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Selfish Genes

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Introduction

In its original formulation, Darwin's theory of evolution by natural selection was based upon individual organisms. It is individuals that vary in phenotype, individuals that struggle to survive environmental pressures and compete over access to mates, and individuals that vary in fitness according to phenotype. Selfish gene theory, or the gene's-eye view of evolution, however, offers a radically different picture of evolution by natural selection. Tracing its origins to the emergence of population genetics during the modern synthesis of the 1930s, especially to the writings of R. A. Fisher, as well as the social evolution models of W. D. Hamilton, the most ambitious form of the gene's-eye view was spelled out in two later books: George Williams's *Adaptation and Natural Selection* (1966) and Richard Dawkins's *The Selfish Gene* (1976). Under this view of life, the fundamental unit of selection is the gene. Whereas individual organisms are temporary occurrences—present in one generation, gone in the next—genes are potentially immortal and their structure is passed on from generation to generation. As a consequence, the ultimate beneficiary of selection is the gene. Early on in *The Selfish Gene*, Dawkins relates this crucial insight as follows: "They are in you and me; they created us, body and mind; and their preservation is the ultimate rationale for our existence. They have come a long way, those replicators. Now they go by the name of genes, and we are their survival machines" (p. 21). Few phrases in science have caught the imagination of laymen and professionals alike the way "selfish genes" has done. The concept touches on several questions of interests to both biologists and philosophers, including how to articulate general principles of evolution and the units and levels of selection debate. The concept has contributed to the study of new biological phenomena, such as selfish genetic elements, greenbeard genes, and extended phenotypes. Finally, its association with selfishness and altruism has led to it being featured heavily in broader debates about morality and ethics.

Original Works

Two books stand out in the origin story of selfish gene thinking. The first of these was Williams 1966, in which "selection at the genic level" is held as a contrast to group selection explanations for traits, especially in relation to social behavior. *The Selfish Gene* (Dawkins 1976), published a decade later in 1976, was aimed at a broader audience and argued forcefully for genes to occupy the central role in evolutionary explanations. Both are very readable, and still offer excellent introductions to the gene's-eye view of evolution.

Dawkins, R. 1976. *The selfish gene*. Oxford: Oxford Univ. Press.

The million-copy bestseller that coined several of the terms used in the debate, including selfish genes, replicator, survival machine, and meme.

Williams, G. C. 1966. *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton, NJ: Princeton Univ. Press.

Williams's critique of the poor use of the concept of adaptation among contemporary biologists, especially with respect to group selection. Together with *The Selfish Gene*, introduced the gene's-eye view of evolution to biology.

General Overviews

Both Williams and Dawkins later published books that address critiques of their views, and present slightly updated versions of their arguments (Williams 1992, Dawkins 1982). Dawkins recently published a short essay reiterating his general views on evolution and selection (Dawkins 2016). David Haig has written extensively about value of the gene's-eye perspective for a variety of problems in social evolution, the field of research that aims to establish the evolutionary principles that explain the ways in which individuals interact with each other (Haig 1997, Haig 2012). Gardner and Welch 2011 use optimization models to provide what the authors describe as a "formal theory of the selfish gene" and use this formalization to discuss a comprehensive catalogue of common criticisms of selfish genes. Akçay and Van Cleve 2016, a review of fitness concepts, includes a discussion of how the gene's-eye view of fitness corresponds to other accounts. Finally, the debate about the value of selfish genes as a general model of evolution also coincided with, and contributed to, the rise of philosophy of biology as a distinct discipline. As a consequence, several philosophical books provide comprehensive summaries of the many abstract issues related to the selfish gene debate. Godfrey-Smith 2014 is a general introduction to the philosophy of biology and includes a good chapter on selfish genes. Okasha 2006 extensively discusses selfish genes in the context of the levels of selection debate.

Akçay, E., and J. Van Cleve. 2016. There is no fitness but fitness, and the lineage is its bearer. *Philosophical Transactions of the Royal Society Series B* 371:20150085.

An up-to-date review of various fitness concepts, including that of the gene's-eye view.

Dawkins, R. 1982. *The extended phenotype*. Oxford: Oxford Univ. Press.

The sequel of *The Selfish Gene* in which Dawkins replies to critics and spells several implications of the gene's-eye view. Introduces the concept of extended phenotypes.

Dawkins, R. 2016. Evolvability. In *Life: The leading edge of evolutionary biology, genetics, anthropology, and environmental science*. Edited by J. Brockman, 1–16. New York: Harper Perennial.

A short recent essay laying out Dawkins's views on evolution and selection forty years after *The Selfish Gene*.

Gardner, A., and J. J. Welch. 2011. A formal theory of the selfish gene. *Journal of Evolutionary Biology* 24:1801–1813.

Uses optimization theory to develop a model of a gene as a "fitness-maximizing agent." Also discusses several common criticisms of the gene's-eye view.

Godfrey-Smith, P. 2014. *Philosophy of biology*. Princeton, NJ: Princeton Univ. Press.

A recent introduction to the philosophy of biology from a leader in the field. Includes a good section on the philosophical issues associated with selfish genes.

Haig, D. 1997. The social gene. In *Behavioural ecology*, 4th ed. Edited by J. R. Krebs and N. B. Davies, 284–304. Oxford: Blackwell Science

Outlines how a gene's-eye view helps illuminate several questions in social evolution.

Haig, D. 2012. The strategic gene. *Biology and Philosophy* 27:461–479.

Clarifies how gene selectionists use terms like "gene" and "environment" in an unusual way compared to other biologists.

Okasha, S. 2006. *Evolution and the levels of selection*. Oxford: Oxford Univ. Press.

A superb introduction to the general levels of selection debate with a comprehensive chapter dedicated to the gene's-eye view.

Williams, G. C. 1992. *Natural selection: Domains, levels, and challenges*. New York: Oxford Univ. Press.

An updated take of Williams's view on several issues in evolution; develops a new informational account of what should count as a gene.

Precursors to Selfish Gene Thinking

Selfish gene thinking has two main conceptual precursors, population genetics (formed in the "modern synthesis" of the 1930s) and social evolution theory (from the 1960s). The former formally characterized the process of natural selection as changes in the frequency of allelic variants. The latter outlined how the process of natural selection required fitness maximization of allelic variants across individual contexts, rather than being confined to self and direct descendants. Williams and Dawkins drew on both traditions in formulating their argument.

Population Genetics

When Darwin and Wallace first conceived the process of natural selection, heredity was loosely defined—that offspring resembled parents. The work of Mendel and later the "early geneticists" (such as Morgan, Punnett, and Bateman) established inheritance as particulate. In the standard diploid model, there are two copies of each genetic factor in an individual of which one is randomly passed into each gamete, and thus progeny. This means of inheritance was then synthesized with Darwinian gradualism to form the discipline of population genetics, a movement commonly termed the "modern synthesis" (Provine 1971). In particular, R. A. Fisher's *The Genetical Theory of Natural Selection* (Fisher 1930) formally reconceptualized evolution as a process of allele frequency changes in the genepool, rather than a process that followed individuals directly. Edwards 2014 shows how many of the assumptions of the gene's-eye view can be traced back to Fisher's writings.

Edwards, A. W. F. 2014. R. A. Fisher's gene-centred view of evolution and the Fundamental Theorem of Natural Selection. *Biological Reviews* 89:135–147.

A review showing how many of the assumptions of the gene's-eye view originated with Fisher's writing.

Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford: Oxford Univ. Press.

Fisher's major contribution to the modern synthesis, which laid the foundation for much gene's-eye thinking and the study of population genetics. Variorum edition published in 1999.

Provine, W. B. 1971. *The origins of theoretical population genetics*. Chicago: Univ. of Chicago Press.

The best historical review of the history of population genetics. The 2001 edition includes a new afterword.

Social Evolution Theory

In addition to population genetics, the second strand of thinking that promoted the gene's-eye view was developments in the study of social behaviour by George C. Williams, Robert Trivers, John Maynard Smith, and in particular W. D. (Bill) Hamilton. During the 1960s, group selection (the belief that selection acted to create adaptations at the group and species level) was prevalent, a historical period documented by Borrello 2010. In the preface to the 1996 edition of *Adaptation and Natural Selection*, Williams recounts his unhappiness after attending

a seminar by the prominent behavioral ecologist A. E. Emerson. To Williams, Emerson and other contemporaries used the concept of adaptation too loosely. In particular, explanations of apparently altruistic acts (ones which are costly to the bearer and beneficial to the receiver) were commonly made in terms of group advantages without proper evidence. Hamilton's work on the evolution of altruism revealed the rationale underlying many apparent cases of altruism. In his original 1963 paper Hamilton demonstrated that "despite the principle of 'survival of the fittest' the ultimate criterion that determines whether [a gene for altruism] G will spread is not whether the behavior is to the benefit of the bearer but whether it is of benefit to the gene G" (Hamilton 1963). Hamilton's insight, formalized in Hamilton 1964, was that selection acted not only on direct fitness—how a trait affected your survival and the number of descendents you yourself produced—but also on the fate of relatives. This logic holds as relatives are statistically more likely than random individuals to carry the same variant (e.g., promoting altruism to kin) by virtue of shared descent. Hamilton's work gave rise to two important concepts: the method of inclusive fitness (which allows us to account for how behavior affects other individuals including kin), and the process of kin selection (selection for behaviors that aid kin), the latter being a term coined by John Maynard Smith (Maynard Smith 1964). The insight that selection does not simply maximize the fitness of a variant in terms of direct descendants represented an important erosion of the primacy of individual reproduction, developing a series of behaviors best understood from a gene's-eye perspective. Maynard Smith 1987 is a nice personal discussion of gene, individual, and group selection modeling approaches.

Borrello, M. E. 2010. *Evolutionary restraints: The contentious history of group selection*. Chicago: Univ. of Chicago Press.

A history of the group selection controversy.

Hamilton, W. D. 1963. The evolution of altruistic behaviour. *The American Naturalist* 97:354–356.

Hamilton's first paper on what is now referred to as kin selection. Introduces a gene's-eye view to the problem of altruism.

Hamilton, W. D. 1964. The genetical evolution of social behaviour I, II. *Journal of Theoretical Biology* 7:1–52.

Hamilton's major paper on the theory of inclusive fitness.

Maynard Smith, J. 1964. Group selection and kin selection. *Nature* 201:1145–1147.

A short paper introducing the term "kin selection" to distinguish Hamilton's theory from group selection models.

Maynard Smith, J. 1987. How to model evolution. In *The latest on the best: Essays on evolution and optimality*. Edited by J. Dupré, 119–131. Cambridge, MA: MIT.

Discusses various modeling strategies in evolution and explains why he prefers gene-centered models.

Dawkins's Immediate Motivators Surrounding Publication of *The Selfish Gene*

The run-up to the publication of *The Selfish Gene* is covered in the first volume of Dawkins's autobiography (Dawkins 2013) and in the second volume he discusses how his views have developed over the years (Dawkins 2015). In particular, Dawkins himself notes that the book is built on a series of lecture notes he had developed to communicate Hamilton's theory of inclusive fitness to undergraduate students (Dawkins 2013, p.200). De Chadarevian 2007 used files from Oxford University Press to outline the publishing origin of the book. Dawkins's editor at Oxford University Press, Michael Rodgers, has also recounted his own experience with the publishing process (Rodgers 2014).

Dawkins, R. 2013. *An appetite for wonder: The making of a scientist*. London: Bantam.

The first volume of Dawkins's autobiography, covering the time up until the publication of *The Selfish Gene*.

Dawkins, R. 2015. *A brief candle in the dark: My life in science*. London: Bantam.

The second volume of Richard Dawkins's autobiography, focuses on his life after the publication of *The Selfish Gene*.

De Chadarevian, S. 2007. The selfish gene at 30: The origin and career of a book and its title. *Notes and Records of the Royal Society* 61:31–38.

Uses papers from the Oxford University Press archives to review the editorial background to *The Selfish Gene*.

Rodgers, M. 2014. *Publishing and the advancement of science: From selfish genes to Galileo's finger*. London: Imperial College.

Dawkins's editor at Oxford University Press describes his life in science publishing, with large chunks devoted to the origin of *The Selfish Gene*.

Initial Reactions to *The Selfish Gene* from biologists

The reception of *The Selfish Gene* markedly contrasted with that of Williams's *Adaptation and Natural Selection*, the book on which it is partly built. While *Adaptation and Natural selection* received generally positive book reviews (Lewontin 1966 called it "excellent" in *Science* and Slobodkin 1966 praised the book in *The Quarterly Review of Biology*), *The Selfish Gene* generated very mixed (and very strong) contrasting views. Bill Hamilton wrote an enthusiastic review for *Science* (Hamilton 1977a) and Bateson 1978 was generally positive, but quipped that by Dawkins's reasoning a bird is just a nest's way of making another nest. Over the years Bateson would remain a friendly sparring partner. Langley 1977 wrote a scathing review for *Bioscience*, calling it "shallow and untrue to the science of evolutionary biology" and "a nuisance to the knowledgeable reader and misleading to the layman." In a similar vein, Richard Lewontin's review for *Nature* (Lewontin 1977a) was entitled "Caricature of Darwinism" and called Dawkins's adaptationist thesis "Panglossian" (two years before the famous Spandrels of San Marco paper with Stephen Jay Gould) (Lewontin 1977a). Lewontin's tone led Bill Hamilton to write a letter of protest to the editor (Hamilton 1977b), where he called the review a "disgrace" and compared it to Bishop Wilberforce's attack on Darwin and Huxley at the British Association meeting in 1860. Lewontin 1977b in turn replied in an equally ill-tempered fashion. Michael Wade, writing in *Evolution*, presented a more technical critique of the book, focusing on two points (Wade 1978). First, contrary to Dawkins (and Hamilton and Maynard Smith), Wade argued that kin selection is a kind of group selection. Second, Wade argued that Dawkins ignored epistasis, the concept that survival and reproduction of an individual is not simply an additive property of the particular variants in the genome, but that the impact of a particular variant can depend in complex ways on the presence/absence of variants of other genes. Wade wrote that Dawkins's thesis would have worked "if evolution in natural populations followed the paradigm developed by R. A. Fisher." Indeed, Dawkins refers to Fisher as the greatest biologist of the 20th century, a point approvingly picked up by Hamilton in his review. The critique that natural selection cannot "see" individual genes, only bodies, was also the major theme of Stephen Jay Gould's first take on the book (Gould 1977).

Bateson, P. 1978. The Selfish Gene. *Animal Behaviour* 26:316–318.

A critical but friendly and constructive review.

Gould, S. J. 1977. Caring groups and selfish genes. *Natural History* 86:20–24.

Gould's first commentary of *The Selfish Gene*, arguing that postulating selection at the gene level is nonsensical.

Hamilton, W. D. 1977a. The play by nature. *Science* 196:757–759.

A very supportive review of *The Selfish Gene*.

Hamilton, W. D. 1977b. The Selfish Gene. *Nature* 267:102.

Hamilton's angry letter to the editor following Lewontin's review.

Langley, C. H. 1977. A little Darwinism. *BioScience* 27:692.

A scathing review of *The Selfish Gene*.

Lewontin, R. C. 1966. Adaptation and Natural Selection. *Science* 152:338–339.

In contrast to *The Selfish Gene*, Lewontin was impressed by *Adaptation and Natural Selection*.

Lewontin, R. C. 1977a. The Selfish Gene. *Nature* 266:283–284.

Lewontin's highly critical review that prompted Hamilton's 1977 letter of protest.

Lewontin, R. C. 1977b. The Selfish Gene. *Nature* 267:202.

Lewontin's reply to Hamilton's complaint about his review of *The Selfish Gene*.

Slobodkin, L. B. 1966. The light and the way in evolution. *The Quarterly Review of Biology* 41:191–194.

Enthusiastic review of *Adaptation and Natural Selection*.

Wade, M. J. 1978. The Selfish Gene. *Evolution* 32:220–221.

Critical review that focused on group selection and epistasis.

What Is a (Selfish) Gene?

The definition of a "gene" in selfish gene theory differs from that used in classical or molecular biology. For example, in molecular biology, a gene has often been thought of as encoding a particular RNA or protein that then has function. The evolutionary concept of the gene is broader than this—it requires integrity over generations, but does not explicitly require the encoding of a single product, nor is it necessarily associated with DNA-based inheritance.

Biological Evolution

The gene's-eye view envisions the history of life as a struggle between competing selfish genes. So what is a gene? In *Adaptation and Natural Selection*, Williams defined a gene to mean "that which segregates and recombines with appreciable frequency" (Williams 1966, cited under Original Works, p. 24). Similarly, Dawkins in *The Selfish Gene* (p. 28) emphasized that the material basis of genes must persist across generations: "a gene is defined as any portion of chromosomal material that potentially lasts for enough generations to serve as a unit of natural selection." This definition is often referred to as the "evolutionary gene" concept and differs substantially from how molecular biologists typically use the word. Griffiths and Stotz 2013 provides a good overview of how different kinds of biologists use the word. The definition of evolutionary genes has further changed over the years, a development well described by Sterelny and Griffiths1999 (chaps. 3–5) and Haig 2006. For example, Williams 1992 (cited under General Overviews, p. 11) seeking a definition that did not require a gene to be made of DNA refined his definition to make the gene a unit of information: "DNA is the medium, not the message. A gene is not a DNA

molecule; it is the transcribable information coded by the molecule . . . the gene is a packet of information, not an object." Moreover, different opinions of whether selfish genes are best perceived as physical objects (tokens) or sets of information distributed across individuals (types) is provided in exchanges by David Haig (Haig 2012, cited under General Overviews) and Andy Gardner (Gardner 2014). In a recent paper, Stencel and Crespi 2013 developed a definition of a genome inspired by the evolutionary gene concept. Lastly, in light of selection occurring on non-coding elements (e.g., introns, upstream regulatory sequences, microRNAs), it is also necessary to look beyond the protein coding sequence itself for gene identity, as mutations outside of coding regions control gene expression and RNA splicing, which alongside protein sequence control the phenotypic effect of the protein. Indeed, a "selfish gene" need not encode protein at all—it may simply be a variant that controls the expression of other genes.

Gardner, A. 2014. Genomic imprinting and the units of adaptation. *Heredity* 113:104–111.

Uses the same optimization approach as Gardner and Welch 2011 (cited under General Overviews to study genomic imprinting. Includes a discussion whether selfish genes should be thought of as types or tokens.

Griffiths, P., and K. Stotz. 2013. *Genetics and philosophy: An introduction*. Cambridge, UK: Cambridge Univ. Press.

An overview of the philosophical issues related to genetics and surveys the different ways genes have been defined by biologists over the years.

Haig, D. 2006. The gene meme. In *Richard Dawkins: How a scientist changed the way we think*. Edited by A. Grafen and M. Ridley, 50–65. Oxford: Oxford Univ. Press.

A discussion of the particular way gene selectionists use the word gene.

Stencel, A., and B. Crespi. 2013. What is a genome? *Molecular Ecology* 22:3437–3443.

Uses Dawkins and Williams's original definition of an evolutionary gene to develop an analogous definition of a genome.

Sterelny, K., and P. E. Griffiths. 1999. *Sex and death: An introduction to philosophy of biology*. Chicago: Univ. of Chicago Press.

A general text book on the philosophy of biology, which includes several chapters dedicated to the role of both genes in general, and selfish genes in particular, in evolutionary theory.

Cultural Evolution

In the last chapter of the first edition of *The Selfish Gene*, Dawkins began developing an account of cultural evolution. To do so, he introduced the term "meme" to serve as a unit of cultural transmission parallel to that of genes in organic evolution. Examples of memes suggested by Dawkins included "tunes, ideas, catch-phrases, clothes fashions, ways of making pots or of building arches" (Dawkins 1976, cited under Original Works, p. 206). Memes as a theory of cultural evolution attracted both supporters and critics. Philosopher Daniel Dennett is a supporter and used it to develop a theory of mind in *Consciousness Explained* (Dennett 1991), and so is physicist David Deutsch, who incorporated replicators (both genes and memes) as one of the four strands of his Theory of Everything in *The Fabric of Reality* (Deutsch 1997). The most ambitious attempt to develop a comprehensive theory of memes was Susan Blackmore's *The Meme Machine* (Blackmore 1999, a book that came with a foreword by Dawkins. A journal dedicated to the study of memes, the *Journal of Memetics – Evolutionary Models of Information Transmission* existed online between 1997 and 2005. Aunger 2001 brought together both supporters and critics of memes, and catalogues a variety of views on the topic. Recent reviews of cultural evolution more broadly provide comprehensive treatments of the history of the study of cultural evolution and why memetics never really caught on (e.g., Lewens 2015).

Aunger, R., ed. 2001. *Darwinizing culture: The status of memetics as a science*. Oxford: Oxford Univ. Press.

An edited volume, covering a variety of opinions on memetics.

Blackmore, S. 1999. *The meme machine*. Oxford: Oxford Univ. Press.

The most comprehensive development of the concept of memetics. Includes a foreword by Dawkins.

Dawkins, R. 1999. Foreword. In *The meme machine*. Edited by S. Blackmore, vii–xvii. Oxford: Oxford Univ. Press.

Dawkins expresses his excitement for how the field of memetics had expanded since the publications of *The Selfish Gene* and replies to a series of common criticisms of the concept.

Dennett, D. C. 1991. *Consciousness explained*. Boston: Little, Brown

Dennett's account of the evolution of consciousness, written for a general audience. His argument gives memes a key role.

Deutsch, D. 1997. *The fabric of reality*. New York: Viking.

A physicist's attempt to develop a "theory of everything," which relies on replicators, both genes and memes, to cover the informational part.

Lewens, T. 2015. *Cultural evolution*. Cambridge, UK: Cambridge Univ. Press.

An up-to-date account of the study of cultural evolution more generally, including the current state of memetics.

Developments of the Selfish Gene Concept

The selfish gene concept has been discussed and developed greatly in the last forty years. First, the difference between individual and gene in evolution has been made clearer in the concept of replicator and vehicles. Second, the concept of extended phenotype placed the impact of the gene beyond the limits of the individual that carried it, to include modifications to the environment encoded by the gene. Third, empirical advancements inspired by the genes-eye view were made in the form of the concepts of selfish genetic elements and greenbeard genes. Fourth, discussions of selfish genes played a key role in attempts to integrate the processes of selection across levels of biological organization through the concept of "levels of selection." Finally, selfish gene thinking was used to explain changes in levels of biological organization and function, the "major evolutionary transitions."

Replicator and Vehicles

An early critique of the gene's-eye view was that natural selection cannot "see," that is, act on, individual genes, but only individual organisms (e.g., Gould 1977, cited under Initial Reactions to *The Selfish Gene* from Biologists). The formulation of natural selection developed by Dawkins and Darwin contrasts in that the former emphasizes the passing of a structure (the replicator) across generations, and the latter the life, death, and reproduction of organisms. Critics have argued that whatever the unit of selection, it must survive and reproduce in nature, which genes cannot do. To address this disagreement, philosopher of biology David Hull (Hull 1980, Hull 1981, Hull 1988) introduced the concepts of replicator and interactors. Following Dawkins, he defined replicators as an entity whose structure is passed on intact across generations. Interactors, however, are cohesive wholes that interact with the environment, a role typically played by individual organisms, and so cause replicators to be passed on. Thus, replicators cover one aspect of selection, heredity transmission of information. In organic evolution, genes play the role of replicator, but the concept has also been expanded to cultural evolution with memes. Interactors, on the other hand, represent the second element of selection, ecological interaction. Interactors live and produce

progeny, but are themselves not transmitted. This distinction came to play a crucial role in the levels of selection debate and Godfrey-Smith 2000 offers a comprehensive review of the role of the replicator in evolutionary theory. Dawkins 1982 made a similar distinction, but preferred the term vehicle to Hull's interactor. Though similar, interactors and vehicles are not identical. Vehicle is in line with Dawkins's emphasis on organisms as a means to an end for replicators. Indeed, he has argued that thinking in terms of vehicles can often be misleading. In *The Extended Phenotype*, Dawkins offers a friendly rebuke to Hamilton for not "following his ideas through to the logical conclusion" (Dawkins 1982, cited under General Overviews, p. 194), meaning explaining all selection as replicator selection. As he would put it in a later paper: "I coined the vehicle not to praise it but to bury it" (Dawkins 1994). While Dawkins's nomenclature clearly favors replicators over vehicles, Hull's interactor is on equal footing. Furthermore, Hull allowed for a broader conception of replicators, including asexual organisms and even sexual ones if the genetic diversity was low enough, something that Dawkins rejects.

Dawkins, R. 1982. Replicators and vehicles. In *Current problems in sociobiology*. Edited by King's College Sociobiology Group, 45–64. Cambridge, UK: Cambridge Univ. Press.

Dawkins presents his distinction between replicator and vehicles, an argument elaborated upon in *The Extended Phenotype*.

Dawkins, R. 1994. Burying the vehicle. *Behavioral and Brain Sciences* 17:616–617.

A commentary on a review paper on group selection by Elliot Sober and David Sloan Wilson in the same journal. Emphasizes that the key player in evolution is not the vehicle, but the replicator.

Godfrey-Smith, P. 2000. The replicator in retrospect. *Biology and Philosophy* 15:403–423.

A comprehensive historical review of the idea of replicators. Dedicated to the memory of David Hull and so pays particular attention to his concept of interactors.

Hull, D. L. 1980. Individuality and selection. *Annual Review of Ecology and Systematics* 11:311–332.

A hugely influential paper that did a lot to focus the levels of selection debate. Makes the distinction between replicators and interactors and suggests that much disagreement is because authors talk past each other in relation to these issues.

Hull, D. L. 1981. The units of evolution: A metaphysical essay. In *Populations: Controversies over the units of selection*. Edited by R. N. Brandon and R. M. Burian, 142–160. Cambridge, MA: MIT.

As the title suggests, this paper focuses on issues central to metaphysics and Hull uses replicator and interactors to develop a general account of evolution.

Hull, D. L. 1988. *Science as a process*. Chicago: Chicago Univ. Press.

The book mainly focuses on the parallels between evolutionary change in biology and the historical development of science, but also includes a succinct summary of his replicator-interactor distinction.

Extended Phenotypes

The publication of new editions of *The Selfish Gene* has twice involved new forewords (1989, 2006). The 1989 edition also added two new chapters and extensive endnotes, discussing particular criticisms and perceived misunderstandings. The year 2016 marked the 40th anniversary of *The Selfish Gene* and the new edition includes a newly written epilogue. However, it is in Dawkins's second book, *The Extended Phenotype*, where the gene's-eye view and its implications are spelled out most clearly. Indeed, the first edition had the subtitle "the gene as the unit of selection," later changed to the "the long reach of the gene." Unique among his books in being aimed at

professional biologists, it is described by Dawkins in the opening of the book as a work of “unabashed advocacy,” laying out the gene’s-eye view of the world. In addition to addressing various criticisms of *The Selfish Gene*, Dawkins develops several new ideas, all with the aim of replacing the individual with the gene as the central unit of selection. In particular, the idea of extended phenotypes and the existence of selfish genetic elements are used to demonstrate the utility of the gene’s-eye perspective. Originally introduced at a talk at the International Ethological Conference in Bielefeld, Germany, in 1977 (published as Dawkins 1978), extended phenotypes are defined as phenotypic effects of a gene beyond the physical body in which the gene resides. Paradigm examples include beaver dams, bird’s nests, and parasites manipulating the behavior of their hosts. The extended phenotypic effects of parasites are also at the heart of the argument of Dawkins 1990 to demote the organism from occupying the central role in evolutionary explanations. Hughes, et al. 2012 is an edited volume reviewing all aspects of host manipulation by parasites, and includes a foreword by Dawkins. A recent empirical study is Weber, et al. 2013, whose authors dissected the genetic architecture of the size and shape of brown mice burrows. In 2004, the journal *Biology and Philosophy* invited four commentators to reflect upon the legacy of *The Extended Phenotype* (Jablonka 2004, Laland 2004, Turner 2004), to which Dawkins wrote an extensive reply (Dawkins 2004). Bateson later commented on some arguments raised by Dawkins (Bateson 2006). In all, these exchanges highlight the differences in opinion on the value of extended phenotypes.

Bateson, P. 2006. The nest’s tale. A reply to Richard Dawkins. *Biology and Philosophy* 21:553–558.

Bateson’s reply to Dawkins 2004; highlights their disagreements that go back to Bateson’s original review of *The Selfish Gene*.

Dawkins, R. 1978. Replicator selection and the extended phenotype. *Zeitschrift für Tierpsychologie* 47:61–76.

Paper based on Dawkins’s conference talk, introduces the extended phenotype concept for the first time.

Dawkins, R. 1990. Parasites, desiderata lists and the paradox of the organism. *Parasitology* 100:S63–S73.

Connects parasites and selfish genetic elements to show that individual organisms are not unified units but a compromise of competing fitness interests.

Dawkins, R. 2004. Extended phenotype—But not too extended. A reply to Laland, Turner and Jablonka. *Biology and Philosophy* 19:377–396.

A rare recent technical paper from Dawkins where he replies to three commentaries on *The Extended Phenotype*.

Dawkins, R. 2012. Foreword. In *Host manipulation by parasites*. Edited by D. P. Hughes, J. Brodeur, and F. Thomas, xi–xiii. Oxford: Oxford Univ. Press.

Foreword to an edited volume on research on how parasites may manipulate the behavior of their hosts (a classic example of an extended phenotype).

Hughes, D. P., J. Brodeur, and F. Thomas, eds. 2012. *Host manipulation by parasites*. Oxford: Oxford Univ. Press.

An edited volume on one of the best example of an extended phenotype: the manipulation of host behavior by parasites.

Jablonka, E. 2004. From replicators to heritably varying phenotypic traits: The extended phenotype revisited. *Biology and Philosophy* 19:353–375.

A critical commentary on the gene-centered approach. Argues among other things for an expanded notion of heredity. One of three commentaries replied to by Dawkins 2004.

Laland, K. 2004. Extending the extended phenotype. *Biology and Philosophy* 19:313–325.

One of three commentaries replied to by Dawkins 2004, focuses on the similarities between extended phenotypes and the concept of “niche construction.”

Turner, J. S. 2004. Extended phenotypes and extended organisms. *Biology and Phylosophy* 19:327–352.

A critique of the extended phenotype and gene’s-eye view from a physiological perspective. One of three commentaries replied to by Dawkins 2004.

Weber, J. N., B. K. Peterson, and H. E. Hoekstra. 2013. Discrete genetic modules are responsible for complex burrow evolution in Peromyscus mice. *Nature* 49:402–405.

A recent empirical example demonstrating the genetic basis of an extended phenotype in nature: the shape of mice burrows.

Selfish Genetic Elements

Another empirical observation that played a key role in promoting the utility of the gene’s-eye view was the existence of selfish genetic elements (SGEs; historically also referred to as ultraselfish genes, selfish DNA, genomic outlaws, self-promoting elements, and parasitic DNA). SGEs are genes that have the ability to promote their own transmission at the expense of organismal fitness, as measured in terms of inclusive fitness. The discovery of selfish genetic elements goes back some one hundred years, but it took a while for their evolutionary implications to be appreciated. Ågren 2016 traces the intertwined histories of the selfish gene thinking and the empirical study of selfish genetic elements. One example of a historical study that predates *The Selfish Gene*, but nevertheless used a language very similar to Dawkins, was Gunnar Östergren’s 1945 discussion of how B chromosomes could spread in a population despite their lack of positive fitness effects on the host plant (Östergren 1945). The landmark papers Doolittle and Sapienza 1980 and Orgel and Crick 1980 on selfish DNA published back-to-back in *Nature* marked the beginning of serious empirical study of selfish genetic elements, and both papers cite Dawkins’s writings as an inspiration. These papers also promoted the view that genome size was a product (at least in part) of the dynamics of transposable elements—genetic elements that could replicate within the genome and whose accumulation may be costly. This ran contrary to the prevailing view that genome size was an adaptive trait at the individual level. Another early example was Cosmides and Tooby 1981, which took a gene’s-eye perspective on the conflicts between the biparentally inherited nuclear and uniparentally inherited organellar genomes. David Haig drew heavily on the gene’s-eye view in his pioneering theoretical work on genomic imprinting, the phenomenon where the expression of the two gene copies within an individual differs with the copy inherited from the father showing repeatable patterns of down or upregulation compared to the maternal copy (Haig 2002 is a collection of his papers). Hurst, et al. 1996 provided one of the earliest reviews of genomic conflicts. Other key reviews are Hurst and Werren 2001, which focuses on the importance of selfish genetic elements in genome evolution, and Werren 2011, which discusses their role in the evolution of new traits. Burt and Trivers 2006 is a book-length treatment of the biology of selfish genetic elements and remains the most comprehensive treatment of the topic.

Ågren, J. A. 2016. Selfish genetic elements and the gene’s-eye view of evolution. *Current Zoology* 62:659–665.

Reviews the parallel histories of the gene’s-eye view and the empirical study of selfish genetic elements.

Burt, A., and R. Trivers. 2006. *Genes in conflict: The biology of selfish genetic elements*. Cambridge, MA: Belknap.

A superb book and the most extensive review of selfish genetic elements.

Cosmides, L. M., and J. Tooby. 1981. Cytoplasmic inheritance and intragenomic conflict. *Journal of Theoretical Biology* 89:83–129.

An early adopter of the gene’s-eye view to explain conflict between mitochondrial and nuclear genes.

Doolittle, W. F., and C. Sapienza. 1980. Selfish genes, the phenotype paradigm and genome evolution. *Nature* 284:601–603.

One of two landmark papers on selfish DNA published back-to-back in *Nature*.

Haig, D. 2002 *Genomic imprinting and kinship*. Piscataway, NJ: Rutgers Univ. Press.

A collection of papers on genomic imprinting, many of which draw heavily on a gene's-eye view.

Hurst, L. D., A. Atlan, and B. O. Bengtsson. 1996. Genetic conflicts. *The Quarterly Review of Biology* 71:317–364.

Early key review that provides a very thorough treatment of theory and data on selfish genetic elements as well as an argument for the importance of conflict in evolution.

Hurst, G. D., and J. H. Werren. 2001. The role of selfish genetic elements in eukaryotic evolution. *Nature Reviews Genetics* 2:597–606.

Comprehensive review on how selfish genetic elements play a key role in the evolution of genomes.

Orgel, L. E., and F. H. C. Crick. 1980. Selfish DNA: The ultimate parasite. *Nature* 284:604–607.

The second of two landmark papers on selfish DNA published back-to-back in *Nature*.

Östergren, G. 1945. Parasitic nature of extra fragment chromosomes. *Botaniska Notiser* 2:157–163.

Published three decades before *The Selfish Gene*, this article argues in favor of a gene's-eye perspective to understand the population biology of B chromosomes.

Werren, J. H. 2011. Selfish genetic elements, genetic conflict, and evolutionary innovation. *Proceedings of the National Academy of Sciences (USA)* 108:10863–10870.

A comprehensive review of the biology of selfsh genetic elements and their evolutionary implications.

Greenbeard Genes

Hamilton 1964 (cited under Social Evolution Theory) postulated that social evolution could occur not just as determined by genealogical relatedness (as envisaged in kin selection), but also in terms of altruistic actions directed at other bearers of the gene variant, irrespective of genealogical relatedness. In *The Selfish Gene*, Dawkins developed this argument in the form of "greenbeard" genes. The "greenbeard" concept concerns the recognition of other individuals carrying the gene variant through a phenotypic badge (a green beard), and alteration of behavior toward this individual according to whether the individual carried a matching badge. For instance, if there are two co-inherited genetic variants, one of which promoted helping individuals with a green beard, and the other growing a green beard, then this could spread through natural selection, as it would direct altruism toward individuals that bear the gene variant. Distinct from classic kin selection, greenbeards would operate beyond genealogical kin to any bearer of the variant, which could be through deep descent. A well-studied case in nature is the *gp9* locus in *Solenopsis* fire ants (Keller and Ross 1998). Fire ants are typical eusocial insects in that they form large colonies where some individuals breed, and other individuals (workers) assist others to breed while themselves not breeding. Worker individuals carrying one allelic variant kill any individual without the allele that attempts to initiate reproduction in the colony, but will permit reproduction by individuals that carry the same variant (all irrespective of relatedness). Consistent with its role as a greenbeard, this locus encodes an odorant binding protein—involved in recognition by scent. Another well characterized example of a greenbeard locus is the

flocculation gene *FLO1*, which causes budding yeast individuals to stick together—but only if they have the same variant of *FLO1* (Smukalla, et al. 2008). Gardner and West 2010 synthesizes case studies to outline four types of greenbeard. On one axis, greenbeards may act through helping other bearers (as envisaged by Dawkins and is the case with *FLO1*) or by harming non-bearers (as for *gp-9*). On a second axis, the actor may perform a fixed behavior that then has a differential impact depending on the variant in the receiver, or may act facultatively, only directing the behavior at recipients carrying particular variants. The fire ant example, for instance, is a case of a variant directing harming behavior at non-carriers. Examples of all four types have been discovered in natural systems. Biernaskie, et al. 2011 use mathematical models to explore under what conditions greenbeards will behave as selfish genetic elements.

Biernaskie, J. M., S. A. West, and A. Gardner. 2011. Are greenbeards intragenomic outlaws? *Evolution* 65:2729–2742.

Theory paper exploring scenarios of when greenbeard genes will be in conflict with the rest of the genome.

Gardner, A., and S. A. West. 2010. Greenbeards. *Evolution* 64:25–38.

Review of the greenbeard concept, introducing the four ways in which a locus can be a greenbeard, alongside empirical case studies of each type.

Keller, L., and K. G. Ross. 1998. Selfish genes: A green beard in the red fire ant. *Nature* 394:573–575.

Early description of a greenbeard in fire ants.

Smukalla, S., M. Caldara, N. Pochet, et al. 2008. *FLO1* is a variable greenbeard gene that drives biofilm-like cooperation in budding yeast. *Cell* 135:727–737.

Empirical example of a greenbeard locus in yeast.

Levels of Selection

Since *Adaptation and Natural Selection* and *The Selfish Gene* were both highly critical of the idea of group selection, the gene's-eye view has been at the center of much onward debate over the units and levels of selection: Does selection work principally at the level of gene, individual, group or species? Okasha 2006 (cited under General Overviews) and Lloyd 2012 both provide extensive reviews of the whole debate, with large chunks dedicated to the role of the gene's-eye view, while Patten 2010 offers a more succinct introduction. Brandon and Burian 1986, a collection of key papers on the levels of selection debate to date, offers an interesting insight to the historical context of the debate. Istvan 2013 specifically discusses the disagreement between Dawkins and Gould over the levels of selection. Reeve and Keller 1999 in the introduction to an edited volume on the levels of selection suggest that much of the arguments over levels of selection are a waste of time. Sober and Wilson 1998 deals with what the authors consider the unfair dismissal of group selection. Wilson 2005 and Walsh 2015 are both philosophical accounts that discuss the historical role of genes and organism in evolutionary explanations. Finally, Peter Godfrey-Smith 2009 developed the concept of Darwinian populations as an alternative to the separation between replicators and vehicles (but see Queller 2011 for how this can be reconciled with a gene's-eye view).

Brandon, R. N., and R. Burian, eds. 1986. *Genes, organisms, populations: Controversies over the units of selection*. Cambridge, MA: MIT.

A classic collection of previously published papers related to the levels of selection debate. Provides an interesting historical window into the debate.

Godfrey-Smith, P. 2009. *Darwinian populations and natural selection*. Oxford: Oxford Univ. Press.

One of the most highly praised books in philosophy of biology of recent years. Includes a fair discussion of the limitations of the replicator-vehicle distinction as a general account of evolutionary theory.

Istvan Jr., M. A. 2013. Gould talking past Dawkins on the unit of selection issue. *Studies in History and Philosophy of Biological and Biomedical Sciences* 327–335.

A discussion of the disagreements between Dawkins and Gould over the levels of selection.

Lloyd, E. 2012. Units and levels of selection. In *The Stanford Encyclopedia of Philosophy*. Edited by N. Zalta. Stanford, CA: Stanford Univ.

Encyclopedia entry on the history of the levels of selection debate, showing that much disagreement arises because people talk past each other trying to answer different questions.

Patten, M. M. 2010. Levels of selection. In *Encyclopedia of animal behavior*. Edited by M. Breed and J. Moore, 272–276. Oxford: Academic Press.

A brief but useful summary of the many issues involved in the levels of selection debate.

Queller, D. C. 2011. A gene's eye view of Darwinian populations. *Biology and Philosophy* 26:905–913.

Commentary on Peter Godfrey-Smith's Darwinian population concept, showing how it can be reconciled with a gene's-eye view.

Reeve, H. K., and L. Keller. 1999. Levels of selection: Burying the units-of-selection debate and unearthing the crucial new issues. In *Levels of selection in evolution*. Edited by L. Keller, 3–14. Princeton, NJ: Princeton Univ. Press.

The introductory chapter in an edited volume dedicated to the levels of selection questions. Argues that much of early debate was semantic and not very useful.

Sober, E., and D. S. Wilson. 1998. *Unto others: The evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard Univ. Press.

A book that played a key role in bringing group selection back into serious discussions concerning levels of selection and the evolution of altruistic behavior. The account is divided into two sections, one on the biology and one on the psychology of altruism.

Walsh, D. M. 2015. *Organisms, agency, and evolution*. Cambridge, UK: Cambridge Univ. Press.

Argues that the modern synthesis, while empirically very successful, puts too much emphasis on genes at the expense of organisms.

Wilson, R. A. 2005. *Genes and the agents of life*. Cambridge, UK: Cambridge Univ. Press.

Philosophical account about what the proper "agents" should be in evolutionary theory. Relates aspects in the levels of selection debate to broader philosophical issues.

The Major Transitions in Evolution

The role of selfish gene thinking in explaining long-term evolutionary trends is also contentious. Biologists have long recognized that life is organized in a hierarchical fashion. Genes form chromosomes that make up genomes; eukaryotic cells contain up to three separate genomes (nuclear, mitochondria, chloroplast); cells come together in multicellular organisms, which in turn can form eusocial societies. Buss 1987 transformed the levels of selection question from being about the consequences of hierarchy to also trying to understand why the hierarchy evolved in the first place. Following Maynard Smith and Szathmáry 1995, the origin of new levels of hierarchy is usually referred to as a major transition (or sometimes evolutionary transitions in individuality). Buss was critical of the gene's-eye view, which he contrasted with his own hierarchical approach. Maynard Smith and Szathmáry 1995, on the other hand, put the gene's-eye view at the heart of their account. In many ways, Michod 1999 synthesized these two traditions by developing formal population genetic models of transitions, but verbally conceptualized them using the language of multilevel selection. Bourke (Bourke 2011, Bourke 2014) is a strong proponent of the gene's-eye view as the key to understand the major transitions. Calcott and Sterelny 2011 is an edited volume where diversity of voices on the topic of major transitions are collected.

Bourke, A. F. G. 2011. *Principles of social evolution*. Oxford: Oxford Univ. Press.

Ambitious book that a gene's-eye view of inclusive fitness theory provides the key to studying the major transitions in evolution. Good balance between theory and data.

Bourke, A. F. G. 2014. The gene's-eye view, the major transitions and the formal Darwinism project. *Biology and Philosophy* 2:241–248.

Commentary on Alan Grafen's formal Darwinism project, calling for putting the gene, rather than the individual organism, at the center of the effort.

Buss, L. W. 1987. *The evolution of individuality*. Princeton, NJ: Princeton Univ. Press.

The first comprehensive argument that individuality, and the hierarchical organization of complex life, is a derived character in need of explanation. In some ways, a precursor to Maynard Smith and Szathmáry 1995 but favored a hierarchical rather than a gene-centred approach.

Calcott, B., and K. Sterelny, eds. 2011. *The major transitions in evolution revisited*. Cambridge, MA: MIT.

An edited volume with contributions from both philosophers and biologists focusing on how the study of major transitions have changed over the years and the current standing of the field.

Maynard Smith, J., and E. Szathmáry. 1995. *The major transitions in evolution*. Oxford: Oxford Univ. Press.

Landmark publication introducing the concept of major transitions, which dramatically transformed the levels of selection question.

Michod, R. E. 1999. *Darwinian Dynamics: Evolutionary transitions in fitness and individuality*. Princeton, NJ: Princeton Univ. Press.

Introduced several key ideas and some of the first and still influential mathematical models in the study of transitions in individuality.

Critiques of Selfish Gene Thinking

Selfish gene thinking was and remains controversial. Critiques vary from overreliance of the concept on genotype-phenotype determinism, the intentionality inherent in the term "selfish," a lack of rigor compared to formal mathematical approaches within population genetics, and

the weakness of the concept in cases when traits are determined by multiple genetic loci.

The Gene's-Eye View Denies Human Agency

Dawkins famously described organisms as "lumbering robots," which lead several early critics to accuse him of genetic determinism, the idea that only genes matter in the development of a trait. This was a major theme of, for example, Lewontin 1977a (cited under Initial Reactions to *The Selfish Gene* from Biologists) and Lewontin, et al. 1984 critiques. However, the gene's-eye view does not deny that environmental factors play a crucial role in development. This criticism was dealt with in, for example, Dawkins 1982 (cited under General Overviews) and has not played an important role in the subsequent debate about the gene's-eye view. Critics also picked up on other implications of the book for human ethics (e.g., Stent 1977, Midgley 1979). The commentary by the English philosopher Mary Midgley is perhaps the most notable. In particular, Midgley took issue with the way Dawkins, and other biologists, use the word "selfish." Believing that Dawkins argued that selfish genes meant that individuals were automatically egoistical, she also misunderstood how genes could be selfish to begin with. She began her review with: "Genes cannot be selfish or unselfish, any more than atoms can be jealous, elephants abstract or biscuits teleological." This review lead to Dawkins 1981a, a spirited reply in the same journal entitled "In Defence of Selfish Genes." Midgley has continued her discussion of the moral implications of the ideas presented in *The Selfish Gene* through her career. In particular, she has argued against what she considers an unsound and dangerous focus on individualism. Her book *The Solitary Self: Darwin and the Selfish Gene* (Midgley 2010) is the most up-to-date account of her views. Finally, the gene's-eye view became embroiled in the accusations of racism that featured heavily in the sociobiology debate (comprehensively reviewed in Segerstrale 2000). One expression of the high tempers of this debate was Steven Rose's letter to *Nature* (Rose 1981) calling on Richard Dawkins and John Maynard Smith to clearly dissociate themselves from the appropriation of their work by racist organizations, which Dawkins 1981b did.

Dawkins, R. 1981a. In defence of selfish genes. *Philosophy* 56:556–573.

Dawkins's spirited response to Mary Midgley's commentary on *The Selfish Gene*.

Dawkins, R. 1981b. Selfish genes in race and politics. *Nature* 289:528.

Following the call from Rose 1981, Dawkins takes a clear stand against the suggested racist implications of sociobiology.

Lewontin, R. C., R. Rose, and L. J. Kamin. 1984. *Not in our genes*. New York: Pantheon.

Inspired by their shared Marxist ideology, the authors launch a spirited attack on sociobiology. The book has been accused of misrepresenting the views of their scientific opponents.

Midgley, M. 1979. Gene juggling. *Philosophy* 4:439–458.

Infamous commentary on *The Selfish Gene* by the philosopher Mary Midgley. Accused Dawkins of advocating egoism in human morality. The paper led to Dawkins's spirited 1981 reply.

Midgley, M. 2010. *The solitary self: Darwin and the selfish gene*. Durham, UK: Acumen.

A fine example of Midgley's writing. Focuses on the common intellectual roots she sees between selfish gene thinking and an overreliance on individualism in modern society.

Rose, S. 1981. Genes and race. *Nature* 289:335.

Letter to the editor of *Nature* calling on John Maynard Smith and Richard Dawkins to distance themselves from the use of sociobiology by racist organizations, such as the UK's National Front.

Segerstrale, U. 2000. *Defenders of the truth: The battle for science in the sociobiology debate and beyond*. Oxford: Oxford Univ. Press.

A fine and exhaustive account of the many intricate issues and large personalities of the so-called sociobiology controversy.

Stent, G. S. 1977. You can take the ethics out of altruism but you can't take the altruism out of ethics. *The Hastings Center Report* 7:33–36.

A critical review of *The Selfish Gene* focusing on the implications for human ethics.

Genes Cannot Have Intentions

Several authors have taken issue with the use of intentional language—"selfish"—for genes. Charlesworth 2006 in a discussion about selfish genetic elements also questions the utility of such language, arguing the verbal model is imprecise and unhelpful compared to the predictive precision of the evolutionary process represented by standard population genetic models. Dawkins 1976 (cited under Original Works), anticipating the critique, argues: "If we allow ourselves the license of talking about genes as if they had conscious aims, always reassuring ourselves that we could translate our sloppy language back into respectable terms if we wanted to, we can ask the question, what is a single selfish gene trying to do?" Dawkins (p. 88). Here, the use of intentional language is argued to be a heuristic tool that helps guide the development of more formal models, which then represent the ultimate test of scientific validity for a particular proposition. This quote was also the starting point for a paper by Gardner and Welch 2011 (cited under General Overviews), which used optimization tools from behavioral ecology to model genes as agents seeking to maximize their inclusive fitness.

Charlesworth, B. 2006. Conflicts of interest. *Current Biology* 16:R1009–R1011.

A review of Burt and Trivers 2006 (cited under Selfish Genetic Elements) on selfish genetic elements. Criticizes the use of intentional language at the gene level.

Not All Genes are Selfish

Even if we recognize the heuristic value of using intentional langue, should all genes be considered selfish? There is a view that the term selfish should be reserved for cases of selfish genetic elements (SGEs). Selfish genetic elements are distinct in that their spread *requires* the disruption of individual fitness and some authors argue that the notion of selfish genes should thus be restricted to selfish genetic elements (e.g., Burt and Trivers 2006, cited under Selfish Genetic Elements and Gardner and Welch 2011, cited under General Overviews). In a similar vein, Yanai and Lercher 2016, while paying homage to *The Selfish Gene*, argue that a metaphor of a "society of genes" is a more productive way to think about evolution.

Yanai, I., and M. Lercher. 2016. *The society of genes*. Cambridge, MA: Harvard Univ. Press.

Explicitly inspired by *The Selfish Gene*, the authors develop the metaphor of the society of genes to emphasize the cooperative aspects of gene interactions.

Bookkeeping Does Not Imply Causality

Several authors (originally Sober and Lewontin 1982 and Sober 1983; and later Dover 2000, Gould 2001, Gould 2002, Bar-Yam and Sayama 2006) have argued that the gene's-eye conflates causality with bookkeeping. These critics agree that population genetics provides a way to represent all evolutionary change as changes in gene frequency in a population over time. However, they note that this is simply a means of tracking change, and represents a means of bookkeeping rather than a validation of the gene's-eye view of selection. Rosenberg

1983 argued that Sober and Lewontin 1982 confused mathematical modeling with causal theory, a charge Sober and Lewontin 1983 replied to. Elizabeth Lloyd's book-length treatment of the abstract structure of evolutionary theory sided with Sober and Lewontin in the question (Lloyd 1988). Parts of this debate continue to this day (see Ongoing Philosophical Discussion of the Gene's-Eye View of Evolution). Critics also argue that it is a mistake to assign causality to genes, rather than, for example, individual organisms. In support of this, it is well established that a gene's fitness depends on its genetic background, such that a variant may be under positive selection in some backgrounds, and others under negative selection in others. Such epistatic effects mean that it is problematic to view genes in isolation (see Wade 1978, cited under Initial Reactions to The Selfish Gene from Biologists). This point is often illustrated with the example of heterozygote advantage in diploid systems, that is, situations where the heterozygote genotype is fitter than either of the homozygous genotypes. The fitness of each allele can be calculated by averaging across genotypes (a point captured in Dawkins's famous rowing analogy in *The Selfish Gene*; see Dawkins 1976, cited under Original Works, p. 40). To critics, this is a mistake and the selection coefficients determined this way is a statistical artifact, not a true representation of causality. In the case of heterozygous advantage, fitness is most properly assigned to the diploid genotype. Okasha 2004 discusses this "averaging fallacy" and how it relates to similar issues in the group selection debate. He also introduces the distinction between the gene's-eye view as a causal process and as a useful heuristic perspective.

Bar-Yam, Y., and H. Sayama. 2006. Formalizing the gene centered view of evolution. In *Unifying themes in complex systems*. Edited by A. A. Minai and Y. Bar-Yam, 215–222. Heidelberg, Germany: Springer.

Mathematical paper that argues against Dawkins's rowing analogy, that genic fitness effects can be calculated by averaging across individuals.

Dover, G. 2000. Anti-Dawkins. In *Alas poor Darwin: Arguments against evolutionary psychology*. Edited by H. Rose and S. Rose, 55–77. New York: Harmony.

Essay directed at the general public highly critical of the gene's-eye view. Argument focuses especially on how epistatic interactions makes it impossible to assign fitness effects to individual genes.

Gould, S. J. 2001. The evolutionary definition of selective agency, validation of the theory of hierarchical selection, and the fallacy of the selfish gene. In *Thinking about evolution*, 2d ed. Edited by R. S. Singh, C. B. Krimbas, D. B. Paul, and J. Beatty, 208–234. Cambridge, UK: Cambridge Univ. Press.

Reiterates and spells out several themes of Gould's critique of selfish genes, including reductionism, hierarchical selection and that selection cannot act on individual genes.

Gould, S. J. 2002. *The structure of evolutionary theory*. Cambridge, MA: Harvard Univ. Press.

Gould's last major publication. Summarizes Gould's views on evolutionary biology, including his attacks on selfish genes, across some fourteen hundred pages.

Lloyd, E. A. 1988. *The structure and confirmation of evolutionary theory*. Princeton, NJ: Princeton Univ. Press.

A book that covers several issues relating to the philosophy of evolutionary biology. Includes a dedicated chapter to the gene's-eye view that especially focuses on the bookkeeping objection.

Okasha, S. 2004. The "averaging fallacy" and the levels of selection. *Biology and Philosophy* 19:167–184.

Discusses the critique that fitness of a gene cannot be averaged across genotypes, which is how the gene's-eye view handles cases like heterozygote advantage. Links the genic case to an analogous debate in the group selection controversy.

Rosenberg, A. 1983. Coefficients, effects, and genic selection. *Philosophy of Science* 50:332–338.

A commentary on Sober and Lewontin's influential 1982 paper. Argues that Sober and Lewontin confused mathematical modeling with causal theory.

Sober, E. 1983. *The nature of selection: Evolutionary theory in philosophical focus*. Cambridge, MA: MIT.

A crucial book in the history of the philosophy of biology that touches on several issues in evolutionary theory. Provides a comprehensive account of Sober's many disagreements with the gene's-eye view.

Sober, E., and R. C. Lewontin. 1982. Artifact, cause and genic selection. *Philosophy of Science* 47:157–180.

One of the most influential critiques of the gene's-eye view. In particular, this piece argues that the gene's-eye conflates causality with bookkeeping.

Sober, E., and R. C. Lewontin. 1983. Reply to Rosenberg on genic selections. *Philosophy of Science* 50:648–650.

A brief reply to Rosenberg's 1983 critique of their paper. Rejects the charge that they confuse mathematical modeling tools with accounts of causality.

Genes Do Not Have a Privileged Role in a Causal Account of Development

Under the gene's-eye view, genes are the units of inheritance. Critics have argued that other entities are stably inherited and play an important causal role in the development of phenotypes. This was the theme of developmental systems theory (Gray 1992, Oyama 2000) and of Denis Noble's long-standing argument that the gene's-eye view misrepresents the relationship between genotype and phenotype and so hinders the synthesis of physiology and evolutionary biology (Noble 2006, Noble 2011). The call for an expanded notion of inheritance is also a feature of biologists arguing for the so-called "extended evolutionary synthesis" to replace the modern synthesis of the 1930s (Jablonka and Lamb 2005; Laland, et al. 2014).

Gray, R. 1992. Death of the gene: Developmental systems strike back. In *Trees of life: Essays in philosophy of biology*. Edited by P. Griffiths, 165–209. Dordrecht, The Netherlands: Springer.

An attack on the centrality of genes in evolutionary explanation from one of the main proponents of developmental systems theory. Argues that genes do not have a special role in causal explanations.

Jablonka, E., and M. Lamb. 2005*. Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. Cambridge, MA: MIT.

An ambitious call for extending the notion of heredity beyond genes to also include epigenetic signals, behavior, and symbols (language). A key implication of this argument is that such extension invalidates the gene's-eye view.

Laland, K., T. Uller, M. Feldman, et al. 2014. Does evolutionary theory need a rethink? *Nature* 514:161–164.

Commentary including two groups of researchers of contrasting views. The disagreement is over whether the gene-centred modern synthesis needs to be replaced by an "extended evolutionary synthesis" that pays closer attention to alternative inheritance mechanisms.

Noble, D. 2006. *The music of life*. Oxford: Oxford Univ. Press.

A popular science account of Noble's longstanding critique of the gene's-eye view. Shares many themes with Noble 2011 and presents the developing field of systems biology as a better way to conceptualize evolution.

Noble, D. 2011. Neo-Darwinism, the modern synthesis and selfish genes: Are they of use in physiology? *Journal of Physiology* 589:1007–1015.

Argues that the gene's-eye view distorts the relationship between genotype and phenotype and so prevents the integration of evolutionary biology and physiology.

Oyama, S. 2000. *The ontogeny of information*: *Developmental systems and evolution*. 2d ed. Durham, NC: Duke Univ. Press.

Extensive book from one of the main proponents of developmental systems theory as an alternative to the gene's-eye view.

Selfish Genes and the Philosophy of Biology

Scientific concepts only rarely feature in philosophical discussion. Selfish gene thinking is a major exception, being both examined extensively as a concept by philosophers, and to some extent also synthesized into philosophical treatments. Indeed, debates over the validity of the gene's-eye view were essential as philosophy of biology developed into its own independent discipline.

Selfish Gene Theory as a Contribution to Philosophy

In the preface to the second edition of *The Selfish Gene*, Dawkins remarked: "One critic complained that my argument was 'philosophical,' as though that was sufficient condemnation." Without doubt, the gene's-eye view greatly influenced both biologists and philosophers. Indeed, while Williams's *Adaptation and Natural* selection had received some attention from philosophers of science (e.g., Wimsatt 1970), *The Selfish Gene* created more widespread philosophical debate. Daniel Dennett provided the afterword to *The Extended Phenotype* and in Dennett 2006 he lays out how *The Selfish Gene* shares many of the qualities of philosophy at its best. Dennett's own major contribution to the philosophy of biology, *Darwin's Dangerous Idea* (Dennett 1995), also draws heavily on Dawkins's thinking and offers a strident defense against critics, especially Stephen Jay Gould. Similarly, Helena Cronin's philosophical treatise of the study of altruism and sexual selection (Cronin 1991) is an ally in the same cause.

Cronin, H. 1991. *The ant and the peacock: Altruism and sexual selection from Darwin to today*. Cambridge, UK: Cambridge Univ. Press.

Shows how a gene's-eye view offers useful perspective on two classic Darwinian problems, the evolution of altruism and sexual selection.

Dennett, D. C. 1995. *Darwin's dangerous idea*: *Evolution and the meaning of life*. New York: Simon & Schuster.

Greatly inspired by Dawkins gene's-eye view, this is also an extensive defense against the critique of writers like Stephen Jay Gould.

Dennett, D. C. 2006. *The Selfish Gene* as a philosophical essay. In *Richard Dawkins: How a scientist changed the way we think*. Edited by A. Grafen and M. Ridley, 101–115. Oxford: Oxford Univ. Press.

Outlines how Dawkins's verbal conceptual argument, pushing a thesis to its logical conclusion, is what makes *The Selfish Gene* philosophy of biology at its best.

Wimsatt, W. C. 1970. Adaptation and natural selection. *Philosophy of Science* 37:620–623.

Book review showing the many philosophical implications of *Adaptation and Natural Selection*.

Ongoing Philosophical Discussion of the Gene's-Eye View of Evolution

In addition to the levels of selection debate outlined above, selfish gene thinking has contributed to several other debates within philosophy. Many contemporary disagreements about the gene's-eye view can be traced back to Sober and Lewontin's influential paper (Sober and Lewontin 1982, expanded in Sober 1983; both cited under Bookkeeping Does Not Imply Causality), which among other things introduced the bookkeeping argument mentioned earlier. One influential paper inspired by Sober and Lewontin was Sterelny and Kitcher 1988 which introduced the concept of pluralistic genic selection. Genic pluralism is analogous to the Necker cube idea introduced by Dawkins 1982 (cited under General Overviews) in *The Extended Phenotype* and suggests that gene's-eye view is a valuable heuristic perspective that is causally equivalent to a more traditional perspective seeing evolution through the lens of individual organisms. No perspective is empirically more correct than the other. Sterelny and Kitcher's paper reignited the literature and resulted in a long and rather technical debate, touching on several philosophical concepts, including causality, pluralism versus monism, and instrumentalism versus realism (Sober 1990; Kitcher, et al. 1990; Waters 1991; Lloyd 2005; Waters 2005; Lloyd, et al. 2005; Brandon and Nijhout 2006; Weinberger 2011). These papers can be challenging for biologists without formal training in philosophy, but highlight the depth and diversity of the philosophical implications of the selfish gene concept. Okasha 2006 (chap. 5) (cited under General Overviews) and Lloyd 2012 (cited under Levels of Selection) provide clear summaries of key concepts.

Brandon, R. N., and H. F. Nijhout. 2006. The empirical nonequivalence of genic and genotypic models of selection: A (decisive) refutation of genic selectionism and pluralistic genic selectionism. *Philosophy of Science* 73:277–297.

Proposes to show why genic and genotypic (usually meaning diploid) population genetic models are not equivalent, as is often suggested by proponents of so-called genic pluralism.

Kitcher, P., K. Sterelny, and C. K. Waters. 1990. The illusionary riches of Sober's monism. *Journal of Philosophy* 50:158–161.

A reply to Sober's critique of Sterelny and Kitcher 1988 that focuses on whether a given selective event can be described by multiple equivalent perspectives (pluralism) or if there is one correct one (monism).

Lloyd, E. A. 2005. Why the gene will not return. *Philosophy of Science* 72:287–310.

Philosophical paper from one of the premier experts on the topic. Rejects the call for "genic pluralism," the viewpoint that gene's-eye and individual-level thinking provide complementary (rather than competing) accounts of evolution, with no view being more correct than the other.

Lloyd, E. A., M. Dunn, J. Cianciollo, and C. Mannouris. 2005. Pluralism without genic causes. *Philosophy of Science* 72:334–341.

Lloyd's most recent contribution to the long-going debate over genic pluralism and monism.

Sober, E. 1990. The poverty of pluralism: A reply to Sterelny and Kitcher. *Journal of Philosophy* 87:151–158.

A commentary on Sterelny and Kitcher 1988. Rejects their account of genic pluralism.

Sterelny, K., and P. Kitcher. 1988. The return of the gene. *The Journal of Philosophy* 85:339–361.

A key paper that outlines the author's genic pluralism idea, the idea that viewing evolution from the gene's-eye or individual view provide heuristically different but empirically equivalent accounts of selection events, a proposition that has prompted much debate.

Waters, K. C. 1991. Tempered realism about the force of selection. *Philosophy of Science* 58:553–573.

Links the disagreements about genic pluralism to the philosophical debate about scientific realism.

Waters, K. C. 2005. Why genic and multilevel section theories are here to stay. *Philosophy of Science* 72:311–333.

Further elaborates Water's account of both genic pluralism versus monism and the role of realism in evolutionary explanations.

Weinberger, N. 2011. Is there empirical disagreement between genic and genotypic selection models? A response to Brandon and Nijhout. *Philosophy of Science* 78:225–237.

A rejection of Brandon and Nijhout's argument that genic and genotypic accounts of evolution are predictively equivalent.

Historical Reflections

The huge commercial and academic success of *The Selfish Gene* has meant that a lot has been written about the book itself. For the thirtieth anniversary former graduate students Alan Grafen and Mark Ridley edited a *festschrift* to celebrate Richard Dawkins's contributions to evolutionary biology (Grafen and Ridley 2006). Several contributions dealt specifically with *The Selfish Gene*. For example, Dennett 2006 (cited under Selfish Gene Theory as a Contribution to Philosophy) discussed the philosophical contribution of the book and Haig 2006 (cited under Biological Evolution) the concept of a selfish gene. Grafen 2006 argues that the book was more than a popularization of previous ideas and constitutes an intellectual contribution in itself. Sociologist of science Ullica Segerstrale reviewed the broader cultural context of the so-called sociobiology debate, of which *The Selfish Gene* was very much a part in her book *Defenders of the Truth* (Segerstrale 2000, cited under The Gene's-Eye View Denies Human Agency). Sterelny 2007 outlines the disagreements between Dawkins and Stephen Jay Gould over evolutionary theory more broadly. More recently, an episode of the BBC 4 series *A Beautiful Mind* includes extensive interviews with Dawkins and several colleagues, reflecting on the influence of Dawkins's writings. Finally, Ridley 2016 wrote an essay that praises the book's influence forty years on, whereas Gardner 2016 offers a slightly more critical take. In a paper marking the semi-centennial of Williams's *Adaptation and Natural Selection*, Boomsma 2016 highlights its enduring value for the study of adaptation.

BBC 4. 2012. *A Beautiful Mind: Richard Dawkins*. Television (25th April 2012).

Documentary about the intellectual contribution of Richard Dawkins to evolutionary biology.

Boomsma, J. J. 2016. Fifty years of illumination about the natural levels of adaptation. *Current Biology* 26:pR1250–R1255.

Outlines George Williams's contribution to the study of adaptation.

Gardner, A. 2016. The strategic revolution. *Cell* 166:1345–1348.

Discusses *The Selfish Gene*, with particular focus on the role of "strategic thinking" and the role of genes contra individual organisms in evolutionary explanations.

Grafen, A. 2006. The intellectual contribution of *The Selfish Gene* to evolutionary theory. In *Richard Dawkins: How a scientist changed the way we think*. Edited by A. Grafen and M. Ridley, 66–74. Oxford: Oxford Univ. Press.

Outlines how the book was more than a popularization of other peoples' ideas. Chapter in the *festschrift* dedicated to Dawkins for the thirtieth anniversary of *The Selfish Gene*.

Grafen, A., and M. Ridley, eds. 2006. *Richard Dawkins: How a scientist changed the way we think*. Oxford: Oxford Univ. Press.

Edited *festschrift* dedicated to Dawkins for the thirtieth anniversary of *The Selfish Gene*. Includes sections on his writing style and views on religion, in addition to all aspects of his contribution to evolutionary biology.

Ridley, M. 2016. In retrospect: *The Selfish Gene*. *Nature* 529:462–463.

A salutary celebration of *The Selfish Gene* for its fortieth anniversary.

Sterelny, K. 2007. *Dawkins vs. Gould: Survival of the fittest*. Cambridge, UK: Icon.

A summary of the many disagreements between Richard Dawkins and Stephen Jay Gould on the state of evolutionary theory.

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