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Original Article Conditional helping and evolutionary transitions to eusociality and cooperative breeding

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The nonreproductive helpers of many arthropod, bird and mammal species are a perennial puzzle for evolutionary biologists. Theory and evidence suggests that helping is favored by high relatedness between social partners and by certain ecological factors. I suggest that the availability of information on reproductive value may be another important factor predicting whether helping evolves. Using simple models, I show that conditional helping strategies, in which individuals assess the reproductive value of themselves and their relatives and then help conditionally, evolve more easily than unconditional helping strategies. The models also identify conditions that cause parent–offspring conflict over helping strategy and produce predictions regarding the evolution of honest signaling and parental effects. Crucially, the evolution of facultative helping can select for specialization in helping, which in turn selects for more frequent helping, creating positive feedback. Facultative helping might thereby act as stepping-stone to advanced forms of obligate helping.

Key words: altruism, cooperation, maternal effects, parent-offspring conflict, sociality.

INTRODUCTION

The evolution of altruism is puzzling because natural selection typically favors self-interest. Altruists that give up reproduction in order to help others are particularly difficult to explain, because genes encoding sterility are never directly transmitted. Nonreproductive helpers have therefore been argued either to have cryptic means of acquiring direct fitness (e.g., by occasionally inheriting the nest or territory and starting to breed; Woolfenden and Fitzpatrick 1978; Leadbeater et al. 2011) or to propagate their genes indirectly by augmenting the fitness of close relatives (Hamilton 1964).

Eusociality and cooperative breeding (sensu Crespi and Yanega 1995) are relatively rare across taxa, implying that the inclusive fitness returns are too low for nonreproductive helpers to evolve in most species. Relatedness among siblings is comparatively high among eusocial insects and cooperatively breeding vertebrates, or at least in their ancestors (Hughes et al. 2008; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012), suggesting that high within-family relatedness (e.g., because of monogamy; Boomsma 2007) is one requirement for the evolution of advanced sociality. Ecological and life history correlates of sociality have also been proposed: for example, eusociality and cooperative breeding are

© The Author 2014. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com thought to be associated with taxa in which the available habitat is largely saturated, the nest or territory is a valuable and scarce resource, and in which breeders are comparatively long-lived (e.g., Bennett and Faulkes 2000; Hatchwell and Komdeur 2000; Duffy 2003; Koenig and Dickinson 2004). Such factors affect the reproductive value (i.e., the expected contribution to the future population; Fisher 1930) of actors and recipients. For example, breeders' average reproductive value will typically be higher when they have low extrinsic mortality, and ecological factors influencing the availability of empty breeding sites affect reproductive value (Alizon and Taylor 2008). Because reproductive value factors into inclusive fitness decisions (Frank 1998), factors such as these may be very important to the evolution of eusociality and cooperative breeding.

Conditional Helping as a Stepping-Stone to Advanced Sociality

The availability of information on the individual-specific costs and benefits of helping might be another key factor determining whether a solitary species evolves eusociality/cooperative breeding. For helping to be selectively advantageous, the net inclusive fitness benefits of helping must exceed those of not helping. If individuals have no knowledge of factors that affect the relative fitness returns of helping for them specifically, they must rely solely on evolutionary information. That is, the population-wide average inclusive

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fitness benefits of helping must be greater than its average costs for helping to be positively selected. However, when individuals are able to gauge the inclusive fitness consequences of helping that apply to them specifically, they could evolve to help only when it is particularly advantageous. Such conditional helping may evolve more easily than unconditional helping; if so, the availability of information that facilitates conditional helping might be important to the evolution of eusociality and cooperative breeding.

Consider the following formulation of Hamilton's rule, which is weighted by the reproductive value of the actor and recipient: rBv_p – $Cv_a > 0$, where B and C are the benefits and costs of the social behavior to the recipient and actor respectively, r is their relatedness, and v_p and v_a are the reproductive values of the recipient and actor, respectively (Frank 1998). It is clear that altruism is more likely to be favored when the actor's reproductive value is low and that of the recipient is high. For individuals that always perform the helping behavior (e.g., they always become a helper at their mother's nest), this inequality becomes $\bar{r}B\bar{v}_p - C\bar{v}_a > 0$, where the bars denote the average values of these parameters for actors and the potential recipients they encounter. By contrast, the invasion criterion for individuals playing a conditional strategy in which they only provide help when r, v_p , and v_a are sufficiently favorable may be written as $B(\bar{r} + \delta_1)(\bar{v}_p + \delta_2) - C(\bar{v}_a + \delta_3) - y > 0$, where y represents the costs of being selective, and the δ terms control when the behavior is expressed relative to \overline{r} , $\overline{v_{\rho}}$, and $\overline{v_{a}}$. For example when δ_{1} and δ_{2} are positive, individuals only help recipients with higher relatedness and reproductive value than the average potential recipient that is encountered. When δ_{3} is positive, they only help when their own reproductive value is lower than average (I assume $\delta_{3} \leq \overline{v_{a}}$).

Therefore, facultative helping can evolve but unconditional helping cannot when $B(\bar{r} + \delta_1)(\bar{v_p} + \delta_2) - C(\bar{v_a} + \delta_3) - y > 0 > \bar{r}B\bar{v_p} - C\bar{v_a}$. This condition is more likely to hold for any given relatedness structure and *B*:*C* ratio when the δ terms are large and *y* is small, that is, when conditional helping is stringent and the costs of choosiness are low. This inequality demonstrates that facultative helping based on variation in relatedness and/or reproductive value can sometimes invade a nonhelping population in parameter spaces in which unconditional helping cannot.

Though this result is somewhat obvious, it has important implications. The evolution of facultative helping could often act as a stepping-stone toward more extensive helping strategies, including obligate, unconditional helping (Figure 1). Once facultative helping has evolved, it could select for adaptations to a social lifestyle that would be selected against in a nonhelping population. Adaptations to sociality could affect the costs and benefit terms C and B. For example, individuals adapted to helping could confer higher



Figure 1

Hypothesized role of conditional helping as a stepping-stone in the evolution of obligate helping. In this example, only some mothers (those above the line) are initially worth helping. In each panel, the mother bee above the line is of high quality, and the one below is of low quality (small bees represent offspring). 1) Initially, maternal quality is not apparent and all offspring disperse rather than helping, because unconditional helping would yield lower inclusive fitness returns than dispersal. 2) Later, maternal quality becomes discernable by offspring, for example via a signal or cue associated with fecundity or condition. 3) Offspring might then evolve a conditional helping strategy, such as "help rear the offspring of mothers expressing the signal." 4) The evolution of helping will select for traits that make alloparental care more efficient. 5) Helping might become more common, further strengthening selection on helping ability, potentially producing positive feedback. Eventually, helping may become obligate.

benefits on recipients, increasing *B*. Adaptations to helping might also have antagonistic pleiotropic effects on fitness as a nonhelper, reducing *C*. Subsequently, less stringent conditional helping could invade, causing helping behaviors to be expressed more often. This would further strengthen selection for traits that improve fitness under sociality, potentially causing positive feedback. Eventually, obligate helping could become the optimal strategy. This hypothesis predicts that the availability of information on reproductive value might be an important prerequisite for the evolution of advanced sociality, since conditional helping requires individuals to possess information on their social partners and/or themselves.

Here, I use models to illustrate that reliable information about the reproductive value of oneself and others can make nonreproductive helpers more likely to evolve. The first model shows that various forms of conditional helping can often invade in parameter spaces in which unconditional helping cannot and identifies conditions affecting what form of helping evolves. The model also makes predictions about the extent and evolutionary consequences of parent–offspring conflict over offspring helping strategy. The second model shows that the invasion of conditional helping can select for alleles for specialization in helping, which can provide a route to the evolution of obligate helping in parameter spaces in which it was initially inferior to nonhelping strategies.

MODEL 1: EVOLUTION OF FACULTATIVE AND UNCONDITIONAL HELPING

Model 1 aims to identify factors that affect the evolution of conditional helping based on reproductive value and to illustrate that conditional helping can evolve relatively easily in a biologically explicit model. I consider the evolution of nonreproductive helpers that stay at their natal nest to help their mother rear additional siblings. In light of phylogenetic data suggesting high intrafamily relatedness at the origin of eusociality and cooperative breeding (Chapman et al. 2000; Hughes et al. 2008; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012), and because my focus here is on facultative helping based on reproductive value rather than relatedness (the latter has been investigated previously; e.g., Agrawal 2001; Rousset and Roze 2007), I assume that all females mate singly. Relatedness among siblings is therefore invariant and high.

I consider a meta-population subdivided into i patches of sexual haploid individuals, which have discrete generations. The lifecycle is typical of a primitively social hymenopteran such as a Halictid bee or *Polistes* wasp (though the model's qualitative conclusions likely generalize to other taxa such as cooperatively breeding birds). The clearest biological interpretation of the model is that mated females rear 2 clutches of offspring, and then die. The first clutch

of offspring is exclusively female, while the second clutch contains both sexes. Females born in the first clutch can either remain with their mother and become nonreproductive helpers or disperse and attempt to breed in the next cohort. Whether a first-clutch female helps or disperses depends on her own genotype and, potentially, on her reproductive value and that of her mother (Table 1). All individuals born in the second clutch disperse and attempt to breed in the next cohort. An equally valid biological interpretation of the model is that the first and second clutches are not temporally separated: the "first-clutch" females (i.e., the subset of females that potentially become helpers) are born at random intervals among their nonhelping ("second clutch") siblings, the number of which depends on the number of helpers that the nest produces. For simplicity, and because this situation most closely matches Hymenopteran biology (e.g., Field et al. 2010), I will continue to speak of first and second clutches.

I assume that females differ in their reproductive value, and that the majority of reproductive value is randomly determined for each individual by the environment (i.e., there is a negligible correlation for reproductive value between mothers and offspring or between siblings). For simplicity, reproductive value can take only 2 possible values: low and high. Reproductive value determines the size of a female's second clutch (see below). A proportion f of females is born with high reproductive value, while the remainder (1 - f) has low reproductive value (mnemonic: f means "frequency of fecund females"). Furthermore, individuals carry a single locus (termed the "helping strategy" locus) with 5 possible alleles, which controls the helping strategy of females born in the first clutch; this locus is not expressed in males or in other types of females. Each allele codes for one of the 5 helping strategies described in Table 1. In short, one allele encodes the strategy Never help, one encodes Always help, and the others produce the helper phenotype conditional on the individual's own reproductive value, its mother's reproductive value, or both.

The strategies in Table 1 were chosen because 5 is the maximum number of possible helping strategies when reproductive value falls into 2 categories, excluding strategies that are inferior to a less behaviorally complex strategy. For example, *Help if you have high reproductive value* was excluded because conditions allowing this strategy to beat *Never help* always favor helping in low reproductive value females as well. Therefore, one of the simpler strategies *Never help* and *Always help* is always superior to *Help if you have high reproductive value*. For similar reasons, I excluded the nonsensical strategies *Help if mother has low reproductive value* and *Help if mother has lower reproductive value than you*.

Both low and high reproductive value females produce n female offspring in their first clutch, where n is the expected clutch size (n was set to 1 in all simulations, since trial simulations showed it had

Table 1

Descriptions of the 5 strategies encoded	l by the 5 alleles at the he	elping strategy locus in Models 1 and 2
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Allele	Strategy	Description
1	Never help	Individuals playing this strategy always disperse and never help.
2	Help if you have low reproductive value	These individuals become helpers when they have low reproductive value, irrespective of their mother's reproductive value.
3	Help if mother has high reproductive value	These individuals become helpers whenever their mother has high reproductive value, irrespective of their own reproductive value.
4	Help if mother has higher reproductive value than you	These individuals only help when they have low reproductive value and their mother has high reproductive value.
5	Always help	These individuals always help and never disperse.

Only offspring born in the first clutch face the decision to help or disperse: second clutch offspring always disperse.

no qualitative effect on the results). The expected size of the second clutch for a low reproductive value female with \mathcal{N}_{help} helpers at her nest is $n(1 + b\mathcal{N}_{help})$, where *b* determines the magnitude of the effect of helpers on maternal fecundity ($b \ge 0$; for simplicity, I assume linear, additive effects of helpers on maternal fitness). The expected size of the second clutch of a high reproductive value female is $nx(1 + b\mathcal{N}_{help})$, where *x* determines how much more fecund high reproductive value females are than low reproductive value females ($x \ge 1$). All breeding females and their helpers die following production of the second clutch.

In some runs of the model, I assumed no sex ratio adjustment: the first clutch was always all-female, and the second had an even sex ratio. However, I suspected that this situation might substantially hinder the evolution of helping, since nests with helpers would then produce a greater proportion of dispersing males than females, incurring a disadvantage because of the "rarer sex" effect (Fisher 1930; Gardner and Ross 2013). Therefore, in other runs, I assumed that mothers adjust the sex ratio of their second clutch, such that the sex ratio across the entire meta-population is even (e.g., because loci controlling the sex ratio co-evolve and compensate for population-level changes in helping frequency). Such sex ratio adjustment assumption is not overly unrealistic for eusocial hymenopterans, which modulate the sex ratio of their sexual (nonworker) brood independently of the large number of all-female workers they produce (Boomsma and Grafen 1991; Gardner and Ross 2013).

A proportion *m* of dispersing offspring (i.e., nonhelping firstclutch females and all second clutch individuals) entered a pool of migrants that was divided equally among the patches, while the remainder (1 - m) stayed in their natal patch (m = 0.05 in all simulations). Females mate with a single randomly chosen local male (males may mate multiply) and then attempt to found a new colony. To prevent exponential population growth, I imposed a carrying capacity. Both local and global population regulation were considered, in separate simulation runs. Under local regulation, patches containing more than k/i individuals were culled down to size k/i; under global regulation, the population as a whole was culled until it contained k or fewer individuals (k = 1000 in all simulations).

In each run of the simulation, I initiated a starting population containing a uniformly distributed random number of colonies between 0 and 1000 of each of the 50i possible types of colonies (i.e., 5 maternal genotypes \times 5 mate genotypes \times 2 levels of maternal reproductive value $\times i$ possible locations). The simulation then calculated the expected number of each possible type of individuals in the first and second broods for each of the 50icolony types, implemented breeding, dispersal, mating and density regulation, and replaced the old population with the new one. This procedure was repeated iteratively, updating the expected numbers of the 50i colony types each time. The simulation is deterministic; that is, it always produces the same results for a given initial condition. However, because the initial conditions were randomly determined in each run, I could test for sensitivity to initial conditions by comparing the outcomes of nearby parameter spaces, as well as rerunning the model. After 10000 generations, the allele frequencies were computed. All runs were inspected to confirm that allele frequencies had reached a stable equilibrium.

Factors Affecting the Evolution of Helping Strategy

The effects of f, x, and b on the evolutionarily outcome are shown in Figure 2. Firstly, one can see that the outcome was insensitive



Figure 2

The evolutionary stable strategy (or strategies) for different values of f, x, and b when offspring control their own helping strategy. Colors that match the legend show that a single strategy has fixed, while intermediate colors indicate stable coexistence of 2 or more strategies. As b increases, the parameter space in which *Never help* (red) is an evolutionarily stable strategy shrinks. First, *Never help* gives way to Strategy 4 (green), which in turn is replaced by Strategies 2 and 3 (orange and yellow) and the unconditional helping Strategy 5 (blue) at high b values.

to the initial conditions: although I only ran each combination of f, x, and b once using random initial allele frequencies, neighboring parameter spaces almost always reached the same (typically monomorphic) equilibrium. Accordingly, recreating the entire figure using new simulation runs produced near-identical results (not shown). Figure 2 assumes i = 10 patches, global density regulation, and also that nests adjust the sex ratio of their offspring to compensate for population-wide rates of helping; however, varying these assumptions produced similar or identical figures (this is also true of subsequent figures).

When offspring assistance provided meager benefits to maternal fecundity (b = 0.1), the allele encoding the strategy *Never help* often fixed. However, the allele for the stringent conditional Strategy 4, *Help if mother has higher fecundity than you*, could also fix, provided that high reproductive value females were very fecund relative to low reproductive value ones (high *x*). When b = 0.4, the strategy *Help if mother has high fecundity* could beat Strategy 4, provided that both *f* and *x* were sufficiently high. The parameter *f* affects the reproductive value of the extra sisters that are produced by helping the mother, so higher values of *f* favor less stringent forms of helping.

Higher benefits of offspring help to maternal fecundity (b = 1.5) increased the parameter space in which *Help if mother has high fecundity* beat *Help if mother has higher fecundity than you*, by making helping even more beneficial. There was also a region in which *Help if you have low fecundity* was the winning strategy, replacing *Help if mother has higher fecundity than you*. Lastly, when helping is highly beneficial (b = 2.1), *Always help* fixed in much of the parameter space. The region with high *f*, high *x* and b = 2.1 appeared to be polymorphic for Strategies 3 and 5. However, this result likely reflects the simulation taking a very long time to converge on Strategy 5, since Strategies 3 and 5 have increasingly equivalent fitness as $f \rightarrow 1$.

These results illustrate that information is vital to the evolution of helping, provided that the benefits of help to the recipient (b) are low. However, information can become redundant when helping provides sufficiently large inclusive fitness benefits, for example because b, f, and x are high. This conclusion is evident from the replacement of conditional helping strategies with either a less stringent conditional helping strategy (i.e., Strategy 4 being outcompeted by Strategies 2 or 3) or by unconditional helping. Moreover, one can show by setting the starting frequencies of alleles 2, 3, and 4 to zero that conditional helping can invade a nonhelping population more easily (i.e., at lower values of b, f, and x) than unconditional helping (cf. Figure 2 and Supplementary Figure S1), supporting the earlier algebraic argument involving Hamilton's rule.

Mother-Offspring Conflict Over Helping

I next modified Model 1 to investigate the potential for conflict between mothers and first-clutch offspring over the helping behavior of the latter. A powerful method for determining the optimal offspring phenotype from the mother's perspective is to transfer genetic control of the offspring phenotype to the mother (Frank 1998). I therefore modified the model such that the helping phenotype of all first-clutch females depended on the allele present in the mother, rather than in the offspring (half of which carry a paternally inherited allele). For example, all low reproductive value offspring born in the first clutch of a high reproductive value mother carrying the Strategy 4 allele would become helpers. By comparing the evolutionary outcomes under offspring and maternal control, one can identify zones in which mothers and offspring have divergent evolutionary interests. These zones of conflict ultimately derive from relatedness asymmetries within the family (Trivers 1974).

The evolution of helping strategies under maternal control is shown in Figure 3 for the same parameter space as in Figure 2. The results are qualitatively similar, except that mothers favor more extensive helping for any given combination of b, f, and x. For example, when b = 0.4, the stringent strategy *Help if mother has higher reproductive value than you* takes up a smaller area in Figure 3 than in Figure 2, and the strategy *Always help* is favored when b = 1.5for many combinations of f and x. However, there are substantial areas of overlap, in which the same strategy *evolves* under both offspring and maternal control. As expected, *Always help* can invade *Never help* more easily under maternal control than offspring control (Supplementary Figure S2). Under maternal control, there were still many parameter spaces in which conditional helping can invade a nonhelping population, but *Always help* cannot (cf. Figure 3 and Supplementary Figure S2).

This model provides interesting insights into the consequences of mother–offspring conflict over helping for the evolution of signals and cues. If offspring evolve to conditionally help mothers that have cues or signals that indicate high reproductive value, mothers might benefit from evolving dishonest signals that exaggerate their quality, allowing them to always receive help. Mothers might also evolve to disguise cues to their fecundity. Such adaptations would represent a "selfish maternal effect" (sensu Marshall and Uller 2007), since they are causal effects of a maternal trait on offspring phenotype, which increase offspring number at a cost to the inclusive fitness of individual offspring.

Intuitively, one might predict that maternal deception would place selection on offspring to revert to a nonhelping strategy. However, the model provides little evidence that maternal dishonesty could cause the collapse of helping: there are few parameter spaces in which the fitness of strategies are ranked Conditional helping > Never help > Always help from the offspring perspective, yet mothers are fittest with Always help. Instead, comparison of Figures 2 and 3 and Supplementary Figure S1 reveals that dishonest signaling might paradoxically allow more frequent helping to evolve. For example, when b = 1.5, offspring favor the conditional Strategies 2-4, while mothers often favor Always help. If mothers then evolved to exaggerate their reproductive value, offspring would not regress to Never help, because this strategy provides them with lower fitness than Always help (Supplementary Figure S1). Offspring could however benefit from adaptations that allowed them to see through dishonesty and discern maternal reproductive value, and again help conditionally. Alternatively, offspring could increase their fitness by evolving to specialize in helping at the expense of independent breeding (see Model 2), in effect "accepting their fate" as obligate helpers.

There are also parameter spaces in which mothers and offspring both favor conditional helping (e.g., zones with the same color in Figures 2 and 3). In these cases, both parties increase their fitness through the honest transfer of information. That is, low quality mothers would benefit from making their offspring aware of their quality, so that the offspring "knew" to disperse. Signals of maternal quality would remain honest even in the absence of mechanisms that enforce honest signaling, such as handicap or index processes (reviewed in Holman 2012). Dishonesty is disadvantageous to mothers in these parameter spaces because of its indirect costs, namely the lost fecundity of the offspring that are "tricked" into becoming helpers.



Figure 3

The evolutionary stable strategy (or strategies) for different values of f, x, and b when mothers control the helping strategy of their offspring. Mothers favor more extensive helping than do offspring. For example, mothers sometimes favor *Always help* in parameter spaces in which offspring are selected to help conditionally.

Lastly, there are zones in which offspring evolve to become helpers only when they have low reproductive value, but mothers benefit from being helped by both high and low value offspring. As explained in the discussion, this could select for mothers that manipulate the reproductive value of their offspring (e.g., by stunting their growth), thereby inducing them to stay.

MODEL 2: CONDITIONAL HELPING AS A STEPPING-STONE TO OBLIGATE HELPING

Model 2 adds a second locus with two alleles "A" and "a", termed the "specialization" locus, which has antagonistic pleiotropic effects on helping and dispersal in offspring. Model 2 aims to investigate the hypothesis illustrated in Figure 1.

The "a" allele coded for specialization in dispersal: all individuals carrying this allele behave exactly as in Model 1. Specifically, they had an effect b on the size of their mother's first clutch when they became helpers, and they always survived dispersal. The "A" allele coded for specialization in helping and was beneficial when expressed in first-clutch females that become helpers but detrimental when in expressed in dispersing first-clutch females. Helper females that carry the "A" allele increased their mother's fecundity by a factor of b', where $b' = b(1 + \alpha)$ and $\alpha \ge 0$. Therefore in Model 2, the size of the second clutch was equal to $n(1 + bN_{help} +$ $b' \mathcal{N}_{help}$), where \mathcal{N}_{help} and \mathcal{N}_{help} are the number of helpers carrying the "a" and "A" alleles, respectively (as before, the size of the second clutch is multiplied by x for mothers with high reproductive value). However, dispersing first-clutch females carrying the "A" allele were assumed to die during dispersal with probability β . The specialization locus was assumed to have no effects on males, or females other than first-clutch females. I envisage the specialization locus as affecting any trait that has antagonistic pleiotropic effects on the ability to provide help and to successfully disperse, which could be behavioral, physiological, developmental, or morphological. Model 2 allows for linkage between the helping strategy and specialization loci, which recombine with probability γ ($0 \le \gamma \le 0.5$).

The helping strategy locus (Table 1) is predicted to affect the strength and direction of selection on the specialization locus, because it controls the frequency with which helping and dispersal are performed. Specifically, when alleles causing high rates of helping and low rates of dispersal are present at high frequencies at the helping strategy locus, selection on the "A" allele will be more positive, all else equal.

Figure 4 shows the joint evolution of helping strategy and specialization in helping. As predicted, the evolution of conditional helping strategies in a largely nonhelping initial population can allow the "A" allele to invade, in spite of its costs when expressed by dispersing first-clutch females. The invasion of the "A" allele increases the relative fitness of strategies that confer high rates of helping, allowing unconditional helping (as well as less stringent forms of conditional helping) to reach higher frequencies. In Figure 4's parameter space, *Always help* is unable to invade *Never help* directly when the "a" allele is fixed, showing that the invasion of the "A" allele was essential for the invasion of *Always help*.

In Figure 4A (which assumes offspring control over helping strategy), the "A" allele has no fitness effects ($\alpha = \beta = 0$) and so remained at its initial frequency of 0.001. Meanwhile, the stringent conditional helping Strategy 4 invaded and fixed. Figure 4B shows the same parameter space, except that $\alpha = 5$ and $\beta = 0.1$ (i.e., "A" individuals are 5× better at augmenting maternal fecundity if they become helpers but have a 10% chance to die if they disperse after being born in the first clutch). First, Strategy 4 invaded, allowing allele "A" to increase in frequency. After that, the presence of specialized helpers in the population allowed the less stringent



Figure 4

Conditional helping can provide a stepping-stone to unconditional helping in parameter spaces in which unconditional helping could not evolve in one step. In the left panels, the "A" allele has no fitness effects ($\alpha = \beta = 0$), while on the right, it confers an advantage to helpers and a disadvantage to dispersers ($\alpha = 5$, $\beta = 0.1$). On the left, the conditional Strategies 4 (offspring control; panel A) or 2 (maternal control; panel C) are able to invade the largely nonhelping initial population and go to fixation. In panels B and D, conditional strategies increase in frequency, allowing the "A" allele to follow. This is turns facilitates the evolution of conditional helping. The figure assumes b = 0.8, f = 0.25, x = 2 and global density regulation, that is, a parameter space in which Strategy 5 cannot invade Strategy 1 when the "a" allele is fixed. Strategies 2–5 are present at initial frequencies of 1%.

conditional Strategy 2 to replace Strategy 4. Later still, Strategy 2 was superseded by unconditional helping (Strategy 5). Similar results were obtained assuming maternal control over offspring helping behavior (Figure 4C,D). The stepping-stone effect was observed in many other parameter spaces, for example, for b = 0.4 and b = 1.5 (Supplementary Figures S3 and S4).

Assuming low rates of recombination ($\gamma = 0.001$) between the helping strategy and specialization loci had no effect on the evolutionary outcome (Supplementary Figure S5). However, strong linkage allowed the population to reach equilibrium more rapidly, because it prevents recombination from breaking up high fitness allelic combinations (e.g., the Strategy 5 and "A" alleles). As in Model 1, assuming local rather than global competition did not affect the evolutionary equilibrium, only the speed with which it was reached (slower under soft selection).

Lastly, I note that similar results would have likely been produced had I assumed that the "A/a" locus controlled specialization to sociality in mothers, for example, by increasing their fitness when living with helpers at a cost to their fitness when reproducing alone.

DISCUSSION

I first considered the evolution of conditional helping dependent on the actor's own reproductive value, that of its mother, or both. Model 1 confirmed that conditional helping can sometimes invade a nonhelping population in cases in which unconditional helping cannot and identified factors determining what form of conditional helping evolves. Secondly, comparison of the optimal offspring helping strategies from the perspective of offspring and mothers revealed zones of conflict, as well as zones of mutual agreement. These results have implications for the evolution of signaling and parental effects. Lastly, Model 2 supported the "stepping-stone" hypothesis outlined in Figure 1: conditional helping may facilitate the evolution of unconditional helping in parameter spaces in which it would not otherwise be favored, by allowing selection to favor adaptations to sociality.

Information and evolutionary transitions to sociality

Model 1 showed that conditional strategies, in which individuals become sterile helpers depending on their own or the recipient's reproductive value, can invade a nonhelping population even when the benefits of help to recipients are relatively modest. Unconditional helping strategies are unable to invade unless helping confers a comparatively strong benefit on the recipient's fitness. Therefore, the availability of reliable information on reproductive value may be an important predictor of whether eusociality/cooperative breeding evolves in a population without alloparental care.

Furthermore, the invasion of conditional strategies can allow alleles that are beneficial when expressed in helpers, but are otherwise deleterious, to increase in frequency. Conditional helping might therefore be a transitory state on the way to more frequent or extensive forms of helping, including obligate sterility (Figure 1). At the origin of eusociality or cooperative breeding, both breeders and helpers will usually lack adaptations to a social lifestyle, meaning that helping yields meager inclusive fitness returns relative to evolutionarily derived lineages. For example, the solitary ancestors of honeybees would not possess the full complement of social signals (such as the dance language that facilitates group foraging), and their queens would have been less long-lived and fertile. In the language of the present model, b and v_p will be comparatively low at the origin of helping. The present model shows that conditional helping can evolve comparatively easily, paving the way for alleles that increase b at a cost to other fitness components (e.g., fitness when solitary). Although not explicitly modeled, Model 2 would probably have produced similar results had I assumed that the "A/a" locus controlled specialization to sociality in mothers, for example, by increasing their fitness when living with helpers at a cost to their fitness when reproducing alone. That is, the evolution of conditional helping might pave the way for adaptations to sociality in parents as well as in offspring.

The information used to inform conditional helping might come from environmental sources; for example, individuals could gauge their chances of successful dispersal from local climatic conditions or assess their mother's future fecundity by the quality of her territory. Young Seychelles warblers are more likely to stay and help when their parents' territory is of high quality relative to others nearby (Komdeur 1992), and Halictus rubicundus sweat bees are eusocial when the climate is sufficiently warm (Field et al. 2010; Soro et al. 2010). Biotic sources of information might be even more important. For example, individuals might breed or help depending on their own nutritional, hormonal or immune state (e.g., Amdam et al. 2007), or their perception of the density of competitors. They might assess their parents' quality using cues, for example the size of the clutch in which they were reared. Alternatively, parents may produce signals with the express purpose of advertising their reproductive value to their offspring, as discussed in the next section.

The stepping-stone hypothesis (Figure 1) could be tested using comparative analysis. A candidate taxon would be bees, in which facultative and obligate helping have arisen multiple times (Schwarz et al. 2007). For example, I would predict that evolutionary transitions from solitary brood rearing to obligate sociality would be less common than from facultative to obligate sociality.

Sociality and fecundity signaling

Chemical signals associated with high reproductive value that induce helping appear ubiquitous in present-day social insects (e.g., Monnin 2006; Le Conte and Hefetz 2008; Heinze and d'Ettorre 2009; Holman 2012; Van Oystaeven et al. 2014). In bees, ants, wasps, and termites, queens produce chemicals that affect worker behavior and physiology, and in many cases, these chemicals are produced in particularly high quantities by especially fecund queens (e.g., D'Ettorre et al. 2004; Monnin 2006; Holman et al. 2010). Phylogenetic evidence suggests that these chemicals predate the evolution of eusociality in multiple lineages, suggesting that chemical cues of fecundity existed in solitary ancestral species (Van Oystaeyen et al. 2014). Therefore, prototypical workers may have had sufficient information to employ conditional helping strategies. Chemical signals produced by dominant breeders are also thought to inhibit subordinate reproduction in many cooperatively breeding mammals (e.g., Creel and MacDonald 1995; Saltzman et al. 2008; Holmes et al. 2009). Chemical signals of fecundity would also likely have been present in the solitary ancestors of mammalian cooperative breeders, because chemical signaling is widely used to identify fertile mates (Wyatt 2003). Cooption of sexual fertility signals as social signals might have occurred in many diverse social taxa.

There is also evidence that chemical signals of fecundity are unfakeable in social insects. In the ant *Lasius niger*, a chemical fecundity signal that sterilizes workers is affected by juvenile hormone, which also has strong effects on fecundity (Holman 2012). There is a genetic correlation between the signal and fecundity, suggesting queens could not easily evolve stronger signaling without also evolving higher fecundity (Holman et al. 2013). If chemical fecundity signals were also unfakeable in ancestral species, they could have provided prototypical workers with assurance that their mother was worth helping (see also Keller and Nonacs 1993; Heinze and d'Ettorre 2009).

Parental effects, conflict, and sociality

Following Wolf and Wade (2009), I define maternal and paternal effects as causal influences of parental genotype or phenotype on offspring phenotype. Model 1 showed that there are zones of conflict in which offspring benefit from dispersing to breed when they have high reproductive value, while mothers would benefit most if all first-clutch offspring stayed and helped. Mothers might then be selected to evolve a "selfish maternal effect" (Marshall and Uller 2007) that confers control over offspring reproductive value, improving the number of offspring produced at a cost to the fitness of the affected offspring.

As outlined below (and in the above discussion of queen pheromones that induce helping in social insects), maternal effects that induce helping in offspring appear to be common. I stress however that these interactions might sometimes be mutually beneficial, as illustrated by my models, and should not be assumed to represent conflict without additional evidence. This is true even for maternal effects that appear harmful to human observers. For example in queenless *Diacamma* ants, breeding females mutilate the wing buds of newly hatched females, permanently preventing them from becoming breeders (Baratte et al. 2006). Daughters acquiesce provided that the mutilator is mature and highly fertile; if she is not, they aggressively resist and seek to become a breeder themselves. This suggests that submitting to mutilation (the maternal effect) benefits individuals if the dominant is mature (Baratte et al. 2006) and suggests the involvement of honest signals of fecundity.

In cooperatively breeding mammals, dominant breeders sometimes use physical aggression to control the reproductive physiology of subordinates (Creel et al. 1992; Kutsukake and Clutton-Brock 2006; Young et al. 2006) and induce them to help (Reeve 1992). In harvester ants, queens control the caste of their offspring by differentially depositing hormones in their eggs (Schwander et al. 2008). Queens rear the first brood of offspring in wasps and sweat bees and can control offspring fecundity and caste by restricting food (O'Donnell 1998; Kapheim et al. 2011; Brand and Chapuisat 2012). Maternal effects also influence offspring development into winged and wingless forms in some insects (Braendle et al. 2006; Schwander et al. 2008), suggesting mothers can sometimes control dispersal ability. Conversely, in cooperatively breeding birds, there appears to be little evidence that parents attempt to lower offspring fecundity in order to receive more helpers (see Russell and Lummaa 2009), though they may skew the sex ratio toward the sex that provides help (Griffin et al. 2005).

In the present context, there may be interesting differences between maternal and paternal effects. In monogamous taxa, fathers and mothers should often have identical evolutionary interests regarding offspring help, and hence the model also predicts paternal effects on traits affecting offspring helping propensity. For other mating systems, the predicted parental effects may be more complex. For example under polyandry, fathers may favor dispersal in their offspring more than mothers, because the fathers are unrelated to some of the additional offspring that would be produced if their offspring stayed to help. Therefore under polyandry, maternal effects that increase helping rates seem more likely to evolve than paternal effects. This inter-parental conflict might even select for genomic imprinting of loci that affect helping and dispersal propensity (Queller 2003; Dobata and Tsuji 2012; Holman and Kokko 2014). I also note that the tendency of fathers to favor less helping and increased dispersal under polyandry adds another reason why monogamy favors the evolution of sociality (Boomsma 2007): under monogamy, both parents are more likely to be united in their desire to induce helping phenotypes in the offspring via parental effects. This mechanism seems most relevant to taxa in which males associate with their offspring and thus have more power to affect offspring phenotype, such as some social vertebrates, termites, and thrips, but not Hymenoptera.

CONCLUSIONS

Conditional helping strategies might evolve more easily than unconditional strategies. Therefore, taxa in which offspring have a reliable means of assessing their own fecundity and survival prospects, as well as the quality of their parents, may be more likely to evolve sociality. Facultative helping might act as a stepping-stone toward more advanced, obligate forms of helping. Additionally, parents are predicted to sometimes manipulate the information available to their offspring or to control offspring quality so as to make helping the best option, though there were many zones in which mothers and offspring both favor conditional helping. Therefore, maternal effects and signals that induce helping should not be assumed a priori to result from conflict. The model suggests that parental manipulation and dishonesty might promote eusociality more often than cause its collapse, not least because manipulated offspring have two routes to higher fitness: escaping the manipulation, or adapting to their new role as obligate helpers.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco. oxfordjournals.org/

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