

Chapter 8

Kin selection and the gene's eye view of evolution

Despite the principle of “survival of the fittest”, the ultimate criterion which determines whether an allele will spread is not whether the behavior is to the benefit of the behaver but whether it is to the benefit of the allele, and this will be the case if the average net result of the behavior is to add to the gene-pool a handful of genes containing the allele in higher concentration than does the gene-pool itself. W. D. Hamilton

8.1 Why self-sacrifice?

We saw in previous chapters that natural selection favors mutant alleles causing their carriers to have an increase in fecundity or survival relative to those in the population. However, in social insects, such as ants, termites, or bees, individuals often forgo their own reproduction to help produce siblings and sometimes even sacrifice themselves defending a colony. Reproductive sterility such as seen in social insects has been around for millions of years and thus must be adaptive, but it poses a serious “evolutionary puzzle”, since any allele that causes an individual to forego reproduction or destroy itself should be selected against. Sterile social insects really puzzled Darwin and remained an evolutionary puzzle for about a century.

The reason why sterility can be adaptive was given by W. D. Hamilton in 1963. He showed that an allele causing an individual to sacrifice itself can nevertheless be favored by natural selection if the behavior benefits replicate copies of that allele in other individuals. If the reproductive benefit to the *recipient* of the selfless (or altruistic) action is greater than the reproductive cost to the individual performing the action, the *actor*, and if actor and

recipient are *related*, then an allele causing selflessness (or altruism) will be favored by natural selection, since on average the fitness of the allele is increased by self-sacrifice. Selection indeed favors alleles that leave on average most replicate copies in the offspring generation, regardless of how it affects particular individuals carrying the allele. This suggests that selection occurs at the level of the gene and not at the level of the individual.

This change of perspective, focusing on genes rather than on individuals, not only explains the evolution of selflessness (or altruism), but allows to better understand the evolution of many other phenotypes, in contexts as diverse as conflict within the family, to the evolution of multicellularity, or even warfare in pre-state societies. This has resulted in the most important change of thinking about the evolution of life since Darwin's theory of natural selection. The goal of this chapter is to study natural selection when interactions occur between relatives. Also called *kin selection*, this gene-centered perspective of evolution will provide us with novel insights about how evolution happens. In order to understand kin selection, we first need to understand the concept of genetic relatedness between individuals.

8.2 Relatedness

Phenotypic similarities between individuals are common, for instance between parent and offspring or between siblings. Siblings often look more similar compared to a pair of individuals randomly chosen in the population. Likewise, individuals in the same ethnic group share more similar phenotypes than individuals from different groups. This phenotypic similarity stems from the fact that individuals are genetically *related*, meaning that they are more likely to share identical alleles than individuals randomly sampled from the population. This occurs when two individuals have a common ancestor, like a parent or a grand-parent, so that the alleles they carry are identical-by-descent, i.e., they both carry an allele that descends from the same allele in the common ancestor (say an allele in a grand-father or a great-grand mother).

In order to quantify how a pair of relatives (a parent and an offspring, two siblings, two cousins) are more likely to share identical alleles than two individuals sampled randomly from the population, we introduce the *relatedness coefficient* r between two individuals, which is defined as the probability that a gene taken in one individual under scrutiny (usually thought to be the actor of some behavior) has an *identical-by-descent* copy of that gene in the second individual (usually thought to be the recipient of some behavior). This means that with probability r , the two genes under consideration descend from the same gene in a common ancestor.

Relatedness between parent and offspring

To better understand the concept of relatedness, let us evaluate the relatedness between parent and offspring under random mating (no sexual selection or mate choice). And let us consider the relatedness from the perspective of an offspring. We thus seek the probability $r_{o,p}$ that a gene in the offspring is identical-by-descent has a copy that is identical-by-descent with a gene in the parent under focus (either the father or the mother). The relatedness between an offspring and a given parent (Mom or Dad) is equal to

$$r_{o,p} = \frac{1}{2}. \quad (8.1)$$

This equation can be understood by considering the two following mutually exclusive events.

- With probability 1/2, the gene in the offspring comes from the parent under focus (either Mom or Dad), and is then necessarily (probability one) identical-by-descent to a gene in the parent.
- With probability 1/2, the gene sampled in the offspring comes from its other parent (either Mom or Dad). Then, under random mating, this gene is unrelated (probability zero) to any gene in the the parent under focus.

Hence, under random mating, the relatedness between an offspring and its parent is simply 1/2 and can be thought as the fraction of genes the two have in common.

Relatedness between full siblings

Let us now consider the relatedness between full siblings, who have the same mother and father. Here, we seek the probability r_{sib} that a gene in an offspring under focus has a copy that is identical-by-descent with a gene in its sibling. This is equal to

$$r_{sib} = \frac{1}{2} \times \frac{1}{2} + \frac{1}{2} \times \frac{1}{2} = \frac{1}{2}, \quad (8.2)$$

which can be understood by considering the two following mutually exclusive events.

- With probability 1/2, the gene in the offspring under focus comes from its mother. In this case, the maternal gene in the sibling is identical-by-descent to the focal's offspring maternal gene with probability 1/2. Because individuals are not inbred, such that parents are unrelated, this is the only way how the maternal gene in the sibling can be identical-by-descent to the maternal gene in the offspring under focus.
- With probability 1/2, the gene in the offspring under focus comes from its father. In this case, the paternal gene in the sibling is identical-by-descent to focal's offspring paternal gene with probability 1/2. Because individuals are not inbred, such that parents are unrelated, this is the only way how the paternal gene in the sibling can be identical-by-descent to the paternal gene in the offspring under focus.

Hence, under random mating, the relatedness between sibling is, $1/2$, is equivalent to the relatedness between parent and offspring.

8.3 Evolutionary invasion analysis for relatives

8.3.1 Gene fitness

Now equipped with the concept of relatedness, we can start to investigate how selection operates when interactions occur between relatives. First, to understand what happens selection in the simplest context under such interactions, we focus on interactions within the family (parent-offspring or sibling interactions). And consider only the fate (invasion or extinction) of an allele A arising as a single copy in a population otherwise monomorphic for B (just like in the chapters on adaptive dynamics and sexual selection).

When A arises as a single copy, the individual in which the mutation appears is necessarily heterozygote AB, expressing phenotype by x . Even if allele A slightly increases in frequency in the population, individuals expressing x will still be heterozygote (since to form an homozygote two A carriers must mate, which is unlikely when allele A is relatively rare in the population). Thus, in order to determine whether allele A is favored by selection (or will go extinct) when at low frequency in the population, we only need to consider the fitness of an heterozygote individual and can neglect homozygotes for A. However, we need to take into account the fact that an A carrier may interact with a relative. Hence, we denote by $w(x, x_r)$ the expected fitness (per ploidy) of an individual with phenotype x when interacting with a relative that expresses phenotype x_r , and where these interactions occur in a population where individuals at large are homozygote for B have phenotype y .

The key point now is that, depending on whether it inherited allele A or B, the relative may either be a heterozygote for A or a resident homozygote (i.e., $x_r \in \{x, y\}$). So, the average fitness of an heterozygote individual expressing phenotype x in a population where individuals express phenotype y is

$$W(x, y) = rw(x, x) + (1 - r)w(x, y). \quad (8.3)$$

This is the expected fitness of a focal heterozygote individual and can be understood as follows.

- Given that the focal individuals carries A, there is a probability r that a gene taken randomly in the relative of the focal individual is identical-by-descent and therefore is also A. Hence, the two individuals carry the A allele because they inherited it from a common ancestor. In other words, the focal individual interacts with probability r with another heterozygote individual.

- Given that the focal individual carries A, there is a probability $1 - r$ that a gene

randomly taken in the relative is not identical-by-descent to the A allele. In other words, with probability $1-r$ the focal interacts with a homozygote individual for the resident allele.

What is crucial to understand about eq. (8.3) is that interacting individuals are more likely to carry the same allele than are two individuals taken randomly from the population. Equation (8.3) shows that fitness $W(x, y)$ is the average fitness of an individual carrying A over the different interactions backgrounds: either interacting with a AB individual or a BB individual, with probability r and $1-r$ respectively. This shows that it is important to distinguish between two concepts of fitness:

- *Individual fitness* $w(x, x_r)$, which is the expected number of offspring produced by a focal individual, and is thus a measure of fitness defined at the individual level.

- *Gene fitness* $W(x, y)$, which is the expected number of gene copies produced over one generation by an average mutant copy.

In a resident population, the average fitness (per ploidy) of a carrier of the B allele is necessarily equal to one, since at a demographic equilibrium each gene just replaces itself (recall eq. 6.2 for haploids and eq. 7.4 for diploids). As a consequence, we have that allele A is disfavored by selection if

$$W(x, y) \leq 1. \quad (8.4)$$

If this inequality is satisfied, an individual carrying A produces on average one (or less than one) replica copy of allele A, which henceforth cannot spread in the population (conceptually eq. 8.4 is the same as eq. 6.3 of the chapter on adaptive dynamics and eq. 7.5 of the chapter on sexual selection).

8.3.2 Uninvadability

We can now characterize the condition under which a phenotype (strategy) is uninvadable by any other strategy. A resident strategy y is said to be *uninvadable* if

$$W(x, y) \leq 1 \quad \forall x \in \mathcal{X}. \quad (8.5)$$

Hence, an uninvadable strategy is resistant to invasion by any mutant phenotype.

As in the previous chapters, it is useful to define the selection gradient at the resident phenotypic point y as the marginal change in fitness:

$$S(y) = \left. \frac{\partial W(x, y)}{\partial x} \right|_{x=y}. \quad (8.6)$$

This is indicative of whether changing strategy at y is profitable and thus predicts the direction of evolution at y . A *singular* strategy y^* solves

$$S(y^*) = 0, \quad (8.7)$$

and such a strategy is convergence stable, i.e., an attractor of the evolutionary dynamics, if it satisfies

$$\left. \frac{dS(y)}{dy} \right|_{y=y^*} < 0. \quad (8.8)$$

This means that the selection gradient $S(y)$ in the resident population is y is a monotonic decreasing function in y in the neighborhood of y^* , such that $S(y) > 0$ for some resident population where $y < y^*$ and $S(y) < 0$ for some resident population where $y > y^*$. This means that mutants arising in a resident population y that is in the neighborhood of y^* will be favored by selection if the phenotypic value of the mutant is closer to y^* compared to the resident (e.g., eq. 6.29 from chapter 6).

The above shows that the three concepts of singular strategy, convergence stable strategy, and uninvadable strategy, also apply to the case of interactions among relatives. The expression for the selection gradient, however, is likely to be different, but how?

8.4 Hamilton's rule

If we substitute eq. (8.3) into eq. (8.6), we find that the selection gradient can be written as

$$S(y) = \frac{\partial w(x, x_r)}{\partial x} + \frac{\partial w(x, x_r)}{\partial x_r} r, \quad (8.9)$$

where all derivatives are evaluated at $x = x_r = y$ (see Derivation 1). Fitness $w(x, x_r)$ can be interpreted as the expected fitness of an individual with phenotype x when interacting with a sibling that expresses phenotype x_r in a population where individuals at large have phenotype y . The first partial derivative, $\partial w(x, x_r)/\partial x$, can be interpreted as representing the effect a focal individual (when varying its strategy) has on its own fitness, and is therefore called the *direct effect* on fitness. The second partial derivative, $\partial w(x, x_r)/\partial x_r$, represents the effect of the relative (when varying its strategy) on the fitness of a focal individual, and is therefore called the *indirect effect* on fitness. Since relatedness r is the proportion of genes that a relative shares with a focal individual, it provides a measure of the extent to which the relative will change its strategy when the focal individual does.

The direct effect is often denoted by $-c$, with c standing for “cost” (i.e., $-c = \partial w(x, x_r)/\partial x$). The indirect effect is often denoted by b for “benefit” (i.e., $b = \partial w(x, x_r)/\partial x_r$). In terms of these notations, the selection gradient is positive, $S(y) > 0$, if

$$rb - c > 0. \quad (8.10)$$

Namely, allele A is favored by selection if the indirect benefit weighted by relatedness is larger than the direct cost. This condition is known as *Hamilton's rule*. Importantly, nothing in the model forces the direct effect, $-c$, to really be a fitness cost: c can be < 0 but also > 0 such that there can be a direct benefit $-c > 0$ to the actor. But the notation does emphasize that it is possible for a behavior to be costly at the individual level and be nevertheless favored

by natural selection because it benefits the gene lineage causing the action. Hence, what matters for natural selection is not the fitness of the individual but the fitness of the gene.

The signs of the cost and benefit terms, c and b , in fact, allow us to operationally classify social behavior in terms of four broad categories as follows.

- **Altruism.** This is defined as occurring when $-c < 0$ and $b > 0$. In other words, there is a fitness cost to self but a fitness benefit to others.

- **Cooperation** (narrow sense “mutualistic cooperation”). This is defined as occurring when $-c > 0$ and $b > 0$. Here, we have a fitness benefit to self and a fitness benefit to others.

- **Selfishness.** This is defined as occurring when $-c > 0$ and $b < 0$. Here, we have a fitness benefit to both self but a fitness cost to others.

- **Spite.** This is defined as occurring when $-c < 0$ and $b < 0$. Here, we have a fitness benefit to both self and others.

These terms are also often used in economics and the social sciences to label behaviors. It is thus worth emphasizing that the above definitions are based on reproductive fitness, which is an operational quantity. In contrast to terms such as “well-being” or “utility”, fitness has a clear unit of measurement and can thus be estimated in the wild.

8.5 Evolution of self-sacrifice

We illustrate the above concepts by applying Hamilton’s rule to the evolution of self-sacrifice. To do so, we consider the life cycle that we already assumed in the previous chapter and that is as follows. (1) Adult individuals gather resources (possibly involving density dependent competition) and produce offspring with a fecundity that depends on the amount of resources they obtain. (2) All adults die and offspring survive to adulthood to form the next generation of adults.

We study the invasion of a mutant phenotype with a probability x of self-sacrificing itself for a relative with phenotype x_r , when the population is monomorphic in y . Here, we assume self-sacrifice to increase a relative’s survival probability. We write $s_J(x, x_r)$ for the expected (density-independent) survival probability of an offspring with phenotype x when interacting with a sibling with phenotype x_r . In order to model self-sacrifice, we assume that the survival probability of an individual with self-sacrificing probability x when its sibling expresses self-sacrifice probability x_r is given by

$$s_J(x, x_r) = (1 - x)(s_b + Bx_r). \quad (8.11)$$

Here, $1 - x$ is the probability that the individual does not sacrifice itself for its relative, s_b is the baseline survival probability of the individual, and B is the increase in own survival

when the individual has not committed self-sacrifice but interacts with a self-sacrificing sibling (and who does so with probability x_r).

Assuming density-independent selection, we can write the fitness of a focal individual with self-sacrificing probability x when its sibling expresses self-sacrificing probability x_r in a population where the self-sacrificing probability is y as

$$w(x, x_r) = k s_J(x, x_r), \quad (8.12)$$

where k is a constant of proportionality that takes into account density-dependence and offspring production by the focal individual when it has reached adulthood.

Substituting the survival function (eq. 8.11) into the fitness function (eq. 8.12), and in turn the fitness function into the selection gradient (eq. 8.9), allows us to compute the direct effect on fitness as

$$\left. \frac{\partial w(x, x_r)}{\partial x} \right|_{x=x_r=y} = -k(s_b + By). \quad (8.13)$$

Since this is negative, it is a fitness cost, which amounts to the survival probability $s_b + By$ of an individual that has not self-sacrificed itself. On the other hand, the indirect fitness effect is

$$\left. \frac{\partial w(x, x_r)}{\partial x_r} \right|_{x=x_r=y} = k(1 - y)B, \quad (8.14)$$

which is an increase in survival weighted by the probability of being alive (otherwise no indirect benefit could be obtained). Hence, this is a fitness benefit.

Adding up direct and indirect fitness effects gives the selection gradient on the probability of self sacrifice,

$$S(y) = k [-(s_b + By) + rB(1 - y)]. \quad (8.15)$$

The sign of the selection gradient depends on y , which allows us to evaluate the singular strategies satisfying $S(y^*) = 0$. There is a unique solution given by

$$y^* = \frac{rB - s_b}{B(1 + r)}. \quad (8.16)$$

This singular probability of self-sacrifice increases with relatedness and is positive if $rB > s_b$ (see Fig. 8.1); namely, if the gain in survival weighted by relatedness exceeds the loss of survival from increasing the probability of self-sacrifice.

Computing the derivative of the selection gradient evaluated at the singular point (eq. 8.16) and rearranging produces

$$\left. \frac{dS(y)}{dy} \right|_{y=y^*} = -\frac{B(1 + r)^3}{r(s_b + B)^2} < 0. \quad (8.17)$$

This shows that the singular strategy is convergence stable, i.e., an attractor of the evolutionary dynamics. It can also be shown that this strategy is uninvadable strategy as well.

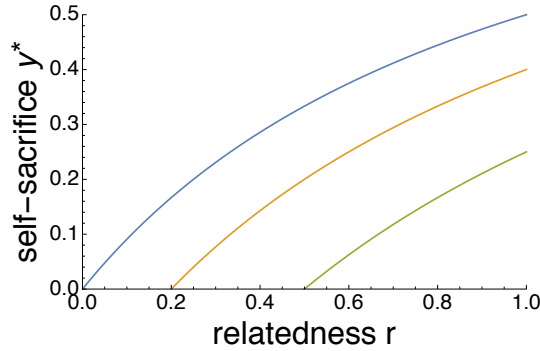


Figure 8.1: Converges stable level of self sacrifice given by eq. (8.16) and depicted as a function of r . Parameters are $B = 0.5$ and $s_b = 0$ (blue), $s_b = 0.1$ (yellow), and 0.25 (green).

8.6 Evolutionary economics within the family: conflict or cooperation?

Interactions among family members such as between parents and offspring or between siblings are common in nature. Many animals indeed care for their young. But the duration of such care and the distribution of resources between offspring vary enormously, depending on various sets of behaviors.

We saw that as a consequence of sexual reproduction, parents and their offspring are only genetically related by one half. Put another way, they are not genetically identical. This suggests that natural selection will shape a differential expression of genes in parents and offspring for behaviors affecting both individuals, since their (evolutionary) incentives are not properly aligned, for instance when it comes to the amount of care a parent should provide to the offspring. We now investigate how the provisioning of care is determined by kin selection, and see how this can lead to parent-offspring conflict.

8.6.1 Allocation controlled by parents

In order to carry out an evolutionary analysis of resource allocation to offspring, we take the case of a mother with two offspring and first assume that she is in control of the allocation of resources. Suppose that the mother has one unit of some resource and she allocates a proportion x of this resource to its first offspring and proportion $1 - x$ to its second offspring. We assume that resources increase offspring survival and we denote by $s(x)$ the survival of an offspring, who receives x unit of resources from its mother.

We can then let the fitness of a mutant mother with trait x , in a population monomorphic for y , be proportional to the sum of the survival of her two offspring:

$$w(x, y) = k [s(x) + s(1 - x)] \quad (8.18)$$

for some constant k taking density-dependence into account.

As an explicit example, we assume that the survival function as a function of any argument z is

$$s(z) = z^{1/2}, \quad (8.19)$$

which is concave in z , taking the value $s(0) = 0$ when $z = 0$ and $s(1) = 1$ when $z = 1$. Since the mother is in control of the trait, then it is a similar model to sex-specific trait expression model of chapter 7. Substituting the fitness function (eq. 8.18) along with the survival function eq. 8.19) into the selection gradient (eq. 7.7), we have

$$\begin{aligned} S(y) &= k \left[\left. \frac{\partial s(x)}{\partial x} \right|_{x=y} + \left. \frac{\partial s(1-x)}{\partial x} \right|_{x=y} \right] \\ &= k \left[\frac{1}{2y^{1/2}} - \frac{1}{2(1-y)^{1/2}} \right] \end{aligned} \quad (8.20)$$

where the first term in brackets is the marginal benefit from allocating more resources to the first offspring, while the second term is the marginal cost of thus depriving the second offspring by doing so. From eq. (8.20), we can write the singular strategy y^* satisfying the condition:

$$S(y^*) = 0 \quad \Longleftrightarrow \quad \frac{(1-y^*)^{1/2}}{2} = \frac{(y^*)^{1/2}}{2}. \quad (8.21)$$

This means that the singular strategy y^* must balance out marginal benefit and cost, such that

$$y^* = \frac{1}{2}. \quad (8.22)$$

Since the returns of investing into each offspring are exactly the same, the marginal benefit and cost in eq. (8.21) will equalize when the mother allocates an equal amount of resources to each offspring. Hence a mother has no advantage to favor one offspring over the other (provided they are of equal condition), and this result actually applies regardless of the exact shape of the survival function $s(x)$, as long as it is concave.

8.6.2 Allocation controlled by offspring

Suppose that now the offspring can have full control over the allocation of the one unit of parental resource. Since there are two offspring, we assume that each offspring has an equal chance of gaining control over resource allocation, i.e., we toss a coin to determine which offspring controls resource allocation. Let x be the phenotype of a focal offspring in the pair

when it is the one in control of the resources allocated. With this, the expected survival of a focal offspring with allocation level x when its sibling expresses allocation level x_r is

$$s_J(x, x_r) = \frac{1}{2}s(x) + \frac{1}{2}s(1 - x_r). \quad (8.23)$$

This can be understood by noting that with probability $1/2$ the focal offspring is in control of the trait and then has survival $s(x)$, while with probability $1/2$ its sibling is in control of the trait, in which case it obtains $1 - x_r$ amount of resources, since x_r is the amount claimed by the sibling, and the survival of the focal is therefore $s(1 - x_r)$.

To obtain the fitness to a focal individual with allocation level x when its sibling expresses allocation level x_r in a population where individuals at large express allocation level y , we use eq. (8.12). Substituting the survival function (eq. 8.23) along with the explicit expression of individual survival (eq. 8.19) into the fitness function (eq. 8.12) and, in turn, fitness into the selection gradient (eq. 8.9), gives the following expression for the selection gradient on allocation level

$$\begin{aligned} S(y) &= \frac{k}{2} \left[\left. \frac{\partial s(x)}{\partial x} \right|_{x=y} + r \left. \frac{\partial s(1 - x_r)}{\partial x_r} \right|_{x_r=y} \right] \\ &= \frac{k}{2} \left[\frac{1}{2y^{1/2}} - r \frac{1}{2(1 - y)^{1/2}} \right], \end{aligned} \quad (8.24)$$

where the first term is the marginal benefit from claiming more resources, while the second term is the marginal cost when one sibling claims more resources. A singular strategy y^* must balance marginal benefit and cost, and from eq. (8.24) we can write this as

$$\frac{(1 - y^*)^{1/2}}{2} = r \frac{(y^*)^{1/2}}{2}. \quad (8.25)$$

By contrast to the case of parental control where allocation of resources to both offspring are equally valued (see eq. 8.21), under offspring control, the marginal cost in eq. (8.24) is discounted by r .

Battleground

The condition for a singular strategy (eq. 8.25) shows that if $r = 0$, an individual should claim all resources $y = 1$ as there are only benefits of increasing resource consumption; the left hand side of eq. (8.25) is positive, while the right hand side is zero. When $r = 1$, the singular strategy should be $y = 1/2$, which is the resource allocation favored by the mother (since eq. 8.25 is then equivalent to eq. 8.21). Hence, as relatedness between offspring decreases, an offspring will tend to claim more resources than its mother is willing to give. As a result there will be a battleground over resource allocation if $r < 1$. The battleground between a parent and an offspring is thus over the allocation $y \in [0.5, 1]$ in a family with two siblings.

From eq. (8.25), we find that there is unique singular strategy given by

$$y^* = \frac{1}{1 + r^2}, \quad (8.26)$$

which takes value $y^* = 1$ if $r = 0$ and $y^* = 1/2$ if $r = 1$. It can be checked that this is a convergence stable and an uninvadable strategy.

From battleground to resolution

The above results demonstrate that there is a potential conflict between parent and offspring over resource allocation, but this does not allow us to make predictions on the allocation of resources observed in nature. To that end, one needs to understand the mechanism through which parents and offspring influence the conflict resolution. Understanding how natural selection shapes the outcome of the conflict is much more complicated than showing that a potential conflict exist. Two broad categories of conflict outcomes have been proposed.

- Only the parent can influence the outcome. This is predicted on the supposition that parents are stronger and can always enforce their optimal allocation by *force majeure*.
- Both the parent and the offspring can influence the outcome. In many mammals and birds offspring communicate their needs to parents by various sounds. One expects that offspring will solicit their parents as much as they can, and may evolve psychological manipulation mechanisms to favor more allocation of resources for themselves (tantrums may be an example of that). Parent may then respond to solicitation and/or evolve measures to avoid manipulation.

Empirical evidences indeed suggest that selection will shape a differential expression of genes in parents and offspring concerning resource allocation, but the exact genetic mechanism by which this occurs is not known. Further, since parents and offspring can be considered to play a repeated game, it is very difficult to make clear theoretical predictions on outcomes observed in nature.

8.7 Appendix

Derivation 1. We here prove eq. (8.9). To that end, we first note that from eq. (8.3), the expression for gene fitness $W(x, y)$ is

$$W(x, y) = rw(x, x) + (1 - r)w(x, y). \quad (8.27)$$

Differentiating, we can write

$$\left. \frac{\partial W(x, y)}{\partial x} \right|_{x=y} = r \left(\frac{\partial w(x, x_r)}{\partial x} + \frac{\partial w(x, x_r)}{\partial x_r} \right) + (1 - r) \frac{\partial w(x, x_r)}{\partial x}, \quad (8.28)$$

where we use the fact that we can write $\partial w(x, x) / \partial x = \partial w(x, x_r) / \partial x + \partial w(x, x_r) / \partial x_r$ and $\partial w(x, y) / \partial x = \partial w(x, x_r) / \partial x$ when all derivatives are evaluated at $x = x_r = y$. Adding up the first and last term with common factor $\partial w(x, x_r) / \partial x$ in eq. (8.28), we have

$$S(y) = \left. \frac{\partial W(x, y)}{\partial x} \right|_{x=y} = \left. \frac{\partial w(x, x_r)}{\partial x} \right|_{x=x_r=y} + r \left. \frac{\partial w(x, x_r)}{\partial x_r} \right|_{x=x_r=y}. \quad (8.29)$$
