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The evolution of cooperative breeding through group augmentation

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Some individuals (helpers) in cooperatively breeding species provide alloparental care and often suppress their own reproduction. Kin selection is clearly an important explanation for such behaviour, but a possible alternative is group augmentation where individuals survive or reproduce better in large groups and where it therefore pays to recruit new members to the group. The evolutionary stability of group augmentation is currently disputed. We model evolutionarily stable helping strategies by following the dynamics of social groups with varying degrees of subordinate help. We also distinguish between passive augmentation, where a group member benefits from the mere presence of others, and active augmentation, where their presence as such is neutral or harmful, but where helping to recruit new group members may still be beneficial if they in turn actively provide help for the current reproductives ('delayed reciprocity'). The results show that group augmentation (either passive or active) can be evolutionarily stable and explain costly helping by non-reproductive subordinates, either alone or leading to elevated help levels when acting in concert with kin selection. Group augmentation can thus potentially explain the weak relationships between relatedness and helping behaviour that are observed in some cooperatively breeding species. In some cases, the superior mutualistic performance of cooperatively behaving groups can generate an incentive to stay and help which is strong enough to make ecological constraints unnecessary for explaining the stability of cooperatively breeding groups.

Keywords: altruism; cooperative breeding; eusociality; kin selection; delayed benefits; delayed reciprocity

1. INTRODUCTION

Ever since Hamilton (1964) formulated the notion of inclusive fitness, cooperatively breeding species have been seen as ideal candidates for testing the hypothesis of kin-selected altruism. However, while many studies have quantified substantial inclusive fitness benefits to subordinates who help to raise new offspring at the nests of their kin, instead of attempting to reproduce on their own (reviewed in Emlen 1991), helping does not appear to be restricted to groups of closely related members. An early study of pied kingfishers (*Ceryle rudis*) (Reyer 1980) identified 'secondary' (unrelated) helpers, who 'apply' to several breeding pairs but are accepted as helpers only when food is scarce. Subsequently, many studies of cooperatively breeding birds have found unrelated helpers (for reviews, see Stacey & Koenig 1990; Cockburn 1998), and differences in relatedness do not appear to explain any variance in helping behaviour in some bird and mammal species (Duplessis 1993; Piper 1994; Dunn *et al.* 1995; Delay *et al.* 1996; Heinsohn & Legge 1999; Clutton-Brock *et al.* 2000)—and, in some cases, help is preferentially directed to unrelated offspring (Magrath & Whittingham 1997). Although helping behaviour is undoubtedly most common in familial groups (Emlen 1995), the general conclusion from studies of cooperative breeding is that helping behaviour is not strictly restricted to interactions among kin.

Clearly, alternative or additional explanations for helping in cooperatively breeding groups are needed, and several have been suggested (reviewed in Jennions & Macdonald 1994; Cockburn 1998). These include helping as an unselected behaviour (Jamieson 1989; but see Brown & Vleck 1998; Clutton-Brock *et al.* 1998), as a means of gaining parenting experience (Skutch 1961; Lancaster 1971), as a means of acquiring social status (Zahavi 1977; Roberts 1998), or as 'payment of rent' (Gaston 1978), where subordinates benefit by waiting for future breeding opportunities, but are permitted to do so only if they help to boost the dominant breeder's productivity. The focus of this paper is on a further explanation, namely group augmentation (Woolfenden 1975; Rood 1978; Brown 1987). Here, individuals are assumed to survive or reproduce better in larger groups and they therefore benefit from raising new group members even if these are unrelated. This argument may take the explicit form of 'delayed reciprocity', in which individuals help to recruit new group members who will later actively help them (Ligon & Ligon 1978; Wiley & Rabenold 1984).

The stability of group augmentation is currently disputed. It is not easy to see how helping based on such delayed benefits could spread (e.g. Cockburn 1998, p. 159), and there is a lack of theoretical work addressing the stability of such behaviour. Models of cooperative breeding have focused almost exclusively on kin selection as an explanation for helping behaviour, ignoring benefits that individuals may enjoy in groups of different sizes (Emlen 1982; Brown & Pimm 1985; Mumme *et al.* 1989; Motro 1993; Queller 1994). In a notable exception, Wiley & Rabenold (1984) modelled the evolution of helping through delayed reciprocity, showing that helping behaviour which reduces survival early in life can be selectively favoured if it leads to greater fecundity or survival later. However, even their model did not address

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the evolutionary stability of helping fully. This would require one to demonstrate that it does not pay for an individual to 'cheat' by helping less than others (and, consequently, being more likely to obtain a breeding position) while still inheriting the helpers raised by other group members. Wiley & Rabenold (1984, p. 618) argued that cheating is selected against because the cost–benefit balance of helping repeats itself in each generation that queues for dominance, but did not specify why exactly a selfish mutant that disrupts this balance should not spread.

In this paper, we develop a more comprehensive model of the evolution of helping that permits us to examine the evolutionarily stability of group augmentation, including delayed reciprocity. We track the dynamics of births and deaths in groups of different sizes, as group dynamics may profoundly influence the evolution of cooperation (Avilés 1999). The model allows us to compare the importance of group augmentation versus kin selection by determining how evolutionarily stable help levels change as a function of relatedness and by using parameters that determine the dynamics of births, deaths and dispersal in the group. Helping that is solely based on kin selection should disappear if relatedness is set to zero, whereas benefits from group augmentation will vanish if the group retains none of the offspring produced.

2. THE MODEL

We wish to determine the circumstances under which subordinate group members gain by staying in an association and helping dominant individuals to raise more offspring. If a subordinate is related to the dominant, this behaviour obviously yields indirect, kin-selected fitness benefits. However, it may also yield direct advantages later in life if a helper increases the chances that it later finds itself later in a group of beneficially large size.

In order to assess these possibilities, we first outline a basic model framework that specifies the survival probabilities and reproductive opportunities of group members in the absence of helping behaviour. We then go on to incorporate helping, by allowing subordinates to boost the productivity of the dominant member of the group at the cost of a reduction in their own survival chances. This extended model allows us to determine the evolutionarily stable level of help, while taking into account both the indirect, kin-selected benefits that helping yields, and the contribution it makes to group augmentation. The latter effect is incorporated into the model by allowing that the probability of recruitment may depend on productivity (more help leads to greater productivity, which leads to a higher probability that an offspring is recruited to stay in the group). However, we also investigate the case where all offspring disperse and recruitment is thus independent of productivity. This alternative allows us to study the evolution of helping in the absence of group augmentation.

(a) *The basic framework*

We focus on a group that may range in size from 1 to N members (we assume that individuals in excess of this number will disperse rather than joining or remaining in the group, because queuing for breeding status becomes inefficient at larger group sizes); (see Kokko & Sutherland 1998; Field *et al.* 1999). All group members are related to each other with an average coefficient of relatedness r. While this simplification ignores any individual differences in relatedness (tracking these greatly complicates models even if group sizes are fixed) (Johnstone *et al.* 1999), our model still captures the essence of the problem of alternative helping explanations, such as whether and when kin selection is necessary for helping to evolve (if it is, helping will not evolve if $r = 0$ among all group members). In addition, in order to provide a conservative estimate of subordinates' benefits when staying in groups, we restrict our attention to cases in which breeding is restricted to the dominant member of the group. Helping is costly for subordinates and they will trade off any direct or indirect benefits of helping against their survival (Heinsohn & Legge 1999). Their expected fitness includes the chance to eventually accede to the dominant's position. Given the subordinates' interest in future breeding possibilities such groups can be stable when composed of either kin or non-kin individuals (Kokko & Johnstone 1999; Ragsdale 1999).

Even in the absence of specialized helping behaviour, the productivity of the dominant individual, which is denoted by k, may depend upon the number of subordinates present. We will therefore write k_n for the reproductive success (during a single breeding season) of an unaided dominant in a group of size n. Similarly, the chance of an individual surviving from one breeding season to the next may be influenced by group size and by rank. We will therefore write $s_{i,n}$ for the survival probability of the ith ranking individual in a group of size n.

The group represents a strict queue, so that, whenever an individual dies, surviving group members of lower rank move up one place in the dominance hierarchy. In this way, a subordinate may eventually accede to dominance status following the death of all higher ranking group members. In addition, for groups less than the maximum size N, there is the possibility of recruiting new group members who will join the bottom of the dominance hierarchy. The probability of recruiting at least one new member between one breeding season and the next may depend upon the group's reproductive output, k; this will be denoted $a(k)$.

If any subordinate member of the group chooses to disperse and attempt to breed independently, it will succeed in doing so (i.e. in becoming a lone dominant breeder) with probability x. Low values of x thus indicate strong ecological constraints (as in reproductive skew models) (Reeve 1998; Johnstone 2000).

(b) *Incorporating helping behaviour*

We incorporate the possibility of helping in the model by allowing subordinate group members to boost the dominant's reproductive success (and, thus, indirectly, the chances of recruiting new group members) at the cost of a reduction in their own survival chances. Each subordinate in the group can choose to offer a help level h, which is measured as an increase in the dominant's productivity. The dominant's total productivity k is then equal to the basic value described above (k_n) plus the sum total of all help given by subordinate group members. Formally,

$$k = k_n + \sum_{i=2}^{i=n} h_i, \tag{1}$$

where h_i denotes the help offered by the subordinate of rank i. Consequently, the chances of recruiting one new group member (assuming that the group is smaller than the maximum size N) is equal to

$$a(k) = a\left(k_n + \sum_{i=2}^{i=n} h_i\right). \tag{2}$$

Since several new recruits may enter the group simultaneously if the dominant is sufficiently productive, we assume that the probability of recruiting at least n group members is $a(k)^n$ (again provided that this does not exceed the maximum group size).

When the effects of helping are taken into account, a subordinate's chance of survival from one breeding season to the next, which is $s_{i,n}(h)$, is equal to the basic value described above ($s_{i,n}$ for the ith ranking individual in a group of size n) reduced by a factor dependent on h, the level of help it gives to the dominant. Formally,

$$s_{i,n}(h) = s_{i,n}(0)(1 - h^{\Phi}), \tag{3}$$

where Φ is a positive constant that determines how rapidly survival declines with the amount of help offered. A high value of Φ indicates that survival will only begin to decline significantly when a large amount of help is offered, whereas a small value indicates that survival declines rapidly even for small amounts of help (figure 1).

(c) *Calculating the evolutionarily stable level of help*

The evolutionarily stable helping strategy, H^*, specifies the level of help offered by a subordinate of rank i in a group of size n (for every possible combination of i and n), which is denoted by $h^*_{i,n}$. This strategy was sought iteratively according to the following steps (see Appendix A for details).

(i) Pick a candidate helping strategy H.
(ii) Write down an expression for the expected lifetime inclusive fitness of a mutant individual who adopts an alternative strategy H' in a population that adopts the strategy H. This expression takes account of all possible transitions of the individual in the group hierarchy, as well as of current and future changes in group size (including the risk of group extinction).
(iii) Choose the mutant strategy H' which maximizes the inclusive lifetime fitness calculated in step (ii).
(iv) Replace the population strategy H with the best mutant strategy H', which was calculated in step (iii) and repeat steps (ii)–(iv) until H converges to an equilibrium H^*.
(v) Check that subordinates do best to stay and offer the levels of help specified by H^* rather than dispersing to attempt to breed independently.

While the above procedure is simple in principle, the calculations required in step (ii) (to obtain an expression for the fitness of a mutant individual who adopts a strategy H' in a population that adopts the strategy H) become increasingly lengthy and involved as the range of possible group sizes increases. We therefore only present results only for maximum group sizes of $N = 2$ and $N = 3$. The details of these calculations are given in Appendix A.

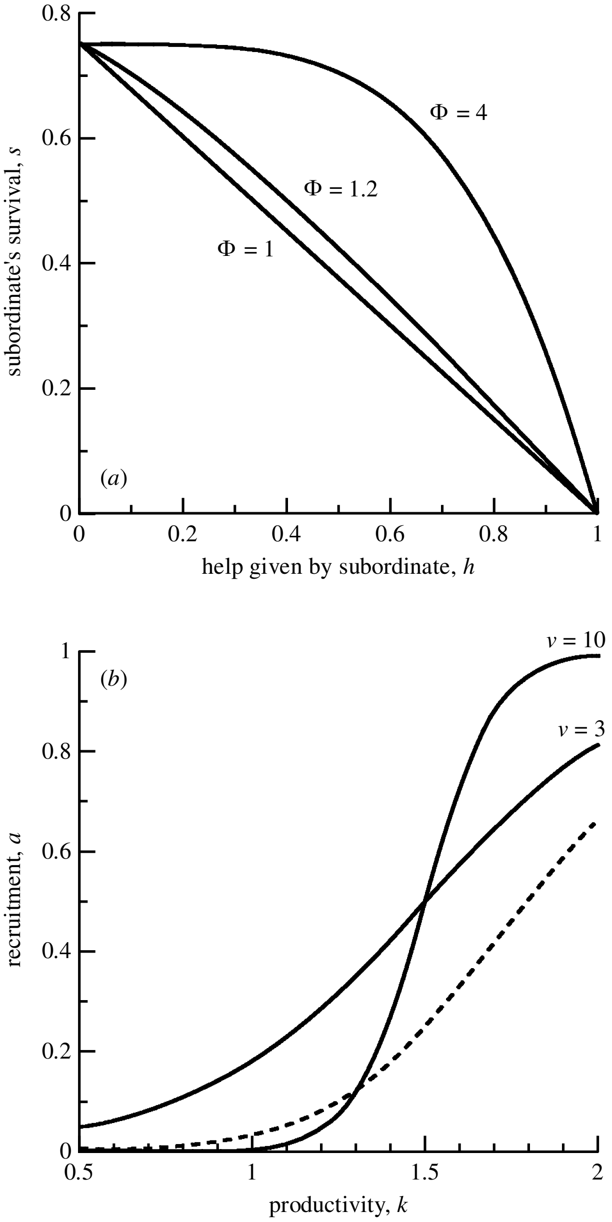

Figure 1. Model assumptions on (a) the level of helping h and the survival s of the helper (exemplified with $s(0) = 0.75$), and (b) the current productivity of the group, k, and the recruitment probability to the group, $a(k)$. The parameter Φ scales the cost of helping, while ν determines how strongly recruitment $a(k)$ responds to changes in productivity k. Large values of ν indicate that helping (an increase in k) is efficient, i.e. it strongly enhances recruitment. The dashed line additionally exemplifies the probability $a(k)^2$ of gaining two recruits in the case $\nu = 3$, if group size permits (maximum group size $N = 3$). The equation for $a(k)$ is $a(k) = (1 + \exp(-\nu(k - 1.5)))^{-1}$.

3. RESULTS

The results show that it is important to consider two different kinds of benefit that group augmentation may bring: 'passive' benefits that depend solely on the presence of other group members rather than their behaviour, and

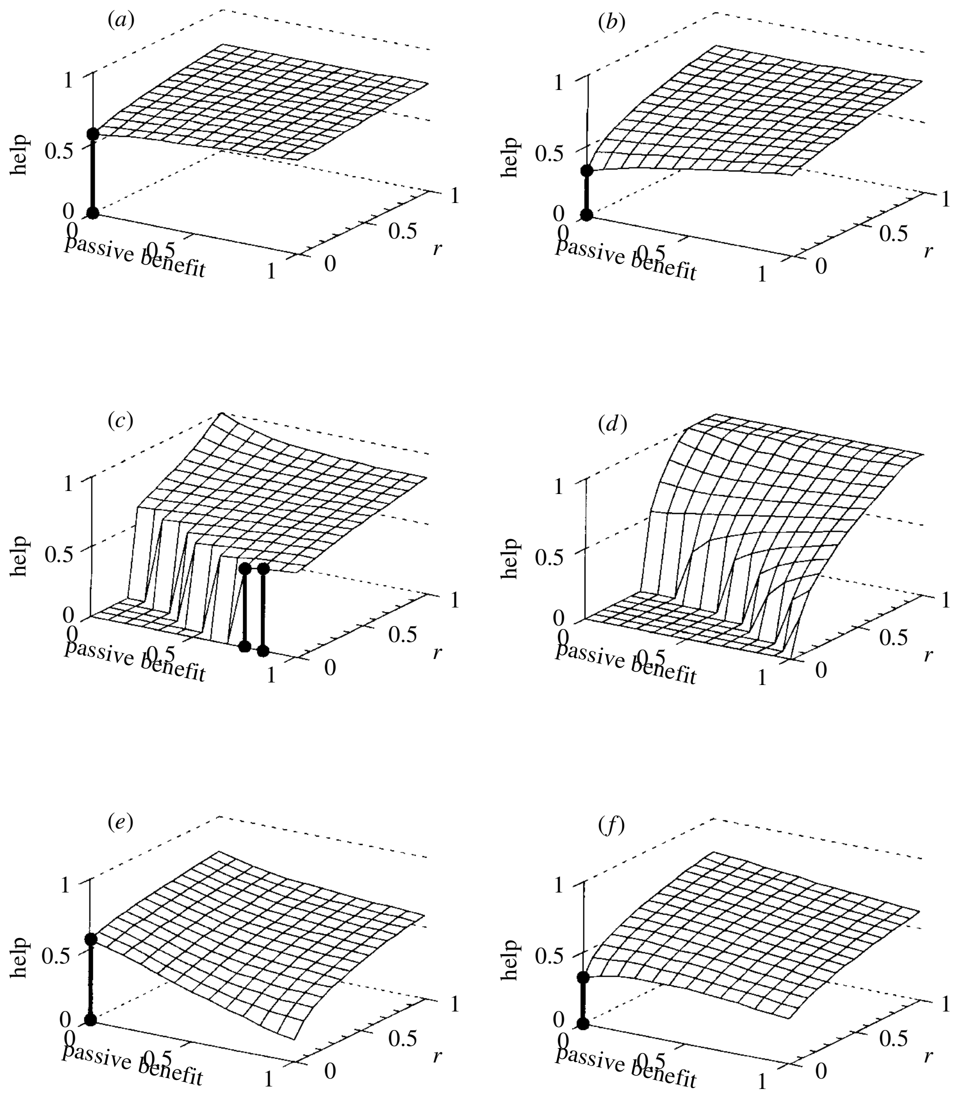

Figure 2. The evolutionarily stable strategy of group augmentation-based helping with maximum group size $\mathcal{N} = 2$. The subordinate's equilibrium help levels h^* are indicated for different values of relatedness r and the magnitude of passive benefits for the group when group size is changed from 1 to 2. Connected dots mark cases where not helping ($h = 0$) is also an evolutionarily stable strategy. (*a–d*) The passive benefit enhances the survival of all group members, with benefit being defined as the fraction by which mortality $(1 - s)$ is reduced in groups of two individuals compared to solitary breeders. (*e–f*) The passive benefit equals an automatic increase in the productivity of the dominant, i.e. $k_2 - k_1$ (helping h will then further increase the productivity). (*a*) Efficient helping ($\nu = 10$) with slowly increasing costs ($\Phi = 4$), (*b*) inefficient helping ($\nu = 3$) with slowly increasing costs ($\Phi = 4$), (*c*) efficient helping ($\nu = 10$) with rapidly increasing costs ($\Phi = 1$), (*d*) inefficient helping with rapidly increasing costs ($\Phi = 1$) and (*e*,*f*), slowly increasing costs ($\Phi = 4$) with passive productivity enhancement with either (*e*) efficient or (*f*) inefficient helping. The other parameter values used in all examples are $s_{1,1} = s_{1,2} = s_{2,2}(0) = 0.5$, $k_1 = k_2 = 1$ and $x = 0.01$.

'active' benefits that depend on the help that new members may offer. The latter represents a form of delayed reciprocity, in which individuals help to recruit new group members who will later help them. We deal with these two types of benefit separately in turn in § 3(a,b). For simplicity, we present results based on the particular cost and recruitment functions shown in figure 1. Our conclusions remain robust to changes in these functions, provided that helping entails accelerating survival costs and enhances group productivity. In each case, we first consider the results of the model for the smallest possible group with one helper and a dominant ($\mathcal{N} = 2$). We then show that the evolutionary stability of group augmentation is not an artefact of assuming that the low maximum group size restricts helpers to work alone, but that helping can also be evolutionarily stable also in larger groups ($\mathcal{N} = 3$) where individual helpers are allowed to decide their help levels independently.

(a) *Result 1: helping can evolve through group augmentation if larger group sizes yield automatic 'passive' benefits to group members*

When large groups offer passive benefits to the individual, the model reveals that it may prove advantageous for a subordinate to provide aid even if it is completely unrelated to any of the offspring it helps to rear (figure 2 shows positive help levels with $r = 0$). This means that group augmentation alone can provide sufficient reason for subordinates to help. Moreover, if recruitment to the group is low for an unaided dominant but increases sharply at a sufficient help level (figure 1*b* with $\nu = 10$), group augmentation may become the most important factor behind help. Under these circumstances, unrelated subordinates will offer almost the same level of help as related individuals (figure 2*a*) and both will tolerate substantial reductions in survival for doing so. Only if helping has a weaker effect on recruitment does kin selection become important in addition to group augmentation, with kin individuals helping more than non-kin (figure 2*b*). Positive relatedness is a more important requirement for helping in cases where even a small level of help is costly to give (figure 2*c*,*d*).

Although group size benefits underlie the argument behind group augmentation, the precise amount of help offered can prove insensitive to the magnitude of these benefits (figure 2*a*,*b*). This is because, once helping takes over as a strategy in the population, active benefits are generated which reduce the sensitivity to initial, passive benefits (see § 3(b)). Furthermore, even where this is not the case, the correlation between passive benefits and help may be positive or negative. When larger group sizes lead to increased survival, greater passive benefits are likely to favour more help (e.g. figure 2*c*,*d*). In contrast, when larger group sizes lead to increased productivity of the dominant (rather than survival of all group members), greater passive benefits may lead to less help being offered (figure 2*e*,*f*). This is simply because passive enhancement of productivity means that helpers need to do less actively in order to achieve the desired rate of recruitment.

In larger groups ($N = 3$), the solutions become more complicated, but with a similar main conclusion: passive benefits can favour helping as a means to augmenting the group. However, the amount of help given does not always increase with the magnitude of passive benefits. In addition, because of differences in both the probability and the benefits of recruiting new group members, two helpers together may give either more or less help than a solitary helper (figure 3).

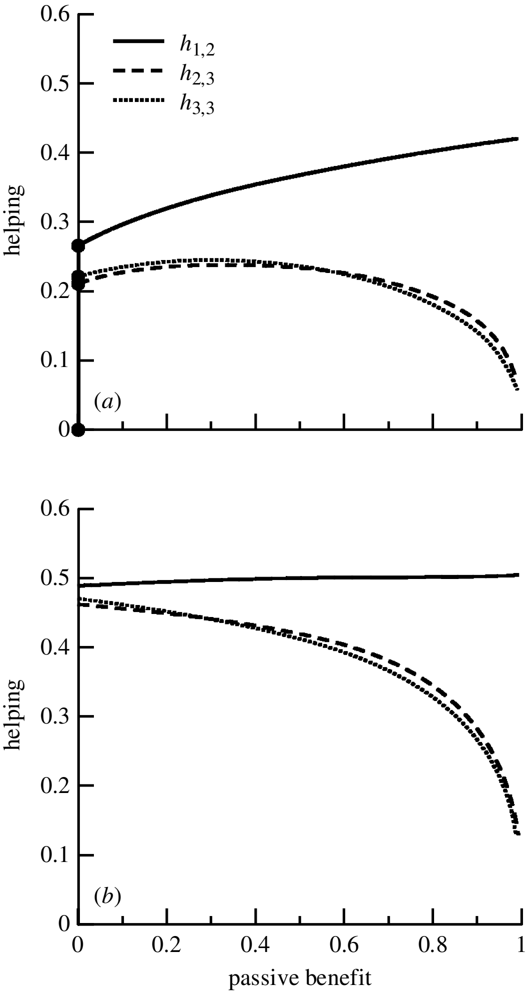

Figure 3. Augmentation in groups of maximum size $N = 3$, either (*a*) in groups of unrelated individuals or (*b*) in groups with average relatedness $r = 0.5$. The solid line indicates help given by a sole subordinate in a group of two individuals, the dashed line indicates helping by the higher ranked sub-ordinate in a group of three individuals and the dotted line gives the help levels of the lower ranked subordinate in that group. The passive benefit is assumed to reduce mortality as in figure 2*a*–*d*, but with full reduction achieved only in groups of three individuals; groups of two individuals are assumed to achieve half of the reduction in mortality. Connected dots mark cases where not helping ($h = 0$) is also an evolutionarily stable strategy, as in figure 2. The parameter values used are $s_{1,1} = s_{1,2} = s_{2,2}(0) = s_{2,3}(0) = s_{3,3}(0) = 0.75$, $k_1 = k_2 = k_3 = 1$, $\nu = 3$, $\Phi = 4$ and $x = 0.01$.

(b) *Result 2: even if individuals gain no automatic 'passive' benefits by recruiting new group members, 'active' benefits (in the form of delayed reciprocity) may provide a stable reason to help*

Assuming a complete absence of kin-selected benefits of helping and passive benefits of group augmentation, leads to the cases marked with dots in figures 2*a*,*b*,*d*,*e*, and figure 3*a*. These feature two possible equilibria (which are indicated by connected dots in the figures): either no help ($h = 0$), or, more interestingly, an evolutionarily stable strategy (ESS) with a positive level of help. This positive level is generally smaller than expected in the presence of passive benefits or kin selection. Its existence proves that active benefits of group augmentation, i.e. delayed reciprocity, can provide a sufficient reason to help, as suggested by Wiley & Rabenold (1984). This equilibrium is stable even though individual subordinates have the option to 'cheat' and refrain from helping.

It should also be noted that this reciprocity does not require that helpers have always been partly or completely reared by the same individual they are now helping (and, thus, the usage of the term 'reciprocity' in this context may be criticized) (see also Brown 1987). Instead, helping may be an evolutionarily stable rule of behaviour in a group that aims to raise new group members, which will in turn adopt this behaviour. 'Deceiving' offspring into believing that they are related to their rearer (Curry & Grant 1990; Connor & Curry 1995) is not necessary for this behaviour to evolve. A natural requirement for delayed reciprocity is that helping enhances recruitment to the group (i.e. at least some of the offspring that the subordinate helps to raise are retained). However, the initial recruitment enhancement from small help levels need not be strong (figure 4) (reciprocal helping is stable at any $\nu > 0$).

The initial origin of delayed reciprocity may appear problematic (e.g. Cockburn 1998) as the 'no help' state is also stable in the cases discussed above (figures 2 and 3).

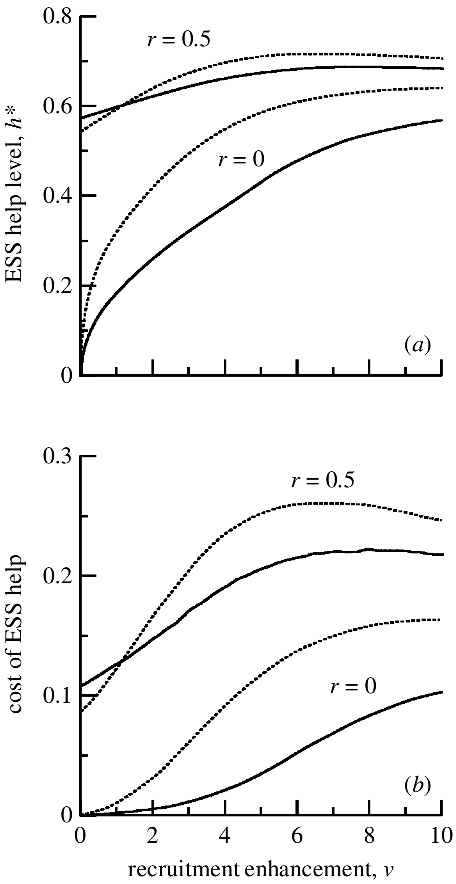

Figure 4. The interaction between kin selection and group augmentation in the two-player game. The parameter ν indicates the impact that helping has on recruitment (figure 1*b*): $\nu = 0$ assumes no impact and, thus, prevents any effect of group augmentation (all offspring disperse). Evolutionarily stable helping is indicated for unrelated ($r = 0$) and related ($r = 0.5$) subordinates as both (*a*) evolutionarily stable help levels h^* and (*b*) costs expressed as a fraction by which subordinates accept to reduce their survival. Solid lines indicate help in the absence of passive benefits and dotted lines assume higher survival in larger groups. The parameter values used are $k_1 = k_2 = k_3 = 1$, $\Phi = 4$ and $x = 0.01$ and either $s_{1,1} = s_{1,2} = s_{2,2}(0) = 0.5$ (solid lines) or $s_{1,1} = 0.5$ and $s_{1,2} = s_{2,2}(0) = 0.6$ (dotted lines). The alternative 'no help' equilibrium also exists in all cases where relatedness $r = 0$ (not shown).

To put it simply, if the whole population is in a non-helping state, it does not pay an individual to help to recruit new group members in the hope of obtaining help from them later. Therefore, some degree of initial helping tendency is needed in the population before helping that is solely based on active group augmentation can evolve. This degree depends crucially on the costs associated with small amounts of help given. If the costs of low levels of help are small (figure 1*a* with high Φ), even a tiny chance that another subordinate will adopt a helping strategy suffices to trigger a transition towards the helping equilibrium as this will bring about a small (and, later, when helping increases, larger) delayed benefit for an individual that helps to rear such offspring. This process whereby helping 'takes off' is conceptually similar to a model of direct (non-delayed) reciprocity with increasing investments (Roberts & Sherratt 1998).

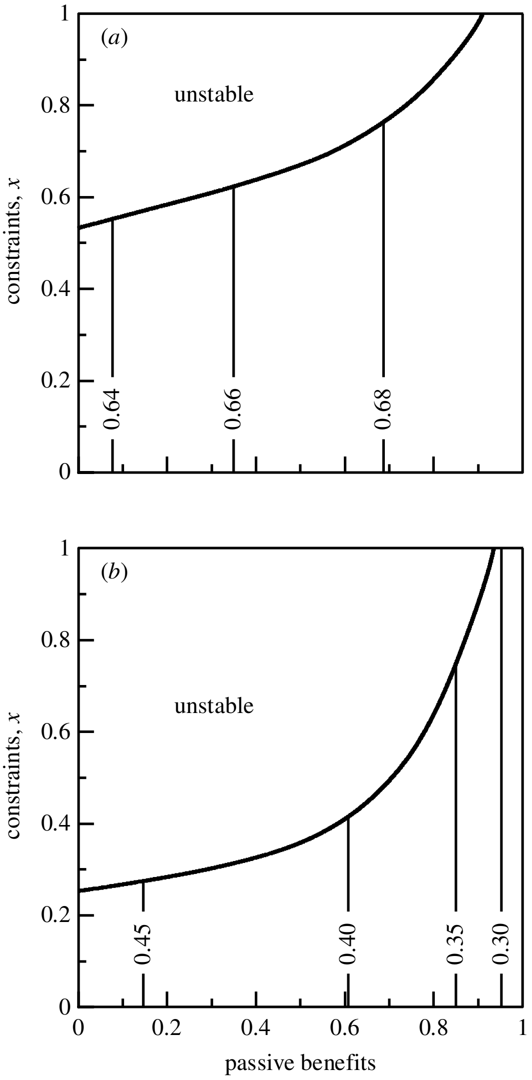

Figure 5. Ecological constraints do not affect help levels in stable groups, but they do determine the threshold at which dispersal occurs. Passive benefits are defined as in figures 2*a–d* for groups with maximum sizes is set to (*a*) two or (*b*) three (in the latter case, survival is assumed to be equal in groups of two or three). In the unstable region, the success of a disperser (x) is large enough that the lowest ranking subordinate disperses rather than stays and helps and the given group size is not attained. Contour lines give evolutionarily stable strategy help levels for the lowest ranking subordinate of stable groups; these depend on the magnitude of passive benefits, but not on constraints (x). The parameter values used are $k_1 = k_2 = k_3 = 1$, $s_{1,1} = s_{1,2} = s_{2,2}(0) = s_{2,3}(0) = s_{3,3}(0) = 0.5$, $r = 0.25$, $\Phi = 4$, and $\nu = 10$.

(c) *Result 3: group augmentation and kin-selected helping can interact to produce highly elevated levels of help compared to helping expected by kin selection alone*

As described in § 3(b) group augmentation can in principle explain helping even in completely unrelated groups, although in its most conservative form (in the absence of any passive benefits of large aggregations) it requires some initial tendency for individuals to provide small amounts of help. 'Unselected' helping (Jamieson 1989) is one possible reason for such a tendency. Kin selection obviously provides another reason. Therefore, we may suspect that kin selection and group augmentation can interact to provide particularly favourable conditions for the evolution of helping behaviour. Indeed, we find that group augmentation can push help in kin groups to much more costly levels. In the example in figure 4, related subordinates accept reductions of 20% or more in their survival prospects if their help strongly enhances group recruitment (high ν), whereas they stop at a *ca*. 10% reduction if their help only contributes to the production of related dispersing offspring, but not to recruitment ($\nu = 0$), thus disabling group augmentation.

(d) *Result 4: delayed mutualistic benefits of helping may stabilize groups even in the complete absence of ecological constraints*

Finally, the model reveals that the mutualistic benefits of being a member of a large, well-functioning group may reduce the influence of ecological constraints on breeding behaviour. Recent models of cooperative breeding with an unequal division of reproduction (reproductive skew models) typically view helping as an automatic consequence of a subordinate's decision to stay in a group because breeding opportunities elsewhere are limited (reviewed in Reeve 1998; Johnstone 2000). However, we find that, for a staying subordinate, the level of help it offers evolves according to parameters that describe the dynamics of the group, but irrespectively of the degree of ecological constraint (x) that made the subordinate stay in the first place (figure 5). In other words, once an individual has chosen to stay, the relative merits of the worse alternative (dispersal) do not affect its subsequent behaviour. This emphasizes the need for an independent treatment of the decision to help from the decision to stay (Emlen 1982; Brown 1987). This independence has not been considered in recent models of reproductive skew nor in other treatments of the evolution of helping in cooperatively breeding groups (e.g. Pen & Weissing 2000) even though reproductive skew theory itself, when extended to consider delayed benefits, predicts that dominants are often expected to accept subordinates even if they offer no help (Kokko & Johnstone 1999).

On the other hand, group augmentation by itself can increase the benefits of staying as a subordinate as compared to dispersing to breed alone. When the benefits to be gained from group augmentation are large it may become so beneficial to remain in a large group that delayed dispersal together with substantial helping may be favoured even if there are no ecological constraints on independent breeding at all (i.e. stable groups can be found in the unconstrained case $x = 1$) (figure 5). This is particularly remarkable since our model does not allow for any reproduction in subordinates and, thus, takes a very conservative view of the benefits that accrue to subordinates in groups.

4. DISCUSSION

Our model shows that group augmentation (including delayed reciprocity as its active form) can account for costly helping by non-reproductive subordinates, either alone or in concert with kin selection. This is despite the fact that our model gives each subordinate the freedom to 'cheat' and reduce its help level, with the consequence of lower survival costs and, hence, higher chances of acquiring the status of the dominant, a status which is furthermore conservatively assumed to be the only state in which reproductive benefits occur. How can such stability be explained?

In our model, we distinguished between active and passive forms of group augmentation, and found both as valid explanations for helping. Whenever increasing group size brings automatic passive benefits, the mutualistic logic of augmentation is easy to explain: it pays for everyone to keep a group large if this will offer shelter for each individual and the main point of a model is to contrast the immediate survival costs of helping with the longer term survival benefits that operate via group size (see Wiley & Rabenold 1984). The stability of active augmentation, i.e. delayed reciprocity, needs more explanation. By active augmentation we mean a situation where new recruits are of no benefit to the group (and may be even harmful) unless they provide help. Thus, individuals need to rely on the 'faith' that offspring they help to raise will in turn adopt the helping strategy, even if unrelated; automatic benefits from their presence are assumed to be absent.

Active augmentation indeed turns out to be evolutionarily stable, but stability does not follow from the 'uninterrupted chain of benefits' argument provided by Wiley & Rabenold (1984). Rather, stability requires that helping has accelerating costs combined with a sufficiently strong effect of each helper on recruitment. It is conceivable that accelerating costs are a biologically reasonable assumption: the occasional feeding of nestlings is likely to be a disproportionately cheap action compared to increasing the time spent feeding which leaves in the end leaves no time for self-maintenance. Under these circumstances a cheating mutant that reduces its level of help will not enjoy a large increase in survival (it shifts in a decelerating direction of the cost curve), but will suffer from a significant risk that it will inherit a smaller group of helpers later. Reduced performance of small groups, including an increased risk of group extinction, is commonly found in cooperatively breeding species (Courchamp *et al.* 1999), and can therefore select against cheating and stabilize help levels. Even if inherited helpers do not 'punish' a cheat by providing less help, but instead help more to compensate for a reduced group size (as is found, for example, in white-winged choughs *Corcorax melanorhamphos* (Heinsohn & Cockburn 1994) and suricates *Suricata suricatta* (Clutton-Brock *et al.* 1998)), the cost of living in a smaller group can still impose a significant penalty on cheats, because the remaining helpers are not expected to compensate fully for the loss in numbers. Moreover, even if they did, the burden of doing so would reduce their survival, thereby tending to further diminish the group size further.

A major prediction from our model is that group augmentation may be triggered by helping that is originally kin selected but, once it is established in a population, the benefits of group augmentation may in some cases be sufficiently great to render differences in relatedness practically irrelevant. Such cases are expected when recruitment to the group is strongly dependent on productivity, which in turn strongly depends on the amount of help offered. Measures of the group's success in group augmentation-based helping should thus increase with the addition of each new individual. If there are sex differences in dispersal, the predictions of the group augmentation model are that help should mainly be given by the philopatric sex, and help should also be given preferentially to offspring of that sex (for a more detailed discussion of sex differences in helping, see Cockburn (1998)). Finally, group augmentation could explain why group members may even actively attempt to attract new recruits from outside (Heinsohn 1991).

The model of group augmentation also offers some new insight into the role of ecological constraints which prevent independent breeding and, therefore, force subordinates to join groups. Such constraints are currently considered a major explanatory factor behind cooperative breeding (Koenig *et al.* 1992; Emlen 1995, 1997; Reeve 1998; Johnstone 2000; but see also Hatchwell & Komdeur 2000; Kokko & Lundberg 2001). Our model includes constraints but also shows that, given sufficiently superior performance of individuals in mutualistic groups, subordinates may gain by remaining in groups even in the complete absence of such constraints. Possible examples are provided by acorn woodpeckers *Melanerpes formicivorus* living in unsaturated habitats (Stacey & Ligon 1987) where the benefits of collective food hoarding can favour group living even if vacant breeding sites are available and by guira cuckoos *Guira guira* (Macedo & Bianchi 1997) and gray-backed fiscal shrikes *Lanius excubitorius* (Zack & Ligon 1985) which likewise remain social despite vacancies. Such situations can be generated by our model even though it takes a very conservative view of the advantages subordinates can gain: they are assumed to obtain no direct reproduction until the dominant dies and have to pay substantial costs for helping.

Mutualistic benefits of helping behaviour may thus, in some cases, prove to be an essential factor in the maintenance of group living itself. It is intriguing that taking group dynamics into account may stabilize apparently altruistic behaviour even in cases where strict rules of reciprocity do not exist and there is thus no guarantee that a single individual will ever be 'paid back' the help it has given. This highlights the need for considering the fitness of social individuals in the context of the dynamics of the groups they are living in.

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APPENDIX A

Solving the ESS requires stating the lifetime inclusive fitness of a mutant group member with helping strategy H' when the population uses a strategy H. We give a full account of the solution with maximum group size $N=2$ only and sketch the extensions needed to form the case $N=3$.

When $N=2$, individuals can occur in three different states: as lone breeders, as dominant breeders in a group of two and as subordinates in a group of two. The survivals of these individuals are $s_{1,1}$, $s_{1,2}$ and $s_{2,2}$, respectively; of these the last is dependent on the subordinate's level of help h, i.e. $s_{2,2}(h) = s_{2,2}(0)(1-h^{\Phi})$.

A strategy H needs to specify only the level of help h $(0 \leqslant h \leqslant 1)$ offered by the subordinate in a group of two. The direct lifetime fitness $W'_{2,2}$ of a mutant subordinate using a value h' in a population using a level h is solved from equations that relate each individual's fitness to its possible future states (see Kokko & Johnstone (1999) for a similar derivation with fixed helping behaviour). As an example, a lone breeder gains k_1 fitness units from its current breeding and, additionally, survives with probability $s_{1,1}$. If it survives, it remains alone with probability $1-a(k_1)$ and gains a new subordinate with probability $a(k_1)$. These transitions give

$$W_{1,1}(h) = k_1 + s_{1,1}\{[1-a(k_1)]W_{1,1}(h) + a(k_1)W_{1,2}(h,h)\}. \qquad \text{(A1)}$$

Similar expressions build the fitness for a dominant with a subordinate,

$$\begin{aligned} W_{1,2}(h',h) = k_2 + h' + s_{1,2}\{&[1-s(h')][1-a(k_2+h')]W_{1,1}(h) \\ &+ [1-s_{2,2}(h')]a(k_2+h')W_{1,2}(h,h) + s_{2,2}(h')W_{1,2}(h',h)\} \end{aligned} \qquad \text{(A2)}$$

and, for a subordinate,

$$\begin{aligned} W_{2,2}(h',h) = s_{2,2}(h')\{&(1-s_{1,2})[1-a(k_2+h')] \\ &W_{1,1}(h) + (1-s_{1,2})a(k_2+h')W_{1,2}(h,h) + s_{1,2}W_{2,2}(h',h). \end{aligned} \qquad \text{(A3)}$$

Here, it is important to distinguish between the mutant's own helping behaviour and the help that it will receive later. $W_{1,1}(h)$ is a lone dominant breeder's direct fitness in a population where the overall helping behaviour equals h. $W_{1,2}(h',h)$ is a dominant's fitness if it currently has a mutant helper that uses h', but any other future helpers will use the population-wide strategy h. $W_{2,2}(h',h)$ is a subordinate mutant's fitness if its own help equals h' but, when it accedes to any other status, it will receive a help level h. These rules ensure that a mutant is free to try 'cheating' by offering less help but still gaining the population-wide helping level once it becomes dominant.

The iterative procedure replaces the population-wide strategy h with the mutant's strategy h' which maximizes the subordinate mutant's inclusive fitness $W_{2,2}(h',h) + r\,W_{1,2}(h',h)$.

Iteration converges to the help level h^* which forms the ESS H^*. It is then checked that the subordinate does not do better by dispersing, i.e.

$$W_{2,2}(h^*,h^*) + rW_{1,2}(h^*,h^*) \geqslant (x+r)W_{1,1}(h^*). \qquad \text{(A4)}$$

The maximum group size $N=3$ follows a similar procedure, but with six individual states: a lone breeder, a dominant with one subordinate, a dominant with two subordinates, a single helper in a group of two, the first helper in a group of three and the second helper in a group of three. In addition, where group size permits, we need to distinguish between the probability of recruiting one (probability $a(k)-a(k)^2$) and two (probability $a(k)^2$) new group members. Thus, the transitions become considerably more complex. As an example of one out of 24 possible transitions, the first helper in a group of three becomes a dominant with one helper if it survives, if the dominant breeder dies and if either the second helper survives and there are no new recruits or if the second helper dies and there is one new recruit. We do not present a complete list of these transitions. The strategy H consists of help levels of the lone helper in a group of two, the first helper in a group of three and the second helper in a group of three: $H = \{h_{2,2}, h_{2,3}, h_{3,3}\}$. Each helper maximizes the inclusive fitness of its own state. The outcome of the iteration does not depend on whether one or all of the components of H are allowed to change at a time.

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