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Ecological and demographic correlates of cooperation from individual to budding dispersal

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Abstract

Identifying the ecological and demographic factors that promote the evolution of cooperation is a major challenge for evolutionary biologists. Explanations for the adaptive evolution of cooperation seek to determine which factors make reproduction in cooperative groups more favourable than independent breeding or other selfish strategies. A vast majority of the hypotheses posit that cooperative groups emerge in the context of philopatry, high costs of dispersal, high population density, and environmental stability. This route to cooperation, however, fails to explain a growing body of empirical evidence in which cooperation is not associated with one or more of these predictors. We propose an alternative evolutionary path towards the emergence of cooperation that accounts for the disparities observed in the current literature. We find that when dispersal is mediated by a group mode of dispersal, commonly termed budding dispersal, our mathematical model reveals an association between cooperation and immigration, lower costs of dispersal, low population density, and environmental variability. Furthermore, by studying the continuum from the individual to the partial and full budding mode of dispersal, we can explicitly explain why the correlates of cooperation change under budding. This enables us to outline a general model for the evolution of cooperation that accounts for a substantial amount of empirical evidence. Our results suggest that evolution may have favoured two major contrasting pathways for the evolution of cooperation depending on a set of key ecological and demographic factors.

Introduction

Understanding the origin of cooperation poses a problem for evolutionary biologists (Hamilton, 1964, 1996; Maynard Smith & Szathmáry, 1996; West *et al.*, 2007). Natural selection favours those individuals who are best adapted to their environment so that, through differential reproduction, their genetic variants become over-represented in the gene pool of future populations (Darwin, 1959; Fisher, 1930; Price, 1970). It is then puzzling why individuals are willing to suffer a reproductive cost to help with the reproduction of their social partners. Hamilton's inclusive fitness theory provides an answer: natural selection promotes the costly transfer of resources to others whenever donors and beneficiaries are closely related (Hamilton, 1964). When social interactions occur between genetically related individuals, donors still increase their own genetic representation in future generations, albeit indirectly, through copies of their genes that are present in the beneficiaries of their actions (Hamilton, 1964, 1970).

Limited dispersal, whereby individuals tend to remain near their place of birth, provides a simple and general mechanism for generating groups of close relatives. As a result, limited dispersal is often central to theories pertaining to the evolution of cooperative societies (Hamilton, 1964; West *et al.*, 2007). This idea has motivated an extensive literature on the multiple ecological and demographic factors that lead to the evolution of limited dispersal, and ultimately to the evolution of cooperative breeding (e.g. Emlen, 1982, 1991; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2004, 2016). Among these factors, environmental stability, high costs of dispersal, and high density of the population have all been identified as major factors promoting the evolution of limited dispersal and / or cooperation (Komdeur, 1992; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2016). For instance, in the social allodapine bee *Exoneura nigrescens*, the removal of nesting sites leads to higher philopatry (Langer *et al.*, 2004). In the paper wasp *Mischocyttarus mexicanus*, solitary nesting is more common when population density is low, and nest availability and quality is high (Gunnels *et al.*, 2008). In the Seychelles warblers, a sudden availability of breeding sites has been shown to disrupt both kin groups and cooperative behaviour (Komdeur, 1992). In African mole-rats, a comparative analysis has shown an association between harsh environments and low food density with the size of social groups (Faulkes *et al.*, 1997). In the Hornbills avian family, a phylogenetic analysis found a positive association between climatic stability and cooperative reproduction (Gonzalez *et al.*, 2013).

Several authors have attempted to synthesise this wealth of empirical findings to produce a general model of the ecological and demographic factors influencing the evolution of cooperation. For instance, the “habitat saturation” hypothesis, emphasises the role of population density in the evolution of limited dispersal, and how this favours the evolution of cooperation (Selander, 1964; Brown, 1974; Emlen, 1982). The “benefits of philopatry” hypothesis, emphasises the role of the benefits obtained in the natal nest, and how this facilitates cooperation (Stacey & Ligon, 1987, 1991). Notwithstanding the specific emphasis of each model, they all converge on the importance of ecological and demographic constraints for the evolution of delayed or limited dispersal as a primary factor favouring the evolution of cooperative behaviour (Emlen, 1982, 1991; Koenig *et al.*, 1992; Hatchwell & Komdeur, 2000).

In an increasing number of species, however, the ecological constraints model seems to be at odds with the empirical evidence, which has shown instances where cooperation is not associated with one or more classic predictors of sociality. In several species, cooperation has been found to be associated with immigration, such as in wild western gorillas (*Gorilla gorilla*; Bradley *et al.*, 2007), white-winged choughs (*Corcorax melanorhamphos*; Heinsohn *et al.*, 2000), long-tailed tits (*Aegithalos caudatus*; Sharp *et al.*, 2008), or in a ciliate protozoa (*Tetrahymena thermophila*; Schtickzelle *et al.*, 2009; Jacob *et al.*, 2016). Further molecular analysis, in gorillas, white-winged choughs, and long-tailed tits, has shown a high degree of kinship among immigrants (Heinsohn *et al.*, 2000; Bradley *et al.*, 2007; Sharp *et al.*, 2008). These findings are consistent with a group mode of dispersal, commonly termed 'budding' (e.g. Goodnight, 1992; Gardner & West, 2006), a behaviour also observed in other social species such as in bacteria (*Myxococcus xanthus*, Velicer & Yu, 2003), and banded mongooses (*Mungos mungo*, Cant *et al.*, 2001; Nichols *et al.*, 2012). This empirical evidence suggests an alternative evolutionary path to the emergence of cooperation, in which cooperation is mediated by the budding mode of dispersal, and yet this problem has received surprisingly little attention (for a review see Cote et al. 2017). Specifically, how different ecological and demographic factors, such as environmental stability and the cost of dispersal, influence the evolution of budding dispersal and cooperation remains unexplored.

Here we develop a theoretical model to study how multiple ecological and demographic factors influence the evolution of dispersal under budding and how this, in turn, influences the evolution of cooperation. We describe how temporal variation in resource availability mediates multiple variables such as the genetic relatedness among social partners and the intensity of kin competition. We then study how these variables mediate the evolution of dispersal and how this influences the evolution of cooperative behaviours.

The Model

Life-cycle

Here we provide a description of the life cycle of our model organism, a visual depiction of which can be found in Figure 1. We assume a population of asexually-reproducing and haploid individuals subdivided into a very large number of patches (i.e. an infinite island model; Wright, 1931; Hamilton & May, 1977; Rodrigues & Gardner, 2012). A fraction p of these patches is habitable, while a fraction 1-p is uninhabitable. Each habitable patch is occupied by n mothers. Uninhabitable patches lack resources to sustain life, and therefore they are "empty". Each of the n mothers has a very large number of offspring, $F(x_A,y_A)$, which is a function both of the focal mother's investment in cooperation, $x_{A,}$ and the focal groups', including the focal mother, average investment in cooperation, $y_{A,}$ in a population where the average investment in cooperation is z_A. We discuss the social behaviour in more detail below. After social interactions and reproduction, mothers die. Juveniles become adult females, who form buds. We assume that each bud has n adults. Each bud disperses to a random patch in the population with probability z_D and remains in its natal patch with probability 1-z_D. Migrant buds are assumed to survive dispersal with probability 1-k, where k is the cost of dispersal. After dispersal, in the previously occupied patches, there is competition between migrant and native buds for the n available breeding sites, whilst in previously empty patches, competition occurs among immigrant buds only. Only one bud wins, the remainder buds die. After group competition, there is an exchange of adult females between patches, so that adult females remain in their patch with probability 1-m, and move to another patch with probability m. The exchange of adult females between patches sustains some genetic variation within each group, which would otherwise be clonal (cf. Gardner &

West, 2006). We can also interpret migration as a mutation rate, which can be considered as interchangeable in, for example, bacterial populations (e.g. O'Brien *et al.*, 2013). As migration, mutation introduces within-group variation, and in the context of our model is conceptually equivalent. Following movement of adult females, the ecological state of patches may change. With probability α habitable patches produce a surplus of resources so that all offspring born in the patch are viable. However, with probability 1-α, disturbances (such as wildfires or floods) destroy all the available resources, which leads to the premature death of all of the resident mothers. With probability β, uninhabitable patches do not recover and remain barren, whilst with probability 1-β, uninhabitable patches recover their viability and become habitable again. After these ecological changes, the life-cycle of our model species returns to its starting point.

Methods and Analysis

We employ the neighbour-modulated approach to kin selection (Taylor & Frank, 1996; Frank, 1998; Rodrigues & Gardner, 2013b) to determine how natural selection acts on the adaptive evolution of dispersal and cooperation. We first analyse the evolution of dispersal, and we then focus on the evolution of cooperation (see Appendix for details).

Hamilton's Rule: Dispersal

We find that the condition for natural selection to favour the evolution of dispersal, a form of Hamilton's rule (Hamilton, 1964; Charnov, 1977), is given by:

$$-v_{\mathrm{O}} + (1-k)(pv_{\mathrm{O}} + (1-p)v_{\mathrm{E}}) + v_{\mathrm{O}}hR > 0, \tag{1}$$

where: $v_O = \omega_O\alpha/(\alpha+1-\beta)$ is the reproductive value of a juvenile competing for a breeding site in an occupied patch, where $\omega_O = 1/((1-z_D)+z_Dp(1-k))$ is the probability that a focal individual wins a breeding spot, and $\alpha/(\alpha+1-\beta)$ is the relative probability that the patch remains habitable; $v_E = \omega_E(1-\beta)/(\alpha+1-\beta)$ is the reproductive value of a juvenile competing for a breeding site in an empty patch, in which $\omega_E = 1/(z_Dp(1-k))$ is the probability that a focal individual wins a breeding spot, and $(1-\beta)/(\alpha+1-\beta)$ is the relative probability that an empty patch becomes habitable; $h = (1-z_D)/((1-z_D)+z_Dp(1-k))$ is the probability that a random individual, after dispersal, was born in the focal patch; and $R = 1/(n-(n-1)(1-m)^2)$ is the relatedness among group members.

The left-hand side (LHS) of inequality (1) readily yields an inclusive fitness interpretation of the behaviour. The first term represents a direct fitness cost of dispersing to a juvenile. A disperser loses a reproductive value v_O, which is the reproductive value she would have won had she decided to stay in her natal patch. The second term represents a direct fitness benefit of dispersing to the focal juvenile. She survives dispersal with probability $1-k$. With probability p, she arrives at an occupied patch, in which case she obtains a reproductive value v_O, whilst with probability $1-p$, she arrives at an empty patch, in which case she obtains a reproductive value v_E. Finally, the third term represents an indirect fitness benefit to the focal juvenile. With probability h the benefit goes to a native individual whose relatedness to the focal individual is R, and where the beneficiaries obtain a reproductive value v_O.

Hamilton's Rule: Cooperation

We focus on a social trait in which a mother pays a fecundity cost C to provide a fecundity benefit B to her social partners, including herself. The condition for natural selection to favour the evolution of cooperation is then given by

$$-Cv + BvR - (B - C)v_{\mathrm{P}}hR > 0, \qquad (2)$$

where v is the reproductive value of an offspring at birth and $v_{\mathrm{P}} = (1\text{-}z_{\mathrm{D}})v_{\mathrm{O}}$ is the philopatric component of an offspring's reproductive value. That is, an offspring remains in its natal patch with probability $1\text{-}z_{\mathrm{D}}$, in which case it obtains a reproductive value v_{O}.

The LHS of inequality (2) readily yields an inclusive fitness interpretation of the behaviour. The first term represents a direct fitness cost to the focal mother. She has C fewer offspring, whose reproductive value would have been v. The second term represents an indirect fitness benefit to the focal mother. Her behaviour improves the fecundity of all group members by a total of B offspring, whose reproductive value is v, a benefit that must be discounted by the relatedness R. Finally, the third term represents an inclusive fitness cost to the focal mother. Her behaviour displaces B-C offspring, who were born in the local patch with probability h. Each displaced offspring represents a cost v_{P} to the actor, a cost that must be discounted by the relatedness R.

The cost and benefit of cooperation are given by the slopes of fecundity on the phenotype of individuals (i.e. $-C = \partial F(x_{\mathrm{A}},y_{\mathrm{A}})/\partial x_{\mathrm{A}}$, and $B = \partial F(x_{\mathrm{A}},y_{\mathrm{A}})/\partial y_{\mathrm{A}}$); see Appendix D for details). We assume that fecundity depends on the relative competitiveness of each mother within each group, and on the public good available to each group member. Investment in cooperation (x_A) decreases an individual's relative competitiveness within each group but increases the amount of the public good available. In order to plot ES cooperation strategies, we assume that the fecundity of a focal individual is given by $F(x_A,y_A) = ((1-x_A)/(1-y_A))y_A$ (cf. Frank, 1994). Thus, $C(z_A) = z_A/(1- z_A)$, and $B(z_A) = 1/(1- z_A)$. In the appendix, we show that the specific functional form does not have a qualitative impact on our results.

Hamilton's rule and inclusive fitness

Above we have considered a particular partition of Hamilton's rule, in which each additive term represents a selective pressure and where the costs (C's) and benefits (B's) are given in number of offspring. In the original formulation of Hamilton's rule, however, selection is partitioned into additive direct and indirect fitness components, and costs and benefits are given in terms of fitness (Hamilton 1964). This original formulation of Hamilton's rule can be recovered by re-arranging the LHS's of inequalities (1) and (2) and by considering the 'others-only' coefficient of relatedness, rather than the 'whole-group' coefficient of relatedness (Pepper 2000). Hamilton's rule for the evolution of dispersal becomes

$$-\underbrace{\left(v_O - (1-k)(pv_O + (1-p)v_E) - v_O h\frac{1}{n}\right)}_{c} + \underbrace{v_O h\frac{n-1}{n}}_{b} r > 0, \qquad (3)$$

where: c is the fitness cost of the behaviour; b is the fitness benefit of the behaviour; and r is the 'others-only' relatedness between actor and recipients. The direct fitness effect is then given by $–c$ whereas the indirect fitness effect is given by br. Likewise, Hamilton's rule for the evolution of cooperation becomes

$$-\underbrace{\left(Cv - Bv\frac{1}{n} + (B-C)v_{\mathrm{P}}h\frac{1}{n}\right)}_{c'} + \underbrace{\left(Bv\frac{n-1}{n} - (B-C)v_{\mathrm{P}}h\frac{n-1}{n}\right)}_{b'} r > 0. \qquad (4)$$

Evolutionarily Stables Strategies

Our aim is to find the Evolutionarily Stable (ES) dispersal, denoted by z_{D}^*, and the ES investment in cooperation, denoted by z_{A}^*. An evolutionary singular dispersal (or cooperative) strategy occurs when natural selection favours neither a slight increase nor a slight decrease in the probability of dispersal (or in cooperation). This evolutionary equilibrium occurs when the corresponding LHS of Hamilton's rule is null. A joint evolutionary singularity strategy (z_{D}^*,z_{A}^*) occurs when the LHS of both Hamilton's rules, as given by inequalities 1 and 2, are simultaneously null. We investigate both the convergence and evolutionary stability of these joint optimal strategies. To determine the evolutionary stability of the evolutionary singularities, we construct a genetic model that is equivalent to our kin selection model (Ajar, 2003; Wild, 2011; Rodrigues & Johnstone, 2014; Appendix E). We use this genetic model to check the validity of the analytical results derived from our kin selection model, and to check the convergence stability (Christiansen, 1991; Eshel, 1996), and the evolutionary stability (Maynard Smith & Price, 1973; Metz & Gyllenberg, 2001; Ajar, 2003; Rodrigues & Johnstone 2014) of the joint optimal strategies (Appendix E). Our analysis suggests that all evolutionary singular strategies are both convergence and evolutionarily stable (Appendix F).

Results

Here we describe the evolution of cooperation and dispersal with respect to the cost of dispersal (k), proportion of habitable patches (p), and the temporal stability of the local environment (τ), where $\tau = \alpha - (1 - \beta)$. We explore how the different model parameters influence the ES dispersal rate (z_D^*) and the ES investment in cooperation (z_A^*). We analyse our results in terms of the relative direct ($\upsilon_D = (1-k)(pv_O+(1-p)v_E)/v_O$) and relative indirect ($\rho_D = v_O hR/v_O$) benefits of dispersal, and in terms of the relative kin-selected benefits ($\upsilon_A = vR/v$), and the relative kin competition costs ($\rho_A = v_P hR/v$) of cooperation (Figures 2 - 4).

How does the cost of dispersal influence cooperation (Figure 2)? We find that, in general, higher costs of dispersal have a negative impact on the evolution of cooperation (Figure 2 (*d*)). When many dispersers die in transit between patches, fewer immigrants arrive at each patch. This increases kin competition, which disfavours the evolution of cooperation (Figure 2 (*c*)). In addition, higher dispersal costs reduce the benefits of dispersal (Figure 2 (*a*)), which leads to lower ES dispersal rates. This, in turn, further increases the intensity of kin competition, and the corresponding costs associated with cooperation. Counter to intuition, when the environment is unstable and the cost of dispersal is already high, dispersal tends to rise with increasing cost of dispersal (Figure 2 (*b*)). This is because higher costs of dispersal increase the competition among close relatives, and therefore it also increases the indirect fitness benefits to dispersers. In other words, even if a disperser is likely to perish in a dispersal event, they will indirectly benefit as their kin left behind will benefit from reduced competition within the patch. How does the cost of dispersal in unstable environments influence the evolution of cooperation? Two opposing factors drive the evolution of cooperation. First, the cost of dispersal leads to less immigration and therefore to higher kin competition for local resources. Second, higher kin competition leads to higher dispersal rates, which in turn erodes kin competition. Overall, the cost of dispersal increases the intensity of kin competition, which disfavours the evolution of cooperation (Figure 2).

How does habitat occupancy (p) mediate investment in cooperation (Figure 3)? We find that when the local environment is stable (temporal correlation, $\tau \approx 1$), cooperation increases with habitat occupancy. By contrast, when the local environment is unstable ($\tau << 1$), cooperation decreases with habitat occupancy (Figure 3 (*c* & *d*)). In stable environments, barren patches rarely become fertile again, and therefore any immigrant that lands in one of these patches is unlikely to reproduce. As a result, higher habitat occupancy decreases the chances that dispersers migrate to a barren patch, which increases the expected direct benefits of dispersal, which leads to higher ES dispersal rates (Figure 3 (*a* & *b*)). Higher dispersal rates from occupied patches reduce the intensity of local kin competition, and therefore cooperation becomes more beneficial (Figure 3 (*d*)).

When the local environment is unstable ($\tau < 1$), higher habitat occupancy leads to lower direct benefits of dispersal (Figure 3 (*a*)). The value of occupied patches is now greatly reduced because: (i) they have higher competition (as they have philopatric individuals and not only immigrants), and (ii) they may be more likely to become extinct (if $\tau < 0$). When the fraction of poor quality occupied patches increases in the population, dispersal is disfavoured (Figure 3 (*b*)). This is because dispersers are more likely to find themselves in a poorer patch after dispersal. Low dispersal rates increase the intensity of local kin competition, and this disfavours the evolution of cooperation (Figure 3 (*c*)).

How does temporal correlation (τ) influence the potential for cooperation (Figure 4)? We find that the potential for cooperation decreases as the environment becomes more stable

(Figure 4 (*c* & *d*)). Stable environments reduce the direct fitness benefit of dispersal (Figure 4 (*a*)), which disfavours the evolution of dispersal (Figure 4 (*b*)). This leads to an increase in the intensity of kin competition, which disfavours costly investments into cooperative behaviours (Figure 4 (*c* & *d*)). In addition, temporal stability increases the value of occupied patches, which also increases the costs associated with kin competition (Figure 4 (*c*)). This additional factor further disfavours investment into cooperation (Figure 4 (*d*)).

Finally, what is the relationship between dispersal and cooperation? For a large range of parameter values, we find a positive correlation between dispersal and cooperation when we vary a model parameter (Figure 5). Exceptions occur when the cost of dispersal is high and the environment is unstable (Figure 5 (*a*, *b* & *d*)). In this case, the ES dispersal rate of juveniles increases with the cost of dispersal. Higher dispersal rates directly oppose higher costs of dispersal, with the former acting to alleviate kin competition and the latter increasing kin competition. This latter effect is stronger than the former and, as a result of higher net kin competition, investment into cooperation decreases with increasing dispersal rates. At intermediate levels of environmental stability, we also find a negative correlation between the dispersal rate of juveniles and investment in cooperation as patch occupancy increases (Figure 5 (*f*)). In some areas of parameter space the model is biologically unrealistic (represented by grey shaded areas on Figure 5). Here, there isn't a realistic combination of parameter values (α and β) that gives values of τ and p that could occur in nature (e.g. if $\tau = -1$, and $p = ¼$, then α is negative ($-\,^{1}/_{2}$)).

Individual, partial and complete budding dispersal

Above, we have explored how budding dispersal influences general patterns of cooperation as a function of the different model parameters. Here, we explore these results in three main directions. First, we investigate cases where the migration rate is set to zero. Next, we explore cases where the size of each bud is allowed to vary in relation to patch size. Finally, we explore a clonal expansion scenario, whereby each patch is colonised by a single individual who then produces offspring that fill up all of the available breeding sites.

Migration rate -- In the previous sections, we have assumed that there is an exchange of individuals between groups after the dispersal stage, which sustains some within-group genetic variation. Here we explore some of the consequences of having no exchange of individuals between groups ($m \rightarrow 0$). Under this scenario, if we assume a saturated population (i.e. $p = 1$), we recover Taylor's (1992) result for the evolution of cooperation when there is a single breeder per patch, in which case Taylor's condition for the evolution of cooperation becomes $B > C$. In this case, individuals invest all of their resources into cooperation (i.e. $z_A^* = 1$), irrespective of the dispersal rate. Similarly, we also recover Hamilton & May's (1977) result for the evolution of dispersal, where the ES dispersal rate is $z_D^* = 1/(1+k)$. In other words, we find that clonal groups behave as if they were individuals, and we recover the classic results of Taylor (1992) and Hamilton & May (1977).

Bud size -- Above, we showed that for a wide range of the parameter space we discover an unexpected positive correlation between dispersal and cooperation when individuals disperse in groups, where the size of each dispersing group, denoted by n_B, was assumed to exactly match patch size (i.e. $n_B = n$; Figure 5). Here, we relax this assumption and explore this result further by taking into account the size of the bud (n_B) relative to the number of available breeding sites (n). In particular, we assume that the size of each bud (n_B) can be less than, or greater than, the number of available breeding sites, with $n_B \in \{1, 2, \ldots, n, n+1, \ldots\}$. Thus, when $n_B = 1$, we have a pure individual mode of dispersal; when $1 < n_B < n$, we have a partial budding dispersal mode; and when $n_B \geq n$, we have a complete budding mode of dispersal. In the main model, we also assumed that all individuals had exactly the same fecundity. Here, we relax this assumption and we consider that a single dominant individual has higher fecundity the $n - 1$ subordinate individuals. Thus, $F_H \geq F_L$, where F_H is the fecundity of the dominant individual and F_L is the fecundity of a subordinate individual (see Appendix G for details).

As shown in Figure 6, we find that both dispersal and cooperation increase with bud size, irrespective of patch size. In particular, we find that in the limit case, under the individual mode of dispersal (i.e. $n_B = 1$), the optimal levels of dispersal and cooperation are relatively low. As bud size increases, both dispersal and cooperation gradually rise until bud size becomes equal to, or greater than, the number of breeding spots (i.e. $n_B \geq n$ and all breeding spots are filled by individuals from the same bud), at which point both dispersal and cooperation stabilise at their highest values.

The effect of temporal stability, i.e. τ, on the optimal level of cooperation strongly depends on the mode of dispersal. Under the individual mode of dispersal (i.e. $n_B = 1$), temporal stability and cooperation are positively correlated. Stable environments select against dispersal, which increases relatedness, and higher relatedness, in turn, favours cooperation. Unstable environments select for dispersal, which decreases relatedness. Lower relatedness, in turn, selects against cooperation. This pattern gradually changes as bud size increases and beyond a threshold bud size the coefficient of temporal stability and cooperation become negatively correlated. As under the individual mode of dispersal, stable environments are associated with philopatry and unstable environments with dispersal when bud size increases. However, the effects of philopatry and dispersal on cooperation differ when bud size increases beyond the set threshold. Under such scenario, philopatry becomes associated with strong kin competition, which leads to the evolution of lower levels of cooperation. Dispersal becomes associated with weak kin competition, which leads to the evolution of higher levels of cooperation.

Clonal expansion -- Akin to full budding dispersal is clonal colonisation. To consider this scenario, we modify the model of the previous section. In particular, we consider that a single individual colonises a patch with multiple available breeding spots that remain open. The coloniser takes up the dominant position, and then reproduces clonally, with the offspring taking up all other available breeding spots and adopting the role of subordinates (see Appendix I for details). Under these conditions, we find that the dynamics of dispersal and cooperation are similar to those observed under full budding dispersal. In particular, we find that high levels of cooperation evolve irrespective of temporal stability and of patch size (see Figure I in Appendix I).

Discussion

Identifying the ecological and demographic factors that shape the evolution of cooperation has been a long-standing problem for evolutionary ecologists (Koenig & Dickinson, 2004, 2016; West *et al.*, 2007). The “habitat saturation” hypothesis, for instance, suggests that high population density tends to disfavour immigration, and as a result favours the evolution of cooperation (Salender, 1964; Brown, 1974; Emlen, 1982). The “benefits of philopatry” hypothesis emphasises the benefits obtained in the natal patch as a force driving philopatry, which in turn promotes cooperative behaviour (Stacey & Ligon, 1987, 1991). Independently of the specific viewpoint of each different hypothesis, the common idea is that cooperation evolves in the context of environments with strong ecological and demographic constraints on dispersal and independent breeding, of which environmental stability, high costs of dispersal, and high population density are usually regarded as the primary constraining factors (Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2016).

Recent observational and experimental studies, however, have uncovered variation in cooperation that is not explained by these models. A common thread across these studies is the existence of budding or some form of group dispersal (e.g. Heinsohn *et al.*, 2000; Williams & Rabenold, 2005; Bradley *et al.*, 2007; Sharp *et al.*, 2008; Jacob *et al.*, 2016). This observation has led us to advance the central hypothesis of our study where we propose that budding may mediate a shift in the ecological and demographic variables shaping the evolution of cooperation. To test this hypothesis, we developed a kin-selection theoretical model in which we varied key factors to study their effect on the evolution of dispersal and ultimately on the evolution of cooperation. Our model supports our initial hypothesis, as we found that under budding dispersal, cooperation becomes associated with environmental instability, immigration, low costs of dispersal, and low population density. These results provide a foundation for a general model for the evolution of cooperation in which its correlates are in contrast with the ecological and demographic correlates proposed by the hypotheses based on ecological constraints.

Support for our findings comes from different lines of research. For instance, white-winged choughs are cooperative breeders who live in groups of relatives that show some degree of reproductive skew. Social groups can last for several generations, but ecological perturbations can lead to their demise. In one of such instances, severe droughts resulted in high mortality and group fragmentation (Heinsohn *et al.*, 2000). New groups were readily established, each comprised of sub-groups of close kin and individuals of different origins. After the establishment of new groups, reproductive skew was immediately developed, and researchers found a positive correlation between reproductive success and the number of relatives present in the new groups (Heinsohn *et al.*, 2000). Long-tailed tits are also cooperative breeders that show relatively high levels of dispersal, in which dispersers often fail to establish independent breeding. Sharp *et al.* (2008) has shown that around 40% of the failed breeders become helpers at an established nest, with over 30% joining the nest of a close relative. These cases illustrate situations where there is an association between relatively high immigration, high relatedness and cooperation, and in the case of white-winged choughs high environmental instability, as outlined in our model.

In our model, and in white-winged choughs, dispersal is partially driven by ecological disturbances. We can expect, however, that in some cases, dispersal may be caused by other factors that vary over time. For instance, sex-biased dispersal is common in sexually reproducing species, a behaviour that is often driven by the costs of inbreeding. In lions, males are the dispersing sex, while females are philopatric. Dispersal by males is particularly important when their own daughters become adult group members, in which case the costs of inbreeding rapidly escalate. Males may disperse solitarily but also in groups of different sizes, and they are more likely to associate in groups when close kin are available. Groups of males are more likely to take over a pride, and therefore improve their reproductive success (Packer *et al.*, 1991). In brown jays, males are also the dispersing sex. Immigration is often made in groups, and not random, as males are more likely to disperse to a group where other close relatives are already present (Williams & Rabenold, 2005). This suggests that kin selection and cooperation is associated with both budding and dispersal.

We also uncover the result that bud size relative to number of available breeding spots drives both the potential for cooperation and dispersal, especially under more unstable environments. This analysis provides a continuum between the individual mode of dispersal to complete budding dispersal. Cooperative breeders such as the western bluebird (*Sialia* Mexicana) and the superb fairy-wren (*Malurus cyaneus*), will often delay dispersal when food is scarce and competition for quality patches is high. Here, quality patches do not often become available, so a kin group is established and cooperative behaviours persist. However, when quality patches become available helpers will prefer to disperse individually and breed (Dickinson *et al.*, 2014; Pruett-Jones & Lewis, 1990). As such, cooperation is established when patches are stable even under individual dispersal, however, when new patches become available relatedness will decline as groups disperse and cooperation is unlikely to be maintained.

At the other end of the spectrum are eusocial insects who need a cooperative group to establish a new nest site. When a colony of honey bees (*Apis mellifera*) divide, the old queen will swarm with several thousand workers to find a new patch, leaving remaining resources to colony members and a new queen (Camazine *et al.*, 1999). Here, the quality and quantity of resources in a patch will determine dispersal rate, and cooperation will remain high during dispersal through budding.

Dispersal in other eusocial insects, such as the drywood termite (*Cryptotermes secundus*) where patch resources are limited, is dependent on ecological factors such as food availability. When food becomes scare in the nest, there is an increase in maturation of individuals into dispersing sexuals that go on to colonise new nests as a single monogamous queen (clonal colonisation in our model) (Korb and Schmidinger, 2004). Here, patch quality determines dispersal rate, and although individual dispersal is established, clonal colonisation of empty patches ensures high relatedness and maintains selection for dispersal. These examples demonstrate the vital role ecological determinants play in the evolution of dispersal and how the dispersal strategy can act to disrupt or maintain cooperative behaviours during dispersal events, depending on whether dispersal is budding or individual.

In many cases, testing theoretical predictions linked to dispersal and cooperation is not experimentally tractable in vertebrates and higher organisms. However, experimental approaches using single cellular organisms highlights the critical role of dispersal strategy in maintaining cooperative groups during dispersal events. These studies reveal budding as a key factor for resolving conflicting selective pressures between cooperation and kin competition (Kümmerli *et al.*, 2009; Taylor *et al.*, 2013; Jacob *et al.*, 2016). For example, using a ciliated protozoan model system (*Tetrahymena thermophile*) Jacob *et al.* (2016) found that the aggregative behaviour of the strain (determined by their genotype) altered the plastic reaction norms of dispersal behaviour. Specifically, cooperation and dispersal are maintained via the avoidance of kin-competition through long distance dispersal, and the maintenance of kin structure thorough group dispersal.

Reflecting on the results gained in this study, it is interesting to consider the parallels that may be important for vector-borne diseases, such as malaria. Malaria often exists within a host as a mixed-genotype infection, i.e. they are frequently dispersing to occupied patches (Read *et al.*, 2002). But kinship patterns observed within an infected host suggest that relatedness within the mosquito vector (i.e. during dispersal) is high (Nkhoma *et al.*, 2012). Moreover, it seems that parasites can discriminate between related and non-related malaria parasites (Reece *et al.*, 2008), suggesting kin structure to be important to the success of the parasitic lifecycle. If relatedness within the vector is high, then relatedness is not destroyed by dispersal, and a type of budding dispersal is established. Besides, theoretical work has shown that both high competition within a mixed-genotype infection (Read *et al.*, 2002) and long distance transmission mechanisms (such as those that are vector-borne; Boots & Sasaki, 1999) will select for more virulent pathogens. The consequence of this higher virulence are more unstable patch dynamics (because the host dies more quickly), and our work predicts this will also select for a higher dispersal rate. In support of this theory, a recent study found that passaging the parasitic nematode, *Heterorhabditis floridensis*, under conditions that resulted in low relatedness within new hosts led to reduced growth and lower virulence. In contrast, passaging under conditions that led to high relatedness within the new host led to higher growth and more virulent strains (Shapiro-Ilan & Raymond, 2016). This empirical result matches the predictions made above; nematodes that disperse to a new host while maintaining kin structure will have increased growth, resulting in decreased patch stability (as host mortality increases). These specific examples illustrate how a budding group remains competitive when entering a colonised patch, however, what remains to be experimentally tested is the longer term evolutionary consequences. Does intense within patch competition reduce patch stability and subsequently select for higher dispersal?

Our results suggest that the role of the demographic and ecological correlates of cooperation strongly depend on group size. Despite this, group size has been relatively neglected in the classic hypotheses for the evolution of cooperation (Selander, 1964; Brown, 1974; Emlen, 1982; Stacey & Ligon, 1987, 1991), which have largely focused on identifying the ecological and environmental factors that lead to group formation and sociality. Our results suggest a more complex picture for the evolution of cooperation, where group size plays a pivotal role. For instance, when group size is small, the effect of environmental stability of cooperation significantly depends on the mode of dispersal. When individuals disperse independently, the degree of environmental stability has a large impact on cooperation. By contrast, when individuals disperse in a group, the degree of environmental stability has little impact on cooperation. This pattern, however, is reversed when individuals live in large social groups.

Our results contrast with the idea that dispersal and cooperation should in general be negatively correlated, as proposed by classic hypotheses, such as the "habitat saturation" (Selander, 1964; Brown, 1974; Emlen, 1982) or the "benefits of philopatry" hypothesis (Stacey & Ligon, 1987, 1991). Another exception to the classic literature is the study of Le Galliard et al. (2005) that also found a positive correlation between dispersal and cooperation. However, the reasons underlying the positive correlation are diverse. In Le Galliard et al., an elevated cost of mobility leads to an increase in both dispersal and cooperation. In our study, by contrast, increased cost of dispersal leads to a decrease in both dispersal and cooperation. In Le Galliard et al., increased dispersal and cooperation occurs because the cost of mobility raises the levels of local aggregation. In our study, decreased dispersal occurs because of the direct effect of the cost of dispersal. As such, decreased cooperation occurs because costly dispersal decreases dispersal rates, and lower dispersal rates raises kin competition, which ultimately leads to decreased cooperation.

Understanding the evolutionary consequences of the complex interactions between dispersal and cooperation is a non-trivial task. Species will differ in many respects regarding their life-cycle, breeding system, and genetics. Extending our model to take into account species-specific biological factors presents an exciting and promising line of future research. For example, we might consider populations in which group size varies (e.g. Rodrigues & Gardner, 2013a) or cases in which group members differ in their quality (e.g. Rodrigues & Gardner, 2013b). Furthermore, one may also consider situations in which, alongside the evolution of dispersal, budding itself is also an evolving trait rather than a fixed parameter. Our analysis here provides a general framework to build and extend upon, so we might understand how budding influences the joint evolution of dispersal and cooperation within the context of a complex biological system.

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Tables

Table 1 | Defined list of parameters used in model

Parameter	Definition
α	Probability that a patch will remain habitable
β	Probability that a patch will remain inhabitable
k	Cost of dispersal
m	Probability that an adult female moves to a new patch (facilitating genetic exchange)
n	Number of mothers within a patch
p	Proportion of habitable patches
τ	Temporal patch stability
x_A	Focal mother's investment in cooperation
y_A	Focal group's average investment in cooperation
z_A	Population's average investment in cooperation

z_D	Probability of dispersing

Figures Legends

Figure 1 | Lifecycle described by the model. Groups of mothers (*n*) exist within habitable patches (white), also present are non-habitable patches (grey). Individuals within the focal patch will produce $F(x_A, y_A)$ offspring, yield is determined as a function of the focal mother's investment in cooperation, x_A, and the focal group's average investment in cooperation, y_A . Mature adult buds will disperse to all patches (z_D) or remain in their natal patch ($1 - z_D$) and compete for patch occupancy; migration between patches facilitates genetic exchange between buds (*m*). Patch quality has the potential to change after bud dispersal and competition, a patch may remain habitable (α), become inhabitable ($1 - \alpha$), remain inhabitable (β), or become habitable ($1 - \beta$). Buds within inhabitable patches will perish; the cycle begins again.

Figure 2 | [*a*] The direct (υ_D; solid lines) and indirect (ρ_D; dashed lines) benefit of dispersal as a function of the cost of dispersal (*k*). [*c*] The kin selected benefit (υ_A; solid lines) and the kin competition cost (ρ_A; dashed lines) as a function of the cost of dispersal (*k*). [*b*,*d*] The ES dispersal rates (z_D^*) and the ES investment in cooperation (z_A^*) as a function of the cost of dispersal (k). Parameter values: [*a*-*d*] $m = 0.01$, $n = 5$, $p = 0.5$, [*a*,*c*] $z_D = 0.5$.

Figure 3 | [*a*] The direct (υ_{D}; solid lines) and indirect (ρ_{D}; dashed lines) benefit of dispersal as a function of patch occupancy (p). [*c*] The kin selected benefit (υ_{A}; solid lines) and the kin competition cost (ρ_{A}; dashed lines) as a function of patch occupancy (p). [*b*,*d*] The ES dispersal rates (z_{D}^*) and the ES investment in cooperation (z_{A}^*) as a function of patch occupancy (p). Parameter values: [*a-d*] $m = 0.01$, $n = 5$, $k = 0.5$, [*a*,*c*] $z_{\mathrm{D}} = 0.5$.

Figure 4 | [*a*] The direct (υ_{D}; solid lines) and indirect (ρ_{D}; dashed lines) benefit of dispersal as a function of the temporal correlation (τ). [*c*] The kin selected benefit (υ_{A}; solid lines) and the kin competition cost (ρ_{A}; dashed lines) as a function of the temporal correlation (τ). [*b*,*d*] The ES dispersal rates (z_{D}^*) and the ES investment in cooperation (z_{A}^*) as a function of the temporal correlation (τ). Parameter values: [*a-d*] $m = 0.01$, $n = 5$, $p = 0.5$, [*a*,*c*] $z_{\mathrm{D}} = 0.5$.

Figure 5 | Sign of the correlation between dispersal and cooperation; as the cost of dispersal changes [panels *a-d*], as the patch occupancy changes [panels *e-g*], and as the temporal correlation changes [panel *h*], as a function of model parameters. The grey regions are not mathematically tractable. The sign is given by the partial derivatives of the ES strategies with respect to ∂ variable (either k, p, or τ) for each combination of parameter values. Parameter values: [*a-h*] $m = 0.01$, $n = 5$. [*a*,*e*] $\tau = 0.0$ [*b*,*f*] $\tau = 0.5$. [*c*,*g*] $\tau = 1.0$. [*d*,*h*] $p = 0.5$.

Figure 6 | ES dispersal and cooperation strategies under individual dispersal, and partial and complete budding dispersal. Bud size (n_B) changes relative to patch size (n) under variable temporal instability (τ) ranging from – 1.0 to 1.0 (see legend). Parameter values: $k = 0.5$, $p = 0.5$, $F_{\mathrm{L}} = F_{\mathrm{H}}/10$, $m = 0.01$.