© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

CHAPTER ONE

Social Behavior and Evolutionary Thought

1.1 Explanations for Apparent Design

Animals, plants, and other organisms appear to be designed for some purpose. While the ultimate purpose may not always be clear to us, observers of the natural world can readily understand sophisticated "devices" such as the wing and the eye to be "designed" for flight and sight, respectively. Until the mid-nineteenth century, natural philosophy explained design in nature as being due to, and evidence for, the existence of a supernatural creator. One of the most famous late examples of this tradition is William Paley's "argument from design" [Paley, 1802]; on discovering a pocket watch lying on a heath, the conclusion of any reasonable person is that, due to its apparent complexity and its evident purpose, it must have been designed, and therefore a designer (the watchmaker) must exist. Paley went on to argue that, should the discovered watch have an internal mechanism capable of producing copies of itself, the rational discoverer would still conclude that it had been designed for this purpose, in addition to its purpose of telling the time, and must still therefore have a designer. Similarly, the apparent complexity in construction of animals and plants, and fitness for a purpose which includes reproduction, means they must have been designed, and therefore a designer (God) must exist. Under such a view, of course, an anthropocentric natural theologist might conclude that the animals and plants around us have been designed, by the supernatural creator, with the primary purpose of giving us food to eat, natural resources with which to make things, and so on.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

With the work of Charles Darwin and of Alfred Russel Wallace [Darwin and Wallace, 1858, Darwin, 1859], an alternative explanation for the appearance of design arrived and, simultaneously, the question of the ultimate purpose of organisms was answered. The ultimate purpose of organisms was to compete for individual reproduction, and the result of such competition was that natural selection would progressively improve their suitability for this purpose, thereby giving them the appearance of design. If flight would increase the chances of individual reproduction for members of a species, for example, then natural selection acting on heritable variation over many generations could fashion limbs into wings, and then progressively optimize them for the purposes of aerodynamically efficient flight. Design and purpose in nature were both explained, and the explanations did not suggest a supernatural designer.

Darwin and Wallace amassed significant empirical support for the theory of evolution through natural selection, in collections of animals from around the globe,[1] and Darwin also interacted with practitioners of artificial selection, such as pigeon breeders and farmers. Yet the new evolutionary theory was formulated without knowledge of how characteristics, which natural selection was supposed to act on, were inherited by offspring from their parents. In fact, only 8 years after Darwin and Wallace's papers were read at the Linnean Society in London, Gregor Mendel discovered the particulate nature of inheritance in an abbey in Brno, through his experiments on pea morphology [Mendl, 1866]. Despite being contemporary with and crucially relevant to the theory of natural selection, Mendel's results were ignored for over 30 years [Bateson, 1909]. Initially thought to be a replacement for Darwinian evolution, the field of genetics was ultimately reconciled with natural selection in a mathematical framework that came to be known as the "modern synthetic theory of evolution," or "modern synthesis" for short [Huxley, 1942]. Primarily the work of three pioneers, Sewall Wright, J.B.S. Haldane, and R. A. Fisher (e.g., [Wright, 1932, Haldane, 1932, Fisher, 1930]), the modern synthesis gave a formal mathematical structure to Darwin and Wallace's ideas that would enable them to be developed into a predictive theory as never before. Of particular importance, in *The Genetical Theory of Natural Selection* Fisher mathematically formalized individual reproductive success, which lies at the original heart of natural selection theory [Fisher, 1930]. Thus, with a few exceptions as discussed below, in explaining adaptation the modern synthesis firmly set the focus of natural selection at the level of the individual and their own direct reproduction.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

1.2 Natural Selection and Social Behavior

Although the examples described above of traits "designed" through natural selection are physical body parts, behaviors also have genetic components, and therefore can be shaped by natural selection. As William D. Hamilton put it very pithily, "It is generally accepted that the behaviour characteristic of a species is just as much the product of evolution as the morphology" [Hamilton, 1963]. Behaviors that improve the reproductive success expected by an individual often have a negative impact on reproduction of members of the same species; one obvious example is behaviors involved in competition over mates, such as in display and fighting by red deer stags (figure 1.1); by monopolizing access to females, a male improves his own reproductive success at the expense of other males. Natural selection theory as developed by Darwin, Fisher, and others has no problem explaining the evolution of such behaviors; indeed it predicts them. This theory acts according to the reproductive success of individuals, and when the side effects of any trait are to modify the reproductive success of unrelated individuals, these are irrelevant.

Other individual behaviors seem to impact on the reproduction of others in a much more "deliberate" manner, however. Examples of such *social behaviors* abound in the natural world. Quite possibly the most well-known examples are among the social insects, considered by Darwin himself [Darwin, 1859]. In these insect species, reproductive division of labor is observed, with one or more castes helping to raise offspring other than their own; this is referred to as *eusociality* [Crespi and Yanega, 1995]. The simplest pattern is that the daughters of a single reproductive female, the queen, forage for, defend, and raise her offspring. These worker daughters either have suppressed levels of reproduction, as in the honeybee *Apis mellifera* where workers may both reduce their own levels of reproduction and destroy eggs laid by other workers [Ratnieks and Visscher, 1989], or are completely functionally sterile, as in several species of leafcutter ant for example (figure 1.2). *Cooperative breeding* is also observed in vertebrates, including many species of birds (e.g., figure 1.3) and mammals, such as meerkats (*Suricata suricatta*; e.g., [Clutton-Brock et al., 1998]) and naked mole rats (*Heterocephalus glaber*; [Jarvis, 1981]).[2] Cooperative breeders exhibit similar behaviors to eusocial species, in that helpers forage for, and guard, the offspring of a single breeding pair, although helpers do not form a distinct caste and may subsequently become reproductives themselves [Crespi and Yanega, 1995]. The presence of helpers has been shown to improve reproductive success by the breeding pair (e.g., [Hatchwell et al., 2004]),

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.



Figure 1.1: A red deer stag (*Cervus elaphus*). Stags possess large antlers which impact on performance in fights, dominance rank, and hence access to fertile females. Maintenance of a harem of females, and hence increased reproductive success, negatively impacts on the reproductive success of other males in the population. However, natural selection theory (as developed by Darwin, Fisher, and others) acting on individuals explains the evolution of antlers since the successful male's net personal reproduction is increased as a result of having them. Photograph by Loeske Kruuk, reproduced from [Kruuk et al., 2014] with the permission of the photographer.

yet the helpers necessarily forego their own reproduction while caring for offspring that are not their own (e.g., [Emlen, 1982]).

Less frequently appreciated, social behavior is also observed in microbes including amoebae and bacteria [West et al., 2007a]. In social amoebae (*Dictyostelium* sp.; figure 1.4) normally free-living individuals aggregate at times of ecological stress, with some amoebae sacrificing themselves to form a structure that raises other individuals up in order to facilitate their dispersal to new, potentially richer,

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

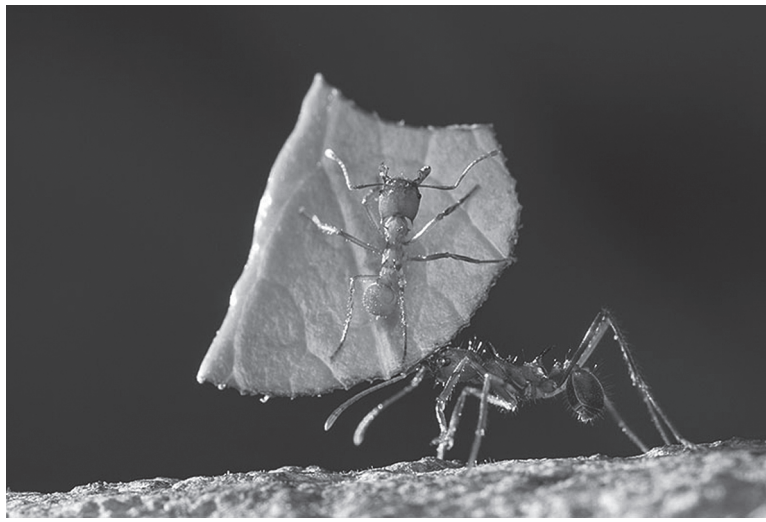


Figure 1.2: Leafcutter ants of the genus *Atta* have morphologically distinct worker castes [Wilson, 1980], such as this forager (carrying leaf) and minim (sitting on leaf). In eusocial insect colonies, a worker caste or castes are either partially or totally functionally sterile, reducing or foregoing individual reproduction in order to support the reproduction of their mother. *Atta colombica* workers, although still possessing functioning ovaries, are effectively sterile [Dijkstra et al., 2005, Dijkstra and Boomsma, 2006]. Photograph by Chris Tranter, reproduced with permission of the photographer.

locations (figure 1.4) [Raper, 1984]. In the bacterium *Pseudomonas aeruginosa*, as in many other microorganisms, individuals secrete siderophores, which scavenge iron from insoluble forms in the environment. Siderophore production is individually costly in metabolic terms, resulting in a reduced growth rate, but this is offset by the increase in growth rate that siderophores facilitate when iron is scarce [Griffin et al., 2004, Jiricny et al., 2010] (figure 1.5A). However, siderophores secreted by individual bacteria can also facilitate iron uptake by neighboring individuals, allowing them to benefit from an increased growth rate, even if those neighbors did not contribute to siderophore production themselves [Griffin et al., 2004, Jiricny et al., 2010] (figure 1.5B).

Less munificent examples of social behavior have also been described. Let us take one important example: bacterial production of bacteriocins. Production of colicins by the bacterium *Escherichia coli*, for example, is fatal for producing cells, as well as killing neighboring cells within a narrow phylogenetic range [Riley and Wertz, 2002]. Thus, bacteriocin production is personally costly (colicin producers pay the ultimate price of death, thereby ceasing personal reproduction),

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.



Figure 1.3: A long-tailed tit chick (*Aegithalos caudatus*) is fed an invertebrate by an adult helper. Long-tailed tits are facultatively cooperative breeders; individuals that have failed to breed successfully themselves may help to raise the offspring of another breeding pair by feeding their chicks until independence [Hatchwell and Sharp, 2006, Hatchwell et al., 2014]. Photograph by Ben Hatchwell, reproduced with permission of the photographer.

as well as costly to the targets of the behavior. Similarly, *Pseudomonas* bacteria produce individually costly pyocins that inhibit growth of strains that do not possess corresponding immunity genes [Michel-Briand and Baysse, 2002], as illustrated in figure 1.6.

Some purely physical traits can also have positive or negative social effects on conspecifics. One example is aposematism, for example in caterpillars (figure 1.7), in which individuals evolve both to be unpalatable to predators, and to bear conspicuous markings that indicate their unpalatability. As described below, Fisher himself considered the problem of aposematism, the initial evolution of which would be personally costly since conspicuous markings increase the probability of detection by a predator. A conspicuous distasteful individual being consumed would benefit aposematic members of the same species, however, by informing the predator that conspicuous markings mean unpalatability and thereby deterring them [Fisher, 1930].[3] Thus, while many social effects on conspecifics are due to behavior, not all are.

Examples such as these, and many others, have long presented a puzzle for evolutionary biology. The puzzle is that, under Darwin's and Fisher's views of

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

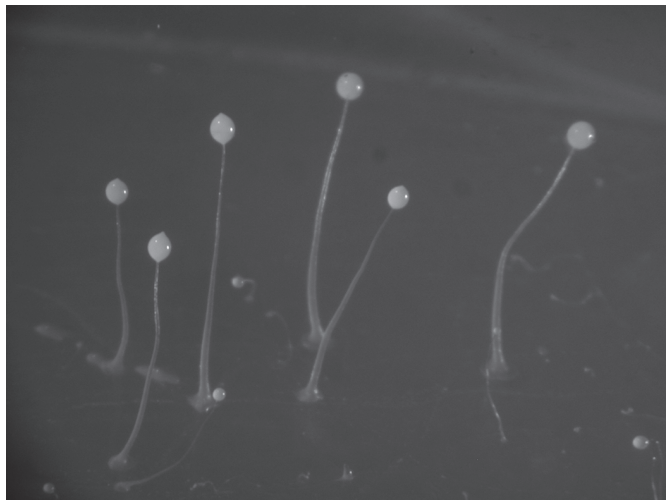


Figure 1.4: Various social amoebae such as *Dictyostelium discoideum* exhibit primitive multicellularity under certain conditions. When resources are locally depleted, free-living amoebae aggregate to form a multicellular "slug," which migrates and then produces a stalk topped by a fruiting body. Only amoebae in the fruiting body become spores and therefore potentially reproduce; all members of the stalk die in raising the fruiting body high enough to disperse spores effectively [Raper, 1984]. Photograph by Kevin Foster, reproduced with permission of the photographer.

natural selection acting on personal reproduction, it seems to make no evolutionary sense for individuals to reduce their personal reproductive success, possibly to zero, in order to have an effect on the reproduction of others. Natural selection should favor traits that *increase* personal reproductive success, hence personally costly traits of the kind described above should experience negative selection, and be eliminated from any population in which they appear. Yet the examples we have just seen seem not to be of transient social behaviors in the process of being weeded out by natural selection, but rather of stable evolutionary outcomes; eusociality has evolved multiple, independent times in the social insects, for example, and persisted for millions of years (e.g., [Hughes et al., 2008]). The crucial question, therefore, is how can evolutionary theory be extended to accommodate these obvious biological facts?

1.3 Arguments for Group Benefit

Darwin himself was concerned with explaining the evolution of apparent self-sacrifice, commenting on sterility in the social insects in *On the Origin of Species*

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

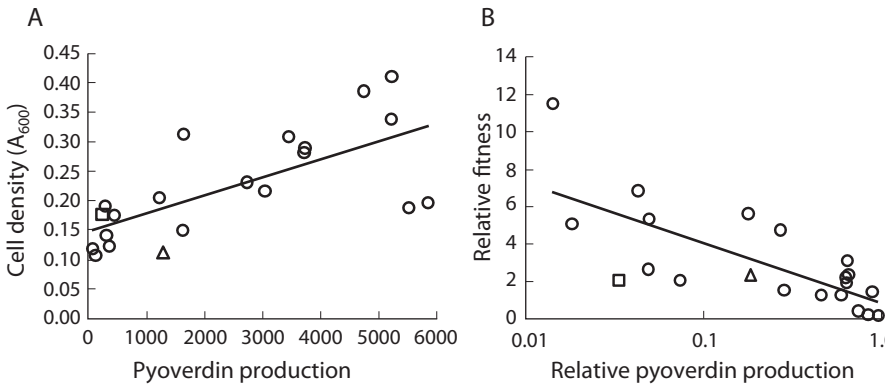


Figure 1.5: Fitness consequences of production of a siderophore (pyoverdin) in *Pseudomonas aeruginosa*. (A) Cell density in monocultures of different *P. aeruginosa* mutant strains in iron-limited environments, plotted against strain pyoverdin production per cell; when soluble iron is scarce, pyoverdin production positively correlates with higher cell densities, indicating that it is beneficial for population growth. (B) Relative competitive ability of different *P. aeruginosa* mutant strains in competition with the wild type, plotted against relative strain pyoverdin production; the negative correlation indicates that pyoverdin production is individually costly. In both figures, plot markers indicate mutant strains having different provenance. Figures redrawn from [Jiricny et al., 2010].

[Darwin, 1859]. Interestingly, Darwin was not concerned with sterility per se, which he considered could be explained by selection acting at the level of the family (i.e., colony), but rather how morphologically varied worker castes could evolve when they left no offspring to inherit their variation [Ratnieks et al., 2010]. Darwin resolved this problem by analogy to the selection of well-flavored vegetables or beef cattle. Once a vegetable or a cow has been consumed and found to be tasty it is unavailable for production of further similarly tasty individuals; yet horticulturists and beef farmers had long known that by breeding from closely related individuals in the vegetable patch or herd, offspring with similar characteristics could be produced [Darwin, 1859, Ratnieks et al., 2010].

Just over 10 years later, in *The Descent of Man*, Darwin discussed the potential for competition between human groups to favor those groups containing more "courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other." Darwin noted that in inter-group conflict, groups with the highest numbers of such individuals would tend to be victorious, all else being equal. Yet he also noted that within those same groups, the same such individuals would be at a disadvantage; "therefore it hardly seems

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

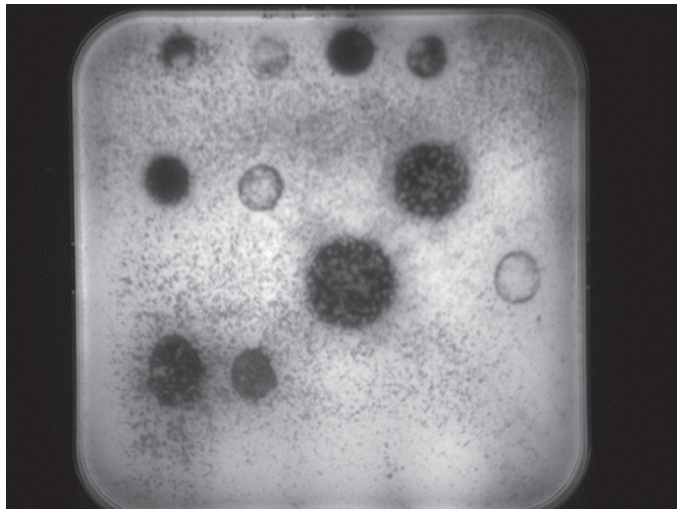


Figure 1.6: A "bacterial lawn" of a single strain of *Pseudomonas aeruginosa*, isolated from a pulmonary infection. Supernatant spots, containing pyocins, from 25 environmental and clinical strains of *P. aeruginosa* have been imposed on the lawn. Where growth of the lawn is inhibited under a spot (dark disks), this is due to action of the pyocins in the spot, and lack of appropriate pyocin-immunity genes in the lawn [Michel-Briand and Baysse, 2002]. Photograph by Melanie Ghoul, reproduced with permission of the photographer.

probable, that the number of men gifted with such virtues, or that the standard of their excellence, could be increased through natural selection, that is, by the survival of the fittest" [Darwin, 1871].

Darwin understood that, technically, selection could act at multiple levels in a biological hierarchy. Samir Okasha [Okasha, 2006] traces the full development of these ideas back to August Weismann [Weismann, 1903]. Darwin, however, also noted the fundamental difficulty with selection acting, in the way he described, at a higher level than the individual; while between-group selection would favor groups containing more individuals with prosocial behaviors, defined as behaviors that benefit others, within the group these behaviors would be individually costly and hence disfavored by natural selection at the level of the individual.

Despite Darwin's clear statement of the fact that individual selection would run counter to selection acting at higher levels, by the early twentieth century it was typical to invoke benefits to the group, or the species, as explanations of perceived adaptations. Among the most famous examples are V. C. Edwards's explanations of population regulation, such as through individual restraint in reproduction, as

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.



Figure 1.7: Several insects and vertebrates such as caterpillars (e.g., *Arsenura armida*, pictured) and frogs ([Santos et al., 2003]) have evolved to be unpalatable, and to signal this unpalatability to predators via conspicuous warning markings. As noted by [Fisher, 1930], evolution of such a trait under natural selection acting at the level of the individual is problematic, as unpalatable and conspicuous individuals will bear a higher probability of being detected and eaten by a predator who has not yet experienced their unpalatability. Photograph by Artour Anker, reproduced with permission of the photographer.

being due to adaptation for the benefit of the population [Wynne-Edwards, 1962]. In response, George C. Williams argued comprehensively for the need to ascribe adaptation to the lowest plausible level, and distinguish adaptations from inevitable side effects. Thus, considering evolution of deer in response to predation, he argued that natural selection acting on individuals would give rise, as a side effect, to a "herd of fleet deer"; however selection on the group, he argued, would not be sufficiently powerful to shape an adapted group, a "fleet herd of deer," in which individuals each occupied distinct behavioral roles designed, in their interaction, to reduce the group's overall predation risk [Williams, 1966]. While Williams explicitly recognized the potential for selection acting between groups, which he took to be groups of unrelated individuals, rather than families or other relatives, like Darwin he ascribed the ultimate adaptive power to natural selection acting on individuals.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

While for unrelated groups Williams gave primacy to individual-level selection producing individual-level adaptation, he noted that this was insufficient to explain many apparent incidents of self-sacrifice, such as the example of sterility in social insect workers introduced above. Williams did recognize and tackle this problem [Williams, 1966], but the priority belongs to another researcher whose work he referred to.

1.4 Enter Hamilton

The problem of providing an evolutionary explanation of self-sacrifice by individuals, as it stood in the mid-twentieth century, can be described no better than in the first published[4] biological writings of William D. Hamilton:[5]

> It is generally accepted that the behavior characteristic of a species is just as much the product of evolution as the morphology. Yet the kinds of behavior which can be adequately explained by the classical mathematical theory of natural selection are limited. In particular this theory cannot account for any case where an animal behaves in such a way as to promote the advantage of other members of the species not its direct descendants at the expense of its own. The explanation usually given for such cases and for all others where selfish behavior seems moderated by concern for the interests of a group is that they are evolved by natural selection favoring the most stable and co-operative groups. But in view of the inevitable slowness of any evolution based on group selection compared to the simultaneous trends that can occur by selection of the classical kind, based on individual advantage, this explanation must be treated with reserve so long as it remains unsupported by mathematical models. [Hamilton, 1963]

Hamilton went on to outline the evolutionary explanation of altruism, or self-sacrifice to benefit others, as follows:

> Despite the principle of "survival of the fittest" the ultimate criterion that determines whether [gene for altruism] G will spread is not whether the behavior is to the benefit of the behaver but whether it is of benefit to the gene G.… With altruism this will happen only if

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

> the affected individual is a relative of the altruist, therefore having an increased chance of carrying the gene, and if the advantage conferred is large enough compared to the disadvantage to offset the regression, or "dilution," of the altruist's genotype in the relative in question. [Hamilton, 1963]

In sketching his new theory, Hamilton proposed that selection would favor the altruism gene G whenever

$$K > \frac{1}{r}, \tag{1.1}$$

where K is the ratio of the advantage conferred on recipients to the cost to the behaver, and r is a measure of genetic relatedness. Equation (1.1) is the first form of what came to be known as Hamilton's rule, a summary statement of when natural selection favors self-sacrificing behavior. The following year, Hamilton presented the mathematical basis for his suggestions [Hamilton, 1964a, Hamilton, 1964b]. What Hamilton achieved in these three papers was, as he put it, "an extension of the classical theory" [Hamilton, 1963], showing that genes within individuals should value not only the reproductive success of their bearer, but also the reproductive success of other individuals within the population who might carry the same gene with some degree of certainty. The "extension of the classical theory" was to observe that what mattered for natural selection was not simply the direct reproductive success of an individual (their *direct fitness*), but also their indirect reproduction via relatives containing the same genes, whose reproduction their own behavior had impacted on (their *indirect fitness*). Hamilton labeled this extended fitness as *inclusive fitness*, and described it thus:

> Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbors. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects. [Hamilton, 1964a]

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

As a simple word equation,

$$\text{inclusive fitness} = \text{direct fitness} + \text{indirect fitness}, \tag{1.2}$$

where "direct fitness" in the above equation is the classical Darwinian/Fisherian conception of the fitness that natural selection acts on. In conceptualizing inclusive fitness, Hamilton had thus proposed what was arguably the most important extension of evolutionary theory since 1859. There were hints of such ideas before 1963 and 1964, however. Hamilton himself identified many of these [Hamilton, 1963], the most obvious being the recognition that parental care of offspring involves self-sacrificial behavior on the part of the parent, yet is consistent with standard Darwinian evolution. Hamilton also referred to R. A. Fisher's explanation of the evolution of aposematism (figure 1.7), which considered benefits to siblings from the evolution of conspicuous markings indicating distastefulness, that could arise only in the case that the unpalatable bearer of the markings was consumed and therefore forfeited all future reproduction [Fisher, 1930]. Hamilton noted, however, that Fisher did not consider benefits to relatives more distant than siblings; J.B.S. Haldane on the other hand did consider likelihoods of more distant relatives, up to cousins, containing genes for behavior when he laid out the evolutionary logic for a decision over whether to jump into a river to save a drowning child [Haldane, 1955], as Hamilton acknowledged [Hamilton, 1963].[6] Yet despite these isolated and partial appreciations of how self-sacrificing behavior might evolve, the priority remains with Hamilton for conceptualizing the solution so generally, and for presenting the first mathematical formalization of the arguments [Hamilton, 1963, Hamilton, 1964a, Hamilton, 1964b].

1.5 Multilevel Selection Theory

Inclusive fitness is not the only way of conceptualizing selection acting on social behaviors. An alternative viewpoint seems to spring from the earlier, discredited, view of adaptations for the benefit of the group [Wynne-Edwards, 1962] in that it considers group-level fitness. However, this new version of group selection theory explicitly decomposes total selection acting on a population into between-group selection, and within-group selection [Price, 1972a]. For altruism, it follows that when

$$\text{between-group selection strength} > \text{within-group selection strength}, \tag{1.3}$$

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

altruism will be favored overall in a population[7] [Hamilton, 1975, Wilson, 1975a]. This theory has been labeled *group selection* [Price, 1972a, Hamilton, 1975] and *trait-group selection* [Wilson, 1975a], but is increasingly described as *multilevel selection* [Okasha, 2006]. Multilevel selection will be used in this book to describe scenarios in which condition (1.3) predicts the evolution of social behavior; most models of "group selection" postulated in the literature are of this type [Okasha, 2006].

Multilevel selection cannot explain the evolution of group-level adaptation, as early group selectionists believed [Okasha, 2006]; the problem is that when within-group selection is present then individual-level adaptations will be favored over group-level adaptations [Gardner and Grafen, 2009, Okasha and Paternotte, 2012]. However, multilevel selection theory is increasingly seen as an alternative to inclusive fitness theory, and one that is more general in its applicability. The details of these claims are given in later chapters, as is the demonstration that the multilevel selection rule (condition (1.3)) and Hamilton's rule (condition (1.1)) can always be applied to the same social trait, and always predict the same direction of selection.

1.6 The Generality of Inclusive Fitness Theory

This chapter has provided a brief historical introduction to the problem of apparent design in biology, evolutionary explanations of this, and in particular, evolutionary explanations of individual behaviors that appear designed to benefit not the individual themselves, but other members of their species. For other historical reviews of evolutionary theory, particularly with respect to the evolution of social behavior and the role of design in biological thought, the interested reader should see [Foster, 2009, Gardner and Foster, 2008, Gardner, 2009].

Despite the elegant simplicity of inclusive fitness theory, both in extending Darwinian theory, and also in explaining the evolution of self-sacrificing behavior, it has attracted criticism from some quarters, even fifty years after its advent. One particular line of criticism holds that multilevel selection is a more general theory of social evolution than is inclusive fitness theory. These misunderstandings will be identified and addressed later in this book, and provide one of the main motivations for its writing. The overarching motivation of this book is, however, to demonstrate and celebrate the generality of inclusive fitness theory, with a focus on its fundamental evolutionary logic. The remainder of the book is laid out as follows. The first

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

third of the book presents the basic mathematical theory of natural selection, and inclusive fitness theory. Chapters 2 and 3 present two complementary approaches to building mathematical models of natural selection: the replicator dynamics and the Price equation, respectively. The replicator dynamics provide a very simple model of selection, and are used in chapter 2 to illustrate the action of natural selection on various kinds of social behavior, including nonadditive behaviors, when interactions are between nonrelatives. The Price equation, introduced in chapter 3, allows very general statements about selection to be formulated, and is used in chapter 4 to formalize the logic of inclusive fitness theory and derive Hamilton's rule in its simplest form, as well as show its equivalence with the multilevel selection approach.

The second third of the book treats more complicated social scenarios, and shows how inclusive fitness theory deals with these. Chapter 5 explores the outcomes of selection when interactions are nonadditive and occur between relatives, and explains two main approaches to generalizing Hamilton's rule to deal with such interactions. Chapter 6 considers behaviors that are expressed conditional on the phenotype of others, including the classic "greenbeard" thought experiment proposed by Hamilton [Hamilton, 1964b], and introduces a further generalization of Hamilton's rule to deal with such behaviors. Chapter 7 shows how the multiple versions of Hamilton's rule give different evolutionary explanations for certain traits such as greenbeards, and also how one can translate between these different versions. Chapter 9 deals with the problem of correctly defining fitness costs and benefits in inclusive fitness theory, when competition occurs between offspring who are relatives.

The final chapters of the book deal with more philosophical issues in inclusive fitness theory, to do with explanation of the results of selection in ultimate causal terms. Chapter 8 considers which of the equivalent alternative partitions of fitness, including inclusive fitness, and group fitness, can be interpreted as being subject to selection in a meaningful way, and also reviews proposals for classifying different evolutionary processes involved in the selection of social behavior. Chapter 9 reviews the definition of evolutionary fitness, and shows how its misinterpretation explains many previous misunderstandings as to whether inclusive fitness theory always makes accurate predictions. Finally, chapter 10 reviews the limitations of the analyses presented in this book, directing the reader to additional mathematical techniques, as well as considering the empirical support for inclusive fitness theory, and more advanced topics in the field.

For general queries, contact webmaster@press.princeton.edu