

### Original Article

## Persistent Misunderstandings of Inclusive Fitness and Kin Selection: Their Ubiquitous Appearance in Social Psychology Textbooks

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**Abstract:** Inclusive fitness theory and kin selection theory are among the most recognizable theories associated with evolutionary biology and psychology—they are also among the most widely misunderstood. The problem begins early, in undergraduate psychology textbooks. Here, ten social psychology textbooks were reviewed, and they were all found to contain at least one form of misunderstanding. Because these misunderstandings appear to result partly from people’s intuitions about kinship and adaptive behavior (which are not necessarily in line with the scientific theories), writers must be especially vigilant in order to combat the misunderstandings.

**Keywords:** altruism, genetic similarity, inclusive fitness, kin selection, misunderstandings.

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### Introduction

*Inclusive fitness theory* and the closely associated *kin selection theory* (Hamilton, 1964; Maynard Smith, 1964) are among the most important ideas in evolutionary biology and psychology. They are also among the most widely misunderstood ideas, generating several pieces of corrective text over the years (e.g., Daly, Salmon, and Wilson, 1997; Dawkins, 1979; Mealey, 1985; Tooby and Cosmides, 1989). Despite these corrective attempts, many misunderstandings persist. In many cases, they result from conflating “coefficient of relatedness” and “proportion of shared genes,” which is a short step from the intuitively appealing—but incorrect—interpretation that “animals tend to be altruistic toward those with whom they share a lot of genes.” These misunderstandings don’t just crop up occasionally; they are repeated in many writings, including undergraduate psychology textbooks—most of them in the field of social psychology, within sections describing evolutionary approaches to altruism.

This article has the following objectives: (a) reiterate the key aspects of inclusive fitness theory and kin selection theory, (b) describe some of the common misunderstandings of the theories, (c) review passages from several undergraduate social psychology textbooks and identify the specific misunderstandings, and (d) point to some

possible reasons why these theories are so often misunderstood. Given the apparent failure of previous corrective attempts in stamping out the misunderstandings, it's unclear whether this article will have any impact on psychology textbook writers. But, assuming that these writers were not being deliberately erroneous, perhaps bringing the misunderstandings to attention might induce at least some writers to be more vigilant in the future. (In all quoted passages below, all emphases are original; spelling and formatting has been modified to conform to this journal's house style.)

*Inclusive Fitness and Kin Selection*

Inclusive fitness theory pertains to the *evolutionary emergence of genes*, and it pertains principally to genes underlying behaviors that influence other individuals. Although it may be handy to assume that individual organisms generally act in ways that maximize their inclusive fitness, inclusive fitness is not a property of individuals—it represents the cumulative effects of genes that underlie specific behaviors (see Tooby and Cosmides, 1989). Nor does inclusive fitness theory imply that all genes under all circumstances are driven to maximize copies of themselves at the expense of non-copies.

As a thought experiment, imagine a population of organisms in which no single gene in these organisms' bodies codes for behavior that influences other organisms (a scenario that must have existed at some point in the past). In such a state, the mere fact that two closely related individuals happen to "share genes" isn't enough to engender altruistic behavior. Any two genes, replica or not, are "selfish" competitors for limited resources (Dawkins, 1976). In such a population, no tendency toward kin altruism—or any preferential treatment of others, for that matter—would be observed. Imagine further that a mutant gene emerged in a parent organism making it confer benefits to its offspring, even at costs to itself. Now, here is the reason—the only reason—that genetic relatedness matters: Assuming diploid sexual reproduction, there would have been 50% probability that each of the parent organism's offspring would inherit this particular mutant gene. Therefore, as long as the benefits conferred to the offspring (multiplied by the probability of inheritance) outweighed the costs incurred by the parent (with benefits and costs measured in terms of reproductive success), this mutant gene would have been selected over its alleles—and this would be kin selection. Observation of parental care in animals today shows that such selection processes indeed occurred in the past, resulting in a species-typical tendency to invest in offspring.

The same reasoning applies to altruistic behavior between other genetic relatives. In Hamilton's (1964) own words,

A gene causing its possessor to give parental care will then leave more replica genes in the next generation than an allele having the opposite tendency. The selective advantage may be seen to lie through benefits conferred indifferently on a set of relatives each of which has a half chance of carrying the gene in question. From this point of view it is also seen, however, that there is nothing special about the parent-offspring relationship except its close degree and a certain fundamental asymmetry. The full-sib relationship is just as close. If an individual carries a certain gene the expectation that a random sib will carry a replica of it is again one-half (pp. 1–2). For a gene to receive positive selection, it is not necessarily enough that it should increase the fitness of its bearer above the average if this tends to be done at the

heavy expense of related individuals, because relatives, on account of their common ancestry, tend to carry replicas of the same gene. (p. 17)

Hamilton couldn't have been clearer: Inclusive fitness theory—as applied to altruistic behavior—pertains only to the genes that underlie altruistic behavior. All of the remaining genes in organisms' bodies are completely irrelevant to the discussion. You and I (and most other humans, and even some nonhuman animals) may possess identical genes that give rise to, say, the liver. But this doesn't mean that I (or my liver genes) will necessarily care about your (or your liver genes') welfare.

Hamilton's simple ideas were quickly and widely misconstrued, prompting Dawkins (1979) to write a paper titled "Twelve misunderstandings of kin selection." And several writers since then have attempted to emphasize the key points of Hamilton's theory. For instance, Krebs (1987) wrote,

The reason why relatedness is important in Hamilton's formula is because the coefficient of relatedness between two individuals is equivalent to the probability that they share a gene for altruism, not because they share a high proportion of other, nonaltruistic genes. By some measures, all humans share more than 99% of their genes, and, indeed, there is 98% genetic overlap between chimpanzees and humans. (p. 93)

Similarly, Mealey (1985) wrote,

It is not the *proportion* of genes shared with another which is relevant for altruistic behavior; it is the *probability* that the two individuals share the "altruism gene". . . . That altruism can evolve is by virtue of this 0.5 probability of sharing the altruism allele and is totally independent of the fact that genes at other loci are also shared. Altruistic behavior, therefore, is contingent solely on the likelihood that another shares this particular allele at a particular locus, not on overall genotypic or phenotypic similarity. (pp. 572–573)

As Krebs (1987) and Mealey (1985) have stressed, the relatedness coefficients for different classes of kin (.50 for offspring and siblings, .25 for grandchildren, etc.) specify only the *probability of sharing a particular allele by common descent*, a value that allows one to model the selection of genes underlying specific forms of kin altruism. Applying Hamilton's rule ( $rB > C$ ), one can see that genes underlying altruism toward siblings (which can evolve if  $B > 2C$ ) have a very good chance of evolving by kin selection, whereas genes underlying altruism toward cousins (which can evolve if  $B > 8C$ ) are far less likely to evolve (contrary to common belief, Hamilton's theory does not imply that a person will give his or her life for nine cousins—it states merely that a gene underlying such behavior could be selected). Genes for altruism toward even more distant kin simply have no realistic chance of evolving strictly by kin selection. For example, with respect to a second cousin, the benefits to the recipient must outweigh the costs to the altruist by at least thirty-two-fold (using the example of sacrificing one's life, it's difficult to imagine a situation in which one would have a chance to give one's life to save the lives of thirty-three second cousins). A proper account of altruism by kin selection thus demands that we consider such probabilities for each class of kin, in conjunction with other important considerations, such as generation asymmetries in investment and reproductive value.

For now, the most important points are that (a) the relatedness coefficients matter principally "in the beginning," when genes underlying kin altruism first emerge and become selected, and (b) Hamilton's rule provides only the formal constraints on what *can*

evolve—it is not a descriptive theory of altruistic behavior. Once the genes underlying kin altruism did evolve and propagate, they would have gone on to reside in most individuals within a species. In other words, kin altruism would have become a species-typical adaptation (in the parlance of game theory, kin altruism would have become an *evolutionarily stable strategy*). This has some counterintuitive implications that contribute to the misunderstandings. Dawkins (1979) wrote,

The logical outcome of the statement that, say, sibling altruism is favored by natural selection, is that the relevant genes will spread to fixation. Virtually all individuals in the population will be sibling altruists. Therefore, if they did but know it, they would benefit the gene for sibling altruism just as much by caring for a random member of the species as by caring for a sibling! . . . To put it this way is to expect animals, even genes, to play God. Natural selection is more mechanical than that. The kin altruism gene does not program individuals to take intelligent action on its behalf; it specifies a simple behavioral rule of thumb such as “feed squawking gapes in the nest in which you live.” It is this unconscious rule that will become universal when the gene becomes universal. (p. 192)

The fact that kin altruism—and the genes that give rise to it—is universal doesn’t imply that it would no longer be adaptive to selectively allocate resources to kin; it continues to be an evolutionarily stable strategy that would out compete indiscriminate altruism (see Dawkins, 1979).

In short, when we observe present-day animals behaving altruistically toward kin, we are not observing an inherent tendency to respond altruistically to absolute degrees of “shared genes” detected online; we are observing animals that are executing—mechanically—evolved programs for kin altruism (or, more accurately, programs for altruism toward animals who frequently enough happen to be kin). These evolved programs are not omniscient; most of the available research indicates that they are gene-blind algorithms, operating according to heuristics such as “be altruistic toward those who are familiar or those who look and smell like you” (Hauber and Sherman, 2001; Rendall, 2004).

#### *Persistent Misunderstandings and Their Appearance in Social Psychology Textbooks*

In identifying misunderstandings in textbooks, it’s useful to specify exactly what they are. Described below are three of the most commonly recurring misunderstandings.

**Misunderstanding 1:** “The *coefficient of relatedness* (the probability of sharing a gene by common descent) is equal to the *proportion of shared genes* (or *genetic similarity*)—for example, people share 50% of their genes with their siblings.”

**Misunderstanding 2:** “Inclusive fitness / kin selection implies that animals have a tendency to be altruistic toward individuals with whom they share a lot of genes—be they close relatives or simply *genetically similar* individuals—in order to increase the odds of passing on their (unspecified) genes.” This misunderstanding appears especially frequently in text, and it goes hand-in-hand with the failure to specify that kin selection pertains only to genes underlying altruistic behavior toward kin. It also reveals a deeper erroneous assumption—that all genes inherently recognize copies of themselves and/or are inherently driven to proliferate those copies (a formal version of this idea, called the “green-beard effect,” is theoretically plausible, but has little empirical support; for an exception, see Keller and Ross, 1998).

**Misunderstanding 3:** “Hamilton’s rule and/or the notion of inclusive fitness describe the actual operation of altruistic behavior—for example, people will help a sibling in a given situation if the benefits to the sibling are more than twice the costs to self.” This misunderstanding is difficult to identify objectively, as many writers deliberately simplify the concept of inclusive fitness by depicting organisms as though they behave in ways that maximize their inclusive fitness. Thus, perhaps misunderstanding 3 can truly be said to exist when Hamilton’s rule is described as directly predicting altruistic behavior.

Presented below are passages from ten recent undergraduate social psychology textbooks describing the role of kinship (and evolution) in human altruism. *Social psychology* textbooks were reviewed in particular, because nearly all of them mention inclusive fitness and/or kin selection within chapters on altruism (or “prosocial behavior”). Of the 10 books reviewed here, the majority of them (or their alternate edition) were listed on the Web site of the Social Psychology Network ([www.socialpsychology.org/texts.htm](http://www.socialpsychology.org/texts.htm)). Thus, at the time of this writing, these books likely represented the most commonly used social psychology textbooks. Following each passage, the specific misunderstanding(s) conveyed by the passage are identified.

(1) Aronson, Wilson, Akert, and Fehr (2004):

One way that evolutionary psychologists attempt to resolve this dilemma [of altruism] is with the notion of **kin selection**, the idea that behaviors that help a genetic relative are favored by natural selection (Hamilton, 1964; Meyer, 1999). People can increase the chances that their genes will be passed along not only by having their own children, but also by ensuring that their genetic relatives have children. Because a person’s blood relatives share some of his or her genes, the more that person ensures his or her survival, the greater the chance that his or her genes will flourish in future generations. Thus, natural selection should favor altruistic acts directed toward genetic relatives. There is support for this notion in the animal kingdom, particularly among social insects. Les Greenberg (1979), for example, released bees near a nest protected by guard bees, and observed which ones the guards admitted to the nest and which ones they rebuffed. He had bred the intruders to be of varying genetic similarity to the guards. Some were siblings, some were cousins, and some were more distant relatives. (The guards could tell how related they were to the bees by their odors.) Consistent with the idea of kin selection, the guard bees were much more likely to admit bees that were close relatives. (p. 390)

This passage contains misunderstanding 2.

(2) Baron, Byrne, and Branscombe (2006):

Studies of various species indicate that the greater the genetic similarity between two individual organisms, the more likely it is that one will help the other when help is needed (Ridley and Dawkins, 1981). Evolutionary theorists have coined the term *selfish gene* to describe this phenomenon. That is, the more similar individual A is to individual B, the more genes they probably have in common. If so, when A helps B, some portion of A’s genes will be more likely to be represented in future generations because of the genetic overlap of the two individuals (Rushton, Russell, and Wells, 1984). From this perspective, altruism doesn’t necessarily benefit the individual who helps, but it is adaptive because adaptation is not limited to the individual and his or her reproductive fitness, but also to inclusive fitness—natural

selection that favors behaviors that benefit whoever shares our genes (Hamilton, 1964; McAndrew, 2002). . . . Even though risking one's life to save the life of another person doesn't seem adaptive, it is adaptive *if* the person being saved is genetically similar to the rescuer (Burnstein, Crandall, and Kitayama, 1994). (p. 409)

This passage contains misunderstanding 2. (As an aside, these authors refer to the evolutionary approach to altruism as the “genetic determinism model,” which is unfortunate.)

(3) Brehm, Kassin, and Fein (2005):

Shouldn't any genetically based propensities for helping have dropped out of the gene pool long ago? No. There is an alternative to individual survival. You can also preserve your genes by promoting the survival of those who share your genetic make-up, even if you perish in the effort to help them. By means of this indirect route to genetic survival, the tendency to help genetic relatives, called **kinship selection**, could become an innate characteristic—that is, a characteristic that is not contingent on learning for its development, although it can be influenced by learning, culture, and other factors. (p. 353)

This passage contains misunderstanding 2, and it introduces a new term—“kinship” selection.

(4) Brown (2006):

In the 1960s, several scientists offered resolutions to the apparent contradiction between survival and self-sacrificing behavior (for reviews, see Hoffman, 1981; Wilson, 1975). Three mechanisms were identified. The first, known as **kin selection**, builds on Darwin's original theory by maintaining that natural selection operates at the level of the gene, not the individual (Dawkins, 1976). From this perspective, anything that enhances the reproductive success of one's genes is selected for. Because we share our genes with relatives, we can increase our “inclusive fitness” by helping our kin survive (Hamilton, 1964). Consider a father with three children. Since he shares one-half of his genes with each child, he can maximize his genetic fitness by sacrificing his own life for theirs. More formally, Hamilton's rule maintains that helping will occur when  $rb - c > 0$ , where  $r$  = Relatedness of two individuals,  $b$  = Benefits to the recipient, and  $c$  = Costs to the benefactor. To demonstrate this formula's application, if the recipient of helping is a sibling ( $r = 0.5$ ), the benefit to the sibling must be more than twice the cost of helping. If the recipient is an aunt, uncle, grandparent, nephew or niece ( $r = 0.25$ ), the benefit must be more than four times the cost of helping (and so on). (p. 448)

This passage contains misunderstandings 1 and 3. Immediately following this passage, Brown (2006) goes on to describe reciprocal altruism and group selection, and then describes how researchers test “the evolutionary model” of helping:

Evolutionary models of helping hinge on two testable propositions: (1) People can identify those who are genetically similar to them, and (2) people are more willing to help those who are genetically similar to them than those who are genetically dissimilar. . . . The evidence that humans can also detect genetic similarity is less direct, but there is reason to believe they can (for reviews, see Porter, 1987; Rushton, 1989). . . . Later in life, people tend to form closer bonds with those who are genetically similar to them. For example, friends are more genetically similar to

one another than are acquaintances or nonfriends, and married couples are more genetically similar to one another than are romantically involved but unmarried couples. . . . The evidence supporting the proposition that people help those who are genetically similar to them is fairly plentiful. Anthropological studies show that in countries around the world, people are more apt to help close family members and kin than those who are less genetically similar to them (Essock-Vatale [*sic*] and McGuire, 1985). Moreover, identical twins (who share 100 percent of their genes) are more apt to help each other than fraternal twins (who share 50 percent of their genes) are (Segal, 1984). These findings lend credence to the maxim “Blood is thicker than water” (Neyer and Lang, 2003; Webster, 2003). (pp. 448–449)

This second passage contains misunderstandings 1 and 2, and conflates kinship with genetic similarity more than once.

(5) Franzoi (2006):

Evolutionary theorists contend that it is not individual survival that is important, but rather, it is *gene* survival that promotes reproductive fitness (Archer, 1991). Because your blood relatives share many of your same genes, by promoting their survival you can also preserve your genes even if you don’t survive the helpful act. This principle of **kin selection** states that you will exhibit preferences for helping blood relatives because this will increase the odds that your genes will be transmitted to subsequent generations (Zahavi, 2003). (p. 536)

This passage contains misunderstanding 2.

(6) Gilovich, Keltner, and Nisbett (2006):

One evolutionary explanation for altruism is based on the concept of **kin selection**, which refers to the tendency for natural selection to favor behaviors that increase the chances of survival of genetic relatives (Hamilton, 1964). This derives from an individual’s inclusive fitness, which as we have noted is an evolutionary tendency to look out for oneself, one’s offspring, and one’s close relatives together with their offspring, so that one’s genes will survive. Thus, from the perspective of kin selection, people should be more likely to help those who share more of their genes, helping siblings more than first cousins, first cousins more than second cousins, and so on. Much altruism, therefore, is not really selfless, for it is designed to help individuals who share their own genes. By helping relatives survive, people help their own genes survive so that they can be passed on to future generations. A first prediction guided by the kin selection thesis is that we should have a highly developed capacity to recognize kin. This would help us with the important task of determining whom to help and whom to ignore. Indeed there is evidence that at least some nonhuman animals reared apart can recognize their kin through specific visual cues and smells (Rushton, Russell, and Wells, 1984). Human mothers can recognize their new babies from photographs, even when they have had very little contact with the baby (Porter, Cernoch, and Balogh, 1984), and from smells left by the baby on T-shirts (Porter, Cernoch, and McLaughlin, 1983). . . . In a puzzle task that required cooperation, identical twins, who share all their genes, were found to cooperate about twice as often (94 percent) than fraternal twins (46 percent) who share only half of their genes (Segal, 1984; see also Burnstein, 2005). (pp. 541–542)

This passage contains misunderstanding 1 and 2.

(7) Kenrick, Cialdini, and Neuberg (2005):

This distinction between personal survival and genetic survival is incorporated in Hamilton's concept of **inclusive fitness**, the likelihood that one's genetic makeup will be preserved not just in one's own offspring but also in the offspring of any relatives. The distinction is a profound one for understanding and predicting when helping will occur because it implies that people may well accept personal risks and losses if, in the process, they increase their inclusive fitness—the chance their genes will survive. Consequently, we should be willing to risk even our own survival, if it increases the chance that more copies of our genes will survive in any relatives we help. The evidence is overwhelming that individuals prefer to help those to whom they are genetically related. Many animal species aid their relatives—feeding, defending, and sheltering them—in direct relation to their degree of relatedness: An animal tends to help most those with which it is more likely to share genes through ancestry (Greenberg, 1979; Sherman, 1981). In large measure and in a large number of cultures, we humans show the same pattern (Burnstein, Crandall, and Kitayama, 1994; Cunningham, Jegerski, Gruder, and Barbee, 1995; Neyer and Lang, 2003). (pp. 282–283)

This passage contains misunderstanding 2.

(8) Michener, DeLamater, and Myers (2004):

Evolutionary psychology and a related theoretical perspective called **sociobiology** (Archer, 1991; Buss, 1999; Ketelaar and Ellis, 2000; Wilson, 1975, 1978) have constructed a response to the problem of altruism and have assembled evidence that supports their view (Buss and Kenrick, 1998; Krebs and Miller, 1985). To understand how helping can make sense in an evolutionary context, it is important to appreciate that the perpetuation of genes is important, rather than the perpetuation of physical attributes (Dawkins, 1976). In this view, the “fittest” animal is the one that passes on its genes to subsequent generations. This can happen either by the animal itself producing offspring or by the animal's close relatives, such as brothers, sisters, and cousins (who share many of its genes) producing offspring. It is true that altruistic behavior will not have survival value for an individual. But altruistic acts can increase the survival of one's genes if those altruistic acts are directed toward others who share the same genes—a phenomenon called **kin selection** (Hamilton, 1964; Meyer, 1999). If an individual helps his or her close relatives, that act increases the chances that those relatives will survive and eventually have offspring. As the relatives share many genes with the altruistic individual, the reproduction of these relatives passes many of the altruist's own genes to the next generation (Krebs and Miller, 1985; Ridley and Dawkins, 1981). Consider a mother bird that sacrifices herself to save the lives of her eight babies. Each of the babies carries half of the genes of the mother; thus, between them, they have four times as many of the mother's genes as she does herself. (pp. 250–251)

This passage contains misunderstandings 1 and 2.

(9) Myers and Spencer (2004):

You share one-half of your genes with your brothers and sisters, one-eighth with your cousins. **Kin selection**—favoritism toward those who share our genes—led the evolutionary biologist J. B. S. Haldane to jest that while he would not give up his life for his brother, he would sacrifice himself for *three* brothers—or for nine cousins. Haldane would not have been surprised that, compared to fraternal twins,



genetically identical twins are noticeably more mutually supportive (Segal, 1984). . . . We share common genes with many besides our relatives. Blue-eyed people share particular genes with other blue-eyed people, for example. How do we detect the people in which copies of our genes occur most abundantly? As the blue-eyes example suggests, one clue lies in physical similarities (Rushton et al., 1984). Also, in evolutionary history genes were shared more with neighbors than with foreigners. Are we therefore biologically biased to act more altruistically toward those similar to us and those who live near us? In the aftermath of natural disasters and other life-and-death situations, the order of who gets helped would not surprise an evolutionary psychologist: the young before the old, family members before friends, neighbors before strangers (Burnstein, et al., 1994; Form and Nosow, 1958). (pp. 300–301)

This passage contains misunderstandings 1 and 2.

(10) Olson, Breckler, and Wiggins (2008):

One explanation [for altruism] is an evolutionary one, based on the principle of **inclusive fitness** (Hamilton, 1964). This principle refers to the idea that some social behaviors have been selected during the course of evolution because they increase the survival of our *genes*—not necessarily within us, but within other relatives (Kenrick, Li, and Butner, 2003). For example, a father who rescues his daughter is improving the odds that some of his own genes will survive—whether or not he survives. In early human history, people lived in small hunter–gatherer bands, in which members were highly interdependent and often related. Therefore, altruism toward any member of the band could potentially benefit one’s own genes as well. (pp. 464–465)

This passage contains misunderstanding 2, and it presents the unexamined—and implausible—idea that altruism toward “any member of the band” would be sufficient to drive kin selection.

In sum, every textbook reviewed above contained at least one misunderstanding. A recurring theme was that altruism toward kin or genetically similar others preserves one’s genes (not a single textbook passage specified that it is genes underlying altruism toward kin that matter for kin selection); another recurring theme was that natural selection favors altruism toward kin or genetically similar others. Of course, natural selection favors no such thing; only when genes *for* kin altruism emerge, they may—under specific circumstances—outcompete their alleles. Rather than presenting purely scientific theories of evolution and kin selection, many textbooks seemed to be presenting a mixture of theory and intuition (discussed further below). Perhaps not surprisingly, writers of evolutionary psychology textbooks have taken care not to repeat these misunderstandings—indeed, they explicitly caution readers against them. For instance, Barrett, Dunbar, and Lycett (2002) wrote,

Hamilton’s solution to the problem of altruism, therefore, was to argue that a gene for altruism could evolve under Darwinian selection if the altruist’s behavior allowed a genetic relative that shared the same gene to reproduce more than it would otherwise have done. . . . The degree of relatedness,  $r$ , measures the probability that any two individuals share the *same* gene because they inherited it from the same common ancestor. (Note that even in the best textbooks [for example, Wilson, 1975] it has sometimes been defined—incorrectly—as the

proportion of all genes held in common. Defining it this way can give rise to misleading results.). (pp. 26–27)

Likewise, Buss (2008) wrote,

The key point to remember is not that people's behavior will necessarily conform to the logic of inclusive fitness. Hamilton's rule is not a psychological theory. Instead, the key is that Hamilton's rule defines the conditions under which adaptations for aid to kin can evolve. It defines the selection pressure to which genes for altruism—indeed any genes—are subject. Any traits that happen to enter the population through mutation and violate Hamilton's rule will be ruthlessly selected against. Only those genes that code for traits that fulfill Hamilton's rule can spread throughout the population and hence evolve to become part of the species-typical repertoire. This is sometimes called an *evolvability constraint* because only genes that meet the conditions of Hamilton's rule can evolve. (p. 232)

Unfortunately, given the relative rarity of proper courses on evolutionary psychology, the students most likely to acquire the misunderstandings are probably also the least likely to have them corrected.

#### *Why the Misunderstandings Persist*

The pesky persistence of these misunderstandings suggests that they might not be due simply to writers' carelessness—there may be psychological biases that inflict lay people and textbook writers alike. One possibility is that the misunderstandings are intuitively appealing to our essentialist minds: People believe that biologically related organisms share some underlying essence—blood, for example (e.g., Waxman, Medin, and Ross, 2007)—and genes are an appealing substitute for that essence. Another possibility is that they are intuitively appealing to our teleological minds: People tend to perceive purpose and goal-directedness everywhere (e.g., Keleman, 2004), and the idea that biological organisms have been “designed to serve the goal” of increasing inclusive fitness may all too easily be interpreted literally (see also Shtulman, 2006, for broader differences between naïve and scientific theories of evolution).

Along these lines, it's particularly illuminating that when the textbooks mentioned kin-recognition mechanisms at all, they emphasized phenotype-matching mechanisms (e.g., identifying kin by smell) and ignored association-based mechanisms (e.g., using proximity as a kinship cue), despite the fact that association-based mechanisms lie at the heart of kin recognition (Lieberman, Tooby, and Cosmides, 2007; Rendall, 2004). This probably isn't coincidental: Kin-detection-at-first-sight flows from our intuition that kin share some underlying essence to be detected. Association-based mechanisms, strictly speaking, have nothing to do with true “recognition” of kin, and they are more famous for misfiring (e.g., warblers feeding cuckoo chicks), which doesn't click with our intuition that kin share essence.

Natural biases aside, sometimes the misunderstandings may simply reflect carelessness: Heuristics such as “organisms should behave in ways that maximize their inclusive fitness” or “siblings share 50% of their genes” might serve the purpose for psychology textbook writers, who invoke inclusive fitness and kin selection mostly as a rhetorical device when describing evolutionary approaches to human altruism (particularly as an alternative to social and cultural approaches). In at least one instance, these misunderstandings were a part of explicit theorizing (genetic similarity theory; Rushton et

al., 1984), which was widely discredited precisely for propounding these misunderstandings (e.g., Daly et al., 1997; Mealey, 1985; Tooby and Cosmides, 1989). Apparently, many textbook writers missed this discussion, as they allude to genetic similarity theory in describing kin selection theory. (Perhaps some textbook writers place all “evolutionary” explanations in the same corner to ease comparisons with “non-evolutionary” explanations; but one can only speculate—the psychology of textbook writing is beyond the scope of this article.)

## **Conclusions**

As shown above, it’s easy to slip into an intuitively appealing but incorrect way of conceptualizing inclusive fitness and kin selection—thinking of organisms as bundles of self-replicating essence inherently driven to boost its concentration in the world. To properly educate our students, we need to more rigorously explain and distinguish the concepts of inclusive fitness (the cumulative effects of a gene on its possessor, as well as kin who have inherited the same gene), kin selection (the natural selection of genes underlying kin-helping tendencies), kin altruism (the kin-helping tendencies, comprising the proximate psychological motives), and kin recognition (the mechanical process that mediates the kin-helping tendencies).

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