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No Synergy Needed: Ecological Constraints Favor the Evolution of Eusociality

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ABSTRACT: In eusocial species, some individuals sacrifice their own reproduction for the benefit of others. It has been argued that the evolution of sterile helpers in eusocial insects requires synergistic efficiency gains through cooperation that are uncommon in cooperatively breeding vertebrates and that this precludes a universal ecological explanation of social systems with alloparental care. In contrast, using a model that incorporates realistic ecological mechanisms of population regulation, we show here that constraints on independent breeding (through nest-site limitation and dispersal mortality) eliminate any need for synergistic efficiency gains: sterile helpers may evolve even if they are relatively inefficient at rearing siblings, reducing their colony's per-capita productivity. Our approach connects research fields by using hypotheses developed for cooperative breeding to explain the evolution of eusociality. The results suggest that these hypotheses may apply more generally than previously thought.

Keywords: social evolution, altruism, helping, ecological constraints, evolutionary simulation.

Introduction

An apparent implication of the “struggle for existence” in nature is that organisms are predisposed to be selfish and fierce competitors. Nonetheless, highly social (eusocial) insect species exhibiting altruistic behavior have come to dominate many terrestrial ecosystems (Wilson 1990). Eusocial societies (*sensu* Crespi and Yanega 1995) consist of at least two castes of individuals that become irreversibly behaviorally distinct before reproductive maturity, with members of a less reproductive caste behaving altruistically toward a more reproductive caste. When eusociality evolves via the subsocial route, as considered in this article, the less reproductive caste originates from nondispersing offspring helping their mother. Eusociality is distinguished from cooperative breeding, which is defined as alloparental care without castes. The transition to eusociality has occurred repeatedly during the course of evolution (Crespi 1996), but its

underlying causes remain a subject of debate (Nowak et al. 2010; Abbot et al. 2011). Because sterile helpers, as found in eusocial insects, should generate benefits to their colony that outweigh their lack of own reproduction, explaining their evolution has been linked to the question (Queller and Strassmann 1998, p. 169) “how can an individual provide greater gains to a colony than to her own offspring, even though she carries out the same kinds of tasks in each case?” The suggested answers to this question invoke synergistic mechanisms by which colony members are more effective jointly than individually, such that their coordinated or complementary actions elevate colony productivity beyond the expectation of linear increase based on colony size. Two main mechanisms for creating synergy have been suggested. The “life insurance” mechanism assumes that, while n individuals may jointly produce n times as many offspring as any of them alone, the expected number of surviving offspring may increase more than n -fold if the colony ensures the survival of the dependent young even in the event of their mother's death (Gadagkar 1990). The “fortress defense” mechanism assumes that synergy arises in the context of agonistic interactions, where groups of individuals may jointly be able to defend a resource that they could not defend alone (Queller and Strassmann 1998). Since these mechanisms are distinct from each other and neither appears to apply to most social vertebrates, Queller and Strassmann (1998) concluded that the hope for a universal ecological explanation of cooperative social systems may be doomed. It has also been argued that strict monogamy, by ensuring that helpers are equally related to their siblings as they would be to their own offspring, is the only mating system that will make weak synergistic effects sufficient to select for sterile helpers, whereas other mating systems require larger and less plausible synergistic effects (Boomsma 2007; West and Gardner 2010). In contrast to these views, we show here that sterile helpers can evolve in the absence of synergy, defined here as any mechanism that would increase colony productivity beyond the expectation of linear increase based on (constant) colony size. Provided that ecological constraints strongly limit their op-

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opportunities for independent breeding, sterile helpers can evolve even if they are far less efficient than their mother at raising offspring, thus reducing their colony's per-capita productivity.

Ecological constraints that have been suggested to favor cooperative breeding include mortality faced by dispersing individuals and scarcity of available nest sites (or territories; Emlen 1982). To evaluate the impact of these factors on the evolution of eusociality, we use a population dynamics model that quantifies the conditions under which a sterile helper caste can evolve, and subsequently be stable, from a solitary ancestral species. We vary the mortality faced by dispersing individuals under two modes of population regulation, which for simplicity we model as alternatives: (1) "fecundity limitation," where fecundity is density dependent because of competition for biotic resources that can be transformed into offspring, and (2) "nest-site limitation," where the transition toward becoming a breeder is density dependent because of competition for nest sites or territories. We also vary our assumptions regarding the genetic system (haplodiploidy vs. diplodiploidy), the mating system (monandry vs. biandry), and the sex-specific predisposition for helping.

Methods

We use a modeling approach that tracks the demographic and genotypic composition of a population over ecological and evolutionary time, rather than considering what is optimal from the perspective of some focal individual or colony (Nowak et al. 2010; Fromhage and Kokko 2011). Our model is designed to reflect the empirical viewpoint that transitions to eusociality have occurred overwhelmingly via the subsocial route (i.e., parents and offspring remained in association through nondispersal of offspring; Bourke 2011), from monogamous ancestors (Hughes et al. 2008; Boomsma 2009; Cornwallis et al. 2010) with some degree of maternal care (progressive provisioning; Andersson 1984). However, we consider both monandry and biandry to compare the effect of the mating system to those of other potential promoters of social behavior. We do not aim to model any particular species or to cover the full diversity of ecological and life-history details of social insects. Instead, we assume a simplistic life cycle that allows us to focus on the processes we consider essential to the point we wish to make.

Consider a class-structured, infinite, panmictic population, where females of the breeder class rear their offspring and, once matured, offspring leave their natal nest to join the classes of dispersed males and dispersed females. Dispersed males remain in this class, continuously searching for mating opportunities, until they die. Dispersed females join the breeder class, thus completing the life cycle, when

they find a mate and a nest site. We call this a solitary life cycle. For simplicity, we consider a single locus with two alleles affecting offspring dispersal: the wild-type (solitary) allele a and the mutant (eusocial) allele A . This single mutation can be thought of as a switch that can suppress a preexisting behavior, such as dispersal from the nest. Such a phenotypic effect is consistent with findings that some known genes (or small ensembles of genes) can cause major changes in social behavior by silencing mutations in preexisting traits (Ross and Keller 1998; Abouheif and Wray 2002). If A is expressed, the carrier stays in her natal nest as a sterile helper and helps her mother to rear more offspring. We consider that expression of A may be sex limited, so that only females may become helpers. Colonies of size n have $(n - 1)$ helpers, since every colony has to have a breeder. We assume that beyond some maximum colony size N there is no space for further helpers, leading to unconditional dispersal of offspring produced in size N colonies. Depending on the dominance/recessiveness assumption (table A5; tables A1–A11 available online), offspring who carry allele A stay as helpers in colonies of size $n < N$. Theoretically, N can be arbitrarily large. Biologically, however, since we are interested in the origin of eusociality, we choose N to be a relatively small number, and we are not focusing on how maximum colony size can itself be subject to selection when sociality has already been initiated. To reflect empirical findings suggesting that helpers can increase both colony productivity and survival (Hogendoorn and Zammit 2001; Langer et al. 2004; Zammit et al. 2008; Brand and Chapuisat 2014), we use functions $f(n)$ and $m(n)$ to define the breeder's fecundity and mortality, respectively, in a nest of size n as

$$f(n) = f_0[1 + b(n - 1)] \quad (1)$$

and

$$m(n) = \frac{m_0}{1 + \alpha(n - 1)}, \quad (2)$$

where the parameters f_0 and m_0 are a breeder's intrinsic fecundity and mortality rate, respectively, in the absence of helpers and density dependence, and b and α are the increments to a breeder's fecundity and life expectancy, respectively, caused by adding one more helper to her nest. The primary sex ratio is even, with equation (1) describing production of each offspring sex. We distinguish between K colony types (based on genotype combinations of breeders and their mates; tables A1–A4) and N colony sizes, denoting as $X_{k,n}$ the density of colonies of type k and size n . Offspring with genotype π , born in a colony of size n , become helpers with probability $q_{\pi,n}$ (table A5). Thus, the probability of any given offspring becoming a helper in a colony of type k and size n is given by $\varphi_{k,n} = \sum_{\pi} \omega_{\pi,k} q_{\pi,n}$, where $\omega_{\pi,k}$ is the proportion of offspring (of a given sex) be-

ing born with genotype π (tables A1–A4) and the summation is over all offspring genotypes. The dynamics of the population can be described by the following system of ordinary differential equations. The density x_π of unmated dispersed females with genotype π changes with time t as

$$\frac{dx_\pi}{dt} = \sum_{k=1}^K \sum_{n=1}^N [f(n)X_{k,n}(1 - q_{\pi,n})\omega_{\pi,k}] - x_\pi \left(m_x + \beta \sum_{\pi} y_\pi \right) \quad (3)$$

(see table A6 for more details on the terms). Here, the summation covers colonies of any type k and size n from which unmated females with genotype π disperse at the rate given in square brackets. The negative term to the right of the square brackets represents dispersed females who either die (at rate m_x) or become breeders (at rate $\beta \sum_{\pi} y_\pi$). Here, β is a parameter controlling mate search efficiency and y_π is the density of potential mates of any genotype π . To facilitate comparison between mating systems, we assume that monandry and biandry do not differ in the rate at which dispersed females establish colonies. Biologically, this can be interpreted as males occurring in aggregations, such that a female always finds a second male once she finds a first. The density of dispersed males of any genotype π changes over time, according to similar influx and decay rates, as

$$\frac{dy_\pi}{dt} = \sum_{k=1}^K \sum_{n=1}^N [f(n)X_{k,n}(1 - q_{\pi,n})\omega_{\pi,k}] - y_\pi m_y \quad (4)$$

(see table A7 for more details on the terms), where m_y is the mortality rate of males. We assume that males can mate multiple times, but their matings are limited by their short life span. The density of colonies of type k and size $n = 1$ changes over time as

$$\frac{dX_{k,1}}{dt} = \beta\chi_k - [\varphi_{k,1}f(1) + m(1)]X_{k,1} + m_h X_{k,2} \quad (5)$$

(see table A8 for more details on the terms), where m_h is the mortality rate of helpers. Here, χ_k is the number of matings giving rise to colonies of type k (see tables A1–A4), and hence the term $\beta\chi_k$ is a measure of successful matings giving rise to colonies of type k . This formulation allows two interpretations. First, the transition toward becoming a breeder may be instantaneous upon mating, implying either that nest sites are abundant or that mating takes place at empty nest sites. Alternatively, $\beta\chi_k$ can be interpreted as an average rate at which dispersed females (who may or may not have mated but have yet to find a nest site) become breeders. In any case, the proportionality between search efficiency β and the transition rate toward the breeder class offers a convenient way of modeling nest-site limitation (see below). The terms in square brackets represent colonies that leave size category $n = 1$ because of colony growth or

breeder death, and the rightmost term represents colonies that enter this size category through death of a helper in a colony of size $n = 2$. Following similar logic, the density of type k colonies of intermediate size (where $1 < n < N$) changes as

$$\frac{dX_{k,n}}{dt} = \varphi_{k,n-1}f(n-1)X_{k,n-1} - [\varphi_{k,n}f(n) + m(n) + (n-1)m_h]X_{k,n} + nm_h X_{k,n+1} \quad (6)$$

(see table A9 for more details on the terms), and the density of type k colonies of maximum size (where $n = N$) changes as

$$\frac{dX_{k,N}}{dt} = \varphi_{k,N-1}f(N-1)X_{k,N-1} - [m(N) + (N-1)m_h]X_{k,N} \quad (7)$$

(see table A10 for more details on the terms). To apply the concept of density dependence to an infinite population, we envisage a population inhabiting an infinite area, in which ecological processes depend on the number of entities present per area unit (i.e., density). Specifically, we model density dependence by letting vital rates depend on density D_i and carrying capacity C_i as

$$\phi(D_i, C_i) = \begin{cases} 1 - \frac{D_i}{C_i} & D_i \leq C_i \\ 0 & D_i > C_i \end{cases} \quad (8)$$

In order to model fecundity limitation, we limit breeders' fecundity by replacing $f(n)$ with $\phi(D_T, C_T)f(n)$, where $D_T = \sum_n \sum_k nX_{k,n} + \sum_\pi (x_\pi + y_\pi)$ is total population density and C_T is its carrying capacity. Alternatively, to model nest-site limitation, we replace β with $\phi(D_B, C_B)\beta$, where $D_B = \sum_n \sum_k X_{k,n}$ is breeder density and C_B is its carrying capacity. This substitution gradually reduces the rate of colony foundation toward 0, as empty nest sites become rare. It is worth noting that, under nest-site limitation, competition between dispersed females implies lower per-capita chances of colony foundation when there are more competitors. Our model accounts for this via a series of feedbacks: other things being equal, increasing the density of dispersed females in our model will increase population-wide colony foundation in the short term, which in turn reduces nest-site availability (i.e., the difference $C_B - D_B$), which in turn reduces the per-capita rate of colony foundation.

We implement this model computationally by projecting the population toward its asymptotic state, using the Euler approximation. We focus on stable asymptotic states rather than initial transient dynamics, because we are interested in long-term evolutionary outcomes. However,

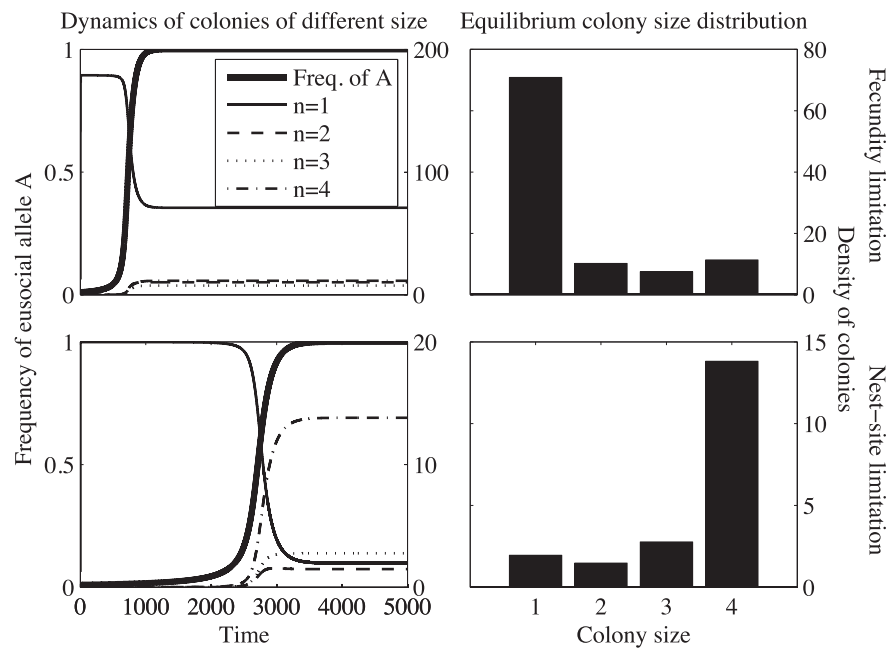


Figure 1: Dynamics of colonies of different size and the respective equilibrium colony size distributions when a recessive eusocial allele *A* invades: frequency of eusocial allele *A* (bold solid line), colonies of size $n = 1$ (solid line), colonies of size $n = 2$ (dashed line), colonies of size $n = 3$ (dotted line), colonies of size $n = 4$ (dash-dotted line). The helper phenotype is expressed only in females. Parameter values: $b = 5$ (for the fecundity limitation case): helpers are relatively efficient at raising offspring; $b = 0.5$ (for the nest-site limitation case): helpers are relatively inefficient at raising offspring; $\alpha = 0$, $N = 4$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. Initial condition: the frequency of allele *A* is 1%.

we provide some examples of initial transient dynamics of colonies of different size, when eusocial allele *A* invades (fig. 1).

Results

To show under what conditions eusociality is predicted to evolve, we plot evolutionary outcomes in parameter space. First we assume that the eusocial allele *A* is initially rare; then we reverse this situation and assume that the eusocial allele is initially common. In this way, we account for both invasion and stability of the eusocial strategy. The model allows us to distinguish three areas of parameter space: (1) a “eusocial area,” where the eusocial allele spreads to fixation for any initial condition, (2) a “mixed area,” where either allele spreads if rare, leading to stable polymorphism, and (3) a “solitary area,” where the solitary allele spreads to fixation for any initial condition.

Nest-site limitation greatly broadens the conditions of social benefits under which a sterile helper caste can evolve and be stable (figs. 2, 3). Compared to the effect of nest-site limitation, the qualitatively similar effects of haplodiploidy and monandry are of much smaller magnitude (figs. 2,

B5; figs. B1–B10 available online). Under fecundity limitation, many colonies fail to reach the size at which offspring of any genotype disperse (fig. 1). We find the following interacting effects between life-history traits and density-dependence modes: high intrinsic fecundity promotes eusociality under nest-site limitation but not under fecundity limitation (fig. 3); conversely, high mortality of dispersing individuals (m_x and m_y) and low search efficiency β promote eusociality under fecundity limitation (fig. 4) but not under nest-site limitation (fig. B4).

Our definition of synergy requires that a colony held constant at size n obtains more than n times the lifetime reproductive success of a solitary breeder; formally, $f(n)/m(n) > nf_0/m_0$. Expressed in terms of equations (1) and (2), this can be written as $\alpha + b + \alpha b(n - 1) > 1$, which simplifies to $b > 1$ in the simplest case, where helpers affect only fecundity but not longevity (i.e., $\alpha = 0$), and to $\alpha > 1$ if helpers affect only longevity but not fecundity (i.e., $b = 0$). If helpers elevate both breeder fecundity and longevity, the interaction term is positive ($\alpha b(n - 1) > 0$), and it increases with the number of helpers present in a colony. Under both density-dependence modes, there are parameter combinations where eusociality evolves even when

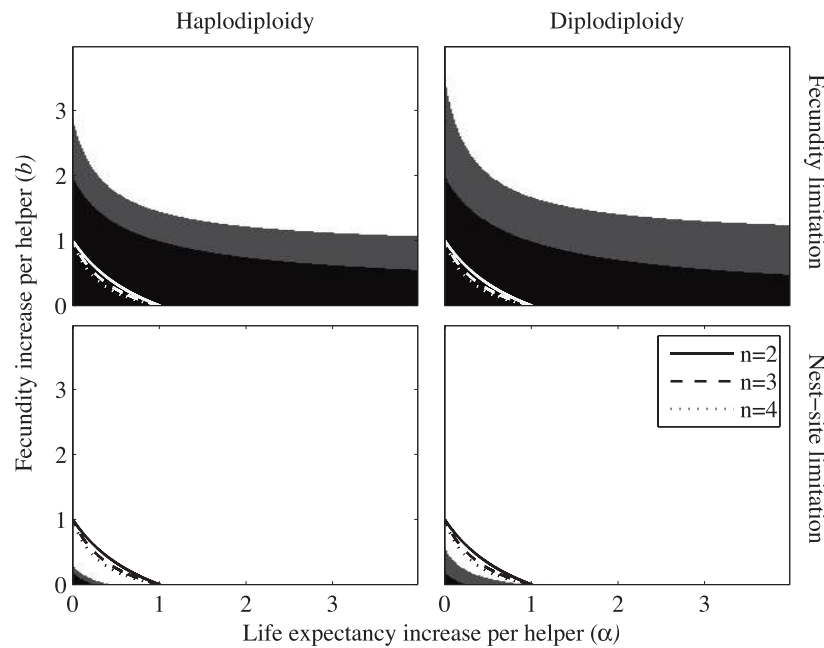


Figure 2: Evolution and stability of a recessive eusocial allele A in social benefits parameter space (b ; α) under monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. Initial conditions: (1) the frequency of allele A is 1%; (2) the frequency of allele A is 99%. The lines satisfy the expression $f(n)/m(n) = nf_0/m_0$ for $n = 2, 3, 4$, such that synergy exists above the line for colony size n .

helpers are much less efficient than their mother at rearing offspring ($b < 1$ and $\alpha = 0$), that is, in the absence of synergy (figs. 1–4). Note that eusociality can evolve even when helpers increase only breeder longevity (see the region where $\alpha > 0$ and $b = 0$ in fig. 2), in contrast to a result presented by Nowak et al. (2010). These results are robust regarding the dominance/recessiveness assumption of the eusocial allele (figs. B1–B3, B6) as well as regarding the assumption about sex-limited expression of the helper phenotype (figs. B7, B8). They are also robust to limiting the number of helpers to one per colony (i.e., $N = 2$), an assumption that excludes any cascading effects of helpers producing more helpers, which produce more helpers, and so on (figs. B9, B10).

Next, we analyze the mechanisms behind these numerical results. A comprehensive analytic solution is beyond our reach because selection at the focal locus depends on colony dynamics in complicated ways. (Note that relatedness at the focal locus between a helper and its dispersing siblings does not follow simple pedigree relations, because the eusocial allele affects dispersal.) Nevertheless, we can gain insight into the link between ecology and selection on the basis of the heuristic principle that, other things being equal, selection for helping will be stronger when more siblings are raised per helper. For simplicity, we focus on the case where helpers provide social benefits in terms of

fecundity ($b > 0$) but not longevity ($\alpha = 0$; the argument can also be extended for $\alpha > 0$).

Consider a helper who raises siblings at b times the rate at which its mother could raise offspring alone. From equation (1) and the expected duration $1/(m_0 + m_h)$ while both helper and mother remain alive, this amounts to B additional siblings raised during the helper's lifetime, where $B = 2bf_0\phi/(m_0 + m_h)$ under fecundity limitation and $B = 2bf_0/(m_0 + m_h)$ under nest-site limitation. These expressions for B illustrate several points. (1) Fecundity limitation reduces B , thus weakening selection for helping, because $\phi < 1$ (see eq. [8]). (2) Under nest-site limitation, higher intrinsic fecundity f_0 increases B . Under fecundity limitation, however, higher f_0 also has a counteracting effect, namely, increasing population density D_T , which lowers ϕ . (3) Dispersal mortality does not affect B under nest-site limitation. Under fecundity limitation, however, increase in dispersal mortality and/or decrease in search efficiency increases ϕ , and hence B , via its negative effect on population density D_T . (4) Under nest-site limitation, even relatively inefficient helpers (i.e., with $1 > b > 0$) may raise many siblings, provided that intrinsic fecundity f_0 is sufficiently high.

It is interesting to note how B relates to breeders' reproductive value in an initially solitary population. Demographic equilibrium implies that each breeder produces,

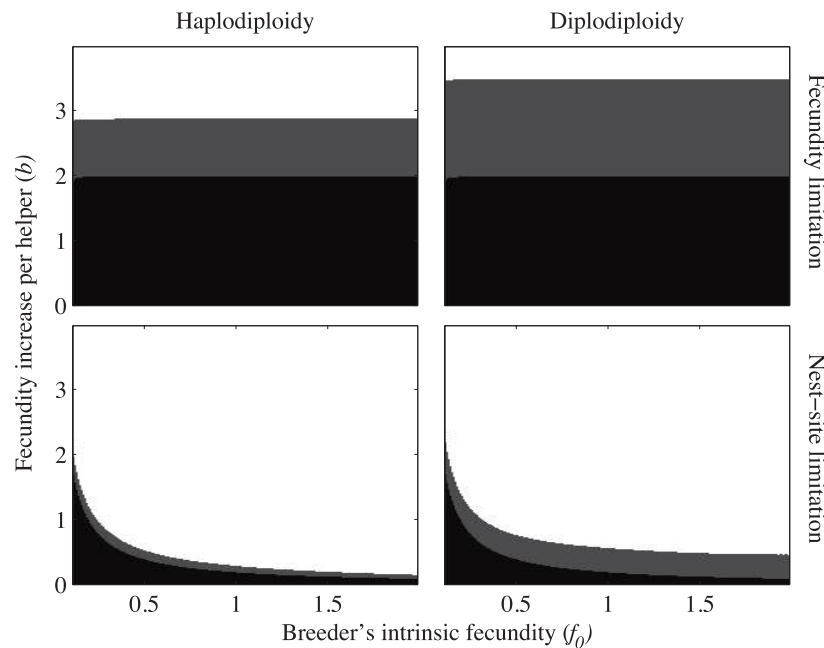


Figure 3: Evolution and stability of a recessive eusocial allele A in parameter space $(b; f_0)$ under monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $\alpha = 0$, $C_T = 400$, $C_B = 20$. Initial conditions: (1) the frequency of allele A is 1%; (2) the frequency of allele A is 99%.

on average, exactly one new breeder during its lifetime; otherwise the population would grow or shrink. This implies that dispersing daughters become breeders with probability $1/d$, where d is the expected number of daughters produced during a breeder's lifetime. Dispersing daughters' reproductive value (V_d), expressed in terms of breeders' reproductive value (V_b), is therefore $V_d = (1/d)V_b$. Setting $V_d = 1$ by convention, this yields $V_b = d$. Calculat-

ing d as the product of breeders' life expectancy ($1/m_0$) and rate of producing daughters, breeders' reproductive value is $V_b = f_0\phi/m_0$ under fecundity limitation and $V_b = f_0/m_0$ under nest-site limitation. Comparing the expressions for V_b and B reveals that any parameter that affects V_b also affects B in the same direction. In other words, helpers of given efficiency (in terms of b) can expect to raise more siblings in ecological settings in which breeders have high

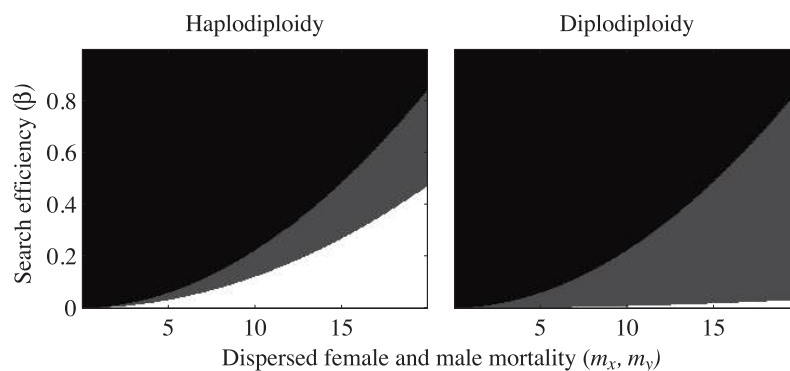


Figure 4: Evolution and stability of a recessive eusocial allele A in parameter space $(\beta; (m_x, m_y))$ under fecundity limitation and monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 100$, $m_0 = m_h = 0.1$, $b = 0.5$, $\alpha = 0$, $C_T = 400$. Initial conditions: (1) the frequency of allele A is 1%; (2) the frequency of allele A is 99%.

reproductive value. Furthermore, since there is no limiting term ϕ in the reproductive value of breeders under nest-site limitation, the difference in reproductive value between breeders and dispersers can be much larger in ecological settings where nest-site limitation is the main constraint on population growth.

Discussion

Our model shows that ecological constraints can strongly favor the evolution of eusociality. Intuitively, this can be explained as follows. If empty nest sites are rare, dispersing daughters have a low chance of becoming breeders, especially when they are numerous because of high fecundity. Low chances of independent breeding imply that daughters have low reproductive value compared to their mothers. In this situation, even a small proportional increment made to a mother's fecundity can outweigh a daughter's low chance of own reproduction, meaning that helping need not be very efficient in order to evolve. A similar argument holds if dispersing daughters have low chances of independent breeding for other reasons, such as high dispersal mortality (fig. 4). This result was partly anticipated by Queller (1989), on the basis of a model that did not include population regulation but instead specified a priori a focal individual's probability s of raising independent offspring (see app. C; apps. A–D available online). He concluded that, by choosing to help, the individual can raise brood sooner and can therefore shorten the period in which its own death would result in reproductive failure. Put another way, his model suggests that, when given a choice between raising siblings or accepting probability $s < 1$ of raising the same number of (equally valuable) offspring, the individual should choose the former option. However, while Queller defined s as the survival probability between egg laying and offspring independence, in the present context it is more pertinent to define s as a focal individual's probability of raising independent offspring if it attempts to disperse, accounting for any risks between dispersal and the onset of reproduction. We elaborate below how Queller's perspective complements our insights regarding the link between population regulation and selection for helping.

Existing models of social evolution with population regulation have assumed either nest-site limitation (Lehmann et al. 2008; Nonacs 2011; McLeod and Wild 2013) or fecundity limitation (Nowak et al. 2010; Fromhage and Kokko 2011), but we are aware of only one model that has attempted a comparison between these two, that of Pen and Weissing (2000). Surprisingly, Pen and Weissing (2000) came to the opposite conclusion that, in the absence of nest (or territory) inheritance, ecological constraints are irrelevant for the evolution of helping. This apparent con-

tradiction with our results stems from their implicit assumption (see app. D) that the number of siblings raised per helper is independent of ecological conditions (density dependence) and species-specific characteristics (intrinsic fecundity). We find this assumption potentially misleading, for the following reason. In species in a given ecological setting where unaided breeders can rear (say) 0.5 offspring per time unit, to rear one additional sibling per time unit a helper would need to be twice as efficient as her mother, implying synergistic interactions of improbable magnitude. Compared to this, in species where unaided breeders rear 10 offspring per time unit, the same absolute increment of one extra sibling seems trivial and could be achieved by a much less efficient helper. To avoid this problem and to make species comparable despite ecological differences, here we describe brood-rearing efficiency of helpers in relation to that of their mothers. In appendix D, we show that an accordingly modified version of Pen and Weissing's model yields results consistent with ours. Perhaps surprisingly, as recognized by Pen and Weissing (2000), ecological constraints do not affect a dispersing offspring's expected reproductive success, because "the smaller the probability that a disperser ever obtains a territory, the larger must be the reward for those that eventually do obtain a territory, because fewer individuals will be the progenitors of the next generation" (p. 2415). Even so, ecological constraints affect selection for helping through their effect on fecundity, which determines how many siblings can be reared by a helper of given efficiency. If dispersers have low chances of becoming breeders ($s \ll 1$), population stability requires that breeders raise many offspring, which occurs under conditions where helpers can also rear many siblings with relative ease (see above). This allows helpers to outweigh their lack of own reproduction, or, paraphrasing Haldane (1955), to "save" enough siblings to give up their own life. These considerations are consistent with, and complementary to, Queller's insight of how low s favors the evolution of helping.

Here we have modeled eusociality without the possibility of nest inheritance by helpers. While we recognize that nest inheritance can provide a strong additional incentive for philopatry (Pen and Weissing 2000), we have excluded it here because it is not compatible with caste specialization involving helper sterility. By focusing on helping that is not selfish reproductive queuing in disguise (or caused by manipulative mothers temporarily getting the upper hand in a parent-offspring conflict; Craig 1979), we aim to make our model more suitable for predicting long-term evolutionary trends toward advanced eusociality.

It has long been hypothesized that nest-site (or territory) limitation can promote temporary helping behavior in cooperatively breeding vertebrates, such as birds (Koenig and Dickinson 2004), voles (Lucia et al. 2008), salamanders

(Harris et al. 1995), and ciclids (Bergmüller et al. 2005; Stiver et al. 2006; Heg et al. 2011), and that high dispersal mortality may have a similar effect (Emlen 1982). Although temporary helping may be less costly than permanent commitment to a helper caste, our study supports earlier verbal arguments (Andersson 1984; Keller 1995) that both phenomena could nevertheless be shaped by similar selective forces. Consistent with our results, there is much evidence that dispersing females' probability of successfully starting a new nest is extremely low in ants, bees, and termites (Hölldobler and Wilson 1990, 2009; Thorne 1997). While the precise mechanisms responsible for this are notoriously hard to quantify (Keller 1995), scarcity of suitable nest sites probably plays a major role in this context, at least in cavity-dwelling species that are incapable of constructing their own nests (Foitzik and Heinze 1998; Langer et al. 2004; Dew et al. 2012; Yip et al. 2012) and in insects that build energetically costly nests and therefore prefer to reuse old nests (Field et al. 1998). It is unclear, however, to what extent these contemporary findings are representative of ancestral conditions. Comparative analyses of estimated ancestral states are necessary to test our prediction that eusociality should evolve more readily in lineages characterized by low success of independent breeding attempts (because of high dispersal mortality and/or nest-site limitation combined with high fecundity).

The role of haplodiploidy and frequency-dependent selection in our model is also worth mentioning. The positive effect of haplodiploidy on eusociality is mediated by positive assortment between cooperative genotypes, the underlying mechanism of which is explained by Fromhage and Kokko (2011). We have assumed that expression of helper phenotypes depends on colony size, such that newly produced offspring of any genotype will disperse while a colony is at its maximum size. Dispersers from such colonies therefore carry an unbiased sample of their founders' alleles, whereas dispersers from smaller colonies carry a sample biased toward solitary genotypes. This bias against the eusocial allele is less prevalent if colonies reach their maximum size quickly, as happens under haplodiploidy because of positive assortment of cooperative genotypes (Fromhage and Kokko 2011). Similar effects of haplodiploidy are absent in models that do not include colony dynamics (Gardner et al. 2012; Rautiala et al. 2014). The stable coexistence of both eusocial and solitary alleles in a mixed area of parameter space indicates negative frequency-dependent selection. This arises by a "free-rider" effect at the allelic level, whereby rare solitary alleles increasingly participate in obtaining social benefits when they co-occur with eusocial alleles in the same colony.

A common formulation of Hamilton's rule, $r_B B > r_C C$, states that an altruistic behavior is favored by selection when the number of relatives gained (B ; here, expected ad-

ditional siblings), weighted by the actor's relatedness to them (r_B), exceeds the number of relatives lost (C ; here, expected own offspring), weighted by the actor's relatedness to them (r_C). This formulation assumes that relatives gained and relatives lost have the same reproductive value, as would be the case if they were otherwise indistinguishable offspring who were raised either by their sister or by their mother, respectively. In this context it has been argued that at the origin of eusociality, before the evolution of specialized adaptations for group living, the ratio B/C cannot be expected to greatly exceed 1, because, "for example, feeding a sibling is unlikely to be hugely more beneficial than feeding an offspring by the same amount" (West and Gardner 2010, p. 1342). This view has been used to support the claim that origins of eusociality must pass through a narrow "monogamy window," where potential helpers' equal relatedness to their offspring (r_C) and their (full) siblings (r_B) is necessary to fulfill Hamilton's rule despite B/C being only marginally greater than 1 (Boomsma 2007, 2009, 2013). However, in the light of Queller's (1989) model as well as our own, we argue that ecological constraints on independent breeding make $B/C \gg 1$ plausible even at the origin of eusociality, if any relatives lost as a consequence of helping were only a remote possibility in the first place (limiting the expected number of own offspring, C , in Hamilton's rule), whereas relatives gained (expected additional siblings, represented by B) are an immediate possibility. This eliminates the need to postulate mechanisms at the origin of eusociality by which helpers could increase the per-capita productivity of their colony. This argument is consistent with Queller's (1989) model, by setting $r = r^*$, $b = b^*$, and $s \ll s^*$ in his equation (2) (app. C) and adapting the notation $s^* b^* = B$ and $sb = C$. Doing so also clarifies which factors are incorporated above in the coefficients C (namely, survival during dispersal, probability of successful nest establishment, and offspring produced over the life time of a breeder) and B (a helper's survival until raising the first sibling and the expected number of siblings raised from that point onward).

Since we have modeled the evolution of eusociality from a solitary life cycle, our model does not predict the taxonomic distribution of eusociality, as compared to that of cooperative breeding. For example, our model does not explain why birds have repeatedly evolved cooperative breeding but never eusociality, whereas both cooperative breeding and eusociality are well represented in insects. In this respect, we agree with earlier suggestions that remating promiscuity may preclude eusociality in some systems by eroding within-nest relatedness over time, to the disadvantage of permanently committed helpers (Boomsma 2007, 2009, 2013). In addition, any trade-offs between behavioral flexibility and other aspects of helper performance might well operate somewhat differently across taxa.

One limitation of our model is that it assumes a nonseasonal environment, thus excluding any effects that a bivoltine life history might have on the evolution of eusociality in temperate climates (Seger 1983; Stubblefield and Charnov 1986). Nevertheless, we expect that processes similar to those described in our model may operate also in temperate climates. For example, even if nest sites are easy to find for the first swarming insects in spring, any potential dispersers of their offspring generation will still face a situation where many nest sites are already occupied, which may limit their chances of independent breeding. It is also worth noting that Queller's (1989) model, whose results are consistent with ours, made no particular assumption about seasonality.

In conclusion, we have identified two mechanisms, nest-site limitation and high dispersal mortality, that can impose ecological constraints favoring the evolution of eusociality. Both mechanisms work by creating a mother-daughter asymmetry in reproductive value, whereby helping daughters have little to lose compared to the potential indirect benefits available to them through helping. Both mechanisms also allow breeders to express high fecundity, making it tempting to speculate that high fecundity per se could be regarded as a promoter of eusociality. It is worth noting, however, that high fecundity will not create a mother-daughter asymmetry in reproductive value unless mothers also possess some advantage over their daughters, for example, in terms of resource possession or life expectancy. We argue that density-regulation mechanisms, acting in concert with life-history traits and relatedness-enhancing mechanisms, are key to understanding the origin of altruistic behavior.

We end by quoting Dawkins (1989, p. 295): "Your [monogamous] mother is as genetically valuable to you as an identical twin, or as yourself. Think of yourself as an offspring-producing machine. Then your monogamous mother is a (full) sibling-producing machine, and full siblings are as genetically valuable to you as your own offspring. Of course, this neglects all kinds of practical considerations. For instance, your mother is older than you, though whether this makes her a better or worse bet for future reproduction than you yourself depends on particular circumstances." Here we have highlighted circumstances that make mothers a "better bet" for future reproduction, predisposing them as recipients of their offspring's help.

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