

Group augmentation and the evolution of cooperation

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The group augmentation (GA) hypothesis states that if helpers in cooperatively breeding animals raise the reproductive success of the group, the benefits of living in a resulting larger group – improved survival or future reproductive success – favour the evolution of seemingly altruistic helping behaviour. The applicability of the GA hypothesis remains debatable, however, partly owing to the lack of a clear conceptual framework and a shortage of appropriate empirical studies. We conceptualise here the GA hypothesis and illustrate that benefits of GA can accrue via different evolutionary mechanisms that relate closely to well-supported general concepts of group living and cooperation. These benefits reflect several plausible explanations for the evolutionary maintenance of helping behaviour in cooperatively breeding animals.

The evolution of cooperative breeding and the GA hypothesis

The evolution of cooperative breeding, where non-breeding individuals seemingly act altruistically by foregoing reproduction and behave as alloparents in the reproductive attempts of others ('helpers'; e.g., nest building, tending and protecting young, territory defence [1,2]), has served as a model for the study of evolutionary mechanisms of cooperation in general. The provision of alloparental care is associated with substantial costs (e.g., risk and energy expenditure [3]), and helpers should thus benefit from doing so in order to outweigh these costs. Even so, the relative importance of the various proposed mechanisms that may explain the evolution of helping behaviour (indirect fitness benefits resulting from raising kin, and direct benefits of enhanced own survival and future reproduction) is subject to ongoing debate [4–9].

Although traditionally mainly indirect benefits have been considered to explain cooperative behaviour, it becomes increasingly clear that mechanisms increasing the direct fitness of helpers may also be important [8–16]. A frequently suggested mechanism underlying

Glossary. GA benefits classified within the framework of general cooperation theory

Cooperative groups involve three parties (breeders, helpers, and recruits) (Figure 2), and the fitness effects of cooperation potentially apply at two time-periods, namely (i) during the period in which helpers recruit new individuals (e.g., indirect benefits), and (ii) when these recruits later may affect the Darwinian fitness of (former) helpers. The latter reflects the benefits that the presence or behaviour of recruits exert on helpers as predicted by the GA hypothesis; the concepts of this cooperation show considerable overlap with the concepts of broad-cooperation and group-living theory [10]. These concepts of general cooperation are addressed in this article.

The semantics of social evolution is highly diverse [78]. For clarity we therefore define crucial terms used in this article. Specific examples are given in the text and in Table 1. It is useful to distinguish between 'passive' and 'active' benefits exerted on helpers by their recruits. In a theoretical study [16], passive benefits have referred exclusively to mutualistic effects in the short term (survival benefits resulting merely from the presence of additional group members and thus not from their behaviour), and active benefits have referred exclusively to future reciprocal cooperation of recruits for the benefit of former helpers after these have become breeders (Figure 2). The use of the terms active and passive may be confusing in the framework proposed here (Table 1) because short-term survival benefits (defined as passive GA in [16]) may in fact derive from the passive presence as well as from active behaviour of recruits (mutual or reciprocal behavioural interactions, respectively). By the same token, long-term or delayed benefits (defined as active GA in [16]) to former helpers may – in addition to active behaviour – also result simply from the passive presence of recruits. To root the concepts of GA unambiguously within general cooperation theory we therefore adopt the distinctions of benefits that may apply in the short- or long-term, and that can derive from mutualism or reciprocity. We define these terms below.

- **Mutualism:** or behaviour with mutual benefits to actor and receiver. This denotes behavior directly causing fitness benefits to each actor, while raising the fitness of receivers as well [32]. It is irrelevant whether the behaviour has been selected only by its fitness benefits to the actor [in which case the benefits to the partner(s) would be a mere by-effect], or by fitness effects on the partner(s) as well [79]. We stress that we use the term mutualism in an intra-specific context.

- **Reciprocity:** Behaviour with negative instantaneous fitness effects to the actor that are compensated by behaviour of the receiver benefiting the original actor [37,80,81]. In other words, an individual invests in another by adopting costly behaviour, and the receiver in return invests in costly behaviour towards the actor.

- **Short-term benefits of GA:** fitness benefits to a helper caused by the positive effect of recruits (that were produced through the influence of the helper) on helper survival during the coexistence of helper and recruits in the group. These benefits may result from the mere presence of additional group members (dilution effects or safety-in-numbers), from mutually beneficial behaviours (e.g., joint territory defence, vigilance), or from reciprocal behavioural interactions between helpers and recruits (e.g., allogrooming).

- **Long-term benefits of GA:** fitness benefits to a former helper, resulting from the presence or action of recruits (that were produced through the influence of the helper), which help the former helper in reproduction or enhance its survival chances. This can occur when a former helper has ascended to breeder status in its resident territory or after a helper has dispersed together with its recruits to breed independently elsewhere. These benefits may result from the mere presence of additional group members or from beneficial behaviours of recruits towards the former helper.

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such direct benefits is described by the GA hypothesis, which proposes that helpers gain fitness benefits by enhancing group size if the recruits that are produced as a result of helping behaviour in turn increase the survival and/or reproduction of helpers [8–10,16–19]. However, the importance of GA as a general evolutionary mechanism selecting for helping behaviour has been questioned [1,20].

We believe that lack of conceptual rigor regarding the different evolutionary concepts underlying potential benefits of GA, and the absence of a clear distinction of the conditions under which these benefits may apply, impede a prudent evaluation of the importance of the GA hypothesis to explain helping behaviour in specific cases and the evolution of cooperative breeding in general. Partly because of this shortcoming, empirical tests of the GA hypothesis are rare [6,7,9,21], and supporting results are not necessarily placed explicitly in the specific context of GA [22]. In agreement with Bergmüller *et al.* [10], we argue that the GA hypothesis is based on well-supported concepts derived from general cooperation theory, the main assumption being that it pays helpers to invest in enhancing group size (Figure 1) [16]. We aim here to develop a framework to evaluate whether benefits of GA can explain costly helping behaviour in cooperatively breeding animals (see Glossary). We use this framework to review evidence for each of four potential components of GA – short- and long-term mutualism, and short- and long-term reciprocity – and we outline directions for future studies to test the GA hypothesis.

Testing the GA hypothesis

For the GA hypothesis to apply, several prerequisites must be met (Figure 1). First, helping behaviour should result in enhanced recruitment through increased reproductive success of breeders, and these additionally produced offspring (i.e., recruits) should stay together with the helper for some time. In many species this is the case: helpers have a positive effect on reproductive output in several cooperatively breeding mammals [23], birds [24], fishes [25,26], insects [27], and spiders [28], and recruits typically stay in the group with the helpers [1,2]. Unlike, for example, when helpers gain indirect benefits or help to be allowed to stay in the group ('pay-to-stay' [14,29,30]), improvement of the reproductive success of a group does not necessarily imply a role for GA in the evolution of helping behaviour. Therefore, it is necessary to evaluate (i) whether and how recruits improve the direct fitness of helpers, and (ii) whether helpers invest accordingly.

A cooperation framework to assess the ultimate benefits of GA

Group size benefits

Helping behaviour can be selected when helpers benefit from recruits in terms of survival or reproduction. Therefore, it is important to consider that two main concepts of cooperation have been described in general cooperation theory (Glossary and Table 1), and these may apply similarly to how recruits can benefit helpers. First, inevitable mutualistic benefits to group members may result from the mere presence of other individuals through dilution of

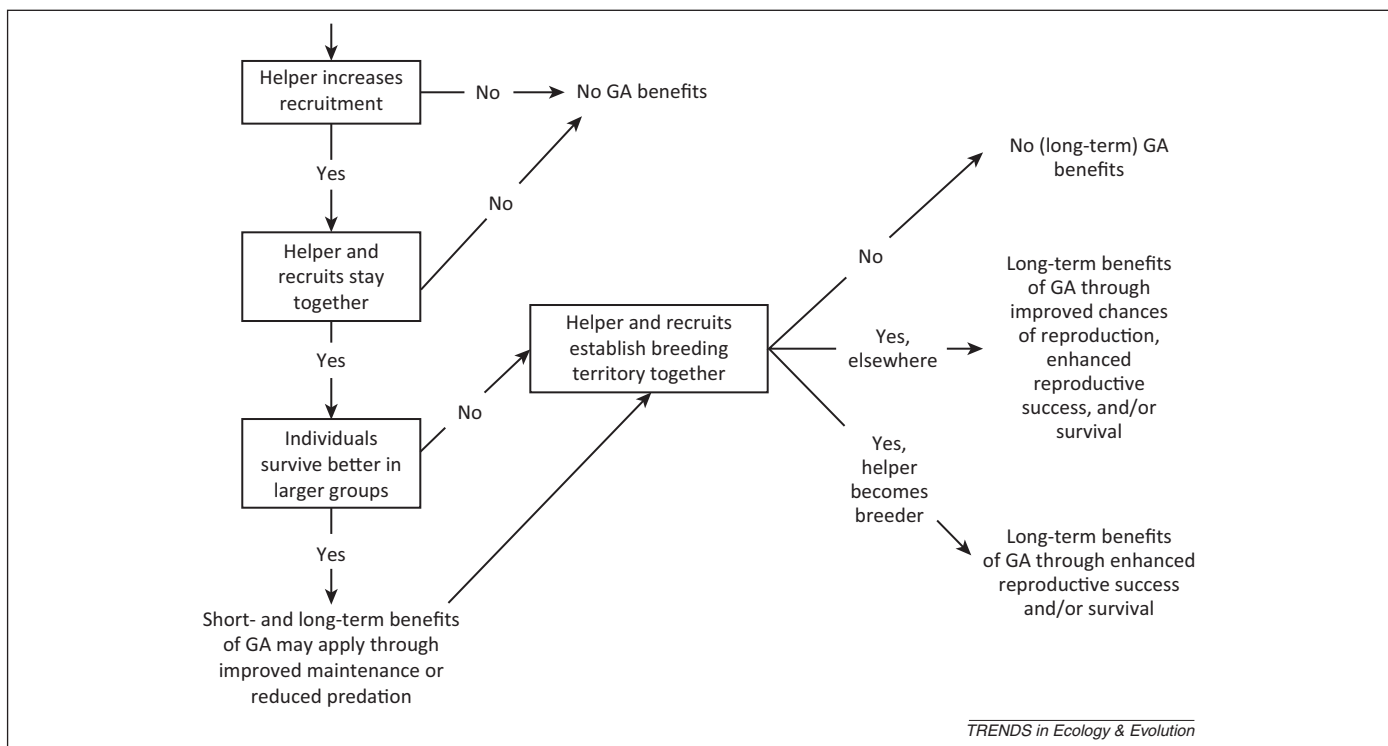


Figure 1. Flow chart of prerequisites for different components of group augmentation (GA). For GA to select for helping behaviour, first and foremost the behaviour of helpers must result in an increase in group size and the produced recruits must stay with the helper for some time. The benefits that these recruits provide to helpers may be an enhancement of survival and/or reproduction in the short- or long-term. These benefits can be mutualistic, because they also fulfil self-serving functions to all parties, or they may characterise a simultaneous or delayed reciprocal relationship (i.e., exchanged investments) between helpers and recruits [16,19] (Table 1). Note that, when these prerequisites are met, GA will inevitably lead to selection on helping behaviour, but its importance in explaining variation in helping behaviour relative to alternative mechanisms needs further exploration (see main text).

Table 1. The main components of the GA hypothesis, including short-term and long-term fitness benefits derived from a mutualistic or reciprocal relationship between helpers and recruits. For each concept preconditions are described and specific theoretical and empirical examples are given.

Concept	Fitness benefits to helpers	Mechanisms of how benefit to helpers can arise	Preconditions/favourable conditions ^a	Examples of general cooperation theory	Models specifically for cooperative breeders ^b
Short-term mutualism	Recruits benefit helpers by their presence or behaviour (survival and condition benefits)	<p>Reduced predation Safety in numbers^c Predator confusion^c Vigilance [33,42] Predator repellence [25,42]</p> <p>Enhanced health or condition Food acquisition or processing [34,51] Time saving (e.g., increased food intake through reduced vigilance) [35,36] Thermoregulatory effects [52,53]</p>	Survival benefits should be considerably large (e.g., at high predation risk [82])	<p>Selfish herd [31,41] By-product mutualism [83] Pseudo-reciprocity [84] Interdependence [85] Cooperative predator defence game [82,86] Interspecific mutualisms [87]</p>	<p>Passive GA [16] Safe haven [88]</p>
Short-term reciprocity	Recruits and helpers benefit from reciprocal support (survival and condition benefits)	<p>Reduced predation Alarm calling [49] Shared vigilance [33,42] Predator repellence [25,42]</p> <p>Improved health or condition Food acquisition or processing [34,51] Allogrooming [37]</p>	Survival benefits should be considerably large (e.g., at high predation risk) [82]	<p>Iterated prisoners dilemma game [80] Commodity trading [80] Direct reciprocity [89] Network- and generalised reciprocity [90–93] Partnership [94] Cooperative predator defence game [82,86] Interdependence [85]</p>	<p>Pay-to-stay [30,95] Interdependence Partnership [94]</p>
Long-term Mutualism	Recruits benefit helpers by their presence or behaviour in the future by enhanced survival, condition, chances of reproduction and/or reproductive success of helpers	<p>Reduced predation Safety in numbers^c Predator confusion^c Increased vigilance [33] Predator repellence [21,43]</p> <p>Improved health or condition Joint dispersal [55] Load-lightening of cooperators [1] Territory expansion [58]</p> <p>Enhanced chances of reproduction Group stability [21,43] Territory defence [32,58,60] Joint dispersal [54]</p>	Helpers should be able to acquire breeding position	<p>Communal territory defence [96] Interspecific mutualisms [87]</p>	<p>Passive GA [16] Social queuing and territory inheritance [88]</p>
Long-term reciprocity	Recruits benefit helpers by investing in helpers' future survival, condition, chances of reproduction and/or reproductive success	<p>Reduced predation Alarm calling [49] Shared vigilance [33] Predator repellence [43]</p> <p>Enhanced reproductive success Territory expansion [58] Recruits become helpers [19]^d</p>	Helpers should be able to acquire breeding position Queues for inheritance of the breeding position should be stable [16] and breeder turnover should be high [12], or helpers and recruits should disperse jointly	<p>Communal territory defence [96] Network- and generalised reciprocity [90–93]</p>	<p>Social queuing and territory inheritance [88] Delayed reciprocity [19] Active GA [16] Generational mutualism [2]</p>

Table 1 (Continued)

Concept	Fitness benefits to helpers	Mechanisms of how benefit to helpers can arise	Preconditions/favourable conditions ^a	Examples of general cooperation theory	Models specifically for cooperative breeders ^b
		Enhanced chances of reproduction Territory defence [32,58,60] Joint dispersal [54] Territory budding [62] Coalition formation [54]			

^aWithin each concept, preconditions do not necessarily apply to all mechanism of how benefits to helpers arise. For example, if helpers cannot inherit a breeding position, then the mechanism of enhanced chances of reproduction does not apply, but 'long-term mutualism' may still arise in the form of reduced predation risk.

^bSee also Boxes 1 and 2.

^cAlthough in many cooperative breeders individuals survive better in larger groups, there is currently no experimental proof for safety-in-numbers and predator confusion in cooperatively breeding species.

^dDelayed reciprocity (with former recruits that help former helpers to produce new recruits) can be selected because of the cascading effect of reciprocal benefits (Figure 2). The former helpers benefit by the alloparental investment of the recruits they have helped to produce, whereas the former recruits will benefit in the future from the help they will obtain from the new recruits they are helping to produce; kinship effects notwithstanding [16,19].

predation risk ('safety-in-numbers' [31]) and/or from self-serving acts of group members, such as vigilance behaviour, predator repellence or food finding [32–36]. Second, reciprocal benefits can emerge if helpful behaviour is returned in some form by the receiver, such as predator mobbing, food sharing, or care for one another by mutual grooming [37–40]. It is important to distinguish between these two possibilities because reciprocity, but not mutualism, involves investment in others that is itself costly (Glossary). Hence, two different evolutionary mechanisms (mutualism and reciprocity) can be involved in the selection of helping by GA.

When interested in the selection of helping by GA, 'short-term' and 'long-term' benefits of cooperation should also be distinguished [38]. We refer to short-term benefits when recruits enhance survival prospects of helpers during the coexistence of helpers and recruits in the group, and to long-term benefits when recruits improve the success of (former) helpers in independent reproduction. This distinction partly overlaps with 'active' and 'passive' GA benefits as referred to by Kokko *et al.* [16], but there are important differences (Glossary).

Short-term benefits of GA

The idea that the short-term benefits helpers gain from recruits can select for helping behaviour is appealing because of its simplicity [16]. The only condition for this to apply is that recruits produced through the influence of helpers must improve the survival of helpers. Theoretical work has shown that helping behaviour can evolve when such survival benefits exceed the costs of helping (Box 1). There are two main ways in which the presence or behaviour of recruits can benefit helpers on such a short time-scale (Table 1), namely through (i) reducing predation or (ii) improving the health or body condition of helpers.

(i) Recruits can reduce the predation risk of helpers by providing safety-in-numbers through risk dilution, predator confusion, or by contributing to vigilance and predator repellence. Dilution and predator-confusion effects [32,41] are hard to determine and have to our knowledge not been tested explicitly in cooperative breeders. However, there are several examples of recruits enhancing the survival of helpers through increased vigilance and/or predator repellence.

For instance, mongooses (dwarf mongoose *Helogale parvula* and meerkats *Suricata suricatta*) have higher survival probability in larger groups [23,42,43], mainly because of greater vigilance and better predator repellence [8,33,42,44], which is a behaviour that has been observed also in many other cooperative breeders (e.g., [45–47]). Such benefits can affect behavioural decisions of individuals, as suggested by results from choice experiments in the Lake Tanganyika cichlid *Neolamprologus pulcher*: helpers were found to prefer to join a group instead of breeding independently elsewhere, and helpers in groups survived better because of the defence against predators by group members [25,29]. Individuals in large groups of this species were shown to have higher survival rates [46,48]. Whether

Box 1. Theoretical models of short-term benefits gained from living in large groups

Several theoretical models addressed the significance of short-term benefits for the evolution of cooperation in general and for cooperative breeders in particular (see references in Table 1). The 'passive GA hypothesis' model by Kokko *et al.* [16] predicts that helping in cooperative breeders can be evolutionarily stable if the (survival) benefits to helpers of additionally raised offspring outweigh the (survival) costs of helping. Garay [82] and Garay and Varga [86] have shown that survival benefits are likely to occur when individuals in groups are exposed to fewer attacks by predators, through either dilution effects or active predator repellence. The maintenance of cooperation between group members resembles a 'chain reaction' because when a group member is saved from predation its presence or behaviour will enhance the future survival of other group members. Garay's model [82] is therefore an example of principles described in models of 'partnership' [94] and 'interdependence' [85]. Interdependence has been defined as 'an individual's stake in another', where the stake is an increase in fitness that depends on the fitness of others [85]. Such partnerships may be formed between unrelated group-members, and individuals may even invest more (e.g., take more risk) in individuals with whom they have such a bond than they would invest in kin [94]. These models seem appealing because, unlike in models of reciprocity (see [8]), memory of reciprocal acts by others is not required and the risk of exploitation (where some individuals 'cheat' by taking advantage of others without performing costly acts themselves) is small owing to the 'uninterrupted chain of benefits' deriving from such partnerships [16,85,94]. As such, this mechanism resembles the scenario of generalised reciprocity [90–92] where also no memory of individual acts is required but the potential risk of exploitation still does not prevent the evolution of cooperation.

vigilance and predator repellence reflect mutualism or reciprocity depends on the direct costs and benefits to the actor, which are often hard to determine. If, for instance, alarm-calling is involved to warn group members of approaching predators, then it probably reflects reciprocity because callers put themselves at risk for others (e.g., [47,49]; but see [44]). In addition, helpers may reduce predation risk by preparing shelters, as exemplified by the digging effort of Lake Tanganyika cichlids [13] and meerkats [50].

(ii) Recruits can also provide short-term benefits to helpers by improving their condition and health, for instance by improved food finding or processing, as illustrated by collective acorn-hoarding of acorn woodpeckers *Melanerpes formicivorus* [51] and cooperative hunting of African wild dogs *Lycaon pictus* [34]. In addition, recruits can reduce the opportunity costs of helpers (i.e., time investment) because the vigilance of recruits may reduce the time spent in such behaviour by other group members [35,36]. Moreover, roosting in groups reduces energy expenditure in some cooperatively breeding birds (green woodhoopoes *Phoeniculus purpureus* [52] and long-tailed tits *Aegithalos caudatus* [53]). Short-term benefits of improved condition can apply also through reciprocal acts such as grooming each other to remove ectoparasites [40].

We point out that helpers do not necessarily always benefit from additional group members in the short term. Large groups may yield survival disadvantages (e.g., due to competition for food, predator attraction, or parasite transmission) and, in systems where this is the case, short-term benefits of enhanced group size can probably not explain helping behaviour, at least not in (very) large groups. Nonetheless, from the above mentioned examples it is clear that short-term benefits received from other group members are common in cooperative breeders, and theoretical studies suggest that such benefits can be large enough to outweigh the costs of helping (Box 1).

Long-term benefits of GA

Long-term benefits of GA apply when recruits enhance either the chances of successful independent breeding by (former) helpers or their reproductive success once they become breeders. Similar to short-term benefits, recruits can also reduce predation risk or enhance the health or condition of helpers in the long term (Table 1). Such beneficial effects can derive from mutualism or reciprocity and may apply, for instance, through a safety-in-numbers effect by risk dilution or predator confusion, either when former helpers have inherited a breeding position and recruits are now their helpers in the group, or when recruits have dispersed together with the former helpers [54]. The latter has been demonstrated in Arabian babblers *Turdoides squamiceps*, where individuals dispersing together suffer less body-mass loss than individuals dispersing alone [55]. Recruits can also decrease the workload of helpers if they share in the care for subsequent offspring ('load-lightening' [1,56,57]). In addition, larger groups may allow territory expansion, and this can improve helper survival because of access to more or better resources [58].

Long-term benefits can be accrued by increasing the chances of reproduction of the former helpers via the actions of their former beneficiaries (Table 1). In cooperative

Box 2. Theoretical models of long-term benefits caused by former recruits

As illustrated by several theoretical models ([88,96] and references therein), territory inheritance can be an important determinant for the evolution of group living. Therefore, recruits improving the chances of helpers to inherit a territory (for instance through cooperative territory defence or enhanced group stability [96,97]) may be a strong selective force for helping to raise recruits. Furthermore, former recruits can enhance the reproductive success of former helpers when the latter have ascended to breeding status and the recruits now act as helpers (Figure 2). This was suggested by a model based on long-term data for stripe-backed wrens, *Campylorhynchus nuchalis*, where individuals queuing for a breeding position gained Darwinian fitness owing to enhanced productivity in larger (inherited) groups which they had helped to produce [19]. A model developed to study this possibility [16] suggested, however, that other evolutionary mechanisms favouring helping behaviour (such as indirect fitness benefits) must initially apply to select for cooperative breeding in the first place [16].

societies, breeding vacancies are often scarce and competition for breeding positions is intense [59], and the probability of establishing or inheriting a territory may therefore be an important determinant of the lifetime Darwinian fitness of helpers (Box 2). As such, helpers may benefit from recruits if larger groups are more stable over time or are less likely to be taken over by conspecifics [60], as is the case in Lake Tanganyika cichlids [21] and meerkats [43]. Hover wasp *Liostenogaster flavolineata* groups that were experimentally reduced by group member removal were more likely to disappear, illustrating that larger groups enhance the chances of inheritance of a breeding position [61]. Similarly, individuals in larger groups may benefit from forming alliances or coalitions that increase dispersal and/or settlement opportunities [54]. In meerkats, larger groups produce larger dispersing coalitions that experience lower costs of dispersal and are better able to found new groups or to take over established groups (A.J. Young, PhD thesis, University of Cambridge, 2003; see also [55]). Alternatively, if larger groups are able to expand their territory, individuals may more easily bud off part of the territory to reproduce independently [62].

Helpers can also gain long-term benefits of enhanced reproductive success when they inherit the breeding position and former recruits are still present to help them to raise their offspring [17–19] (Figures 1,2). In many cooperative breeders, a proportion of helpers can inherit their home territory [9,11,12,17–19,23,58,63–66]; for example, in green woodhoopoes [63] and female dwarf mongooses [23], 58% and 43% of breeding positions, respectively, are obtained by inheritance. In such systems improvement of reproductive success in larger groups could drive the evolution of helping behaviour through delayed (or 'long-term') reciprocity of former recruits who help former helpers to produce new recruits. Such a system may maintain itself through the cascading effect of reciprocal benefits (Figure 2). For such long-term benefits to be a reason for helping, hierarchical queues for inheritance among helpers should be stable. Social queuing has been reported in cooperatively breeding mammals [64], birds [9], fish [15], and insects [65]. Social queues can be stabilised, for instance, by size or age differences between helpers, where larger or older helpers are ranked more highly [47,65,67].

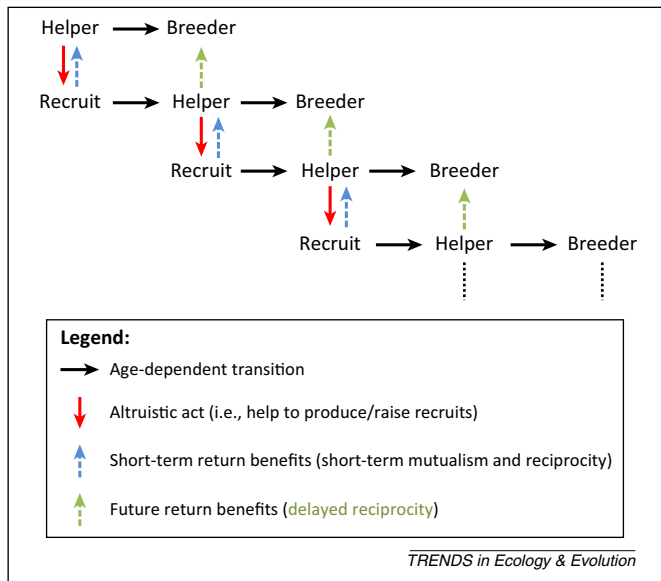


Figure 2. The cascading effect of short-term and delayed (or long-term) reciprocity between helpers and their recruits, where helpers enhance the production of recruits – which in turn become helpers after transition of their former helper to breeder status.

Stable queues will select for the production of new recruits by helpers because the latter eventually will not only inherit a breeding position but also a group of helpers (the former recruits), and this exemplifies the benefits of GA by delayed reciprocity [16,19] (Figure 2).

Testing the GA hypothesis: predictions of helper investment

Improvement of helper fitness by recruits inevitably selects for helping behaviour. However, it is important to determine the importance of GA relative to other fitness effects when aiming to understand the adaptive processes underlying variation in helping behaviour. Alternative evolutionary mechanisms explaining helping behaviour are not mutually exclusive [9,16], and different mechanisms may predict similar investment strategies. It may therefore be difficult to disentangle the mechanisms driving the evolution of cooperation in empirical studies (Table 2). However, this should not prevent us from separating them conceptually to understand which evolutionary mechanisms can contribute to the cooperative behaviour.

In fact, it is likely that a general mechanism such as GA, which includes ubiquitous fitness benefits such as safety-in-numbers, will inevitably select for cooperative behaviour even if other benefits favouring helping behaviour are also involved (e.g., indirect fitness benefits). Once it is established that GA benefits are likely to apply in a specific system, and in which way, several *a priori* predictions can be made regarding investment in recruits by helpers to determine the relative importance of GA in explaining variation in helping behaviour [6,9] (Table 2). We stress that some of the predictions of GA outlined below are similar for other mechanisms. Therefore, if the aim is to exclude alternative hypotheses, tests of additional predictions may be required (see section ‘Disentangling different hypotheses explaining helping behaviour’ below). If predictions of the GA hypothesis are not supported, however, this will provide evidence against selection based on GA benefits.

Although we highlight several examples below that show evidence for group-size benefits to helpers, we highlight here that for specific studies ideally experimental scrutiny should test whether recruits affect components of the fitness of helpers (e.g., survival, resource access, condition, dispersal ability, or future reproductive success). This may be conducted by removing or adding recruits at an early stage (e.g., dependent nestlings) to minimise confounding effects of disruption of group dynamics.

Predictions of the GA hypothesis: helping effort

(i) If GA applies, helping effort is expected to be higher in small groups than in large groups. Small groups should benefit from a larger number of individuals, whereas above a particular group size individuals might suffer from increased competition over food, predator attraction, or parasite transmission. In other words, the utility of group size may show diminishing returns, although we should point out that reduced helping effort in larger groups could also reflect ‘load-lightening’ because additional help would have no or little further effect on increasing group size. As predicted, individuals in larger groups help less in some species: a group-size manipulation experiment in Lake Tanganyika cichlids showed that helpers visited breeding shelters more when 40% of the helpers were removed, and this might indicate an increase in helping behaviour because eggs and larvae are tended inside these shelters [26]. In experiments in fish [68] and birds [69], helpers compensate for an

Table 2. Some predictions of alternative hypotheses of helping that differ from the predictions of GA

Alternative hypotheses to explain helping behaviour	Predictions of respective hypotheses	Corresponding predictions of the GA hypothesis
Indirect fitness benefits (kin selection)	Helping effort is adjusted to the degree of relatedness [6,7,9] ^a	Helping effort is independent of the degree of relatedness
Parentage acquisition (direct fitness benefits)	Brood care depends on the production of own offspring [98]	Helping is independent of the parentage of dependent young
Pay-to-stay (reciprocal trading)	Helping is adjusted to the demands of breeders [29,68]	Helping is independent of the demands of breeders
Social prestige (signaling of quality)	Helpers obtain breeding status depending on previous helping effort ^b	Helping levels do not predict the acquisition of breeder status

^aNote that absence of adjustment of care to the degree of relatedness does not necessarily imply that helping behaviour is not selected for by indirect benefits: individuals may for example not discriminate when help (and thus discrimination errors) is relatively cheap [99], or they may not discriminate because they normally care for close kin because of relatively low variation in relatedness [77].

^bNo reference is provided here because to our knowledge social prestige has not yet been demonstrated in cooperative breeders [20].

experimental reduction in helping by other group members by increasing their work effort, and this suggests an advantage derived from the behavioural effort of additional group members.

(ii) If dispersal is sex-biased, GA predicts that the philopatric sex should invest more in helping behaviour than the dispersing sex because philopatric individuals benefit from increased group size for longer. If joint dispersal is not practised, long-term benefits of GA will even be restricted completely to the philopatric sex. As such, greater helping effort by females was suggested in Lake Tanganyika cichlids [70] in which females are much more likely to inherit the territory than males [12]. In meerkats, philopatric females invest more in female offspring [22], suggesting strategic investment in anticipating future help from recruits when they inherit the breeding position. In addition, older individuals of the dispersing sex (with no or limited opportunities for territory inheritance) that are closer to dispersal gain little from recruiting additional group members if joint dispersal is not practiced, whereas younger individuals may still gain benefits while remaining in the group. Dispersing group members should therefore invest less in helping shortly before dispersal, as is indeed observed in meerkats and cichlids [22,71]. Alternatively, in species where individuals disperse together in same-sex coalitions, individuals should invest mostly in same-sex recruits that may join them in dispersal. The latter may partly explain why female meerkat helpers, who disperse in same-sex coalitions, invest more in female than in male recruits [22].

(iii) Individuals with the best prospects of attaining a breeding position should help more because the benefits of territory inheritance and recruitment of future helpers are restricted to helpers that eventually acquire breeding status. This is the case in purple-crowned fairy-wrens *Malurus coronatus* where helpers of unrelated opposite-sex breeders are more likely to inherit a vacant breeding position than related helpers, and such individuals invest more in the brood [9]. Moreover, older and/or larger individuals are often more likely to acquire breeding status than younger smaller ones, and should thus invest more in helping. In Lake Tanganyika cichlids, larger helpers that are more likely to inherit the territory indeed invest more in territory defence and maintenance [15,45].

It should be noted that the above-mentioned predictions concerning helping effort are not always straightforward in light of the GA hypothesis. For instance, if helping has substantial costs, individuals that are most likely to attain breeding status might be selected to contribute less to optimise their breeding condition: low-ranked hover wasps with poor prospects for direct reproduction, for instance, help more than do high-ranked individuals with good chances to inherit the breeding status [72]. Moreover, GA predicts that older and larger individuals help more, but such a pattern may also be explained by the fact that the relative costs of helping may be lower for these individuals.

Disentangling different hypotheses explaining helping behaviour

We should be aware that, in addition to GA, other fitness effects can select for helping behaviour, such as the

production of close kin, acquisition of a share in parentage, attainment of resource access (pay-to-stay), or the acquisition of social prestige. As explained in previous studies and reviews [8,9,14,15,20], predictions of alternative hypotheses explaining helping behaviour may overlap with those of the GA hypothesis. For instance, kin selection theory also predicts an increase in *per capita* helping effort if the number of helpers is reduced (prediction 1 above). Similarly, depending on the specific conditions of a system, GA (long-term benefits), pay-to-stay, parentage acquisition, and social prestige can all predict an increase in helping behaviour with fewer helpers. Furthermore, GA, pay-to-stay and social prestige are all expected to lead to more helping effort by the philopatric sex (prediction 2 above). Therefore, to assess the likelihood that GA or alternative hypotheses can explain helping behaviour in particular systems, alternative explanations should be evaluated by appropriate experimental tests of predictions derived from alternative hypotheses (Table 2; see also [9]).

Alternative means to increase group size

Apart from helping to raise offspring, there are alternative ways to increase group size, for example by recruiting or kidnapping (unrelated) individuals from outside the group [73–75]. Such behaviour provides strong evidence for the GA hypothesis. It seems, however, that these forms of group size enhancement are rare [74,75]. One explanation for such rarity might be the severe damage that members of foreign groups can cause, for example by performing cannibalism instead of brood care [76]. Another reason might be that accepting mature floaters can pose a threat to the reproduction of group members [67] because floaters might aim to take over the breeding position or challenge the queue for such positions. Finally, if unrelated individuals improve the survival of group members (which typically will also affect the relatives of each group member), then accepting unrelated group members would imply that indirect benefits and GA benefits act in concert [9,16].

Concluding remarks

GA has been one of the most commonly proposed hypotheses to explain helping behaviour by direct fitness benefits in cooperatively breeding animals. So far, however, a detailed outline of the separate concepts included in the GA hypothesis has been lacking, and this might be responsible for the view that the hypothesis merely serves as ‘a rubbish bin for results that cannot be explained otherwise’ [20]. The GA hypothesis includes several concepts that need to be distinguished: short- and long-term benefits, benefits accrued through mutualistic or reciprocal relationships between helpers and recruits, fitness benefits generated through enhancement of helper survival (either through reduced predation or improved condition), their chances of reproduction, or future reproductive success. Our review of theoretical and empirical studies shows that all these concepts may, in principle, promote the evolution and maintenance of cooperative breeding. It is now to be tested whether these benefits can explain the large variation in helping behaviour within and among cooperative breeders (*sensu* [77]). As such, this outline should provide a guideline for future empirical and theoretical studies to

test the relative importance of the GA hypothesis for the explanation of cooperative breeding and advanced sociality.

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