . Therefore the survival probability of a younger sibling of genotype  $Aa$  is  $r\Pi^2(x_1, x_2) + (1 - r)\Pi^2(\bar{x}_1, x_2)$ . Since  $Aa$  genotypes are equally likely to be cast as older or younger siblings, the survival probability of a randomly selected  $Aa$  genotype is

$$\begin{aligned} & \frac{1}{2} (r\Pi^1(x_1, x_2) + (1 - r)\Pi^1(x_1, \bar{x}_2)) + \frac{1}{2} (r\Pi^2(x_1, x_2) + (1 - r)\Pi^2(\bar{x}_1, x_2)) \\ = & \frac{1}{2} [r (\Pi^1(x_1, x_2) + \Pi^2(x_1, x_2)) + (1 - r) (\Pi^1(x_1, \bar{x}_2) + \Pi^2(\bar{x}_1, x_2))] \\ = & \frac{1}{2} \tilde{V}(x, \bar{x}) \end{aligned} \tag{20}$$

The survival probability of a randomly selected  $aa$  genotype is simply

$$\tilde{V}(\bar{x}, \bar{x}) = \frac{1}{2} (\Pi^1(\bar{x}_1, \bar{x}_2) + \Pi^2(\bar{x}_1, \bar{x}_2)). \tag{21}$$

Therefore a dominant mutant gene can invade a population of  $\bar{x}$  strategists if carriers of the mutant gene use a strategy  $x$  such that  $\tilde{V}(x, \bar{x}) > \tilde{V}(\bar{x}, \bar{x})$  and they cannot invade if  $\tilde{V}(x, \bar{x}) < \tilde{V}(\bar{x}, \bar{x})$ . These facts allow us to state the following proposition, which generalizes Proposition 1 to the case of asymmetric 2-sibling games.

**Proposition 6** *In an asymmetric 2-sibling game, if a single genetic locus determines an individual's actions in each of the two possible roles, then a necessary condition for a monomorphic population of  $\bar{x}$ -strategists to resist invasion by dominant mutants is that  $\bar{x}$  is a symmetric Nash equilibrium for the two-player game with the semi-Kantian fitness function  $\tilde{V}(\cdot, \cdot)$  defined in Equation 19. A sufficient condition is that  $\bar{x}$  is a strict symmetric Nash equilibrium for this game.*

## Separate, Unlinked Genes

Suppose that the genes that determine a child's behavior if it is born as an older sibling and the genes that control its behavior if it is born as a younger sibling

are found in two distinct genetic loci. Assume further that these loci are not “linked,” so that mutations at one locus are uncorrelated with mutations at the other. Consider a monomorphic population in which normal individuals are of genotype  $aa$  in the locus that controls behavior if they are the older sibling and of genotype  $bb$  in the locus that controls behavior if they are the younger sibling. These individuals are said to be of genotype  $aabb$ . They take action  $\bar{x}_1$  if born as the older sibling and  $\bar{x}_2$  if as the younger sibling.

Consider a mutant gene  $A$  such that individuals who are of genotype  $Aa$  at the locus controlling behavior-if-older take action  $x_1$ . Since mutations at either locus are rare and mutations at the two loci are uncorrelated, almost all individuals carrying the mutant  $A$  gene will be of genotype  $Aabb$ . Moreover, almost all carriers of the  $A$  gene will be born to one parent of genotype  $aabb$  and one parent who is of genotype  $Aabb$ . Individuals of genotype  $Aabb$  the mutant action  $x_1$  if they are born as older siblings and the normal action  $\bar{x}_2$  if born as younger siblings.

On average, half of the offspring of genotype  $Aabb$  will be older siblings and half will be younger siblings. An older sibling of genotype  $Aabb$  will take action  $x_1$  and its younger sibling, whether of genotype  $Aabb$  or of genotype  $aabb$ , will take action  $\bar{x}_2$ . Therefore the survival probability of an older sibling of genotype  $Aabb$  is  $\Pi(x_1, \bar{x}_2)$ . A younger sibling of genotype  $Aabb$  will take action  $\bar{x}_2$ . With probability  $1/2$ , its older sibling will be of genotype  $Aabb$  and take action  $x_1$  and with probability  $1/2$ , its older sibling will be of genotype  $aabb$  and take action  $\bar{x}_2$ . Therefore the survival probability of a younger sibling of genotype  $Aabb$  is  $\frac{1}{2}\Pi(x_1, \bar{x}_2) + \frac{1}{2}\Pi(\bar{x}_1, \bar{x}_2)$ . Since  $Aabb$  genotypes are equally likely to be born as older siblings and as younger siblings, the survival probability of a randomly selected  $Aabb$  genotype is:

$$\frac{1}{2}\Pi^1(x_1, \bar{x}_2) + \frac{1}{4}\Pi^2(x_1, \bar{x}_2) + \frac{1}{4}\Pi^2(\bar{x}_1, \bar{x}_2) \quad (22)$$

The survival probability of a randomly selected  $aa$  genotype is

$$\frac{1}{2} (\Pi^1(\bar{x}_1, \bar{x}_2) + \Pi^2(\bar{x}_1, \bar{x}_2)). \quad (23)$$

Therefore a dominant mutant gene  $A$  can invade a monomorphic population of  $aabb$  genotypes if

$$\frac{1}{2}\Pi^1(x_1, \bar{x}_2) + \frac{1}{4}\Pi^2(x_1, \bar{x}_2) + \frac{1}{4}\Pi^2(\bar{x}_1, \bar{x}_2) > \frac{1}{2} (\Pi^1(\bar{x}_1, \bar{x}_2) + \Pi^2(\bar{x}_1, \bar{x}_2)). \quad (24)$$

Inequality 24 is equivalent to:

$$\frac{1}{2}\Pi^1(x_1, \bar{x}_2) + \frac{1}{4}\Pi^2(x_1, \bar{x}_2) > \frac{1}{2}\Pi^1(\bar{x}_1, \bar{x}_2) + \frac{1}{4}\Pi^2(\bar{x}_1, \bar{x}_2), \quad (25)$$

which in turn is equivalent to:

$$H^1(x_1, \bar{x}_2) > H^1(\bar{x}_1, \bar{x}_2). \quad (26)$$

It follows that a necessary condition for a monomorphic population of  $aabb$  genotypes to resist invasion by a dominant mutant gene that makes older siblings use a strategy  $x_1$  is that  $H^1(x_1, \bar{x}_2) \leq H^1(\bar{x}_1, \bar{x}_2)$  for all possible strategies  $x_1$ . Similar reasoning shows that a *sufficient* condition for a monomorphic population of  $aabb$  genotypes to resist such an invasion is that  $H^1(x_1, \bar{x}_2) < H^1(\bar{x}_1, \bar{x}_2)$  for all possible strategies  $x_1$ .

A parallel line of reasoning applies to a dominant mutant  $B$  gene such that  $aaBb$  genotypes take action  $x_2$  rather than the normal action,  $\bar{x}_2$ . Putting these results together, we have:

**Proposition 7** *In an asymmetric 2-sibling game, if the genes that determine a child's behavior when it is born as an older sibling and the genes that control its behavior when it is born as a younger sibling are found in two distinct genetic loci, then a monomorphic population in which older siblings take action  $\bar{x}_1$  and younger siblings take action  $\bar{x}_2$  resists invasion by dominant mutants only if  $(\bar{x}_1, \bar{x}_2)$  is a Nash equilibrium for the asymmetric game in which player 1 has the inclusive fitness payoff  $H^1(\cdot, \cdot)$  and player 2 has the inclusive fitness payoff  $H^2(\cdot, \cdot)$ . A sufficient condition for this population to resist invasion is that  $(\bar{x}_1, \bar{x}_2)$  is a strict Nash equilibrium for this game.*

A pair of actions  $(\bar{x}_1, \bar{x}_2)$  is seen to be a Nash equilibrium for the asymmetric game with payoff functions  $H^1(\cdot, \cdot)$  and  $H^2(\cdot, \cdot)$  if and only if the strategy  $\bar{x} = (\bar{x}_1, \bar{x}_2)$  is a symmetric Nash equilibrium for the symmetric game in which the payoff function is given by  $\tilde{H}(x, y) = H^1(x_1, y_2) + H^2(y_1, x_2)$ . Therefore Proposition 4 has the following corollary.

**Corollary 2** *In an asymmetric 2-sibling game, if the genes that determine a child's behavior in its two possible roles are found in two distinct genetic loci, then a monomorphic population in which older siblings take action  $\bar{x}_1$  and younger siblings take action  $\bar{x}_2$  resists invasion by dominant mutants only if  $\bar{x} = (\bar{x}_1, \bar{x}_2)$  is a symmetric Nash equilibrium for the symmetric payoff function  $\tilde{H}(x, y)$ . A sufficient condition for this population to resist invasion is that  $(\bar{x}_1, \bar{x}_2)$  is a strict symmetric Nash equilibrium for this game.*

## Strategic complementarity and substitutability

In a two-player asymmetric game, two strategies  $x = (x_1, x_2)$  and  $y = (y_1, y_2)$  are said to be *strategic complements* if the expected total payoff to the two players when they “coordinate” by randomly choosing one of the two strategies and both playing it exceeds the expected total payoff when they “diversify” by randomly assigning one of the strategies to one player and the other strategy to the other player. Strategies are said to be *strategic substitutes* if the total payoff is higher if the players diversify than if they coordinate. A more formal statement of this definition is:

**Definition 1** *Define  $\tilde{\Pi}(x_1, x_2) = \Pi^1(x_1, x_2) + \Pi^2(x_1, x_2)$ . For any two strategies  $x = (x_1, x_2)$  and  $y = (y_1, y_2)$ , let*

$$C(x, y) = \tilde{\Pi}(x_1, x_2) + \tilde{\Pi}(y_1, y_2) - \tilde{\Pi}(x_1, y_2) - \tilde{\Pi}(y_1, x_2). \quad (27)$$

The strategies  $x = (x_1, x_2)$  and  $y = (y_1, y_2)$  are said to be strategic complements if  $C(x, y) \geq 0$  and strategic substitutes if  $C(x, y) \leq 0$ .

In the case of differentiable payoff functions, strategic complementarity and substitutability are related in a simple way to the cross-partial derivatives of the payoff functions.

**Lemma 6** *Let the set  $S$  of possible strategies be a convex set and let the function  $\tilde{\Pi}(x_1, x_2)$  be twice continuously differentiable. Then the matrix of cross partials  $\tilde{\Pi}_{12}(x_1, x_2)$  is positive semi-definite for all  $(x_1, x_2) \in S$  if and only if every pair of strategies in  $S$  are strategic complements, and negative semi-definite for all  $(x_1, x_2) \in S$  if and only if every pair of strategies in  $S$  are strategic substitutes.*

For games in which there is strategic complementarity or strategic substitutability, there is a nice, crisp relationship between Nash equilibrium for the game with the semi-Kantian payoff function  $\tilde{V}(\cdot, \cdot)$ , and Nash equilibrium for the corresponding asymmetric game with inclusive fitness payoff function  $\tilde{H}(\cdot, \cdot)$ .

Straightforward calculation shows the following:

**Lemma 7** *for any pair of strategies,  $x = (x_1, x_2)$  and  $\bar{x} = (\bar{x}_1, \bar{x}_2)$ ,*

$$\tilde{V}(x, \bar{x}) - \tilde{V}(\bar{x}, \bar{x}) = \tilde{H}(x, \bar{x}) - \tilde{H}(\bar{x}, \bar{x}) + rC(x, \bar{x}). \quad (28)$$

The following result is almost immediate from Lemma 7.

**Proposition 8** *In an asymmetric two-sibling game: If every pair of strategies are strategic complements, then a Nash equilibrium for the game with inclusive fitness payoffs is also a Nash equilibrium for the corresponding game with a semi-Kantian payoff function. If every pair of strategies are strategic substitutes, then a Nash equilibrium for the game with semi-Kantian payoffs is also a Nash equilibrium for the game with inclusive fitness payoffs.*

In an additive game between siblings,  $C(x, y) = 0$  for all  $x = (x_1, x_2)$  and  $y = (y_1, y_2)$ , so that all strategies are strategic complements, as well as strategic substitutes. This implies the following Corollary to Proposition 5.

**Corollary 3** *In an additive, asymmetric two-sibling game, a Nash equilibrium for inclusive fitness payoffs is a Nash equilibrium for semi-Kantian payoffs.*

# Appendix

## A Additive Games Between Relatives

The class of additive games between relatives is defined as follows. There is a population of individuals such that each individual  $i$  interacts with a finite set  $S_i$  of relatives, bearing specific familial relationships to that individual, grandparent, parent, sibling, aunt, uncle, cousin and so on.<sup>15</sup>

For each individual  $i$  and each of  $i$ 's relatives  $j$ , there is a set  $A_{ij}$  of possible actions that  $i$  could take toward  $j$ . Define a function  $c_i(\cdot)$  such that  $c_i(a_{ij})$  is the "cost" to  $i$  of taking action  $a_{ij}$  towards  $j$ . Also, for each of  $i$ 's relatives  $j \in S_i$ , define a function  $b_{ji}(\cdot)$  so that  $b_{ji}(a_{ji})$  is the "benefit" conferred on  $i$  by the action  $a_{ji}$  taken by  $j$  toward  $i$ . Let  $a_i$  be the vector of all actions taken by  $i$  toward its relatives and let  $(a_1, \dots, a_n)$  be a list of the vectors of actions taken by all individuals toward their relatives. The probability that individual  $i$  survives to reproductive age is the sum of benefits that  $i$  receives from its relatives minus the cost of  $i$ 's own action. This can be expressed as:

$$\Pi^i(a_1, \dots, a_n) = \sum_{j \in S_i} b_{ji}(a_{ji}) - \sum_{j \in S_i} c_i(a_{ij}). \quad (29)$$

In a population of individuals playing additive games with their relatives, the *inclusive fitness*  $H_i$  of individual  $i$  is defined by the equation:

$$H^i(a_1, \dots, a_n) = \Pi^i(a_1, \dots, a_n) + \sum_{j \in S_i} r_{ij} \Pi^j(a_1, \dots, a_n) \quad (30)$$

where  $r_{ij}$  is the degree of relationship between individuals  $i$  and  $j$  and where  $\Pi^i(a_1, \dots, a_n)$  is defined by Equation 29.

## B Proofs of Propositions in the Text

### Proof of Proposition 1

A mutant  $A$  gene can invade a monomorphic population of  $aa$  genotypes if the reproduction rate of  $A$  genes exceeds that of normal  $a$  genes. The reproduction rate of  $A$  genes will be greater than (less than) that of  $a$  genes if the probability that an  $Aa$  heterozygote child survives to adulthood is greater than (less than) the probability that a randomly selected child of genotype  $aa$  survives to adulthood.

If mating is monogamous, an  $Aa$  genotype born to one  $Aa$  and one  $aa$  parent will be matched with an  $Aa$  sibling with probability 1/2 and with an  $aa$  sibling with probability 1/2. Since  $Aa$  genotypes use strategy  $x$  and  $aa$  genotypes use

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<sup>15</sup>A single individual will typically bear different familial relationships to several other people. For example Arthur can simultaneously be Betty's brother, Fred's son, and Curious George's uncle.

strategy  $\bar{x}$ , the survival probability of an  $Aa$  is  $\Pi(x, x)$  if its sibling is an  $Aa$  genotype and  $\Pi(x, \bar{x})$  if its sibling is an  $aa$  genotype. Therefore the survival probability of an offspring of genotype  $Aa$  is  $V(x, \bar{x}) = \frac{1}{2}\Pi(x, x) + \frac{1}{2}\Pi(x, \bar{x})$ .

If mating is not monogamous, then two children who share the same mother might not have the same father. If the mutant gene is not sex-linked, then 1/2 of the children of genotype  $Aa$  are born to an  $Aa$  mother and an  $aa$  father and 1/2 are born to an  $aa$  mother and an  $Aa$  father. If the mother is of type  $Aa$ , then the probability that a child of  $Aa$  has an  $Aa$  sibling is 1/2. But if the father is of type  $Aa$ , then the probability that the child is paired with a sibling of type  $Aa$  is only  $s/2$  where  $s$  is the probability that the two siblings share the same father. The probability, therefore, that a child of genotype  $Aa$  is paired with a sibling of genotype  $Aa$  is therefore  $1/4 + s/4$ . The probability that a child of the rare mutant genotype  $Aa$  survives to adulthood is therefore  $V(x, \bar{x}) = r\Pi(x, x) + (1 - r)\Pi(x, \bar{x})$ , where  $r = 1/4 + s/4$  is the ‘‘coefficient of relationship between siblings’’. (In the special case of monogamy,  $s = 1$  and  $r = 1/2$ .)

The function  $V(\cdot, \cdot)$  is seen to be the same as Grafen’s personal fitness function. Let  $S$  be the set of possible strategies for a sibling. If for some strategy  $x \in S$ ,  $V(x, \bar{x}) > V(\bar{x}, \bar{x})$  then a monomorphic population of  $aa$  genotypes who take action  $\bar{x}$  could be invaded by a dominant mutant gene  $A$  such that  $Aa$  genotypes take action  $x$ . It follows that a necessary condition for a monomorphic population of  $\bar{x}$ -strategists to resist invasion by dominant mutants is that  $V(x, \bar{x}) \leq V(\bar{x}, \bar{x})$  for all  $x \in S$ . Similar reasoning shows that a sufficient condition for a monomorphic population of  $\bar{x}$ -strategists to resist invasion by dominant mutants is that for all  $x \in S$ , if  $x \neq \bar{x}$  then  $V(x, \bar{x}) < V(\bar{x}, \bar{x})$ . This establishes that the strategy  $\bar{x}$  must be a symmetric Nash equilibrium for the game with payoff function  $V$ .

■

## Proof of Lemma 1

From Equation 8, it follows that

$$V_1(\bar{x}, \bar{x}) = \sum_{k=1}^{N-1} p(k)\Phi_1(x, \bar{x}, k). \quad (31)$$

The gradient of  $\Phi(x, \bar{x}, k)$  with respect to  $x$  is:

$$\begin{aligned} \bar{\Phi}_1(x, \bar{x}, k) &= \frac{\partial \Pi^1(x, \overbrace{x, \dots, x}^{k \text{ times}}, \overbrace{\bar{x}, \dots, \bar{x}}^{n-k-1 \text{ times}})}{\partial x} & (32) \\ &= \Pi_1^1(x, \overbrace{x, \dots, x}^{k \text{ times}}, \overbrace{\bar{x}, \dots, \bar{x}}^{N-k-1 \text{ times}}) + k\Pi_2^1(x, \overbrace{x, \dots, x}^{k \text{ times}}, \overbrace{\bar{x}, \dots, \bar{x}}^{n-k-1 \text{ times}}) & (33) \end{aligned}$$

Equation 34, below, follows from Equations 31 and 33. Equation 35 then follows from the fact that for the probability distribution  $p(k)$ ,  $\sum_{k=0}^{n-1} p(k) = 1$  and  $\sum_{k=0}^{n-1} p(k)k = (n - 1)r$ .

$$V_1(\bar{x}, \bar{x}) = \sum_{k=0}^{n-1} p(k) \Pi_1^1(\bar{x}, \overbrace{\bar{x}, \dots, \bar{x}}^{n-1 \text{ times}}) + \sum_{k=0}^{n-1} p(k) k \Pi_2^1(\bar{x}, \overbrace{\bar{x}, \dots, \bar{x}}^{n-1 \text{ times}}) \quad (34)$$

$$= \Pi_1^1(\bar{x}, \overbrace{\bar{x}, \dots, \bar{x}}^{n-1 \text{ times}}) + (n-1)r \Pi_2^1(\bar{x}, \overbrace{\bar{x}, \dots, \bar{x}}^{n-1 \text{ times}}) \quad (35)$$

Differentiating Equation 10, we find that

$$H_1(x, y) = \Pi_1^1(x, y, \dots, y) + r(n-1) \Pi_1^2(x, y, \dots, y) \quad (36)$$

Therefore

$$H_1(\bar{x}, \bar{x}) = \Pi_1^1(\bar{x}, \bar{x}, \dots, \bar{x}) + (n-1)r \Pi_2^1(\bar{x}, \bar{x}, \dots, \bar{x}) \quad (37)$$

$$= V_1(\bar{x}, \bar{x}). \quad (38)$$

■

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