Communal breeding: A social take on survival of the fittest.

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Summary

Communal breeding is a highly researched behaviour found in many different vertebrate species. There are some long standing researches in different cooperative breeding species to understand the behaviour. For example the study of the Seychelles warbler by lead by Komdeur, or the study of meercats lead by Clutton-Brock. These studies have shown a lot about the behaviour patterns of these communally breeding animals. But is this behaviour evolutionary stable? What is known about the cooperative breeders will be analysed to answer this question.

Introduction

Communal breeding is a concept where, sometimes unrelated(Clutton-Brock 2009), individuals of the same species give birth, or lay their eggs in the same territory and raise the offspring together. This concept is found and studied among different species and taxa. This behaviour is however, from a darwinistic evolutionary perspective, not easy to explain. Evolution is the survival of the fittest, or the best adapted individual. It is not just the “fittest” individual that survives in these cases; a weaker individual can procreate under the protection of a stronger individual.

Communal breeding involves all forms of care for the offspring, however, this can take a lot of different forms between species(Jennions and Macdonald 1994). Not only the group size differs, but also the makeup of the group. For example it might consist of only kin with two breeders, or it could be mostly non-related individuals with different nests which they all take care for. In even rarer cases there might be joint nesting where two individuals give birth to their young in the same nest site. All of these types will be called communal breeding in this paper.

Looking from an evolutionary perspective, there must be an advantage for forgoing reproduction and helping another with their offspring. Possible ecological factors could make an individual stay in their parental territory or forgo reproduction all together (Zöttl *Et al.* 2013). Even if an individual chooses to help rearing another’s offspring, will the communal breeders still compete by giving their own young an advantage?

The reproductive skew model is introduced to better understand communal breeding. This model tries to determine the dynamic of these breeding collaborations. A dominant individual exists within this model that recruits and benefits from one or more subordinate individuals to help defend the territory and to help raise the offspring. These two alternate models are taken into account(Magrath *Et al.* 2004).

The concession model is a model in which the dominant individual has perfect control over the subordinates (optimal skew). The dominant individual can give the subordinates a durable incentive, they do concessions on their own reproduction, or they can remain the only breeder by not allowing the subordinate to breed. The subordinate can only leave and search for another territory or stay. This model predicts that the related individuals will stay, because of inclusive fitness. The subordinates still gain fitness over raising others young and the dominant hardly loses their fitness(Magrath *Et al.* 2004).

The restraint model Is a model in which the dominant only has the power to evict an individual from the territory; it cannot fully control the share of reproduction from a subordinate. The dominant individual will tolerate more subordinate reproduction if the inclusive fitness for dominants is high enough. Selection on kin is lower in this model, because all subordinates can reproduce in theory. Thus the subordinate takes a greater part in reproducing which is determined by what the dominant will tolerate(Magrath *Et al.* 2004).

This communal breeding behaviour is found throughout different vertebrae species and even some insects show this behaviour(Kalinova *Et al.* 2009; Hoermann Et al. 2013). It is studied among different species to understand how it exactly works, but what makes these species breed together? And is it even evolutionary stable? In this paper, I will assess different ecological factors that may influence species to breed communally, and look at the advantages of this behaviour. I will eventually look at the competition within the breeding group.

Territorial conditions

Safety comes in numbers is a well-known saying that stems from the Latin proverb, *Defendit numerus*. It states that an individual is safer when it is not alone but when it is surrounded by others. The diluted risk of predation by the presence of other individuals alone could be a reason for communal breeding, which also has advantages in foraging and food sharing (kingma *Et al.* 2014; Kokko *Et al.* 2001). In the next chapter, I will explore the costs and the benefits of having a group in a territory.

A territory has to meet a few conditions to be a viable territory(Zöttl *Et al.* 2013). A territory has to have enough shelter, breeding sites and food available to sustain an individual or a group. Each of these conditions is influenced by the size of the group that lives within the habitat.

<u>Food availability</u>

The amount of food available is highly influenced by the number of individuals in a certain sized territory. However, the amount of food needed in a territory is mostly affected by the number of individuals in a territory. The territory needs a larger amount of food to sustain a group and thus to feed each individual compared to just one or two individuals. This can be solved by dominating a bigger territory that houses enough food, which is harder to defend due to the increased size, or by a territory which is richer in food and therefore more prone to invasions.

A group that cooperates within a territory can create a buffer in food availability at times when food is harder to find, for example after heavy rainfall or a drought. A larger group will find more food at a faster rate (Pulliam and Millikan 1982; Gordon 1954). This will also help the survivability of the young if the group takes care of each other's young.

Accordingly, the amount of food is a driving factor if a territory is able to sustain a group. However, a group can make it easier to sustain themselves in a territory; it is a buffer for harsher times when it is easier to find food. Group foraging also reduces the anti-predator vigilance for each individual. The territory adjustments for sustaining a group brings some defense problems. This will be discussed in the next few paragraphs.

<u>Territory defense</u>

Defending a territory takes a lot of energy; the territory owner has to keep an eye out for intruders at all times and it has to defend it when it notices an intruder. A larger group reduces the risk of getting its territory invaded. The chances of successfully noticing an invader increase when there are more individuals that can spot an intruder. The amount of energy used for defending a territory should decrease per individual if more are defending the same territory.

Safety comes in numbers for defending your territory against intruders, but being in a bigger group can make them a more desirable target for predators, because the predator can quickly detect a bigger group. However, the same assumption as discussed above does not only apply to intruders, but it also works for the defence against predators as is shown by Jungwirth *Et al.* (2015). The individual's effort of anti-predator behaviour is reduced for each individual, especially for the focal group (or breeders).The energy, which is saved by reducing their anti-predator efforts and by relying on their subordinates, can be used for raising their offspring.

Heg *Et al.* (2005) have shown that bigger groups have a higher survival rate, and this was confirmed by Jungwirth *Et al.* (2015) who also found that different groups in a denser also have a higher survival rate. This means that it is favourable for a breeder to attract helpers, and if the breeders have a good territory, the helpers should join the territory (Zöttl *Et al.* 2013). The survival rate of the whole group increases, which helps breeders to spend more energy on raising their young, and the helpers might have the inclusive fitness.

<u>Breeding/ nesting sites</u>

When a young in a communal breeding group is old enough, it can leave the parental territory and look for a breeding ground of its own, or it can delay its dispersal and help with the next brood. An individual has to find a habitat with a good nesting site and a partner to nest with to start breeding. This is not always possible however, as one of the more common explanations for delayed dispersal is habitat saturation.

The habitat saturation hypothesis states that if an individual becomes of reproductive age, it cannot find a suitable reproductive vacancy. The individual can stay in its natal territory and help raise its parents' young and wait for a vacancy in this territory or neighbouring territories. It can also look for a vacant territory at the risk of not finding one, and consequently becoming a "floater", which means that it roams between territories (Ekman *Et al.* 2014). There is little evidence on this however, when it comes to mammals (Walters *Et al.* 2004). Creating suitable breeding vacancies should favour dispersal and independent breeding, but there are a few observations that have shown that dispersal decisions are not dependent on the vacancy of breeding area's (Russel 2004; Cheeseman *Et al.* 1993; Clutton-Brock *Et al.* 1999a; Creel and Creel 2001)).

The Seychelles warbles (*Acrocephalus sechellensis*), a bird that is only found on the small island group Seychelles in the Indian Ocean, are a good example of the impact habitat saturation can have on a population. Seychelles warbler territories are normally occupied by a single pair of dominant birds, one of each sex. About 30% of the territories also contain one or more helpers, and they can be male and/ or female. These helpers lack a suitable nesting site. This was demonstrated when vacancies were created by translocating the breeders from a habitat; the habitat was immediately taken by subordinates from other territories (Komdeur 1992; Richardson *Et al.* 2002, 2007). The individuals also immediately started to breed independently and refused to help when they were translocated to an uninhabited island.

Joint nesting might also be a result of a scarcity in breeding sites. This way of nesting, where two individuals nest in the same space, is scarce but not uncommon, and it is mostly found in birds like the Seychelles warbler (Komdeur *Et al.* 2016), guira cuckoo (Macedo 2016) and hooded crow (McIvor and Healy 2015). However, a better example might be the burying beetle (*Nicrophorus vespilloides*), a species that breeds in the cadaver of a small animal. The burying beetle detects a cadaver up to several kilometres away (Kalinova *Et al.* 2009; Hoermann *Et al.* 2013). When the cadaver is found the beetle starts burying and prepping it for breeding, and it might start this process alone or it could wait for another beetle to arrive. *N. vespilloides* has been found breeding with another female beetle on the same cadaver or a male and female pair. Staying together or even allowing another female to breed on a claimed cadaver might be a result of scarcity in cadavers, and they can take advantage of this; breeding together makes the breeding ground more defendable.

Costs and benefits for the breeder

A breeder benefits from having a helper, as discussed before. Defending the territory and helping to find food are good examples of these advantages, as is the reduction of infant care costs. The infant care costs are the costs of rearing one infant to a stage in its life where it does not need the adult to look after it or to feed the infant. The infant care costs are the energy that is needed to defend the home range of the parents and the energy that is needed to find enough food to feed the infant. These costs are simulated by the size of the home range and the body weight of the infant (Díaz-Muñoz 2016). Thus, having helpers that rear the infants helps the breeder to reduce the costs per infant. This leads to more successful breeding attempts and more offspring. But does a breeder have costs for allowing helper(s) in its territory?

The likelihood of a successful pregnancy of the golden lion tamarin (*Leontopithecus rosalia*) is increased in the presence of additional group members (Díaz-Muñoz 2016) as is with meerkats (Clutton-Brock and Manser 2016). It is even necessary for the breeder of some species to have helpers for a successful breeding cycle, for example the white-winged choughs (*Corcorax melanorhamphos*) (Heinsohn and Legge 1999). This might even point to an evolutionary necessity for communal breeding; the white-winged choughs experience this due to a specific foraging niche, where a steep learning curve prevents the young from fledging too early and helping their parent raise their siblings. Nevertheless, all these cases show that group augmentation, where the group size is actively increased by all the members of the group trough recruitment(kokko *Et al.* 2001; Kingma *Et al.* 2014), is important for the breeder to have a successful breeding attempt.

A breeding pair must have incentives for their offspring or floaters to attract helpers, and to stay and help them raising their young. If the breeders have a rich territory, this could be incentive enough. Especially when it is rare to have your own territory, as is the case with the Seychelles warbler where the islands on which the birds are found are small and isolated (Komdeur 1992). There is not enough space on these islands for each bird to have its own territory, and the younger birds stay in the territory and feed of it. This means however, that the breeding pair has to share their food with the helper.

Another incentive to let a helper stay, is to allow some of the helpers to reproduce themselves. This is a costly offer; not only do the breeders have to share the food and safety of the territory, but some of the infants that live there are not their own and this diverts the helpers attention from the young of the dominant breeding pair. The dominant breeding pair can counter this by ensuring that the largest amount of offspring is theirs, or the helpers which are allowed to breed, have to be their offspring or kin. The dominant pair will then have inclusive fitness from the breeding helpers. In this case, the dominant breeder loses some of its total breeding success, but still keeps the largest overall success.

Thus the breeders gain many advantages by having helpers, but it is not without losing some of its reproductive success. However, even if the cost of having helpers reduces some of the reproductive success of the breeder, having helpers increases the overall reproductive success in most cases. Thus, the negative effect of having helpers might be reduced to almost zero due to these helpers.

Costs and benefits for the helper

As expected, helping is not completely costless. Therefore, the question rises what benefits the helpers get by communal breeding. It is a costly endeavour to rear young, and especially if they are not your own. Some studies indicate that the inclusive fitness of the helper compensates this, but it is already shown that helpers are not always related to the young they are rearing. In that case, the inclusive fitness argument fails, and there have to be other factors which indicate that helping is a viable strategy.

The inclusive fitness for the related helpers is one of the benefits from a darwinistic perspective. Since the helper is related to the breeders and the infant, at least some its genes will proceed to the next generation. Following this argument, it is more advantageous to help raise your siblings rather than non-related infants. Besides, at what point do you decide not to help raise your family because your inclusive fitness is too low.

The infant care cost will reduce if more individuals care for fewer young. This means that more young could be raised by the group. Reducing the infant care cost could put the breeder in a position where it could allow the helpers to reproduce within its own territory. A helper could also sneak a young of its own in the brood of the breeder, at which point it will raise it like one of its own.

The study by Clutton-Brock *Et al.* (1998) shows that a non-breeding meerkat helper takes care of the young while the breeders are out foraging. This will cost the helper dearly, because it loses 1,3% of its body weight on average. Gaining breeding experience could be a reason why a helper would go through such a trial. This is shown in the study about Seychelles warblers by Komdeur *Et al.* (2016) where experienced breeders, inexperienced breeders and experienced helpers were transferred to a new island. It appeared that the experienced helpers were as successful in reproduction and finding good breeding territories as the experienced breeders. The inexperienced were less successful. This same concept could account for the offer the meerkat helpers are making.

Territory inheritance could also be a good incentive for helpers. After the original owner of the territory dies or becomes too old to breed, the territory could go to one of the helpers. This sounds as a good incentive though, because a good territory provides a better chance for successful reproduction. However, the longest waiting helper does not automatically inherit a territory, and the breeding position might even go to a floater (Kokko and Ekman 2002; komdeur *Et al.* 2016).

Although the inheritance of the territory is not a leading argument, Ekman *Et al.* (2004) stated that a good territory could be a good incentive for delayed dispersal and thus for helping. This derives from the notion that a good territory helps the helper to gather strength and energy to eventually compete for a mate or territory of its own.

Thus, from an evolutionary perspective, it makes sense to choose for a helping strategy. Although the helping individual forgoes at least some its reproductive success, the strategy prepares the individual to reproduce on its own. The helping strategy also gives the helper an advantage when it chooses to look for its own territory and for a breeding partner.

Competition

This dynamic with dominant breeders and subordinate helpers looks like a stable and advantageous strategy for all parties involved. However, since evolution is about survival of the fittest, or as Darwin called it "the struggle for life", this implies competition. But which is a better way to survive, competition or cooperation? Or is there still a lot of competition among the communal breeders?

If we look at the two models which are used to describe communal breeding, there is already some competition described in the model. Each of the models implies a struggle between the breeders and helpers where both parties try to maximise their gain. In the concession model, the breeder has more control, but it has to offer some of her own reproductive success or other advantages to attract and keep helpers. The restraint model allows even more power for the helper when the helper is weaker than the dominant breeder, but it can do what it wants up to a certain point where the breeder doesn't allow or tolerate it anymore and consequently evicts the helper from the territory. Thus, competition might be a given even when the species are cooperating.

Sneaking is a well-known tactic that is found in different types of dominant subordinate relationships. This means that a subordinate will try to mate with another individual in the group with the intent that the subordinate raises the offspring of the subordinate as its own. This tactic is shown be used in a communal breeding situation by Jennions and Macdonald (1994), in which the breeder doesn't allow helpers to breed.

Consequently, the breeder could practice infanticide as a defence against "sneaking" behaviour. This behaviour is observed in the meerkat species. A dominant female meerkat will act hostile towards other pregnant females in het group during pregnancy, and it will therefore prevent other females to become pregnant, or it will induce abortions due to stress. Even when the dominant female is not pregnant, a subordinate pregnant female might be expelled from the group until she gives birth (Clutton-Brock and Manser 2016).

If the species nest together there is still competition. The guira cuckoo removes the eggs from the nest that are not her own (Macedo 2016). This is despite the fact that it is known for breeding with more than one individual in one nest; a nest of the guira cuckoo could contain up to 24 eggs from up to 7 different females. Macedo even hypothesises that the species could differentiate between the freshness of the laid eggs, and that a breeding female will reject the eggs which are laid later than her own. Even though this species breeds and rears the young together, each female tries to give their young an advantage and tries to maximise their own fitness.

These examples of competitive behaviour in communal breeding models are very darwinistic; in maximizing the fitness, an individual will benefit from breeding in a group or from rearing the young together. However, this impedes on the stability that the communal models bring and it seems to work against the effectiveness and collective benefits that breeding together might bring.

Discussion

Breeding together and sharing the care for raising offspring has its advantages. As discussed before, it is easier for a bigger group to defend against intruders and predators. However, most of these advantages have already been found by species who just live in groups or herds. The evolutionary advantage of communal breeding must therefore come from something else, and this is not the reason why a species would breed together.

However, if the species has a specific and limited habitat, communal breeding could be a viable survival strategy. This is due to the fact that the limited nesting sites are created by a group living in a limited habitat, and living in groups still aids in territory defence, which is a bigger factor if all territory is limited. In this case, all the advantages of group living apply, but it has the added advantage of the breeding pair that maximizes their breeding potential. This could be one of the major reasons why a species would breed communally.

The breeding pair benefits the most from the whole communal breeding system. This is the territory owner and it maximizes its breeding potential by allowing other individuals in its territory. At first, the dominant breeders impede on their own breeding success, due to the lesser amount of food available to fatten up for nesting, and to get it back later in the reproduction cycle. The breeder can raise more young successfully if it has more help, and thus the reproductive success increases for the breeder. This makes the strategy viable and evolutionary stable for the breeders. There are cases however, where this has taken a form of necessity, like the white-winged choughs, and thus the advantage for the breeders is gone.

There are also many advantages for the helpers, but they are all future or circumstantial based. The advantages for the helpers include fitness or experience. Although these advantages in experience are substantial, as was shown by Komdeur et al. (2016), the question remains if an individual should better try to start breeding and learn from trial and error. When trying to breed, the individual at least raises its own offspring and maximizes its fitness this way. This, combined with the competition strategies that are still present in the communal breeding species, might be better for helpers to try and breed themselves.

This leads me to the conclusion that communal breeding is an evolutionary stable strategy. The competition within the communal breeders is still darwinistic, and is a great example of survival of the fittest; the strongest individual within the communal breeders has the most offspring and the highest fitness.

However, the only way this behaviour will show itself, is when circumstances will force the species, due to the limited habitat (Seychelles warbler), scarcity in nesting sites (burying beetle) or other reasons, like what happened to the white-winged choughs. These examples show that there is an external force that forces both or one of the parties to accept the other.

I will also state that in most of these cases, the helper is forced into the helping position, because the helper does not benefit as much and the breeder will have strengthened most in many cases. It is easier and less costly for a breeder to accept helpers than it is for a helper to forgo its own reproduction and help, even if the breeders are its own parents.

This makes communal breeding an adaptive strategy, and if we can show this in a controlled environment there is the possibility we could see this behaviour in species we haven't seen communal breeding thus far.

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