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Why do unrelated individuals within the same species cooperate?

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ABSTRACT

Gradually it becomes apparent that helping behaviour between unrelated individuals within the same species is more common than was thought. The benefits that affects these individuals are direct, but the exact benefits and their role in the evolution and maintenance of cooperation remain unclear. In this thesis I will therefore summarize what the known direct benefits are. The benefits can affect the fitness of the helper by increasing his own survivability or his reproductive success. The survivability is enhanced through the lowering of stress and food sharing. The reproductive success is enhanced through thermoregulation in bat crèches and in cooperative breeding through future territory and mate access and development of parenting skills. Aside from the benefits of helping, there are also costs that need to be considered. Investment plays a big role in social networking and maintaining successful cooperative systems. When there is little evidence for direct or indirect fitness benefits, manipulation is likely to cause seemingly altruistic behaviour. Summarizing all direct benefits found in cooperation between non-relatives, it can be concluded that direct benefits play a major role in the evolutionary maintenance of cooperative behaviour.

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INTRODUCTION

Group dynamics and group augmentation are popular subjects within the biological sciences. By understanding the structure of a group, intraspecific social behaviours are better understood. These insights contribute to different scientific fields like behavioural and conservation biology, neurosciences and psychology.

Group dynamics and augmentation are heavily researched. However, underlying structures and behaviours remain unclear or debated. The group augmentation hypothesis is an example of this. It states that in cooperative breeding species, helpers gain the benefits of living in a larger group – such as more possible mates and safety-in-numbers – by increasing the reproductive success of the group. This would increase the chance of the evolution of seemingly altruistic behaviour. Though this is a reasonable explanation, it remains unclear if the hypothesis holds in real life situations (Kingma et al., 2014).

A lot of research was conducted about cooperation within species (Clutton-Brock, 2002; Clutton-Brock, 2009). It was thought that cooperation almost solely occurred between relatives, and that cooperation between non-relatives was very rare or manipulation rather than cooperation. Benefits derived from helping relatives are called indirect benefits (see *Direct and indirect benefits* for more detail).

Until recently, kin-selection was thought to be the major cause of the evolution of cooperative breeding (Clutton-Brock, 2002). In avian species, the majority of cooperation is observed in kin-based societies/structures (Hatchwell, 2009). With kin-selection as primary cause, it was widely believed that only indirect benefits were a motivation for cooperation. However, recently interest in cooperation between unrelated individuals emerged. This kind of behaviour appears to be more common than previously assumed. Benefits that directly affect the helper, relative or not, are called direct benefits (see *Direct and indirect benefits*). In some species the benefits seem straightforward, while in other species the beneficial aspects remain obscure, since these aspects only come to be much later in time. It is also not clear if the animals are aware of potential benefits and only help non-kin if they gain these benefits.

For example, of 406 bird species that are known to be cooperative breeders, there are 213 species for which data is available (Rhiel, 2013). Of these 213 species 30% consist of groups with mixed helpers (related and unrelated), and 15% consist of groups with exclusively unrelated helpers.

Likewise, bats are known for their cooperative behaviour. The groups they form are often composed of unrelated animals (Carter et al., 2013; Carter et al., 2015; Wilkinson et al., 2015). The most common forms of social behaviour within bat species are roosting (sleeping in colonies), social hunting, sharing of food with bats in need, and caring for juveniles by giving milk and babysitting crèches.

To get a deeper understanding of seemingly altruistic behaviour between unrelated individuals, it is necessary to understand the causes of such behaviour. Accordingly, the thesis at hand asks: *why do unrelated individuals help each other?* To be more specific, I will explore what kind of direct benefits the helpers get from their cooperative behaviour and what role these benefits play in the evolution and maintenance of cooperation. Since helping behaviour is a broad subject, I will focus on help during breeding, raising juveniles and food sharing. Among others, this will include thermoregulation, donating food, crèche formation, and territory and clutch defence. The helping behaviours will be divided by their benefits; ones that increase survivability and ones that increase reproductive success.

RELATEDNESS

Because this paper will specifically look at behaviour of unrelated individuals, the term *relatedness* needs to be defined. Relatedness is a gradient of similarity between the genes of two different individuals. Identical twins are 100% related, siblings are 50% related, whilst cousins are 25% related (see table 1). The table shows clearly how relatedness declines when the percentage of shared DNA decreases. It is difficult to draw the line between related and unrelated. Articles discussing differences between related and unrelated individuals frequently omit this definition. They compare related and unrelated individuals while they do not define when exactly two individuals are not related. Because the line between related and unrelated is absent in the source material for this paper, I will define individuals as related or unrelated as done in the articles used. I will therefore tentatively assume that all articles have drawn the same line in genetic similarity when dividing relatives and nonrelatives.

Relationship	Average DNA shared %
Identical twin	100%
Parent / Child	50%
Full Sibling	50%
Grandparent / Grandchild	25%
Aunt / Uncle / Niece / Nephew	25%
Half Sibling	25%
First Cousin	12.5%
Half-Aunt / Half-Uncle / Half Niece / Half-Nephew	12.5%
Half-First Cousin	6.25%
First cousin once removed	6.25%
2 nd cousin	3.13%
2 nd cousin once removed	1.5%

Table 1 Average DNA shared between relatives (23andme, 2018)

DIRECT AND INDIRECT BENEFITS

The gains non-relatives garner through cooperation are direct benefits. These are benefits that affect the helping individual directly (Clutton-Brock, 2009; Kingma et al., 2011; Kingma et al., 2014). In contrast, indirect benefits do not benefit the helper itself directly, but the survival of his genes increases by helping individuals that carry a part of the helpers genes. Though the name can lead to some confusion, direct benefits can either be short-term or long-term benefits, or both.

Direct benefits can increase fitness in two ways; by increasing survivability of the individual and/or by increasing its reproductive success. The benefits increasing the chance of survival are gains that improve overall health, increase foraging time and success and lower predation risk. Benefits increasing reproductive success increase the chance of reproduction and the survivability of the offspring. A benefit can affect one of the two, but often affects both. For example, when bats leave their offspring in crèches, the female lowers her level of stress and increases her foraging time, which is beneficial for her chance of survival (Wilkinson et al., 2015). On the other hand, thermoregulation through huddling together in the crèches keeps the juvenile bats warm, which is beneficial for offspring survival (see also the next two paragraphs).

SURVIVABILITY

The lowering of stress is one of the major direct benefits of cooperation, increasing overall health of the individual. Lowering stress is induced by different mechanisms. The main mechanisms are allogrooming, increasing the amount of free time and conserving energy. In common vampire bats, social grooming is mainly seen as a way of networking, compensation for not sharing food (Wilkinson et al., 2015) and reducing infections (Carter & Leffer, 2015). In wild baboons it has been shown that social grooming increases the survivability of offspring (Silk et al., 2003). Here too, the grooming is seen as a form of networking and social inclusion. The female baboons that had better social contact and were more socially integrated in the group, were more successful in raising their offspring. The latter two mechanisms –increase of free time and conservation of energy – occur in alloparenting. Alloparenting is displayed when females leave their offspring in crèches, as seen in

greater spear-nosed bats (Wilkinson et al., 2015). The free time and energy gained by this mechanism is used to forage, which lowers stress of starvation.

Social foraging can be beneficial when the success rate of foraging together is higher than the success rate of foraging alone. For the individual this means that either the intake rate or the food quality have to be higher when foraging together, even though the food is shared. This is seen in multiple species of bats (Wilkinson et al., 2015) where an individual shows others – related or not – a patch of insects through vocal signalling. Since these patches change and move rapidly they are much easier to find in group hunting. The signalling individual invests in its social network and expects the favour to be returned in the future. An exception to this is when social foraging is used to compensate for babysitting females. Alloparental care, in the means of crèches, increases the free time of females donating their young. This time is mostly used for foraging. The females that look after the young thereby give up their foraging time. The babysitters hereby depend on the reciprocity of the other bats. Those are expected to let the babysitters know where food patches are through vocal signalling.

Donating food to those in need can be life-saving helping behaviour. Though the helper does not immediately receives benefits from it, it does create a social network. This highly increases the chance that the helper will be fed in the future by those helped. Wilkinson and Carter have studied this in common vampire bats (Carter & Wilkinson, 2013; Carter & Wilkinson, 2015; Wilkinson et al., 2015) and concluded that bats in need are significantly more fed by those that they had helped in the past, excluding relatives in the empirical studies (see *Case studies*).

Case studies: social food sharing in common vampire bats

Common vampire bats (*Desmodus rotundus*) are known for sharing food with other bats in need. They donate by regurgitating blood to both kin and non-kin. At first it was thought that sharing with unrelated bats was the result of both direct and indirect fitness effects, as suggested by Wilkinson in an early paper from 1984. Later on, some researchers suggested that food-sharing with non-kin was only due to indirect fitness effects, like harassment and indiscriminate altruism (Clutton-Brock, 2009; Paolucci et al., 2006; Foster, 2004). Clutton-Brock suggests that simpler mechanisms, like intra-specific mutualism and manipulation, probably cause non-kin cooperation. In his review he discards reciprocity due to lack of evidence. However, in the past five years Carter and Wilkinson published two more articles in which they conducted experiments to test these hypotheses. These articles support the belief that direct fitness benefits do affect food sharing among unrelated bats (Carter & Wilkinson, 2013; Carter & Wilkinson, 2015).

CASE STUDY 1: RECIPROCITY PREDICTS FOOD SHARING

In a 2-year experiment, Carter and Wilkinson (2013) tested if common vampire bats only shared blood due to indirect fitness benefits. They took away individuals and did not feed them for 24 hours, then placed them back in the colony and observed if they would be fed. They also measured who would feed the fasted bat and if the donor or receiver initiated the sharing.

The results show that donors initiated food sharing more often than receivers. This undermines the harassment theory that suggests that receivers harass donors until they share blood. How much a bat had received food in previous interactions was the best indicator to predict if the bat would share food. Previously received food predicted 8.5 times better if a bat would share food than relatedness did.

The experiment supports the hypothesis that direct fitness benefits – reciprocal help and allogrooming – also play a role in food sharing, not just indirect fitness benefits – harassment and kin-selection. Mainly female bats participated in food sharing and the sharing never occurred between two male bats. Of the sharing pairs, 64 percent were not related. Per donation the donor lost about 5 percent body mass, and with that the receiving bat could usually recover about 20 percent of the weight lost. It seems that social bonding increases the food sharing rate and plays a major role in stabilizing this kind of behaviour.

CASE STUDY 2: HELPING NON-KIN CAN EXPAND FOOD SHARING NETWORK

In a following experiment, Carter and Wilkinson (2015) measured the donating behaviour with female receivers only. 14 females were fasted 6 times. 28 other bats could possibly donate blood to the females. Donations from the main donors, most of the time related bats, were prevented. They measured the donating behaviour of the 28 possible donors.

The experiment gave three major results. The first was that the fasted females received less food when the bats that previously shared food with them were removed. This means that donors are specific and cannot be switched. They also found that the removing of the main donor increased the variance of the food sharing in the other bats. Some bats increased their sharing a lot, while others almost stopped sharing. Finally, they found that the receivers that had donated more blood with non-related female bats in the years before the experiment were more popular among the donors; these bats had more donors and received more blood than the others. The previous food sharing of the fasted bats with non-kin male bats and related male and female bats did not increase the popularity of the fasted bats. It has to be taken into account that the main donor was excluded in this experiment, which could explain why sharing with relatives did not change popularity. From the increase in donating popularity due to helping non-kin females in the past, Carter and Wilkinson concluded that helping non-kin could expand the donating network of the female vampire bats.

REPRODUCTIVE SUCCESS

Social thermoregulation possibly explains why female greater spear-nosed bats that babysit crèches actively guard unrelated fallen juveniles (Wilkinson et al., 2015). Social thermoregulation occurs when a group of animals roost together. When huddling, individuals can use the body heat of others to warm themselves, and thus reducing their own energy input. Roosting occurs within groups of adults, but is also commonly seen when juveniles are put together in crèches. Especially when the young animals are yet to grow fur, huddling together can drastically cut back individual energy costs for thermoregulation. In the first few weeks of their life, young spear-nosed bats face high death rates. Therefore, social thermoregulation may play an essential role in increasing their survivability. This would make it beneficial for females to guard unrelated fallen pups. An important factor supporting this theory is that the guarding female is always a recent mother. In Wilkinson's study, a guarding female always had a young of less than two weeks old; a pup without fur. Every surviving pup in the crèche would thereby enhance the survivability of the guardians own offspring.

In avian species, cooperative breeding can be put into two systems of stable, social group formation (Rhiel, 2013). The first is *pair nesting*, where groups consist of only one breeding pair and the other birds are helpers. The second system is *cooperative polygamy*. Here, the groups consist of more than two birds that share one single clutch and reproduce together. In both systems non-breeding helpers may be present. In cooperative polygamy this is not certain however. In reality, the two systems are not distinct but are two ends on a spectrum of cooperation. When the two systems are combined, 55% of the groups consist of mainly related birds, 30% consist of both related and unrelated birds, and 15% consist of mainly unrelated birds.

Moving to another group can be favoured over staying in the group of the parents, because the helper would gain access to a future mate and territory more quickly. In another group where the relatedness is low, the helper will not have to wait until the dominant breeder is unrelated. In his maternal group it might have to wait a long time for this to happen. First it would have to wait for both parents to die. Then there is a high chance that an older, related helper with more dominance would claim the same-sex breeding spot (Rhiel, 2013). The amount of time the helper would have to wait before it can breed would be so long that it becomes more beneficial to move to another group.

Helpers can benefit from nest-care by gaining experience in territory-defence and parenting behaviour. In some species, enhanced breeding success through skill-development is not found or debunked (Cockburn, 1998). However, the benefit of this skill-development has been proven in an experiment with Seychelles warblers (Komdeur, 1996) and was recently observed in the hair-crested

drongo (Lei et al., 2016); both passerine bird species. In Komdeurs experiment, Seychelles warblers (*Acrocephalus sechellensis*) with different breeding and helping experience were placed in unoccupied, high-quality territories and were then monitored while breeding. Birds with previous breeding or helping experience raised juveniles faster than birds without any experience. Only first-time breeders gained benefits from previous helping experience; after the first breeding attempt experience did not accumulate. Lei's study showed that breeding success in the hair-crested drongo (*Dicrurus hottentottus*) mainly depended on the experience of the breeding male. Clutch-size or condition was not affected. Only predation-rates where; suggesting that inexperienced males were worse at nest- and territory-defence. Though the study of Lei does not show results for helping experience, it does show that experience in breeding improves breeding success. Together with Komdeurs study this shows that breeding experience – be it through nest-care of own juveniles or nest-care by helping other breeders – has a positive effect on reproductive success in beginning breeders.

In pair-nesting, helping kin may be preferred over non-kin, but helping non-kin can still be preferred over breeding alone, due to higher survivability in group-living (Rhiel, 2013). This is most commonly seen in obligate cooperative species, where breeding alone may be impossible due to lack of space for territories or the high competitive pressure of other, group-living breeders. However, in some facultative cooperative species helping is also found to be evolutionary stable, where chance of breeding success may simply be higher in groups than when breeding alone.

In cooperative polygamy, social nesting can increase the survivability of group members. This would make it favourable for non-relatives to help with nests of non-kin. The groups are better in defending the territory or are better in feeding the juveniles, or both. These benefits can increase survivability more than the costs of shared reproduction decrease survivability (see also *Group augmentation hypothesis*). It has to be noted that cooperative polygamy can arise in two ways; one through competitive reproductive behaviour, and one where the benefits of group-living highly affects all group members. In the latter we can speak of direct fitness benefits. Clutton-Brock (2002; 2009) prefers to see this kind of behaviour as mutualism rather than cooperation.

Group augmentation hypothesis

According to the group augmentation hypothesis, the evolution of helping behaviour in a cooperatively breeding species is favoured because living in a larger group increases the fitness of the helpers. In cooperatively polygamous birds (where multiple birds breed together and may have helpers), the fitness is increased due to better territory defence and feeding juveniles in a better, more efficient way. Thus, increasing the reproductive success of the whole group by helping others is beneficial for the helper, even if the breeders and helpers are not related. Aside from cooperative breeding, safety-in-numbers is also a benefit that can be derived from the group augmentation theory. This is seen in fish where the predation pressure is so high, that group-living becomes obligatory (Fischer et al., 2014).

In a 2014 review, Kingma et al. concluded that there are different evolutionary mechanisms that can cause the benefits known for the group augmentation hypothesis. In order to use the hypothesis, Kingma placed the GA hypothesis in a framework of the general cooperation theory and tried to define it clearly, something that had not been done up until then. Though he concluded that different mechanisms can cause the same beneficial outcomes, Kingma insisted that it is necessary to have a clear concept and separation of the different possible causes. This conceptualization will create a better understanding of which evolutionary mechanisms are plausible and what combinations of these mechanisms are likely to occur, in the current state of research as well as in future research.

Kingma also stressed that it is important to look at different evolutionary mechanisms simultaneously in order to find patterns. In his analysis, some mechanisms have only significant meaning when different factors are simultaneously tested. He looked at different factors influencing the helping effort of subordinates in cooperative breeding species *Malurus coronatus*. The

probability to gain the territory in the future was individually not significant as a factor. However, together with relatedness it got a significant impact. Kingma found that the probability to gain territory in the future influenced the effect of feeding effort due to relatedness.

Contradicting the group augmentation theory, in most avian species that breed cooperatively with non-related helpers, the young birds leave their maternal nest to find another group (Rhiel, 2013). They do this rather than staying and increasing the group-size. This is even the main reason that helpers are non-related in these species.

COSTS OF COOPERATION

Though this thesis focuses on the direct and indirect evolutionary benefits that cause and maintain cooperation, costs are also an important factor that has to be taken into account. Just like benefits gained from cooperation, costs of cooperation influences the behaviour of an individual. There are two forms of costs to be considered; resulting from cooperation or causing it. Costs may be caused by the cooperative behaviour, in the form of *investment*, but costs may also be an important factor that drives individuals to cooperate, in the form of *punishment* or *manipulation*.

Investment is often seen in cooperative breeding species. The helper invests in his future by helping the dominant breeding pair raise their offspring. This increases the experience of the helper in successfully caring for juveniles and defending territory. This is also an investment in a way that the helper could replace one of the dominant breeders if the breeder passes away. In that case it is beneficial for the helper not to be related to the dominant breeder of the opposite sex. As stated in Kingma's analysis (2011), kin-selected benefits arise from investment in related individuals and benefits from group augmentation arise from investment in own future helpers.

Investment plays a very big role in the helping behaviour of bats and is key in creating their social networks. Investment becomes apparent in babysitting of greater spear-nosed bats, social foraging in multiple species of bats and social food sharing of common vampire bats (Carter and Wilkinson, 2013; Carter and Wilkinson, 2015; Wilkinson et al., 2015). The paragraphs about food sharing and case studies above show more detail. By guarding juveniles in crèches, signalling others where food patches are and donating blood to other bats, the vampire bats create a social network. This social networking occurs between both related and unrelated individuals. The investing individuals expect that the favour is returned in the future; according to the tit-for-tat theory. The bats are so developed that they can remember different encounters with individuals. This makes them capable of scoring how much individual bats have given and received donations.

In manipulative behaviour, strategies are used purely to maximize one's own fitness. Harassment and punishment are both tactics that can be used to manipulate (Clutton-Brock, 2009). In these cases helper is forced to act cooperatively because it would be punished otherwise. On the other hand, punishment and harassment can also be used in order to avoid cheating in reciprocal systems. In obligatory group-living, an individual can be manipulated into helping by the dominant breeding pair; also known as the pay-to-stay theory. Obligatory group-living happens when there is too little space for new territories or when the predation risk is high, as seen in the daffodil cichlid (Fischer et al., 2014).

In the daffodil cichlid (*Neolamprologus pulcher*), a cooperative breeding species, helpers are being punished if they are idle (Fischer et al., 2014). In the field experiment of Fischer, dominant breeders would act aggressive towards helpers that were disabled to help, and the helpers had to leave for at least 24 hours. However, this only occurred in small cooperative breeding groups. This was likely because the dominant breeders found it more difficult to distinguish helpers in bigger groups. It has to be noted that the daffodil cichlid is an obligatory cooperative breeding species; due to high predation risk they cannot live alone. According to the pay-to-stay hypothesis a) subordinates need to earn their stay by helping, and b) dominants able to punish idle subordinates.

The social networks in bats are not maintained by harassment or manipulation. The harassment hypothesis was suggested by Clutton-Brock in 2009 to explain food-sharing among unrelated individuals. However, the experiment of Carter and Wilkinson in 2013 showed that harassment was

not a predictor of food donations among vampire bats. They also suggested that both donating and receiving bats gained direct fitness benefits from food-sharing (for more detail see case study 1).

DISCUSSION

The direct benefits increase the helpers survivability or increase its reproductive success. Survivability is enhanced by the lowering of stress and food sharing. Stress decrease can be achieved through alloparenting – like babysitting of crèches – and allogrooming. Food sharing is seen in the form of food donation, for example when common vampire bats regurgitate blood to those in need, and in the form of social hunting, as seen in multiple bat species that use vocal signalling to show a food patch to the group. In both forms the direct benefits for the helping individuals are return of favours in the future. The tit-for-tat theory and social networking are obvious mechanisms explaining food sharing. Social networking is a driving factor in the maintenance of cooperative behaviour. Therefore, social networking between non-kin within bat species can be a maintaining factor in seemingly altruistic behaviour.

The reproductive success is enhanced by social thermoregulation and cooperative breeding. Thermoregulation happens in bat crèches when the juveniles have yet to obtain fur. By huddling the juveniles stay warm and therefore have a higher chance to survive. Cooperative breeding mainly occurs in bird species, where helpers defend the territory and the clutch. Direct benefits derived from cooperative breeding are increased chance to obtain territory and mates in the future, and developing parenting skills.

Costs of cooperation, either causing the behaviour or resulting from it, can be equally influential on behaviour as benefits are. Investment plays a big role in social networking and maintaining successful cooperative systems. Manipulation and punishment may play a big role in seemingly altruistic behaviour, and have to be kept in mind when there is a lack of evidence for direct or indirect benefits (Clutton-Brock et al., 2009). Helping behaviour is easily considered to be cooperation, even when the evidence is not that strong. Therefore, defining behaviour as cooperation needs to be done cautiously.

It is important to look at multiple benefits simultaneously in order to find the true significance of different benefits (Kingma et al., 2011). A benefit might not show significance if it is measured alone. However, it may show significance once it is analysed together with another benefit.

The lack of clear differentiation between relatives and non-relatives needs to be considered when comparing results of multiple studies. If there is no clear definition what percentage of genetic similarity defines two individuals as related, inconsistency between different studies remains. Therefore, every study needs to name their defined genetic distinction between kin and non-kin.

Though the helping behaviour may be selfish on an evolutionary level, it is unclear if the intention of the individual is. It may be that the helping individual is not aware of these mechanisms and consciously operates unselfish. The intention of the individual can be unselfish if the individual is not aware of the benefits it receives from the help he provides. According to Frans de Waal this is the base for the evolution of empathy. He defines empathy as a proximate mechanism for helping behaviour (de Waal & Suchak, 2010).

Summarizing all direct benefits found in cooperative behaviour between unrelated individuals, it can be concluded that direct benefits support the evolutionary maintenance of cooperation. Cooperative behaviour might have evolved through kin-selection with indirect fitness benefits as base causes, but direct benefits became more important throughout time. Direct benefits now play a major role in the evolutionary stability of cooperation.

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