

a0005 **Evolution of Altruism**

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**Glossary**

d0005 **Altruist** An individual performing a behavior that confers a fitness cost to itself but provides a fitness benefit to others.

d0010 **Defector** An individual that gains benefits from the altruistic behavior of others but does not behave altruistically itself.

d0015 **Fitness** A measurement of an organism's ability to survive and reproduce.

d0020 **Greenbeard gene** A gene that encodes (1) a distinct phenotype, (2) the ability for the bearer to recognize

this phenotype in others, and (3) an alteration of behavior toward others based on detection of this phenotype (where those with the phenotype are helped or those lacking the phenotype are harmed).

**Positive assortment** A situation in which individuals within a population preferentially interact with similar types (e.g., A's interact preferentially with other A's and B's interact preferentially with other B's).

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s0005 **The Paradox of Altruism**

p0005 In *The Origin of Species*, Charles Darwin describes the inevitable 'struggle for existence' that organisms experience in competing for limited resources. Such fierce competition places a premium on maximization of personal fitness. Under such a view, the evolution of behavior in which an individual sacrifices its own well-being to help others appears plainly untenable. Yet our observations of the natural world reveal that altruistic behavior is commonplace, from unicellular prokaryotes to mammals. Amoebae sacrifice their lives to aid starving relatives in migration, vampire bats share food with hungry neighbors, and male wild turkeys will sacrifice their own mating success to help secure females for their brother, just to name a few examples.

p0010 When used in everyday language, altruism refers to the 'selfless' motives or intentions that direct the behavior of one individual toward another. However, in evolutionary biology, altruism refers to the *effects* of a behavior without regard to intention or motivation. The effects of an organism's behavior can be quantitatively measured in terms of the costs and benefits to an individual's reproductive fitness or the number of offspring. A behavior is said to be biologically altruistic when it results in a reproductive fitness cost to the actor while conferring a fitness benefit to a recipient, regardless of the conscious intention of the actor. The challenge is how such a behavior, which is seemingly antithetical to natural selection, can evolve.

p0015 Darwin himself clearly appreciated this challenge. By way of a solution, he proposed that altruistic behavior of individuals produced better social *groups*, which could supplant groups composed of more selfish members. Thus, he shifted the level of selection from individuals to groups to deal with the paradox of altruism. While group-level selection has been a contentious topic, Darwin's original proposition does offer an alternative way of viewing social interactions. For instance, social behavior in eusocial insects can be seen from the vantage of individual insects (an *individualist* perspective) or from the vantage of colonies (a *collective* perspective). In this article,

we will discuss how different representations of fitness, which focus alternatively on either the individual or the group, have led to subtly different definitions of altruism. Although there are general conditions that favor altruism in its different guises, the different definitions of altruism do require formally different resolutions to the paradox of altruism.

**Individualist versus Collective Representations of Altruism**

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In much of what follows, we will make use of a simple example. p0020 Imagine a large population of asexual organisms that come in two varieties: altruist and defector. Every generation, groups of size  $n$  form, in which fitness-affecting interactions occur (see **Table 1** for descriptions of all parameters used in this chapter). Let  $\alpha_x$  and  $\delta_x$  be the fitness of an altruist and a defector, respectively, in a group with  $x$  altruistic group mates. These parameters measure the fitness of *individuals*, and thus we refer to this representation as an *individualist* perspective (see **Figure 1** for an example with a single group). The subscript  $x$  (where  $0 \leq x \leq n-1$ ) refers to the social context (or neighborhood) of the target individual.

However, one can also shift focus to the *groups*. Let  $\pi_i$  be the p0025 productivity of a group with  $i$  altruists. This can be obtained by summing the fitnesses of every group member. We must also describe how much of this total productivity is claimed by each type of individual (altruist or defector). Let  $\phi_i$  be the fraction of the group productivity that is altruistic in a group starting with  $i$  altruists. These parameters define a *collective* perspective, where groups of organisms are assigned productivities ( $\pi_i$ ) that are split between defectors and altruists ( $\phi_i$ ) (see **Figure 1**). Here, the subscript  $i$  (where  $0 \leq i \leq n$ ) refers to a property of the higher level entity (i.e., group composition).

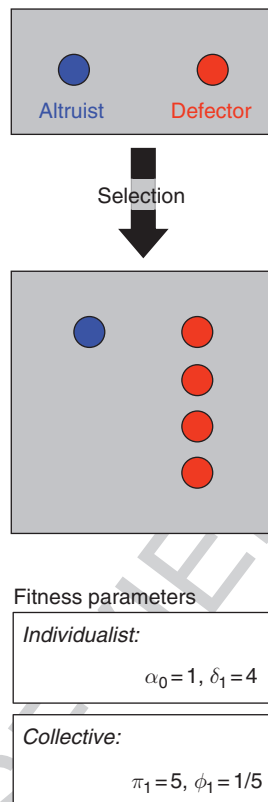
One can translate from the individualist perspective to the p0030 collective perspective and vice versa. Nonetheless, these different perspectives emphasize different aspects of selection in group-structured populations. Indeed, as we outline below, different definitions of altruism find natural homes in these different perspectives.

2 Evolution of Altruism

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**Table 1** Model parameters and descriptions

Parameter	Description
$\alpha_x$	The fitness of an altruist with $x$ altruistic group mates
$\delta_x$	The fitness of a defector with $x$ altruistic group mates
$\pi_i$	The productivity of a group with $i$ altruists
$\phi_i$	The altruistic fraction of group productivity in a group with $i$ altruists
$n$	Group size
$z$	Baseline fitness for an individual (given a linear fitness structure)
$b$	Benefit an altruist provides to each group mate (given a linear fitness structure)
$B$	Benefit an altruist provides to all group mates ( $B = b(n-1)$ ) (given a linear fitness structure)
$c$	Personal cost an altruist incurs (given a linear fitness structure)
$n^*$	Group size before in-group reproduction (for the model illustrated in <a href="#">Figure 5</a> )
$p_i$	Frequency of altruists in a group with $i$ altruists ( $p_i = i/n$ )
$\bar{p}$	Frequency of altruists in the population
$\sigma_p^2$	Variance of in-group altruist frequency



**Figure 1** Different representations of fitness. An altruist (blue circle) and a defector (red circle) comprise a group. Offspring (after selection) are shown below their parents. Fitnesses can be defined from an individualist perspective ( $\alpha/\delta$ ) or a collective perspective ( $\pi/\phi$ ).

**The Definitions of Altruism**

The following *individual-based* definition of altruism is most easily expressed using an individualist perspective:

$$\alpha_x < \delta_x \quad [1]$$

for all  $x$ , where  $0 \leq x \leq n-1$ , and

$$\alpha_{x-1} < \alpha_x \quad [2]$$

$$\delta_{x-1} < \delta_x \quad [3]$$

for all  $x$ , where  $1 \leq x \leq n-1$ . As outlined by condition [1], this individual-based definition requires that a switch from a defector to an altruist (keeping neighborhood composition constant) is always costly for a focal individual. The benefit of altruism is gauged by conditions [2] and [3], which state that the fitness of either an altruist or a defector always increases with the number of altruists in its neighborhood ( $x$ ).

A second definition of altruism shifts focus to collectives by considering the effects of altruists on group productivity as well as their fate within groups:

$$\phi_i < \frac{i}{n} \quad [4]$$

for all  $i$ , where  $1 \leq i \leq n-1$ , and

$$\pi_i < \pi_{i+1} \quad [5]$$

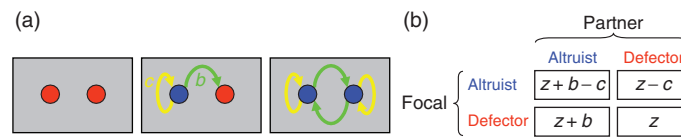
for all  $i$ , where  $0 \leq i \leq n-1$ . Condition [4] states that the frequency of altruists within a group after selection ( $\phi_i$ ) must be lower than the frequency before selection ( $i/n$ ). Thus, the cost of altruism is defined by a drop in altruist frequency within mixed groups (i.e., groups with both altruists and defectors). The benefit of altruism is given by condition [5], which states that group productivity increases with the frequency of altruists in the group. Conditions [4] and [5] can be thought of as a *multilevel* definition of altruism where altruists are selected against within groups, but groups with more altruists have higher productivity.

To illustrate the difference between these two definitions of altruism, we make use of a *linear* fitness structure. Specifically, the altruist helps each group mate have an extra  $b$  offspring at a cost of  $c$  offspring to itself, while the defector does nothing to benefit its group mates. For  $n=2$ , [Figure 2\(a\)](#) illustrates the interactions and [Figure 2\(b\)](#) gives the fitnesses.

From the individualist perspective, the linear fitness structure is

$$\alpha_x = z - c + bx \quad [6]$$

$$\delta_x = z + bx \quad [7]$$



**Figure 2** The linear fitness structure. (a) Altruists and defectors are shown as blue and red circles, respectively. Groups of size 2 are shown. The altruist increases the fitness of its partner by  $b$  (green arrow) at a cost of  $c$  (yellow arrow) to its own fitness. (b) The fitness matrix for (a) is given. The entries in the table refer to the fitness of the row (focal) player when paired with the column (partner) player. The parameter  $z$  is the baseline fitness.

for all defined  $x$ . The parameter  $z$  is the baseline fitness (i.e., fitness in the absence of social interaction). From the collective perspective, the fitness structure is

$$\pi_i = nz + (B - c)i \quad [8]$$

$$\phi_i = \frac{[z - c + b(i - 1)]i}{nz + (B - c)i} \quad [9]$$

for all defined  $i$ . The parameter  $B$  is the cumulative benefit a single altruist provides to all of its group mates ( $B = b(n - 1)$ ).

By plugging eqns [6] and [7] into eqns [1]–[3], we see that the linear fitness structure satisfies the definition of individual-based altruism if  $c > 0$  (the altruist incurs a personal cost) and  $b > 0$  (the group mate of the altruist enjoys a benefit). As Figures 3(a) and 3(b) show, costs and benefits of individual-based altruism are measured by how altruistic behavior alters the fitness of *individuals*.

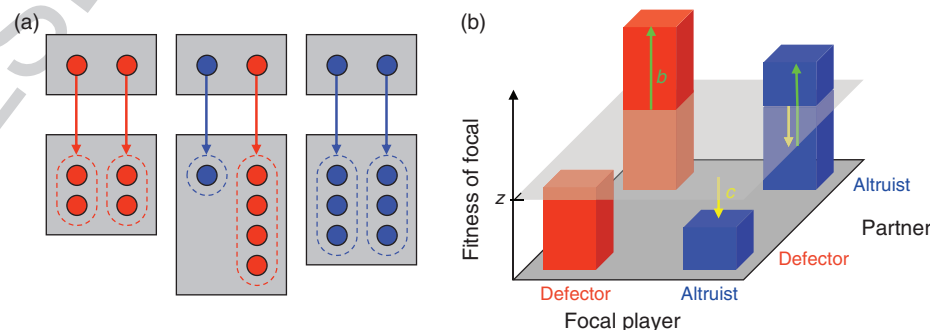
By plugging eqn [9] into eqn [4], we see that  $b + c > 0$  guarantees that the frequency of altruists within a group always decreases over a selective episode under a linear fitness structure. Note that  $b + c$  is the difference in fitness between a defector and an altruist in the same group; a positive difference means that an altruist suffers a fitness cost relative to a defector in its group. The benefit of multilevel altruism derives from the increase in group productivity as more altruists populate a group. By plugging eqn [8] into eqn [5], we see that if the benefits to the group mates of an altruist outweigh its personal cost (i.e.,  $B > c$ ), then groups benefit from altruism under a linear fitness structure. The same example illustrating the individual-based perspective is redrawn in Figures 4(a) and 4(b) to illustrate this multilevel view. For multilevel altruism, the fitness cost incurred by an altruist relative to a defector in its group forces down the in-group frequency of altruists. Benefits are measured by how *group* productivity swells as a function of this altruistic group character.

If  $B > c > 0$ , the linear fitness structure (eqns [6] and [7] or [8] and [9]) satisfies both the individual-based and multilevel definitions of altruism. However, these definitions are not equivalent. As an example, consider a linear fitness structure in which  $c < 0$  and  $|b| > |c|$ . Here, the altruist helps itself, but helps each group mate more. This fitness structure would qualify as multilevel altruism, but not as individual-based altruism (it has also been called ‘weak altruism’). Furthermore, there are other definitions of altruism that are also distinct (e.g., defining benefit as the lift in fitness to the complement of a focal individual changing from a defector to an altruist). These different definitions will directly impact the evolutionary hurdles that an ‘altruist’ faces; thus, it is important to clearly define the type of ‘altruism’ under focus before considering its evolution.

### The Conditions for the Evolution of Altruism

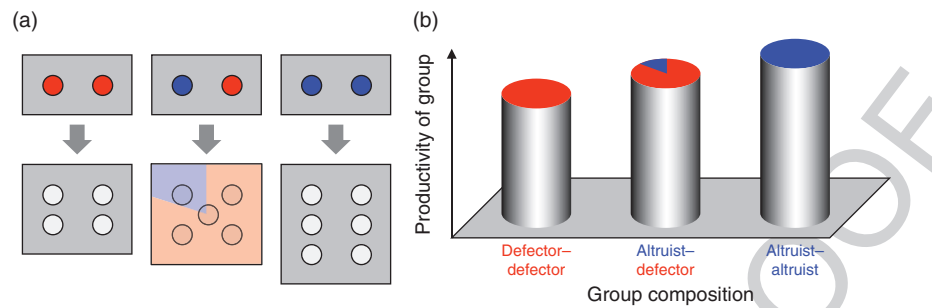
Let us return to our original example of a population of asexual organisms comprised of both altruists and defectors. Imagine that groups of size  $n$  form anew every generation and then dissolve after selection, which is the classic ‘trait group’ model. If group formation occurs at random, then altruism by the individual-based definition cannot evolve. We note that altruism by other definitions (e.g., weak multilevel altruism) can evolve under random group formation. However, the evolution of individual-based altruism requires *nonrandom* group formation. One salient form of nonrandom grouping involves relatives finding themselves in the same group.

To illustrate this, imagine a population of altruists and defectors, where groups of size  $n^*$  form. Within each group, there is an episode of random reproduction whereby  $n$  offspring are produced and the parents die. That is, there is no fecundity selection at this stage. Within the groups

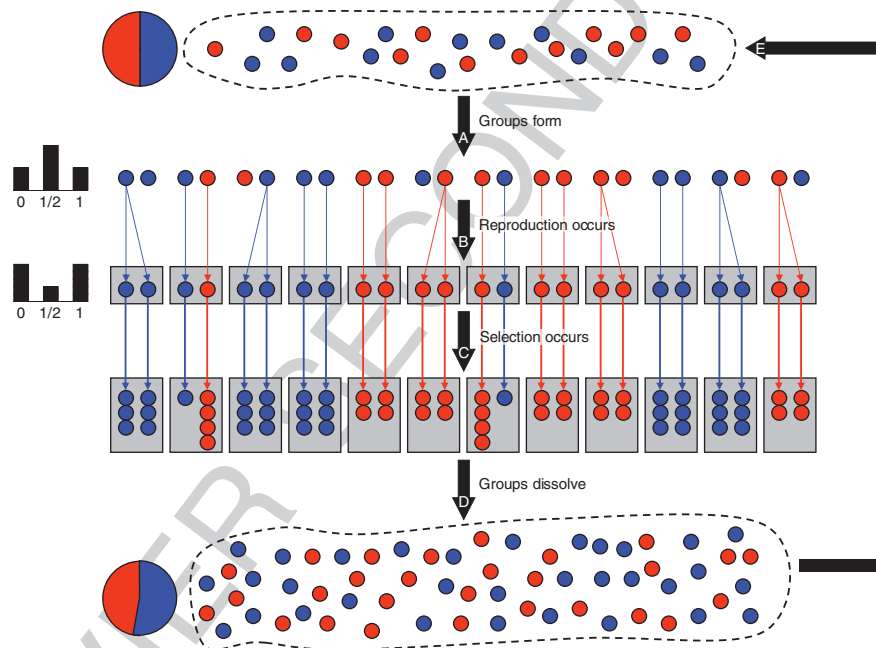


**Figure 3** Individualist representation of the linear fitness structure (where  $n = 2$ ,  $z = 2$ ,  $b = 2$ ,  $c = 1$ ). (a) The offspring of each individual is placed directly below it. This schematic emphasizes the productivity of each individual (the dashed enclosure at the end of the arrow emanating from the individual). (b) The graphical representation of linear fitness structure for pairs. The translucent plane gives the baseline fitness (at a value of  $z$ ). Switching from a defector to an altruist (compare neighboring red and blue bars) always involves a cost of  $c$  (yellow arrows). Switching the partner from a defector to an altruist (compare bars of the same color) always involves a benefit  $b$  (green arrows). Thus, costs and benefits are measured in terms of changes to the fitnesses of individuals.

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**Figure 4** Collective representation of the linear fitness structure (where  $n = 2, z = 2, b = 2, c = 1$ ). (a) The focus is on the productivity of groups (measured by the number of offspring after selection). For mixed groups (the mixed pair in this case), we must also specify what fraction of that productivity is claimed by the altruist (here  $1/5$ ). (b) The graphical representation of linear fitness structure of pairs. Here, the cost of altruism involves a drop in altruistic frequency within the mixed pair (from  $1/2$  before selection to  $1/5$  – given by the pie chart – after selection). The benefit of altruism is that the productivity (height of the cylinders) increases with the number of altruists in the group.



**Figure 5** A life cycle involving interactions between relatives. (A) From a pool of altruists (blue circles) and defectors (red circles), groups of size  $n^*$  form (here  $n^* = 2$ ) at random. The group frequency distribution is shown to the left of the groups, where each bar measures the frequency of groups with a fraction  $p$  of altruists (here  $p = 0, 1/2, \text{ or } 1$ ). (B) Reproduction occurs without fecundity selection (i.e., the average number of offspring is the same for the altruist and the defector). However, in some groups, multiple offspring come from the same parents. Parents die leaving offspring groups of size  $n$  (here  $n = 2$ ). The new group frequency distribution is shown to the left of the groups. (C) Selection occurs where a second set of offspring are produced (i.e., altruists and defectors have fitnesses dependent on their social context). (D) The groups dissolve and (E) the next generation begins. Altruist and defector frequencies at the level of the entire population are given by the pie charts (altruists increase in frequency across the generation shown here).

of  $n$  individuals, selection occurs. Here, we will assume a standard linear fitness structure. This life cycle is illustrated in **Figure 5** with  $n^* = n = 2$ . Altruists increase in frequency if

$$B\left(\frac{1}{n^*}\right) > c \quad [10]$$

The probability that two individuals in a group of size  $n$  are identical by descent is  $1/n^*$ . In this asexual system, if we are in the same group, the probability that your parent was also mine is 1 over the number of potential parents. For example, if  $n^* = 1$ , then we are guaranteed to be clones. The quantity  $1/n^*$  is the coefficient of relatedness ( $r$ ) for

this simple example, and we see that eqn [10] is an instance of Hamilton's rule:

$$Br > c \quad [11]$$

As Hamilton pointed out, the critical ingredient for the evolution of altruism is positive assortment of types. This need not occur through direct common descent (although it often may). For instance, assume that both altruists and defectors form homogeneous groups with probability  $F$  and form groups at random with probability  $(1 - F)$ . In this case, altruism with a linear fitness structure can evolve if

$$BF > c \quad [12]$$



p0090 Thus, the degree of association with like types ( $F$ ) plays the role of relatedness here. Generally, to overcome the evolutionary obstacle inherent in individual-based altruism, altruists must disproportionately benefit from altruism. As genetic or ecological factors change to increase  $r$  (or  $F$ ), such disproportionate benefit occurs.

p0095 In order to derive conditions [10]–[12], one begins with the simple requirement that the average fitness of the altruist is greater than that of the defector:

$$\bar{a} > \bar{\delta} \quad [13]$$

p0100 Such a condition is natural within the individualist perspective, which focuses on individual fitness. However, we can also incorporate the properties of groups, leading to a different condition, which finds a home in the collective perspective. Specifically, altruists can evolve if

$$\text{cov}(\pi, p) + \text{ave}[\pi(\phi - p)] > 0 \quad [14]$$

where  $p$  is the frequency of altruists within a group (i.e., in a group of size  $n$  with  $i$  altruists,  $p_i = i/n$ ). Equation [14] is derived from the famous Price equation. The covariance (cov) measures how group productivity ( $\pi_i$ ) changes as in-group altruist frequency ( $p_i$ ) changes. Recall that, by the multilevel definition of altruism, this is guaranteed to be positive because productivity always rises with altruist frequency (see condition [5]). The average (ave) measures the change in altruist frequency within groups ( $\phi_i - p_i$ ) weighted by group productivity. By the multilevel definition of altruism, this is guaranteed to be negative because the frequency of altruists within mixed groups drops over a selective episode (condition [4] ensures  $\phi_i < i/n = p_i$ ). Altruism evolves when the magnitude of the covariance outweighs the magnitude of the average. Within multilevel selection theory, these two quantities represent opposing ‘forces’ of selection, where the covariance term measures between-group selection *for* altruism and the average term measures within-group selection *against* altruism. As **Figure 5** illustrates, the frequency of altruists within every mixed group can decrease over a selective episode (gray-filled groups in **Figure 5**), whereas the frequency of altruists at the level of the population can increase (pie charts in **Figure 5**). This occurs when there is a strong positive covariance between group productivity and in-group altruist frequency (as in **Figure 5**).

p0105 For the linear fitness structure, condition [14] reduces to

$$(B - c)\sigma_p^2 > (b + c)(\bar{p}(1 - \bar{p}) - \sigma_p^2) \quad [15]$$

where  $\bar{p}$  is the average altruist frequency within groups and  $\sigma_p^2$  is the variance in altruist frequency within groups. As this variance increases, we see that the between-group term (on the left of the inequality) increases and the within-group term (on the right of the inequality) decreases, such that altruism is more likely to evolve.

p0110 In the case illustrated in **Figure 5**, the variance increases as the size of the parental bottleneck ( $n^*$ ) shrinks. From the vantage of Hamilton’s rule, a small bottleneck increases the coefficient of relatedness ( $1/n^*$ ). From the vantage of Price’s decomposition, a small bottleneck increases the variance in altruist frequency within groups ( $\sigma_p^2$ ); in **Figure 5**, reproduction has the effect of shifting weight to the tails of the group frequency distribution, which leads to higher variance. Either way, small bottlenecks lead altruists to interact disproportionately

with other altruists. *Positive assortment* is at the core of the evolution of simple forms of altruism.

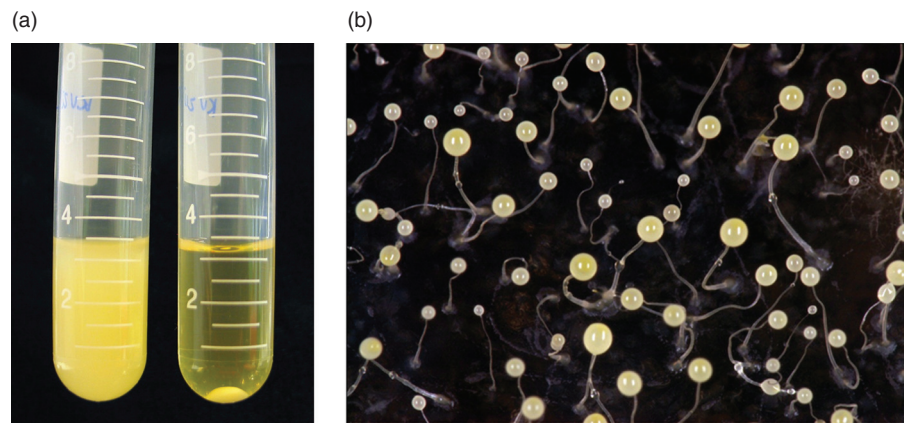
We see that, as altruists encounter disproportionately p0115 greater numbers of altruists in their groups, the evolution of altruism becomes more likely. From a genetic point of view, the genes underlying altruism are more likely to spread when their carriers disproportionately benefit from altruism, that is, when the genes positively assort. Positive assortment can result naturally from certain forms of dispersal. For instance, with limited dispersal in relatively sessile organisms, one’s neighbors are also more likely to be one’s relatives. Even with highly mobile organisms, positive assortment can be generated if altruistic behavior improves environmental quality, and organisms preferentially disperse from low- to high-quality environments. Positive assortment can also arise via active choice of social contacts. For instance, there is evidence that altruistic behavior is preferentially directed toward relatives in turkeys, mole rats, lions, hyenas, elephants, and baboons. In these species, altruism can evolve through kin selection. Although altruistic action often transpires between genetic relatives, it is possible for altruism to evolve under other scenarios. We end this article with a focus on cases of positive assortment that are ‘built into’ the genes for altruism; that is, the very gene(s) responsible for an altruistic action also ensures that organisms with copies disproportionately benefit from altruism, despite genealogical relatedness at the rest of the genome.

### The Self-Recognition of Altruism

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As Hamilton first proposed, organisms could make use of p0120 recognition systems that allow them to discern altruists from non-altruists and respond by either helping altruists or harming non-altruists. Such altruist recognition genes were later named ‘greenbeard genes’ by Dawkins in 1976. The idea was that a gene would encode some distinct phenotype – a green beard – but would also encode the ability to detect other greenbeards (or non-greenbeards) and preferentially help these other greenbeards (or harm the non-greenbeards). Thus, greenbeard genes have three major effects: (1) expression of a perceptible trait, (2) recognition of this trait, and (3) differential behavior based on whether or not this trait is perceived. While the existence of such genes may seem far-fetched, they have been discovered in a wide range of taxa.

One class of greenbeard genes involves preferential p0125 help directed between greenbeard carriers. In the yeast *Saccharomyces cerevisiae*, expression of the *FLO-1* gene produces specific cell-surface proteins that can bind one another to form a biofilm-like complex of linked cells. Although cells expressing *FLO-1* confer a fitness cost (slower growth), cells within the biofilm gain protection from biological and chemical antimicrobials. In addition, the preferential interaction between *FLO+* cells through reciprocal cell-to-cell adherence helps to exclude *FLO-defectors* (cells that do not produce biofilm proteins). Thus, such binding can be thought of as a form of ‘recognition’. The greenbeard *FLO-1* gene encodes both an altruistic behavior (biofilm formation) and a recognizable trait that brings together altruists. A similar example has been described in *Dictyostelium discoideum*, a single-celled amoeba that preferentially forms fruiting bodies with those altruistically expressing certain cell adhesion proteins (**Figure 6**).



**Figure 6** Systems in which greenbeard genes have been discovered. (a) Live culture of yeast (left) and subsequent biofilm formation (right). Photo courtesy of Kevin Verstrepen. (b) Fruiting bodies in *D. discoideum*. Photo courtesy of Owen Gilbert.

A second class of greenbeard genes involves spite, wherein greenbeards harm non-greenbeards. Some strains of *Escherichia coli* produce colicins, antimicrobial proteins that kill resource competitors. Colicin production is encoded on a plasmid with three tightly linked genes that encode the colicin, an immunity protein that binds and neutralizes the colicin, and a lysis protein that facilitates cell lysis and the subsequent release of the colicin into the environment. Thus, the release of the colicin is extremely costly (a lethal event) and occurs only in a small fraction of the producers. When there is colicin in the external milieu, latent producers (those with the plasmid, but not actively expressing the colicin or lysis protein) are protected by their immunity protein (which is constitutively expressed), while cells lacking the plasmid will die. Latent producers then benefit from the resources liberated by elimination of their colicin-sensitive competitors. Therefore, the colicin complex is a greenbeard: cells with the colicin plasmid incur a cost to harm cells without the plasmid, indirectly benefiting other cells with the plasmid. A spiteful greenbeard has also been discovered in the red fire ant, *Solenopsis invicta*. This ant maintains multiple queen colonies and all egg-laying queens from the wild are heterozygotes at the Gp-9 locus (*Bb*). Researchers artificially induced *BB* homozygotes to develop as reproductive queens and found that they were more likely to be attacked and killed by workers than *Bb* queens. In addition, workers with the *Bb* genotype were most likely to be the attackers. Workers appeared to distinguish *BB* from *Bb* queens by odor, suggesting that the Gp-9 locus is linked to a pheromone-expressing gene.

Thus, we see that the positive assortment favoring altruism can be built into (or closely linked to) the genetic basis for altruism. Greenbeards are taxonomically cosmopolitan (reported in bacteria, protists, fungi, and animals) and provide a connection between altruistic activity and the very conditions favoring its evolution.

### Conclusions

The existence of self-sacrificial prosocial behavior is paradoxical from a traditional evolutionary perspective. Thus, the ubiquity of altruism in natural systems demands an explanation. Here, we have focused on the evolution of altruism through natural selection. We have suggested that selection in social systems

can be represented in two different ways, either with a focus on individuals (individualist perspective) or with a focus on groups of individuals (collective perspective). The perspective taken can influence the way that altruism is defined and the precise conditions necessary for its evolution. However, both perspectives show that altruists tend to fare better when altruists can positively assort. While positive assortment can occur through a number of mechanisms, in some cases, it results from the very genetic basis of altruism.

**See also:** Group Selection (00663); Kin Selection: Hamilton's Theory (00677).

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### Relevant Websites

- <http://depts.washington.edu/kerrpost/Public/GlenneyKerr2012> – Provides derivations for several of the equations found in this article. [bib0185](#)

### Biographical Sketches



Carrie Glenney received her BS degree in biology from the University of Washington in 2009. She is currently working toward a PhD degree in biology at the University of Washington in the Kerr lab. She is interested in a range of topics in the field of evolutionary biology and is currently exploring the diversification of toxin and immunity proteins produced by *Escherichia coli*.



Ben Kerr received his PhD in biological sciences from Stanford University in 2002. While at Stanford, he worked with Marcus Feldman on modeling the evolution of flammability in resprouting plants, the evolution of animal learning, and the evolution of altruism. He also worked with Brendan Bohannon on experimental evolution within microbial systems and with Peter Godfrey-Smith on some philosophical issues arising in the levels of selection controversy. Kerr then spent 3 years as a postdoctoral research associate at the University of Minnesota, where he worked with David Stephens on modeling impulsive behavior in blue jays, with Tony Dean on the evolution of cooperation within a microbial host–pathogen system, and with Claudia Neuhauser on spatial dynamics within model population genetic systems. Kerr joined the faculty of the University of Washington in 2005. His lab currently uses a combination of mathematical analysis, computer simulation, and laboratory experiments with microbes to explore theoretical and empirical perspectives on topics in ecology, evolutionary biology, and the philosophy of biology.