

Promiscuity and the evolution of cooperative breeding

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Empirical data suggest that low levels of promiscuity have played a key role in the evolution of cooperative breeding and eusociality. However, from a theoretical perspective, low levels of promiscuity can favour dispersal away from the natal patch, and have been argued to select against cooperation in a way that cannot be explained by inclusive fitness theory. Here, we use an inclusive fitness approach to model selection to stay and help in a simple patch-structured population, with strict density dependence, where helping increases the survival of the breeder on the patch. Our model predicts that the level of promiscuity has either no influence or a slightly positive influence on selection for helping. This prediction is driven by the fact that, in our model, staying to help leads to increased competition between relatives for the breeding position—when promiscuity is low (and relatedness is high), the best way to aid relatives is by dispersing to avoid competing with them. Furthermore, we found the same results with an individual-based simulation, showing that this is not an area where inclusive fitness theory ‘gets it wrong’. We suggest that our predicted influence of promiscuity is sensitive to biological assumptions, and that if a possibly more biologically relevant scenario were examined, where helping provided fecundity benefits and there was not strict density dependence, then low levels of promiscuity would favour helping, as has been observed empirically.

Keywords: promiscuity; cooperative breeding; relatedness; dispersal; inclusive fitness

1. INTRODUCTION

It has been argued that monogamy or low levels of promiscuity have played a key role in favouring the evolution of cooperative breeding and eusociality. Hamilton’s inclusive fitness theory [1–3] explains how cooperation can be favoured when it is directed towards relatives who also carry the gene for cooperation. Higher levels of promiscuity would decrease relatedness within family groups (figure 1*a*), which could therefore reduce selection for staying and helping in the natal family group [4]. Empirical support for this idea has come from the observations that (i) eusociality has only evolved in species with strict lifetime monogamy, and (ii) both the occurrence and amount of cooperative breeding in birds are negatively correlated with the level of promiscuity [5,7–9].

However, it is unclear whether greater promiscuity should always select against staying to help in natal groups. From an empirical perspective, some of the highest promiscuity rates ever recorded are cooperative breeders, such as the superb fairy wren and the Australian magpie [5]. From a theoretical perspective, previous predictions have been based on either verbal or heuristic models. More explicit models, which allow the action of selection to emerge as a consequence of demographic assumptions, have shown that an increased relatedness will not always favour cooperation because it can be negated by increased local competition between relatives (reviewed by West *et al.*

[10] and Lehmann & Rousset [11]). Furthermore, some theoretical models make the opposite prediction, showing that because higher relatedness within groups leads to increased competition between relatives, selection can favour dispersal away from the natal group to reduce competition between relatives (figure 1*b*; e.g. [6,12–16]). Finally, a recent attempt by Nonacs [17] to explicitly model the effect of promiscuity on cooperation with population genetic simulations found that the level of promiscuity had little effect, or even a positive effect, on selection for cooperation, possibly suggesting that this is an area where inclusive fitness theory ‘gets it wrong’.

Here, we use an inclusive fitness approach to model how promiscuity influences selection to stay and help in natal groups. Our aim is to consider the simplest possible scenario to explicitly examine how the level of promiscuity, through its effect on within-group relatedness, has multiple consequences. Our approach is therefore analogous to that taken by Taylor [18], when considering how limited dispersal influences cooperation. In particular, we examine how lower levels of promiscuity lead to higher within-group relatedness, which can, in turn, increase the indirect benefits of both staying to help relatives and dispersing to reduce competition among relatives [19]. In addition, we check the validity of our inclusive fitness model by comparing its predictions with that made by an individual-based model.

2. THE MODEL

We consider a population of cooperatively breeding, diploid individuals. To address the effect of promiscuity on cooperative breeding behaviour, we must assume

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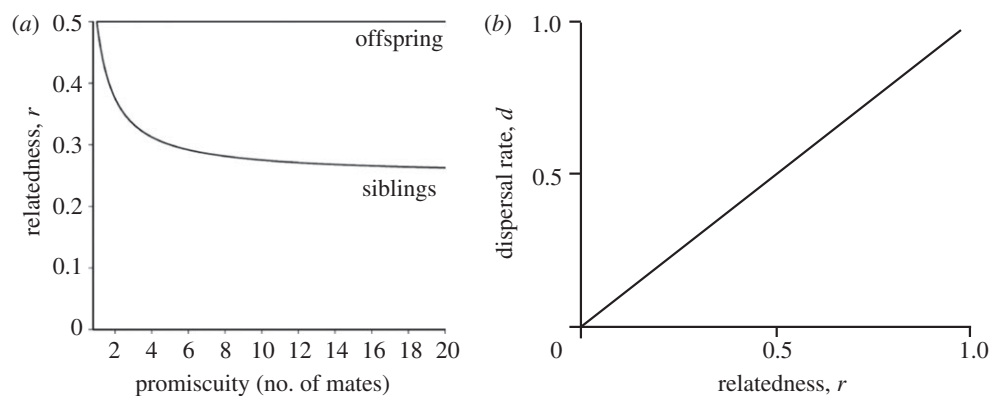


Figure 1. Promiscuity, relatedness and dispersal rate within family groups. (a) Promiscuity and relatedness. Promiscuity (number of mates) plotted against the mean genetic relatedness between potential helpers and both their siblings and offspring. An individual is always related to its offspring with $r = 0.5$. However, as promiscuity increases, the relatedness to siblings decreases from $r = 0.5$ to 0.25 (full-siblings to half-siblings) [4]; redrawn from [5]. (b) Higher relatedness within groups can lead to increased competition between relatives, which selects for dispersal away from natal groups to reduce competition between relatives [6].

that the individuals are sexual. In order to avoid complications of modelling different sexes, we assume that individuals are sexual hermaphrodites.

We assume that the population is subdivided into a very large, but fixed, number of breeding patches (say, p patches). Each patch is of equal quality and supports one adult breeder at a time, plus a large number of juvenile offspring. In nature, the cooperative behaviour of juvenile helpers can increase the breeder's survival and/or fecundity [20–22]. We focus on the former case, where the survival of the breeder is boosted by the presence of helpers. We avoid the latter case in order to avoid complications associated with the cascading effects that fecundity benefits exert on breeder fitness (more helpers result in more offspring, producing greater numbers of helpers, which in turn increases fecundity further, etc.) [23,24].

Since juvenile helpers often direct their help towards the individual(s) occupying the same patch on which helpers themselves were born (e.g. helpers help their own parents [25,26]), we assume that an offspring's tendency to help is linked to its decision to disperse. In other words, an offspring that remains on its natal patch does so in order to help the incumbent breeder, while an offspring that disperses from its natal patch will compete (without helping) on a new patch for the opportunity to breed, which occurs upon the (possible) death of a breeder. We explain our assumptions about the basis for an individual's 'tendency' to help (or 'decision' to not disperse) in greater detail below. For now, simply note that all helpers exert the same level of effort, and it is just this 'tendency' to help that varies among individuals in our model population.

Now suppose we observe the population described above at discrete, evenly spaced points in time. We assume that, between successive observations, the following series of five events occurs:

- *Mating*. Each breeder chooses exactly M mates from the global population of breeders. Mate choice occurs uniformly at random, and with replacement. Note that larger M indicates that breeders are more promiscuous.
- *Birth*. Each breeder produces a very large number (K) of offspring, and each offspring carries one chromosome pair. An offspring's 'maternally' inherited chromosome is one of the two chromosomes (chosen uniformly, at

random) belonging to the local breeder, while the offspring's 'paternally' inherited chromosome is one of two chromosomes (chosen uniformly, at random) belonging to one of the breeder's M mates (chosen uniformly, at random with replacement). The local breeder, then, will be considered 'mother' to offspring produced on her patch, while the local breeder's mates will be considered potential 'fathers'. Of course, the local breeder will also be potential 'father' to offspring produced off-site, while the local breeder's mates will also be 'mother' to offspring produced on the patches they themselves occupy.

- *Dispersal*. Genes found on the chromosomes carried by an individual offspring determine d , the probability with which that individual disperses from its natal patch. We assume that maternally inherited and paternally inherited genetic information contribute equally and additively to the offspring's dispersal phenotype. Thus, we treat d as the mean of two phenotypes: one that would be produced by two identical copies of the maternally inherited gene, and a second that would be produced by two identical copies of the paternally inherited gene. We assume that offspring that disperse successfully find their new patch by choosing from among the p patches in the population uniformly at random. Note that there is a possibility that an offspring actually disperses to its natal patch, and in this case becomes a non-helping, individual-in-wait. Since offspring that do not disperse stay to help the incumbent breeder, the probability $1 - d$ quantifies an individual's aforementioned 'tendency' towards helping.
- *Helping*. Once the decision to help/disperse has been made, the direct benefit to the breeder can accrue. We assume that breeder mortality decreases at a rate proportional to the total number of helpers found on its patch immediately following dispersal. We assume that the constant of proportionality is small (say, of order $1/K$), and model the probability of breeder mortality with the function

$$\mu(\bar{d}) = \exp\{-k(1 - \bar{d})\}, \quad (2.1)$$

where k is a positive constant that controls how quickly breeder mortality decays with increasing

numbers of helpers (larger k means helping is more effective at reducing mortality), and where \bar{d} is the mean d among a breeder's current brood of offspring. Given this model for breeder mortality, we model the probability of breeder survival as

$$S_b(\bar{d}) = 1 - \mu(\bar{d}). \quad (2.2)$$

- *Competition for vacant patches.* If a breeder survives, then we assume it retains its patch, and breeds there again in the next time step. However, if a breeder does not survive, then we assume that competition for the vacant patch occurs among helpers (those native offspring that did not disperse) and non-helping individuals-in-wait (those non-native offspring that dispersed to the contested patch). Because a helper may compete for a breeding site more/less successfully than a non-helper owing to, for example, different territory inheritance patterns [21], costs of dispersal [27] or costs of helping [20], we introduce a positive constant c that allows the competitive ability of a non-helper to vary relative to that of a helper. When $c > 1$, a non-helper has a competitive advantage over a helper; when $c < 1$, a non-helper has a competitive disadvantage; and when $c = 1$, helpers and non-helpers are competitively equivalent. Mathematically, c acts as a competitive weight given to non-helpers, so that the terms

$$\frac{1}{\text{no. helpers} + c \cdot \text{no. non-helpers}}$$

and

$$\frac{c}{\text{no. helpers} + c \cdot \text{no. non-helpers}}$$

express the probability that a given helper and a given non-helper, respectively, secure the breeding site on which they compete.

When the competition phase is complete, all unsuccessful competing offspring die (this includes offspring competing on patches where the incumbent breeder survived), and the cycle repeats.

3. METHODS OF ANALYSIS AND RESULTS

We analysed the model using the neighbour-modulated (direct) fitness approach of Taylor and Frank [13,28,29]. For convenience, our inclusive fitness treatment assumes that the number of patches (p) and brood size (K) are both very large (ideally infinite). We make the standard suite of genetic assumptions (weak selection, additive gene action, etc.), discussed in detail elsewhere [23,28,30–33].

We show in the electronic supplementary material that, given the life-history assumptions described above, the marginal inclusive fitness of a focal juvenile with a reduced tendency to help (i.e. increased tendency to disperse) can be described by

$$\begin{aligned} \Delta W = & (1 - S_b) \left[\frac{(c-1)}{(1-d+cd)} \right] & \text{I} \\ & + \bar{R} S'_b & \text{II} \\ & + r(1 - S_b) \left[\frac{1}{(1-d+cd)} \right] & \text{III} \\ & - r S'_b, & \text{IV} \end{aligned} \quad (2.3)$$

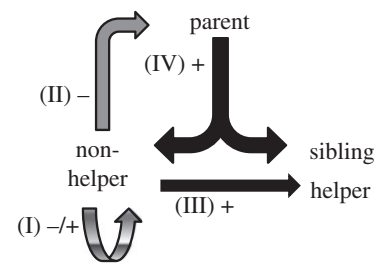


Figure 2. The costs and benefits of dispersing from the natal patch. Roman numerals relate to the lines of equation (2.3). – is a cost, + is a benefit: (I) –/+ is the direct cost/benefit associated with a decreased/increased chance of becoming a breeder; (II) – is the cost of decreasing parent survival; (III) + is the benefit of dispersing, leading to decreased competition among siblings; (IV) + is the benefit of decreasing parent survival, leading to increased chances of the helper or siblings becoming a breeder.

where S'_b is the marginal survival of the breeder (this is negative, since increased dispersal leads to reduced breeder survival), $\bar{R} = 0.5$ is the average relatedness between a juvenile and its parent, and r is the average relatedness between a focal juvenile and the average juvenile that competes on the focal juvenile's natal patch. The coefficient r can be written as $r = [(1-d)/(1-d+cd)] [(1/M) + 1]/4$, where M is the number of different mates a breeder has (i.e. M is the degree of promiscuity).

Equation (2.3) shows that the inclusive fitness effects of reduced helping (i.e. increased dispersal) are given by four components (figure 2):

- (I) The direct fitness effect of reduced helping. That is, the difference between the focal individual's own probability of securing a breeding site in the case that it disperses (i.e. does not help), and the focal individual's own probability of securing a breeding site in the case that it does not disperse (i.e. does help). When $c > 1$, this term counts as a benefit, and when $c < 1$, this term counts as a cost.
- (II) The reduction in adult breeder survival that is associated with reduced help. This term counts as a cost, since $S'_b = -k\mu < 0$.
- (III) Reduced local competition due to the focal individual's increased tendency to disperse (i.e. decreased tendency to help). This is a benefit given to the average juvenile that competes on the focal juvenile's natal patch.
- (IV) The benefit of increased opportunity to succeed the current breeder. When there is less help available to the breeder, adult survivorship is decreased, which in turn increases the probability that the local breeding site will become available to a juvenile competing on the patch. Again, this benefit is given to the average juvenile that competes on the focal juvenile's natal patch.

The sign of ΔW determines when reduced helping confers a selective advantage. Reduced helping is favoured when $\Delta W > 0$ and is disfavoured when $\Delta W < 0$. When $\Delta W = 0$, the population-wide level of helping is at an equilibrium. Simple algebra shows that the sign of ΔW is determined by a quadratic function of d , so it is possible to provide an exact expression for the equilibrium value

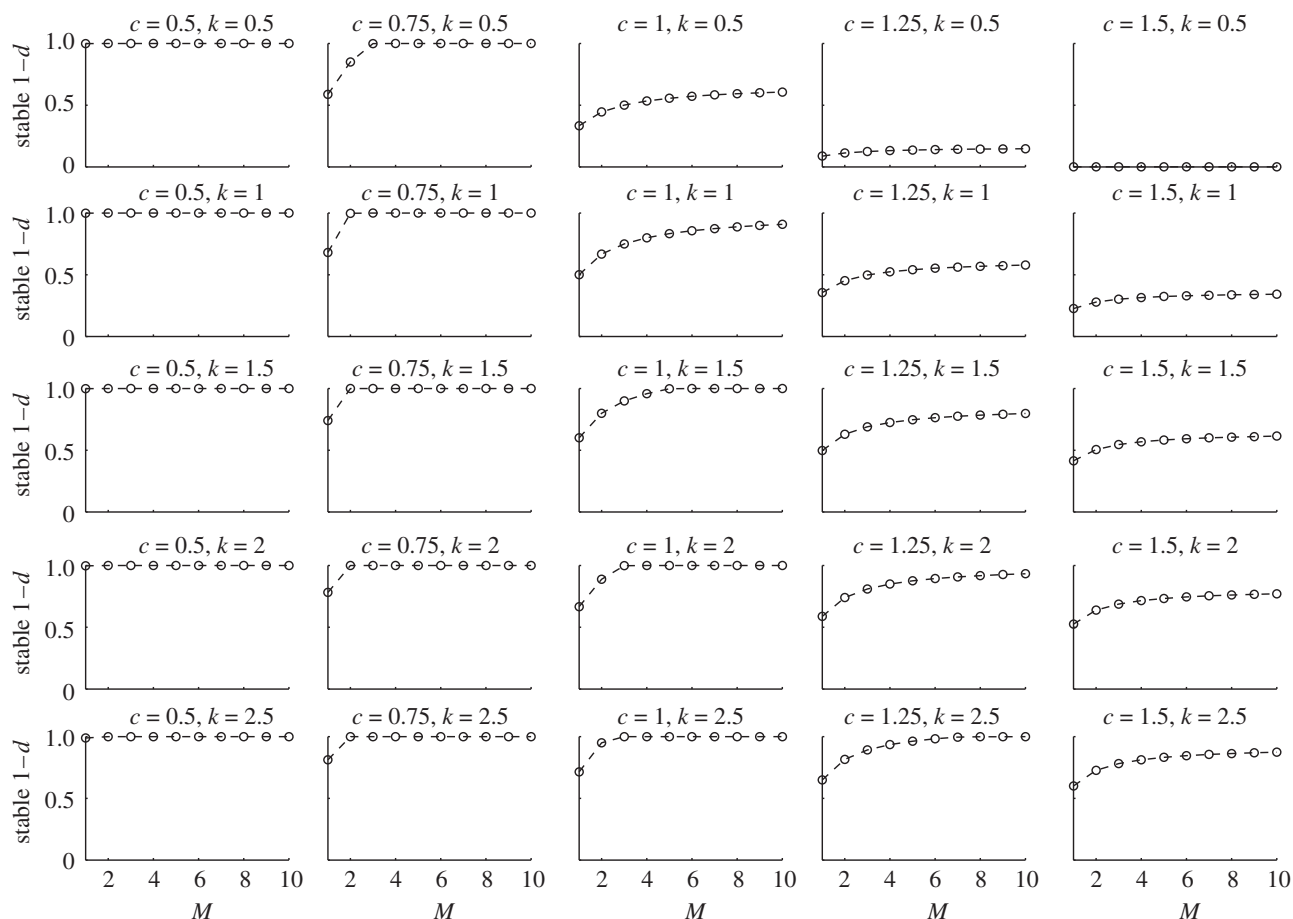


Figure 3. Helping and promiscuity. The predicted rate at which individuals stay and help ($1-d$) is plotted against the level of promiscuity (M), for different rates of the competitive ability of non-helpers (c) and the survival benefit conferred upon breeders (k). The proportion of individuals selected to stay and help decreases with increased competitive abilities of non-helpers, c , and with decreased survival benefit conferred upon breeders, k .

of d , when it exists. That said, the expression for such a d is complicated, and its existence requires that a second complicated expression (in mathematical terms, the second expression is called the discriminant) be positive. To avoid complicated mathematical expressions that convey no biological insight, and to explore the possibility that long-term action of selection leads to non-equilibrium levels of behaviour, we turned to numerical simulation.

Our numerical procedure began by assuming a set of initial conditions that covered the entire range of phenotype space evenly. In this way, the numerical procedure simulated several evolutionary trajectories simultaneously. Any given trajectory was constructed by using the most recently observed population average d to calculate ΔW . When ΔW was positive (respectively negative) the population average d was increased (respectively decreased) by an amount that was proportional to ΔW itself. These two basic steps were repeated until all trajectories of a given simulation run were sufficiently close to one another.

We found that the predicted level of helping increased with increasing promiscuity (figure 3). Hence, the tendency to help juveniles born on the same patch increased with decreasing relatedness (from increasing promiscuity). The reason for this is that the rate of promiscuity only has consequences for lines III and IV in equation (2.3). Promiscuity does not influence either direct fitness consequences (line I) or relatedness to parent (line II). In contrast, lower levels of promiscuity lead to a higher relatedness to other helpers on a patch,

which increases the indirect benefit of dispersing to reduce competition for relatives. We checked the validity of our inclusive fitness result with an individual-based simulation of the model system (see the electronic supplementary material for details of the assumptions and a version of the script used to generate simulation results), which gave the same results (figure 4).

4. DISCUSSION

Our model predicts that selection for staying to help (i) either shows no relationship or increases with higher levels of promiscuity, (ii) is decreased when non-helpers are more likely to inherit a territory (higher c), and (iii) increases when helping provides a greater survival benefit to the breeder (figure 3). In addition, we found close agreement between the predictions of our inclusive fitness analyses and an individual-based simulation (figure 4).

Our model shows that, even in a very simple scenario, the consequences of promiscuity for the level of cooperation can be far more complicated than expected from heuristic and verbal arguments (see equation (2.3) and figure 2). Previous theoretical arguments have focused on how promiscuity reduces relatedness to siblings, and hence reduces the indirect benefit of staying to help, leading to the prediction that promiscuity selects against helping (figure 1). However, when all the population level consequences of staying to help are explicitly modelled, there can also be indirect costs of staying to help. Specifically, staying to

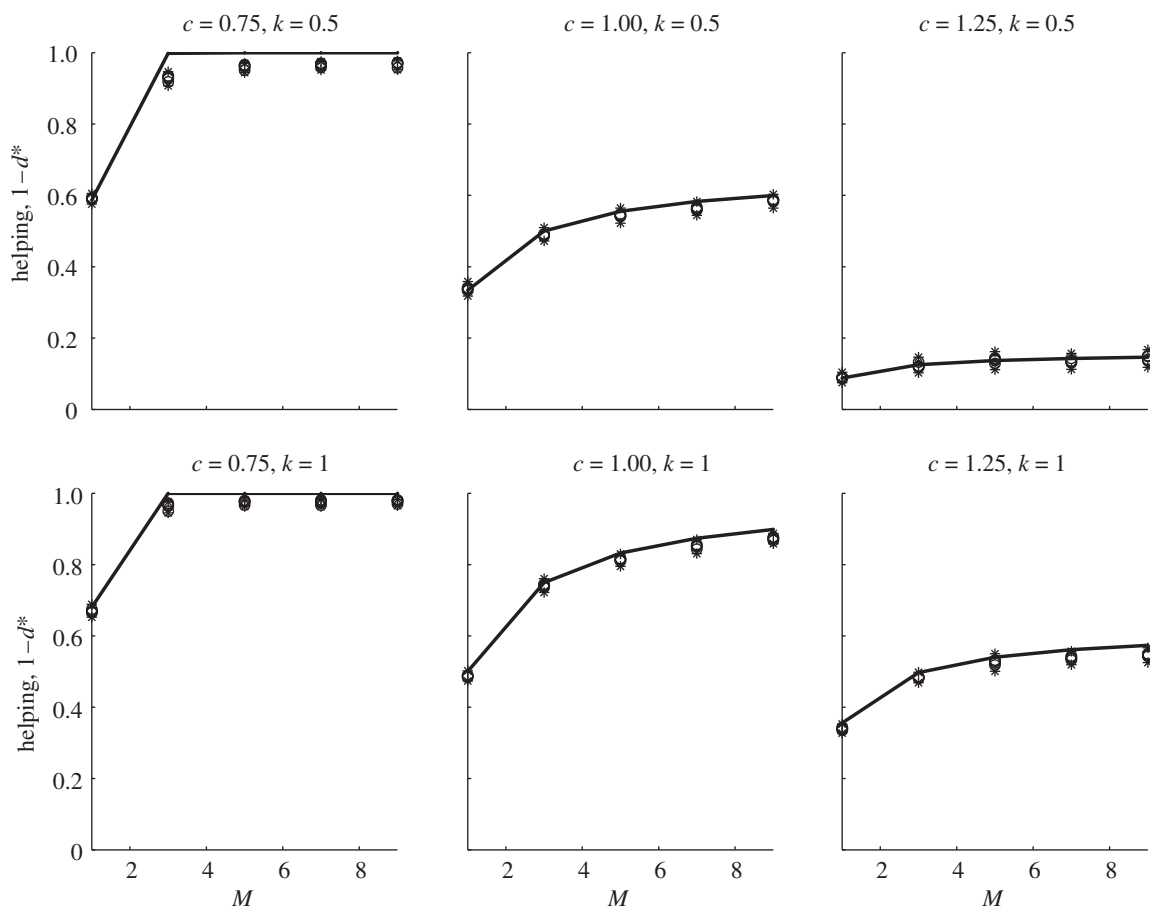


Figure 4. Inclusive fitness versus simulations. The predicted rate at which individuals stay and help ($1 - d$) is plotted against the level of promiscuity (M), for different rates of the competitive ability of non-helpers (c) and the survival benefit conferred upon breeders (k). The results obtained using inclusive fitness theory (solid lines) and individual-based simulations (dots) are in close agreement.

help increases the chance both that the breeder survives and that the helper inherits the patch if the breeder dies (lines IV and III of equation (2.3), respectively). Consequently, staying to help decreases the chance that another sibling who has stayed to help will inherit the patch.

Why does our model predict that promiscuity has either no effect or a positive effect on selection to stay and help (figures 3 and 4)? Equation (2.3) shows that in our model, staying to help has four fitness consequences: (I) direct cost of not dispersing to breed elsewhere; (II) indirect benefit of increased survival of parent; (III and IV) indirect cost of creating greater competition for non-dispersing siblings by reducing the likelihood that the breeder will die, and the helper staying to compete for the breeding spot if the breeder dies. The indirect benefit of staying to help (II) is not altered by promiscuity, because the helper is always related to their parent by $R = 0.5$. Consequently, the effect of promiscuity is driven by its indirect cost of making greater competition for siblings (III and IV). Lower levels of promiscuity lead to a higher relatedness between siblings, which favours dispersal to reduce the competition that these siblings face. Another way of looking at this is that low promiscuity does favour helping, but that the way to help siblings is to disperse away (to reduce competition), rather than to stay and help. This illustrates the general point that verbal arguments can be misleading because they focus on conspicuous traits and ignore less conspicuous consequences.

From a theoretical perspective, one of the most important points that arises from our model is that, even in a simple situation, things can be more complicated than expected. Specifically, competition between relatives can either negate or reverse predictions that follow from simple intuition. In this respect, our paper is analogous to when Taylor [18] showed that limited dispersal did not necessarily favour cooperation, because it could also lead to increased competition between relatives. A major theme since Taylor's pivotal paper has been examining exactly what kind of demographic factors lead to limited dispersal favouring cooperation (reviewed by West *et al.* [10] and Lehmann & Rousset [11]). Analogously, we are not saying that the idea that monogamy and low levels of promiscuity will favour cooperation is wrong, but rather saying that this requires certain biological assumptions, the biological relevance of which we discuss below. This illustrates Boomsma's point [7,8] that monogamy is necessary, but not sufficient for the evolution of eusociality.

A problem with our model is that by concentrating on survival benefits, it neglected one of the main aspects of helping that we had hoped to capture—the benefit to siblings from staying to help. Extending our model to include survival benefits to siblings did not change things (results not shown), because the strict density dependence means that this is cancelled out by the increased competition that it also creates. If dispersal

and helping were allowed to coevolve, we would also expect similar results, because dispersal reduces the kin-selected benefit of helping (line II of equation (2.3)), and hence selects for helping to be conditional upon not dispersing, as we have assumed [34]. We suggest that the best avenue for future research is to take an entirely different approach, and examine fecundity benefits in a population where there is not strict density dependence [23,24,35–37]. This task will be non-trivial, as even the simple scenario we considered here, with only survival effects and strict density dependence, led to a model that we had to solve numerically, rather than analytically. We suggest that this alternative approach captures a more biologically useful scenario than the one we modelled, and would lead to a negative correlation between selection to stay to help and promiscuity, as has been found in the empirical literature [5,7–9]. Noteworthy here is that the species where the benefits of helping are primarily on the survival of breeders, the superb fairy-wren, also has one of the highest levels of promiscuity [22].

Finally, our results contradict the possibility that the influence of promiscuity on the evolution of cooperation could be an area where inclusive fitness theory makes ‘spurious predictions’ [17]. Nonacs [17] found that a population genetic simulation predicted a flat or slightly positive relationship between promiscuity and helping, and contrasted this with arguments based on kin selection theory that promiscuity should select against cooperation (e.g. [4,5,7,8]). However, he did not also construct an inclusive fitness model, and so he was comparing scenarios with very different assumptions, rather than comparing different theoretical approaches (for a related example on the evolution of dispersal, see pp. 117–120 of [13]). We have found the same pattern as Nonacs with an inclusive fitness analysis, and also shown that when population genetic simulations are produced for the same scenario, they give the same results. This is not surprising, given the large literature showing the equivalence of different approaches [32,33,38–40]. More generally, the comparison of our simulation with inclusive fitness analyses supports the previous suggestion that the inclusive fitness approach will often be computationally simpler, and hence facilitate both the deriving of predictions and our conceptual understandings of why those predictions arise ([39], p. 671; [13], p. 120; [41], p. 119).

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