

Review

Reproductive value and the evolution of altruism

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Altruism is favored by natural selection provided that it delivers sufficient benefits to relatives. An altruist's valuation of her relatives depends upon the extent to which they carry copies of her genes – relatedness – and also on the extent to which they are able to transmit their own genes to future generations – reproductive value. However, although relatedness has received a great deal of attention with regard to altruism, reproductive value has been surprisingly neglected. We review how reproductive value modulates patterns of altruism in relation to individual differences in age, sex, and general condition, and discuss how social partners may manipulate each other's reproductive value to incentivize altruism. This topic presents opportunities for tight interplay between theoretical and empirical research.

Reproductive value

Natural selection arises when individuals that differ genetically also differ in their reproductive success. However, individuals may vary systematically in reproductive success for reasons other than the genes they carry, and this variation can have important consequences for natural selection. For example, if males and females were always equal from the perspective of natural selection, parents would simply maximize their number of offspring, and the sex ratio of the brood would be an irrelevant detail. However, males and females are not necessarily equal: if, for any reason, there is a biased sex ratio, then newborns of the rarer sex will, on average, leave more descendants than newborns of the more common sex, under diploid inheritance [1]. In panmictic populations this leads natural selection to favor parents who invest more heavily in offspring of the rarer sex, which tends to neutralize any population bias in investment into one sex over the other [1–4]. The **rarer-sex effect** (see [Glossary](#)) highlights a more general principle of how natural selection acts in relation to class-structured populations.

To solve the problem of **class structure**, Fisher [1] developed the concept of **individual reproductive value**, which measures how well individuals of a particular age, sex, or any other type of class transmit copies of their genes to future generations. The reproductive value of an individual is given by the combined reproductive value of all her offspring, in which the contribution of each offspring is weighted by the genetic share of the individual in that offspring ([Box 1](#)) [1,5]. Put another way, reproductive value measures the relative probability that a gene picked at random from the distant future traces its origin to the focal individual in the present generation, and it is this quantity – rather than number of offspring or grandoffspring *per se* – that defines the proper measure of Darwinian fitness. Fisher [1,6] introduced the concept in relation to age-structured populations, and used data from the 1911 Australian census to show how female reproductive value increased during childhood as the individual approached reproductive maturity, peaked shortly thereafter, and then declined towards zero at older ages. From the standpoint of natural selection, the life of an individual is most valuable when her reproductive value peaks.

Reproductive value considerations are crucial when individuals must decide how to behave towards their relatives [13,16,17]. **Inclusive fitness** theory shows that an individual should

Highlights

Reproductive value describes the asymptotic genetic contribution made by an individual – or a particular segment of the population – to future generations.

Reproductive value is an important factor in social evolution that has been relatively neglected in the study of altruistic behavior.

We provide an overview of how reproductive value modulates the evolution of altruism in populations that are subdivided according to age, sex, and general condition.

We discuss how social partners may manipulate each other's reproductive value as a means to incentivize altruism.

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Box 1. Reproductive value and Hamilton's rule

The total reproductive value of a class of individuals is the probability that a gene picked at random from the distant future traces its ancestry back to this class in the present generation. Accordingly, **class reproductive value** (c) describes the relative importance of this segment of the population from the perspective of natural selection, and hence coincides with the concept of **force of selection** in relation to a particular class [1,7,8]. This can be calculated directly from the 'gene flow' between the different classes [9] using mathematics analogous to the way in which Google calculates the PageRank of webpages [10,11]. For example, in haplodiploid species with non-overlapping generations, daughters inherit half of their genes from their mothers (i.e., $1 - \phi = 1/2$), and half from their fathers (i.e., $\phi = 1/2$), whereas sons inherit all of their genes from their mothers (i.e., $\mu = 1$, $1 - \mu = 0$). This implies that the class reproductive value of females satisfies $c_f = (1 - \phi)c_f + \mu c_m = 1/2 c_f + c_m$, and the class reproductive value of males satisfies $c_m = \phi c_f + (1 - \mu)c_m = 1/2 c_f$ (Figure 1). Using matrix notation, we can rewrite these equations as:

$$\begin{pmatrix} c_f & c_m \end{pmatrix} = \begin{pmatrix} c_f & c_m \end{pmatrix} \begin{pmatrix} 1/2 & 1/2 \\ 1 & 0 \end{pmatrix} \quad [I]$$

or $\mathbf{c} = \mathbf{cP}$, where \mathbf{P} is the gene-flow matrix and $\mathbf{c} = (c_f \ c_m)$ is the dominant left-eigenvector of \mathbf{P} . Following the convention that class reproductive values sum to unity, this yields $c_f = 2/3$ and $c_m = 1/3$. Under neutrality, the reproductive value of a class is shared equally among all the individuals of that class, such that **individual reproductive value** (v) satisfies $c_f = v_f u_f$ for females and $c_m = v_m u_m$ for males, where u_f and u_m are the equilibrium frequencies of the two classes.

Reproductive value provides one of the three measures of value that feature in the general version of **Hamilton's rule** of inclusive-fitness theory, the other two being relatedness and fitness effect [12–15]. To illustrate, consider an altruistic behavior in which a daughter forgoes her own clutch of C offspring to help her mother raise B extra offspring. Hamilton's rule is given by:

$$-((1-z)v_f r_{F \rightarrow D} + z v_m r_{F \rightarrow S})C + ((1-z)v_f r_{F \rightarrow F} + z v_m r_{F \rightarrow M})B > 0 \quad [II]$$

where $r_{F \rightarrow D}$ is the relatedness between mother and daughter, $r_{F \rightarrow S}$ is the relatedness between mother and son, $r_{F \rightarrow F}$ is the relatedness between sisters, $r_{F \rightarrow M}$ is the relatedness between sister and brother, and z is the sex ratio. The selective advantage of altruism increases as the life-for-life relatedness valuation of the siblings of the focal female, namely $R_S = (1 - z)v_f r_{F \rightarrow F} + z v_m r_{F \rightarrow M}$ increases relative to that of her own offspring, in other words $R_O = (1 - z)v_f r_{F \rightarrow D} + z v_m r_{F \rightarrow S}$.

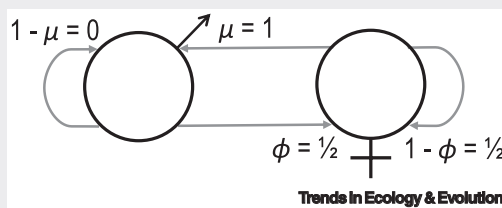


Figure 1. Gene-flow coefficients under haplodiploidy.

value each of her social partners according to how well they transmit copies of her genes. This is not only a matter of the extent to which they carry copies of her genes (**relatedness**) but also concerns the ability of each social partner to transmit copies of their own genes to future generations (reproductive value). Hamilton [17] was the first to integrate the concept of reproductive value into the theory of inclusive fitness by defining **life-for-life relatedness** as relatedness multiplied by the ratio of the recipient and actor reproductive values, in the context of understanding the evolution of social behavior in insects (Box 1). Despite these early insights, the crucial role of reproductive value in driving the evolution of **altruism** has been overshadowed by research on relatedness. To remedy this we provide an overview of ways in which reproductive value may modulate patterns of altruism – in relation to individual differences in age, sex and general condition – across the natural world (Figure 1 for illustrative examples).

Glossary

Altruism: one of four types of social behaviors (the others being cooperation, selfishness, and spite) in which the actor pays a fitness cost and the recipient enjoys a fitness benefit.

Class reproductive value: the probability that a gene picked at random from the distant future traces its ancestry back to an individual belonging to this class in the present generation.

Class structure: non-genetic differences between individuals that affect reproductive success.

Force of selection: the relative importance of selection in relation to a particular class, which is equal to the class reproductive value.

Hamilton's rule: the condition for natural selection to favor a trait of interest, emphasizing the distinction between direct versus indirect components of the inclusive fitness of an individual.

Inclusive fitness: the success of an individual in transmitting copies of her genes to future generations, both directly through her own reproduction and also through the reproductive success of her genetic relatives.

Individual reproductive value: the probability that a gene picked at random from the distant future traces its ancestry back to this individual in the present generation.

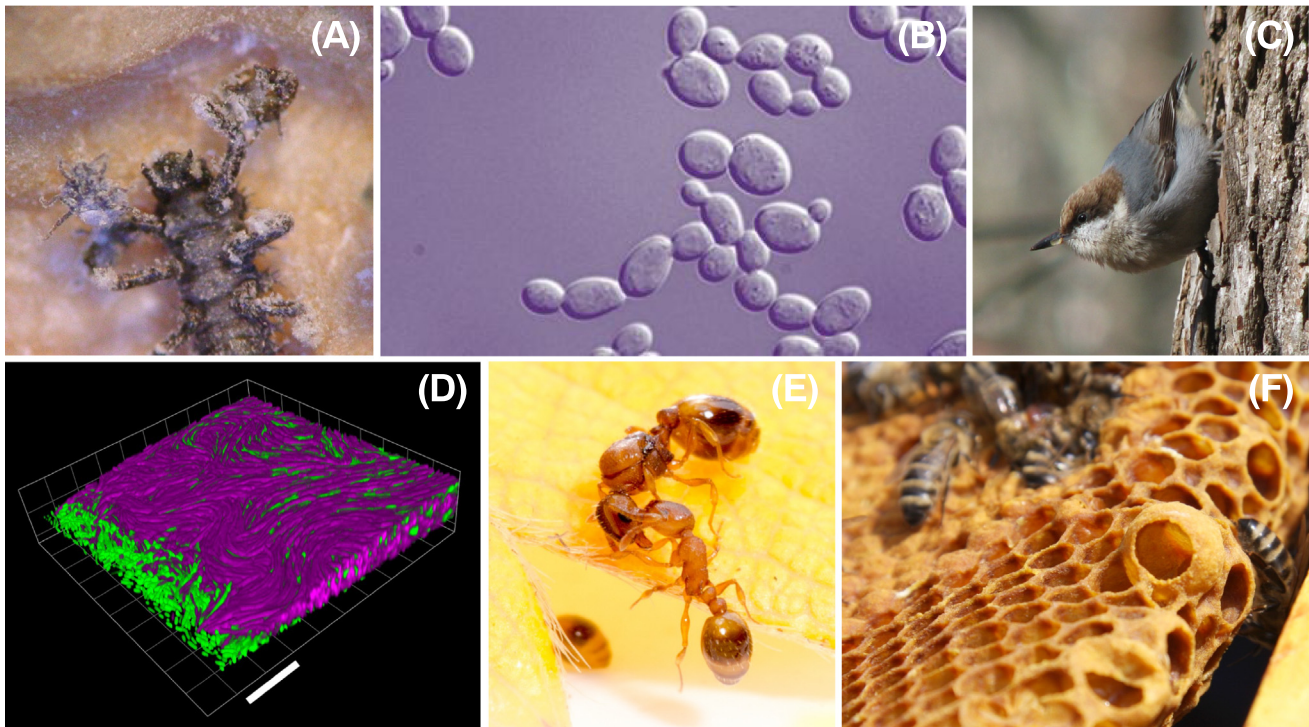
Life-for-life relatedness: a measure of value that combines individual reproductive value and genetic relatedness.

Manipulated altruism: voluntary altruism that is incentivized following manipulation of the reproductive value of the actor.

Programmed cell death (PCD): a genetically determined process that leads to death of the focal cell.

Rarer-sex effect: the reproductive value advantage enjoyed by individuals of the less-common sex.

Relatedness: the extent to which recipients of a behavior have genes in common with the actor.



Trends In Ecology & Evolution

Figure 1. Reproductive value and the evolution of altruism across species. (A) In gall-forming aphids (*Quadrartus yoshinomiya*), only juveniles and elders engage in self-sacrificing altruistic behavior, presumably because of their lower reproductive value [18,19] (credit Keigo Uematsu). (B) In budding yeast (*Saccharomyces cerevisiae*), low-reproductive value senescing cells undergo programmed cell death that benefits their colony mates [20–22] (credit Scott Stevens). (C) In brown-headed nuthatches (*Sitta pusilla*), there is a strong positive correlation between male-biased adult sex ratios and the prevalence of helping by males [23,24] (credit Vicky DeLoach). (D) In bacteria (*Escherichia coli*), self-sacrifice by low-reproductive value cells (purple cells) helps to defend the clonal colony from competitors [25,26] (credit Elisa Granato). (E) In ants (*Temnothorax crassispinus*), infected workers leave the nest, whereas infected queens remain [27] (credit Julia Giehr). (F) In honeybees (*Apis mellifera*), females reared in smaller comb cells develop as workers, whereas females reared in larger cells develop as queens [28] (credit Maja Dumat: CC BY2.0).

Age structure

Organisms experience dramatic changes in their personal circumstances during the course of their lives, and these changes may lead to the reproductive value of an individual varying as a function of her age [1,29]. Accordingly, if a prospective altruist is contemplating risking her own life to save that of a social partner, then in addition to their relatedness she should also take into account both her age and that of her social partner. All else being equal, we expect individuals of ages associated with lower reproductive value to be more inclined towards altruism, and individuals of ages associated with higher reproductive value to more frequently enjoy the benefits of this altruism (Box 2) [29,30].

A striking example of age-dependent altruism is provided by the gall-forming aphid *Quadrartus yoshinomiya* (Figure 1A) [18,19,33]. This aphid lives in leaf-galls wherein a single foundress gives rise to a colony of clonally related individuals, and among the hazards experienced by such colonies is predation by ladybirds (Coccinellidae). When a ladybird threatens the colony, some individuals immediately respond by attacking the predator, which improves the overall survival of the colony while incurring a higher risk of death for the attacking individuals. From a relatedness perspective, all colony members are equally related, and thus in this respect they should all be equally inclined towards altruism. However, from a reproductive value perspective we would expect those age groups associated with lower reproductive value to have a greater

Box 2. Age structure

Age-structured populations are those containing coexisting individuals who were born at different times, and where the fertility and survival of an individual may depend on her age. In general, we can describe such populations by considering n age classes, where n represents the maximum lifespan of an individual, and by considering that age- i individuals produce f_i offspring and survive with probability s_i to become age- $i+1$ individuals (Figure I). These quantities form a projection matrix \mathbf{L} which in the context of age-structured populations is often called the Leslie matrix [29,31]. The Leslie matrix is given by:

$$\mathbf{L} = \begin{pmatrix} f_1 & f_2 & \dots & f_n \\ s_1 & 0 & \dots & 0 \\ 0 & s_2 & \dots & 0 \\ \dots & \dots & \dots & 0 \\ 0 & 0 & s_{n-1} & 0 \end{pmatrix} \quad [I]$$

The reproductive value of an age- i individual is $v_i/v_1 = f_i\lambda^{-1} + s_i\tilde{v}_i$, where λ is the leading eigenvalue, $\tilde{v}_i = \sum_{j=i+1}^n f_j/s_j\lambda^{i+1}$ is her residual reproductive value, $l_i = s_1s_2\dots s_{i-1}$ is the probability that an individual survives to age- i , and $l_1 = 1$. Because the reproductive value of individuals may vary with their age, age structure can have important consequences for the evolution of altruism. To illustrate, consider an altruistic behavior in which the actor pays a survival cost C to provide a survival benefit B to the recipient. Because the behavior affects survival, the proper weights in Hamilton's rule are given by the residual reproductive value of actor and recipient [29,30], and therefore Hamilton's rule is given by:

$$-C\tilde{v}_\alpha + B\tilde{v}_\rho r_{\alpha \rightarrow \rho} > 0 \quad [II]$$

where $r_{\alpha \rightarrow \rho}$ is the relatedness between the age- α actor and the age- ρ recipient. Inequality [Figure II] can be rearranged into the form $C/B < A_{\alpha \rightarrow \rho}$, where $A_{\alpha \rightarrow \rho} = (\tilde{v}_\rho/\tilde{v}_\alpha)r_{\alpha \rightarrow \rho}$ represents the 'potential for altruism' – the point at which the costs and benefits of altruism break even (i.e., $A_{\alpha \rightarrow \rho} = C/B$) [30,32], and where selection for altruism increases with the potential for altruism. Often, the residual reproductive value of organisms in natural populations peaks at an intermediate age. In such cases the potential for altruism is highest among younger or older individuals, and when the recipients are middle-aged individuals (Figure II). Thus, reproductive value may explain the patterns of altruism observed in aphids, where altruism is carried out by both juveniles and elders but not by middle-aged individuals (main text).

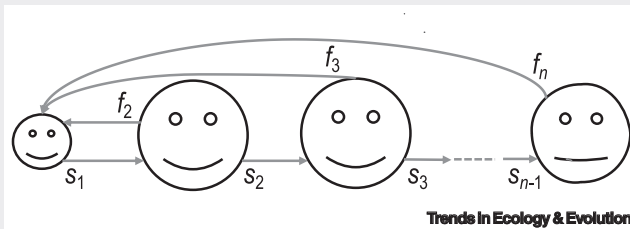


Figure I. The genetic contributions of individuals as a function of age.

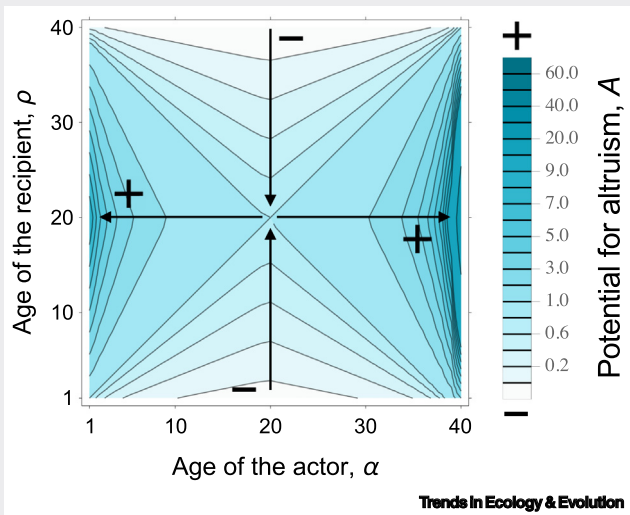


Figure II. Potential for altruism as a function of actor and recipient age. Parameter values: $s_i = 0.9$, $r_{\alpha \rightarrow \rho} = 1$, $f_i = i$ (if $i < A/2$), $f_i = A - i$ (if $i \geq A/2$).

potential for altruism (Box 2), and indeed this is what is observed. The altruistic defenders are drawn from the youngest and oldest cohorts within the colony, with pre-reproductive colony members attacking the ladybird with their mouthparts, post-reproductive individuals secreting a sticky substance that they use to glue themselves to the ladybird, and reproductive members of the colony refraining from such altruistic defense [18,19]. Reproductive value appears to be especially relevant here because the incidence of altruism does not simply depend on the present reproductive status of individuals within the colony (non-reproductive versus reproductive age classes) but more specifically upon their future reproductive potential (Box 2). For example, among the pre-reproductive age classes, the incidence of altruism is significantly higher among first-instar nymphs – whose reproductive value is expected to be relatively low because they are further from attaining reproductive maturity – than among second-instar nymphs – whose reproductive value is expected to be relatively high because they are closer to attaining reproductive maturity. This hypothesis warrants further empirical testing.

Age-dependent altruism has also been identified in unicellular organisms (Figure 1B). Many unicellular organisms – such as the bacteria *Escherichia coli* and *Caulobacter crescentus* and the budding yeast *Saccharomyces cerevisiae* – divide asymmetrically, such that the two cells resulting from a division may differ in their relative sizes, the age of the cell poles, and the number of senescent cell components [34,35]. In such situations, the two cells are better viewed as an older, larger mother and a younger, smaller daughter, rather than as two equally sized daughters [36], where older cells experience both replicative and chronological aging [36–38]. The concept of aging may also be applied to whole colonies of unicellular organisms, where older colonies show greater cell differentiation in terms of older, nondividing cells appearing in the center of the colony and younger, dividing cells at its periphery [21]. **Programmed cell death (PCD)** – a genetically regulated process leading to the fragmentation of cells in an orderly fashion that is not seen in other types of cell death [39–41] – is widespread among microbes and appears to represent an altruistic adaptation because cells that undergo PCD may relax local competition for resources, impede the spread of parasites, and even provide food for their neighbors [20,42–44]. Studies of PCD in yeast have shown that it occurs more frequently in older cells [20] and in older colonies [21,22]. Accordingly, age-related differences in reproductive value may be crucial in shaping the evolution and incidence of PCD, although explicit investigation of this hypothesis remains to be undertaken.

When older, lower reproductive value individuals invest more in altruism than do other age classes, this can further exacerbate age-related differences in reproductive value and hence act to further promote altruism by older-aged individuals. In humans and cetaceans, female reproduction ceases long before the typical age of natural death, resulting in a substantial post-reproductive life that has baffled generations of evolutionary biologists [45–47]. The 'grandmother hypothesis' is a strong candidate for explaining menopause, and this suggests that older females altruistically forgo reproduction to improve the reproductive success of their relatives by relaxing competition for reproductive resources and diverting their own resources into allo-maternal care [47,48]. Although relatedness is key under this hypothesis, reproductive value may also modulate the evolution of menopause in multiple ways. For instance, if reproductive effort is less effective later in life, then reproductive restraint and associated altruistic traits, including menopause, become less costly. A lower reproductive effectiveness – and concomitant lower reproductive value – in older females is expected for multiple reasons: in humans, maternal mortality, offspring mortality, and offspring genetic disorders all increase with maternal age [49,50]; in killer whales (*Orcinus orca*), the mortality of the offspring of older females can be 1.7-fold higher than of the offspring of younger females [48]. Moreover, by lowering the reproductive value of older age classes, it is

possible that reproductive altruism has even been responsible for exacerbating reproductive senescence, further contributing to the evolution of a prolonged post-reproductive lifespan.

Sex structure

The total reproductive value of newborns of each sex is fixed – and, crucially, is independent of the sex ratio – under a stable age distribution [1,51,52]. Accordingly, the average reproductive value of newborns of a given sex is inversely proportional to the number of newborns of that sex in the population [1]. This is the basis for Fisher's [1] rarer-sex effect which tends to equalize parental investment in each sex because the reproductive value returns from each unit of investment are greater if it is invested in the rarer sex. The rarer-sex effect also has consequences for the evolution of altruism because individuals of the more common sex have less to lose than individuals of the rarer sex, such that we would often expect individuals of the more common sex to be more predisposed towards altruism (Box 3) [53].

Sex differences in reproductive value appear to play a key role in the sociality of the brown-headed nuthatch *Sitta pusilla* (Figure 1C). Experiments wherein adult sex ratio (ASR) was manipulated over a span of 5 years found a strong correlation between sex ratio, given by the proportion of males, and the proportion of helpers [23]. In male-biased treatments, they showed a significant increase in the frequency of male helpers; in female-biased treatments, they showed an increase in the frequency of female helpers. These results are consistent with the general hypothesis that the more common sex in the population experiences fewer reproductive opportunities [24,55], and that this promotes the evolution of reproductive value-driven altruism as an alternative inclusive fitness-maximizing strategy (Box 3).

Comparative analyses provide further support for a link between biased ASRs and altruism. A phylogenetically controlled comparative analysis of 188 bird species found a positive correlation between cooperative breeding and male-biased sex ratios [55]. This study also found a positive association between male-biased sex ratios and male-biased helper sex ratios. In another study, a comparison of six populations of wild shorebirds found an association between sex differences in apparent juvenile survival and ASRs (Box 3) [56]. Furthermore, biased ASRs are associated with a higher prevalence of nest desertion by the rarer sex, and this suggests that the more common sex is more willing to bear the costs of parental care [56]. In general, these studies support the idea that altruism is favored among individuals of the more common sex, but disfavored among individuals of the rarer sex (Box 3).

The link between sex ratio and sex-specific altruism may lead to coevolutionary feedback [53,57]. If individuals of one sex have a greater tendency to help their parents with the rearing of their siblings, then parents may be favored to bias their sex allocation towards the more-helpful sex in what is termed 'local resource enhancement' [58]. The resulting sex-ratio bias may then act to favor further increases in altruism by individuals of the more common sex because of their lower reproductive value [53]. This dynamic may result in extreme sex-ratio bias, and an amplification of the sex-difference in helping, to the extent that the sex ratio is evolutionarily labile – although the positive feedback process is predicted to halt before reproductive individuals of either sex are lost entirely [52,56]. This potentially explains the single-sex workforce in haplodiploid insect societies (such as ants) where the sex ratio is readily adjusted by controlling the proportion of fertilized versus unfertilized eggs, versus the mixed-sex workforce of diplodiploid insect societies (such as termites) in which sex ratio is expected to be relatively more constrained [53,57].

Sex differences in reproductive value can also be an important factor modulating the evolutionary dynamics of symbionts and their hosts. For instance, some insects – such as the ladybird *Adalia*

bipunctata and the butterfly *Acraea encedon* – carry *Wolbachia* as a maternally inherited endosymbiont [59,60]. In these species, *Wolbachia*-infected male offspring die early in development, which can be considered to be an act of altruism on the part of the *Wolbachia* carried by these males, and which benefits the related *Wolbachia* carried by their sisters through relaxation of

Box 3. Sex structure

To illustrate how sex may influence the evolution of altruism we consider a sex-structured population, that includes female and male sex classes, as well as juvenile and adult age classes. Juvenile females and males survive to adulthood with probability s_{JF} and s_{JM} , respectively. Adult females survive with probability s_{AF} , and produce fz sons and $f(1-z)$ daughters. Adult males survive with probability s_{AM} , and father Mf offspring, where M is the number of mating partners per male. The genetic contribution of mothers (or fathers) to daughters is $1-\phi$ (or ϕ) and to sons is μ (or $1-\mu$). Thus, the gametic success of adult females through daughters is $f_{F\rightarrow F} = (1-\phi)f(1-z)$ and through sons is $f_{F\rightarrow M} = \mu fz$, whereas the gametic success of adult males through daughters is $f_{M\rightarrow F} = \phi Mf(1-z)$ and through sons is $f_{M\rightarrow M} = (1-\mu)Mfz$ (Figure 1). The full-gametic matrix is then given by:

$$A = \begin{pmatrix} 0 & (1-\phi)f(1-z) & 0 & \phi Mf(1-z) \\ s_{JF} & s_{AF} & 0 & 0 \\ 0 & \mu fz & 0 & (1-\mu)Mfz \\ 0 & 0 & s_{JM} & s_{AM} \end{pmatrix} \quad [I]$$

We find that the adult sex ratio (ASR) is $\zeta = q_{AM}/(q_{AM} + q_{AF})$, where $q_{AM} = (\lambda - s_{AF})s_{JM}z$ and $q_{AF} = (\lambda - s_{AM})s_{JF}(1-z)$, and the reproductive values are $v_{JM} = \chi_m/z$ for juvenile males, $v_{JF} = \chi_f/(1-z)$ for juvenile females, $v_{AM} = \chi_m\lambda/s_{JM}z$ for adult males, and $v_{AF} = \chi_f\lambda/s_{JF}(1-z)$ for adult females, where $\chi_m = \phi/(\phi + \mu)$ and $\chi_f = \mu/(\phi + \mu)$ correspond to the class reproductive values of newborn males and females, respectively [54]. We ask who is under more selection for altruism, juvenile males or females, or adult males or females. Hamilton's rule is given by:

$$-C\tilde{v}_a + B\tilde{v}_p r_{a-p} > 0 \quad [II]$$

where \tilde{v}_a (or \tilde{v}_p) is the residual reproductive value of the actor (or recipient), and r_{a-p} is the relatedness between the actor and the recipient. Assuming that adult females are the recipients, the potential for altruism of a juvenile (or adult) male and a juvenile (or adult) female is then given by $A_M = (\chi_f s_{JM} z) / (\chi_m s_{JF} (1-z)) r_M$ and $A_F = r_F$, respectively. We find that selection favors juvenile (or adult) male altruism when the ASR becomes male-biased, which can occur for two main reasons: male-biased primary sex ratios and higher juvenile-female mortality (Figure 2). For instance, in the scenario shown in Figure 2, if the survival of juvenile females is 0.4, and that of males is greater than 0.4, then males are favored to help more ($A_M > A_F$).

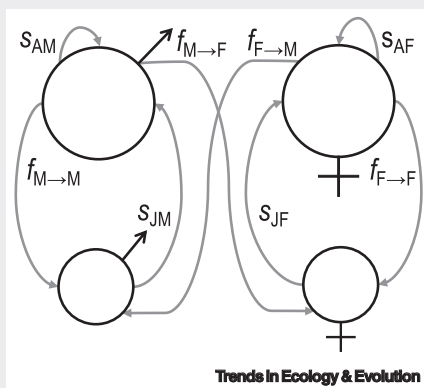
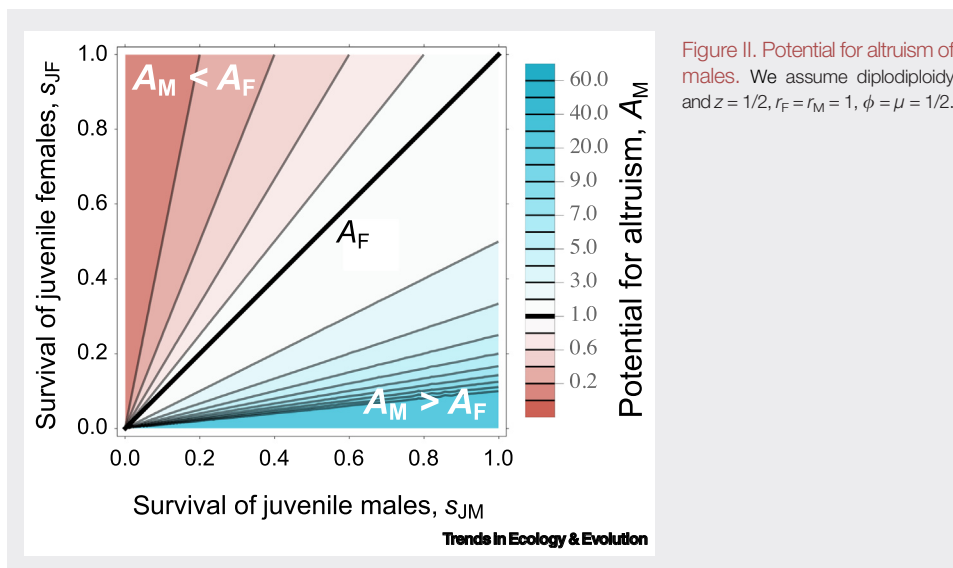


Figure 1. The genetic contributions of individuals, through sons and daughters and survival, as a function of age and sex.

resource competition [61]. This sex-specificity of *Wolbachia*-induced killing makes sense in light of reproductive value because, although males carry *Wolbachia*, they do not transmit it to their descendants and hence, from the perspective of the endosymbiont, males have zero



reproductive value and inclusive fitness is maximized by promoting female reproductive success. Although the basic logic of *Wolbachia*-induced male killing has long been understood [60], explicitly framing in terms of reproductive value shows the connection with sterile workers in ants, and male-biased helping in birds, that represent different facets of the link between sex-specific reproductive value and altruism in which low reproductive value individuals show a disproportionate tendency towards altruism. Indeed, this connection highlights that *Wolbachia*-induced female-biased sex ratios might even drive a female bias in helping in the host population, a possibility which may warrant future theoretical and empirical exploration.

Condition structure

We have focused so far on how two classic examples of class structure – age and sex – modulate variation in reproductive value among individuals. Other factors that are not necessarily associated with age and sex – such as social rank, nutritional state, or resource availability – can also drive individual variation in reproductive value and concomitant patterns of altruism (Box 4) [62–64]. We term this 'condition structure'.

Differences in the individual condition of cells in the slime mould *Dictyostelium discoideum* appear to explain differences in their proclivity to altruism. The multicellular phase of *D. discoideum* begins when solitary cells run out of food and start to aggregate; the multicellular form then moves to the soil surface where it forms a fruiting body in which ~80% of the cells become reproductive spores and ~20% become non-reproductive stalk cells. Stalk cells thus represent a striking form of reproductive altruism because their deaths help spore cells to disperse and colonize other areas. Several experiments have shown that the developmental switch that determines whether a cell becomes a spore or a stalk is not expressed at random: instead, cells have a higher tendency to become stalk cells if they are leaner after undergoing cell division, or if they are nutritionally deprived (reviewed in [66,67]). We can use reproductive value to interpret and explain these observations: it is likely that starved cells have lower reproductive value than their well-nourished counterparts and, as a result, the cost of altruism is lower if borne by starving cells (Box 4). The extent to which this mechanism is stable depends on the average relatedness within groups of slime mould cells during aggregation, where lower relatedness would potentially favor a higher

proportion of cheats among the spore cells. Further empirical investigation and the development of more detailed theoretical models will be necessary to properly evaluate this hypothesis.

Reproductive value may also modulate collective defense strategies in microbial populations (Figure 1D). In the bacterium *Escherichia coli*, when populations come under attack, a fraction of the population undergoes suicide to release exotoxins that kill rival bacteria [25,68]. The cells that undergo suicide tend to be those that have suffered DNA damage [25,26], which reduces their reproductive value, and may explain why they participate in the altruistic defense of the population (Box 4) [15,26]. Other forms of DNA damage-mediated self-sacrificing behavior include the provisioning of nutrients to surviving cells or defense mechanisms against the spread of bacteriophage infection [69].

The evolution of social immunity strategies may also hinge upon differences in reproductive value (Figure 1E). When social partners live in close proximity, individuals can engage in more selfish self-immunity strategies, or more altruistic social-immunity strategies, including self-sacrificing

Box 4. Condition structure

We illustrate how differences in condition among individuals can modulate the evolution of altruism. We assume three classes of adult individuals – high-quality (H), medium-quality (M), and low-quality (L) – that each reproduce asexually [15]. Adults survive with probability s_i , where i denotes the quality of the individual. All adults produce f offspring, but offspring survival, denoted by S_i , is correlated with parental quality, such that $S_H \geq S_M \geq S_L$. With probability $x_{i \rightarrow j}$, offspring of i -quality parents become j -quality adult breeders, where $\sum_{j \in \{H,M,L\}} x_{i \rightarrow j} = 1$ (Figure I). Thus, the condition-specific fecundity of an i -quality individual is given by $f_{i \rightarrow j} = fS_i x_{i \rightarrow j}$. The fitness matrix is then given by parental survival matrix and the fertility matrix:

$$A = \begin{pmatrix} s_L & 0 & 0 \\ 0 & s_M & 0 \\ 0 & 0 & s_H \end{pmatrix} + \begin{pmatrix} f_{L \rightarrow L} & f_{M \rightarrow L} & f_{H \rightarrow L} \\ f_{L \rightarrow M} & f_{M \rightarrow M} & f_{H \rightarrow M} \\ f_{L \rightarrow H} & f_{M \rightarrow H} & f_{H \rightarrow H} \end{pmatrix} \quad [I]$$

The reproductive value of an i -quality individual is given by $v_i = s_i v_i + \lambda v_i$, where $V_i = S_i \sum_{j \in \{H,M,L\}} x_{i \rightarrow j} v_j$ is the reproductive value of the offspring of an i -quality parent. We consider a behavior in which an i -quality actor pays a fertility cost C_i to provide a fertility benefit B_i to a j -quality recipient. Hamilton's rule is given by:

$$-C v_i + B v_j r_{i \rightarrow j} > 0 \quad [II]$$

where $r_{i \rightarrow j}$ is the relatedness between the actor and the recipient. Assuming that the offspring quality does not depend on the quality of the parent, in other words $x_{i \rightarrow j} = x_j$, the potential for altruism between an i -quality and a j -quality individual is $A_{i \rightarrow j} = (S_j/S_i) r_{i \rightarrow j}$. Thus, because $S_H \geq S_M \geq S_L$, lower-quality individuals are more likely to be altruists than higher-quality individuals. For instance, when the relative quality of high-quality individuals (H) increases, their predisposition for helping individuals of inferior quality (M and L) decreases (Figure II, third column). Note that fertility effects require the weighting of costs and benefits by the reproductive values of the offspring [54,65]. By contrast, if the behavior entails survival effects, the weighting is given by the residual reproductive values of the actors and recipients (e.g., [65]). In such cases, individuals with lower residual reproductive value are more predisposed to altruism.

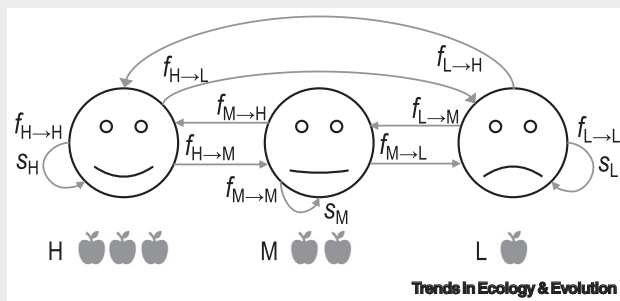
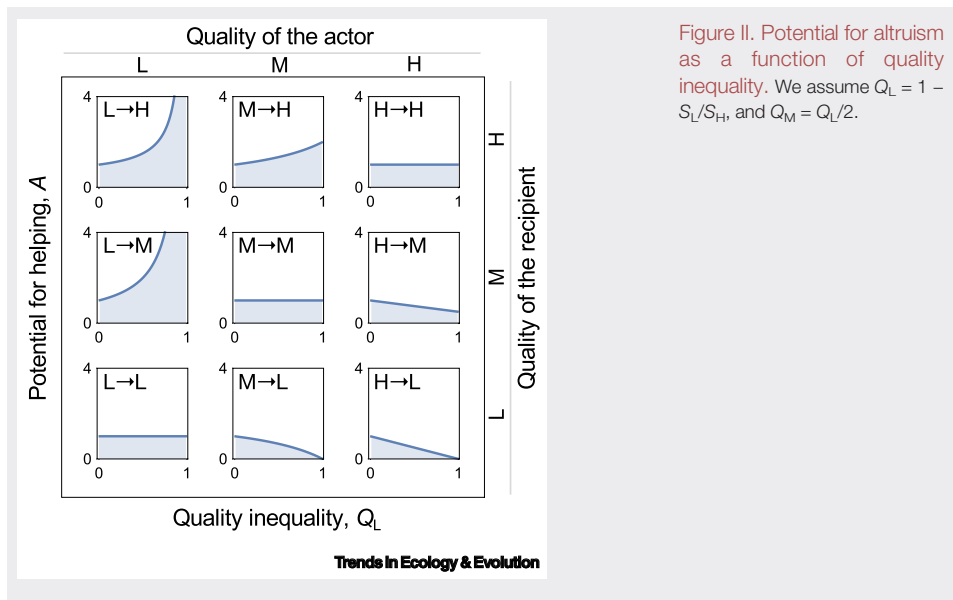


Figure I. The genetic contributions of individuals, through offspring and survival, as a function of class.



behaviors that prevent the transmission of pathogens to social partners [70–72]. Because death entails the loss of residual reproductive value, we expect low reproductive value individuals to invest more in social immunity than do high reproductive value individuals (Box 4). Some evidence supports this prediction. In the ant *Temnothorax crassispinus*, queens and workers respond differently when treated with the entomopathogenic fungus *Metarhizium brunneum*. Although low reproductive value workers altruistically remove themselves from the nest, irrespective of their reproductive status, high reproductive value queens always remain in the nest and are only removed by workers if they eventually die from the infection [27]. The pattern among workers is less clear, and reproductive workers apparently show the same rate of self-removal as non-reproductive workers, although this might be explained if the workers have similar future reproductive value irrespective of their current reproductive status. More generally, differences in the altruistic behavior of infected individuals – that have poor reproductive prospects – versus their noninfected counterparts represent fertile ground for further theoretical and empirical investigation into the role of reproductive value in modulating the evolution of altruism.

Manipulated altruism

As we have discussed in the previous text, the predisposition to altruism may depend on the reproductive value of the actor and the recipient, and factors such as sex, age, and condition can modulate reproductive value. However, variation in reproductive value can also result from the manipulative actions of a social partner [73]. A manipulator can reduce the reproductive value of an unwitting victim as part of a self-serving strategy in which their lowered reproductive value incentivizes the victim to voluntarily help the manipulator or her close relatives. We call this **manipulated altruism**.

Evidence for self-serving reproductive value manipulation is perhaps best illustrated by bees [74,75]. All female larvae in the Mexican stingless bee *Melipona beecheii* are reared in similarly

sized cells, and ~20% of the larvae develop into queens – well above the rate that would be optimal in terms of maximizing the productivity of the colony [28]. By contrast, in the honeybee *Apis mellifera* most female larvae are reared in relatively small, poorly provisioned cells whereas a small fraction are reared in large, well-provisioned cells, and the females eclosing from small cells overwhelmingly develop as workers, whereas those eclosing from large cells develop as queens (Figure 1F). Although it is possible for larvae in small cells to develop as queens (and, indeed, a very small proportion do), the resulting small queens have such poor reproductive prospects that, for most of the larvae finding themselves in small cells, their inclusive fitness interests are better served by developing as workers. In this way, the larvae are manipulatively incentivized – rather than directly forced – into making caste fate decisions that are more in line with optimal production of queens by the colony [28]. Manipulated altruism appears also to occur in the subsocial bee *Ceratina calcarata*, where mothers manipulate the quantity and quality of pollen given to their first daughter such that she develops as a dwarf daughter who is incentivized to forage and help her mother to rear her younger siblings rather than pursuing her own reproductive career [76].

Concluding remarks

The evolution of sociality depends on opportunities for cooperation and the extent to which social partners share genes. This has been the focus of a large body of research on social evolution that seeks correlations between levels of altruism and relatedness. However, relatedness is not the only predictor of altruism – reproductive value is also important, and its role has been relatively neglected (see Outstanding questions). All else being equal, individuals with a lower expected reproductive value should be more willing to risk their lives for the good of others than are those with higher expected reproductive value.

Reproductive value-driven altruism plays a key role in the evolution of division of labor and in morphological specialization of castes within highly integrated social groups. Both processes are crucial for major evolutionary transitions [77–80]. Although high relatedness is a necessary condition for major transitions, it is not sufficient [77,81,82]. During all stages of major transitions, from group formation to group transformation [77], populations suffer dramatic changes in class structure and in the distribution of reproductive value. Despite this, the significance of reproductive value in major evolutionary transitions remains largely unexplored [83].

Environmental factors can introduce important differences in reproductive value and mediate the evolution of altruism and key fitness traits. Explicitly considering reproductive value in population biology and conservation can enhance our understanding of the dynamics of populations, including niche expansion and biological invasions [84–86], and improve conservation efforts. Anthropogenic-driven environmental changes have a profound impact on the class structure of populations. These include changes in the distribution of resources and habitat connectivity, which can lead to evolutionary mismatches analogous to the self-defeating efforts of conservationists whose provision of extra food for the endangered kākāpō (*Strigops habroptilus*) led to the birds producing strongly male-biased clutches in the following season [87]. More generally, considerations of class structure will facilitate the development of more ecologically realistic models that consider the interactions between a wide range of genetic and environmental factors in driving the evolution of altruism.

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Outstanding questions

How does reproductive value change with age in microbial populations? In these populations, are altruistic behaviors such as PCD inclusive fitness-maximizing behaviors driven by differences in reproductive value?

How do altruistic behavior and reproductive value coevolve? Does positive feedback between reproductive altruism and reproductive value drive the evolution of single-sex helping in social insects and a prolonged post-reproductive lifespan in humans and killer whales?

In the social amoeba *Dictyostelium discoideum*, how does reproductive value vary among cells and over the different stages of the multicellular development that leads to stalk formation and spore dispersal? Is the nutritional state of cells a key indicator of individual reproductive value?

What is the role of reproductive value in cell differentiation and division of labor within social groups?

Are individuals infected with pathogens more inclined to acts of altruism on account of their lowered reproductive value?

How does variation in reproductive value affect the life cycle and social behavior of pathogens?

How important is manipulated altruism in driving the evolution of altruism? What are the genetic and ecological factors that contribute towards the evolution of manipulated altruism?

The capacity to identify the relative reproductive value of potential social partners can be an important fitness-related trait. To what extent are individuals able to discriminate each other's reproductive values and adjust their social behavior accordingly?

How diverse are reproductive value-discrimination mechanisms, and how are they distributed among the different taxa?

What are the major ecological, demographic, and social factors that generate differences in reproductive value within and among social groups?

Declaration of interests

The authors declare no conflicts of interest.

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What is the role of reproductive value in major evolutionary transitions, and is reproductive value-driven altruism a key factor in these transitions?

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