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KIN SELECTION

Introduction

Kin selection theory is a formulation of natural selection theory that is particularly suitable for understanding cases of reproductive self-sacrifice. For example, sterile workers in insect societies help the queen to reproduce by rearing her offspring. This phenomenon can be favored by natural selection when the workers are genetically related to the queen and thereby help her to transmit genes identical to theirs in the queen. The origin of this idea can be traced back to anecdotal comments by Haldane and Fisher, and even to the *Origin of Species*, but a systematic development of the idea began with Hamilton's development of the concept of inclusive fitness. Natural selection by way of effects on genetic relatives has been named *kin selection*, and can thus occur whenever relatives preferentially interact together, in family-structured or spatially structured populations. The concepts of kin selection theory now provide powerful methods for analyzing models of evolution of social behaviors, including not only reproductive self-sacrifice in social insects but also the occurrence of conflicts within such societies, and more broadly any ecological interaction that includes cooperative or competitive interactions between individuals. The theory has contributed substantially to the development of ideas in diverse fields beyond behavioral ecology, including parasitology, and to the study of epigenetic processes in developmental biology.

General Overviews

The general theory and the diversity of its empirical implications are not generally

covered in a single textbook. Bourke 2011 comes closest to filling this niche. The collection of papers in Hamilton 1996 is a highly recommended reading, showing both significant early steps in the development of kin selection theory and the breadth of its empirical applications, but it is piecemeal and missing recent developments. Some monographs address applications to specific group of organisms or life history traits, largely using kin selection theory as the conceptual framework. The evolution of social insect colonies is surveyed by Crozier and Pamilo 1996, and ants are more specifically discussed in Bourke and Franks 1995. The latter book also provides an accessible introduction to many aspects of the theory itself. West 2009 reviews sex ratio evolution, a favorite topic of many tests of kin selection theory because of the relative ease of controlling the costs and benefits of alternative behaviors. Two more theoretically oriented monographs provide thorough introductions for graduate students and above: Frank 1998 emphasizes abstract general formalisms applicable to any evolutionary scenario, and Rousset 2004 emphasizes the relationship between kin selection, population genetic theory, and demography in structured populations. Marshall 2015 is a booklength defense of the general version of inclusive fitness.

Bourke, A. F. G. 2011. *Principles of social evolution*. Oxford: Oxford Univ. Press.
[ISBN: 9780199231157]

Covers kin selection broadly and in reasonable depth. A more specific aim of the book is to explain in terms of kin selection theory the hierarchical organization of life, of genes in cells, of cells in multicellular organisms, and of organisms in societies.

Bourke, A. F. G., and N. R. Franks. 1995. *Social evolution in ants*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691044279]

Although the book defines ants as its topic, it includes substantial general introductions to kin selection and multilevel selection theories, and substantial discussions of major conceptual issues such as parent-offspring conflict.

Crozier, R. H., and P. Pamilo. 1996. *Evolution of social insect colonies*. Oxford: Oxford Univ. Press. [ISBN: 9780198549437]

Similar in spirit to Bourke and Franks 1995, but covers a broader taxonomic range, delves more into the analysis of models, and more narrowly focuses on sex ratios.

Frank, S. A. 1998. *Foundations of social evolution*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691059334]

The first book-length treatment of inclusive fitness theory, with broad applications and many examples. It also emphasizes regression methods for formulating various expressions for change in allele frequency, but in an abstract way so that some readers may find it difficult to appreciate the precise meaning and limits of the concepts.

Hamilton, W. D. 1996. *Narrow roads to gene land*. Vol. 1. Oxford: Freeman. [ISBN: 9780716745303]

This volume collects all of Hamilton's publications prior to 1981, including works on sex ratio that introduced concepts of game theory and of intragenomic conflict. Each paper is introduced by a commentary describing the intellectual context in which it was developed, often in the form of personal anecdotes.

Marshall, J. A. R. 2015. *Social evolution and inclusive fitness theory: an introduction*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691161563]

Mainly an enthusiastic advocacy of the general version of inclusive fitness against recent criticisms, this book argues more through citations of previous authors than through self-contained, compact arguments. It does not discuss how kin selection arguments are used in game theoretical arguments that form the core of behavioral ecology.

Rousset, F. 2004. *Genetic structure and selection in subdivided populations*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691088167]

Merges methods of kin selection theory, game theory, and population genetics, showing in particular how relatedness relates to descriptions of genetic population structure; how this leads to results for fixation probabilities of mutants, widely used since; and how to interpret fitness costs and benefits in the presence of local competition.

West, S. 2009. *Sex allocation*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691089638]

Extensively covers the literature on sex ratio evolution. Theoretical results are presented but not rederived, and kin selection theory is used as an interpretative tool for

these results.

Textbooks

Although kin selection theory is a population genetic theory, undergraduate population genetic textbooks are often superficial or misleading, offering little more than a vague description of the classical $-c + rb$ formula for inclusive fitness (for a still brief but sound account, see [Charlesworth and Charlesworth 2010](#)). Behavioral ecology textbooks may also be remarkably silent on the topic. However, kin selection sets a good part of the scene in [Davies, et al. 2012](#) and [Alcock 2013](#), and [Westneat and Fox 2010](#) also includes chapters on kin selection theory and social insects. [Dugatkin 2004](#), an animal behavior textbook, provides a clear introduction to the concepts of kin selection theory. Among introductions to modeling in evolutionary biology, [Bulmer 1994](#) and [McElreath and Boyd 2007](#) also offer valuable coverage of kin selection.

Alcock, J. 2013. *Animal behavior: An evolutionary approach*. 10th ed. Sunderland, MA: Sinauer. [ISBN: 9780878939664]

Presents a strong adaptationist perspective of animal behavior based on a gene-centered perspective of evolution. The chapter on kin selection is central but remains very basic.

Bulmer, M. 1994. *Theoretical evolutionary ecology*. Sunderland, MA: Sinauer. [ISBN: 9780878930784]

An introduction with a focus on behavioral ecology and game-theoretical models with simple genetics, including chapters on kin selection and sex-ratio evolution. Although not up-to-date, this is still a good introduction to many modeling techniques in behavioral ecology.

Charlesworth, B., and D. Charlesworth. 2010. *Elements of evolutionary genetics*. Greenwood Village, CO: Roberts and Company. [ISBN: 9780981519425]

A broad coverage of evolutionary genetics, including a brief but sound introduction to inclusive fitness theory.

Davies, N. B., J. R. Krebs, and S. A. West, eds. 2012. *An introduction to behavioural ecology*. 4th ed. Oxford: Wiley-Blackwell. [ISBN: 9781444339499]

A weighty and colorful textbook devoted to explaining behavior through individual

adaptation and inclusive fitness. Remains elementary on the theory but has many illustrative empirical examples.

Dugatkin, L. A. 2004. *Principles of animal behavior*. New York: W. W. Norton. [ISBN: 9780393976595]

Animal behavior presented from both a proximate and ultimate perspective, with clarity and simplicity of the explanations of the concepts. The chapter on kin selection provides a “beginners” introduction on most concepts introduced in this bibliography.

McElreath, R., and R. Boyd. 2007. *Mathematical models of social evolution: A guide for the perplexed*. Chicago: Univ. of Chicago Press. [ISBN: 9780226558264]

A gentle introduction to theoretical models in social evolution. The chapter on kin selection is useful for a clear introduction to the basic concepts, but its overall focus on short-term evolution sidesteps the powerful developments of the long-term approach of kin selection theory (see **Weak Selection and Long-Term Evolution**).

Westneat, D. F., and C. W. Fox, eds. 2010. *Evolutionary behavioral ecology*. Oxford: Oxford Univ. Press. [ISBN: 9780195331936]

Useful for its broad coverage of the field through a variety of perspectives, this volume also includes a chapter on the “indirect genetic effects” approach, which, using the same methods as personal fitness approaches in kin selection theory, partitions the response to selection of a quantitative character, rather than fitness as is sufficient in game theory.

Journals

Papers on kin selection are regularly published in virtually any journal that publishes on evolution or on animal behavior, and can more occasionally be published in other publications bearing on developmental genetics or microbiology. The main current sources for research on kin selection and inclusive fitness are leading journals in evolutionary biology such as ***Evolution***, the ***Journal of Evolutionary Biology***, ***American Naturalist***, ***Behavioral Ecology***, ***Animal Behaviour***, ***Proceedings of the Royal Society B: Biological Sciences*** and ***Philosophical Transactions of the Royal Society B: Biological Sciences***. ***Theoretical Population*

*Biology*** and the ***Journal of Theoretical Biology*** have also published a number of theoretical papers on the subject.

**American Naturalist*[<http://www.press.uchicago.edu/ucp/journals/journal/an.html>]*. 1867–. [class:periodical]

Published by the American Society of Naturalists. Publishes empirical and theoretical research, as well as edited special issues surveying a field. Has traditionally been an outlet for theoretical papers with simple messages.

**Animal Behaviour*[<http://www.journals.elsevier.com/animal-behaviour/>]*. [class:periodical]

Publishes mostly empirical papers and covers the same type of articles as *Behavioral Ecology* with respect to kin selection theory.

**Behavioral Ecology*[<http://beheco.oxfordjournals.org>]*. 1990–. [class:periodical]

Regularly publishes papers on kin selection theory and various of its fields of application, such as parent-offspring conflict and reproductive skew. It is mainly a source of applied and empirical work, but it also publishes some theoretical work on the subject, tailored to specific applications.

**Evolution*[[http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1558-5646](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1558-5646)]*.

Published by the Society for the Study of Evolution, it aims to remain the leading journal in the field. Publish both theory and empirical work, and both research papers, perspectives and commentaries.

**Journal of Evolutionary Biology*[[http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1420-9101](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1420-9101)]*. [class:periodical]

Published by the European Society for Evolutionary Biology, it competes with *Evolution* as a reference journal in the field. Has widely covered kin selection theory in recent years.

**Journal of Theoretical Biology*[<http://www.journals.elsevier.com/journal-of-theoretical-biology/>]*. 1961–. [class:periodical]

Publishes research papers on all fields of theoretical biology. Most famous for

publishing Hamilton's first inclusive fitness paper, and has continued to publish on kin selection theory, but also publishes some of its most extreme criticisms.

**Philosophical Transactions of the Royal Society B: Biological Sciences*[<http://rstb.royalsocietypublishing.org/>]*. [class:periodical]

Published by the Royal Society of London. Publishes edited collections of reviews on a broad array of subjects within biology. An important source for in-depth syntheses, it regularly publishes on behavioral ecology and social evolution.

**Proceedings of the Royal Society B: Biological Sciences*[<http://rspb.royalsocietypublishing.org/>]*. [class:periodical]

Published by the Royal Society of London. Publishes research papers on a broad array of subjects within biology, but has traditionally been an outlet for relatively short, but high impact, papers in evolutionary ecology.

**Theoretical Population Biology*[<http://www.journals.elsevier.com/theoretical-population-biology/>]*. 1970–. [class:periodical]

Publishes mainly mathematical research papers on demography, ecology, epidemiology, evolution, and genetics. A good place for papers examining population genetic and game theoretical underpinnings of kin selection theory.

Main Concepts of Kin Selection Theory

Modern kin selection theory is a set of concepts and modeling techniques used to understand the effects of selection on any biological phenotype; it is most relevant to understand individual phenotypes that affect the fitness of genetically related individuals. These concepts have been gradually improved over the years and subject to intense debate.

Kin Selection

To understand the evolution of a trait that reduces the fitness of an individual expressing it, the gene-centered perspective shows that it is important to consider the average fitness of all individuals in the population who express this trait, and in particular the average fitness of all individuals who bear a particular allele modifying the expression of the trait

(a *modifier* allele). Dawkins 1976 is a classic introduction to the gene-centered perspective. It is generally possible to represent the average fitness effect of the modifier allele as $-c + rb$, where $-c$ is the expected effect of any given copy of the modifier allele on the fitness of the actor, b is the expected effect on the fitness of recipients, and *relatedness* r measures the extent to which recipients are more likely than a random individual in the population to carry the modifier allele. The notation reflects the aim of explaining how an allele that is costly for individuals who express it ($-c < 0$), can still be favored by selection if there are correlated fitness benefits ($br > 0$) to other individuals carrying the modifier allele. However, this representation holds whether $-c$ is negative or not, and whether b is positive or not. In general, c , b and r may depend on the state of the population. Such a representation of the average total fitness effect of an allele was introduced (with different notation) in Hamilton 1964. Maynard Smith 1964 introduced the term *kin selection*, which is said to occur when $rb \neq 0$. Hamilton 1970 emphasized that relatedness is best defined as a regression coefficient. The inclusive fitness effect was first formulated under assumptions including weak selection and additivity of costs and benefits, and Queller 1992 pointed out that the costs and benefits can also be defined as regression coefficients of individual fitness to individual allelic state and to partners' allelic state. This general interpretation of $-c + rb$ provides an exact formulation of the conditions under which biological altruism, as defined by Hamilton 1964, may evolve under natural selection, under strong selection and non-additive costs and benefits. Frank 1997 discussed this as part of a general framework unifying several conceptions of natural selection in quantitative and evolutionary genetics. Gardner, et al. 2011 provides several examples illustrating the generality of the regression version in the presence of non-additive interactions. Lehmann and Keller 2006 emphasized that Hamilton's rule holds even for the evolution of reciprocity or coercive mechanisms that are sometimes proposed as alternative explanations for altruism.

Dawkins, R. 1976. *The selfish gene*. Oxford: Oxford Univ. Press. [ISBN: 9780198575191]

The book that made gene-centered thinking popular. Initially quite controversial, but has entered mainstream thinking in evolutionary biology, certainly not without more privately expressed misgivings. Still a highly recommended reading for anyone

interested in understanding the natural world.

Frank, S. A. 1997. The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. *Evolution* 51:1712–1729.

Provides useful connections between various strands of the theoretical literature by discussing the relationship between the general interpretation of $rb - c > 0$, quantitative genetics, the Price equation, and Fisher's so-called fundamental theorem of natural selection.

Gardner, A., S. A. West, and G. Wild. 2011. The genetical theory of kin selection. *Journal of Evolutionary Biology* 24:1020–1049.

Provides several enlightening applications of Queller's general interpretation of inclusive fitness (see Queller 1992), showing the meaning of the cost and benefits in cases where it had previously been argued that inclusive fitness is not valid, in particular in the classic example of the prisoner dilemma with synergy.

Hamilton, W. D. 1964. The genetical evolution of social behavior. I. *Journal of Theoretical Biology* 7:1–16.

This is the classic reference that introduced the inclusive fitness concept. It represented the change in allele frequency in terms of the inclusive fitness effect $-c + rb$ and further provided definitions of cooperation, selfishness, altruism, and spite relevant for later discussions. Striving with unusual notation to show maximization of inclusive fitness, this paper remains difficult to read.

Hamilton, W. D. 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* 228:1218–1220.

Introduces the use of the Price equation in kin selection, and the first appearance of relatedness as a regression coefficient. Further discusses the evolution of spiteful behaviors, suggesting limited opportunities for such evolution.

Lehmann, L., and L. Keller. 2006. The evolution of cooperation and altruism: A general framework and a classification of models. *Journal of Evolutionary Biology* 19:1365–1376.

Emphasizes that b and c in $rb - c > 0$ can be complicated expressions of the behavior of

interacting individuals under repeated interactions, and that one often has $-c > 0$ under reciprocity and for various coercive mechanisms, which thus do not qualify as altruism as defined in Hamilton 1964.

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

This article introduced the concept of kin selection. Inspired by a reading of the then unpublished work of Hamilton, the paper defines kin selection as the evolution of characteristics that favor the survival of close relatives. It contrasts this definition with group selection, requiring that all members of the group have the same characteristic. Later literature has discussed broader definitions of group selection.

Queller, D. C. 1992. A general model for kin selection. *Evolution* 46:376–380.

Provided the first formulation of a generally valid interpretation of the $-c + rb$ formula, in which $-c$ and b are the partial regression coefficients respectively of an individual's fitness to its own allelic state, and of this fitness to the average allelic state of its social partners. This remains a topic of debate today.

Personal and Inclusive Fitness

Inclusive fitness was first introduced as an interpretation of the results of population genetic models. In particular, the term rb in $-c + rb$ was first introduced by Hamilton with the interpretation that it is the average effects of an actor on the transmission of the allele by the recipients (the *inclusive fitness interpretation*), rather than as the average correlated effects on the carrier of the modifier allele (the *personal fitness interpretation*).

Michod 1982 reviewed population genetic models of social behavior, which are usually formulated in terms of the personal fitness of the carrier of a modifier allele. Maynard Smith 1980 stated that a personal fitness analysis is compatible with the view that the inclusive fitness perspective is a useful guide to intuition about what an individual “should” do to transmit her genes. Grafen 1982 highlighted that measuring personal fitness from actual data is equivalent to measuring inclusive fitness. Frank 2013 reviews the historical change of appraisal of kin selection concepts, from interpretative tools to powerful methods for analyzing models of social behaviors. Hamilton 1970 (cited under *Kin Selection*) and Hamilton 1975 (cited under *Group Selection and Kin Selection*)

are important early steps in this change. Following [Taylor and Frank 1996](#), the personal fitness approach is currently preferred as a starting point of analytical methods that decompose the change in allele frequency in terms of various components of personal fitness. [Wenseleers, et al. 2010](#) provides a simple introduction to these analytical methods (also covered by [Frank 1998](#) and [Rousset 2004](#), both cited under *General Overviews*). [West and Gardner 2013](#) argues that inclusive fitness is distinctively the quantity organisms should appear designed to maximize, building on an interpretation of Fisher's so-called fundamental theorem of natural selection. [Ewens 2014](#) criticizes this interpretation.

Ewens, W. E. 2014. Grafen, the Price equations, fitness maximization, optimisation and the fundamental theorem of natural selection. *Biology & Philosophy* 29:197–205.

A criticism of recent misuses of Fisher's fundamental theorem of natural selection, this paper does not discuss the independent concepts of maximization that arise from the long-term evolution perspective (see *Weak Selection and Long-Term Evolution*).

Frank, S. A. 2013. Natural selection. VII: History and interpretation of kin selection theory. *Journal of Evolutionary Biology* 26:1151–1184.

An overview of the historical development of kin selection theory, mainly until 1998. Documents the evolution of (1) kin selection, from an interpretative tool of population genetic models to a toolkit of methods to analyze models; and (2) inclusive fitness, from an approximate expression of the fitness of a modifier allele to a general and exact version of it.

Grafen, A. 1982. How not to measure inclusive fitness. *Nature* 298:425–426.

Makes the point that simply counting the successful number of offspring of an individual encompasses kinship effects and amounts to an evaluation of the inclusive fitness of the individual.

Maynard Smith, J. 1980. Models of the evolution of altruism. *Theoretical Population Biology* 18:151–152.

Analysis of various models for the evolution of altruistic behavior by first endorsing an "exact" population genetic approach (personal fitness) and then an inclusive fitness

approach. Concludes that the inclusive fitness approach is generally useful to understand the causal components of a model that are often hidden in the precise but more complicated population genetic approach.

Michod, R. E. 1982. The theory of kin selection. *Annual Review of Ecology and Systematics* 13:23–55.

An early review of the population genetic basis of kin selection theory, which is focused entirely on a family-structured model. Emphasizes the correspondence between population genetic approaches under weak selection and inclusive fitness arguments based on “pedigree relatedness,” a correspondence that has since been generalized (see [Rousset 2004](#), cited under *General Overviews*).

Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. *Journal of Evolutionary Biology* 180:27–37.

Describes a simple algebraic technique to analyze models of kin selection from a personal fitness perspective, which has become a component of most current theoretical works. It rests on several theoretical arguments developed later in the literature.

Wenseleers, T., A. Gardner, and K. R. Foster. 2010. Social evolution theory: A review of methods and approaches. In *Social Behaviour: Genes, Ecology and Evolution*. Edited by T. Szekely, A. Moore, and J. Komdeur, 132–158. Cambridge, UK: Cambridge Univ. Press. [ISBN: 9780521883177]

A simple introduction to the methodology of kin selection theory in general, and to the personal fitness approach in particular. Works out several simple examples by starting the analysis with the personal fitness of a carrier of a modifier allele.

West, S. A., and A. Gardner. 2013. Adaptation and inclusive fitness. *Current Biology* 23:R577–R584.

Eloquently argues for using inclusive fitness as a guide for thinking about what individuals should do. However, this paper draws support for this position from the maximization argument in [Grafen 2006](#), which, as discussed in *Maximization of Inclusive Fitness*, may ultimately not be the strongest argument in support of inclusive fitness.

Group Selection and Kin Selection

The idea that natural selection favors altruistic traits that increase the productivity or persistence of some groups is entrenched in public discourse. The emblematic work [Wynne-Edwards](#) 1962 made this an explicit theory of group selection. Kin selection theory was instrumental in providing a common language for discussing gene-centered and group-selection ideas. Indeed, [Dawkins](#) 1982 highlighted that the inclusive fitness perspective retains some group selection perspective, as rb can be interpreted as a value given by an individual to fitness benefits of other individuals in the group. [Hamilton](#) 1975 showed that the partition of the allele effect on individual fitness can be done in terms of relative fitness of individuals within a group, and of group fitness relative to the average fitness of different groups. [Okasha](#) 2006 broadly discusses this and other multilevel selection formalisms. [Bourke](#) 2011 (cited under *General Overviews*) emphasizes the logical validity of such partitions, widely acknowledged in the kin selection literature. [Maynard Smith](#) 1987 emphasized that the existence of group effects does not generally lead to group adaptation. For example, [Nunney](#) 1999 discussed the importance of multilevel selection in the evolution of sexual reproduction, and how it relates to kin selection theory. Various answers have been proposed to the challenge of identifying a biological unit that exhibits adaptation under kin selection. The gene-centered perspective in general suggests that adaptation is an average property over all individuals that carry a given allele, rather than of any one of them. [Haig](#) 2012 proposed that all such individuals can be partitioned in lineages of individuals carrying alleles identical-by-descent, which would then exhibit adaptation. [Van Baalen](#) 2013 proposed to identify unit of adaptations with a probability distribution of allele environments when an allele grows in frequency. Dawkins, R. 1982. *The extended phenotype*. Oxford: Oxford Univ. Press. [ISBN: 9780198576099]

[An in-depth strengthening of the conceptual arguments raised in *The Selfish Gene* \(\[Dawkins\]\(#\) 1976, cited under *Kin Selection*\), bearing in particular on the ideas of fitness, adaptation, and the units of selection. Addressed to professional biologists, but generally accessible, the book emphasizes the distinction between replicators and vehicles \(such as organisms\) that carry them.](#)

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

Suggests that “a cloud of identical-by-descent [gene copies] with the possibility of a division of labor among its parts” may be the unit of adaptation.

Hamilton, W. D. 1975. Innate social aptitudes in man, an approach from evolutionary genetics. In *Biosocial anthropology*. Edited by R. Fox, 133–157. London: Malaby. [ISBN: 9780460140027]

Includes the first (and still a core) formulation of multilevel selection theory. This paper interpreted kinship in kin selection as what can be measured by the traditional computations on pedigrees, while it interpreted the r in inclusive fitness more widely as quantifying any process leading to correlations between social partners.

Maynard Smith, J. 1987. Reply to Sober. In *The latest on the best*. Edited by J. Dupré, 147–149. Cambridge, MA: MIT Press. [ISBN: 9780262040907]

One of the clearest and most concise summaries of key ideas in the group selection debate, distinguishing group adaptation from group selection, and emphasizing that a kin-selected trait (such as sex ratio in a local mate competition model) exhibits individual rather than group adaptation.

Nunney, L. 1999. Lineage selection: Natural selection for long-term benefits. In *Levels of selection in evolution*. Edited by L. Keller, 238–252. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691007038]

A clear discussion of the classical idea that sexual reproduction may evolve by competition between sexual and asexual lineages, and that developmental mechanisms that prevent mutation toward asexuality may have been selected in the same way. Highlights the importance of time-scale arguments in standard approximations of inclusive fitness.

Okasha, S. 2006. *Evolution and the levels of selection*. Oxford: Oxford Univ. Press. [ISBN: 9780199267972]

Primarily a conceptual comparison of variants of multilevel selection theory, this book carefully avoids a number of misconceptions of kin selection found in previous discussions of multilevel selection. Remains critical of how inclusive fitness represents

causal relationships.

van Baalen, M. 2013. The unit of adaptation, the emergence of individuality, and the loss of evolutionary sovereignty. In *From groups to individuals: Evolution and emerging individuality*. Edited by F. Bouchard and P. Huneman, 117–140. Cambridge, MA: MIT Press. [ISBN: 9780262018722]

Discusses the role of various factors, including kin selection, for the formation of associations between individuals, and proposes that the unit of adaptation in spatially structured populations is a probability distribution of the size of a local lineage of individuals sharing alleles identical-by-descent.

Wynne-Edwards, V. C. 1962. *Animal dispersion in relation to social behaviour*. Edinburgh: Oliver and Boyd.

Sparked controversy by explicitly stating the otherwise implicit reasoning of many biologists, according to which whenever group selection and individual selection conflict, “group selection is bound to win” (p. 20), and by interpreting as group adaptations many behavioral traits that have since been understood differently.

Weak Selection and Long-Term Evolution

The components of the inclusive fitness effect, c , b , and r , can be defined exactly and generally in terms of regression coefficients, making no assumption about their underlying determinants, or they can be approximated in different ways. Eshel 1996 expounds the theory of long-term evolution, which is a framework under which different approximations can be used to describe different aspects of the evolution of a character, and distinguishing convergence stable states (toward which a population evolves by successive allele replacements) from evolutionary stability (whether a genetic polymorphism can invade a population at a convergence stable state). Accordingly, Taylor 1989 showed that a first-order approximation of inclusive fitness is appropriate for determining convergence stable states if mutational effects are small, and Ajar 2003 showed how to compute a second-order version appropriate to assess evolutionary stability if mutational effects are small. The first-order approximation underlies most of the results discussed in *Implications of Kin Selection Theory* (with some exceptions

with respect to *Kin Recognition and Greenbeard Alleles*). Therein, the costs and benefits are marginal effects of a small change in behavior, and r is a function of an often simple genealogical structure. As recognized by many early studies reviewed in Michod 1982 (cited under *Personal and Inclusive Fitness*), this provides a rationale for expressing r in terms of probabilities of identity-by-descent (“pedigree coefficients”). Lynch and Walsh 1998 reviews traditional usage of such probabilities in population and quantitative genetics to describe genetic correlations due to family relationships, which can be measured using selectively neutral genetic markers. Likewise, Taylor 1990 showed how the effects of complex demographic structures can be taken into account through the concept of reproductive value, which is computed from a demographic transition matrix unaffected by selection. These terms are independent of the frequency of a modifier allele, so that $-c + rb > 0$ can provide a condition for spread of this allele at all frequencies of the allele in the population. Lehmann and Rousset 2014 emphasizes that this property underlies the relevance of first-order approximations for assessing convergence stability, and that different forms of weak selection lead to different conclusions about frequency dependence.

Ajar, É. 2003. Analysis of disruptive selection in subdivided populations. *BMC Evolutionary Biology* 3:22.

Provides an evolutionary stability condition in the form of a second-order expression for the inclusive fitness of a rare allele. This involves second-order fitness costs and benefits, but also distinguishes relatedness that results from demographic processes independent of selection, and the additional effect on relatedness resulting from selection.

Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. *Journal of Mathematical Biology* 34:485–510.

Surveys work by Eshel and collaborators that distinguished the qualitative features of short- and long-term evolution, as well as convergence and evolutionary stability under long-term evolution. The framework allows mutations with arbitrarily small effects and defines “local” (small effect) analytical criteria to determine convergence and

evolutionary stability.

Lehmann, L., and F. Rousset. 2014. *The genetical theory of social behavior[<http://rstb.royalsocietypublishing.org/content/369/1642/20130357>]*. *Philosophical Transactions of the Royal Society B: Biological Sciences* 369:20130357.

Reviews theoretical underpinnings of social evolution modeling, as well as broader conceptual issues raised by this, such as concepts of separation of time scales, different arguments for the use of reproductive values, and how causal processes extending over several generations can be represented by descriptions of changes over one generation.

Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sunderland, MA: Sinauer. [ISBN: 9780878934812]

An in-depth textbook on quantitative genetics. Chapter 7 provides a survey of the theory of relatedness coefficients computed from pedigree information. Also surveys regression methods considered in general versions of inclusive fitness, such as Queller 1992 and Frank 1997 (both cited under *Kin Selection*).

Taylor, P. D. 1989. Evolutionary stability in one-parameter models under weak selection. *Theoretical Population Biology* 36:125–143.

Aimed to show that the convergence stability condition can be evaluated using the weak selection version of inclusive fitness, defined in terms of relatedness coefficients unaffected by selection, using the same “rare-allele” approximation as Taylor 1990. Emphasized that the evolutionary stability condition cannot be computed in the same way.

Taylor, P. D. 1990. Allele-frequency change in a class-structured population. *American Naturalist* 135:95–106.

Distinguishes class and individual reproductive value, and develops an argument for using reproductive values in kin-selection models. The argument involves both a weak selection approximation and the assumption that the allele is rare, where the latter assumption has been relaxed in later analyses (see Rousset 2004, cited under *General Overviews*).

Maximization of Inclusive Fitness

Hamilton 1964 (cited under *Kin Selection*) not only introduced the inclusive fitness effect $-c + rb$ to describe allele frequency change, but also defined the inclusive fitness of the modifier allele as $1 - c + rb$, and perceived that under some circumstances its average value in the population would be maximized by natural selection. The extent to which this result can be generalized depends on the genetic basis of the trait and on how the b and c of a mutant depend on the population state. **Bürger** 2000 reviews traditional population genetic models that show that even with no dependence on population state, fitness is not necessarily maximized by natural selection when the trait depends on multilocus genetic variation. This fact has prompted population geneticists to probe whether inclusive fitness, at least in the weak selection version discussed by **Hamilton** 1964 (cited under *Kin Selection*), was maximized in one-locus or two-locus models. **Uyenoyama** 1989 provides a thorough analysis of two-locus models of kin selection exhibiting similar complications as in traditional population genetic models. This line of research faded when the long-term evolution perspective gained acceptance (see *Weak Selection and Long-Term Evolution*). In this perspective, one explicitly considers a dependence of fitness on population state. **Eshel, et al.** 1998 formalized the distinct idea that maximization occurs in the sense that the growth rate of any rare mutant is lower than that of the resident at an evolutionary stable state (ESS). Maximization then implies that the first-order term in $-c + rb$ equals zero. **Day and Taylor** 1998 further identified conditions where inclusive fitness, viewed only as function of the resident state, could be maximized at an ESS. **Grafen** 2006 attempted to define another concept of maximization of fitness, where individuals still behave as if they alter their own strategy to maximize their inclusive fitness, but which also appears to be realized only under similar restricted conditions, as in **Day and Taylor** 1998. **Bourke** 2014, a review of field tests of $-c + rb > 0$, attests to the persistent divergences in interpretation of these concepts in the literature. Bourke, A. F. G. 2014. Hamilton's rule and the causes of social evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 369:20130362.

Reviews tests of kin selection theory, and field estimates of $-c + rb$. It finds a weak trend for the latter to be positive, but does not consider that this could be expected

depending on whether or not one adopts the long-term evolution perspective and the definitions of costs and benefit that it entails.

Bürger, R. 2000. *The mathematical theory of selection, recombination, and mutation*. Chichester, UK: Wiley. [ISBN: 9780471986539]

An advanced reference on multilocus genetics, with clear summaries of various segments of the literature, including in particular cases where mean fitness is not maximized globally or locally near a stable equilibrium point in two-locus systems, and applications of the Price formula.

Day, T., and P. D. Taylor. 1998. Unifying genetic and game theoretic models of kin selection for continuous traits. *Journal of Theoretical Biology* 194:391–407.

Emphasizes that standard inclusive fitness calculations are suitable for evaluation of convergence stability, but are inadequate for evolutionary stability. Proposes criteria for evolutionary stability different from those of Ajar 2003 (cited under *Weak Selection and Long-Term Evolution*).

Eshel, I., M. Feldman, and A. Bergman. 1998. Long-term evolution, short-term evolution, and population genetic theory. *Journal of Theoretical Biology* 191:391–396.

Shows that evolutionarily stable strategies can be characterized as the mutant strategies that maximize the growth rate of a mutant when rare in a resident population itself at the evolutionarily stable state, and that this holds even under multilocus systems.

Grafen, A. 2006. Optimization of inclusive fitness. *Journal of Theoretical Biology* 238:541–563.

Attempts to show that inclusive fitness is maximized. Defines inclusive fitness as a function of individual phenotype only and where cost and benefits are then not a function of the population state. This requirement excludes most game theoretical contexts of application of kin selection concepts.

Uyenoyama, M. K. 1989. Two-locus models of kin selection among haplodiploids: Effects of recombination and epistasis on relatedness. In *Mathematical evolutionary theory*. Edited by M. W. Feldman, 174–206. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691085029]

A thorough discussion and endpoint of a thread of works investigating differences between one- and two-locus models of kin selection. Takes the perspective of defining relatedness as what makes Hamilton's rule work, so that it depends on the genetic basis, but cost and benefits are treated as constants.

Criticisms of the Concepts

As a Darwinian theory of the evolution of social behaviors, kin selection theory has been controversial ever since as it came into recognition. [Segerstråle 2000](#) abundantly documents sociological or political objections to sociobiological ideas. Much of these criticisms have little scientific substance. However, incorrect uses of inclusive fitness arguments, including by some of their most vocal advocates, have contributed to the confusion. [Dawkins 1979](#) clarified a number of early misunderstandings. [Grafen 1984](#) further warned about the risk of double accounting of costs and benefits. [Rousset 2004](#) (cited under *General Overviews*) highlighted safe modeling techniques. [Cavalli-Sforza and Feldman 1978](#) and [Bulmer 1986](#) contributed to early debates about inclusive fitness by comparing them to population-genetic modeling techniques based on a dynamical description of all possible configurations of groups in terms of allele frequencies. Two main ideas abated interest for such comparisons. First, the weak-selection version of inclusive fitness is consistent with such alternative population genetic models, in particular more easily recovering the same first-order conditions for convergence stability (see *[Weak Selection and Long-Term Evolution](#)*). Second, [Queller 1992](#) (cited under *Kin Selection*) showed that one can formulate an exact version of inclusive fitness with regression interpretations of cost, benefit, and relatedness (see also [Frank 1997](#), under *Kin Selection*), consistent with other use of regression concepts in evolution (reviewed by [Lynch and Walsh 1998](#), under *Weak Selection and Long-Term Evolution*). More recently, [Allen and Nowak 2015](#) attempted to falsify such uses of regression concepts, with no clear bearing on major insights that have been reached by kin selection arguments. [Okasha 2006](#) (cited under *Group Selection and Kin Selection*) emphasized the persistent criticism that the $-c + rb$ formula does not appropriately represent causal processes of evolution. [Waters 2010](#) criticized the prerequisites of such claims. Several works, including [Ohtsuki 2012](#), show that modern kin selection techniques can yield

informative causal partitions of costs and benefits in specific biological scenarios.

Allen, B., and M. A. Nowak. 2015. Games among relatives revisited. *Journal of Theoretical Biology* 378:103–116.

Claims that the regression version of inclusive fitness is not well defined and relies on an invalid use of statistical inference tools.

Bulmer, M. G. 1986. Sex ratio theory in geographically structured populations. *Heredity* 56:69–73.

Evaluates numerically the fate of a mutant allele in a population genetic model enumerating all possible population states in which a rare allele can be found. Recovers a number of results for the first-order condition of evolutionarily stable sex ratios obtained previously by inclusive fitness arguments, and extends them.

Cavalli-Sforza, L. L., and M. W. Feldman. 1978. Darwinian selection and altruism. *Theoretical Population Biology* 14:268–280.

An illustration of influential early research considering a population genetic model tracking all population states in which an allele can be, and allowing dominance and multiplicative interactions. The authors concluded that comparing cost, benefit, and a single relatedness coefficient was not appropriate for multiplicative interactions.

Dawkins, R. 1979. Twelve misunderstandings of kin selection. *Zeitschrift für Tierpsychologie* 51:184–200.

Debunks various misunderstandings, including some that are still encountered, such as the idea that kin selection is a special, complex kind of natural selection, as opposed to individual selection, or that kin selection theory implies universal altruism because all species members share the majority of their genes.

Grafen, A. 1984. Natural selection, kin selection and group selection. In *Behavioural ecology: An evolutionary approach*. Edited by J. R. Krebs and N. B. Davies, 62–84. London: Blackwell. [ISBN: 9780632009879]

Highlights the distinction between within-group selection and individual selection, the importance of accounting for local competition, and the problem of double accounting of fitness cost or benefits, which has been solved by modern kin selection techniques.

Ohtsuki, H. 2012. Does synergy rescue the evolution of cooperation? An analysis for homogeneous populations with non-overlapping generations. *Journal of Theoretical Biology* 307:20–28.

Analyzes the spread of a mutant allele in a spatially structured population when individuals employ discrete strategies. Decomposes the inclusive fitness effect in terms of pairwise and triplet relatedness coefficients that make the model tractable.

Seegerstråle, U. 2000. *Defenders of the truth: The battle for science in the sociobiology debate and beyond*. New York: Oxford Univ. Press. [ISBN: 9780198505051]

A broad survey of debates following the publications of Wilson's *Sociobiology* and Dawkins' *The Selfish Gene*, this volume includes a description of the intellectual environment of Hamilton and of other early students of kin selection. It documents opposition to kin selection by those who viewed it as a dangerous ideology.

Waters, C. K. 2010. Okasha's unintended argument for toolbox theorizing. *Philosophy and Phenomenological Research* 82:232–240.

Argues that no single partition of fitness effects will identify causal relationships in all its potential applications, and promotes a “toolkit” approach that may use different partitions for different biological scenarios.

Implications of Kin Selection Theory

Kin selection is historically known as an explanation for reproductive sacrifice in insect societies, but it affects all biological taxa. Several broad classes of predictions have been derived from kin selection theory, beyond the simple message that helping relatives may be favored by natural selection.

Kin Conflicts in Insect Societies

Kin selection theory predicts that divergence of interest will occur between individuals as soon as they are not genetically identical. Trivers 1974 showed that this means, in particular, that the same gene may be selected to express conflicting behaviors in a parent and in an offspring, a process known as parent-offspring conflict. Kilner and Hinde 2012 provides a concise overview of parent-offspring theory and empirical studies. The idea of

kin conflict has led to striking results on sex ratio in insect societies. [Hamilton](#) 1972 had already pointed that in haplodiploid insect societies, even sterile workers have reproductive interests that may depart from those of queens, and that workers may gain from investing more in rearing sisters than brothers. [Trivers and Hare](#) 1976 developed the idea, highlighting the case for worker control, and supporting it with evidence for female-biased sex ratio investment in monogynous ants. See chapter 5 of Bourke and Franks 1995 (cited under *General Overviews*) for a later review of such evidence. However, [Boomsma and Grafen](#) 1991 predicted that when there is variation in within-colony relatedness among different colonies (for example, depending on variation in the number of queens per colony), workers may favor either son production or daughter production in their colony. [Meunier, et al.](#) 2008 concluded from a comparative analysis that this prediction explains part of the colony-level variation in sex ratio. [West](#) 2009 (cited under *General Overviews*) discusses several complicating factors. Eusociality can be seen as an extreme case in a continuum of unequal sharing of reproduction among cooperating individuals. [Nonacs and Hager](#) 2011 reviews reproductive skew theory, which examines how this unequal sharing evolves among unrelated or related individuals, and [Wenseleers and Ratnieks](#) 2006 reviews policing theory, which examines how worker sterility is enforced by workers themselves to favor queen reproduction.

Boomsma, J. J., and A. Grafen. 1991. Colony-level sex ratio selection in the social Hymenoptera. *Journal of Evolutionary Biology* 3:383–407.

Predicted the phenomenon of colony variation in sex ratio (“split sex ratios”), from the argument that workers could maximize their inclusive fitness by specializing in the production of the sex to which they are more related than the average worker in the population is related to that sex.

Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics* 3:193–232.

An early discussion of implications of kin selection theory—for example, pointing to the potential for conflict between workers and queens owing to relatedness asymmetries between males and females. This paper is characteristic of Hamilton’s distinctive blend of theoretical insight and natural history knowledge.

Kilner, R. M., and C. A. Hinde. 2012. Parent-offspring conflict. In *The evolution of parental care*. Edited by N. J. Royle, P. T. Smiseth, and M. Kölliker, 119–132. Oxford: Oxford Univ. Press. [ISBN: 9780199692576]

A review covering intrabrood conflict in birds, the contrast between unstable and stable outcomes of joint parent and offspring evolution, and whether stable outcomes appear to lie closer to the parent or to the offspring optimum.

Meunier, J., S. A. West, and M. Chapuisat. 2008. Split sex ratios in the social Hymenoptera: A meta-analysis. *Behavioral Ecology* 19:382–390.

From a meta-analysis of sex ratio variation in twenty-two species of ants, the authors conclude that workers often bias colony sex allocation in their favor, as predicted by split sex ratio theory, even if their control is incomplete and a large part of the variation among colonies has other causes.

Nonacs, P., and R. Hager. 2011. The past, present and future of reproductive skew theory and experiments. *Biological Reviews* 86:271–298.

Reviews both models and tests of reproductive skew theory. Emphasizes the dependence of theoretical predictions on parameters that are difficult to measure, and that patterns of interpopulation variation are better predicted than patterns of intrapopulation variation. Suggests quantitative genetic approaches to assess whether intrapopulation variation is heritable.

Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* 14:249–264.

An offspring may benefit from monopolizing all parental investment, when the parents may benefit from sharing investment between all the offspring. The paper emphasized that offspring control of the outcome of such conflicts had been neglected, and further discussed how relatedness between offspring affects the offspring's best choices.

Trivers, R. L., and H. Hare. 1976. Haplodiploidy and the evolution of the social insects. *Science* 191:249–263.

The first paper to investigate conflicts between workers and queen in insect societies.

Wenseleers, T., and F. Ratnieks. 2006. Enforced altruism in insect societies. *Nature*

444:50.

In many species of ants, workers forgo reproduction despite having functional ovaries. Kin selection theory predicts that when queens are multiply mated, workers should evolve to police other workers from producing males and favor queen-produced males, which is suggested to occur in this empirical study.

Intragenomic Conflict over Gene Expression

Haig 1997 noted that parent-specific expression can be favored by selection in situations when there is an asymmetry in relatedness between the maternally or the paternally inherited allele in an actor, and a random homologous gene taken in a recipient. Predictions based on this idea were developed in particular to explain genomic imprinting, or the different effects of the maternally and paternally derived hemigenomes. Burt and Trivers 2006 reviews how such predictions may explain imprinting in the mouse embryo, and Haig 2013 reviews imprinting in the endosperm of angiosperm seeds. Isles, et al. 2006 argued that the widespread occurrence of parent-specific gene expression in the brain may be the consequence of intragenomic conflict over social interactions with either maternal or paternal relatives. Brandvain, et al. 2011 presented a synthetic modeling framework that has been used to extend and ascertain these ideas under diverse demographic assumptions, where relatedness asymmetries may result from such asymmetric family ties, from female multiple matings, and from sex-specific dispersal. For example, Úbeda, et al. 2014 argued that variation in sex-specific dispersal can explain the dysfunctional features of menopause. Spencer and Clark 2014 reviews many alternative theories that have been developed to explain parent-specific gene expression.

Brandvain, Y., J. van Cleve, F. Úbeda, and J. F. Wilkins. 2011. Demography, kinship, and the evolving theory of genomic imprinting. *Trends in Genetics* 27:251–257.

[Reviews the modern theoretical framework for analyzing selection on parent-specific gene expression in diverse ecological conditions.](#)

Burt, A., and R. Trivers. 2006. *Genes in conflict*. Cambridge, MA: Harvard Univ. Press. [ISBN: 9780674017139]

A fairly comprehensive treatment of manifestations of intragenomic conflict, where the theory is explained verbally, without equations.

Haig, D. 1997. Parental antagonism, relatedness asymmetries, and genomic imprinting. *Proceedings of the Royal Society B: Biological Sciences* 264:1657–1662.

A concise statement of the key steps of the theory of kin-selected genomic imprinting. In particular, it highlights that using the average relatedness over maternally and paternally inherited gene copies implicitly assumes that alleles will result in the same gene expression independently of their origin.

Haig, D. 2013. Kin conflict in seed development: An interdependent but fractious collective. *Annual Review of Cell and Developmental Biology* 29:189–211.

Reviews how far the kin conflict hypothesis explains accumulated knowledge about the effect of genomic imprinting on seed development, in particular the results of crosses between parents with different ploidy levels. Emphasizes the need to consider the possibility that one gene copy affects the expression of the homologous gene copy from the other parent.

Isles, A. R., W. Davies, and L. S. Wilkinson. 2006. Genomic imprinting and the social brain. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:2229–2237.

A review of parent-specific gene expression on genes affecting social behavior. Genomic imprinting on mother-offspring postnatal interactions. Many genes involved in cognition and socially costly behaviors, such as risk-taking, are also imprinted. Alternative explanations, particularly for the many imprinted genes found on sexual chromosomes, are considered.

Spencer, H. G., and A. G. Clark. 2014. Non-conflict theories for the evolution of genomic imprinting. *Heredity* 113:112–118.

Reviews thirteen alternatives to kinship theory for explaining parent-specific gene expression, and concludes that some of these hypotheses may provide tenable explanations for at least some loci.

Úbeda, F., H. Ohtsuki, and A. Gardner. 2014. Ecology drives intragenomic conflict over

menopause. *Ecology Letters* 17:165–174.

An example of possibly many phenomena that could be reconsidered as arising from intragenomic conflict over gene expression, this paper explains the dysfunctional features of menopause as the result of asymmetries in dispersal between males and females, and the variation of symptoms of menopause across human societies as the result of variation in sex-specific dispersal in recent human history.

Kin Recognition and Greenbeard Alleles

Kin selection theory predicts that an actor may prefer to help the most related partners available. Sharp, et al. 2005 experimentally tested that past family interactions are used as cognitive cues for a higher than average probability of sharing genes. But any other cue of gene sharing between individuals may be used. For example, Richard and Hunt 2013 reviews evidence that kin recognition occurs through shared cuticular hydrocarbon profiles in social insects, whose diversity may be controlled by both the colony environment and genetic polymorphisms. Known genetic recognition systems that may serve as a basis for kin recognition are taxonomically widespread, governing the expression of reproductive self-incompatibility in plants and histocompatibility polymorphisms in vertebrates. Saupé 2000 reviews how they control the fusion of vegetative mycelia in fungi. The polymorphisms controlling the fusion of colonies in various marine invertebrates are less well known, but Voskoboinik, et al. 2013 identifies one of them. In a conceptual exercise, Dawkins 1976 (cited under *Kin Selection*) suggested that the same allele could be involved both in self-recognition and expression of the social behavior, a combination Dawkins nicknamed a “greenbeard gene” (see also Dawkins 1982, cited under * Group Selection and Kin Selection*). This differs from the previous cases of kin recognition, in that only some greenbeard alleles recognize themselves in another other individual, whereas mycelium or colony fusion rests on the sharing of any of the alleles at the recognition locus. As found, for example, by Wang, et al. 2013, large blocks of genomes can function in such a way if they are nonrecombining. West and Gardner 2010 reviews further examples, most of which are examples of spiteful behavior directed at individuals harboring a different allele at the recognition locus. However, Queller, et al. 2003 and Smukalla, et al. 2008 described cell adhesion or

flocculation alleles that perform as greenbeard alleles favoring cooperation in slime molds and yeast.

Queller, D. C., E. Ponte, S. Bozzaro, and J. E. Strassmann. 2003. Single-gene greenbeard effects in the social amoeba *Dictyostelium discoideum*. *Science* 299:105–106.

This appears to be the first empirical example of a cell adhesion mutant performing a greenbeard strategy, substantiating an earlier theoretical suggestion by Haig.

Richard, F. -J., and J. H. Hunt. 2013. Intracolony chemical communication in social insects. *Insectes Sociaux* 60:275–291.

A survey of research on nestmate recognition in social insects (termites, social wasps, ants, and social bees).

Saupe, S. J. 2000. Molecular genetics of heterokaryon incompatibility in filamentous Ascomycetes. *Microbiology and Molecular Biology Reviews* 64:489–502.

A short introduction to vegetative incompatibility in Ascomycetes, with a detailed discussion of the understanding of its molecular mechanisms at the time of publication. Although such knowledge has steadily increased since, not much more has been learned about its ecological significance.

Sharp, S. P., A. McGowan, M. J. Wood, and B. J. Hatchwell. 2005. Learned kin recognition cues in a social bird. *Nature* 434:1127–1130.

Kin recognition has been demonstrated in several social bird species. This paper uses playback and cross-fostering experiments to show that long-tailed tits use calls learned from provisioning adults during the nestling period as cues for kin recognition.

Smukalla, S., M. Caldara, N. Pochet, et al. 2008. *FLO1* is a variable green beard gene that drives biofilm-like cooperation in budding yeast. *Cell* 135:726–737.

This paper provides another example of a cooperative greenbeard, providing collective resistance to toxins, and discusses indirect evidence that this is an evolving polymorphism in natural populations.

Voskoboynik, A., A. M. Newman, D. M. Corey, et al. 2013. Identification of a colonial chordate histocompatibility gene. *Science* 341:384–387.

Identifies a single locus involved in genetic recognition in the marine ascidian *Botryllus schlosseri*. Colony fusion only occurs between individuals that share the same allele at this locus.

Wang, J., Y. Wurm, M. Nipitwattanaphon, et al. 2013. A Y-like social chromosome causes alternative colony organization in fire ants. *Nature* 493:664–668.

Workers carrying a certain allele kill new queens who do not harbor this allele. This behavior correlates with variation in many other behavioral and life-history traits. This paper shows that this allele sits within a large chromosome inversion, which prevents recombination with chromosomes not carrying the allele.

West, S. A., and A. Gardner. 2010. Altruism, spite, and greenbeards. *Science* 327:1341–1344.

A brief survey of several topics, this paper is notable for its supplementary material reviewing known cases of greenbeard genes, and also emphasizes that efficient kin discrimination systems are important for the evolution of spiteful behaviors.

Kin Competition

Limited dispersal of juveniles (as observed in most organisms) implies that there will be competition between juveniles remaining in their natal patch. In such conditions, it is not quite obvious what the selection pressure will be on allele increasing the production of juveniles of interaction partners. Wilson, et al. 1992 introduced an emblematic example of this problem, considering the evolution of fecundity benefits in a population divided into small patches with a fixed number of adults in each patch. In that case, the positive fitness consequences of increasing social partners' fecundity are almost exactly balanced by the negative consequences of increased competition between related juveniles. Taylor 1992 showed how inclusive fitness calculations could be used to recover this result.

Modern kin selection techniques allow one to disentangle the role of kin competition and of fitness benefits, which has helped to identify conditions favorable for the evolution of helping. In particular, Taylor and Irwin 2000 showed that overlapping generations with fecundity effects on juvenile dispersal have such a favorable effect. Lehmann, et al. 2006 identified propagule dispersal with competition between groups, and effects of helping on

deme survival and deme carrying capacity, as quite favorable. Rubenstein and Lovette 2007 provides an example of comparative tests of the role of such ecological factors. Additional theoretical and experimental studies cited under *Evolution of Host-Pathogen Interactions* have investigated the effects of limited dispersal on evolution of host resistance to pathogens. In all cases, kin competition tends to offset at a least some part of kin-selected benefits, and Johnstone and Cant 2008 illustrates that this sometimes comes to the point where it becomes more favorable to harm neighbors. Kin competition can affect the evolution of any social trait under localized dispersal. For example, Hamilton and May 1977 recognized that kin competition can play a major role in the evolution of dispersal itself. Likewise, Hamilton 1967 recognized that local competition for mates could explain female-biased sex ratios. Chapters 3–5 of West 2009 (cited under *General Overviews*) reviews extensive later research on sex ratio evolution under local mate competition, and local resource competition, between kins.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.

Showed how local competition for mates selects for female-biased sex ratios. A key step in shifting ideas from group-adaptationism to gene-centered thinking, this paper initiated several major lines, including intragenomic conflict and the application of game theoretical ideas in evolutionary biology.

Hamilton, W. D., and R. May. 1977. Dispersal in stable habitats. *Nature* 269:578–581.

Shows that arbitrarily costly (short of totally lethal) dispersal of juveniles can evolve simply because it reduces the impact of kin competition on the fitness of the parent.

Johnstone, R. A., and M. A. Cant. 2008. Sex differences in dispersal and the evolution of helping and harming. *American Naturalist* 172:318–330.

Explores the impact of sex-biased dispersal on relatedness and on selection for helping and harming behavior among males and females. Shows in particular that when there is a marked sex bias in dispersal, selection will almost always favor harming behavior among individuals of the sex more prone to dispersal.

Lehmann, L., N. Perrin, and F. Rousset. 2006. Population demography and the evolution of helping behaviors. *Evolution* 60:1137–1151.

Relaxes several key assumptions of Taylor's analysis, in particular by allowing patches to change in size, propagule dispersal, and traits reducing patch extinction as well as increasing carrying capacity. Relaxing assumptions often (but not always) reduces the effect of kin competition and results in an increased selection pressure on helping.

Rubenstein, D. R., and I. J. Lovette. 2007. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology* 17:1414–1419.

Provides evidence for the role of temporal variability in rainfall on selection for or against cooperative breeding in forty-five species of African starlings. Although this is broadly consistent with theoretical predictions such as those of Lehmann, et al. 2006, the more specific assumptions of such predictions were not checked.

Taylor, P. D. 1992. Inclusive fitness in a homogeneous environment. *Proceedings of the Royal Society B: Biological Sciences* 249:299–302.

An emblematic illustration of the effects of kin competition, showing in particular that in some conditions, only direct effects of an individual on its own fecundity determine an allele's inclusive fitness. This explains the simulations results of Wilson, et al. 1992.

Taylor, P. D., and A. J. Irwin. 2000. Overlapping generations can promote altruistic behaviour. *Evolution* 54:1135–1141.

Constructs pleasingly simple models investigating the effects of overlapping generations on the evolution of helping behaviors. Some of the interpretations are cryptic.

Wilson, D. S., G. B. Pollock, and L. A. Dugatkin. 1992. Can altruism evolve in purely viscous populations? *Evolutionary Ecology* 6:331–341.

Shows by simulation that under certain assumptions about dispersal and population regulation, helping one's neighbors by increasing their production of juveniles has no net selective effects.

Evolution of Host-Pathogen Interactions

The relatedness between pathogens within an organism should affect the extent to which such pathogens will cooperate to best exploit their host. Thus their degree of cooperation

should differ whether hosts are infected by one parasite, several ones of common origin, or several ones of diverse origin. However, predictions of outcomes of infections in terms of virulence are not straightforward, since virulence may increase as well as decrease with increasing cooperation among pathogens. Frank 1996 reviewed a number of models of parasite virulence in a common inclusive fitness framework, and Chao, et al. 2000 emphasized the differences in outcome whether or not kin competition keeps constant the number of parasites produced by a host. Alizon, et al. 2013 reviewed experiments that have attempted to test such predictions. Any factor that is expected to affect social behavior may be expected to affect virulence evolution. For example, Lion and Boots 2010 suggested that virulence should be maximal at intermediate parasite dispersal, though again the details will be complex. Diseases are often transmitted between relatives, which will share similar resistance or susceptibility alleles to the pathogens. Frank 1998 emphasized that this should affect how much hosts would invest in resistance to parasites. Fukuyo, et al. 2012 and additional experimental studies reviewed in Lion and Gandon 2015 have shown how this can explain the evolution of suicide in bacteria infected by a virus. Schliekelman 2007 pointed out that kin selection effects have been ignored in estimates of the strength of selection on resistance alleles in humans. Alizon, S., J. C. de Roode, and Y. Michalakis. 2013. Multiple infections and the evolution of virulence. *Ecology Letters* 16:556–567.

[Reviews tests of predictions of evolution of virulence, and concludes that taking into account the nature of within-host interactions improves predictions.](#)

Chao, L., K. A. Hanley, C. L. Burch, C. Dahlberg, and P. E. Turner. 2000. Kin selection and parasite evolution: Higher and lower virulence with hard and soft selection. *Quarterly Review of Biology* 75:261–275.

[Highlights the importance of assumptions about group productivity \(here, about the relative numbers of parasites produced by different infected hosts\) on prediction of parasite virulence.](#)

Frank, S. A. 1996. Models of parasite virulence. *Quarterly Review of Biology* 71:37–78.

[A survey of models of parasite virulence, using a kin selection formalism. Emphasizes that earlier analyses had confounded the effect of relatedness among infecting parasites](#)

and other factors.

Frank, S. A. 1998. Inducible defence and the social evolution of herd immunity.

Proceedings of the Royal Society B: Biological Sciences 265:1911–1913.

This paper highlights that host investment in defense against parasites (including vaccines) may be kin selected. It therefore suggests comparing immune responses of individuals whether they live in family groups or not.

Fukuyo, M., A. Sasaki, and I. Kobayashi. 2012. *Success of a suicidal defense strategy against infection in a structured habitat[<http://www.nature.com/articles/srep00238>]*.

Scientific Reports 2:238.

The first of several experimental studies that investigated the effects of kin selection in the evolution of bacterial suicide as a resistance to virus infection, by manipulating bacterial dispersal.

Lion, S., and M. Boots. 2010. Are parasites “prudent” in space? *Ecology Letters*

13:1245–1255.

Using pair-approximation methods to assess the relative effects of parasite relatedness between hosts, and of host demographic structure on the evolution of parasite virulence, this paper finds conditions where parasites evolve maximal virulence at intermediate dispersal rates.

Lion, S., and S. Gandon. 2015. Evolution of spatially structured host-parasite interactions. *Journal of Evolutionary Biology* 28:10–28.

A review based on a unifying model. This paper recovers results similar to those of [Lion and Boots 2010](#) for virulence evolution, and finds that hosts generally evolve stronger defense when they disperse less. It emphasizes the importance of assumptions about the mode of resistance on these conclusions.

Schliekelman, P. 2007. Kin selection and evolution of infectious disease resistance.

Evolution 61:1277–1288.

Taking the example of one of the most studied disease resistance alleles in humans, involved in resistance to HIV but also possibly in past resistance to bubonic plague or smallpox, this paper emphasizes that previous estimates of selection were too low

because they ignored kin selection.

Evolution of Multicellular Organisms

The so-called major evolutionary transition perspective asks, for any kind of group (of genes, of cells, of individuals from different species), what keeps selection acting on within-group selection from disrupting the integration of the group (see Bourke 2011, cited under *General Overviews*). For example, sexual reproduction creates a lot of opportunities for conflicts (see *Kin Conflicts in Insect Societies* and *Intragenomic Conflict over Gene Expression*). The evolution of multicellular organisms has required both specific ecological benefits to them and factors that have reduced the potential for internal conflict. Michod 2007 and Velicer and Vos 2009 provide examples of group benefits in facultatively multicellular organisms. Most multicellular organisms go through a single-cell (and single-genome) stage in their life cycle. Queller 2000 emphasized the distinction between associations of kin vs. non-kin cells, and proposed that a single-cell stage maximizes the relatedness among cells, which reduces the potential for internal conflict. Grosberg and Strathmann 1998 contrasted this with other explanations of the persistence of a single-cell stage. In some microorganisms, genetically distinct individuals can assemble to form differentiated reproductive structures. However, Gilbert, et al. 2007 showed that relatedness is still high enough to deter selfish mutants in a slime mold with such a life cycle. Velicer and Vos 2009 reviews social evolution in Myxobacteria with similar life cycles, which appear to exhibit substantial polymorphisms for social traits. Queller 2000 further considers that relatedness allows the evolution of sterile cells (in other words, a soma), and Fisher, et al. 2013 that this then allows the differentiation of many cell types. Grosberg and Strathmann 2007 further discuss how the loss of cell totipotency, or alternatively the presence of rigid cell walls in plants, further restrain the potential for conflict, preventing selfish somatic mutations (e.g., cancerous ones) from invading the population. In species where fusion between genetically distinct multicellular organisms occurs, fusion appears largely restrained by kin-recognition mechanisms, ensuring high relatedness among the partners (see Saupe 2000 and Voskoboynik, et al. 2013, cited under *Kin Recognition and Greenbeard Alleles*, for examples in fungi and marine invertebrates, respectively).

Fisher, R. M., C. K. Cornwallis, and S. A. West. 2013. Group formation, relatedness, and the evolution of multicellularity. *Current Biology* 23:1120–1125.

Uses comparative methods to test correlations between relatedness and obligate multicellularity, differentiated cell types with loss of totipotency, or cell number in multicellular organisms.

Gilbert, O. M., K. R. Foster, N. J. Mehdiabadi, J. E. Strassmann, and D. C. Queller. 2007. High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. *Proceedings of the National Academy of Sciences of the United States of America* 104:8913–8917.

Shows that the high relatedness in fruiting bodies collected from natural populations of *Dictyostelium discoideum* is sufficient to prevent invasion by selfish mutants in laboratory conditions.

Grosberg, R. K., and R. R. Strathmann. 1998. One cell, two cell, red cell, blue cell: The persistence of a unicellular stage in multicellular life histories. *Trends in Ecology & Evolution* 13:112–116.

Reviews explanations for the persistence of a single-cell stage, as a constraint imposed by sexual reproduction, as a way to control selfish mutants, or as a way of exposing deleterious mutations to selection. Also reviews ecological costs of going through the single-cell stage.

Grosberg, R. K., and R. R. Strathmann, 2007. The evolution of multicellularity: A minor major transition? *Annual Review of Ecology, Evolution and Systematics* 38:621–654.

Broadly reviews the evolution of multicellularity and the mechanisms that restrain the evolution of defecting cells.

Michod, R. E. 2007. Evolution of individuality during the transition from unicellular to multicellular life. *Proceedings of the National Academy of Sciences of the United States of America* 104 (Suppl. 1): 8613–8618.

A discussion of the evolution of a differentiated individual, taking the example of the green alga *Volvox carteri*. In particular, this article reviews works using a mutant-controlling somatic cell differentiation, which provides an estimate of the shape of the

trade-off between somatic and reproductive functions.

Queller, D. C. 2000. Relatedness and the fraternal major transitions. *Philosophical Transactions of the Royal Society B: Biological Sciences* 355:1647–1655.

Emphasizes the distinction between groups of individuals that are similar (groups of kins) and groups of individuals that are different (such as different species) in symbiosis for major evolutionary transitions.

Velicer, G. J., and M. Vos. 2009. Sociobiology of the myxobacteria. *Annual Review of Microbiology* 63:599–623.

Reviews social evolution in these bacteria, with emphasis on the occurrence of cheaters and the factors that prevents them from invading populations. Emphasizes that despite a strong spatial genetic structure, different genotypes are commonly found at the smallest spatial scale.