Revista Filosofía UIS

Bonobos y adopción: un análisis de los presupuestos conceptuales de la cooperación biológica

Adoption and Bonobos: An Analysis of the Conceptual Assumptions within Biological Cooperation

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Artículo de reflexión derivado de investigación
Recepción: 2023/10/04 – Aprobación: 2024/03/12
eISSN: 2145-8529
https://doi.org/10.18273/revfil.v23n2-2024012

Resumen: Martin Nowak (2011; 2013) propone cinco mecanismos para la cooperación biológica: selección por parentesco, reciprocidad directa, reciprocidad indirecta, reciprocidad de red y selección grupal, los cuales deben explicar todo comportamiento altruista. Para poner a prueba esto, se presentan dos casos de adopción y los cuidados aloparentales por parte de dos madres bonobos a huérfanas extragrupales (Tokuyama *et al.*, 2021). Estos casos demuestran que ninguno de los mecanismos propuestos por Nowak logra explicar del todo el comportamiento altruista. Finalmente, este artículo cuestiona los supuestos que subyacen a la teoría de Nowak para concluir que es la insuficiencia explicativa de estos supuestos lo que nos impide dar cuenta de la cooperación biológica en los casos de adopción animal.

Palabras clave: bonobos; cooperación; adopción; racionalidad calculada; genocentrismo.

Abstract: Martin Nowak (2011; 2013) proposes five mechanisms for biological cooperation: kin selection, direct reciprocity, indirect reciprocity, net reciprocity, and group selection, which should explain every altruistic behavior. To test this, this paper presents two cases of adoption and alloparental care from two bonobo mothers to orphans outside of the group (Tokuyama *et al.,* 2021). These cases demonstrate that none of the mechanisms proposed by Nowak accomplishes to explain altruistic behavior altogether. Finally, this paper challenges the assumptions that underlie Nowak's theory to conclude that the explicative insufficiency of these assumptions prevents us from giving an account of biological cooperation in cases of animal adoption.

Keywords: bonobos; cooperation; adoption; reckoning rationality; genecentrism.

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Forma de referenciar (APA): Arias Vélez, M. (2024). Bonobos y adopción: un análisis de los presupuestos conceptuales de la cooperación biológica. *Revista Filosofía UIS, 23*(2), 139-154, http://doi.org/10.18273/revfil.v23n2-2024012

1. Introduction

Since the 1960s, biology has developed arguments to explain the phenomenon of cooperation or altruism in nature[1]. One of the most important theorists in this research is Martin Nowak (2011, 2013), who argues that cooperation, selection, and mutation are principles of evolution. He proposes to describe the rules or mechanisms[2] that allow for the emergence and sustenance of every cooperative act. In this sense, Nowak proposes five biological mechanisms for cooperation that correspond to each biological cooperation theory. Given that those mechanisms summarize all theories related to cooperation and altruism and are conceived as rules that describe the causes of cooperation, one would expect that these mechanisms explain every single case of cooperation in nature. Among the multiple cooperative phenomena, one can find alloparental care, a very costly kind of behavior in which an adult individual takes care of an infant that is not directly his or her offspring: in other words, adoption.

I have two main goals in the present paper: First, I will test Nowak's five biological mechanisms with an empirical case of cooperation- adoption in bonobos. Given that this test concludes that none of the mechanisms proposed by Nowak explain these types of cases, the second goal is to determine which theoretical assumptions underlie those five biological mechanisms. I suggest as my main hypothesis that the explicative insufficiency of these assumptions prevents us from accounting for the cases of cooperation in animal adoption.

To achieve the main goals of the paper, in the first section, I present the five biological mechanisms of biological cooperation proposed by Martin Nowak, in which the theories of altruism and biological cooperation are compiled, summarized, and amplified from the sixties until now. Then, in the second section, I describe two empirical cases of adoption and alloparental caretaking published by Tokuyama and her team in 2021. In the third section, I match the five mechanisms to these cases to show that none of them can account for the cooperative behavior demonstrated in them. In the fourth section, I determine two theoretical assumptions behind the mechanisms proposed by Nowak: genetic selfishness and reckoning rationality. Finally, I present some of the main criticisms of these assumptions and conclude that these assumptions are the culprits for the failure to explain obvious cooperative cases like adoption in bonobos according to the cooperation mechanisms proposed by Nowak.

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[1] The problem of altruism in biology theory is as old as Darwin theory itself. In The Descent of Man (2004), Darwin recognizes that in the nature there are cases of cooperation between individuals or groups, something that he finds extremely intriguing. In this text the English naturalist addresses some cases such as human morality or the sterile castes of social insects. The problem in Darwin is that it is unlikely that those who sacrifice themselves for their fellow will survive, and, therefore, they inherit to their progeny the tendency to act altruistically, which implies that in the future this type of actions will completely disappear. In this sense, altruistic behaviors are problematic for the theory of evolution by natural selection and providing an explanation for them becomes counterintuitive to the fundamental principles of the theory. Darwin (2004) responds to the above by appealing to a kind of group selection. For example, in the case of humans, Darwin (2004) argues that altruistic behavior has been beneficial for some human tribes over others and has allowed them to be naturally selected and given rise to human societies. In his opinion, cooperation is possible in the human species because the rational and moral capacity of them, that allows human beings to understand that helping others guarantees receiving help in the future.

[2] It is important to clarify that the Nowak's mechanism notion does not have the Carl Craver's (2007) sense.

2. Biological mechanisms for the evolution of cooperation

The first mechanism Martin Nowak (2011, 2013) shows is kin selection, originally proposed by William D. Hamilton in his paper *The Genetical Evolution of Social Behavior* (1964). He argued that individuals could engage in self-sacrificial behavior due to the range of genes individuals share with their relatives. Such self-sacrificial behavior would aim to ensure the survival of kin and the genes they share. This way, altruistic behavior guarantees their fitness through their relatives. Hamilton called this "inclusive fitness."

Even though kin selection has been the most common biological mechanism for cooperation in explaining altruistic behavior in many species, researchers started to find cases where organisms cooperated with others with whom they did not share genetic material. For these cases, the second mechanism, which Nowak calls direct reciprocity, was proposed. This mechanism was originally suggested by Robert Trivers (1971), who pointed out that two organisms can cooperate if there is a high probability that these organisms will meet again and that the helped organism will reciprocate the favor received. Trivers' explanation allowed biologists to understand cooperative manifestations such as symbiosis or mutualism between organisms of different species.

Direct reciprocity gained strength thanks to elements incorporated by Robert Axelrod, who, in 1981, put this mechanism to the test through a series of experiments, computations, and game theory. Axelrod (1981) proved that if cooperative relations are modeled through the iterated prisoner's dilemma, direct reciprocity takes the form of an evolutionarily stable strategy called TIT FOR TAT, which entails cooperating in the first move and then replicating the action of the other player. Axelrod found that direct reciprocity in this form could easily beat selfish strategies, establish itself in a community, and persist over time.

The third type of cooperative mechanism is indirect reciprocity, originally proposed by Richard D. Alexander (1987) and developed by Nowak and Karl Sigmund (1998). Nowak (2013) realized that factors can enhance reciprocity in certain populations, and it cannot be guaranteed that two cooperators will meet again. In consequence, in cooperative relations of more than two organisms, the reputation of an altruist is important since it allows others to cooperate with them, even without direct reciprocation.

An extension of these ideas led Nowak to propose the fourth mechanism for biological cooperation: net reciprocity. This mechanism describes a relation between the size of populations, geographic dispersion, and reciprocity. Nowak (2013) points out that cooperating individuals from large populations may start forming groups or networks to help each other. To prove this, Nowak designed a computer game to relate a geographical space with randomly mixed populations of cooperators and egoists and found that both could coexist. Moreover, the dispersion of reciprocity between individuals (regardless of the initial number of cooperators and egoists) always resulted in an abundance of the former.

The last mechanism for cooperation, group selection, was proposed by V. C. Wynne-Edwards (1962) and developed initially by Wilson (1975) and then with Sober (1989, 1994, 1994a), who, since the late 1890s and the early2000s began to reintroduce the debates about the group selection in the field of biology, which had been abandoned since the sixties. These authors showed that the group, as a selection unit, is closely linked to the rise of altruists within groups dominated by egoists. From this, a group perspective could explain many cooperative behaviors, even if this conflicts with the perspective of selection focused on the individual as a unit of natural selection.

The central idea of Sober and Wilsons' proposal (1994) resides in accepting a pluralism of selection units; in other words, natural selection does not operate exclusively on one sole type of unit- whether it is the gene, the individual, or the group that it can operate at various levels of biological hierarchy at the same time. It was sufficient for any of these units to start operating jointly and organically in favor of a common goal for natural selection to favor it. In that case, it would make sense to find altruistic and collaborative behaviors that benefit the group, even if they do not benefit an individual, and yet be naturally selected.

In sum, Nowak (2011) proposes that every cooperation theory can be described as a biological mechanism: kin selection, direct reciprocity, indirect reciprocity, net reciprocity, and group selection. These mechanisms make cooperation possible; cooperative phenomena should only be found within these five mechanisms. In the next section, I will show two cooperative cases that any of these previously explained mechanisms cannot model to argue that such explanatory insufficiency lies in the theoretical assumptions underlying the five mechanisms.

3. Two anomalous cases of extra-group adoption in bonobos

Among the many forms of altruism and cooperation, one of the most intriguing and costly is the adoption- a form of alloparental caretaking characterized by an organism providing for the offspring of other individuals that are not their own. In this section, I will present two cases of adoption in bonobos. I aim to test Nowak's (2011, 2013) biological mechanisms for cooperation. The inability of these mechanisms to account for specific cases of adoption inspires a search for the assumptions that underlie the theories about collaboration. Alloparental caretaking is a type of behavior that is highly costly because the foster mother pays a similar price to that which a biological mother would pay for her offspring.

Furthermore, it is a very rare behavior, even more so when the adopted animal is from outside the group. In a recently published report about extra-group adoption in great apes, Tokuyama *et al.* (2021) observed two female bonobos (*Pan paniscus*) adopting babies from different groups. The first case is as follows:

> **Case I.** A multiparous female (Marie) with existent offspring permanently adopted a baby called Flora, which belongs to a different unknown group. At the moment of adoption, Marie had two infants of her own: Marina (July 2014) and Margaux (March 2017). The observations show that Marie cared for Flora and her biological offspring, providing for her and the other infants.

The care provided by Marie included keeping her infants constantly by her side within less than five meters, carrying them, grooming them, sharing food, nesting, and breastfeeding. Comforting behaviors, such as cuddling or genital-genital rubbing after the infants experience distressing episodes, can also be added to the list. Also, other alloparental behaviors are notable. For example, there were times when Marie carried Flora ventrally while she carried Margaux dorsally. It was also registered that Marie took both infants on her back while Marina, her eldest, walked independently. The research group observed Marina crying and screaming when she tried to ride her mother's back, while Marie rejected her, as happened in April and May of 2020 (Tokuyama *et al.,* 2021). When the bonobos started a trip, researchers observed typical interactions between mothers and their children in Marie and Flora, such as the adopted animal running towards her foster mother as she waited patiently before allowing her to cling to her body.

Researchers noted that they observed Marie breastfeeding Flora occasionally and deduced that Flora was likely drinking milk from her foster mother, given that she had her offspring at the point of adoption (Tokuyama *et al.,* 2021). According to the observations, it stands out that Marina and Margaux never displayed any aggressive behavior towards Flora and were usually seen playing and sharing together.

Furthermore, Marie exhibited typical motherly behavior towards Flora, aimed at encouraging her to walk independently. For example, in August 2019, researchers observed Marie walking away from Flora but stopped when she started screaming. This behavior caused the foster mother to wait until the adopted infant climbed onto her back again (Tokuyama *et al.,* 2021). Despite the frequency of carrying decreasing gradually as Flora grew up, researchers noted that Marie still had her occasionally and continued to provide her with essential maternal care until March 2020, when the observation ended due to the COVID-19 pandemic. The second case is as follows:

> **Case II**. Chio, an adult female without dependent offspring, permanently adopted an infant that did not belong to her group, to which researchers and Ruby. The researchers estimated that Chio should be between 52 and 57 years old by October 2019, when she adopted Ruby. They assumed that the female was postmenopausal. Moreover, researchers pointed out that the adult bonobo had not given birth since 2012, and at that moment, she did not have any offspring in the groups nearest to PW, which was her own. Chio was observed without a baby during the intergroup association between PE and PW on the 28th of September 2019. On the fourth day after the association, researchers noted that Chio was carrying an infawhoRuby that did not belong to PW.

It was observed that the foster mother and the infant were constantly together. Chio carried Ruby dorsally and ventrally, cleaned her up, nested with her, and comforted her with hugs and genital-to-genital rubbings. In November 2019, researchers saw Chio breastfeeding Ruby, and at other times, they observed them sharing food, like fruits. Researchers claim that Ruby was accepted by other group adults who were seen playing with her sometimes, and violent behaviors towards her were never reported.

Now, I will examine if Nowak`s five mechanisms match the previously presented cooperative cases to show that none correspond to the cases. I aim to affirm that such explanatory insufficiency is due to the theoretical assumptions underlying the five mechanisms, which is why it is essential to determine such assumptions.

4. Extra-group adoption in bonobos and the five mechanisms for cooperation

Nowak (2013) claims that the five mechanisms for biological cooperation operate as rules that must be achieved for cooperation to emerge and be sustained. If that is the case, it can be expected that at least one (or more) of the mechanisms should be adequate to explain the two cases presented in the last section. In this section, I will show that none of the mechanisms proposed by Nowak can fully explain and account for these cases.

The first mechanism, kin selection, is considered the primary mechanism involved in the evolution of adoption. However, in the cases described, the foster mothers did not share mtDNA haplotypes with the adopted babies (Tokuyama *et al.,* 2021). This suggests that they were not maternally related to each other. Furthermore, as the researchers reported, none of the adopted animals shared any mtDNA haplotypes with any other female in the group in which they were adopted. From this, it can be concluded that cooperative behavior in cases I and II had a goal to foster direct or indirect fitness.

Another typical argument for alloparental caretaking is the *'learning to mother'* hypothesis, which proposes that alloparental caretaking is a form of learning from which young nulliparous learn to provide attention to babies. This allows them to enhance the odds of survival of their future offspring. The teaching-to-mother hypothesis can be related to Triver's and Axelrod's direct reciprocity, given that both interactions benefit mutually. Moreover, the parameter of discount w (the probability of future reencounters) is greater than the cost-benefit ratio. In other words, the interaction between the mother and the adopted is reciprocal because it allows the adopted individual to reciprocate, in some way, the favor received.

Regarding the cases described by Tokuyama *et al*. (2021), the learning-to-mother hypothesis does not seem to be a viable alternative because the foster mothers did not need, in the moment of adoption, additional training for future nurturing: in case I, the mother already had two dependent offspring before adoption; and in case II, the mother had already had offspring before and was, presumably, postmenopausal, so that she could not give birth again. On the other hand, the adopted babies were female and generally emigrated to other groups when they grew up (Sakamaki *et al.,* 2015). This means that it is doubtful that the adoptee could have reciprocated, in any way, the benefits received. This implies that the probability of a future encounter between the foster mother and the adoptee would decrease progressively over time. The result is that the cost-benefit ratio is smaller, violating the equation $w>c/b$ proposed by Nowak (2013).

For the third mechanism, Tokuyama *et al*. explain the migration process of the young, claiming that the bonobos:

> Form multi-male, multi-female social groups with male philopatry, where males remain in their natal group throughout their life, and females typically emigrate before reaching sexual maturation. Intergroup relationships in bonobos can be tolerant; separate groups sometimes associate for a few days. Individuals usually separate back into their original group when an inter-group association ends, except for nulliparous immigrant females. (2021, p. 2)

From this, indirect reciprocity needs to describe the cooperative relation in adoption adequately. Likewise, this does not account for the rise in fitness of the mothers because it is doubtful that the adoptions brought any specific profit or increased the social status of the foster mothers within the group. In other words, it needs to be clarified what type of benefit exists in adopting an individual who does not have, nor could have, a privileged position within a patrilineal group from which she would have to emigrate when she grows up. In the two cases formerly described, even though the adoption attracted the attention of other females and encouraged them to interact with the foster mother, it did not necessarily improve their social status or reputability.

Given other observations recently published by Tokuyama (2016, 2019) about the same geographical area of study as cases I and II previously described, it is known that net reciprocity plays an important role for bonobos, more specifically for the females, who form female coalitions to defend themselves and others from male aggressions (Tokuyama and Furuichi, 2016). However, this is different from the adoptions described. The adoptions do not respond to actions belonging to networks of females cooperating to adopt orphan babies because neither Marie nor Chio belongs to a particular network, nor do they belong to the same social group, and they have not had contact with each other or are related in any way. Therefore, the cases of extra-group alloparental caretaking exposed by Tokuyama *et al*. (2021) do not correspond to behaviors of net reciprocity, nor is it clear how these can enhance the fitness of the mothers or the adopted.

Competition between groups is common for bonobos, as demonstrated by Tokuyama *et al*. (2019, 2021) in the groups from which the described cases originate. Researchers claim that "although bonobos of different groups can be tolerant of each other, they (especially males) may act aggressively and form coalitions to attack individuals of other groups, suggesting that inter-group competition exists" (Tokuyama *et al.,* 2021, p. 2). Additionally, some experiments with bonobos in captivity have shown that they have long-term memory and can distinguish group members from others who do not belong to their group (Keenan *et al.,* 2016). Considering their strong and stable group affiliations and capacity for recognizing each other, it is doubtful that the adoptions between groups were not accepted. For the cases referred to, it is feasible that the group knew that the adopted infants did not belong to their social group but to another group with which they competed for resources.

As a consequence, I asked why the group members accepted the adoptions. According to the researchers, bonobos are socially tolerant of immaturity. Still, it needs to be clarified how this type of adoption would foster the cooperative mechanism through group selection and how it would enhance fitness. On the other hand, it cannot be asserted that adoption guarantees some alliances with other nearby groups, given that these alliances already happen without the need for adoptions (Sakamaki *et al.,* 2018; Tokuyama *et al.,* 2019, 2021). In the same way, it cannot be asserted that the alloparental caretaking provided by Chio and Marie gave some advantages to their social groups concerning others.

In summary, the cases of alloparental caretaking for extra-group infants formerly described do not explain an increment in fitness using the mechanisms of biological cooperation. It is not kin selection, nor direct or indirect reciprocity, nor net reciprocity, or group selection. This behavior only considerably enhances extra-group relations and intragroup relations. It does not give an adaptive advantage compared to competing groups. Therefore, if none of the five traditional mechanisms for biological cooperation explains these behaviors, to what do cases I and II respond? Why does none of these mechanisms explain a relevant case of biological cooperation?

We should identify the theoretical assumptions behind the evolutionary mechanisms for cooperation to understand their relation to those described and show that these anomalous cases cannot be explained within the theoretical framework proposed by these five mechanisms. More than the assumptions underpinning these mechanisms are needed to explain biological cooperation and exclude too much from their framework. In the last section, I will determine the theoretical assumptions underlying the mechanisms for biological cooperation and address some arguments against them.

5. Genetical selfishness and rationality: the assumptions underlying the biological mechanisms for cooperation.

Every one of the five mechanisms proposed by Nowak (2011, 2013) can be understood as a theoretical framework for biological cooperation. All these mechanisms participate in at least two theoretical assumptions that allow them to see and understand natural phenomena they engage with genetic selfishness and reckoning or economic rationality. The first one, genetic selfishness (the framework centered on genes)[3], is a proposal that underpins much of the conceptual foundation of neo-Darwinism and modern synthesis (Tudge, 2013). This notion proposes that genes are selfish reproducers while organisms are mere vehicles for realizing that goal. Hence, the gene is the principal actor of evolution, and every biological interaction can be reduced to individual genes, with the basic survival function being mere genetic replication. In this sense, every altruistic behavior must be explained by genetic reproduction because an organism is biologically successful if it achieves genetic inheritance to the next generation (fitness).

Many arguments have been against the framework centered on genes, especially its explicative insufficiency throughout biology. Some of the most important ones have come from the Development Systems Theory (DST) and the Extended Evolution Synthesis (EES). In the first case, we can reference the text *The Ontology of Information* (1985) by Susan Oyama, who, through an analysis of the concept of information, accuses gene-centrism of perpetuating the nature/culture dichotomy in the form of the gene/environment relationship. She claims that genes have been understood as the development architects, enjoying certain privileges in these explanations. Oyama (1985) claims that gene-centrism is a new form of preformationism. This implies that the information necessary for development is codified beforehand in the genes. According to her, genes are only one of the factors that influence the development processes, and it should also be recognized that the environment plays an

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[3] Genetical egoism goes back to the book *Adaptation and Natural Selection* (1966) de George C. Williams, although it has been popularized by Richard Dawkins in *The Selfish Gene* (1976).

important role—ontogeny results from the constructive interaction between genetic and environmental factors.

More recently, in the EES, we find the book by Eva Jablonka and Marion Lamb: *Evolution in Four Dimensions* (2014). The authors propose that the notion of genetic heredity is not the only one but rather one of four types of hereditary dimensions equally relevant to a theory of biological evolution. For Jablonka and Lamb, the concept of inheritance generally used by gene-centrism is narrow because it cannot incorporate recent results and ideas from molecular biology or the behavioral sciences. For them, that notion of inheritance needs to be revised for the biology of the XXI century.

So, within the framework of EES, a proposal that tries to challenge the neodarwinist version centered on genes (Laland *et al.,* 2015), Jablonka and Lamb (2014) argue that all living organisms have at least two hereditary systems: (1) the genetic and (2) the epigenetic. Furthermore, many animals can transmit information through (3) systems of behavioral heredity, and human beings can also inherit huge amounts of information through language. That is, humans inherit information through a (4) system of symbolic heredity. These four systems provide meaningful variations in organisms that, according to Jablonka and Lamb, can be naturally selected.

Accepting this proposal allows for a broader vision of evolution, where genes are not the only protagonists of natural selection. According to the authors, it would be inadequate to think of the gene as an individual unit because developments in molecular biology show that genetic networks are composed of hundreds of genes and genetic products that work together to develop a particular trait. In this sense, the classical version proposed by Dawkins and others needs to be revised. According to Jablonka and Lamb, molecular biology has shown that it is no longer correct to think about the gene as an independent and autonomous pathway of DNA that codifies information to produce a protein. On the contrary, what a gene produces depends on other sequences of DNA and the interaction with the environment, as Oyama (1985) pointed out. This means genes only have meaning inside the genetic system, not individually.

Equally, the stability of the DNA does not depend exclusively on genes but on a complex and sophisticated set of mechanisms that work as an integrated whole, not exclusively emanating from a particular gene. From this, we can conclude that the image of evolution as a change in the frequency of one or more independent genes is questionable. The genome is a completely ordered system, not merely collecting isolated genes with individual functions. Following this argument, fundamental phenomena for evolution, such as genetic variability, are understood as system properties controlled by it. In consequence, genes are not the protagonists of evolution, nor can all biological interactions be reduced to individual genes. Also, the basic function of survival is different from genetic replicability. Therefore, it is necessary to think of nature in biology as something that goes beyond a purely genetic and reductionist world vision.

The second assumption invokes economic reckoning rationality[4], which is mathematized using game theory. This theory models interactive economic situations based on the notion of a rational agent that must take into consideration the deliberations of other agents involved, who, at the same time, take into consideration their deliberations (Grüne-Yanoff and Lehtinen, 2012) when deciding or acting. Games are situations designed under specific rules in which rational agents must make choices to maximize utility. They must predict the behavior of other players and modify theirs accordingly. The way to do that is to establish some strategies for playing.

In the 1970s, John Maynard Smith began applying game theory in biology, originally developed in the economic sciences, arguing that natural selection should select organisms that adopt optimal strategies (evolutionary stable strategies) within their contexts, just as the players in Game theory decide to use rational strategy to obtain better rewards (Maynard Smith, 1972). Game theory considers organisms as machines genetically programmed (Dawkins, 1976) with a calculating capacity and motivated only by self-interest (egoism) (Jon Elster, 2011). In this sense, organisms behave as economic agents, and cost-benefit functions define all biological relationships (cooperative or not).

Rationality, as understood by Game theory, has been heavily criticized (Elster, 1979, 2011; Simon, 1995). Most of the arguments against that type of rationality can also be applied to its biological version because the notion of *homo economicus*, upon which the structure of Game theory is built, consists of two main points that play fundamental roles within the evolutionary version of this theory: on one hand, perfect rationality and, on the other, self-interest (egoism), both closely interlinked. It is considered that an agent is rational because it chooses amongst multiple options only the one that maximizes its interest.

One of the strongest arguments against this reckoning rationality is that, in biological terms, regardless of the success of evolutionary Game theory, living organisms are not biologically programmed with perfect economic rationality. The idea that self-interest is the main or the only motivation of living beings, or that they are only looking to maximize their benefit, is not a biological notion but an economic one that has already been strongly criticized in economics. This notion is a characterization of the economic interests of human beings, but it should not be taken as a guide to the motivations of living beings in general. Even for economics, homo economicus, selfish and rational, is not a model (Morgan, 2006). The image of living beings as selfish and only living to maximize utility is an exaggerated straw man of what is thought about the modern consumer. Still, it does not represent how the rest of biological beings live and relate to each other.

Likewise, if living beings are not gifted with perfect rationality, neither should we assume that they are genetically preprogrammed with a set of logical strategies that are expressed as instinctive behavior to address specific situations, nor should we assume that organisms identify Nash's equilibrium as an evolutionary stable strategy that they apply instinctively, or that natural selection favors organisms that choose the best strategy from a

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[4] Reckoning rationality was proposed originally by John von Neuman and Oskar Morgenstern (1947).

collection of choices, as pointed out by Maynard Smith (1972). Thus, if living beings are not economic machines with perfect rationality, they are not calculating players or logical experts in a game like The Prisoners' Dilemma. Biological relationships are highly complex and intricate, so they cannot be reduced to cost-benefit analyses or represented simply as strategic interactions in a game.

As a result, although methodologically successful, the prisoners' dilemma is insufficient in ontological terms. Consequently, Game theory must not be taken as an insightful perspective of rationality, much less its concept of rationality as universal (Grüne-Yanoff and Lehtinen, 2012). It is important to remember that game theory and the games' structure lack any empirical content; they are just tools to model highly hypothetical or exclusively mathematical situations (Grüne-Yanoff and Lehtinen, 2012). They are not an exact representation of interactions in the world but rather fictions from which researchers can extract valuable insights.

Consequently, the mistake is not found in using Game theory to model biological relationships but in attributing idealized characteristics found in Game theory to them. These characteristics are not ontological attributes of biological individuals. Finally, the notion of a rational agent is problematic in biological terms because it implies being able to distinguish the interactions between cooperators clearly. These types of distinctions can be observed among microorganisms that generate cooperative relationships that are highly intricate and often composed of organisms of different species (Dupré, 2012). Hence, the idea of a rational agent, calculating and selfish, is inconsistent with a more precise explanation of the cooperative relationships in nature[5].

These assumptions are a byproduct of the context in which the biological mechanisms for cooperation were postulated, the influences of other problems in biology and philosophy of biology, their relation to the mathematical methods in other sciences such as economics, and how they understand nature. As a worldview, these assumptions, although scientific, have a strong philosophical component, and they pave the ground for biology(or not) to understand a particular phenomenon, in this case, cooperative behaviors such as the ones formerly described. These assumptions are the result of a tendency to justify the idea that, by nature, life is competitive, ferocious, and selfish; the interest in others, in the group or the community in which living beings dwell, is not more than a disguise of their selfish condition and their uninterested rationality, calculating and individualistic.

These ideas have impregnated science in fields as diverse as anthropology, economics, and biology. These philosophical constructions can be tracked for centuries (Tomasello, 2009). Thomas Hobbes (2017) and Niccolò Machiavelli (2008) have already proposed that human nature is ferocious; Adam Smith (2010) defined human nature as a profound love for

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[5] These are not the only arguments against this assumption; there is a vast literature with which one can contrast or develop what has been exposed here. See Zamagni (2006), Kahneman (2011), Bowles (2016), or Thaler (2016, 2018); there are also proposals such as Rampello (2019) that take into consideration a biased rationality, or the ones by Fehr and Gächter (2002), Fehr and Rockenbach (2003), Gintis *et al* (2005), Rockenbach and Milinski (2006) and Patrici Calvo (2018), who reject economic egoism and accept reciprocal cooperation as a factor in economic rationality.

oneself; in a sad poem, Alfred Lord Tennyson (2013) pointed out that nature was red in teeth and claws; Darwin himself (2021) described it as a struggle for survival and even Spencer (1866) said that it was the place where only the fittest could survive. Competition and individualism have been, for centuries, the best description of nature. With the development of molecular biology, the origin of this tendency was clarified: selfishness relied on genes. All these tales are an inheritance of the philosophical selfishness that has survived throughout the ages, where it seems more logical to think that nature is ruled by selfishness and competition. It is upon this that the mechanisms of biological cooperation have been cemented. They, too, have inherited the idea that living organisms are genetically and rationally selfish and individual, perpetuating an idea of life incompatible with the observation of cooperative phenomena such as adoption in bonobos.

6. Conclusion

In conclusion, the assumptions of gene-centrism and reckoning rationality that underlie the five mechanisms of biological cooperation need to be revised to explain the cooperative phenomenon of adoption (alloparental caretaking) in non-human animals such as bonobos. An analysis of these assumptions and the search for more comprehensive theoretical frameworks would allow a better understanding of cooperative phenomena that occur in nature. It is necessary to rethink alternatives to these assumptions and, thereby, alternatives to the five mechanisms to provide a fitting explanation of the cases of cooperation that are beyond their reach, such as the ones presented by Tokuyama *et al*. (2021). It is necessary to reconsider cooperation within an evolutionary perspective that incorporates the new findings in biological research and abandons some notions that hinder their understanding.

For example, it is necessary to examine biological cooperation outside the scope of the framework centered on genes and the proposal of the selfish gene. It would also be required to establish different horizons of understanding to achieve a more holistic and harmonious image of nature. The Evolutionary Extended Synthesis and DST are important breakthroughs along these lines. The abandonment of genetic reductionism would enable us to describe another set of phenomena that the mechanisms proposed by Nowak and the assumptions that lie beneath them leave out, such as the cooperative relationships shown by the cases of adoption in bonobos.

I propose interesting alternatives, such as those presented by Frans de Waal (2008), who suggests that empathy and tolerance evolved to serve the ultimate goal of cooperation: to produce benefits for all who participate (de Waal and Preston, 2017). Two explanations have been proposed for this. The first is that empathy seeks to help the other to improve the helper's internal state. The second is that the helper would expect their favor to be returned in some way in the future (intentionally selfish altruism). This last perspective can be closely related to the mechanism of direct reciprocity and reckoning rationality assumption. Concerning this perspective on empathy and cooperation, de Waal (2008) argues that the return benefits of reciprocal altruistic action generally remain beyond the cognitive horizon of the helper; that is, they occur so far in time that it is difficult to ensure that the animal can relate the consequence to the original act. He also adds that, even if cooperative behavior were based on short-term intrinsic rewards (such as improving the internal state of the helper) or long-term extrinsic rewards (such as a future benefit), none of this would deny an altruistic impulse; indeed, both positions imply it. Thus, de Waal (2008) asserts that empathy evolved as an instinctive mechanism for targeted altruistic behaviors in someone in distress or pain (such as consolation).

Furthermore, he claims that empathy allows a rapid and automatic relationship with the emotional states of others, which serves to regulate social interactions. Given that, it can be thought, as Yamamoto and Takimoto (2012) maintain, that empathy arises to promote prosocial behavior in situations in which animals cannot predict the return benefits, or as Schulz (2017) points out, that empathy is like a tool that has evolved to help in the reliable establishment of cooperative interactions, which makes it a highly adaptive trait. This approach may be a fruitful pathway instead of the five mechanisms of Nowak.

Acknowledgments

This paper was written while I received a research grant from Consejo Nacional de Ciencia y Tecnología (Conahcyt); thank you. Also, I would like to congratulate Juan Felipe Guevara-Aristizábal, Violeta Aréchiga-Córdova, and Siobhan F. Guerrero-McManus for reading and giving helpful comments and corrections on previous versions. In addition, I would like to thank Miguel Rotter for helping me with the English version. Their contributions were significant for the elaboration of this paper.

References

Alexander, R. D. (1987). *The Biology of Moral Systems*. Transaction Publishers.

Axelrod, R. (1981). The Emergence of Cooperation among Egoists. *The American Political Science Review*, 75 (2), 306-318. https://doi.org/10.2307/1961366

Bowles, S. (2016). *Moral Economy. Why Good Incentives Are No Substitute for Good Citizens.* Yale University Press.

Calvo, P. (2018). *The Cordial Economy: Ethics, Recognition and Reciprocity*. Springer

Darwin, C. (2004). *The Descent of Man*. Penguin Classics.

Darwin, C. (2021). *The Origin of Species*. Fingerprint! Publising.

Dawkins, R. (1976). *The Selfish Gene*. Oxford University Press

De Waal, F. (2008). Putting the Altruism Back into Altruism: The Evolution of Empathy. *Annual Review of Psychology, 59(1)*, 279-300. https://doi.org/10.1146/annurev.psych.59.103006.093625

De Waal, F. y Preston, S. (2017). Mammalian empathy: behavioural manifestations and neural basis. *Nat Rev Neurosci 18*, 498–509. https://doi.org/10.1038/nrn.2017.72

Dupré, J. (2012). *Processes of Life: Essays in the Philosophy of Biology*. Oxford University Press.

Elster, J. (1979). *Ulysses and the Sirens: Studies in Rationality and Irrationality*. Cambrige University Press.

Elster, J. (2011). *El desinterés: tratado crítico del hombre económico (I)*. (R. Ancira, trad.). Siglo XXI Editores.

Fehr, E. and Gachter, S. (2002). Altruistic punishment in humans. *Nature, 415*(6868), 137-140. https://doi.org/10.1038/415137a

Fehr, E. and Rockenbach, B. (2003). Detrimental effects of sanctions on human altruism. *Nature, 422*(6928), 137-140.

Gintis, H., Bowles, S., Boyd, R. and Fehr, E. (eds.) (2005). *Moral Sentiments and Material Interests. The Foundations of Cooperation in Economic Life.* The MIT Press.

Grüne-Yanoff, T., and Lehtinen, A. (2012). Philosophy of game theory. In U. Mäki (Ed.), *Philosophy of economics*, (pp. 531-576). North-Holland.

Hamilton, W. D. (1964). The Genetical Evolution of Social Behaviour I and II. *Journal of Theoretical Biology, 7*, 1-16 & 17-52.

Hobbes, T. 2017. *Leviathan.* Penguin Classics.

Jablonka, E. and Lamb, M. (2014). *Evolution in Four Dimensions: genetic, epigenetic, behavioral, and symbolic variation in the history of life.* The MIT Press.

Kahneman, D. (2017). *Pensar rápido, pensar despacio*. Debolsillo.

Keenan, S., Mathevon, N., Stevens, J., Guéry, J. P., Zuberbühler, K. and Levréro, F. (2016). Enduring voice recognition in bonobos. *Scientific Reports, 6*, 1-8. https://doi.org/10.1038/srep22046

Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Muller, G.B., Moczek, A., Jablonka, E., and Odling-Smee J. (2015). The extended evolutionary synthesis: its structure, assumptions and predictions. *Proc. R. Soc. B, 282*, 1-14. https://doi.org/10.1098/rspb.2015.1019

Lord Tennyson, A. (2013). *In Memoriam A. H. H.* CreateSpace Independent Publishing Platform.

Machiavelli, N. (2008). *The Prince.* Oxford University Press.

Maynard Smith, J. (1972). Game Theory and the evolution of fighting. In Maynard Smith, J., *On evolution*. Edinburg University Press.

Morgan, M. (2006). Economic Man as Model Man: Ideal Types, Idealization and Caricatures. *Journal of the History of Economic Thought, 28*(1), 1-27. https://doi.org/10.1080/10427710500509763

Morgenstern, O., and von Neumann, J., (1947). *Theory of Games and Economic Behavior*. Princeton University Press.

Nowak, M. (2013). Five Rules for the Evolution of Cooperation. In Nowak, M. and Coakley, S., (Eds.), *Evolution, games, and God: the principle of cooperation* (pp. 99-114). Harvard University Press.

Nowak, M. and Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring. *Nature, 393*, 573-577. https://doi.org/10.1038/31225

Nowak, M., and Highfield, R. (2011). *SuperCooperator. Altruism, Evolution, and Why We Need Each Other to Succeed.* Free Press.

Rampello, S. (2019). Los sesgos en la toma de decisiones. *Revista Perspectivas de las Ciencias Económicas y Jurídicas, 9*(1), 85-94. http://dx.doi.org/10.19137/perspectivas-2019-v9n1a06

Rockenbach, B. and Milinski, M. (2006). The efficient interaction of indirect reciprocity and costly punishment. *Nature, 444*, 718-723. https://doi.org/10.1038/nature05229

Sakamaki, T., Behncke, I., Laporte, M., Mulavwa, M., Ryu, H., Takemoto, H., Tokuyama, N., Yamamoto, S., and Furuichi, T. (2015). Intergroup transfer of females and social relationships between immigrants and residents in bonobo (Pan paniscus) societies. In Furuichi T., Yamagiwa J., and Aureli F. (Eds) *Dispersing Primate Females*. Primatology Monographs. Springer.

Sakamaki, T., Ryu, H., Toda, K., Tokuyama, N. and Furuichi, T. (2018). Increased frequency of intergroup encounters in wild bonobos (Pan paniscus) around the yearly peak in fruit abundance at Wamba. *International Journal of Primatology, 39*, 685-70. https://doi.org/10.1007/s10764-018-0058-2

Schulz, A. W. (2017). The evolution of empathy. En H. L. Maibom (Ed.), *The Routledge handbook of philosophy of empathy* (pp. 64-73). Taylor & Francis Group.

Simon, H. A. (1955). A behavioral model of rational choice. *Quarterly Journal of Economics, 69*, 99-118. https://doi.org/10.2307/1884852

Smith, A. (2010). *The Theory of Moral Sentiments.* Penguin Classics.

Sober, E. and Wilson, D.S. (1989). Reviving the superorganism. *Journal of theoretical Biology, 136*(3), 337-356. https://doi.org/10.1016/s0022-5193(89)80169-9

Sober, E. and Wilson, D.S. (1994). A Critical Review of Philosophical Work on the Units of Selection Problem. *Philosophy of Science, 61*(4), 534-555. https://doi.org/10.1086/289821

Sober, E. and Wilson, D.S. (1994a). Reintroducing Group Selection to the Human Behavioral Sciences. *Behavioral and Brain Sciences, 17*(4), 585-654. https://doi.org/10.1017/S0140525X00036104

Spencer, H. (1866). *The Principles of Biology: Vol. 1 and 2.* D. Appleton Co.

Thaler, R. (2016). *Todo lo que he aprendido con la psicología económica. El encuentro entre la economía y la psicología y sus implicaciones para los individuos*. Ediciones Deusto.

Thaler, R. (2018). Economía del comportamiento: pasado, presente y futuro. *Revista de Economía Institucional, 38* (20), 9–43. https://doi.org/10.18601/01245996.v20n38.02

Tokuyama, N., and Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour, 119*, 27-35. https://doi.org/10.1016/j.anbehav.2016.06.021

Tokuyama, N., Sakamaki, T., and Furuichi, T. (2019). Inter-group aggressive interaction patterns indicate male mate defense and female cooperation across bonobo groups at Wamba, Democratic Republic of The Congo. *American journal of physical anthropology, 170*(4), 535-550. https://doi.org/10.1002/ajpa.23929

Tokuyama, N., Toda, K., Poiret, M. L., Iyokango, B., Bakaa, B., and Ishizuka, S. (2021). Two wild female bonobos adopted infants from a different social group at Wamba. *Scientific reports, 11*(1), 1-11. https://doi.org/10.1038/s41598-021-83667-2

Tomasello, M. (2009). *Why We Cooperate*. The MIT Press.

Trivers, R. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology, 46* (1), 35-57. https://doi.org/10.1086/406755

Tudge, C. (2013). *Why Genes are Not Selfish, and People are Nice: A Challenge to the Dangerous Ideas that Dominate Our Lives.* Floris Books.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton University Press.

Wilson, D. S. (1975). A theory of group selection. *Proceedings of the national academy of sciences, 72*(1), 143-146. https://doi.org/10.1073/pnas.72.1.143

Wynne-Edwards, V. C. (1962). *Animal Dispersion in Relation to Social Behavior*. Oliver & Boyd.

Yamamoto, S., & Takimoto, A. (2012). Empathy and Fairness: Psychological Mechanisms for Eliciting and Maintaining Prosociality and Cooperation in Primates. *Social Justice Research, 25(3)*, 233-255.

Zamagni, S. (2006). *Heterogeneidad motivacional y comportamiento económico. La perspectiva de la economía civil.* Unión Editorial.