Essay of Comparative Cognition

The evolution of altruism

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Abstract: 146 words

Abstract

Natural selection drives to maximize individual fitness. However, occasionally there are also behaviours that increase the fitness of the others at the expense of the helper's own fitness. Indeed, behaviours such as helping others, sharing food but also self-sacrifice for someone else can be observed in nature. But how could such behaviours have been positively selected over the course of evolution if they lower the fitness of the helping individual? For this reason, altruistic behaviours have been a challenge to Darwinian theory and require further investigation. In this essay, I will assess the mechanisms that can result in altruism. I will discuss key examples of altruism documented in the animal kingdom, both from experimental studies and from direct observations. The goal is to reconstruct the evolutionary history of altruism and to determine the evolutionary forces that have favoured it, separately for kin selection and non-kin cooperation.

Keywords : kin selection, altruism, altruistic behaviour, inclusive fitness

Introduction

Charles Darwin published his book "On the origin of species" in which he presented the theory of evolution by natural selection. This idea suggests that the phenomena of variation, heredity and selection together lead inevitably to a process of evolution. Later, this idea has been combined with genetics to formulate the synthetic theory of evolution, which is based on three components: a heritable variation, a differential reproduction and the effects on population genetics (Rampino, M.R., 2011).

Since our genes also influence our behaviours, these will also be in the grip of an evolutionary process. Which means that the behaviours that will allow a better transmission of our genes will be better selected than the others. We can imagine that the behaviours that allow us to hoard the greatest number of resources to ourselves and maximize our fitness will tend to be favored. Therefore, Darwinian theory predicts that selfish behaviours will always be selected in nature. This is partly true but various altruistic behaviours can be observed in nature.

In order to detect this type of behaviour in nature, we need to find a proper definition. Indeed, many scientists use different definitions and there is no strict consensus of this concept in literature. Some will define altruism with the intention of the action, others will say that the approval by the society is essential (Bykov A., 2017 ; Pfattheicher & al., 2022). However, in the field of biology, most of the time, a behaviour will be considered as altruistic if it tends to increase the fitness of the others at the expense of its own fitness. It is mainly the consequences of a behaviour that will allow the term altruistic to be attributed to a behaviour, and not its intention or its approval by society (Okasha Samir, 2020). Therefore, we will consider an altruistic behaviour as an action that decrease the direct fitness of the actor and increase the direct fitness of the recipient(s). However, why would such a behaviour appear during the evolution? We will see that altruism towards kin and non kin are very different forms of altruism. By means of various examples of altruism occurring in nature, we will also present the theories providing explanations for the existence of such a behaviour. Finally, this will give us the tools to illustrate the evolution of altruism in the phylogenetic tree of life.

Kin selection

According to our definition, helping relatives is also considered as an altruistic behaviour and altruism towards kin is widely spread in nature. This type of altruism can be explained with the theory of the inclusive fitness which measures the fitness of an individual organism in terms of the survival and reproductive success of its kin. Indeed, most of altruistic behaviours can be explained by the fact that their costs are counterbalanced by the benefits received from helping an individual who shares a percentage of the same genes. When an individual carries an “altruistic gene”, there is a probability that its relatives will carry the same gene. Thus, by behaving altruistically with its relatives and increasing their fitness, it is very likely that this “altruistic gene” will spread by natural selection (Pfattheicher & al., 2022).

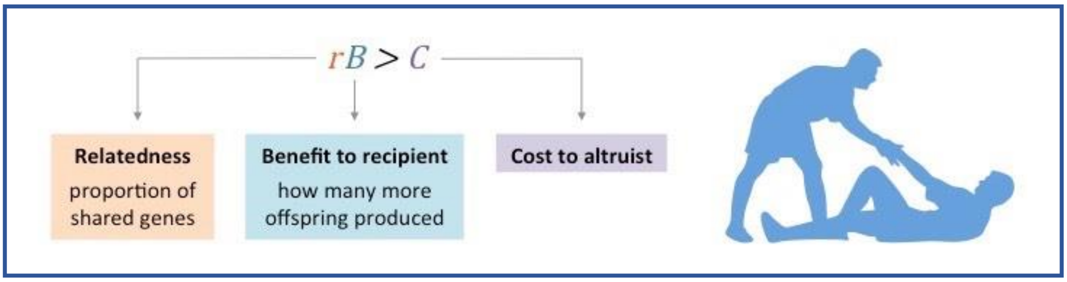

Figure 1 : Hamilton's rule: An altruistic behaviour towards kin is selected when the costs received by the actor (C) are smaller than the benefits received to the recipient (B) multiplied by the degree of relatedness (r). (William Donald Hamilton, 1964)

The Florida scrub jay (*Aphelocoma coerulescens*is) is a bird forming breeding pairs that stay together for the rest of their lives. When an individual fails to find its pair during a breeding season, instead of saving its energy, it will prefer to help other pairs. On average, half of the breeding pairs will receive help from a solitary individual which will assist in giving food to the offspring and defending the nest from predators (Ronald L. Mumme *et al.,* 1989). In 1984, Woolfenden and Fitzpatrick observed breeding pairs who received help and determined the degree of kinship between each breeding pair and the helper. They discovered that, in most of the cases, the helper was related to the breeding pair (Woolfenden, G. E. & Fitzpatrick, J. W., 1984). Thus, most individuals behave altruistically towards their closest relatives which corresponds to the expectations of the inclusive fitness theory.

Examples of altruism towards kin can also be observed in insects. Like ants and bees, termites are eusocial insects. This means that their social structure is characterised by different specialised castes such as reproduction or parental care. In this type of social groups, permanently nonreproducing workers help a few fertile individuals to raise the offspring. The key process explaining the evolution of altruism in nonreproducing workers is the indirect transmission of genes through relatives. This type of social structure is very efficient and contributes to a great ecological success of eusocial species (Laurent Keller & Michel Chapuisat, 2017). *Globitermes sulphureus* is a very common termite species in Southeast Asia (Alain Robert *et al.,* 1996). To fight against their opponents, soldiers primarily use their long mandibles, but they can also sacrifice themselves by expelling a large amount of yellow liquid which is released just behind the prothoracic legs, and which entangles both the termites and their enemies (C. Bordereau *et al.,* 1997). Altruistic self-sacrifice behaviours are common in eusocial species because all individuals of the colony are related. The soldiers do not reproduce so the genes that help the queen to survive without taking in account the survival of the soldiers will be selected and these “altruistic genes” will spread in the colony (Laurent Keller & Michel Chapuisat, 2017).

As altruism towards kin is a very advantageous behaviour in an evolutionary context, it is widely spread in nature. According to our definition, parental care is also a way to behave altruistically. “In bats, as in most other mammals, mothers provide a continuum of protection to their offspring from gestation to weaning” (Thomas H. Kunz and Wendy R. Hood, 2000). Taking care of its offspring is so common among mammals and birds that it is the exceptions that attract our attention (Gubernick, D. J., 2013). But birds are not the only reptiles to take care of their offspring. Crocodiles also show parent-offspring interactions. In their study, Chabert *et al* show that female crocodilians are strongly receptive to the calls of their juveniles. Indeed, substantial records show that fossil archosaurs, which are the common ancestors of birds and crocodilians, also displayed parental care. This provides strong evidence that parental care between birds and crocodiles appeared from a same common ancestor (Chabert *et al*., 2015). However, in contrast to birds and crocodilians, most of reptiles do not provide parental care. We can observe it on some snake species, but it is extremely rare (Dale F. Denardo *et al.,* 2012).

Some altruistic behaviours exist also in other taxa like amphibians or fishes. However, parental care and other altruistic behaviours towards kin are less widespread in aquatic species than in terrestrial ones. Indeed, fishes and most amphibians are used to lay the eggs directly in water. But it is way more difficult to take care of eggs in aquatic habitats rather than on terrestrial ones. According to this, it is more advantageous for an aquatic species to produce more eggs at the expense of giving parental care (Lehtinen, R. M., & Nussbaum, R. A., 2003).

Phylogenetic tree for altruism towards kin

As it is widespread among birds and mammals, altruistic behaviours towards kin probably appeared by homology between them. However, most of reptiles except birds and crocodilians do not behave altruistically towards the offspring. This would suggest that altruistic behaviours appeared by homology in the common ancestor of mammals and reptiles but then disappeared in most species of reptiles like snakes and lizards (see point 2 in Figure 2). However, this can also suggest that altruistic behaviours appeared by convergent evolution between mammals and archosaurs (see point 1 in Figure 2).

However, we also have seen that living on land or in aquatic environments does matter for the evolution of parental care. Aquatic species provide less altruism towards kin than do terrestrial ones. This probably suggest that parental care behaviours appeared when ancestors began to lay eggs in land instead of aquatic habitats and then spread by homology within all mammals and most of reptiles. In addition, as some amphibians, fishes and insects also provide altruistic behaviours towards kin, this type of behaviour could have appeared by homology (see point 3 in Figure 2). However, as it is less frequent in amphibians, fishes or insects than in mammals and reptiles, the probability of a convergent evolution is more possible (see point 2 in Figure 2).

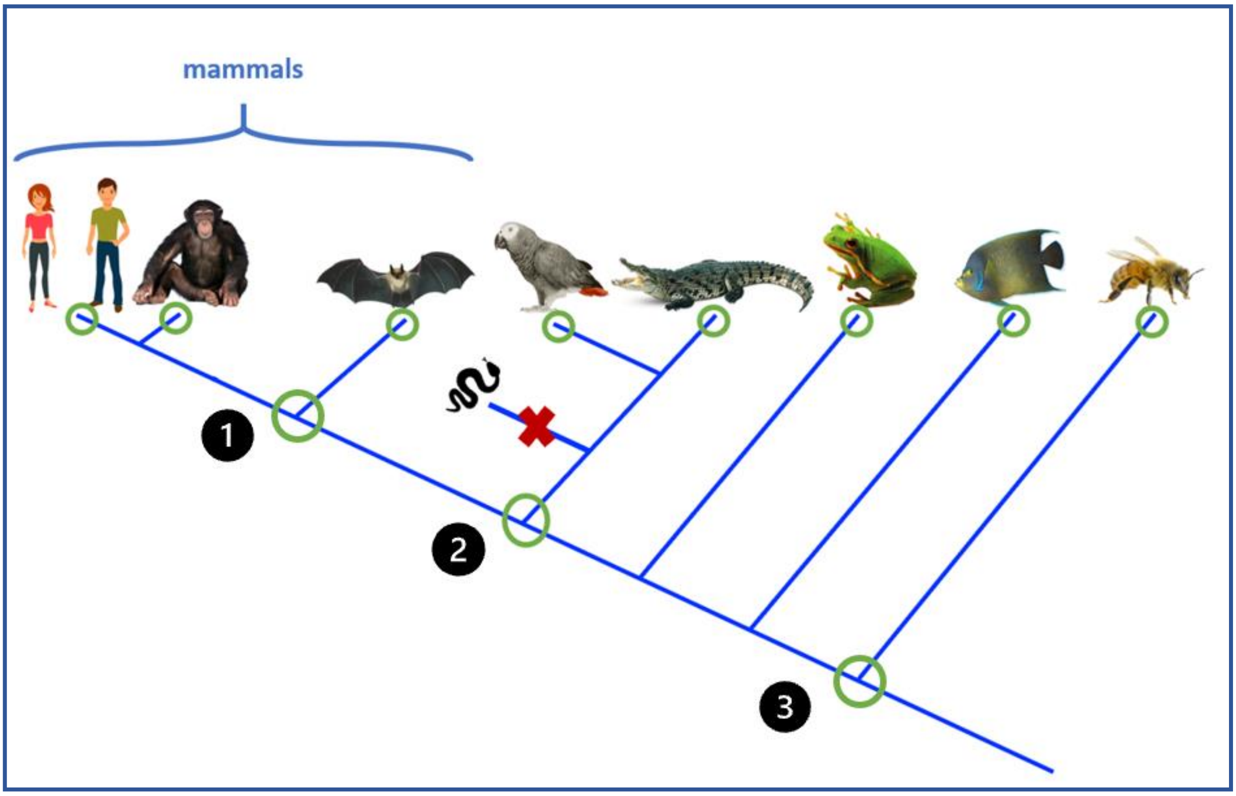

Figure 2: Phylogenetic tree for altruism towards kin. The first point indicates the hypothesis of a convergent evolution between mammals and the others. The second point indicates the hypothesis of a homology between reptiles and mammals and a convergent evolution with amphibians, fish and insects. The point 2 indicates the hypothesis of a homology between all these species.

Altruism towards non kin

As we have seen, altruistic behaviours towards kin can be explained by the inclusive fitness theory. However, altruism towards non kin also exist in nature and cannot be explained by inclusive fitness. This type of behaviours depends on different mechanisms such as reciprocity. Indeed, in some cases, behaving altruistically towards unrelated individuals can be selected by natural selection.

Common vampire bats (*Desmodus rotundus*) feed only on blood and die after 70 h of fasting. However, it is common for this species to live more than 10 years because unfed bats often receive food from roost-mates by regurgitation. In 2013, a study has been published in which the authors suggest that blood sharing dyads in bats would be better explained by reciprocal help than by relatedness or harassment. In the study, some vampire bats have been fasted for 24 hours and returned to the cage with fed groupmates. The relatedness between each individual was estimated by DNA analysis and all social interactions were recorded since the reintroduction of unfed bats. The records showed that donors initiated food sharing more often than recipients, which suggests that the donations were inconsistent with harassment and that donors were behaving altruistically. In addition, as sixty-four per cent of sharing dyads were unrelated, food received was a best predictor of food given across dyads than relatedness. This study shows that the predictive role of reciprocal help can greatly exceeds that of relatedness (Carter & Wilkinson 2013). In this example, costs of helping are offset by the likelihood of the return benefit. Altruism by direct reciprocity can evolve in social groups if individuals can interact with each more than once, and if they can recognize other individuals with whom they have interacted in the past. Altruism by reciprocity has also been found in some species of birds with the suggestion of a convergent evolution (Brucks Désirée & von Bayern Auguste, 2020).

Allomaternal nursing is a rare behaviour in which adults take care of the offspring of other individuals. However, this phenomenon seems to be widespread among some species of primates such as *Cebus Olivaceus* and *Presbytis Johnii.* In addition, allomaternal nursing for these primates seems to be independent of relatedness. Indeed, females facilitated breastfeeding interactions with unrelated infants by raising their arms to expose the nipple, as they would have done with their own infants. As in the case of bats, reciprocity seems to be the mechanism who permitted such a behaviour to evolve. However, instead of direct reciprocity, indiscriminate allonursing seems to be the result of indirect reciprocity. Indeed, allonursing may be a reciprocal behaviour exchanged between adult females via infant nursing. The cost to the mother who lost milk by allonursing is compensated by the high probability that her own infant will also be nursed by other females (Timothy G. O'brien and John G. Robinson, 1991).

We know that humans are more likely to help individuals they have seen help others in previous interactions. One may thus benefit from being altruistic due to gains in "image" (David G. Rand & Martin A. Nowak, 2013). In 2002, Redouan Bshary published an article in which he suggests that image-scoring individuals may be exploitable by cheaters biting cleaner fish. These fish usually feed on parasites by removing it from big species of reef fish. However, cleaner fish can cheat by feeding on client tissue instead of parasites and "cleaners that refrains from taking bites that result in client jolts can be said to behave altruistically compared with conspecifics, that take such bites more regularly" (Redouan Bshary, 2002). But clients approach cooperators and tend to avoid cleaners, that they observe cheating with their current client. The discovery is that cleaners who cheat frequently behave more altruistically with small clients to exploit bigger ones. According to the author, "cheating cleaners use altruism in potentially low-pay-off interactions to deceive and attract image-scoring clients that will be exploited" (Redouan Bshary, 2002).

Phylogenetic tree for altruism towards non kin

As altruism towards non kin is extremely rare in nature, such a behaviour probably appeared by convergent evolution in most of animal species. However, as humans and other primates show similar mechanisms for altruism towards non kin, it is difficult to know if it appeared by analogy or by homology between primates (Felix Warneken *et al.*, 2007).

Other than altruism towards kin, altruism towards non kin seems difficult to observe in insects, amphibians, and most reptiles except birds. However, the lack of information does not prove the absence of altruism towards non kin in these taxa.

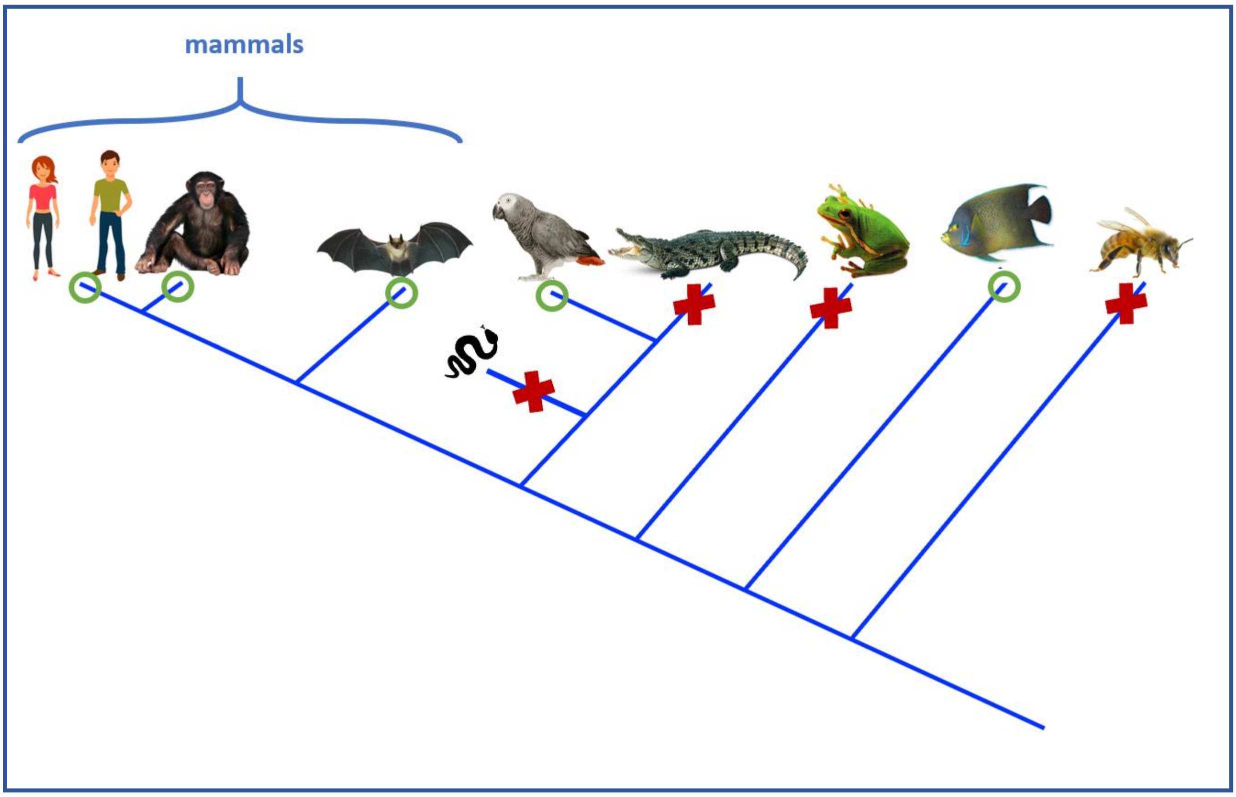

Figure 3: Phylogenetic tree for altruism towards non kin.

Conclusion

As altruism towards kin is common in nature, it probably appeared by homology between a great number of species. On the other hand, as altruism towards non kin is rarer, it probably appeared at different times by convergent evolution. Then, there's no evidence of altruism towards non kin in species that don't behave altruistically towards kin. This could suggest that, at least in some cases, conditions to develop altruism towards kin are included in the conditions to develop altruism towards non kin. It could also suggest that altruism between unrelated individuals evolved from altruism towards kin. Indeed, mutations leading into kin recognition errors could lead to altruistic behaviours between unrelated individuals.

However, the evolutionary origins of altruism towards non kin and the conditions needed to develop such a behaviour are not well known and further research are still needed. In addition, we still don't know if this type of behaviour appeared by analogy or by homology between humans and other primates.

Most studies are mainly based on animal's behaviour observations. However, in my opinion, there is a huge gap on the genetic point of view of this behaviour. Indeed, as behaviours are also dependent of our genes, a better understanding of the genetic origin of altruism could help us answer many questions in this field. Recent studies have shown that oxytocin and vasopressin play an important role in social behaviours and thus, some genetic variants of these neurohormone's receptors could predict the ability for humans to behave more altruistically (Sonne, J. W., & Gash, D. M., 2018). Therefore, studies focusing on the detection of this genetic variants in other animals may allow us to elucidate the origin of altruism.

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Figures

1. Website : Bioninja https://ib.bioninja.com.au/options/option-a-neurobiology-and/a6-ethology/altruism.html