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The risk-return trade-off between solitary and eusocial reproduction

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Abstract

Social insect colonies can be seen as a distinct form of biological organisation because they function as superorganisms. Understanding how natural selection acts on the emergence and maintenance of these colonies remains a major question in evolutionary biology and ecology. Here, we explore this by using multi-type branching processes to calculate the basic reproductive ratios and the extinction probabilities for solitary vs. eusocial reproductive strategies. We find that eusociality, albeit being hugely successful once established, is generally less stable than solitary reproduction unless large demographic advantages of eusociality arise for small colony sizes. We also demonstrate how such demographic constraints can be overcome by the presence of ecological niches that strongly favour eusociality. Our results characterise the risk-return trade-offs between solitary and eusocial reproduction, and help to explain why eusociality is taxonomically rare: eusociality is a high-risk, high-reward strategy, whereas solitary reproduction is more conservative.

Introduction

Eusocial behaviour occurs when individuals reduce their lifetime reproduction to help raise their siblings

(Wilson 1971). Eusocial colonies comprise two castes: one or a few reproductive individuals and a (mostly) non-reproductive, worker caste. These societies thus contain a reproductive division of labour where some individuals reproduce and others forage and provision the young (Hölldobler & Wilson 1990, 2009).

Insect species that have reached this remarkable level of social complexity have proven to be vastly successful in nature, and are thought to comprise nearly 50% of the world's insect biomass (Wilson 1971). Despite the apparent success of this strategy, only 2% of described insect species are eusocial. Here, we use a mathematical approach to improve our understanding of why such a successful life history strategy so rarely evolves.

Eusociality has originated only 12–15 times within the insects, and perhaps 20–25 times within the entire animal kingdom (Wilson 1971). Most of these evolutionary origins have occurred in the order Hymenoptera (the bees, ants and wasps) where there has been a single origin in the ants (Wilson 1971), 2–3 origins in the wasps (Hines et al. 2007), and 4–5 origins in the bees (Cardinal & Danforth 2011; Gibbs et al. 2012). As a result, much focus has been placed on understanding the factors favouring or disfavouring the evolution of eusociality within the social insects (Andersson 1984; Crozier 2008).

There have been a number of attempts to identify some of the key ecological factors associated with the evolution of eusociality. Several precursors for the origins of eusociality have been proposed based on comparative analyses among social insect species – primarily the feeding and defense of offspring within a nest (Andersson 1984). These behaviours are also frequently associated with a subsocial life history, where parents and offspring overlap and occupy the nest simultaneously (Michener 1974; Gadagkar 1990).

In contrast to the relatively few origins of eusociality, losses or reversions back to solitary behaviour appear to be much more common (a very rough estimate indicates a minimum of nine losses within the bees – nearly twice the number of origins; see Wcislo & Danforth 1997; Cardinal & Danforth 2011). This suggests that the evolution of eusociality is difficult to both achieve and maintain. However, some taxa have nonetheless evolved highly complex eusocial behaviours where caste differentiation is determined during development and individuals no longer retain the ability to perform all of the tasks required to reproduce on their own (obligate eusociality) (Batra 1966; Crespi & Yanega 1995). In these cases, no reversions to solitary behaviour have been observed, suggesting that these species have crossed a 'point of no return' where reversion to a solitary life history is no longer possible (Wilson & Hölldobler 2005).

Here we calculate the emergence and extinction probabilities of eusocial vs. solitary reproductive strategies. We use the haploid version of a simple model of eusociality from Nowak et al. (2010). In our model, solitary females produce offspring that leave the nest to reproduce individually, while eusocial females produce a mix of offspring that remain in the natal nest and others that disperse to establish new, eusocial nests. Those offspring that stay augment the size of the colony. We assume that the key reproductive parameters (oviposition rate, successful raising of the young, and expected lifespan of reproductive females) increase with colony size.

Our focus is not on explaining the origins of eusociality, which has already been modelled in Nowak et al. (2010). Instead, we attempt to explain the phylogenetic rarity of this trait by calculating the extinction probabilities of solitary vs. eusocial reproduction in a stochastic model based on the theory of branching processes (Harris 2002). We calculate the probability that a lineage starting from a single, solitary individual faces extinction, and we compare this with the extinction probability of a lineage that starts with a single, eusocial individual.

Intuitively, the eusocial lifestyle appears to be risky because the production of non-reproductive workers

before reproductive offspring results in a delayed reproductive payoff. Furthermore, there is an opportunity cost associated with the non-reproductive offspring that remain in the nest instead of establishing their own lineages. It is largely unknown whether this initial risk associated with eusocial reproduction can later be compensated with higher reproductive rewards. To address this question, we perform a comprehensive assessment of the risks of population extinction for solitary vs. eusocial reproductive life histories. We explicitly take into account the demographic and ecological factors involved in this process.

We calculate and compare the population extinction probabilities and basic reproductive ratios for solitary and eusocial life histories. We show that eusociality is typically a riskier strategy than solitary reproduction unless significant eusocial benefits arise for small colony sizes. We find that, when it is available, obligate eusociality is a more successful strategy than facultative eusociality. These results suggest that the evolution of eusociality is difficult because it requires a high reproductive payoff generated by the immediate production of a small number of workers. We also extend our model to study population competition dynamics between solitary and eusocial lineages under different ecological contexts, and we quantify the role that ecological niches play in facilitating the emergence and maintenance of eusociality. Altogether, these findings can explain both why origins of eusociality are rare but hugely successful and why reversions to solitary behaviour also occur.

Material and Methods

Following the deterministic model of eusociality studied in Nowak *et al.* (2010), here we consider a corresponding stochastic version for the case of asexual reproduction. This model-based approach can be used to evaluate the probability that a single, eusocial foundress in a population of solitary females (e.g. a eusocial mutant) will successfully give rise to a eusocial lineage. We explore this by varying three main parameters: birth rate, b , death rate, d and offspring dispersal probability, q . We relate these variables in two major ways: through the basic reproductive ratio, R_0 , and the extinction probability, p , of a given lineage. These parameters are described in detail below (Table S1).

A solitary individual reproduces at rate b_0 , and dies at rate d_0 . Each offspring of a eusocial queen stays with their mother with probability q ; otherwise she leaves to establish another new colony with probability $1 - q$. A eusocial queen with colony size i reproduces at rate b_i and dies at rate d_i . b_i and d_i are sigmoid functions of the colony size i with the inflection point being at the eusocial threshold m . For simplicity, let us start with assuming b_i and d_i to be step functions of i : for $i < m$, $b_i = b_0$ and $d_i = d_0$; for $i \geq m$, $b_i = b$ and $d_i = d$. Thus, eusociality confers an enhanced reproductive rate and a reduced death rate for a queen whose colony size reaches the eusocial threshold ($i \geq m$): $b > b_0$ and $d < d_0$ (henceforth referred to as the 'eusocial advantage'). Later on, we will verify the robustness of our derived results using more general sigmoid functions (online appendix).

A single foundress can either die or successfully start a lineage by giving birth to another reproductive individual. Each queen reproduces independently of one another. In the light of this, we can use a multi-type branching process to calculate the ultimate *extinction probability*, p , of the lineage initiated by a single founding female. This value represents the chance that a given lineage founded by a single female will go extinct over time $t \rightarrow \infty$. The converse of this is the *emergence probability*, $1 - p$, or the chance that a lineage founded by a single female will persist over time $t \rightarrow \infty$.

Since the daughters who stay with their mother assist to perform tasks for the colony, the whole colony

(consisting of a reproductive queen and non-reproductive workers) can be seen as a sort of superorganism which differs in size and reproductive capacity (b_i, d_i). We thus construct the type space using colony size i (Fig. 1).

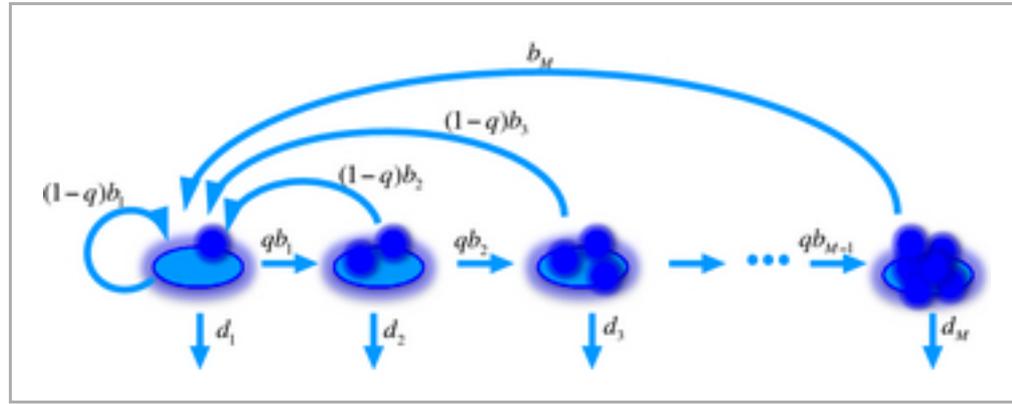


Figure 1.

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Schematic illustration of the stochastic branching model. We describe the stochastic emergence of eusociality using a continuous-time multi-type branching process, in which every colony of size i can be regarded as the i -th type. We set as M the largest possible size of each eusocial colony, and thus there are total M distinctive types. A colony of size i can transform into the one of size $i + 1$ with rate qb_i , reproduces a new colony of size 1 with rate $(1 - q)b_i$, or dies with rate d_i .

For an infinitesimal time interval, Δt , a colony of size i dies with probability $d_i \Delta t$, increases its size to $i + 1$ with probability $qb_i \Delta t$, and gives rise to a new colony of size 1 with probability $(1 - q)b_i \Delta t$. When a colony reaches the maximal size M , the subsequent offspring are required to leave the colony. Thus the colony of size M gives rise to a new colony of size 1 with probability $b_M \Delta t$. For simplicity, we do not consider worker mortality.

Let $f^i(x_1, x_2, \dots, x_M; t)$ denote the joint probability generating function for the number of colonies of size $j = 1, \dots, M$ starting with a single colony of size i at time t . Using the backward equation for this continuous-time multiplicative process, we have

$$\frac{df^i}{dt} = d_i + qb_i f^{i+1} + (1 - q)b_i f^1 f^i - (b_i + d_i) f^i, \quad 1 \leq i < M, \quad (1)$$

$$\frac{df^M}{dt} = d_M + b_M f^1 f^M - (b_M + d_M) f^M, \quad i = M. \quad (2)$$

The initial condition is $f^i = x_i, i = 1, \dots, M$.

The fixed points of the equations are the ultimate extinction probabilities, p_i , of the lineage initiated by a single colony of size i . We will give closed form solutions for the extinction probabilities for general cases.

Results

A population of individuals cannot be sustained without sufficient reproduction. This gives rise to the notion of a 'basic reproductive ratio', R_0 , or the total expected number of (reproductive) offspring produced by an

individual during its lifetime. Simple deterministic models show that supercritical reproduction $R_0 > 1$ is required to sustain a population (e.g. births must exceed deaths). Correspondingly, the condition $R_0 > 1$ also ensures a stochastic supercritical branching process in which the ultimate extinction probability of a given lineage is not definite but less than one.

Solitary reproduction

Returning to our model, for $q = 0$ (e.g. all offspring disperse) the above eqn (1) recovers the case of solitary reproduction. The solitary basic reproductive ratio R_S is

$$R_S = \frac{b_0}{d_0}. \quad (3)$$

The extinction probability, p_0 , of the lineage derived from a single solitary individual can be easily found to be

$$p_0 = \begin{cases} d_0/b_0, & R_S > 1, \\ 1, & R_S \leq 1. \end{cases} \quad (4)$$

Eusocial reproduction with $M = 2$

Let us consider the simplest possible case of eusociality, with $M = 2$ and $m = 2$. This scenario gives us an intuitive understanding of the results obtained with more general cases. The extinction probabilities satisfy the following equations:

$$d_0 + qb_0p_2 + (1 - q)b_0p_1^2 - (b_0 + d_0)p_1 = 0, \quad (5)$$

$$d + bp_1p_2 - (b + d)p_2 = 0. \quad (6)$$

where p_1 and p_2 denote the extinction probability of the lineage initiated by a colony of size 1 and 2, respectively. Because of the eusocial advantage, we set $b > b_0$ and $d < d_0$. We also assume solitary reproduction is supercritical, that is $b_0 > d_0$. We are primarily interested in the extinction probability of the lineage derived from a single eusocial queen, p_1 , which is a function of q :

$$p_1 = \frac{b(b_0 + d_0) + (1 - q)b_0d - \sqrt{(b(b_0 + d_0) + (1 - q)b_0d)^2 - 4(1 - q)b_0b(qb_0d + d_0(b + d))}}{2(1 - q)b_0b}. \quad (7)$$

The formula for p_1 can be simplified for extreme values of q .

For $q \rightarrow 0$,

$$p_1 = \frac{d_0}{b_0}.$$

Note that this is also the ultimate extinction probability of the lineage derived from a single 'solitary' individual.

For $q \rightarrow 1$,

$$p_1 = \frac{d_0}{b_0 + d_0} + \frac{d}{b}.$$

Furthermore, if the following condition holds,

$$\frac{b}{d} > \frac{b_0}{d_0} \left(1 + \frac{b_0}{d_0}\right) \quad (8)$$

We have $\frac{dp_1(q)}{dq} < 0$ and hence $p_1(q)$ is a decreasing function of q , which suggests that a eusocial queen ($0 < q \leq 1$) has a greater emergence probability than a solitary one. We also find that the eusocial basic reproductive ratio,

$$R_E = b_0(1 - q)/(d_0 + b_0q) + bb_0q/[d(d_0 + b_0q)]. \quad (9)$$

Therefore, the following inequality is required for eusocial R_E to be greater than the solitary R_S :

$$\frac{b}{d} > 1 + \frac{b_0}{d_0}. \quad (10)$$

Note that since $b_0/d_0 > 1$, the critical b/d above which eusociality has a greater probability of emergence than solitary, eqn (8), is larger than the b/d obtained by simply requiring that eusocial R_E is greater than solitary R_S , eqn (10). This result can help us to understand why a higher eusocial R_E relative to a solitary R_S alone is not sufficient to guarantee that a higher emergence probability for a eusocial queen relative to a solitary female.

General case with $M > 2$

Supercritical condition for eusociality

We now turn to more general cases with $M > 2$ and $m \geq 2$. For notational simplicity, let us define $\mu_i = b_i q$ for $1 \leq i < M$ and $\mu_M = 0$; $v_i = b_i(1 - q)$ for $1 \leq i < M$ and $v_M = b_M$. Let us now derive the condition for eusocial reproduction to be supercritical. To do this, let us first obtain the expectation matrix \mathbf{K} for the multi-type branching process as given in eqns (1), (2). The element of \mathbf{K} is given by $K_{ji} = \frac{\partial f_i(1, \dots, 1; t)}{\partial x_j}$. Denote by y_i the mean number of colonies of size i and by \mathbf{y} the vector of $[y_1, y_2, \dots, y_M]$. Then the mean behaviour of the branching process is described by

$$\dot{\mathbf{y}} = \mathbf{K}\mathbf{y}, \quad (11)$$

which corresponds to the deterministic ordinary differential equations for eusocial reproduction (Nowak *et al.* 2010). The supercritical branching process requires $\alpha(\mathbf{K}) > 0$, where $\alpha(\mathbf{K})$ is the spectral abscissa (the largest of the real parts of the eigenvalues) of the matrix \mathbf{K} (Harris 2002).

Before proceeding further, let us define two matrices $\mathbf{F} = \{F_{ij}\}$ and $\mathbf{V} = \{V_{ij}\}$ as follows.

$$F_{ij} = \begin{cases} v_i, & i = 1, 1 \leq j \leq M, \\ 0, & \text{otherwise,} \end{cases} \quad (12)$$

$$V_{ij} = \begin{cases} d_i + \mu_i, & i = j, \\ -\mu_{i-1}, & i = j + 1, \\ 0, & \text{otherwise.} \end{cases} \quad (13)$$

We can see that both \mathbf{F} and \mathbf{V} have clear biological interpretations and are the so-called 'next-generation' matrices (Diekmann & Heesterbeek 2000). The entry F_{ij} of matrix \mathbf{F} denotes the rate at which a colony of size j produces new colonies of size i . The entry V_{ij} of \mathbf{V} denotes the (influx) rate at which the class of

colonies of size j move into the class of colonies of size i ($i \neq j$); the diagonal entry (i, i) of \mathbf{V} denotes the total outflux rate of colonies of size i , including the death rate and the rate at which they move into other classes. The inverse of \mathbf{V} is found to be

$$V_{ij}^{-1} = \begin{cases} 1/(d_i + \mu_i), & i = j, \\ \prod_{k=j}^{i-1} \mu_k / \prod_{k=j}^i (d_k + \mu_k), & j < i < M, \\ 0, & \text{otherwise.} \end{cases} \quad (14)$$

It is straightforward to verify the following matrix decomposition:

$$\mathbf{K} = \mathbf{F} - \mathbf{V} = (\mathbf{FV}^{-1} - \mathbf{I})\mathbf{V}.$$

We obtain the supercritical condition after some algebra (Diekmann & Heesterbeek 2000),

$$\alpha(\mathbf{K}) > 0 \leftrightarrow \rho(\mathbf{FV}^{-1}) > 1, \quad (15)$$

where $\rho(\mathbf{A})$ denotes the spectral radius of a matrix \mathbf{A} . Therefore, the eusocial basic reproductive ratio, R_E , can be defined as $\rho(\mathbf{FV}^{-1})$, and has a closed-form expression as follows.

$$R_E = \sum_{i=1}^M \frac{v_i}{\mu_i} \prod_{j=1}^i \frac{\mu_j}{d_j + \mu_j}. \quad (16)$$

It is worth noting that the eusocial R_E is exactly the same as the one obtained by applying the next-generation approach to the deterministic eqn (11) (Diekmann & Heesterbeek 2000). We obtain a supercritical condition for eusociality based on the basic reproductive ratio (R_0). Eusociality has a non-zero chance of emergence if the branching process is supercritical, i.e. $\alpha(\mathbf{K}) > 0$. This condition is equivalent to $R_E = \rho(\mathbf{FV}^{-1}) > 1$. Accordingly, if the eusocial R_E exceeds one, then eusociality can eventually emerge with non-zero probability.

Emergence probability

For general cases with $M > 2$, we can derive a closed form for the emergence probability of a single eusocial queen, $z_1 = 1 - p_1$, as follows. Let the vector $\mathbf{z} = [z_1, z_2, \dots, z_M]$, where z_i is the emergence probability of a single colony with size i . Let $\mathbf{\Lambda} = \text{diag}\{v_1, \dots, v_M\}$ and $\mathbf{I} = \text{diag}\{1, \dots, 1\}$ (the $M \times M$ identity matrix). Using $z_i = 1 - p_i$, we obtain the following ordinary differential equations for the time evolution of \mathbf{z} after simple algebra:

$$\dot{\mathbf{z}} = \mathbf{K}^T \mathbf{z} - z_1 \mathbf{\Lambda} \mathbf{z}, \quad (17)$$

with the initial condition $\mathbf{z}(0) = [1, 1, \dots, 1]$. The ultimate emergence probability can be given by

$$\mathbf{K}^T \mathbf{z} - z_1 \mathbf{\Lambda} \mathbf{z} = (\mathbf{\Lambda}^{-1} \mathbf{K}^T - z_1 \mathbf{I}) \mathbf{\Lambda} \mathbf{z} = 0. \quad (18)$$

For the supercritical branching process, we have $z_i > 0$ for $i = 1, \dots, M$. This leads to

$$\det(\mathbf{\Lambda}^{-1} \mathbf{K}^T - z_1 \mathbf{I}) = 0. \quad (19)$$

It follows immediately that z_1 is determined by the spectral abscissa of $\mathbf{\Lambda}^{-1} \mathbf{K}^T$. Therefore, we obtain the following closed-form solution for z_1 ,

$$z_1 = \max\{0, \alpha(\mathbf{\Lambda}^{-1} \mathbf{K}^T)\}. \quad (20)$$

We note that this closed-form z_1 agrees perfectly with the results obtained by numerically solving the differential equations (Fig. 2). Figure 2 plots the emergence probability and R_E of eusociality as a function of the probability to stay, q , with increasing eusocial birth rates b . For a small eusocial advantage, the emergence probability decreases monotonically with q until reaching certain extinction. As the eusocial advantage further increases, the emergence probability has a peak for intermediate values of q . Eusocial lineages have a greater emergence probability than solitary ones given a sufficiently large eusocial advantage and intermediate values of q .

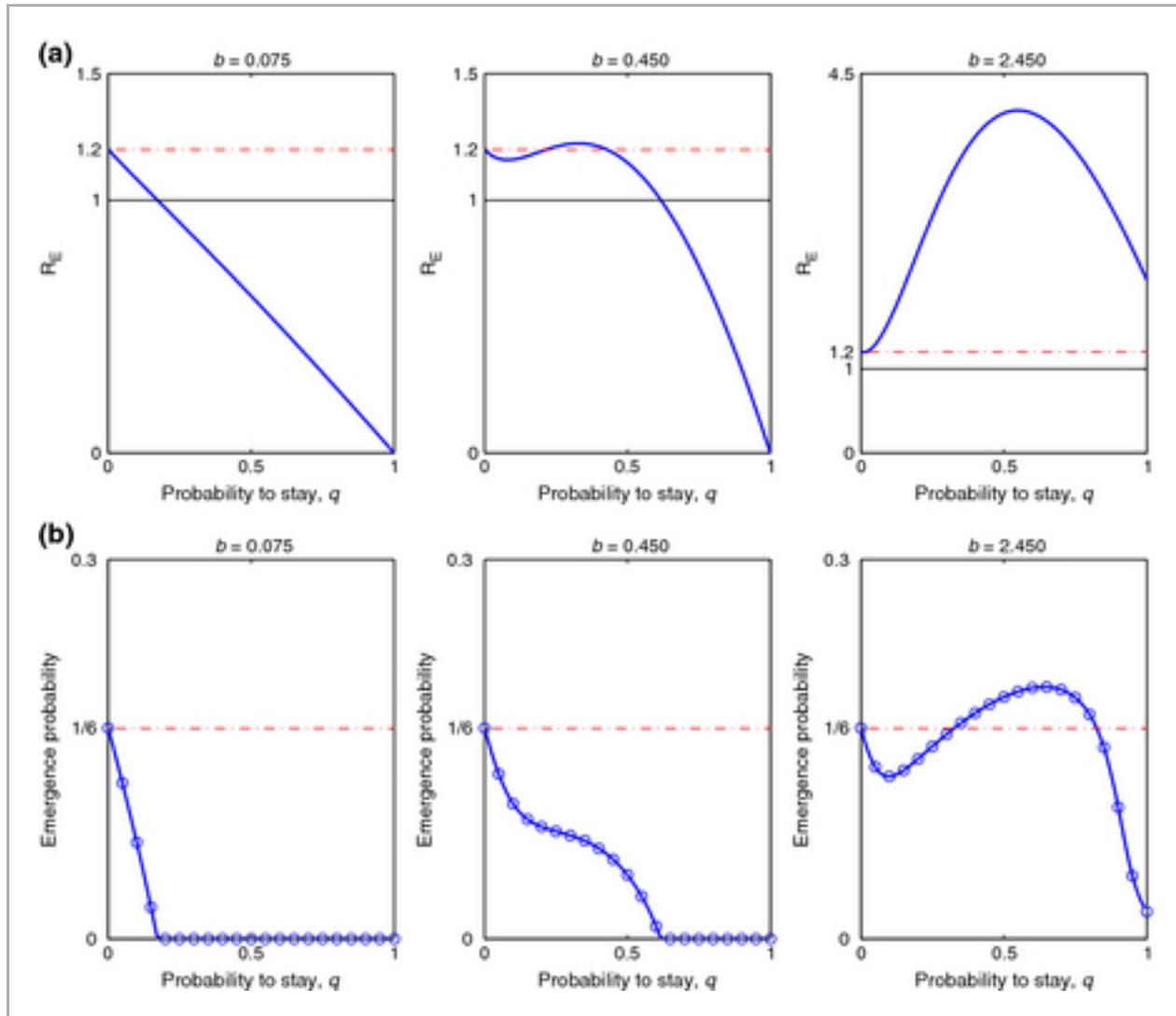


Figure 2.

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Stochastic emergence of eusociality. The upper row (a) shows the eusocial R_E (eqn (16)); the horizontal solid lines are the critical threshold $R_0 = 1$, while the horizontal dot dashed lines are the solitary $R_S = b_0/d_0$. The lower row (b) shows the ultimate emergence probability for one single eusocial queen to establish surviving lineages; the horizontal dot dashed lines are the emergence probability of a single solitary lineage, $(b_0 - d_0)/b_0$. The solid curves are the closed form evaluations of the emergence probabilities as given in eqn (20), and the circles are results obtained by numerically solving the differential equations (eqns (1), (2)). With increasing efficiency of eusocial reproduction (b), there exists an intermediate range of q values such that a single eusocial queen has a higher emergence probability than a solitary lineage. Relating emergence probability to R_E , we find that the condition for the multi-type branching process to be supercritical

(i.e. non-zero ultimate probability for eusociality to emerge) is equivalent to requiring $R_E > 1$.

Parameters: $m = 3$, $M = 100$, $b_0 = 0.12$, $d_0 = 0.1$, $d = 0.05$.

Figure 3 visualises the comparison of the two critical conditions for eusociality to have an advantage over solitary: (1) a higher R_E and (2) a lower extinction probability across the entire parameter space ($b/d, q$). As also shown in Fig. 2, the supercritical condition for a single eusocial lineage to emerge with non-zero probability is exactly equivalent to requiring the eusocial $R_E > 1$ as given in eqn (16) (note that the grey regions in the two panels of Fig. 3 are identical). The critical eusocial reproductive advantages that enable eusociality to outcompete solitary reproductive strategies in terms of establishment probability are much larger than the eusocial R_E simply exceeding the solitary R_S (note that the blue region in the right panel is much smaller, compared with the left panel in Fig. 3).

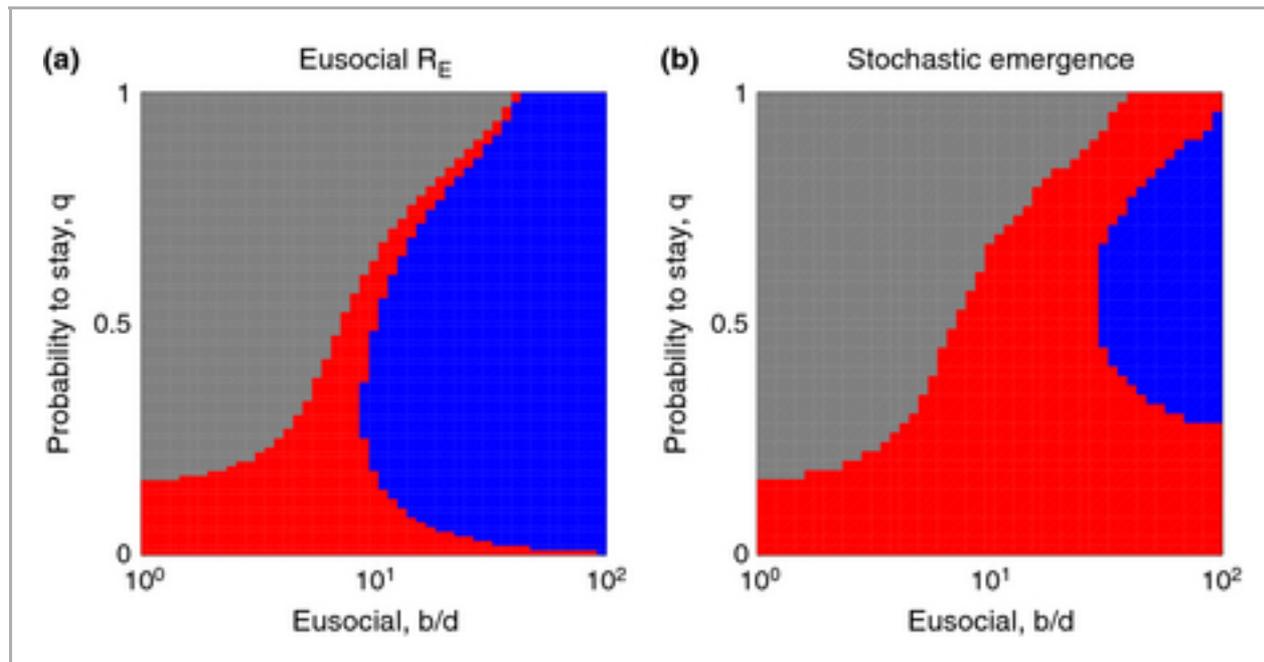


Figure 3.

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Stochastic emergence and R_0 . The plot compares the critical conditions for eusociality to have an advantage over solitary, in terms of higher R_0 and higher stochastic emergence respectively, across the parameter space ($b/d, q$). In the left panel (a), the grey-shaded area denotes the eusocial $R_E < 1$, in the red-shaded area, eusociality has a lower R_0 than solitary, and in the blue-shaded area, eusociality has a higher R_0 than solitary. In the right panel (b), the grey-shaded area denotes definite extinction of eusociality, in the red-shaded area, eusociality has a lower emergence probability than solitary, and in the blue-shaded area, eusociality has a higher emergence probability than solitary. We show that the branching process is supercritical, which is equivalent to $R_E > 1$. Therefore, the grey-shaded areas in both panels are identical. The critical eusocial advantage, b/d , above which eusociality has a higher emergence probability than solitary, is much higher than the one above which eusocial R_E is greater than solitary R_S . Parameters: $m = 3$, $M = 100$, $b_0 = 0.12$, $d_0 = 0.1$, $d = 0.05$.

This result can be intuitively understood as follows. Starting with a single founder queen, each surviving

eusocial colony is likely to go through intermediate stepwise transitions until reaching the largest possible size M . Meanwhile, unlike solitary individuals, when a eusocial colony dies, it inevitably results in the simultaneous loss of all individuals belonging to that colony; much reproductive potential of these colonies with intermediate sizes is thus being wasted. As a consequence, much larger reproductive advantages are required to offset such inefficiency of eusocial reproduction with respect to averting the risk of extinction.

Resilience against extinction: solitary reproduction vs. eusocial reproduction

We find a range of parameters where solitary reproduction is 'unbeatable'. In these cases, as long as the solitary reproductive ratio exceeds a critical value, there is no eusocial advantage that exists where eusocial reproduction would be favoured over solitary reproduction. This may explain why eusociality is taxonomically rare: eusocial life histories can only outcompete solitary ones in scenarios where reproductive payoffs are much higher for eusocial rather than solitary strategies.

For a fixed eusocial threshold m , let us consider the ideal scenario where eusociality is most likely to get established: eusocial lineages become immortal once the colony size reaches m . In this case, the extinction risk lies in the intermediate transition steps and reduces to zero once reaching the threshold size m . Note that $q = 1$ makes it fastest for a single eusocial queen to reach the eusocial threshold and thus the immortal state. There is no intermediate optimal q to this end. Therefore, if the extinction probability, p_1 , of the lineage initiated by a single queen with full eusociality ($q = 1$) is lower than that of a single solitary individual, then it is advantageous for the eusocial queen to utilise a fully eusocial strategy ($q = 1$) to minimise the risk of extinction.

To simplify our notations, we can normalise the birth and death rates with their sum $b_i + d_i$ in the ordinary differential equations in eqns (1), (2) without changing the original fixed points. Let $a_i = b_i / (b_i + d_i)$ for $1 \leq i \leq M$. Then $a_i = a_0 = b_0 / (b_0 + d_0)$ for $i < m$; $a_i = a = b / (b + d)$ for $i \geq m$. The extinction probability, p_1 , of the lineage derived from a single fully eusocial queen is

$$p_1 = \sum_{i=1}^{m-1} (1 - a_0) a_0^{i-1}. \quad (21)$$

The condition for p_1 to be smaller than the extinction probability of the lineage derived from a single solitary individual $p_0 = (1 - a_0) / a_0$ is

$$W_m(a_0) = a_0^{m-1} + a_0^{m-2} + \dots + a_0 - 1 < 0. \quad (22)$$

The above polynomial $W_m(a_0) = a_0^{m-1} + a_0^{m-2} + \dots + a_0 - 1$ always has a unique positive root, denoted by r_m , in $(0, 1)$. Thus, eusociality can have an advantage over solitary (in terms of lower extinction probability) if and only if the ratio of solitary reproduction $a_0 = b_0 / (b_0 + d_0) < r_m$. This yields the critical solitary $R_S(m)$ that always ensures solitary reproduction less prone to extinction than eusocial reproduction for any given eusocial threshold m :

$$\frac{b_0}{d_0} > \frac{r_m}{1 - r_m} = R_S(m). \quad (23)$$

For $m = 2$, $r_2 = 1$. Even so, we stress that this does not mean that eusocial reproduction is less subject to extinction than solitary reproduction for this case with $m = 2$, since this threshold r_2 is calculated with the

assumption of an immortal eusocial queen ($d = 0$). In fact, for eusocial queens without an infinite lifespan ($d > 0$), it requires very large eusocial benefits to reduce the extinction relative to solitary reproduction (Figs. 3 and 4).

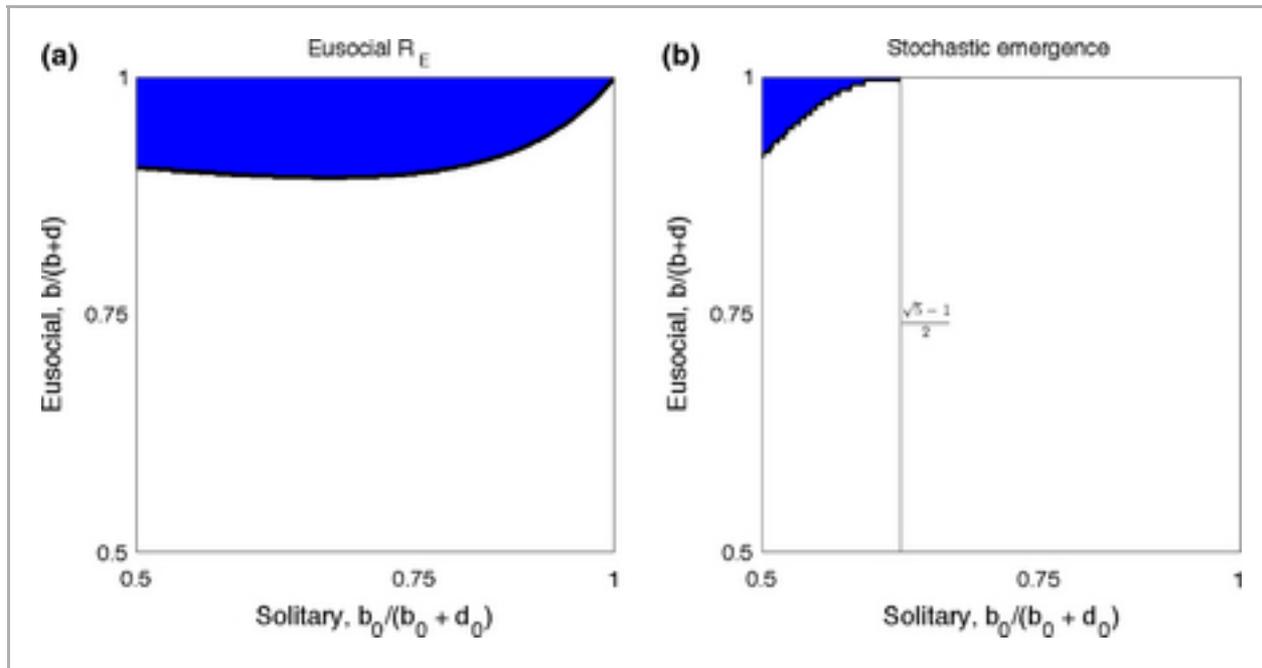


Figure 4.

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Eusocial reproduction may be no better than solitary at averting the risk of extinction. The left panel (a) shows the shaded region where eusocial R_E is larger than solitary R_S . The right panel (b) shows the shaded region where eusociality has a greater chance of emergence than solitary.

Eusociality can have a greater probability of emergence than solitary only when the ratio of solitary reproduction $b_0/(b_0 + d_0)$ is less than a critical threshold, r_m . For the eusocial threshold $m = 3$, $r_m = \frac{\sqrt{5}-1}{2}$. r_m decreases with m and converges to $1/2$ for large m . In contrast, eusociality can always have a larger R_0 than solitary for any given ratio of solitary reproduction $b_0/(b_0 + d_0)$.

Parameters: $m = 3$, $M = 100$.

For $m = 3$ we find

$$r_3 = \frac{\sqrt{5}-1}{2} \approx 0.618,$$

$$R_S(3) = \frac{1+\sqrt{5}}{2} \approx 1.618,$$

We note that this critical value is the 'golden ratio'. For $m = 4$,

$$r_4 = \frac{1}{3} \left(-1 - \frac{2}{(17+3\sqrt{33})^{1/3}} + (17+3\sqrt{33})^{1/3} \right) \approx 0.544,$$

$$R_S(4) \approx 1.193.$$

Because $W_{m-1}(a_0) < W_m(a_0) = (1 - a_0^m)/(1 - a_0) - 2$, the unique root r_m within $(0,1)$ for $W_m(a_0) = 0$ is monotonically decreasing with m and converges to $1/2$ for large m values, which implies that $R_S(m) \rightarrow 1$ for large m . As a result, as the eusocial threshold m increases, it becomes more likely that the solitary reproductive ratio b_0/d_0 exceeds the threshold $R_S(m)$, making it impossible for eusociality to

have a higher probability of emergence than solitary. In other words, the larger m , the more prone eusocial reproduction is to extinction than solitary reproduction.

Figure 4 depicts the parameter region of reproductive rates where eusociality has a higher R_E (left panel) and has a higher emergence probability (right panel) than solitary R_S respectively. Provided with sufficiently large b and small d , the eusocial reproductive ratio can exceed the solitary one (Fig. 4a). Thus, eusocial reproduction is a ‘high reward’ strategy. But if the solitary reproductive ratio is above a threshold value, $R_S(m)$, switching to eusocial reproduction cannot reduce the extinction probability any more than solitary reproduction does, regardless of how large the eusocial advantages are (Fig. 4b). Thus, it is also a ‘high risk’ strategy.

This result mathematically demonstrates the demographic hurdle that eusocial lineages must overcome in order to become established. The eusocial reproductive strategy is risky because of the opportunity costs associated with the non-reproductive offspring that remain in the nest and fail to establish their own colonies and reproduce, as well as the delay in return of eusocial benefits contingent on a certain colony size. These costs associated with eusociality resemble the ‘two-fold cost’ of sexual reproduction where only half of the parental genome is passed on to offspring (Brian 1965).

Roles of ecological niches in origins and reversals of eusociality

In addition to the demographic considerations addressed above, a consideration of the specific ecological context (which determines the competition dynamics between solitary and eusocial strategies) is key to understanding the origin and maintenance of eusociality (Chenoweth *et al.* 2007; Chase & Myers 2011; Kocher *et al.* 2014; Wilson & Nowak 2014). Mathematically, this means that we should consider the scenario where the branching process is dependent on the total population size X . Specifically, we assume that the birth rates of solitary and eusocial lineages are rescaled respectively by a population regulation factor, ϕ_S and ϕ_E ; that is, $b'_0 = \phi_S b_0$, and $b'_i = \phi_E b_i$, and the death rates remain unchanged. For solitary reproduction $\phi_S = 1/(1 + \eta_S X)$ and for eusocial reproduction $\phi_E = 1/(1 + \eta_E X)$, where the coefficients $\eta_S > 0$ and $\eta_E > 0$ quantify the effects of the underlying ecological patch on the population competition dynamics between social forms. The limited carrying capacity introduced in this scenario always leads to the fixation of one strategy or the extinction of both strategies depending on the initial condition, thereby not allowing coexistence between eusocial and solitary in the same ecological patch.

We can still use the extinction probabilities calculated before (i.e. $\eta_S = \eta_E = 0$) to predict the evolutionary outcomes for very small values of η_S and η_E ($0 < \eta_S, \eta_E \ll 1$, which should be relevant because of tremendously high carrying capacity of social insects seen in nature). In the absence of any population competition (i.e. $\eta_S = \eta_E = 0$), coexistence happens with probability $(1 - p_e)(1 - p_s)$, only solitary emerges while eusociality goes to extinction with probability $p_e(1 - p_s)$, only eusociality emerges while solitary goes to extinction with probability $p_s(1 - p_e)$, and both lineages go to extinction with probability $p_s p_e$. Here, p_s and p_e denote the extinction probabilities of solitary and eusocial lifestyles for given initial conditions. Because extinction, if fated to happen, takes place in short time scales for branching processes, the co-existent state that happens with probability $(1 - p_e)(1 - p_s)$ for $\eta_S = \eta_E = 0$ will be dominated by and eventually taken over by the one having a higher effective R_0 in the case of $\eta_S, \eta_E > 0$. To illustrate how our approximation method works, let us consider again the simplest possible case with $M = m = 2$ and $q = 1$. For solitary reproduction, $R_S = \phi_S b_0 / d_0$; for eusocial reproduction,

$R_E = \phi_E^2 bb_0/[d(\phi_E b_0 + d_0)]$. Substituting $X = (b_0 - d_0)/(\eta_S d_0)$ into the inequality of $R_E > 1$, we obtain the critical ratio b/d above which eusociality dominates over solitary,

$$\frac{b}{d} > \left[1 + \frac{\eta_E(b_0 - d_0)}{\eta_S d_0} \right] + \frac{d_0}{b_0} \left[1 + \frac{\eta_E(b_0 - d_0)}{\eta_S d_0} \right]^2. \quad (24)$$

If eusocial reproduction satisfies the above condition, then the emergence probability of eusociality and solitary is $1 - p_e$ and $p_e(1 - p_s)$, otherwise being $p_s(1 - p_e)$ and $1 - p_s$ respectively. Moreover, when solitary and eusocial reproduction fare exactly the same in the ecological patch ($\eta_S = \eta_E$), the above condition can be greatly simplified into $b/d > 2b_0/d_0$. Figure 5 shows that the approximation above works very well for small $\eta_S = \eta_E \ll 1$ and for different initial numbers of solitary individuals. Additionally, it requires greater eusocial advantages for a single, eusocial individual to emerge and eventually take over a larger population of solitary individuals (i.e. larger N_S).

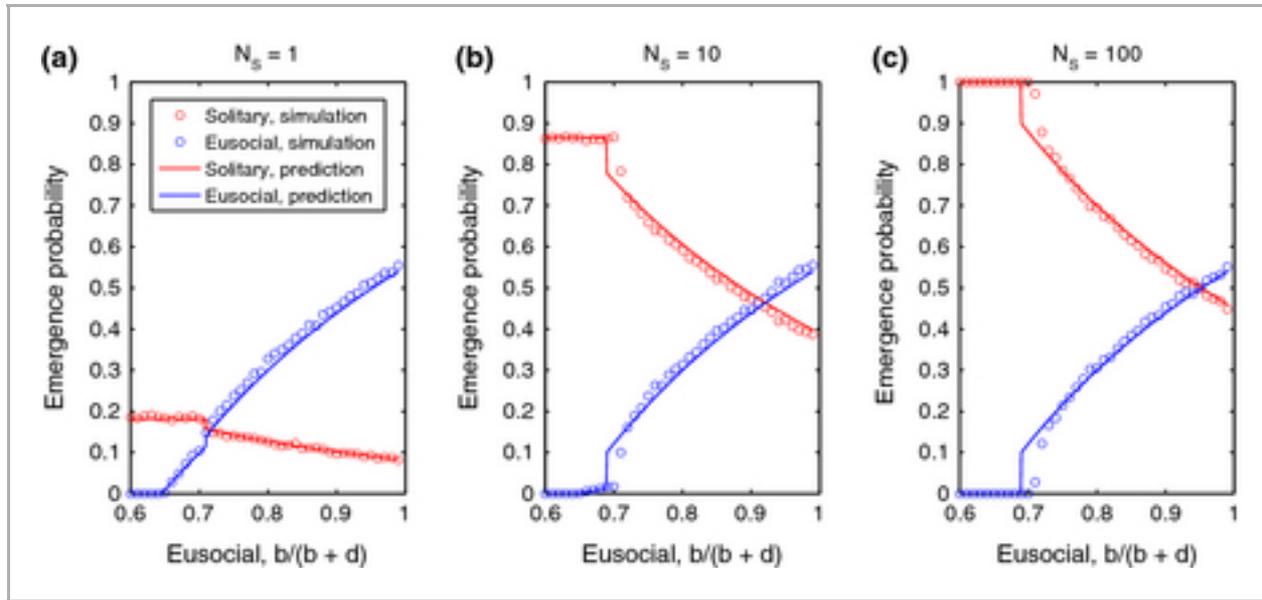


Figure 5.

[Open in figure viewer](#)

Emergence of eusociality from population-size-dependent branching processes. Shown are the emergence probabilities of eusociality and solitary, starting with one single eusocial individual and N_S solitary individuals together ($N_S = 1, 10, 100$, respectively). The branching process is dependent on the total population size, X : the birth rates change as $b'_0 = b_0/(1 + \eta_S X)$ and $b'_i = b_i/(1 + \eta_E X)$ while the death rates remain constant. There is good agreement between predictions (solid lines) and simulations (circles). Parameters: $\eta_S = \eta_E = 0.0001$, $b_0 = 0.55$, $d_0 = 0.45$, $b = 1 - d$, $q = 1$, $m = 2$, $M = 2$.

Finally, let us take into account the effects of ecological niches on the origin and maintenance of eusociality. We simulate the density-dependent branching processes starting with one species almost at carrying capacity in an ecological patch and calculate how likely a single mutant can take over the entire population. As shown in eqn (24), for eusociality it becomes easier to evolve and also more resilient against reversals once established, with decreasing values of η_E/η_S , i.e., when the ecological niche is increasingly biased towards favouring eusocial reproduction. Our analytical predictions agree perfectly with agent-based simulations: as compared to the case where the ecological patch exerts exactly the same effects on solitary

and eusocial reproduction ($\eta_S = \eta_E$, Fig. 6a and b), the presence of an ecological niche that strongly favours eusociality ($\eta_S \gg \eta_E$) makes it easier for eusociality to emerge and is also more robust against invasion by solitary lineages (Fig. 6c and d). These results highlight how the existence of ecological niches that favour eusociality can help eusociality to overcome the aforementioned demographic hurdles.

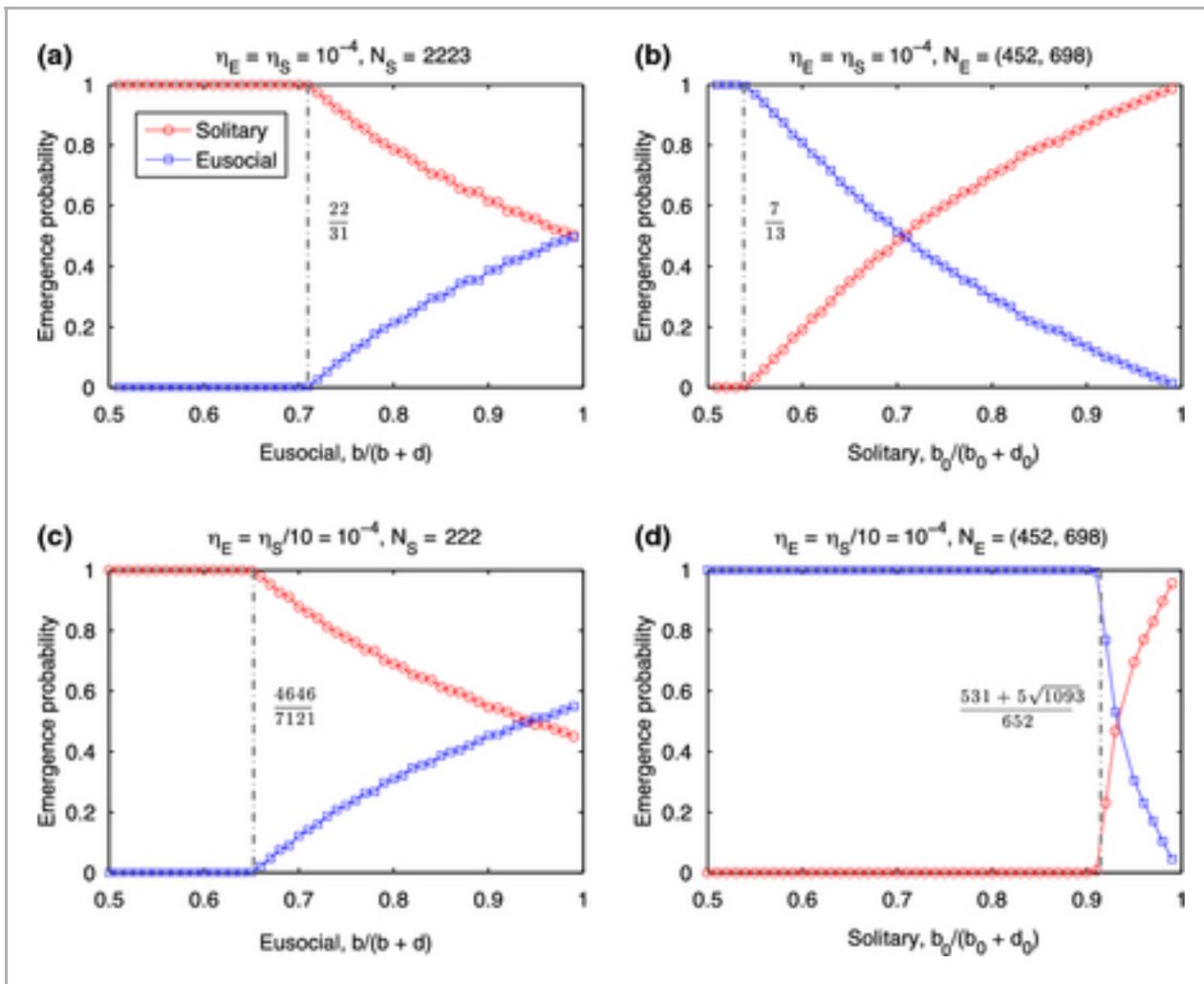


Figure 6.

[Open in figure viewer](#)

Origins and reversals of eusociality depends on the ecological context under consideration. The left panels show the emergence probability of a single eusocial mutant in a population of (a) $N_S = 2223$ and (c) $N_S = 222$ solitary individuals. The right panels (b) and (d) show the emergence probability of a single solitary mutant in a eusocial population consisting of 452 colonies of size 1 and 698 colonies of size 2. In (a) and (b) the ecological patch has exactly the same impact on solitary and eusocial reproduction ($\eta_S = \eta_E$); in (c) and (d) the ecological patch represents a niche that strongly favours the eusocial rather than the solitary lifestyle ($\eta_S \gg \eta_E$). The vertical lines mark the theoretical threshold values, derived from eqn (24), for (a, c) origins and (b, d) reversals of eusociality. Simulation results agree perfectly with the theoretical predications. Parameters: (a, b) $\eta_S = \eta_E = 0.0001$, (c, d) $\eta_S = 0.001$, $\eta_E = 0.0001$, $b = 1 - d$, $b_0 = 1 - d_0$, $q = 1$, $m = 2$, $M = 2$, (a, c) fixed solitary reproduction rates $b_0 = 0.55$, $d_0 = 0.45$, (b, d) fixed eusocial reproduction rates, $b = 0.7$, $d = 0.3$.

Discussion & Conclusion

We have calculated the extinction probabilities associated with solitary and eusocial reproductive strategies. In general, we find that solitary lineages are more stable than eusocial ones and this conclusion is robust to model variations (online appendix, Figs S1 and S2). This finding could help to explain both the relatively few origins of eusociality as well as the many subsequent losses. There are substantial demographic hurdles that make eusociality both difficult to establish and sometimes hard to maintain.

Our comparative results on extinction risk further support the following conclusion: the emergence of eusociality is difficult because it requires relatively large reproductive advantages over solitary strategies. Furthermore, these pronounced advantages have to arise immediately with the production of a small number of workers. We derived a closed-form supercritical condition for eusociality to have a non-zero chance of emergence if and only if the eusocial $R_E > 1$, as given in eqn (16). We show that this R_E , although derived for the stochastic branching process, is exactly the same as the one obtained by the deterministic model in Nowak *et al.* (2010). For eusocial lineages to have a lower risk of stochastic extinction than solitary ones, the reproductive ratio for eusocial queens (R_E) cannot simply exceed that of solitary females (R_S), rather the reproductive advantage for eusocial reproduction must be very large (Fig. 3). Provided sufficiently large reproductive advantages, eusocial queens can always have a larger R_0 than solitary, but only when the ratio of solitary reproduction is lower than a critical value, $b_0/(b_0 + d_0) < r_m$, can eusociality have a lower risk of extinction than solitary (Fig. 4). In other words, eusocial lineages are less likely to become established even though eusocial reproduction can be very advantageous and solitary reproduction is only slightly supercritical. This is an important new insight arising from the present work that helps explain the phylogenetic rarity of eusociality.

In the instances where it has been successfully established, eusociality does appear to confer both higher reproductive output as well as increased offspring survivorship. Evidence from some socially polymorphic species suggests that social colonies do indeed have greater productivity than solitary nests (Smith *et al.* 2007) and can produce more reproductives than solitary species (2–3 reproductive females in solitary *L. albipes* nests vs. 12–20 reproductive females in eusocial *L. albipes* nests; Cecile Plateaux-Quenu, *personal communication* (Plateaux-Quenu 1993; Plateaux-Quenu *et al.* 2000). Eusocial nests often have a higher average productivity per female than solitary nests and/or may be less likely to fail (reviewed in Andersson 1984; Smith *et al.* 2007; Rehan *et al.* 2010, 2011). Several species of allodapine bees show the same patterns: social nesting greatly increases *per capita* brood production, but the benefits of cooperative breeding begin to saturate rapidly after colony sizes exceed a few individuals (Schwarz *et al.* 1998; Tierney *et al.* 2000; Thompson & Schwarz 2006; Chenoweth *et al.* 2007).

The primary factor increasing *per capita* brood production in eusocial nests appears to be decreased brood mortality rather than increased rearing efficiency (Schwarz *et al.* 1998). One of the oft-cited examples of the benefits of social living is that social species are able to reduce their risk of parasitism and predation (Lin & Michener 1972; Evans 1977), which should lead to higher rates of offspring survivorship. For example, *Xylocopa sulcatipes* females are capable of producing both solitary and social nests. Social nests contain a secondary female that acts as a guard at the nest entrance, and her presence significantly reduces the frequency of nest usurpation by other, conspecific females in environments with limited nest-site availability (Stark 1992). Other studies have demonstrated similar benefits in small carpenter bees (*Ceratina* spp.; Sakagami & Maeta 1977; Rehan *et al.* 2010, 2011).

Regardless of the mechanism, it is clear that eusocial colonies containing a small number of workers can gain large reproductive benefits. Surprisingly, in some allodapine bee populations where these large payoffs have been well documented (Schwarz *et al.* 1998; Tierney *et al.* 2000; Thompson & Schwarz 2006; Chenoweth *et al.* 2007), multi-female nests only occur in a small subset of the allodapine populations (Joyce & Schwarz 2006). Our results can explain why – because even with high reproductive rewards, eusociality still carries a higher risk of extinction than their more stable solitary counterparts (Fig. S2).

Our initial analyses were based on a model of eusocial behaviour where offspring dispersal rates were not allowed to vary with the colony size. This approximates a facultatively eusocial colony where all daughters are capable both of reproducing on their own or remaining in the nest as helpers. In this model, facultative eusociality is still capable of emerging with sufficient reproductive payoff and intermediate values of q . These facultative strategies are often observed in nature. For example, some halictid bee species are capable of producing either reproductive daughters or workers in the first brood depending on their local environment (Yanega 1988; Packer 1990; Plateaux-Quenu 1993; Soucy & Danforth 2002; Cronin & Hirata 2003; Field *et al.* 2010). Other species, such as the halictid bee, *Halictus rubicundus* (Yanega 1988), and several wasp species (Haggard & Gamboa 1980; Greene 1984; Kolmes 1986), exhibit ‘graded’ resource allocation strategies where first-brood females are often a mix of workers and reproductives.

In another set of analyses, we allow dispersal to depend on colony size. We found that eusocial advantages are maximised when the first offspring remain in the nest and help increase survival and reproduction of the colony, followed by the production of offspring that disperse to form new colonies (Fig. S1). This is representative of an obligate eusocial colony with a reproductive strategy where the first daughters are required to remain in the nest as workers and are therefore incapable of reproducing on their own. There is substantial evidence that this is indeed the case. Obligate eusociality has evolved several times in the corbiculate bees (honey bees, stingless bees and bumble bees), in vespid wasps (in the Vespinae), and in the ants (Michener 1974), and previous work has demonstrated that among species with an annual life history, this method of resource allocation is the most beneficial (Macevicz & Oster 1976). Furthermore, these species have been estimated to comprise up to 50% of the insect biomass (Wilson 1971), indicating that this strategy is indeed a very successful one. Despite this, obligate (i.e. advanced) eusociality is still relatively rare in comparison to facultative (i.e. primitive) eusociality (reviewed in Kocher & Paxton 2014), suggesting that facultative strategies might be a necessary step on the route to obligate eusociality (as also shown empirically by Cardinal & Danforth 2011).

Finally, we extended our model to explicitly take ecological context into consideration (Figs. 5 and 6). We demonstrated how the presence of ecological niches favouring eusociality can help to mitigate the demographic constraint on the emergence of eusociality as well as protect against potential reversals due to invasion attempts by solitary mutants. This finding is not unprecedented; previous applications of birth-death models have suggested that the origins of eusociality might be most likely to occur in situations where strong ecological constraints favour cooperation (Avilés 1999). For example, harsh and unpredictable conditions are predicted to favour cooperative groups that are better able to acquire food, defend against enemies and rear brood (Wilson 1971; Lin & Michener 1972). Evidence for this has been found in snapping shrimp (Duffy & Macdonald 2010), naked mole rats (Faulkes *et al.* 1997), and some cooperatively breeding birds (Rubenstein & Lovette 2007). Additionally, eusociality could also be associated with the invasion of new adaptive zones, such as the utilisation of novel food resources [as may have been the case of ants and termites (Wilson 1987)]. Our results demonstrate that if there are ecological factors that favour eusocial

lineages, they can help to overcome some of the demographic challenges that inhibit their establishment.

In summary, this work provides key insights into some of the demographic and ecological factors that impact the origins of social behaviour by demonstrating that (at least initially) eusocial strategies are high risk with high reward. Our results suggest that the evolution of social behaviour is difficult, and that the initial origins of eusociality are likely to occur when eusocial advantages in terms of increased survival and reproduction already begin to accrue in colonies of very small size. We have also shown that reversals of eusociality due to invasion by solitary lineages is likely to occur in many circumstances, unless there exist ecological niches strongly favouring the eusocial lifestyle, or with the exception of more advanced forms of obligate eusociality that have crossed a point of no return (Fig. 6). Once eusocial life histories have taken over the population, it is possible that more complex forms of social behaviour can then evolve.

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Authorship

F.F., S.D.K. & M.A.N. conceived the model, performed analyses, and wrote the manuscript.

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