

The evolution of altruism

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Ever since Darwin published *On The Origin of Species* in 1859, the evolution of altruism has been a perennial paradox for evolutionary biologists. In this review, I will discuss three evolutionary paths to altruism – genetic relatedness, reciprocity, and group selection – and examine very recent work that uses social network modeling to help us better understand the evolution of altruism.

Key words: altruism; genetic relatedness; reciprocity; group selection; evolution; social network theory.

КАК ЦИТИРОВАТЬ ЭТУ СТАТЬЮ:

Дугаткин Л.А. Эволюция альтруизма. Вавиловский журнал генетики и селекции. 2017;21(4):487-491. DOI 10.18699/VJ17.267

HOW TO CITE THIS ARTICLE:

Dugatkin L.A. The evolution of altruism. *Vavilovskii Zhurnal Genetiki i Selekcii* = *Vavilov Journal of Genetics and Breeding*. 2017;21(4):487-491. DOI 10.18699/VJ17.267

I never had the pleasure of meeting Dmitri Belyaev, but I feel like I know him. For the last 6 years, my colleague Lyudmila Trut and I have been writing a book on the silver fox domestication experiment. As I did the research for this book, I learned so much about Dmitri Belyaev from Lyudmila, Pavel Borodin, Anatoly Ruvinsky, Misha Belyaev, Nikolai Belyaev and the dozens of people I interviewed during my visits to the Institute of Cytology and Genetics. The more I discovered about him, the more I realized Dmitri Belyaev was not only a brilliant, visionary scientist, and an inspirational leader, he was a kind, gentle, caring man that touched the lives of so many. He was an altruist. And so, in his honor, it seemed appropriate for me to write an article about the evolution of altruism in this special issue.

Within evolutionary biology, altruism is defined as helping others at a cost to self. Dmitri Belyaev was not only an altruist, he expected, in fact demanded, that others be altruistic as well. This is evident in the last interview he did before his death in 1985. In that interview, published in an article entitled “I believe in the goodness of human nature”, Dmitri noted that “In the future we should take great care of human psychology; a lot depends on a social climate, on how people treat each other, and on how a community as a whole will carry out its upbringing and humanitarian functions...” We must foster altruism, he believed, especially in children, among whom

Эволюция альтруизма

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С тех пор как Чарльз Дарвин опубликовал «Происхождение видов» в 1859 г., тема эволюции альтруизма была постоянным парадоксом для эволюционных биологов. В данном обзоре обсуждаются три пути, ведущие к эволюции альтруизма, – генетическое родство, взаимопомощь и групповой отбор. Я также представлю совсем недавнюю работу, в которой использовано моделирование социальной сети, для того чтобы пролить свет на эволюцию альтруизма.

Ключевые слова: альтруизм; генетическое родство; взаимопомощь; групповой отбор; эволюция; теория социальной сети.

Belyaev tells the interviewer “we should recognize their predispositions and support the early goodness in them”. When he was asked “What would you like to wish for mankind in the 21st century?” Belyaev answered, “Be kind and socially responsible, strive for mutual agreement with all people, live in peace” (Belyaev, 1986).

Ever since Charles Darwin published *On the Origin of Species* (1859) evolutionary biologists have been puzzled about the evolution of altruistic behaviors in humans and non-humans. The problem is this: if natural selection favors traits that make organisms better suited to outcompete others in their population – by, for example, favoring superior foragers, fighters, and so on – how could altruism, where individuals help others at a cost to themselves, evolve? Darwin himself was quite worried about this question. In letters to his friends he wrote that his attempt to try and understand how natural selection might favor these sorts of behaviors was driving him “half mad” (Darwin letter to Hooker, February 23, 1858) and in *The Origin*, Darwin noted that altruism among social insects was “one special difficulty, which at first appeared to me to be insuperable, and actually fatal to the whole theory” (Darwin, 1859).

Darwin’s work on domesticated species, especially cattle, eventually led him to develop one hypothesis for the evolution of altruism: that natural selection might favor such behavior

УДК 575.82

Поступила в редакцию 17.10.2016 г.

Принята к публикации 20.12.2016 г.

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when it was directed toward related individuals. He came to think that the “problem” of how natural selection favors altruism “... disappear[s] when it is remembered that selection may be applied to *the family*, as well as the individual and may thus gain the desired end” (Darwin, 1859). As we will see in a moment, Darwin’s ideas were eventually formalized by W.D. Hamilton in his famous inclusive fitness models (Hamilton, 1963, 1964), but before we do this, it is important to note that many fine scientists contributed to the work on altruism between the time of Darwin and Hamilton. Perhaps the most important of these was Petr Kropotkin, whose articles and books on what he called “mutual aid” were the first to seriously explore how altruism could evolve among unrelated individuals (Kropotkin, 1902).

Three paths to the evolution of altruism

In this paper, I will review some of the leading modern hypotheses for the evolution of altruistic behaviors. I begin by outlining three evolutionary paths to altruism and then examine recent attempts to use social network analyses to better understand the evolution of this type of behavior.

Inclusive fitness theory

In the hope that it may provide a useful summary we therefore hazard the following generalized unrigorous statement of the main principle that has emerged from the model. *The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbors’ fitness against his own according to the coefficients of relationship appropriate to that situation.*

W.D. Hamilton. 1964

A little over a century after *The Origin* was published, W.D. Hamilton developed inclusive fitness theory (also known as kin selection theory), which mathematically formalized the idea that genetic relatedness can foster the evolution of altruism (Hamilton, 1963, 1964). Hamilton’s model predicts that altruism is favored by natural selection when:

$$\sum_0^A r \cdot b > c.$$

In this equation, which has become known as Hamilton’s Rule, b is the benefits others receive from the act of an altruist, c is the cost paid by the altruist, r is a measure of genetic relatedness, and A is a count of the individuals affected by the behavior of the altruist. Any factors that increase the variables on the left-hand side of this equation make altruism more likely to evolve; conversely any conditions that increase the value of the right-hand side of the equation make altruism less likely to evolve. As such, a number of general predictions emerge from this equation: i) increasing the genetic relatedness between altruist and recipient favors the evolution of altruism; ii) increasing the benefit the recipient(s) receives favors the evolution of altruism; iii) increasing the number of genetic relatives (A) helped by an act of altruism favors the evolution of altruism; and iv) increasing the cost of an act of altruism decreases the probability that altruism will evolve.

Hamilton’s Rule has generated hundreds of studies of altruism, and in general, the predictions outlined above have been

supported (Dugatkin, 2006; Abbot et al., 2010). There are a number of different kinds of studies that can be used to test Hamilton’s Rule. For example, many studies have looked to see whether high levels of genetic relatedness are associated with increased altruism (prediction (i) from above, (Abbot et al., 2010)). Another way to test the inclusive fitness models is through phylogenetic analysis. Such an analysis was undertaken on altruism in the hymenopteran social insects (e. g. bees, ants, and wasps).

Hymenopterans have an unusual genetic system called haplodiploidy, in which all males are haploid and all females are diploid. This creates very high levels of genetic relatedness among sisters. Full sisters in diploid species have an r of 0.5, but full sisters in hymenopterans have an r of 0.75. With an r of 0.75 between sisters, one would expect high levels of altruism among hymenopteran females and indeed it is the highly related female workers in many species that go to suicidal lengths to defend a hive full of their sisters.

The hypothesis that high genetic relatedness is important to the evolution of altruism in social insects can also be tested using phylogenetic analyses. Genetic relatedness is highest in social insect groups when queens have a single mate; when they are *monandrous*. If queens have multiple mates (if they are *polyandrous*), the average genetic relatedness in groups decreases. This leads to a prediction – eusociality should often be associated with a monogamous mating system. William Hughes and his colleagues tested this idea using already published data that suggested that eusociality has independently evolved five times in bees, three times in wasps, and once in ants (Hughes et al., 2008; Ratnieks, Helantera, 2009).

When we look at modern eusocial hymenopteran lineages we see both monandry and polyandry. But Hughes and his colleagues hypothesized that in order for eusociality to have been favored by natural selection in the evolutionary past of these groups, their evolutionary histories should show monandry as the *ancestral* mating system (Hughes et al., 2008). A phylogenetic analysis of these modern lineages indicates that, as predicted by inclusive fitness theory, monandry was the ancestral state in *all* eusocial lineages examined.

Reciprocity and the evolution of altruism

A second path to the evolution of altruism is via reciprocity. The basic idea in reciprocity-based models is that, under certain conditions, altruism can be favored by natural selection if individuals exchange acts of goodness: that is, in principle, the cost of being a altruist at time T can be compensated if the altruist is helped at some time, $T+1$, in the future by those it helped in the past.

One mathematical tool used to model the evolution of a reciprocal altruism is the prisoner’s dilemma game. Individuals in a prisoner’s dilemma game who use the tit-for-tat (TFT) strategy do very well, especially when they interact often and for long periods of time (Axelrod, Hamilton, 1981; Axelrod, 1984). TFT is a strategy that instructs players to begin their interactions with others by being altruistic, and then to copy what the other individual does. TFT has three attributes that make it a successful strategy: (a) “niceness” – a TFT player is never the first to stop being altruistic; (b) “retaliation” – an individual playing TFT immediately stops being altruistic when his or her partner stops being altruistic; and (c) “forgiv-

ing” – TFT instructs individuals to do what their partner did on the last move, and, so TFT has a memory window only one move back in time. Any act that occurred before one move back in time does not influence the behavior of the individual using the TFT strategy.

A textbook case of altruism via reciprocity is that of blood-sharing behavior in vampire bats (*Desmodus rotundus*). In this species, individuals can starve to death if they do not obtain a new blood meal every few days. Females in a nest of vampire bats sometimes regurgitate blood meals to other bats that have failed to obtain food in the recent past. Wilkinson examined whether reciprocity was an important factor in explaining the sharing of blood meals (Wilkinson, 1984, 1985, 1990, 1992). What he found was that data suggested vampire bats were reciprocal altruists – they remembered who helped them when they were starving and were more likely to give blood to those individuals.

Group selection

A third path to the evolution of altruism is group selection (Wilson, 1975, 1980, 2016; Sober, Wilson, 1998). In group selection models, a group is defined as all individuals that affect one another’s fitness. In group selection models, natural selection operates on two different levels: within groups and between groups. Within-group selection acts against altruists, because altruists, by definition, pay a cost that others do not. Selfish types – those who are not altruists – are favored by within-group selection, because they receive the benefits that altruists provide, but they do not pay the costs. Natural selection between groups favors altruists because groups with more altruists are more productive than groups with fewer altruists. For such group-level benefits to be manifest, groups must differ in the frequency of altruists, and groups must be able to export the increased productivity associated with altruism.

One of the strongest cases to date of group-selected altruism comes from Steve Rissing’s work on the ant, *Acromyrmex versicolor* (Rissing et al., 1989). In *A. versicolor* species, nests are founded by multiple, unrelated queens. The starting nests are underground, and individuals in such nests are protected from most of the predators in their desert environment. Altruism occurs in the feeding behaviors of queens during the early stages of colony foundation. A single queen from the numerous queens in a nest takes on the role of forager. She alone brings back materials for the nest’s fungus garden; the food source for the colony. Foraging behavior is a dangerous activity, in terms of both predators and parasites that queens encounter when they leave their underground nest to forage.

Once a queen becomes a forager, she remains in that role. Only she pays the costs for getting the materials for the fungus colony’s fungus garden, but all queens at her nest share equally in the food produced by the fungus garden. Foraging queens are then altruists; within groups, they benefit others at a cost to self. How then does altruism evolve? The answer is via between-group selection. At a later stage in colony development, “brood raiding” behavior takes place. Brood raiding occurs when workers from one nest capture ants from nearby colonies and raise those captured individuals within their own nests (Wheeler, Rissing, 1975; Ryti, Case, 1984). The probability that a nest survives a period of brood-raiding is positively correlated with the numbers of workers produced

in that nest. And the number of workers produced in the nest is itself positively correlated with how productive a foraging queen is. That is, although within-group selection acts against altruistic queen foragers, between-group selection favors altruism because it increases the nest’s probability of surviving the period of brood raiding (Rissing et al., 1989; Seger, 1989; Cahan, Julian, 1999; Pollock et al., 2004).

Social network approaches to the evolution of altruism

I close this paper by discussing some of the most recent work done on the evolution of altruism. In this work, evolutionary and behavioral ecologists have begun using social network analysis (SNA) to examine altruistic behavior (Dugatkin, Hasenjager, 2015; Hasenjager, Dugatkin, 2015). SNA provides a conceptual framework and a set of mathematical tools to examine the relationship between individual behavior, population structure, and population-level processes (Croft et al., 2008). A social network is often visually depicted as a collection of nodes representing individuals in a population. Behavioral interactions between members of a social network are shown by an edge connecting their two nodes together. Nodes are sometimes assigned traits of the individuals they represent, and edges may be weighted to indicate the relative frequency or intensity of a relationship (e. g., how often two individuals cooperated with each other).

Measures of actual social networks can be compared to simulated social networks to identify significant departures from null expectations, which may suggest important aspects of population social structure that need further investigations (Croft et al., 2008). In addition, a social network is the substrate upon which population-level processes such as information flow are manifest, and so an in-depth knowledge of a population’s social network allows us to better predict these processes and can better our understanding of how social organization influences individual behavior (Croft et al., 2006; Kurvers et al., 2014).

Ohtsuki et al. (2006) found that altruism in a social network can persist if $b/c > k$, where b is the benefit of an act of altruism, c is the cost of the altruistic act, and k is the number of social partners an individual interacts with (more technically, the average degree of the network). This implies that natural selection will favor altruism when individuals have a relatively small number of others with whom they interact.

If altruists can identify other altruists and preferentially interact with them, then altruism can persist even in social networks where they interact with many individuals. Much work suggests that animals have some influence over their network connections, we so might expect to observe such assortative patterns (altruists interacting with other altruists) in the wild, and studies on natural populations of guppies (*Poecilia reticulata*) have indeed found these patterns (Croft et al., 2006).

Policing behavior, where individuals search out and punish those who are not altruists, can be studied using SNAs (Ratnieks, Visscher, 1989; Flack et al., 2006). Flack et al. (2006) used SNA to examine policing in male pig-tailed macaques (*Macaca nemestrina*). Flack first measured social networks for grooming, play and proximity in macaque groups. Next, he removed three high-ranking males who were known to

engage in altruistic behavior by breaking up fights between other group members. When these policing males were absent, aggressive behaviors became more common, and altruism decreased. With the policing individuals gone, other group members played with and groomed fewer partners. They also found that another SNA measure called “reach” – the number of friends of the friends of an individual – decreased. What’s more, the cohesion of the entire society weakened; the population divided into smaller, more homogeneous groups that rarely interacted with those outside their groups. All in all, these structural changes to the social network suggest when policing individuals are removed, altruism decreases and animals adjusted their social networks by maintaining a smaller and less diverse network of connections (Ohtsuki et al., 2006; Santos et al., 2006a, b).

I will end with a study that I think would have made Dmitri Belyaev happy: SNA analysis has been used to study *interspecific* cooperation between humans and dolphins.

For seven years, David Lusseau tracked 64 bottlenose dolphins (*Tursiops truncatus*) in southern New Zealand. After observing more than 1,000 groups that contained subsets of these 64 animals, he used SNA analysis to determine that all these dolphins were part of one large social network. But what Lusseau could not figure out was what benefits the dolphins received by being part of a single large network. What sort of information, if any, was being transferred among members of this social network?

To answer this question Lusseau had to switch the dolphin population he was working with. He began collaborating with Paulo C. Simões-Lopes of the Federal University of Santa Catarina in Brazil, where they studied bottlenose dolphins in Brazil. Earlier, Simões-Lopes had discovered that these dolphins were involved in an amazing interspecific relationship with the local fishermen that fish in their bay.

For the last 200 years or so, fishermen in the Laguna region of Brazil have been casting long nets into the water to catch schools of mullets (*Mugil platanus*). In recent years the fishermen have been receiving help from some of the bottlenose dolphins, who actively herd the mullets towards the nets of the fishermen. The dolphins can see the mullet better than the fishermen, and they slap the water with their heads or tails to tell the fishermen the time and place to cast their nets. As a result, both the fishermen and the dolphins catch more fish than they would without this interspecific cooperation (Lusseau, 2003; Lusseau, Newman, 2004; Lusseau et al., 2006; Daura-Jorge et al., 2012).

Lusseau and Simões-Lopes used SNA to better understand what was happening in this remarkable population of dolphins. Their analysis found that the dolphins in this population subdivided into three subgroups, and individuals spent most of their time in their subgroup, facilitating information transmission among group members. Subgroup 1 had 15 dolphins, and every single dolphin in this subgroup cooperated with the fishermen to help them catch fish. SNA analysis found that this subgroup was highly interconnected, and dolphins in subgroup 1 benefited most (in terms of food acquisition) from their relationship with the fishermen. None of the twelve dolphins in subgroup 2 cooperated with the fishermen and social relationships in this subgroup were weaker than those seen for individuals in subgroup 1.

Subgroup 3 had eight dolphins; seven of the animals did not cooperate with the fishermen – but one dolphin, labeled “Dolphin 20” – did cooperate with the fishermen. And interestingly, it was Dolphin 20 that spent the most time interacting with dolphins in the other two subgroups. Dolphin 20 acted as a sort of liaison among the subgroups. Whether this facilitates more of the dolphins in subgroup 3 to cooperate with the fishermen remains to be seen over time.

Acknowledgements

I would like to thank Pavel Borodin for inviting me to write this review. I also thank Lyudmila Trut, Pavel Borodin, Anatoly Ruvinsky, Misha Belyaev and Nikolai Belyaev for sharing all of their remarkable insights into the life of Dmitri Belyaev.

Conflict of Interest

The author has no conflicts of interest.

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