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Piret Avila

New insights on the role of ecology and life-history in social evolution

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What I cannot create, I do not understand.

(Richard Feynman, 1988)

ABSTRACT

Piret Avila
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Biological altruism, defined as a behaviour that benefits others at an apparent cost to the focal individual, is found abundantly across different levels of biological organization. While kin selection has been useful for explaining both cooperation and conflict in specialized cooperative societies, more theoretical work has to be done to develop models for realistic ecological and life-history contexts. This thesis aims to fill this gap by providing several new insights on the role of ecology and life-history in various social systems. Firstly, I propose a model that incorporates realistic ecological mechanisms of population regulation and study how different population regulation mechanisms affect the evolution of helping behaviour. I show that nest-site limitation strongly favours evolution of helping behaviour even if the helpers are relatively inefficient. I also find that interactions between density dependent mechanisms and life-history traits affect the evolution of social behaviour. Secondly, I consider a resource allocation model for eusocial insect colonies that incorporates the dynamics of colony growth and the conflict between the queen and the workers over the sex ratio. I show that conflict over sex allocation gives rise to a suboptimal pattern of colony growth, while the queen wins the sex allocation conflict. Thirdly, I study optimal reproductive tactics in facultatively cooperative wasps. I show that co-foundress nests and costly helping can evolve even with a low average relatedness between co-foundresses, but only during the initial stages of the nesting cycle. Costly helping during the reproductive phase can only evolve if the relatedness between co-foundresses is high. In conclusion, this thesis demonstrates the importance of considering ecological and life-history aspects in the study of social interactions from early stages of helping behaviour to resolving conflicts in eusocial insect colonies.

Keywords: Eusociality; cooperative breeding; social evolution; evolutionary model; dynamic optimization; game theory; life-history theory.

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LIST OF ORIGINAL PUBLICATIONS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the main text by their Roman numerals I-III. The initial plan for paper I came from Lutz Fromhage (LF), the model was implemented by Piret Avila (PA), and the manuscript preparation was led by PA with contributions from LF. The initial plan for paper II came from Laurent Lehmann (LL) and PA with contributions from LF, the analytical model was developed by PA and LL, the numerical model was developed and implemented by PA, and Mauricio González-Forero (MGF) helped with his knowledge on GPOPS. Manuscript preparation was done by PA with contributions from LL, LF, and MGF. Planning and model development of paper III were done by PA and LF, model implementation was done by PA and manuscript preparation was done by PA with contributions from LF.

I	Avila, P. & Fromhage L. 2015. No synergy needed: ecological constraints favor the evolution of eusociality. The American Naturalist 186: 31-40.
II	Avila, P., Fromhage L., González-Forero M. & Lehmann, L. 2016. Sex ratio conflict affects colony growth in annual haplodiploid social insects. Manuscript.
III	Avila, P. & Fromhage L. 2016. Co-foundress associations in primitively eusocial wasps: a game theoretical approach. Manuscript.

INTRODUCTION

Kin selection and its different formulations

The question of how the cooperative social behaviours have evolved has been one of the fundamental questions of evolutionary biology since the time of Darwin. The idea that organisms are a subject to constant 'struggle for existence' seems to superficially imply that natural selection favours individuals who behave in their own selfish interests. However, animals do not behave selfishly all the time and some animals can even sacrifice their lives for the benefit of other individuals. We can observe a variety of altruistic behaviours in nature and such behaviours are especially common in social insects (ants, bees, wasps and termites), humans, and birds. More generally, all levels of biological organization exhibit some forms of altruistic and cooperative behaviours: different cells in multicellular organisms rely on the cooperation between each other, genes in genomes cooperate with one another, and various cooperative behaviours can be observed in different microorganisms etc. How, then, can altruistic behaviours be so abundant in nature if they appear to make organisms less fit?

In the early 1960s, a graduate student Bill Hamilton proposed a solution to this puzzle. Hamilton argued that if the purpose of reproduction (at least from an evolutionary viewpoint) is to transmit one's genes into the future generations, then the same purpose can also be accomplished by helping relatives to reproduce, taking into account the fraction of genes they are likely to share with the focal individual (Hamilton 1964*a*, *b*). This insight led him to derive a fundamental condition that allows altruistic behaviour to evolve, which became known as the Hamilton's rule. Hamilton's rule states that a gene coding for a social behaviour will be favoured by selection, if and only if, the following condition holds

$$rb > c, \tag{1}$$

where b is the benefit that the behavioural trait confers to the social partner, c is the cost the behaviour imposes on the actor, and r is the relatedness between the actor and its social partner (Hamilton 1964*a*, *b*). The benefit as well as the cost are measured in the units of reproductive fitness. In general, the coefficient of relatedness encompasses any relevant genetic similarity between the actor and its social partner, including genealogical kinship as well as green-beard (Dawkins 1976, Gardner and West 2010) and pleiotropic effects (Hamilton 1975).

Hamilton's theory for explaining altruistic behaviour became known as 'kin selection' theory, although he never used this term himself. Kin selection theory represents an extension to the classical theory of evolution, since it shifted the unit of selection from an individual's level to the level of the gene. This 'gene's-eye view of evolution' puts genes at the centre stage of evolution and individual organisms can be viewed as mere 'vehicles' that genes use to aid their own propagation (Dawkins 1976, 1982). However, kin selection can also be formulated from the organism's point of view if we extend the classical notion of reproductive fitness. According to the theory of kin selection, individuals appear to be maximizing their 'inclusive fitness', which is a sum of the reproductive success they acquire through reproducing themselves ('direct fitness') and through helping relatives to reproduce ('indirect fitness'). Hamilton defined inclusive fitness in his own words as follows:

> Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects. (Hamilton 1964*a*)

Using the concept of inclusive fitness is not the only way to formulate the kin selection theory at the individual's level. An alternative formulation can be obtained if relatedness is interpreted as a degree of correlated interactions. This formulation of kin selection theory is called the 'neighbour-modulated fitness' (or 'direct fitness') framework. In this framework, an individual who carries a gene for altruism has a higher expectation for receiving benefits from its social environment if the relatedness is high enough (Taylor and Frank 1996, Frank 1998, Roze and Rousset 2004). It should be mentioned that indirect fitness and neighbour-modulated fitness formulations are usually considered to be equivalent, since they yield identical results for the evolution of altruistic traits (Taylor and Nowak 2007).

Hamilton derived the original formulation of kin selection theory from a population genetic model based on a single locus, assuming weak selection, additive gene action, and the additivity of the fitness components behind individual actions. Since then, kin selection theory has been developed for more general conditions by numerous authors (e.g., Michod (1982), Queller (1984, 1992), Lehmann and Keller (2006), Lehmann and Rousset (2010, 2014*a*, *b*), Lehmann *et al.* (2016)). Kin selection has been instrumental in understanding various aspects on queen-worker conflict in insect societies, sex ratio evolution, genomic imprinting, reproductive skew, dispersal in animal groups, and the evolution of multicellularity (Abbot *et al.* 2011, Bourke 2011). Yet, surprisingly, for a theory so central to its field and with all of its empirical success, there has been a considerable amount of debate over the accuracy of the mathematical tools it uses, the generality of its implications, and its connection to evolutionary theory in general, especially in the recent years (e.g., Nowak *et al.* (2010), Abbot *et al.* (2011), Nowak *et al.* (2011), Gardner *et al.* (2011), Rousset and Lion (2011), Allen *et al.* (2013), Rousset (2015), Allen and Nowak (2016)).

Eusociality and cooperative breeding in social insects

Social insects are central to the study of social evolution theory, since they represent a vast range of different cooperative social systems. At one end of the extreme, one can find highly complex eusocial societies which include those of many ant and termite species. At the other extreme, there are small groups of cooperatively breeding insects that exhibit a high degree of conflict, such as seen in many species of social wasps.

As we have learned more about the social behaviour of vertebrates and invertebrates, the demarcation between eusociality and cooperative breeding has become blurred, as the existing variation of social systems resembles more of a continuum more than a dichotomy (Sherman *et al.* 1995).

Crespi and Yanega (1995) have proposed one of the clearest definitions of eusociality, as a society that consists of at least two castes of individuals that become irreversibly distinct in behaviour before reaching their reproductive maturity, and in which the members of a less-reproductive caste behave altruistically towards the more-reproductive caste. According to this definition, cooperative breeders differ from eusocial colonies because they do not exhibit irreversible, behaviourally distinct castes, since all individuals in these groups are capable of reproducing. Throughout this thesis, I have adopted these definitions for eusociality and cooperative breeding.

Mechanisms that promote helping

Mechanisms affecting relatedness

According to the kin selection theory, high relatedness between social partners facilitates the evolution of helping behaviour. Here, I discuss two mechanisms that are thought to influence relatedness between social partners.

Monogamy is considered to be important in the systems where helping has evolved via the subsocial route (i.e., where the individuals stay with their mother to help raise siblings) (Boomsma 2007). This is because strict monogamy maintains high relatedness between the offspring of an individual. Empirical evidence, in general, provides support for the importance of monogamy in the evolution of helping behaviour, as many eusocial species exhibit a lifetime of monogamy (Boomsma 2007).

As eusociality is particularly common among the order Hymenoptera, Hamilton conjectured that the Hymenoptera may be predisposed to become eusocial because of their haplodiploid genetic system. In haplodiploids, (diploid) females develop from fertilized eggs and (haploid) males develop from unfertilized eggs. This creates asymmetry of relatedness within family groups. For example, the life-for-life coefficient of relatedness between haplodiploid sisters is 0.75, while between sisters and brothers it is only 0.25. In addition, a haplodiploid mother is equally (0.5) related to her sons and daughters. Here, the life-for-life coefficient of relatedness is the augmented basic (regression) relatedness that also takes into account the relative reproductive value of females compared to males (Bulmer 1994). According to the haplodiploidy hypothesis, daughters possess a large incentive to help their mother to produce sisters, since they are more related to their sisters than to their own offspring (Hamilton 1964*a*, *b*, 1972). However, Trivers and Hare (1976) have pointed out that, given an even sex ratio, the average relatedness between a female and her siblings does not differ between diploids and haplodiploids, since in haplodiploids the high relatedness towards sisters is offset by the low relatedness towards brothers (Trivers and Hare 1976). Additional mechanisms have been invoked that could permit the haplodiploidy hypothesis to work (Seger 1991), but even these mechanisms have been shown to be problematic (Gardner *et al.* 2012). Nevertheless, Fromhage and Kokko (2011) have shown that haplodiploidy can promote evolution of helping via the effect of positive assortment between rare phenotypes.

Intriguingly, social systems where relatedness between social partners is relatively low or consists of completely unrelated individuals can also be found. These examples are more commonly found in cooperative vertebrates (Clutton-Brock 2002, 2009), but there are also some of these instances among ants and social wasps (Bernasconi and Strassmann 1999, Liebert *et al.* 2005, Gadagkar 2016, Field and Leadbeater 2016). In the third chapter of this thesis, I will propose a context-dependent dynamic model to explain how this behaviour could evolve.

Ecological factors

For altruism to be able to evolve there has to be a sufficiently high benefit-to-cost ratio associated with the act of helping. Two main mechanisms for creating high benefit-to-cost ratios have been suggested. One of these, the ‘life insurance’ mechanism can occur in species displaying parental care. According to the ‘life insurance’ mechanism, the individuals raise their offspring in such groups that the orphaned offspring will be brought up by other individuals belonging to the same group (Gadagkar 1990). The other, a so-called ‘fortress defence’ mechanism can arise in the context of agonistic interactions, where the group of individuals have a better chance to defend a shared resource that they would not be able to defend on their own (Queller and Strassmann 1998). However, these mechanisms are relatively specific and neither of them appear to apply to most of the social vertebrates, which led Queller and Strassmann (1998) to conclude that the hope for a universal ecological explanation of cooperative social systems may be in vain.

It has also been proposed that ecological constraints can facilitate helping behaviour. The ecological constraints hypothesis proposes that helping could be favoured in the environments in which the perspective of gaining direct fitness through independent breeding is limited and by helping relatives, individuals are simply making the best out of a bad situation (Emlen 1982, Dickinson and Hatchwell 2004). The ecological constraints hypothesis is supported by the substantial empirical evidence obtained from the cooperatively breeding vertebrates (Hannon *et al.* 1985, Pruett-Jones and Lewis 1990, Komdeur 1992, Harris *et al.* 1995, Dickinson 2004, Bergmüller *et al.* 2005, Stiver *et al.* 2006, Lucia *et al.* 2008, Heg *et al.* 2010, Schoepf and Schradin 2012). However, there is a lack of theoretical support for this hypothesis without invoking direct fitness benefits of helping (Pen and Weissing 2000).

Conflict over sex allocation

Sex allocation refers to the problem of allocating parental resources into producing male and female offspring. In the simplest scenario, selection should favour an unbiased sex allocation at the population level (Fisher 1930). Trivers and Hare (1976) were first to formalize the conflict over sex ratio between the mother-queens and daughter-workers in the eusocial Hymenoptera that arises from the asymmetries relatedness between the members of the colony. They combined sex ratio theory (Fisher 1930) with inclusive fitness theory (Hamilton 1964*a*, *b*) and parent-offspring conflict (Trivers 1974) to show that, while the queen prefers an equal allocation between the two sexes, workers prefer to allocate three times as many resources to the females than to the males.

Resource allocation to reproduction versus growth

One of the most important trade-offs in the life-history of an organism is the allocation of resources between reproduction and growth (Stearns 1992). Allocating resources to somatic growth increases the expected future reproduction, while reproduction provides immediate gains in fitness. The morphological castes of an eusocial insect colony can be interpreted as representing different kinds of effort of a superorganism: workers represent the somatic effort and sexual offspring (new queens and males) represent the reproductive effort. Analogous to the life-history studies of individual organisms one can therefore ask: what is the optimal resource allocation strategy in an eusocial insect colony?

Macevicz and Oster (1976) showed that the optimal resource allocation schedule of an annual eusocial colony proceeds in two distinct phases. First, all effort is directed towards producing workers (ergonomic phase) until a switch happens and then all effort is directed towards producing sexual offspring (reproductive phase) (Macevicz and Oster 1976). This evolutionarily stable strategy of optimal growth is called a 'bang-bang' strategy and it is also found in many annual organisms.

I pointed out in the previous section that there is a conflict between the queen and the workers over sex ratio, such that the queen prefers an unbiased sex ratio whereas the workers prefer a female-biased sex ratio. Can the conflict over sex ratio between the queen and the workers influence the resource allocation between colony growth versus reproductive effort? In past decades, there has been considerable debate over this question. Pamilo (1991) argued that workers should prefer to invest more resources into new queens than workers in contrast to the preference of the queen. Bourke and Chan (1999) pointed out that both parties should prefer the same allocation in order to maximize the production of sexual individuals. Subsequently, Bourke and Ratnieks (1999) suggested that conflict between workers and the queen could arise over the developmental fate of female larvae, with workers preferring a higher amount of female larvae to develop into new queens. Reuter and Keller (2001) showed that, if both parties have means to influence the resource allocation decision, then the conflict over sex allocation results in an overall loss in productivity of the colony, as less than the optimal amount of resources are allocated to worker production. The authors also predicted that the sex ratio among sexual offspring in such a colony should be intermediate between the optima of the queen and the workers. However, their model did not explicitly include time-dependent decision making throughout a colony's ontogeny.

Aims of the thesis

My thesis provides new insights into the theory of social evolution by linking ecology and life-history to some of the fundamental questions of social evolution theory: origin of altruism, conflict between the queen and the workers over sex allocation in eusocial colonies, and the evolution of co-foundress associations with low average level of relatedness.

More specifically, in the first chapter (study I), I demonstrate how ecology and life-history characteristics of a species can affect the origin of altruistic behaviour. I compare how different population regulation mechanisms can effect the evolution of altruistic traits.

In the second chapter (study II), I consider the classical sex ratio conflict between the queen and the workers, taking into account colony ontogeny by explicitly accounting for the population dynamics of colony growth. I study the conflict resolution under different scenarios of power that the workers and the queen have over resource allocation decisions. My analysis provides predictions that make these scenarios empirically distinguishable.

In the third chapter (study III), I considered the optimal reproductive tactics of facultatively cooperative insects. I wanted to study how co-foundress associations and costly helping can evolve in species with a low average level of relatedness.

METHODS

In Chapter I, I use a general population genetic model (Oster *et al.* 1977, Nowak *et al.* 2010, Fromhage and Kokko 2011) which allows to track the demographic and genotypic composition of a population over ecological and evolutionary time. I consider the stable asymptotic state of the population in order to study the long-term evolutionary outcomes of the population under different ecological conditions. I also re-derive some of these results using a direct fitness approach (Taylor and Frank 1996, Pen and Weissing 2000) to show how they relate to previous work on ecological constraints and the evolution of helping behaviour.

In Chapter II, I first use an invasion fitness approach (Lehmann *et al.* 2016). Invasion fitness which is defined as the geometric growth rate (or growth ratio) of the mutant allele in a population, where the mutant allele remains rare in the population. I then use optimal control theory (Sydsæter *et al.* 2008, Bryson and Ho 1975) together with dynamic game theory (Bryson and Ho 1975, Mazalov 2014) to derive the first-order conditions for uninvadability. An uninvadable strategy, in this context, is a strategy that is resistant to the invasion of any mutant strategy and hence it is evolutionarily stable. In addition to finding the first-order conditions for uninvadability, I also used a computational method called the iteration of the best response map (Houston and McNamara 1999), combined with a numerical solver for the problems of optimal control theory, called GPOPS (Patterson and Rao 2014), which uses a direct collocation approach along with various non-linear optimization methods to determine the uninvadable strategies.

In Chapter III, I develop a time and context-dependent model of cooperative breeding, using the iteration of the best response map (with errors in decision making) to find evolutionarily stable strategies (Houston and McNamara 1999).

Note that in Chapter II I use the term 'uninvadable strategy' and in Chapter III, I use 'evolutionarily stable strategy'. I make this distinction because in the first chapter I also provide the local first order conditions for stability in addition to the (global) optimum found by iteration of the best response map. More detailed information about the mathematical methods of these models can be found in the respective chapters.

RESULTS

Chapter I: No synergy needed: ecological constraints favor the evolution of eusociality

The aim of this study is to show how different types of density dependence mechanisms can affect the evolution of eusociality and helping behaviour in general. I also demonstrate that density-dependent mechanisms can interact with the life-history traits to create favourable conditions for the altruistic behaviour to evolve, even if the helpers are relatively inefficient at helping. I use a general population genetic model that incorporates two realistic ecological mechanisms of population regulation: (1) 'fecundity limitation,' in which the resources that affect fecundity are limited and shared between the breeding individuals, and (2) 'nest-site limitation,' where population growth is regulated by having a fixed number of breeding positions or territories available to the individuals. My model allows to draw comparisons between the two density-dependent mechanisms under different genetic systems (haplodiploidy and diplodiploidy), mating systems (monandry and biandry), and the sex-specific predispositions for helping.

I show that nest-site limitation strongly favours the evolution of helping behaviour even if the helpers are relatively inefficient. I also find that the interactions between density dependent mechanisms and life-history traits can have a strong effect on the evolution of social behaviour. For example, I found that high intrinsic fecundity promotes altruistic behaviour if subjected to the nest-site limitation, but not in the case of fecundity limitation. Conversely, high mortality of dispersing individuals promotes altruistic behaviour in the event of fecundity limitation but not in the case of nest-site limitation.

Existing models of social evolution incorporate density dependence by either assuming nest-site limitation or fecundity limitation, but there is only one theoretical study (Pen and Weissing 2000) that has attempted a comparison between these two. Surprisingly, Pen and Weissing (2000) reached the contradictory conclusion mainly that, in the absence of direct fitness benefits of helping, such as nest (territory) inheritance, ecological constraints become irrelevant to the evolution of helping. At the heart of this apparent discrepancy with my results is their implicit assumption that efficiency of helping (number of individuals reared by the helper) is independent of ecological conditions (density dependent mechanisms that regulate population growth) and species-specific characteristics, such as the average number of individuals raised by the mother on her own (intrinsic fecundity of the species). I argue that this assumption is potentially misleading by giving the following example. Let us say that in a given species and at an ecological setting, unaided breeders can rear 0.5 offspring per time unit. Then, for a helper to rear one additional sibling per time unit, the helper would need to be twice as efficient as her mother, which implies synergistic interactions of an improbable magnitude. However, in species in which unaided breeders are able to rear 10 offspring per time unit, the same absolute increment of one extra sibling could be achieved by a considerably less efficient helper and less stringent assumptions about the benefits of helping.

In order to demonstrate that my results are consistent with the direct fitness model (Taylor and Frank 1996) used by Pen and Weissing (2000), I re-derive their results with modifications that allow helping to be influenced by density dependence mechanisms and species-specific intrinsic fecundity. A major contribution of my analysis is to resolve the schism between empirical evidence supporting the hypothesis that ecological constraints can facilitate helping behaviour (Hannon *et al.* 1985, Pruett-Jones and Lewis 1990, Komdeur 1992, Harris *et al.* 1995, Dickinson 2004, Bergmüller *et al.* 2005, Stiver *et al.* 2006, Lucia *et al.* 2008, Heg *et al.* 2010, Schoepf and Schradin 2012) and the lacking theoretical support for this hypothesis. We do not need to invoke direct fitness benefits of helping, such as nest (territory) inheritance, to predict that ecological constraints can influence the evolution of helping.

Chapter II: Sex ratio conflict affects colony growth in annual haplodiploid social insects

Colonies of eusocial insects, much like individual organisms, have to decide how to allocate resources between reproduction and growth. This represents a central life-history trade-off, common to all organisms and super-organisms alike. However, in contrast to different cells in multicellular organisms, individuals in eusocial insect colonies have diverging reproductive optima. For example, in an outbred population, with a single monandrous queen per colony, queens prefer to allocate resources equally among male and female (sexual) offspring, while the workers prefer to invest three times as much resources to females than to males. I study how the conflict over sex allocation can affect the ontogeny of the colony by linking together the dynamics of colony growth with the conflict over sex allocation.

In my analysis, I consider different scenarios of power that workers and the queen can have over the reproductive decisions in the colony, ‘power’ being the ability of a certain party to act towards their fitness optimum. I show that if both parties have some control over the reproductive decision making, then the conflict over sex allocation can give rise to a suboptimal pattern of colony growth, in a way that worker production halts earlier in the season than it would be optimal for maximizing the overall productivity of the colony. The timing of the switch from worker production (ergonomic phase) to producing sexual offspring (reproductive phase) depends on how the power over resource allocation decisions is distributed between the queen and the workers. I reveal how the timing of the switch is affected by life-history traits, such as mortality rates of the individuals in the colony and the per capita productivity of the colony. I also show that the queen is in a strong position to enforce her preference of allocating resources between different sexual offspring. I also show that the queen mating frequency reduces the conflict between the workers and the queen and thus affects the switching time. My model provides testable predictions for the determination of how reproductive decision making is divided between the workers and the queen.

My study shows that conflict resolution which incorporates time-dependent decision making can be different from conflict resolution that averages decisions over time. This highlights the importance of considering the dynamic properties of conflict resolution mechanisms, since the predictions can be qualitatively different compared to time independent conflict resolution mechanisms.

Chapter III: Co-foundress associations in primitively eusocial wasps: a game theoretical approach

Most social insect groups are overwhelmingly composed of close relatives. Intriguingly, there are examples of unrelated helpers in some co-foundress associations that occur in certain ant (Bernasconi and Strassmann 1999) and wasp species (Gadagkar 2016, Field and Leadbeater 2016, Liebert *et al.* 2005). Although relatedness between social partners will, in general, facilitate the evolution of helping behaviour, kin selection seems to be less important in these systems. Moreover, empirical evidence suggests that unrelated females join other nests as subordinates because of the possibility of ultimately inheriting the nest (Leadbeater *et al.* 2011). Nevertheless, for closely related subordinates in the nest, the indirect fitness benefits usually outweigh the direct fitness benefits in this species (Leadbeater *et al.* 2011). The reason behind the unrelated helpers engaging in costly helping behaviour that reduces their chances of inheriting the nest and the low level of re-occurring associations between related wasps remains perplexing.

I show that the high pre-reproductive investment into the nest facilitates co-foundress associations and costly helping even in a population with low average relatedness between the co-foundresses. However, costly only helping takes place during the initial stages of the nesting cycle and halts when the production of sexual offspring begins. Hence, costly helping during the reproductive phase can only evolve if the relatedness between the co-foundresses is high. My model shows that helping at different life cycle stages can be promoted by different ecological factors, sometimes this being followed by aggressiveness in an ultimately selfish strategy.

My model suggests that high costs of building the structure of the nest and producing the first non-reproductive brood may be an important factor in wasp species with very low average relatedness between the co-foundresses. Indeed, there is some empirical evidence to suggest that the structure of the nest of wasp species that exhibit alloparental care is more costly to produce since it contains more protein (Hunt 2007). However, the amount of pre-reproductive investment observed in social wasps today may not be representative of the ancestral conditions under which the co-foundress associations evolved. Since the solitary ancestors of such species must have been reasonably capable of reaching the reproductive phase alone, it appears likely that high requirements of pre-reproductive investment may have evolved after cooperative nesting was already common. Therefore, high relatedness between co-foundresses may have been more important in the initial stages of the evolution of co-foundress associations.

CONCLUSIONS

The fundamental premise of the social evolution theory is that altruistic behaviour can arise through natural selection only if altruistic acts are directed towards the other individuals who also carry the altruistic genes. Hamilton's rule outlines the theoretical foundation for explaining the fundamental conditions under which the altruistic behaviours can evolve. Consequently, determining the underlying factors that increase relatedness between social partners and produce sufficiently high benefit-to-cost ratios associated with the act of altruism are of paramount importance.

Whilst making predictions solely based on relatedness has been relatively straightforward, deriving the benefits and costs of helping in an ecological and life-history context is often challenging. This thesis extends the social evolution theory by showing which ecological conditions and life-history traits are able to facilitate the emergence of specialized cooperative societies. This study resolved some of the issues arising with earlier theoretical work, that provided little support for the hypothesis that ecological constraints can favour helping behaviour, a hypothesis which currently possesses substantial empirical support. I also showed that incorporating life-history and population dynamics of the colony can significantly improve the classical understanding of conflict and cooperation within insect societies. I studied the classical problem of sex ratio conflict in the light of life-history theory and showed that the theoretical predictions differ significantly between the classical models and models that incorporate the life-history of the species. I also proposed a new model for the cooperatively breeding societies, in which time and context-dependent decisions reveal a huge variation between conflict and cooperation at different phases of the life cycle. This model assists in clarification of the role of relatedness for group formation, nest building, and helping during different phases of the life cycle.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Uusia oivalluksia ekologian ja elinkierron merkityksestä sosiaalisuuden evoluutiossa

Darwinistinen ajatus ”olemassaolon kamppailusta” sisältää näennäisesti ajatuksen, että luonnonvalinta suosii itsekkäästi toimivia yksilöitä. Eläimet eivät kuitenkaan aina toimi itsekkäästi ja toisinaan jokin yksilö saattaa jopa uhrata oman henkensä toisten puolesta. Havaitsemme tällaista altruistista toimintaa luonnossa, ja erityisesti sitä esiintyy sosiaalisten hyönteisten (muurahaiset, mehiläiset, ampiaiset ja termiitit), ihmisten ja lintujen keskuudessa. Yleisesti ottaen epäitsekästä ja yhteistyötä tekevää käytöstä tavataan kaikilta biologisten organisaatioiden tasoilta, esimerkiksi solujen, geenien ja mikro-organismien välillä. Kuinka luonnonvalinta voi suosia yksilöitä, jotka toimivat altruistisesti?

Luonnonvalinta suosii epäitsekästä toimintaa, jos sitä ohjaavien geenien kopioita siirtyy menestyksekkäästi sukupolvelta toiselle. Yksilöt voivat siirtää altruistista toimintaa ohjaavia geenejä eteenpäin lisääntymisen ohella myös auttamalla sukulaisiaan lisääntymään, sillä heillä voi myöskin olla suurella todennäköisyydellä kopioita näistä geeneistä. Hamiltonin säännön mukaan luonnonvalinta voi suosia altruismiin ohjaavaa geeniä, jos hyöty b vastaanottajalle kerrottuna vastaanottajan ja toimijan välisen geneettisen sukulaisuuden asteella r on suurempi kuin haitta c toimijalle, toisin sanoen luonnonvalinta voi olla suosiollinen jos $rb > c$. Hamiltonin sääntö ottaa huomioon molemmat tavat siirtää geenejä seuraavalle sukupolvelle ja asettaa yleisen ehdon sille, milloin luonnonvalinta suosii altruistista käyttäytymistä. Tässä väitöskirjassa hyötyjä ja haittoja mitataan lisääntymiskelpoisuuden mukaan. Yksilöiden välisen sukulaisuuden mittaaminen on suoraviivaista, mutta mitä Hamiltonin säännön hyöty b ja haitta c tarkoittavat ekologiassa ja yksilön elämänkierron suhteen on vähemmän selkeää. Suuri osa teoreettisesta tutkimuksesta on toistaiseksi keskittynyt kehittämään yleisiä malleja sosiaalisesta käyttäytymisestä ja erityisesti on painotettu mekanismeja, jotka lisäävät sosiaalisten partnereiden sukulaisuuden astetta. Edelleen on kuitenkin tarvetta yksityiskohtaisemmille malleille, jotka antavat selkeitä ennusteita, ja joita voi soveltaa todellisiin ekologisiin ja elinkierrollisiin systeemeihin. Tämä väitöskirja täyttää tätä aukkoa ja tarjoaa useita uusia oivalluksia liittyen ekologian ja elinkierron rooliin erilaisten sosiaalisten vuorovaikutusten yhteydessä.

Ensimmäisessä kappaleessa kehitän mallin, joka sisältää realistisia ekologisia populaation sääntelymekanismeja ja vertaan kuinka erilaiset sääntelymekanismit vaikuttavat auttamiskäyttäytymisen evoluutioon. Osoitan, että pesäpaikkojen rajoittaminen suosii vahvasti auttamiskäyttäytymisen evoluutiota, ja että tämä pätee vaikka auttaminen olisi suhteellisen tehotonta. Osoitan myös, että populaatiotiheydestä riippuvien ja elinkierrollisten ominaisuuksien vuorovaikutukset voivat merkittävästi vaikuttaa sosiaalisen käyttäytymisen evoluutioon. Korkea luontainen fertiliteetti edistää altruistista käyttäytymistä, kun pesäpaikkoja on rajallisesti, mutta tämä ei päde, jos fertiliteettiä rajoitetaan. Kääntäen, korkea kuolleisuus liikkuvien yksilöiden kesken edistää altruistista käyttäytymistä, kun fertiliteettiä rajoitetaan, mutta ei jos pesäpaikkojen määrää rajoitetaan.

Toisessa kappaleessa kehitän aitososiaalisille hyönteisyhdyskunnille resurssiallokaatiomallin, joka sisältää pesän kasvudynamiikan ja mallintaa kuningattaren ja työläisten välisen epäsuhtaisen sukupuolijakauman konfliktin. Osoitan, että konflikti sukupuolijakaumassa johtaa epäoptimaaliseen kolonian kasvuun samalla kun kuningatar voittaa kyseisen konfliktin. Mallini tuottaa testattavia ennusteita siitä, miten lisääntymispäätökset jakautuvat kuningattaren ja työläisten välillä. Se myös korostaa konfliktien ratkaisumekanismien dynaamisia ominaisuuksia, sillä sen ennusteet voivat olla kvalitatiivisesti erilaisia verrattuna ajasta riippumattomiin ratkaisumekanismeihin.

Kolmannessa kappaleessa tutkin optimaalisia lisääntymistaktiikoita fakultatiivisesti yhteistyötä tekevillä ampiaisilla. Osoitan, että pesien yhteisperustamista ja auttamista oman edun kustannuksella voi kehittyä jopa sellaisissakin populaatioissa, joissa keskimääräinen sukulaisuuden aste pesän perustajien välillä on pieni. Tämä on kuitenkin mahdollista vain pesimissyklin alkuvaiheessa eikä enää lisääntymisvaiheessa. Auttaminen oman edun kustannuksella lisääntymisvaiheessa voi kehittyä vain, jos perustajien välinen sukulaisuuden aste on korkea. Mallini osoittaa, että erilaiset ekologiset tekijät voivat edistää auttamisen kehittymistä eri elämän vaiheissa, ja toisinaan tämä on osa pohjimmiltaan itsekästä strategiaa johon liittyy auttamisen jälkeinen aggressiivisuus.

Yhteenvetona tämä väitöskirja havainnollistaa ekologisten ja elinkierrollisten tekijöiden tärkeyttä sosiaalisten vuorovaikutusten tutkimisessa aina yleisesti auttamiskäyttäytymisen alkuvaiheista konfliktien ratkaisemiseen aitososiaalisissa hyönteisyhdyskunnissa.

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ORIGINAL PAPERS

I

NO SYNERGY NEEDED: ECOLOGICAL CONSTRAINTS FAVOR THE EVOLUTION OF EUSOCIALITY

by

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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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portunities 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

$$f(n) = f_0[1 + b(n-1)] \tag{1}$$

and

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

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) being 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

$$\frac{\mathrm{d}x_\pi}{\mathrm{d}t} = \sum_{k=1}^{K}\sum_{n=1}^{N}[f(n)X_{k,n}(1-q_{\pi,n})\omega_{\pi,k}] - x_\pi\left(m_\mathrm{x} + \beta\sum_{\pi} y_\pi\right) \tag{3}$$

(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

$$\frac{\mathrm{d}y_\pi}{\mathrm{d}t} = \sum_{k=1}^{K}\sum_{n=1}^{N}[f(n)X_{k,n}(1-q_{\pi,n})\omega_{\pi,k}] - y_\pi m_\mathrm{y} \tag{4}$$

(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

$$\frac{\mathrm{d}X_{k,1}}{\mathrm{d}t} = \beta\chi_k - [\varphi_{k,1}f(1) + m(1)]X_{k,1} + m_\mathrm{h}X_{k,2} \tag{5}$$

(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

$$\begin{aligned}\frac{\mathrm{d}X_{k,n}}{\mathrm{d}t} &= \varphi_{k,n-1}f(n-1)X_{k,n-1}\\ &\quad - [\varphi_{k,n}f(n) + m(n) + (n-1)m_\mathrm{h}]X_{k,n} + nm_\mathrm{h}X_{k,n+1}\end{aligned} \tag{6}$$

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

$$\frac{\mathrm{d}X_{k,N}}{\mathrm{d}t} = \varphi_{k,N-1}f(N-1)X_{k,N-1} - [m(N) + (N-1)m_\mathrm{h}]X_{k,N} \tag{7}$$

(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

$$\phi(D_i, C_i) = \begin{cases} 1 - \dfrac{D_i}{C_i} & D_i \le C_i \\ 0 & D_i > C_i \end{cases}. \tag{8}$$

In order to model fecundity limitation, we limit breeders' fecundity by replacing $f(n)$ with $\phi(D_\mathrm{T}, C_\mathrm{T})f(n)$, where $D_\mathrm{T} = \sum_n\sum_k nX_{k,n} + \sum_\pi(x_\pi + y_\pi)$ is total population density and C_T is its carrying capacity. Alternatively, to model nest-site limitation, we replace β with $\phi(D_\mathrm{B}, C_\mathrm{B})\beta$, where $D_\mathrm{B} = \sum_n\sum_k X_{k,n}$ 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 $C_\mathrm{B} - D_\mathrm{B}$), 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,

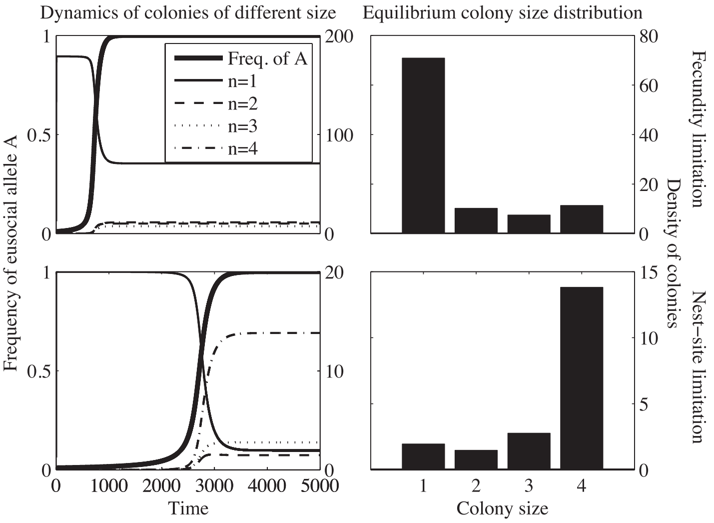

Figure 1: Dynamics of colonies of different size and the respective equilibrium colony size distributions when a recessive eusocial allele *A* invades: frequency of eusocial allele *A* (bold solid line), colonies of size $n = 1$ (solid line), colonies of size $n = 2$ (dashed line), colonies of size $n = 3$ (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

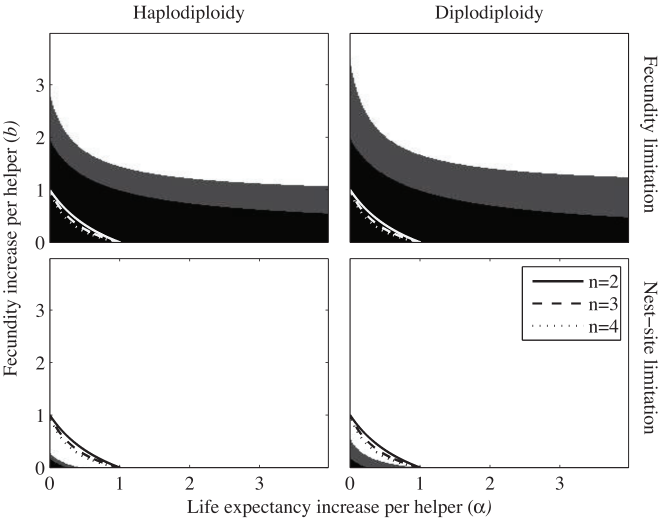

Figure 2: Evolution and stability of a recessive eusocial allele A in social benefits parameter space (b; α) under monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 1$, $\beta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

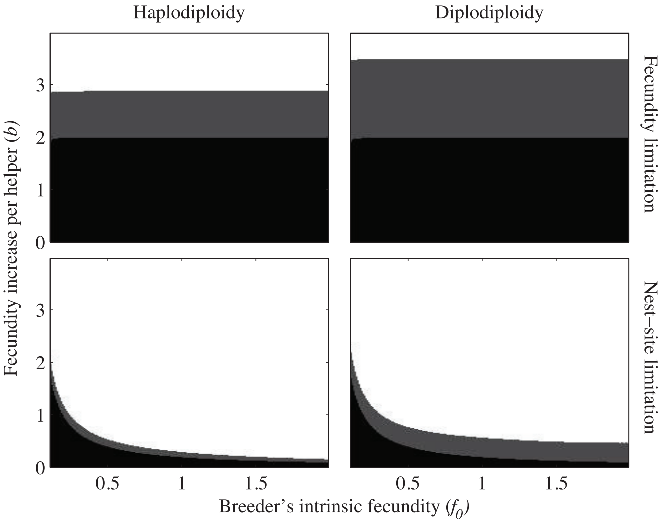

Figure 3: Evolution and stability of a recessive eusocial allele A in parameter space (b; f_0) under monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $\beta = 0.1$, $m_0 = m_x = m_y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

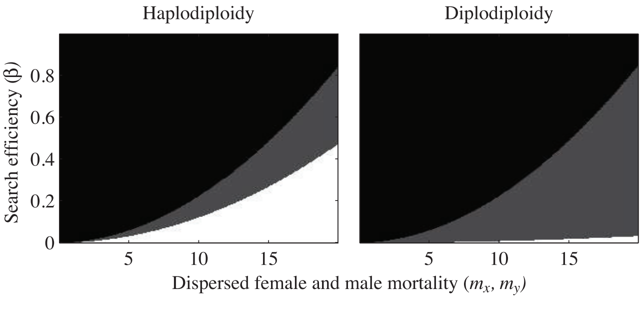

Figure 4: Evolution and stability of a recessive eusocial allele A in parameter space (β; (m_x, m_y)) under fecundity limitation and monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4,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

Acknowledgments

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Appendix A from P. Avila and L. Fromhage, “No Synergy Needed: Ecological Constraints Favor the Evolution of Eusociality” (Am. Nat., vol. 186, no. 1, p. 000)

Supplementary Tables for Methods

Table A1: Colony types and offspring genotypes under haplodiploidy and monandry

k	Female	Male	χ_k	$\omega_{AA,k}$	$\omega_{Aa,k}$	$\omega_{aa,k}$	$\omega_{A,k}$	$\omega_{a,k}$
1	*AA*	*A*	$x_{AA}y_A$	1	0	0	1	0
2	*AA*	*a*	$x_{AA}y_a$	0	1	0	1	0
3	*Aa*	*A*	$x_{Aa}y_A$	1/2	1/2	0	1/2	1/2
4	*Aa*	*a*	$x_{Aa}y_a$	0	1/2	1/2	1/2	1/2
5	*aa*	*A*	$x_{aa}y_A$	0	1	0	0	1
6	*aa*	*a*	$x_{aa}y_a$	0	0	1	0	1

Note: χ_k is proportional to the rate of type *k* colony foundation (reflecting availability of dispersers with suitable genotypes); $\omega_{\pi,k}$ is the proportion of offspring of a given sex with genotype π born in colony *k*, assuming haplodiploidy and monandry.

Table A2: Colony types and offspring genotypes under diplodiploidy and monandry

k	Mate 1	Mate 2	χ_k	$\omega_{AA,k}$	$\omega_{Aa,k}$	$\omega_{aa,k}$
1	*AA*	*AA*	$x_{AA}y_{AA}$	1	0	0
2	*AA*	*Aa*	$x_{AA}y_{Aa} + x_{Aa}y_{AA}$	1/2	1/2	0
3	*AA*	*aa*	$x_{AA}y_{aa} + x_{aa}y_{AA}$	0	1	0
4	*Aa*	*Aa*	$x_{Aa}y_{Aa}$	1/4	1/2	1/4
5	*Aa*	*aa*	$x_{Aa}y_{aa} + x_{aa}y_{Aa}$	0	1/2	1/2
6	*aa*	*aa*	$x_{aa}y_{aa}$	0	0	1

Note: χ_k is proportional to the rate of type *k* colony foundation (reflecting availability of dispersers with suitable genotypes); $\omega_{\pi,k}$ is the proportion of offspring of a given sex with genotype π born in colony *k*, assuming diplodiploidy and monandry.

Table A3: Colony types and offspring genotypes under haplodiploidy and biandry

k	Female	Males	χ_k	$\omega_{AA,k}$	$\omega_{Aa,k}$	$\omega_{aa,k}$	$\omega_{A,k}$	$\omega_{a,k}$
1	*AA*	(*A*, *A*)	$x_{AA}y_A^2/\sum_\pi y_\pi$	1	0	0	1	0
2	*AA*	(*A*, *a*) or (*a*, *A*)	$2x_{AA}y_Ay_a/\sum_\pi y_\pi$	1/2	1/2	0	1	0
3	*AA*	(*a*, *a*)	$x_{AA}y_a^2/\sum_\pi y_\pi$	0	1	0	1	0
4	*Aa*	(*A*, *A*)	$x_{Aa}y_A^2/\sum_\pi y_\pi$	1/2	1/2	0	1/2	1/2
5	*Aa*	(*A*, *a*) or (*a*, *A*)	$2x_{Aa}y_Ay_a/\sum_\pi y_\pi$	1/4	1/2	1/4	1/2	1/2
6	*Aa*	(*a*, *a*)	$x_{Aa}y_a^2/\sum_\pi y_\pi$	0	1/2	1/2	1/2	1/2
7	*aa*	(*A*, *A*)	$x_{aa}y_A^2/\sum_\pi y_\pi$	0	1	0	0	1
8	*aa*	(*A*, *a*) or (*a*, *A*)	$2x_{aa}y_Ay_a/\sum_\pi y_\pi$	0	1/2	1/2	0	1
9	*aa*	(*a*, *a*)	$x_{aa}y_a^2/\sum_\pi y_\pi$	0	0	1	0	1

Note: χ_k is proportional to the rate of type *k* colony foundation (reflecting availability of dispersers with suitable genotypes); $\omega_{\pi,k}$ is the proportion of offspring of a given sex with genotype π born in colony *k*, assuming haplodiploidy and biandry. In column χ_k, the division by $\sum_\pi y_\pi$ ensures that mating with two males takes the same amount of time as mating with one male in the monandry case. We make this assumption to focus on the effect of shared paternity in the comparison between monandry and biandry. This assumption is reasonable if males are numerous and/or occur in the habitat in a clumped fashion, so that a female that finds one male usually find a second male close by.

Table A4: Colony types and offspring genotypes under diplodiploidy and biandry

k	Female	Males	χ_k	$\omega_{AA,k}$	$\omega_{Aa,k}$	$\omega_{aa,k}$
1	*AA*	(*AA*, *AA*)	$x_{AA}y_{AA}^2/\sum_\pi y_\pi$	1	0	0
2	*AA*	(*AA*, *Aa*) or (*Aa*, *AA*)	$2x_{AA}y_{AA}y_{Aa}/\sum_\pi y_\pi$	3/4	1/4	0
3	*AA*	(*AA*, *aa*) or (*aa*, *AA*)	$2x_{AA}y_{AA}y_{aa}/\sum_\pi y_\pi$	1/2	1/2	0
4	*AA*	(*Aa*, *Aa*)	$x_{AA}y_{Aa}^2/\sum_\pi y_\pi$	1/2	1/2	0
5	*AA*	(*Aa*, *aa*) or (*aa*, *Aa*)	$x_{AA}y_{Aa}y_{aa}/\sum_\pi y_\pi$	1/4	3/4	0
6	*AA*	(*aa*, *aa*)	$x_{AA}y_{aa}^2/\sum_\pi y_\pi$	0	1	0
7	*Aa*	(*AA*, *AA*)	$x_{Aa}y_{AA}^2/\sum_\pi y_\pi$	1/2	1/2	0
8	*Aa*	(*AA*, *Aa*) or (*Aa*, *AA*)	$2x_{Aa}y_{AA}y_{Aa}/\sum_\pi y_\pi$	3/8	1/2	1/8
9	*Aa*	(*AA*, *aa*) or (*aa*, *AA*)	$2x_{Aa}y_{AA}y_{aa}/\sum_\pi y_\pi$	1/4	1/2	1/4
10	*Aa*	(*Aa*, *Aa*)	$x_{Aa}y_{Aa}^2/\sum_\pi y_\pi$	1/4	1/2	1/4
11	*Aa*	(*Aa*, *aa*) or (*aa*, *Aa*)	$x_{Aa}y_{Aa}y_{aa}/\sum_\pi y_\pi$	1/8	1/2	3/8
12	*Aa*	(*aa*, *aa*)	$x_{Aa}y_{aa}^2/\sum_\pi y_\pi$	0	1/2	1/2
13	*aa*	(*AA*, *AA*)	$x_{aa}y_{AA}^2/\sum_\pi y_\pi$	0	1	0
14	*aa*	(*AA*, *Aa*) or (*Aa*, *AA*)	$2x_{aa}y_{AA}y_{Aa}/\sum_\pi y_\pi$	0	3/4	1/4
15	*aa*	(*AA*, *aa*) or (*aa*, *AA*)	$2x_{aa}y_{AA}y_{aa}/\sum_\pi y_\pi$	0	1/2	1/2
16	*aa*	(*Aa*, *Aa*)	$x_{aa}y_{Aa}^2/\sum_\pi y_\pi$	0	1/2	1/2
17	*aa*	(*Aa*, *aa*) or (*aa*, *Aa*)	$x_{Aa}y_{Aa}y_{aa}/\sum_\pi y_\pi$	0	1/4	3/4
18	*aa*	(*aa*, *aa*)	$x_{aa}y_{aa}^2/\sum_\pi y_\pi$	0	0	1

Note: χ_k is proportional to the rate of type k colony foundation (reflecting availability of dispersers with suitable genotypes); $\omega_{\pi,k}$ is the proportion of offspring of a given sex with genotype π born in colony k, assuming diplodiploidy and biandry.

Table A5: Probability of helping gene being expressed

$q_{\pi,n}$ (colony size)	Dominant allele *A*	Recessive allele *A*
$q_{AA,n}$ $(n < N)$	1	1
$q_{Aa,n}$ $(n < N)$	1	0
$q_{aa,n}$ $(n < N)$	0	0
$q_{AA,n}$ $(n = N)$	0	0
$q_{Aa,n}$ $(n = N)$	0	0
$q_{aa,n}$ $(n = N)$	0	0
$q_{A,n}$ $(n < N)$	1	1
$q_{a,n}$ $(n < N)$	0	0
$q_{A,n}$ $(n = N)$	0	0
$q_{a,n}$ $(n = N)$	0	0

Note: The probability $q_{\pi,n}$ of an offspring of genotype π staying in a colony of size n as a helper if the eusocial allele *A* is dominant or recessive. If only females can become helpers, then $q_{\pi,n} = 0$ for all males, regardless of genotype and colony size.

Table A6: The dynamics of dispersed females with genotype π follow $dx_\pi/dt = \sum v_i$, with summands v_i as specified

Term	Biological meaning
$v_1 = \sum_k \sum_n f(n)X_{k,n}(1 - q_{\pi,n})\omega_{\pi,k}$	Daughters disperse from colonies of any type and size
$v_2 = -x_\pi \beta \sum_\pi y_\pi$	Dispersed females become breeders
$v_3 = -x_\pi m_x,$	Dispersed female mortality

Table A7: The dynamics of dispersed males with genotype π follow $dy_\pi/dt = \sum v_i$, with summands v_i as specified

Term	Biological meaning
$v_1 = \sum_k \sum_n f(n)X_{k,n}(1 - q_{\pi,n})\omega_{\pi,k}$	Sons disperse from colonies of any type and size
$v_2 = -y_\pi m_y$	Dispersed male mortality

Table A8: The dynamics of colonies $X_{k,n}$ of type k and size $n = 1$ (breeders without helpers) follow $\mathrm{d}X_{k,n}/\mathrm{d}t = \sum v_i$, with summands v_i as specified

Term	Biological meaning
$v_1 = \beta\chi_k$	Rate at which new colonies of type k are founded
$v_2 = -\varphi_{k,n}f(n)X_{k,n}$	Colonies leave the focal size category by helper production
$v_3 = -m(n)X_{k,n}$	Colonies decay through breeder death
$v_4 = m_\mathrm{h}X_{k,n+1}$	Colonies enter the focal size category by helper death in a larger colony

Table A9: The dynamics of colonies $X_{k,n}$ of type k and intermediate size n (with $1 < n < N$) follow $\mathrm{d}X_{k,n}/\mathrm{d}t = \sum v_i$, with summands v_i as specified

Term	Biological meaning
$v_1 = \varphi_{k,n-1}f(n-1)X_{k,n-1}$	Colonies enter the focal size category by helper production in a smaller colony
$v_2 = -\varphi_{k,n}f(n)X_{k,n}$	Colonies leave the focal size category by helper production
$v_3 = -m(n)X_{k,n}$	Colonies decay through breeder death
$v_4 = -(n-1)m_\mathrm{h}X_{k,n}$	Colonies leave the focal size category through helper death
$v_5 = nm_\mathrm{h}X_{k,n+1}$	Colonies enter the focal size category through helper death in a larger colony

Table A10: The dynamics of colonies $X_{k,n}$ of type k and maximal size $n = N$ follow $\mathrm{d}X_{k,n}/\mathrm{d}t = \sum v_i$, with summands v_i as specified

Term	Biological meaning
$v_1 = \varphi_{k,n-1}f(n-1)X_{k,n-1}$	Colonies enter the focal size category by helper production in a smaller colony
$v_2 = -m(n)X_{k,n}$	Colonies decay through breeder death
$v_3 = -(n-1)m_\mathrm{h}X_{k,n}$	Colonies leave the focal size category through helper death

Table A11: Overview of symbols and variables

Symbol	Meaning
A, a	Eusocial allele, solitary allele
b	Number of extra siblings raised by a helper (per offspring the mother could raise alone)
α	Increment to a breeder's life expectancy caused by adding one more helper to her nest
β	Search efficiency coefficient
f_0	Breeders' intrinsic fecundity
$f(n)$	Breeders' fecundity in a size n colony
m_0	Breeders' intrinsic mortality
m_x, m_y, m_h, $m(n)$	Mortality of dispersed females, dispersed males, helpers, and breeders in size n colonies, respectively
χ_k	Mate encounters that give rise to colonies of type k (see tables A1–A4)
$\omega_{\pi,k}$	Proportion of offspring (of a given sex) with genotype π being produced in a type k colony
$q_{\pi,n}$	Probability that an offspring of genotype π, produced in a colony of size n, becomes a helper
$\varphi_{k,n}$	Probability that any given offspring, produced in a colony of type k and size n, becomes a helper
$X_{k,n}$	Density of colonies of type k and size n
x_π	Density of dispersed females of genotype π
y_π	Density of dispersed males of genotype π
n, N	Colony size, maximum colony size
D_T, D_B	Total population density, breeder density
C_T, C_B	Carrying capacity of total population density, carrying capacity of breeder density

Appendix B from P. Avila and L. Fromhage, “No Synergy Needed: Ecological Constraints Favor the Evolution of Eusociality” (Am. Nat., vol. 186, no. 1, p. 000)

Supplementary Figures

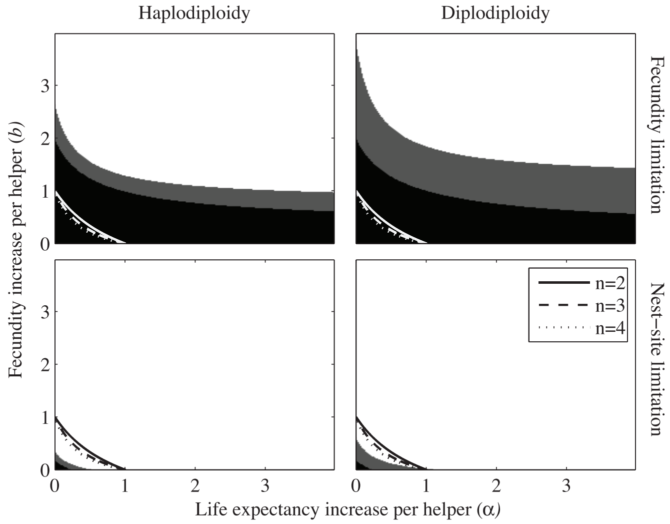

Figure B1: Evolution and stability of a dominant eusocial allele A in social benefits parameter space (b; α) under monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. 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 specified colony size n.

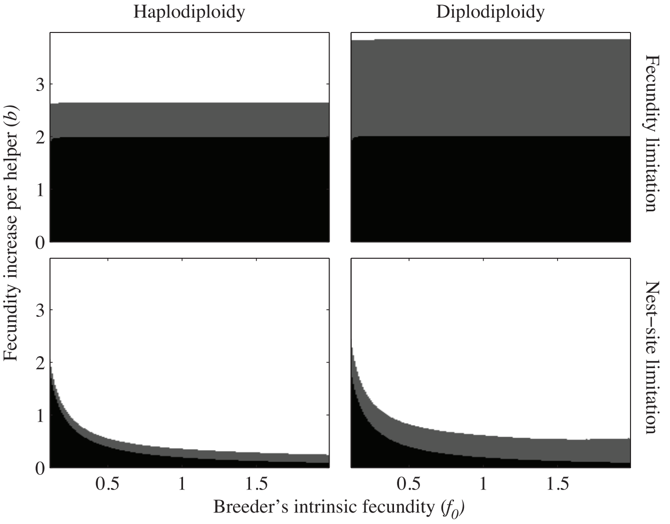

Figure B2: Evolution and stability of a dominant eusocial allele A in parameter space (b; f_0) under monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $\alpha = 0$, $C_T = 400$, $C_B = 20$. Initial conditions: (1) the frequency of allele A is 1%; (2) the frequency of allele A is 99%.

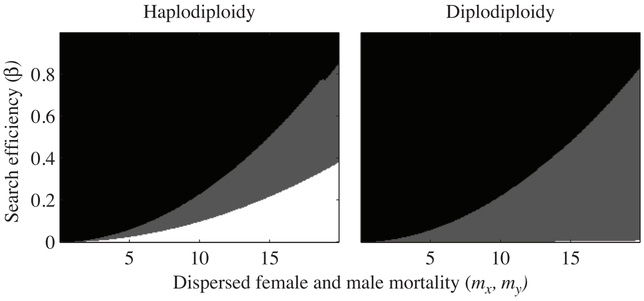

Figure B3: Evolution and stability of a dominant eusocial allele A in parameter space (β; (m_x, m_y)) under fecundity limitation and monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 100$, $m_0 = m_h = 0.1$, $b = 0.5$, $\alpha = 0$, $C_T = 400$. Initial conditions: (1) the frequency of allele A is 1%; (2) the frequency of allele A is 99%.

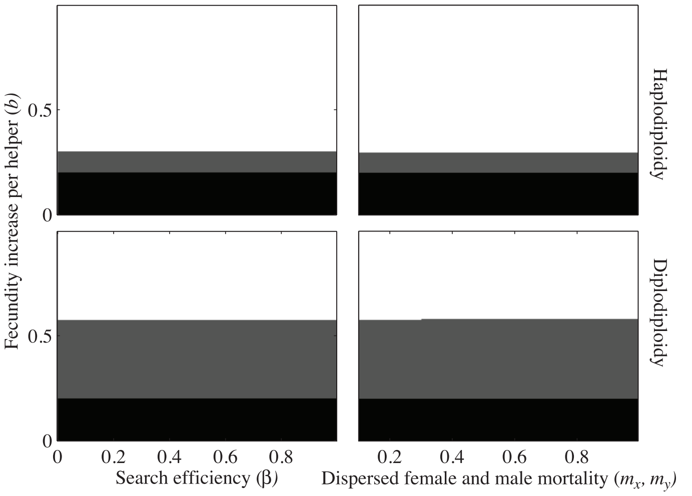

Figure B4: Evolution and stability of a recessive eusocial allele A in parameter space (β; (m_x, m_y)) under nest-site limitation and monandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $m_x = m_y = 0.1$ (if β is a variable), $\beta = 0.1$ (if m_x and m_y are variables), $N = 4$, $f_0 = 1$, $m_0 = m_h = 0.1$, $\alpha = 0$, $C_B = 20$. Initial conditions: (1) the frequency of allele A is 1%; (2) the frequency of allele A is 99%.

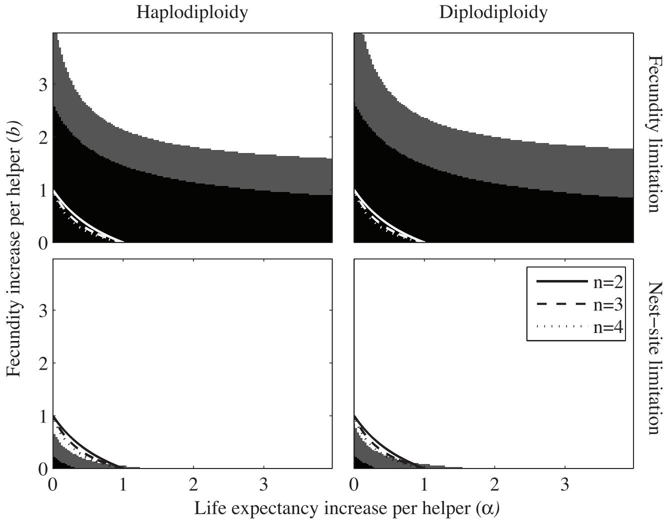

Figure B5: Evolution and stability of a recessive eusocial allele A in social benefits parameter space (b; α) under biandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. 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.

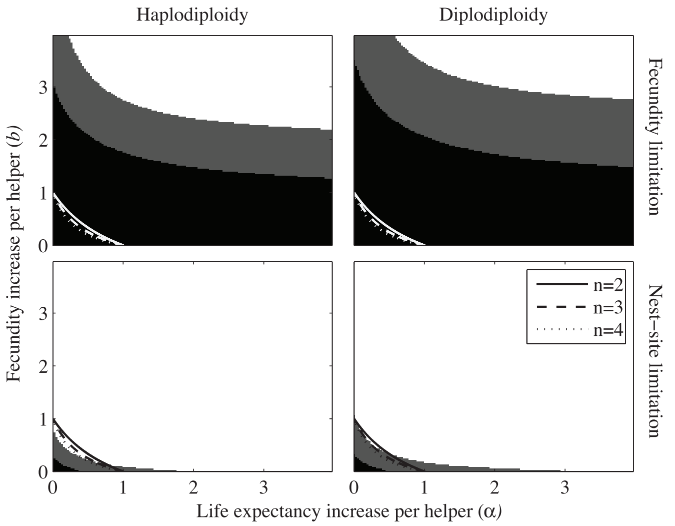

Figure B6: Evolution and stability of a dominant eusocial allele A in social benefits parameter space (b; α) under biandry. The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. 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.

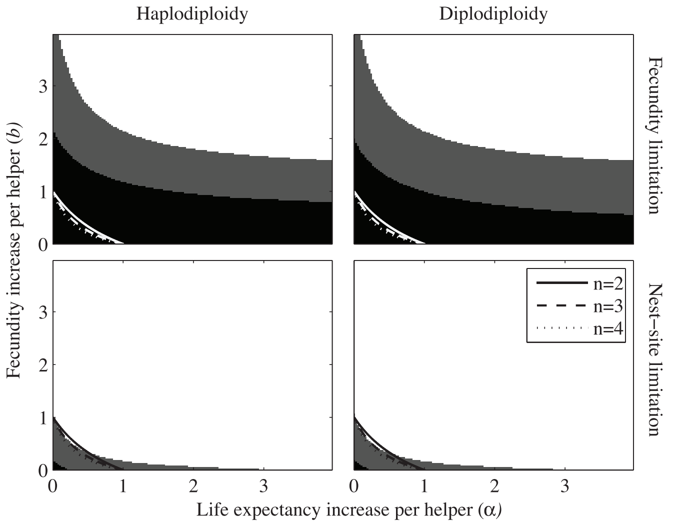

Figure B7: Evolution and stability of a recessive eusocial allele A in social benefits parameter space (b; α) under monandry. The helper phenotype is expressed in both males and females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. 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.

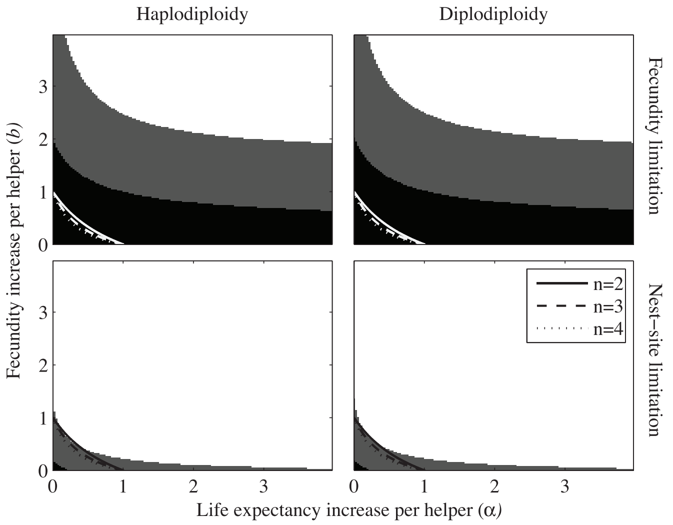

Figure B8: Evolution and stability of a dominant eusocial allele *A* in social benefits parameter space (b; α) under monandry. The helper phenotype is expressed in both males and females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 4$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. 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*.

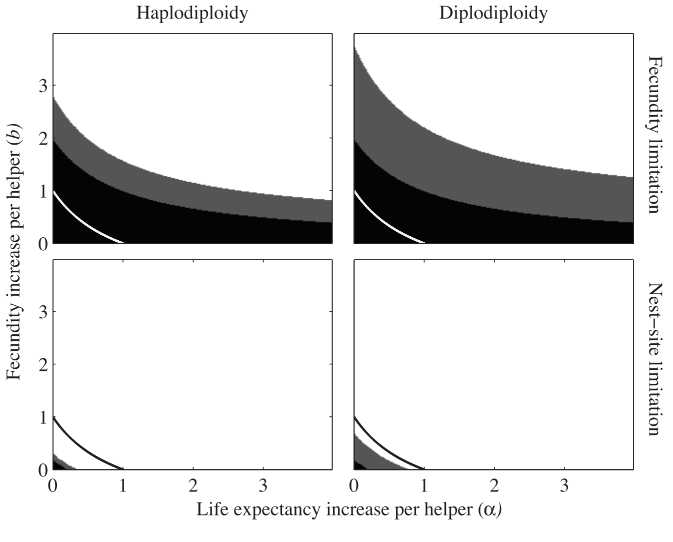

Figure B9: Evolution and stability of a recessive eusocial allele *A* in social benefits parameter space (b; α) under monandry, when there can be only one helper in a nest ($N = 2$). The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 2$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. Initial conditions: (1) the frequency of allele *A* is 1%; (2) the frequency of allele *A* is 99%. The line satisfies the expression $f(n)/m(n) = nf_0/m_0$ for $n = 2$, such that synergy exists above the line for colony size *n*.

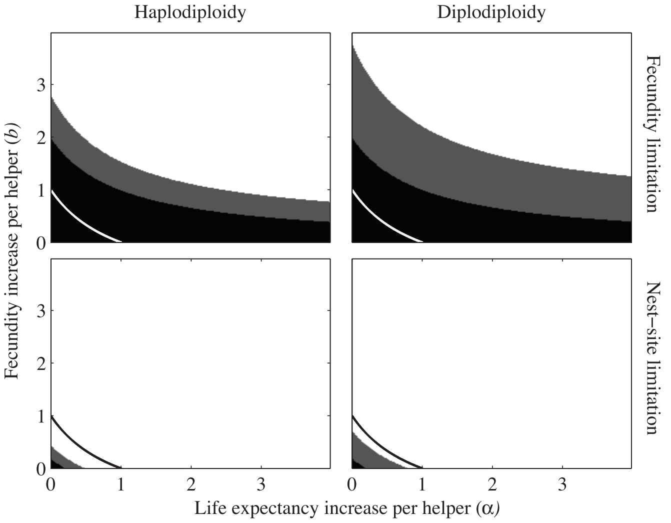

Figure B10: Evolution and stability of a dominant eusocial allele *A* in social benefits parameter space (b; α) under monandry, when there can be only one helper in a nest ($N = 2$). The helper phenotype is expressed only in females. Observed areas: eusocial area (white), mixed area (gray), solitary area (black). Parameter values: $N = 2$, $f_0 = 1$, $\beta = 0.1$, $m_0 = m_x = m_y = m_h = 0.1$, $C_T = 400$, $C_B = 20$. Initial conditions: (1) the frequency of allele *A* is 1%; (2) the frequency of allele *A* is 99%. The line satisfies the expression $f(n)/m(2) = nf_0/m_0$ for $n = 2$, such that synergy exists above the line for colony size n.

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Appendix C from P. Avila and L. Fromhage, “No Synergy Needed: Ecological Constraints Favor the Evolution of Eusociality” (Am. Nat., vol. 186, no. 1, p. 000)

Queller’s (1989) Inequality (2)

For the reader’s convenience, here we reproduce inequality (2) from Queller (1989), which states that selection will favor genes promoting worker behavior over those promoting solitary reproduction when $rsb < r^{*}s^{*}b^{*}$. Here, r is a solitary female’s relatedness to her brood and s is her survival probability until the time she rears her first offspring to independence. Given that she survives this long, b is the number of adult offspring that result from her efforts. On the right-hand side, r^{*}, s^{*}, and b^{*} are the corresponding parameters for a worker, with the latter being what a worker’s efforts add to the colony’s production of reproductives.

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Appendix D from P. Avila and L. Fromhage, "No Synergy Needed: Ecological Constraints Favor the Evolution of Eusociality" (Am. Nat., vol. 186, no. 1, p. 000)

A Modified Version of Pen and Weissing's (2000) Model

Here we show that the results of Pen and Weissing's (2000) model (without territory inheritance) become similar to ours if we express helpers' brood-rearing efficiency as a fixed proportion of solitary breeders' brood-rearing efficiency. For more details, see Pen and Weissing's (2000) original paper. Readers familiar with that work may focus their attention to our equations (D1), (D16), (D25), and (D26).

We assume that breeders' reproductive output has the form

$$F(\bar{x}) = F_0(1 + h\bar{n}(\bar{x})) \tag{D1}$$

(corresponding to eq. [1] in Pen and Weissing 2000), where $x \in [0, 1]$ is the genetically determined tendency to become a helper, $\bar{x}$ is average helping tendency of female offspring, F_0 is the breeder's reproductive output without helpers, h is the contribution per helper, and $\bar{n}(\bar{x})$ is a breeder's expected number of helpers. The crucial modification here is that, in contrast to Pen and Weissing's (2000) equation (1), the contribution of helpers is now proportional to F_0, implying that any population-level processes that limit F_0 will also limit the number of siblings raised per helper. For example, if high population density makes finding food difficult for solitary breeders, it should also be difficult for helpers.

This modification carries over to the transition matrix, which describes the transitions between breeder, waiter, and helper classes. The transition matrix has the form

$$\mathbf{A} = \begin{bmatrix} S_\mathrm{h}S_\mathrm{b} & 0 & xS_\mathrm{b}F(\bar{x}) \\ (1-k)S_\mathrm{h}(1-S_\mathrm{b}) & (1-\alpha)S_\mathrm{w} & (1-k)(1-xS_\mathrm{b})F(\bar{x}) \\ 0 & \alpha S_\mathrm{w} & S_\mathrm{b} \end{bmatrix} \tag{D2}$$

(eq. [2] in Pen and Weissing 2000), where S_b, S_w, and S_h are survival probabilities of breeders, waiters, and helpers, respectively. Waiters have per-capita probability α of obtaining a territory in a given season, and individuals pay survival cost k when dispersing. The transition matrix describes the population dynamics of females following strategy x in a population where the resident strategy is x^*.

We want to know whether a rare mutant with helping tendency $x > 0$ can invade a resident population with monomorphic helping tendency $x^* = 0$. Therefore, we need to assess how this small change in mutant behavior influences the fitness function of the rare mutant $W(x, \bar{x}, x^*)$. Using the direct fitness approach, a small change in mutant behavior x induces the following change in the mutant's fitness

$$\Delta W = \left(\frac{\partial W}{\partial x} + r\frac{\partial W}{\partial \bar{x}}\right)\Bigg|_{x=\bar{x}=x^*} \tag{D3}$$

(eq. [4] in Pen and Weissing 2000).

In a class-structured population, this can be written as

$$\Delta W = \sum_{i,j} u_j^* v_i^* \left(\frac{\partial a_{ij}}{\partial x} + r\frac{\partial a_{ij}}{\partial \bar{x}}\right)\Bigg|_{x=\bar{x}=x^*} \tag{D4}$$

(eq. [5] in Pen and Weissing 2000), where a_{ij} is an element of the transition matrix, u_j^* is the relative frequency of class j in demographic equilibrium, and v_i^* is a class i individual's reproductive value in the resident population. The reproductive values are normalized such that $\sum_i u_j^* v_i^* = 1$, and if the behavior is expressed only in a single class k, then terms $j \neq k$ vanish. Since the positive constant u_k^* does not affect the direction of selection, we can write the fitness function as follows:

$$W(x, \bar{x}, x^*) = \sum_i a_{ik}(x, \bar{x}, x^*)v_i^* \tag{D5}$$

(eq. [6] in Pen and Weissing 2000). After substituting the appropriate elements of the transition matrix, we obtain the following fitness function:

$$W(x, \bar{x}, x^*) = xS_\mathrm{b}F(\bar{x})v_\mathrm{h}^* + (1-k)(1-xS_\mathrm{b})F(\bar{x})v_\mathrm{w}^* + S_\mathrm{b}v_\mathrm{b}^*, \tag{D6}$$

where v_b, v_w, and v_h are reproductive values of breeders, waiters, and helpers, respectively, in the resident population.

The reproductive values v_j^* are the elements of a dominant left eigenvector of the matrix $\mathbf{A}^*$ that results from matrix $\mathbf{A}$ when replacing x with x^*; that is,

$$\mathbf{A}^* = \begin{bmatrix} S_\mathrm{h}S_\mathrm{b} & 0 & 0 \\ (1-k)S_\mathrm{h}(1-S_\mathrm{b}) & (1-\alpha)S_\mathrm{w} & (1-k)F_0 \\ 0 & \alpha S_\mathrm{w} & S_\mathrm{b} \end{bmatrix}. \tag{D7}$$

Thus, we can find the reproductive values v_j^* by solving the system of equations

$$v_j^* = \sum_i a_{ij}^* v_i^* \tag{D8}$$

(eq. [8] in Pen and Weissing 2000). Because only relative reproductive values matter in this context, we can set waiters' reproductive value to be equal to unity, $v_\mathrm{w}^* = 1$, without loss of generality (eq. [9] in Pen and Weissing 2000), leading to the following system of two equations:

$$v_\mathrm{h}^* = a_{11}^* v_\mathrm{h}^* + a_{21}^* + a_{31}^* v_\mathrm{b}^*, \tag{D9}$$

$$v_\mathrm{b}^* = a_{13}^* v_\mathrm{h}^* + a_{23}^* + a_{33}^* v_\mathrm{b}^*. \tag{D10}$$

After substituting the appropriate elements of the transition matrix $\mathbf{A}^*$ and solving the system of equations, we find that

$$v_\mathrm{b}^* = \frac{(1-k)F_0}{1-S_\mathrm{b}}, \tag{D11}$$

$$v_\mathrm{h}^* = \frac{(1-k)S_\mathrm{h}(1-S_\mathrm{b})}{1-S_\mathrm{h}S_\mathrm{b}} \tag{D12}$$

(eqq. [10], [11] in Pen and Weissing 2000). Substituting equations (D11) and (D12) and $v_\mathrm{w}^* = 1$ into equation (D8) leads to the following equation, which holds in a stationary population:

$$\frac{\alpha S_\mathrm{w}}{1-(1-\alpha)S_\mathrm{w}} = \frac{1-S_\mathrm{b}}{(1-k)F_0}. \tag{D13}$$

(eq. [13] in Pen and Weissing 2000).

If competition for breeding sites is density dependent, then

$$\alpha = \frac{(1-S_\mathrm{w})(1-S_\mathrm{b})}{S_\mathrm{w}[(1-k)F_0 - (1-S_b)]} \tag{D14}$$

(eq. [14] in Pen and Weissing 2000), where F_0 is a constant that has to be assigned a priori. If breeders' fecundity is density dependent, then

$$F_0 = \frac{(1-S_\mathrm{b})[1-(1-\alpha)S_\mathrm{w}]}{(1-k)\alpha S_\mathrm{w}} \tag{D15}$$

(eq. [15] in Pen and Weissing 2000), where now α is a constant that has to be assigned a priori. We investigate the effect of selection on helping behavior by applying equation (D3) to equation (D6) and assuming that $x^* = 0$, which entails

$$\Delta W = S_\mathrm{b}F_0[v_\mathrm{h}^* - (1-k)v_\mathrm{w}^*] + rF_0 h\bar{n}'(0)(1-k)v_\mathrm{w}^* \tag{D16}$$

(corresponding to eq. [16] in Pen and Weissing 2000), where a prime denotes differentiation. Note that F_0 appears in the second term on the right-hand side, in contrast to Pen and Weissing's equation (16). Under the condition for demographic equilibrium,

$$u_\mathrm{h}^* = S_\mathrm{h} S_\mathrm{b} u_\mathrm{h}^* + \bar{x} S_\mathrm{b} F(\bar{x}) u_\mathrm{b}^* \tag{D17}$$

(eq. [17] in Pen and Weissing 2000), the expected number of helpers $\bar{n} = u_\mathrm{h}^*/u_\mathrm{b}^*$ in demographic equilibrium can be expressed as

$$\bar{n}(\bar{x}) = \frac{\bar{x} S_\mathrm{b} F_0}{1 - S_\mathrm{b}(S_\mathrm{h} + h\bar{x})} \tag{D18}$$

(eq. [18] in Pen and Weissing 2000).

Differentiation yields

$$\bar{n}'(0) = \frac{S_\mathrm{b} F_0}{1 - S_\mathrm{b} S_\mathrm{h}} \tag{D19}$$

(eq. [19] in Pen and Weissing 2000). The change in the mutant's fitness can now be rewritten as

$$\Delta W = S_\mathrm{b} F_0 [v_\mathrm{h}^* - (1-k) v_\mathrm{w}^*] + rhF_0(1-k)v_\mathrm{w}^* \frac{S_\mathrm{b} F_0}{1 - S_\mathrm{b} S_\mathrm{h}}. \tag{D20}$$

This equation resembles Hamilton's rule, $rb - c > 0$ (up to the factor $S_\mathrm{b} F_0$), such that

$$\Delta W = -c + rb \tag{D21}$$

(eq. [20] in Pen and Weissing 2000), where

$$c = (1-k)v_\mathrm{w}^* - v_\mathrm{h}^*, \tag{D22}$$

$$b = \frac{hF_0(1-k)v_\mathrm{w}^*}{1 - S_\mathrm{b} S_\mathrm{h}} \tag{D23}$$

(see eqq. [21a] and [21b] in Pen and Weissing 2000 for comparison). Substitution of the expressions of reproductive values yields

$$c = \frac{(1-k)S_\mathrm{h}(1 - S_\mathrm{b})}{1 - S_\mathrm{b} S_\mathrm{h}}, \tag{D24}$$

$$b = \frac{hF_0(1-k)}{1 - S_\mathrm{b} S_\mathrm{h}}. \tag{D25}$$

As in Pen and Weissing's model, b can be interpreted as the expected number of siblings raised per helper, which is now, however, proportional to F_0. Helping behavior is favored by selection if $rb > c$, that is, if

$$rhF_0 > 1 - S_\mathrm{h}. \tag{D26}$$

In contrast to Pen and Weissing's (2000) corresponding equation (24), a breeder's fecundity without helpers F_0 appears on the left-hand side. Depending on the mode of density limitation, this condition can be interpreted as follows. Under territory limitation, F_0 is a positive constant that has to be assigned a priori to reflect the focal species' capacity of converting (a constant supply of) resources into offspring; that is, it reflects what we have called "intrinsic fecundity." Since high F_0 makes it easier to fulfill equation (D26), it follows that high intrinsic fecundity facilitates the evolution of helping under territory limitation. Under fecundity limitation, by contrast, F_0 is implicitly a decreasing function of α (according to eq. [D15]), indicating that low probabilities of obtaining a territory facilitate the evolution of helping. This confirms our main result: ecological constraints facilitate the evolution of helping. Moreover, because fecundity limitation acts by reducing the realized value of F_0 (as compared to an otherwise identical species that is subject to territory limitation), our result that territory limitation facilitates the evolution of helping is also implicit in equation (D26).

II

SEX RATIO CONFLICT AFFECTS COLONY GROWTH IN ANNUAL HAPLODIPLOID SOCIAL INSECTS

by

Piret Avila, Lutz Fromhage, Mauricio Gonzáles-Forero
& Laurent Lehmann 2016

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ABSTRACT

In general, the optimal life-history strategy for an annual eusocial colony is thought to proceed in two phases: in the ergonomic phase, all effort is directed towards producing workers; in the reproductive phase, all effort is directed towards producing sexual offspring. Using optimal control theory, we show that conflict over sex allocation between the queen and the workers gives rise to a suboptimal pattern of colony growth while, surprisingly, the queen wins the sex allocation conflict. The suboptimal colony growth is characterized by a premature switch from the ergonomic to the reproductive phase. The timing of the switch depends on how the power over resource allocation is distributed between the queen and the workers, where the power is the ability of a party of interest to act towards their fitness optimum. The timing of the switch is also affected by the life-history traits, such as mortality rates of the individuals in the colony and the per capita productivity of the colony. Our model can be useful for empiricists studying conflict resolution in life-history decisions in annual eusocial insects.

Keywords: Social insects; conflict; sex allocation; colony growth; evolutionary model.

INTRODUCTION

Eusocial colonies, much like individual organisms, have to find a way to resolve the major life history trade-off between reproduction and growth. While unitary organisms consist of clonal cells, eusocial colonies consist of non-clonal individuals whose relatedness to each other is lower than one. Furthermore, the sex-determination system in eusocial Hymenoptera causes relatedness asymmetries among colony members, such that in a colony headed by a singly mated queen the workers are 3/2 more related (genetically) to their sisters than to their brothers, while the queen is twice as related to her sons than to her daughters (in terms of the often used class reproductive value weighted relatedness, the workers are 3 time more "related" to their sisters, while the queen is equally "related" to her sons and daughters). Non-clonal social groups with relatedness asymmetries are subject to potential conflict over resource allocation because different parties in the colony have diverging reproductive optima (Ratnieks *et al.* 2006). For example, in an outbred population, with a single monandrous queen per colony, natural selection on allocation will depend on life-to-life relatedness and favours alleles in queens to equally allocate towards males and females, and alleles in workers to allocate three times as much resources to females than males (Trivers and Hare 1976). Factors, such as multiple related queens per nest, multiple matings by the queen, and worker production of males reduce the extent of the conflict over sex allocation because they cause the worker and queen optima to converge (Ratnieks *et al.* 2006).

Observed colony allocations represents a "conflict resolution", which happens according to the power different parties have over reproductive decisions, where power is the ability of a certain party to act towards their fitness optimum (Beekman and Ratnieks 2003, Helanterä and Ratnieks 2009). Both, workers and the queen, have means to manipulate sex allocation towards their fitness optima. For example, queens control the primary sex ratio by laying fertilized diploid eggs, that develop into females, and haploid unfertilized eggs, that develop into males. Queens can also alter the caste determination of females by producing different types of eggs (Wheeler 1986). Workers can alter the proportion of females developing into queens and workers, as in many species the diet provided to the larvae by workers determines the caste of the female offspring (Ratnieks *et al.* 2006, Schwander *et al.* 2010, Berens *et al.* 2015). Workers can also eliminate male eggs or larvae to redirect resources from male brood to female brood (Sundström *et al.* 1996, Chapuisat *et al.* 1997).

It has been been shown in a static allocation model that if both parties have some control over the resource allocation decision, then the conflict over sex allocation can result in the overall loss in productivity of the colony, as less than the optimal amount of resources are allocated to worker production (Reuter and Keller 2001). In the absence of such conflict, colony productivity should be optimized to allow the maximal amount of sexual offspring to be produced. For this case, it has been shown that by allowing for temporal allocation to occur over the course of colony ontogeny, the optimal resource allocation schedule for an annual eusocial colony proceeds in two distinct phases: in the ergonomic phase, all effort is directed towards producing workers; in the reproductive phase, all effort is directed towards producing sexual offspring (Macevicz and Oster 1976).

In this study, we bring these two approaches on resource allocation in eusocial insects together and show how sex allocation conflict can affect the colony ontogeny by linking together the dynamics of colony growth with the conflict over sex allocation. In our analysis we consider different scenarios of power that workers and the queen can have over reproductive decisions in the colony. Our study shows that conflict resolution over time can be different from conflict resolution that averages decisions over time. This highlights the importance of considering the dynamic properties of conflict resolution mechanisms, since the predictions can be qualitatively different compared to time independent conflict resolution mechanisms.

Our model assumes constant returns to scale between the number of workers and colony productivity in an annual eusocial insect colony with a haplodiploid sex determination system. We assume that the colony is initiated by a single queen ("*monogyny*") and workers are completely sterile. The queen can be mated with only one male ("*monandry*") or with multiple males ("*polyandry*"). We use optimal control theory and dynamic game theory to determine the uninvadable resource allocation strategy of producing workers, queens and males throughout the colony ontogeny for different scenarios of power. Fitness is gained by producing sexual offspring (males and queens) but producing more workers will increase the rate at which resources are acquired from the environment and turned into offspring.

MODEL

Biological scenario

We consider a seasonal population of haplodiploid eusocial insects consisting of a constant number (n) of colonies or breeding sites each occupied by a single queen, where n is a very large number (ideally infinite). The life cycle over a season is assumed to consist of the following four events occurring in cyclic order. (1) *Reproduction*: at the start of a reproductive period of total length T, each queen occupying one of the n breeding sites initiates a colony that grows throughout the period, and where workers, males and new queens are produced. (2) *Dispersal*: juvenile queens and males are assumed to fully disperse out of their natal colony so that no inbreeding, local mate competition, or local resource competition occur. (3) *Mating*: random mating occurs and queens mate with $M \geq 1$ males. (4) *Regulation*: individuals of the parental generation and workers die and juvenile queens randomly compete for vacated breeding slots to form the next generation of adults.

Colony growth

We model explicitly colony population dynamics during stage (1) of the life cycle so that at time $t \in [0, T]$ a focal colony consists of a number $x_{\mathrm{w}}(t)$ of sterile workers, $x_{♀}(t)$ (juvenile) queens, and $x_{♂}(t)$ (juvenile) males. By the term "juvenile" we only want to emphasize that these sexual individuals are regarded as offspring in the current generation and that they will reproduce in the next generation. We are not specifying the ontogenetic state of the offspring at any point in our model. We assume that all such types of individuals are equally costly to produce. Workers acquire resources from the environment to produce offspring. For simplicity, we assume that the availability of resources in the environment is constant in time and the rate at which resources are acquired scales linearly with the colony size. The latter assumption implies that there are enough resources in the environment to sustain constant per worker productivity and the egg-laying rate of the queen is constrained only by the resources available to the colony. Let r denote the net rate at which a worker acquires resources for the colony, measured in offspring produced per unit time. Hence, the parameter r gives the per worker contribution to queen fecundity. We count the colony founding queen as a worker, since she can recover some resources from her body fat and may even forage some additional resources to initiate the colony after which she specializes in egg laying. The number $x_{\mathrm{k}}(t)$ of type $\mathrm{k} \in \{\mathrm{w}, ♀, ♂\}$ individuals in the colony grows according to the equation

$$\dot{x}_{\mathrm{k}}(t) = r a_{\mathrm{k}}(t) x_{w}(t) - \mu_{\mathrm{k}} x_{\mathrm{k}}(t),\ x_{\mathrm{k}}(0) = x_{\mathrm{k}0}, \tag{1}$$

where the "over-dot" notation stands for the time derivative, $a_{\mathrm{k}}(t)$ is the fraction of resources allocated into producing type k individuals at time t, μ_{k} is the mortality rate of individuals of type k, and $x_{\mathrm{k}0}$ is number of type k individuals in the colony in the beginning of the season. The initial condition (number of individuals at the beginning of the season) for the colony is $x_{\mathrm{w}0} = 1$ (one colony founding queen who is counted as a worker), $x_{♀0} = 0$ (no juvenile queens), and $x_{♂0} = 0$ (no juvenile males).

Evolving phenotypes

The dynamics of colony size, given by eq. (1), is governed by the allocation schedule $a_{\mathrm{k}}(t)$, which in turn is determined by two underlying traits. The first trait, $v_{\mathrm{f}}(t)$ gives the proportion of resources allocated to producing females (individuals destined to become workers or queens) at time t. The quantity $1 - v_{\mathrm{f}}(t)$ determines the proportional allocation to males at time t. The second trait, $v_{\mathrm{g}}(t)$ gives the proportion of resources allocated to producing queens from resources allocated to females at time t. Hence, $1 - v_{\mathrm{g}}(t)$ of resources allocated to females at time t are directed towards producing workers. The schematic description of these assumptions is illustrated in fig. 1 and it leads to

$$a_{\mathrm{w}}(t) = v_{\mathrm{f}}(t)(1 - v_{\mathrm{g}}(t)), \qquad a_{♀}(t) = v_{\mathrm{f}}(t) v_{\mathrm{g}}(t), \qquad a_{♂}(t) = 1 - v_{\mathrm{f}}(t). \tag{2}$$

Hereinafter, if we do not want to specify the trait in question, we write $v_{\tau}(t)$, where $\tau \in \{\mathrm{f}, \mathrm{g}\}$. Note that the resource allocation trait $v_{\tau}(t)$ is a function of time, and is defined over the entire growth phase ($t \in [0, T]$).

We consider that allocation strategy to females $v_{\mathrm{f}}(t)$ and to juvenile queens $v_{\mathrm{g}}(t)$ are evolving traits. We will examine three possible scenarios of genetic control over these traits. First, we consider the case where these traits are under the full genetic control of the colony founding queen. Second, we consider the case where workers obtain full control over the reproductive decision making. In the majority of eusocial species, however, it is believed that the most likely scenario is that the queen and the workers share control over the the resource allocation decisions (Trivers and Hare 1976, Bourke and Franks 1995, Helanterä and Ratnieks 2009). Hence, as a third case, we consider the scenario of mixed control, where the queen controls the proportional investment into females versus males $v_{\mathrm{f}}(t)$ and the workers control the proportional investment into new queens versus workers $v_{\mathrm{g}}(t)$. Yet, to be clear, these traits determine the behaviour at the level of the colony rather than behaviour at the level of the individual. Our model of conflict resolution is in accordance to the model by Reuter and Keller (2001), where they also considered these three scenarios. However, the traits in their model were independent of time and thus their conflict resolution was an approximated average over the entire season.

Mutant-resident system

In order to analyse the evolution of $v_{\mathrm{f}}(t)$ and $v_{\mathrm{g}}(t)$ we will perform an evolutionary invasion analysis (e.g., Fisher 1930, Eshel and Feldman 1984, Charlesworth 1994, Ferrière and Gatto 1995, Caswell 2000, McNamara *et al.* 2001, Otto and Day 2007, Metz 2011). That is, we consider the fate (invasion or extinction) of a single mutant allele introduced into a population of resident individuals, where a mutant allele determines the whole allocation schedule throughout colony growth (i.e., an allele determines a trajectory of a trait over $t \in [0, T]$). We thus define a resident resource allocation vector $\mathbf{v} = \{v_{\mathrm{f}}(t), v_{\mathrm{g}}(t)\}_{t=0}^{T}$, which gives the full allocation schedule of a colony, where individuals in control of the resource allocation trait $v_\tau(t)$ carry only resident alleles. It will turn out to be useful to let the mutant resource allocation vector $\mathbf{u} = \{u_{\mathrm{f}}(t), u_{\mathrm{g}}(t)\}_{t=0}^{T}$ to be the full allocation schedule of a colony, where individuals in control of the resource allocation trait $v_\tau(t)$ carry only mutant alleles.

However, since the fate of a mutant is determined when it is rare in the population, we need to consider the frequency of the mutant allele in the individuals who are in control of the resource allocation trait $v_\tau(t)$ when only one of the colony "founding" individuals is carrying a single mutant allele. We also have to take into account that in a haplo-diploid sex-determination system, where females are diploid and males are haploid, the phenotypes of colonies "founded" by mutant females and mutant males will be different, and we thus need further to distinguish the allocation strategy of a colony founded by a focal mutant *heterozygous* female, $u_\tau^{♀}(t)$, from that of mutant haploid male, $u_\tau^{♂}(t)$ (for $\tau \in \{\mathrm{f}, \mathrm{g}\}$). By writing that a mutant male "founds" a colony, we mean that a mutant male has mated with a resident female that gives rise to a focal colony, where the mutant allele is present in the genes of the workers. The distinction between mutant male and female will also turn out to be useful when expressing the colony phenotypes under the various cases of power over the traits.

When party $c \in \{\text{♀}, \mathrm{w}\}$ is in full control of the trait $v_\tau(t)$, then the average phenotype of the colony founded by an individual of sex $s \in \{\text{♀}, \text{♂}\}$, who carries a mutant allele, can be written as

$$u^s_\tau(t) = p^s_c u_\tau(t) + (1 - p^s_c) v_\tau(t) \tag{3}$$

and is thus expressed in terms of the allocation strategy of colonies founded by a *homozygous* individual $u_\tau(t)$. Here, p^s_c is the frequency of the mutant allele in the average individual, who belongs to the party c in control of the trait in the colony, founded by a mutant of sex $s \in \{\text{♀}, \text{♂}\}$.

For queen control, the colony phenotype $u^s_\tau(t)$ is determined by the average frequency of the mutant allele in the colony founding queen. If the colony is founded by a *heterozygous* mutant female then the frequency of the mutant allele in the colony founding queen is $p^{\text{♀}}_{\text{♀}} = 1/2$. Under queen control males have no genetic influence on the resource allocation decisions and thus $p^{\text{♂}}_{\text{♀}} = 0$. Note that female mating frequency will not affect these frequencies under queen control because mutant males have no genetic control over the expression of the trait.

For worker control, the colony phenotype $u^s_\tau(t)$ is determined by the average frequency of the mutant allele in workers. The average phenotype of the colony that is founded by a *heterozygous* mutant female is $p^{\text{♀}}_{\mathrm{w}} = 1/4$ and this frequency is not affected by the number of matings by the queen because a mutant female will only encounter resident males since the mutant allele is considered to be rare. The average phenotype of the colony that is founded by a mutant male is $p^{\text{♂}}_{\mathrm{w}} = 1/(2M)$, where M is the number of matings by a female.

Let $a^s_{\mathrm{k,u}}(t)$ be the the proportion of resources allocated to producing type $\mathrm{k} \in \{\mathrm{w}, \text{♀}, \text{♂}\}$ individuals in the colony founded by a mutant individual of sex $s \in \{\text{♀}, \text{♂}\}$, where the subscript "u" in $a^s_{\mathrm{k,u}}(t)$ emphasizes that it is the mutant allocation strategy, which, according to eq. (2) is

$$a^s_{\mathrm{w,u}}(t) = u^s_{\mathrm{f}}(t)(1 - u^s_{\mathrm{g}}(t)), \qquad a^s_{\text{♀},\mathrm{u}}(t) = u^s_{\mathrm{f}}(t) u^s_{\mathrm{g}}(t), \qquad a^s_{\text{♂},\mathrm{u}}(t) = 1 - u^s_{\mathrm{f}}(t). \tag{4}$$

In a colony founded by a mutant individual of sex s, type $\mathrm{k} \in \{\mathrm{w}, \text{♀}, \text{♂}\}$ individuals grow according to the equation

$$\dot{x}^s_{\mathrm{k,u}}(t) = r a^s_{\mathrm{k,u}}(t) x^s_{w,\mathrm{u}}(t) - \mu_{\mathrm{k}} x^s_{\mathrm{k,u}}(t), \; x^s_{\mathrm{k,u}}(t_0) = x_{\mathrm{k}0}, \tag{5}$$

where $x^s_{\mathrm{k,u}}(t)$ denotes the number of individuals of type k in a colony founded by a mutant individual of sex s.

Invasion fitness

We now have all the elements to obtain an expression for invasion fitness, which allows to ascertain the fate of the mutant allele. Since we have a discrete time reproductive process, invasion fitness is here taken as being the geometric growth rate (or growth ratio) of the mutant. This is the asymptotic per capita number of mutant copies produced by an average trajectory of the mutant lineage descending from the initial mutation, and when overall still rare in the population (Cohen 1979, Tuljapurkar *et al.* 2003).

We will express invasion fitness in terms of fitness functions of juvenile individuals and gene transmission frequencies. The fitness of the juvenile individual alive at T in the current season is its expected number of sexual offspring produced in the following season. The life cycle and our fitness accounting method are illustrated in fig. 2.

Let $w_{s's}(\mathbf{u}^s, \mathbf{v})$ denote the expected number of juveniles of sex $s' \in \{♀, ♂\}$ that descend from a juvenile of sex $s \in \{♀, ♂\}$ carrying the mutant allele. Note, that the fitness function $w_{s's}(\mathbf{u}^s, \mathbf{v})$ is a function of the allocation strategy $\mathbf{u}^s = \{u^s_{\mathrm{f}}(t), u^s_{\mathrm{g}}(t)\}_{t=0}^{T}$ of the colony founded by the mutant individual of sex s, and thus a function of the mutant strategy $\mathbf{u}$ (by way of eq. (3)–(5)), and of the population average allocation strategy $\mathbf{v}$. But since the mutant can be considered to be rare for the invasion analysis, this fitness function is independent of the number (or frequency) of mutants in the population.

Next, we derive the fitness functions $w_{♀♀}(\mathbf{u}^♀, \mathbf{v})$, $w_{♂♀}(\mathbf{u}^♀, \mathbf{v})$, and $w_{♀♂}(\mathbf{u}^♂, \mathbf{v})$. To that end it will be useful to set

$$x^s_{\mathrm{k,u}}(T) = x_{\mathrm{k}}(\mathbf{u}^s), \tag{6}$$

which gives the number of individuals of type k at the end of the season and we emphasize the functional dependence of colony dynamics on the trait $\mathbf{u}^s$; hence, $x_{\mathrm{k}}(\mathbf{v})$ is colony size at the end of the season for a colony monomorphic for the resident.

Because population size is large, a focal (mutant) colony has no impact on the average number of individuals produced in a population and so each season, an average number $nx_♀(\mathbf{v})$ of juvenile queens and $nx_♂(\mathbf{v})$ males mate randomly, after which females compete for the n breeding spots. The probability that a female will gain any of one of the n breeding spots is $n/nx_♀(\mathbf{v})$, and she produces $x_♀(\mathbf{u}^♀)$ daughters and $x_♂(\mathbf{u}^♀)$ to sons. Hence,

$$w_{♀♀}\left(\mathbf{u}^♀, \mathbf{v}\right) = \frac{x_♀(\mathbf{u}^♀)}{x_♀(\mathbf{v})} \qquad \text{and} \qquad w_{♂♀}\left(\mathbf{u}^♀, \mathbf{v}\right) = \frac{x_♂(\mathbf{u}^♀)}{x_♀(\mathbf{v})}. \tag{7}$$

The probability that any of the n new queens who have gained a breeding spot have previously mated with a focal male is $M/x_♂(\mathbf{v})$, and under worker control he will sire $x_♀(\mathbf{u}^♂)/M$ daughters, while under queen control, the male has no control over resource allocation and the fitness function depends only on the resident strategy so that he will sire $x_♀(\mathbf{v})/M$ daughters, whereby

$$w_{♀♂}\left(\mathbf{u}^♂, \mathbf{v}\right) = \frac{x_♀(\mathbf{u}^♂)}{x_♂(\mathbf{v})} \quad \text{(queen control)}, \tag{8}$$

$$w_{♀♂}\left(\mathbf{u}^♂, \mathbf{v}\right) = \frac{x_♀(\mathbf{v})}{x_♂(\mathbf{v})} \quad \text{(worker control)}. \tag{9}$$

Let us denote by $n_{♀,\mathrm{m}}$ ($n_{♂,\mathrm{m}}$) the number of mutant allele copies in females (males) in the population. The change in the vector $\mathbf{n}_\mathrm{u} = (n_{♀,\mathrm{u}}, n_{♂,\mathrm{u}})^\intercal$ of number of gene copies from one generation to the next generation $\mathbf{n}'_\mathrm{u} = (n'_{♀,\mathrm{u}}, n'_{♂,\mathrm{u}})^\intercal$, when the mutant allele is rare is given by the matrix

$$\mathbf{A}(\mathbf{u},\mathbf{v}) = \begin{bmatrix} \gamma_{♀♀} w_{♀♀}\big(\mathbf{u}^{♀},\mathbf{v}\big) & \gamma_{♀♂} w_{♀♂}\big(\mathbf{u}^{♂},\mathbf{v}\big) \\ \gamma_{♂♀} w_{♂♀}\big(\mathbf{u}^{♀},\mathbf{v}\big) & \gamma_{♂♂} w_{♂♂}\big(\mathbf{u}^{♂},\mathbf{v}\big) \end{bmatrix} \tag{10}$$

where $\gamma_{s's}$ is the probability that a gene sampled in an individual of sex $s' \in \{♀, ♂\}$ was contributed by an individual of sex $s \in \{♀, ♂\}$; i.e. transmission frequency of sex s to sex s' (for haplodiploids $\gamma_{♀♀} = 1/2$, $\gamma_{♀♂} = 1/2$, $\gamma_{♂♀} = 1$, $\gamma_{♂♂} = 0$). Hence, elements $a_{s's}$ of matrix $\mathbf{A}$ give the expected number of mutant gene copies in sex $s' \in \{♀, ♂\}$ that descend from an individual of sex $s \in \{♀, ♂\}$ carrying the mutant allele.

The invasion fitness $W(\mathbf{u},\mathbf{v})$ of the mutant is then given by the leading eigenvalue of the matrix $\mathbf{A}$, and this can be expressed as (see Appendix C for the derivation)

$$\begin{aligned} W(\mathbf{u},\mathbf{v}) = {} & \Big[\gamma_{♀♀} w_{♀♀}\big(\mathbf{u}^{♀},\mathbf{v}\big) + \gamma_{♂♀} w_{♂♀}\big(\mathbf{u}^{♀},\mathbf{v}\big)\Big] q_{♀}(\mathbf{u},\mathbf{v}) \\ & + \Big[\gamma_{♀♂} w_{♀♂}\big(\mathbf{u}^{♂},\mathbf{v}\big) + \gamma_{♂♂} w_{♂♂}\big(\mathbf{u}^{♂},\mathbf{v}\big)\Big] q_{♂}(\mathbf{u},\mathbf{v}), \end{aligned} \tag{11}$$

where $q_{♀}(\mathbf{u},\mathbf{v})$ ($q_{♂}(\mathbf{u},\mathbf{v}) = 1 - q_{♀}(\mathbf{u},\mathbf{v})$) is the asymptotic probability that a mutant allele is sampled in a female (male)[1]. Hence, invasion fitness is the average number of mutant copies produced over one time step of the reproductive process by a randomly sampled carrier of the mutant allele from its lineage (Lehmann *et al.* 2016). Because the weights ($q_{♀}(\mathbf{u},\mathbf{v})$ and $q_{♂}(\mathbf{u},\mathbf{v})$) depend on the evolving traits themselves, this expression makes it clear that it is neither colony fitness nor the fitness of a particular individual that is maximized by natural selection, but the asymptotic replication rate of the allele under selection (Dawkins 1978, Haig 2012), which depends on both the fitness of carriers of the mutant allele (the $w_{s's}(\mathbf{u}^s,\mathbf{v})$ functions) and how the mutant allele is distributed across classes (the $q_s(\mathbf{u},\mathbf{v})$ functions).

Uninvadable strategies

Single party control

A mutant strategy $\hat{b}(\mathbf{v})$ that yields the highest invasion fitness for an environment determined by the resident strategy $\mathbf{v}$ is said be the best response to the resident strategy, i.e.

$$W_c(\hat{b}(\mathbf{v}),\mathbf{v}) = \max_{\mathbf{u}\in\mathcal{U}} W_c(\mathbf{u},\mathbf{v}), \tag{12}$$

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[1] $\big(q_{♀}(\mathbf{u},\mathbf{v}), q_{♂}(\mathbf{u},\mathbf{v})\big)$ is the leading right eigenvector of matrix $\mathbf{A}(\mathbf{u},\mathbf{v})$

where $\mathcal{U}$ is the set of strategies, and we have emphasized in the expression of invasion fitness the mode of control of the trait $c \in \{\mathrm{w}, ♀\}$ (which means that $\mathbf{u}^{♀}$ and $\mathbf{u}^{♂}$ in eq. (11) depend on how we model the control over the trait, by way of eq. (3)). The problem of finding the best response $\hat{b}(\mathbf{v})$ for a given environment $\mathbf{v}$ is an optimal control problem (Sydsæter *et al.* 2008, Bryson and Ho 1975), and if the best response of a mutant results in an invasion fitness equal or lower to one ($W_c(\hat{b}(\mathbf{v}), \mathbf{v}) \leq 1$), then the mutant allele will go extinct with probability one (when $n \to \infty$).

A resident strategy $\mathbf{u}^*$ that is resistant to the invasion of any mutant $\mathbf{u} \in \mathcal{U}$ strategy, is a candidate endpoint of the evolutionary process and is thus an uninvadable strategy. It thus follows from eq. (12), that a necessary condition for a strategy $\mathbf{u}^*$ to be uninvadable is that it satisfies

$$\mathbf{u}^* \in \arg\max_{\mathbf{u} \in \mathcal{U}} W_c(\mathbf{u}, \mathbf{u}^*), \tag{13}$$

that is, be a best response to itself. A necessary first-order condition for uninvadability can be obtained by considering a variation in invasion fitness due to a variation in resident schedules for trait type $\tau \in \{\mathrm{f}, \mathrm{g}\}$ only by a small amount ϵ_τ ("weak phenotypic deviation" or "weak selection") relative to the resident (e.g., Taylor 1989, Rousset 2004), so that the mutant can be written as

$$u_\tau(t) = v_\tau(t) + \epsilon_\tau \eta(t), \tag{14}$$

for some change in schedule $\eta(t)$. Hence, we look at a change in the function $v_\tau(t)$ that remains very close to it along the whole trajectory when $\epsilon_\tau \ll 1$. Then a candidate uninvadable strategy for queen ($c = ♀$) or worker ($c = \mathrm{w}$) control of the trait must satisfy

$$\left. \frac{\mathrm{d}W_c(\mathbf{u}, \mathbf{v})}{\mathrm{d}\epsilon_\tau} \right|_{\epsilon_\mathrm{f}=0, \epsilon_\mathrm{g}=0} = 0 \quad \text{for} \quad \tau \in \{\mathrm{f}, \mathrm{g}\}, \tag{15}$$

which is the functional (or variational) derivative of invasion fitness; namely, the infinitesimal change in fitness resulting from a change in the whole mutant schedule. This is an analogue for functions valued traits of the classic first order condition for evolutionary stability (e.g., Eshel 1983: eq. 3, Taylor 1989: eq. 2.1).

Mixed party control

Under mixed control we can no longer use eq. (13) to find the evolutionary stable strategies, since the joint actions of the queen and the workers affect colony state variables (number of different types of individuals in the colony) and through that they affect each other's objectives (invasion fitness functions). For this case, we assume that the queen chooses u_f in order to maximize $W_{♀}(\mathbf{u}_\mathrm{u}, \mathbf{u})$ and workers choose u_g in order to maximize $W_\mathrm{w}(\mathbf{u}_\mathrm{u}, \mathbf{u})$. This problem can then be seen as a so-called differential game (Kamien and Schwartz 2012) with two players (the queen and the workers), who interact repeatedly through colony ontogeny. Under mixed control, the resource allocation schedule $\mathbf{u}^* = (u_\mathrm{f}^*, u_\mathrm{g}^*)$ is uninvadable if

$$u_\mathrm{f}^* \in \arg\max_{u_\mathrm{f} \in \mathcal{U}} W_{♀}\Big((u_\mathrm{f}, u_\mathrm{g}^*), \mathbf{u}^*\Big) \qquad \text{and} \qquad u_\mathrm{g}^* \in \arg\max_{u_\mathrm{g} \in \mathcal{U}} W_\mathrm{w}\Big((u_\mathrm{f}^*, u_\mathrm{g}), \mathbf{u}^*\Big) \tag{16}$$

According to eq.(16) the workers and the queen choose the best strategy possible given what the other party chooses and neither party has an incentive to deviate from their choice (also known as the Nash equilibrium).

RESULTS

In order to determine the uninvadable (evolutionarily stable) strategies, we used an analytical approach to derive the first order results by way of optimal control theory, and a numerical method called the iterative scheme of the best response map (Houston and McNamara 1999, see Appendix C in S.I.), combined with a numerical solver for problems of optimal control theory called GPOPS (Patterson and Rao 2014), which uses a direct collocation approach along with various non-linear optimization methods.

Single-party control

The uninvadable resource allocation schedule $\mathbf{u}^*$ consists of two distinct phases of colony growth: the ergonomic phase and the reproductive phase (see figs. 3-4 and eqs. (B48) and (B49) in Appendix B). Colony growth starts with the ergonomic phase $t \in [0, t_c^*]$ during which only workers are produced. It is followed by the reproductive phase $t \in [t_c^*, T]$ during which only sexual offspring are produced. Here, t_c^* is called the switching time from the ergonomic to the reproductive phase and the subscript $c \in \{♀, \mathrm{w}\}$ emphasizes the mode of control. Hence, the uninvadable allocation schedule in the ergonomic phase is (see Appendix B for the derivation)

$$\mathbf{u}^*\Big|_{[0,t^*]} = \Big(u_{\mathrm{f}}^*(t) = 1, u_{\mathrm{g}}^*(t) = 0\Big). \tag{17}$$

What about the reproductive phase under single party control? In Appendix B, we show that the first order condition for allocating resources to type $\tau \in \{\mathrm{f}, \mathrm{g}\}$ individuals under control mode $c \in \{♀, \mathrm{w}\}$ (given by eq. (15)) yields the following male to female (queen) sex-ratio at the terminal time

$$\frac{x_{♂}(\mathbf{v})}{x_{♀}(\mathbf{v})} = -\frac{\mathrm{d}x_{♂}(\mathbf{z})/\,\mathrm{d}\epsilon_\tau}{\mathrm{d}x_{♀}(\mathbf{z})/\,\mathrm{d}\epsilon_\tau} \times R_c, \tag{18}$$

where R_c is the so-called *relatedness asymmetry* (Boomsma and Grafen 1991). This is the ratio of the relatedness weighted reproductive values of recipients of each sex, from the perspective of a given actor (Boomsma and Grafen 1991: p. 386, see also eq. (B19) in Appendix B). Here, both quantities are evaluated in the absence of selection (as it should be for any first-order condition of evolutionary stability, e.g., Taylor 1989, Rousset 2004). The relatedness asymmetry gives the sex-specific ability of an actor of category c of transferring its genes to the future of the gene pool and is given by

$$R_{♀} = 1 \quad \text{(queen control)}, \qquad\qquad R_{\mathrm{w}} = \frac{M}{2+M} \quad \text{(worker control)}. \tag{19}$$

The left-hand side of eq. (18) also depends on the ratio of males to females marginal products (i.e., the marginal rate of substitution of producing new queens instead of males). This is expressed in terms of the variational derivative $\mathrm{d}x_s(\mathbf{z})/\,\mathrm{d}\epsilon_\tau$ measuring the change in the number of individuals of sex $s \in \{♀, ♂\}$ produced by a colony, where individuals express phenotype $\mathbf{z} = \{z_{\mathrm{f}}(t), z_{\mathrm{g}}(t)\}_{t=0}^{T}$, where $z_\tau(t) = v_\tau(t) + \epsilon_\tau \eta(t)$. If males and females are equally costly to produce and they have the same mortality rate ($\mu_{♀} = \mu_{♂} = \mu$) and the same growth schedule, then the marginal product is 1. Then, eq. (18) returns the classical primary sex-ratio.

Eq. (18) is a dynamic version of the standard static marginal results of sex-ratio theory (e.g., Taylor and Frank 1996: eq. 22). The novelty of eq. (18) is that it results from a time-dependent model, which shows that the relatedness asymmetry and marginal product determine the primary sex ratio regardless of the exact details of colony growth dynamics, and thus returns qualitatively the same results as under any static sex-ratio model for the productivity at the end of the season. Indeed, when males and new queens are equally costly to produce under monandry ($M = 1$), workers prefer to allocate three times as much resources to producing new queens than to males, while the queen prefers equal allocation (respectively $R_{♀} = 1/3$ and $R_{♀} = 1$, see also figs. 5-6). This result is in line with the earlier work on sex allocation preferences of workers and queens in eusocial colonies (Trivers and Hare 1976, Reuter and Keller 2001). In general, under any queen mating frequency ($M \geq 1$) and assuming equal male parentage, the workers prefer to allocate $1/R_{\mathrm{w}} = (2 + M)/M$ times as much resources to queens than males. We can easily see that polyandry reduces the conflict between the queen and the workers, because the sex allocation optimum of the workers approaches the queen's sex optimum as queen mating frequency increases, i.e. $(2+M)/M \to 1$ as M increases. This effect comes from the diminishing relatedness asymmetry within the colony with polyandry, with relatedness asymmetry between workers and their male and female siblings being totally absent, when all the daughters of the queen are inseminated by different fathers (Trivers and Hare 1976, Reuter and Keller 2001).

In conclusion, the uninvadable resource allocation strategy in the reproductive phase, given that mortality of males and new queens is equal to produce, is

$$\mathbf{u}^*\Big|_{[t^*,T]} = \left(u_{\mathrm{f}}^*(t) = \frac{1}{R_c + 1}, u_{\mathrm{g}}^*(t) = 1\right). \tag{20}$$

However, note that $u_{\mathrm{f}}^*(t)$ in eq. (20) is not the only solution that satisfies the first order condition (15). Indeed, it is the only constant function that satisfies the first order condition (given that the mortality rates of new queens and males is equal), but in general, there can be many functions that can produce a sex ratio R_c and thus satisfy eq. (15). In biological terms it means, given that the males and queens have equal mortality, the order of producing males and new queens in the reproductive phase does not affect fitness, as long as they are produced according to the sex ratio R_c by the end of the season T. We can see from fig. 4 that $u_{\mathrm{f}}^{*}(t)$ in the reproductive phase is not a constant function, but the the average allocation over the reproductive phase is indeed $u_{\mathrm{f}}^{*}(t) = 1/(R_{\mathrm{w}} + 1)$.

If we assume that the mortality rate of juvenile queens and males is equal (i.e. $\mu_{♀} = \mu_{♂} = \mu$), we can explicitly calculate the switching time for the uninvadable allocation strategy (see derivation in Appendix B), which is

$$t_c^{*} = T - \frac{\ln\left(1 + \frac{\mu - \mu_{\mathrm{w}}}{r}\right)}{\mu - \mu_{\mathrm{w}}}, \ c \in \{♀, \mathrm{w}\}. \tag{21}$$

Hence, the timing of the switch from the ergonomic to the reproductive phase is equal for queen control and worker control, i.e., $t_{♀}^{*} = t_{\mathrm{w}}^{*}$ and is independent of the number of matings M per queen. This means that both parties agree on the worker production schedule that maximizes the number of sexual offspring produced and disagree only in the reproductive phase about how to allocate resources between new queens and males.

Equation (21) implies that lower worker mortality and higher queen mortality rates result in switching time occurring later in the season. This expression turns out to be identical to eq. (6) of Macevicz and Oster (1976), by setting $r = bR$, $\mu_{\mathrm{w}} = \mu$, and $\mu = \nu$. Note that in our model $1/r$ can be loosely interpreted as the time it takes for one worker to help produce one offspring, i.e. a generation time. For negligible mortality of sexuals ($\mu \approx 0$), we can see that as worker mortality approaches zero (i.e. $\mu_{\mathrm{w}} \to 0$), the switching time approaches to a single generation time, i.e. $t_c \to T - 1/r$. This can be loosely interpreted to mean that in an environment where mortality is low compared to the length of the season T, the switch happens one generation time before the end of the season, i.e. only the last generation of brood is reproductive.

Mixed control

Under mixed control over the resource allocation schedule, the queen controls the primary sex ratio of the colony $u_{\mathrm{f}}^{*}(t)$ and the workers control the proportional allocation to queens versus workers $u_{\mathrm{g}}^{*}(t)$. The uninvadable allocation schedule under mixed control constitutes a situation where the queen cannot increase her fitness by altering $u_{\mathrm{f}}^{*}(t)$ and workers cannot increase their fitness by altering $u_{\mathrm{g}}^{*}(t)$.

Similarly, as under single party control, the uninvadable resource allocation schedule $\mathbf{u}^{*}$ under mixed control also consists of two distinct phases of colony growth: the ergonomic phase and the reproductive phase (see fig. 7 and eqs. (B48) and (B49) in Appendix B). As under the single party control, the uninvadable allocation schedule in the ergonomic phase under mixed control is given by eq. (17) (see also fig. 7). However, the switching time under mixed control is not equal to the switching time under single party control $t_m^{*} \neq t_{♀}^{*} = t_{\mathrm{w}}^{*}$. Thus, the length of the ergonomic and reproductive phase under mixed control is not equal to the length of the ergonomic and reproductive phase under single party control.

Surprisingly, we find that the queen wins the sex allocation conflict as the sexual sex ratio (new queens versus males produced by the end of the season) is always equal under mixed control (see fig. 8). Hence, the uninvadable allocation schedule under mixed control in the reproductive phase is given by eq. (20) for $R_{♀}$. Note that, under single party control, the allocation $u_{\mathrm{f}}^{*}(t)$ in eq. (20) is not the only function that satisfies the first order condition (16), but it is the only constant function that satisfies it. The prediction that the queen wins the sex allocation conflict contradicts the result of Reuter and Keller (2001), where the conflict resolution over resource allocation in eusocial colonies was modelled as a static allocation problem and colony growth was not accounted for. In their study, they found that under mixed control the sexual sex ratio is intermediate between the queen and worker optima. Our result makes intuitive sense, because workers can only influence the sexual sex ratio by starting to produce new queens earlier, but then the queen can respond to that by starting to lay less diploid eggs and more haploid male eggs so that the sex ratio would be still be in the optimum of the queen (see fig. 8, there are equal numbers of new queens and males at time T). Even though the queen wins the sex allocation conflict under our assumptions of the conflict resolution mechanisms, both parties pay a cost because less than the optimal (compare figs. 5, 6, and 8) amount of workers are being produced in the colony.

We find that the length of the ergonomic stage is shorter as the reproductive stage starts earlier in the season (fig. 7). The earlier switching time $t_m^* < t_{♀}^* = t_{\mathrm{w}}^*$ results in smaller colony sizes compared to a situation when a single party monopolizes the control over resource allocation (fig. 8).

If we assume that the mortality rate of juvenile queens and males is equal (i.e. $\mu_{♀} = \mu_{♂} = \mu$), we can explicitly calculate the switching time for the uninvadable allocation strategy under mixed control (see derivation in Appendix B)

$$t_m^* = T - \frac{\ln\left(1 + \theta \frac{\mu - \mu_{\mathrm{w}}}{r}\right)}{\mu - \mu_{\mathrm{w}}}, \tag{22}$$

where

$$\theta = \frac{2 + M}{1 + M}. \tag{23}$$

For negligible mortality of sexuals ($\mu \approx 0$), we can see that as worker mortality approaches zero (i.e. $\mu_{\mathrm{w}} \to 0$), the switching time approaches θ times the generation time, i.e. $t_m^* \to T - \theta(1/r)$. This means that in an environment where mortality is low compared to the length of the season T, the switch happens up to half a generation earlier than is optimal. This means that under monogyny ($M = 1$), where the sex allocation conflict is the highest, the switch t_m happens exactly half a generation earlier than is optimal, and the switching time approaches the optimal switching time as the queen mating frequency increases.

If $1/r$ is large compared to the length of the season T, i.e. reproduction is slow and there are only few generations of offspring produced during the season, this can amount to a big time difference in the onset of early reproduction. The premature switch to the reproductive phase under mixed control is also more pronounced in an environment where worker mortality μ_{w} is high and mortality of sexual offspring μ is low. We can conclude that fast reproduction, low worker mortality, high mortality of sexual offspring, and high queen mating frequency contribute to the premature switch under mixed control t_m^* to approach the optimal switch t_c^* $c \in \{♀, \mathrm{w}\}$ observed under single party control.

The timing of the switch, however, directly influences how large the colonies grow. Note that, by colony size, we mean the number of workers $x_\mathrm{w}(t)$. In our model, the maximal colony size is reached at the start of reproductive phase t_c^* and we call this a colony size $x_\mathrm{w}(t_c^*)$ at its "maturity". We can observe from fig. (9) that under mixed control the colony following the uninvadable resource allocation strategy $\mathbf{u}^*$, will grow larger for higher queen mating frequency.

DISCUSSION

Our model provides predictions for sex-allocation schedules under three possible scenarios of control over reproduction in the colonies of annual eusocial insects: pure worker control, pure queen control, and mixed control. We showed that in a haplo-diploid insect colony, the "bang-bang" strategy of colony growth, that maximizes colony productivity of sexual offspring as predicted by a model with clonal reproduction and full queen control (Macevicz and Oster 1976), is realized only if either the queen or the workers are able to monopolize the control over all resource allocation decisions of the colony. If both parties control some of the reproductive allocation, then the colony growth still follows the "bang-bang" strategy, but the switch from the ergonomic to the reproductive phase happens earlier.

Our model thus predicts that conflict over sex allocation disturbs the worker production schedule under mixed control, but under single party control worker production schedule maximizes colony productivity. This is in accordance with the conflict resolution model by Reuter and Keller (2001). We indeed endorsed their approach on modelling conflict within colony over resource allocation, but extended it by allowing for time-dependent decision making. Contrary to Reuter and Keller (2001), however, we find in our dynamic setting that under mixed control of resource allocation the queen is able to impose her preference over sex allocation. This is because the queen decides the primary sex ratio once the workers stop rearing diploid eggs as workers and hence the workers are forced to rear more males than they would like to. If the sexual sex ratio is observed to be close to the optimum of the workers then we can expect full control of workers over the resource allocation under the assumptions of our model. Our prediction that the queen is in a strong position to impose her preference on sex allocation was anticipated by Bulmer (1981), but in a more restrictive biological scenario. Bulmer (1981) studied sex allocation conflict in annual eusocial colonies and his model did not explicitly include colony ontogeny over a season. The conflict was studied within two time steps at the end of the season and no overlap between generations of workers was assumed. Bulmer (1981) argued that in a population, where the sex ratio is between the optima of the queen and the workers, then in the penultimate generation the queens can start laying only haploid eggs, in which case only males are produced in the colony in that generation, and since no workers are produced, the colony dies one generation before the end of the season. Here, we showed that the queen can control the sex ratio even in less restrictive situations.

Polyandry reduces the potential conflict between the queen and the workers by lowering the relatedness asymmetry between the offspring of the queen. We showed that, as the sex allocation optimum of the workers converges to the queen's optimum due to polyandry, so does the premature switching time under mixed control converge closer to the optimal switching time observed under single party control. This is because the workers gain less benefit from turning worker destined eggs to queens. Similar effects can be expected to hold for other factors that reduce the queen-worker conflict over sex allocation, for example polygyny of related queens or worker production of male eggs (Ratnieks *et al.* 2006, Reuter and Keller 2001).

Comparative studies suggest that population-wide sex allocation in eusocial Hymenoptera is generally close to the worker optimum (Ratnieks *et al.* 2006, Bourke and Franks 1995, Sundström *et al.* 1996), although it is not universal (Helms 1999, Helms *et al.* 2000, Passera *et al.* 2001, Fjerdingstad *et al.* 2002). According to our model, this can only happen when workers have full control over sex allocation decisions. However, if we observe a sex allocation close to the queen optimum, workers might still possess some of the control and then the switching time from ergonomic to reproductive phase and the colony size at the start of reproduction should correlate with the kin structure in the colony under mixed control. We predict that colonies should grow larger if the relatedness asymmetry between the offspring of the queen is reduced through polyandry or polygyny under mixed control. Under single party control, the switching time and colony size should be unaffected by the kin structure in the colony. Correlation between colony size and queen mating frequency has been detected in attine ants (Murakami *et al.* 2000), however the sex ratio in different colonies in this study was in accordance with the predictions for full worker control.

Our model predicts that the onset of early reproduction under mixed control is more pronounced in poor habitats where resource acquisition rate is low and thus reproduction is slow, but colony per-capita productivity still scales linearly as the colony grows. Increased mortality of workers and decreased mortality of sexual offspring also cause the time difference between the optimal switching time and switching time under mixed control to be larger.

Our model predicts that there would be no time period in the season where workers and sexual offspring are produced at the same time. This "bang-bang" strategy of colony growth is exhibited by many annual primitively eusocial species of vespid wasps, bumble bees and sweat bees (see references in Mitesser *et al.* (2007*b*), Crone and Williams (2016)). However, not all annual eusocial insects exhibit the "bang-bang" strategy of growth and reproduction. For example, Greene (1984) has found that many North American vespine wasps depart from a strict "bang-bang" pattern by exhibiting "graded strategies" that contain a period during which sexuals and workers are produced simultaneously. Graded control can evolve in species where colony per-capita productivity is density-dependent (Poitrineau *et al.* 2009). This can happen if worker efficiency or mortality increases with colony size or if queens' egg laying capacity is limited. According to life-history theory, graded control can also evolve as an adaptive bet-hedging strategy in response to environmental fluctuations that can cause the variation in season length or food availability (King and Roughgarden 1982). However, current theoretical predictions imply that the environmental fluctuations alone can not select for graded control as a bet-hedging strategy in eusocial insect colonies (Mitesser *et al.* 2007*a*). It would be interesting to know how the predictions of our model change when assuming colony growth with decreasing returns. We can speculate that as the value of workers diminishes as the colony grows, so does the cost of turning worker destined eggs into workers and so the workers would start producing sexuals earlier in the season.

One of the restrictions of our model is that workers are assumed to be completely sterile. However, parthenogenetic production of males by unmated workers is found in many eusocial Hymenoptera. Worker reproduction can be restrained by workers policing each other. Theory predicts that worker policing should be at its highest at the ergonomic stage, because of the trade-off in worker's effort between reproduction and working (Ohtsuki and Tsuji 2009). Hence, worker reproduction is predicted to increase late in the season. Bulmer (1981) argued that for certain values of return on investment of producing workers, the queen may be able to prevent worker-egg laying in the final generation by limiting the number of diploid eggs and thus forcing workers to rear queen laid males in the penultimate generation. Under the assumptions of his model (non-overlapping generations of workers) this would cause a female biased sex ratio up to 2:1. Our model assumes that individuals in the colony possess some physiological mechanism that enables them to control the switch in reproduction and its timing. The underlying mechanism of the control of the switch from the ergonomic to the reproductive phase is not known. However it has been shown in *Bombus terrestris* that the queen is able to control the switching point endogenously (Holland *et al.* 2013).

In conclusion, we have shown that if both parties have some influence on colony resource allocation then the conflict over sex allocation between the queen and the workers gives rise to a suboptimal pattern of colony growth, characterized by a premature switch from the ergonomic to the reproductive phase and a sex allocation in the queen's optimum.

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Symbol	Meaning
$a_{\mathrm{k}}(t)$	Proportion of resources invested in type k $\in \{\mathrm{w}, ♀, ♂\}$ individuals at time t (population average)
$a^{s}_{\mathrm{k,u}}(t)$	Proportion of resources invested in type k $\in \{\mathrm{w}, ♀, ♂\}$ individuals at time t in a colony "founded" by a mutant individual of sex s
$H_c(\mathbf{x}_{\mathrm{u}}, \mathbf{u}, \lambda, t)$	Hamiltonian function for control mode of the trait $c \in \{\mathrm{w}, ♀\}$
M	queen mating frequency
n	(constant) number of colonies or breeding sites (very large number)
p^{s}_{c}	the frequency of the mutant in the average phenotype of the colony founded by a mutant of sex $s \in \{♀, ♂\}$ under control mode c.
$q_s(\mathbf{u}, \mathbf{v})$	asymptotic probability that a mutant allele is sampled in an individual of sex s
r	colony productivity per colony member (worker)
R_c	critical sex ratio for control mode $c \in \{\mathrm{w}, ♀\}$
r°_{s}	average relatedness between "actors" (queens or workers) and recipients of sex s
t	time of the season defined over a period $[0, T]$
t^{*}_{c}	switching time from ergonomic phase to reproductive phase under control mode$c \in \{♀, \mathrm{w}, m\}$
$u^{s}_{\mathrm{f}}(t)$	proportion of resources allocated to producing females (individuals destined to become workers or queens) at time t in a colony founded by an individual of sex s who carries a mutant allele
$u^{s}_{\mathrm{g}}(t)$	proportion of resources allocated to producing queens from resources allocated to females at time t in a colony founded by an individual of sex s who carries a mutant allele
$u^{s}_{\tau}(t)$	resources allocation trait in a colony founded by an individual of sex s who carries a mutant allele
$\mathbf{u}$	full allocation schedule of a colony, where the individual or individuals in control carry only mutant alleles
$\mathbf{u}^{s}$	full allocation schedule of a colony founded by an individual of sex s who carries a mutant allele
$\mathbf{u}^{*}$	uninvadable (evolutionarily stable) full allocation schedule
$v_{\mathrm{f}}(t)$	proportion of resources allocated to producing females (individuals destined to become workers or queens) at time t (population average)
$v_{\mathrm{g}}(t)$	proportion of resources allocated to producing queens from resources allocated to females at time t (population average)
$\mathbf{v}$	full allocation schedule of a resident (population average) colony
$w_{s's}(\mathbf{u}^{s}, \mathbf{v})$	the expected number of juveniles of sex $s' \in \{♀, ♂\}$ that descend from a juvenile of sex $s \in \{♀, ♂\}$ carrying the mutant allele
$W_c(\mathbf{u}, \mathbf{v})$	invasion fitness of the mutant with the mode of control of the trait $c \in \{\mathrm{w}, ♀\}$
$x_{\mathrm{k}}(t)$	number of type k $\in \{\mathrm{w}, ♀, ♂\}$ individuals in the colony (population average)

$x^{s}_{\mathrm{k,u}}(t)$	number of type $\mathrm{k} \in \{\mathrm{w}, ♀, ♂\}$ individuals in the colony a colony "founded" by a mutant individual of sex s
$x^{*}_{\mathrm{k}}(t)$	number of type $\mathrm{k} \in \{\mathrm{w}, ♀, ♂\}$ individuals in the colony following an uninvadable full allocation schedule $\mathbf{u}^{*}$
$\mathbf{z}$	full resource allocation schedule of a focal colony
α	replacement factor in the iterative scheme of best response map
α°_{s}	normalized neutral reproductive value of an individual of sex s
$\gamma_{s's}$	the probability that a gene sampled in an individual of sex $s' \in \{♀, ♂\}$ was contributed by an individual of sex $s \in \{♀, ♂\}$; i.e. transmission frequency of sex s to sex s'
$\lambda^{s}_{\mathrm{k}}(t)$	a costate variable associated with the state variable $x^{s}_{\mathrm{k,u}}(t)$
ϵ_{τ}	weak phenotypic deviation from the resident phenotype $v_{\tau}(t)$
$\eta(t)$	some change in schedule of the resident phenotype $v_{\tau}(t)$
μ_{k}	mortality rate of type $\mathrm{k} \in \{\mathrm{w}, ♀, ♂\}$ individuals
v°_{s}	neutral reproductive value of an individual of sex s

Table 1: List of symbols and their meaning.

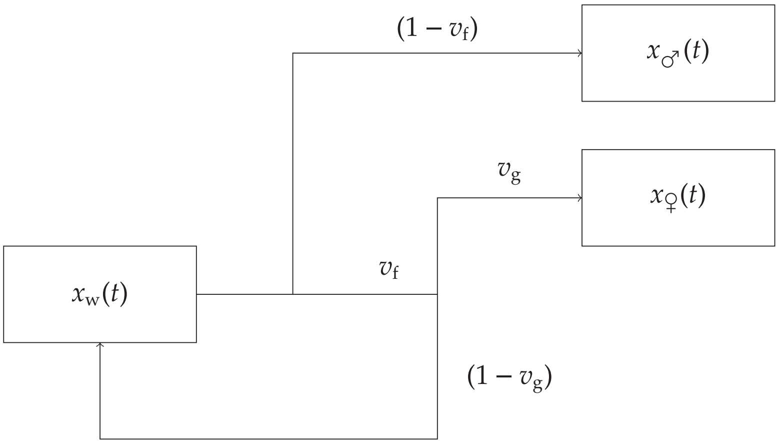

Figure 1: Schematic of the demographic model of the colony. Workers (measured by $x_w(t)$) acquire resources from the environment, from which a fraction $0 \leq v_f \leq 1$ is invested into producing females (either new queens or workers). From resources that are allocated to females, a fraction $0 \leq v_g \leq 1$ is converted into sexual females (new queens).

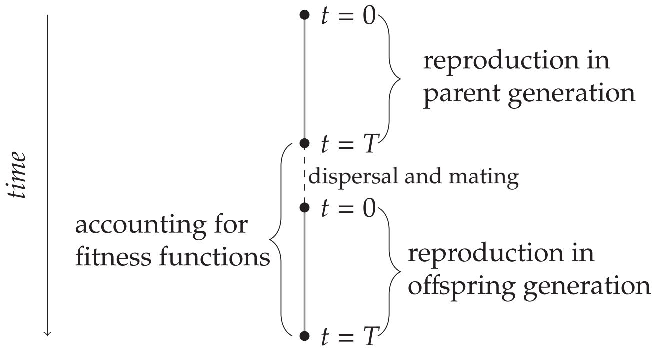

Figure 2: The conceptual graph of the life cycle and accounting for fitness in the model.

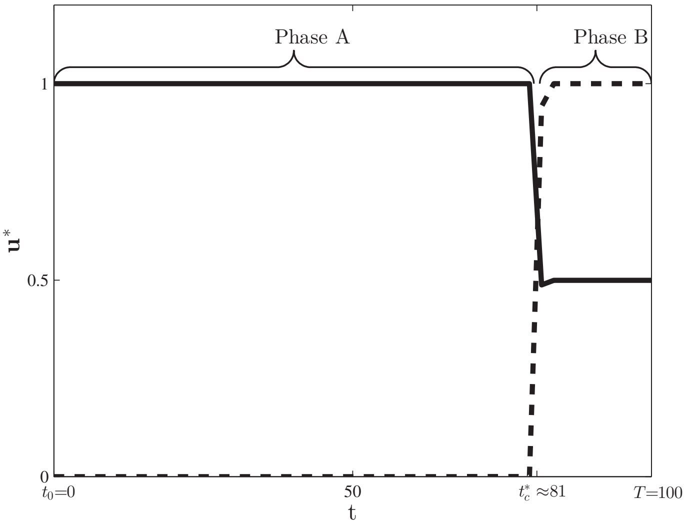

Figure 3: Uninvadable resource allocation strategy $\mathbf{u}^*$ under full queen control and queen monandry ($M = 1$). Primary sex ratio $u^*_{\mathrm{f}}(t)$ (solid line), proportional allocation to queens versus workers from the resources allocated to females $u^*_{\mathrm{g}}(t)$ (dashed line). In the ergonomic phase (phase A) only workers are produced and in the reproductive phase (phase B) equal amount of queens and males are produced. Parameter values: $r = 0.06$, $\mu_{\mathrm{w}} = 0.02$, $\mu_{♀} = \mu_{♂} = 0.005$, $T = 100$.

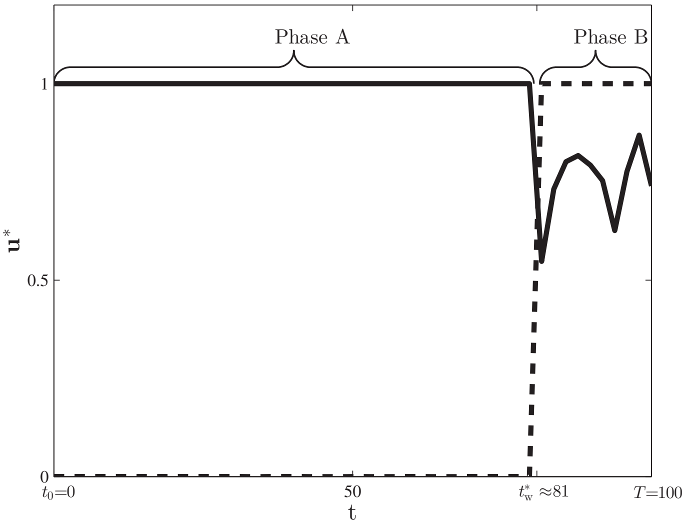

Figure 4: Uninvadable resource allocation strategy $\mathbf{u}^*$ under full worker control and queen monandry ($M = 1$). Primary sex ratio $u_f^*(t)$ (solid line), proportional allocation to queens versus workers from the resources allocated to females $u_g^*(t)$ (dashed line). In the ergonomic phase (phase A) only workers are produced and in the reproductive phase (phase B) three times as many queens are produced than males. Parameter values: $r = 0.06$, $\mu_w = 0.02$, $\mu_♀ = \mu_♂ = 0.005$, $T = 100$. The average primary sex ratio over the reproductive phase is $u_f^*(t) = 0.75$. Note that the reason $u_f^*(t)$ is not constantly equal to 0.75 in the reproductive phase is that the optimal control problem to solve under worker control has twice as many state variables and more complicated objective function (see Appendix B). Hence, the simulation time takes much longer to converge to a straight line. However, this solution still satisfies the first order condition for optimality.

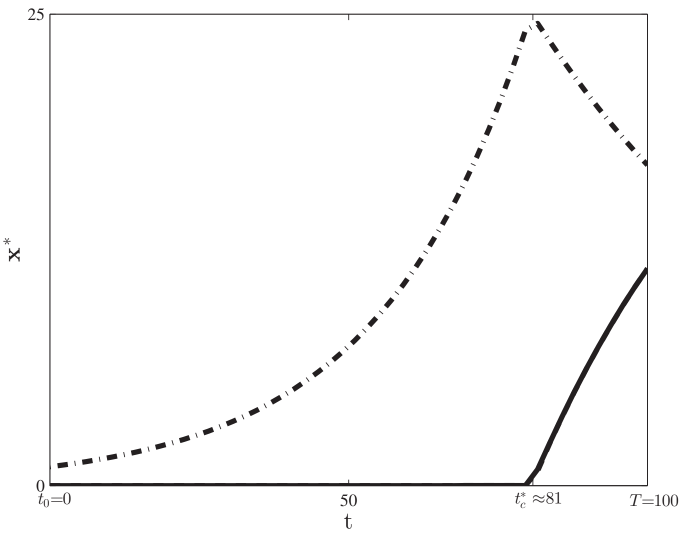

Figure 5: Number of individuals in the colony with the uninvadable resource allocation strategy $\mathbf{u}^*$ under queen control and queen monandry ($M = 1$). Number of queens (solid line), number of males (dashed line) and number of workers (dashed-dotted line). Parameter values: $r = 0.06$, $\mu_{\mathrm{w}} = 0.02$, $\mu_{♀} = \mu_{♂} = 0.005$, $T = 100$.

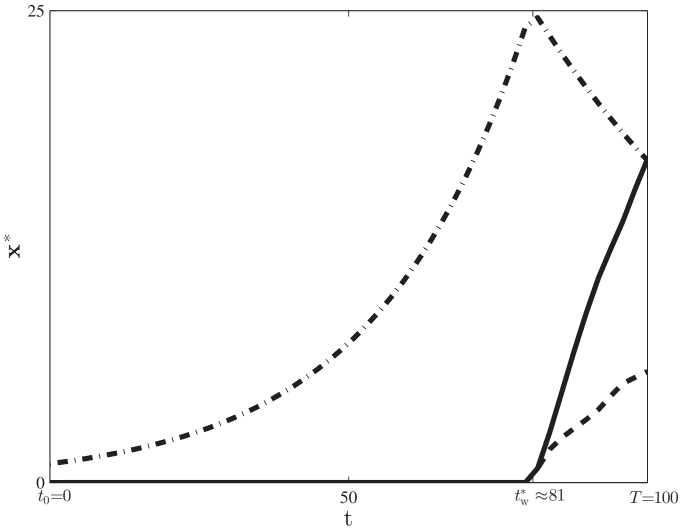

Figure 6: Number of individuals in the colony with the uninvadable resource allocation strategy $\mathbf{u}^*$ under worker control and queen monandry ($M = 1$). Number of queens (solid line), number of males (dashed line) and number of workers (dashed-dotted line). Parameter values: $r = 0.06$, $\mu_{\mathrm{w}} = 0.02$, $\mu_{♀} = \mu_{♂} = 0.005$, $T = 100$.

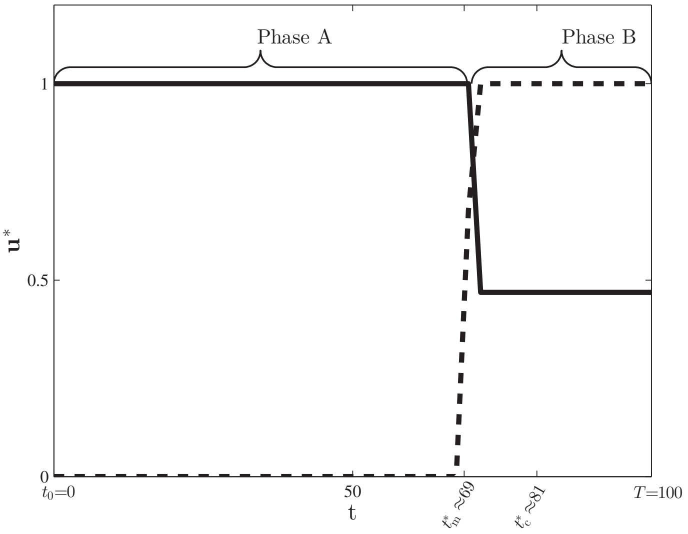

Figure 7: Uninvadable resource allocation strategy $\mathbf{u}^*$ under mixed control and queen monandry ($M = 1$). Primary sex ratio $u^*_\mathrm{f}(t)$ (dashed line), proportional allocation to queens versus workers from the resources allocated to females $u^*_\mathrm{g}(t)$ (solid line). In the ergonomic phase (phase A) only workers are produced and in the reproductive phase (phase B) equal amount of queens and males are produced. Parameter values: $r = 0.06$, $\mu_\mathrm{w} = 0.02$, $\mu_♀ = \mu_♂ = 0.005$, $T = 100$. The average primary sex ratio over the reproductive phase is $u^*_\mathrm{f}(t) = 0.5$.

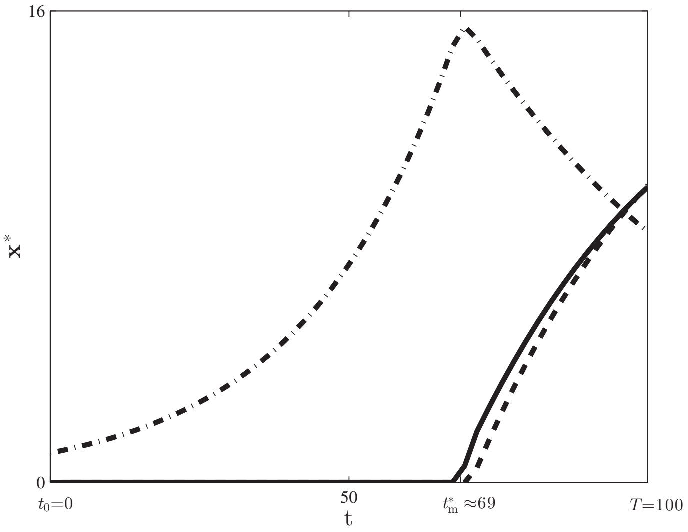

Figure 8: Number of individuals in the colony with the uninvadable resource allocation strategy $\mathbf{u}^*$ under mixed control and queen monandry ($M = 1$). Number of queens (solid line), number of males (dashed line) and number of workers (dashed-dotted line). Parameter values: $r = 0.06$, $\mu_{\text{w}} = 0.02$, $\mu_{♀} = \mu_{♂} = 0.005$, $T = 100$.

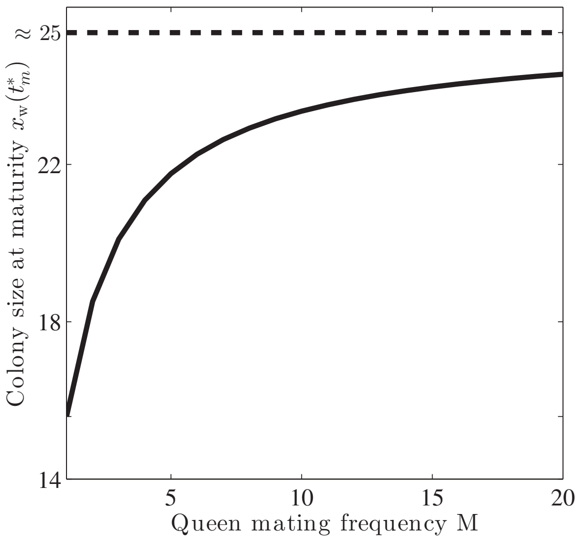

Figure 9: Colony size at maturity $x_{\mathrm{w}}(t_m^*)$ under mixed control as a function of queen mating frequency M for the uninvadable resource allocation strategy $\mathbf{u}^*$. Colony size at maturity $x_{\mathrm{w}}(t_m^*)$ under mixed control (solid line). Colony size at maturity in a colony with no conflict (dashed line). Parameter values: $r = 0.06$, $\mu_{\mathrm{w}} = 0.02$, $\mu_{♀} = \mu_{♂} = 0.005$, $T = 100$.

APPENDIX A: INVASION FITNESS

We here provide a proof for eq. (11). The leading eigenvalue $W_c(\mathbf{u},\mathbf{v})$ of the matrix $\mathbf{A}_c(\mathbf{u},\mathbf{v})$ satisfies $W_c(\mathbf{u},\mathbf{v})\mathbf{q}(\mathbf{u},\mathbf{v}) = \mathbf{A}_c(\mathbf{u},\mathbf{v})\mathbf{q}(\mathbf{u},\mathbf{v})$, where $\mathbf{q}(\mathbf{u},\mathbf{v}) = (q_{\female}(\mathbf{u},\mathbf{v}), q_{\male}(\mathbf{u},\mathbf{v}))^{\intercal}$ is the normalized right leading eigenvector of $\mathbf{A}_c(\mathbf{u},\mathbf{v})$. Pre-multiplying this equation by the vector $(1,1)$ yields eq. (11) and a direct calculation produces

$$q_{\female}(\mathbf{u},\mathbf{v}) = \frac{2\gamma_{\male\female} w_{\male\female}\left(\mathbf{u}^{\female},\mathbf{v}\right)}{2\gamma_{\male\female} w_{\male\female}\left(\mathbf{u}^{\female},\mathbf{v}\right) + \sqrt{A(\mathbf{u},\mathbf{v})} + X(\mathbf{u},\mathbf{v})}, \tag{A1}$$

where

$$A(\mathbf{u},\mathbf{v}) = X(\mathbf{u},\mathbf{v})^2 + 4\gamma_{\female\male}\gamma_{\male\female} w_{\female\male}\left(\mathbf{u}^{\male},\mathbf{v}\right) w_{\male\female}\left(\mathbf{u}^{\female},\mathbf{v}\right)$$

with $X(\mathbf{u},\mathbf{v}) = \gamma_{\female\female} w_{\female\female}\left(\mathbf{u}^{\female},\mathbf{v}\right) - \gamma_{\male\male} w_{\male\male}\left(\mathbf{u}^{\male},\mathbf{v}\right)$.

APPENDIX B: LOCAL UNINVADABILITY

Computing an uninvadable strategy entails establishing an optimal pair

$$(\mathbf{u}^*(t), \mathbf{x}^*(t)) = (u_{\mathrm{f}}^*(t), u_{\mathrm{g}}^*(t), x_{\mathrm{w}}^*(t), x_{\female}^*(t), x_{\male}^*(t))\ \forall t \in [0,T], \tag{B1}$$

which is a solution to eq. (13) for single party control and eq. (16) for mixed control. These are maximization problems with constraints, where the control variables

$$\mathbf{u}_c = (u_{\mathrm{f}}(t), u_{\mathrm{g}}(t)) \tag{B2}$$

must satisfy

$$0 \le u_\tau(t) \le 1\ \forall t \in [0,T],\ \tau \in \{\mathrm{f},\mathrm{g}\}, \tag{B3}$$

while the state variables

$$\mathbf{x}_{\mathrm{u}} = (x_{\mathrm{w,u}}^{\female}(t), x_{\female,\mathrm{u}}^{\female}(t), x_{\male,\mathrm{u}}^{\female}(t), x_{\mathrm{w,u}}^{\male}(t), x_{\female,\mathrm{u}}^{\male}(t), x_{\male,\mathrm{u}}^{\male}(t)) \in [0,\infty[^6 \tag{B4}$$

and the dynamic parameters

$$\mathbf{x} = (x_{\mathrm{w}}(t), x_{\female}(t), x_{\male}(t)) \in [0,\infty[^3 \tag{B5}$$

involved in invasion fitness (eq. (11)) must satisfy the dynamic constraints

$$\begin{aligned} \dot{x}_{\mathrm{k,u}}^{s} &= g_{\mathrm{k,u}}^{s}(\mathbf{x}_{\mathrm{u}}, \mathbf{u}, t), \\ \dot{x}_{\mathrm{k}} &= g_{\mathrm{k}}(\mathbf{x}, \mathbf{v}, t), \end{aligned} \tag{B6}$$

with initial conditions

$$x_{\mathrm{k,u}}^{s}(0) = x_{\mathrm{k}}(0) = x_{\mathrm{k},0} \text{ for k} \in \{\female, \male, \mathrm{w}\}. \tag{B7}$$

Here,

$$\begin{aligned} g^{s}_{\mathrm{k,u}}(\mathbf{x}_{\mathrm{u}}, \mathbf{u}, t) &= r a^{s}_{\mathrm{k,u}}(\mathbf{u}, t) x^{s}_{\mathrm{w,u}}(t) - \mu_{\mathrm{k}} x^{s}_{\mathrm{k,u}}(t), \\ g_{\mathrm{k}}(\mathbf{x}, \mathbf{v}, t) &= r a_{\mathrm{k}}(\mathbf{v}, t) x_{\mathrm{w}}(t) - \mu_{\mathrm{k}} x_{\mathrm{k}}(t), \end{aligned} \tag{B8}$$

where the mutant and resident allocation schedules are given, respectively, by eq. 4 and eq. 2 of the main text.

For single and mixed party control, the characterization of the best response schedule $(\mathbf{u}^{*}(t), \mathbf{x}^{*}(t))$ can be done by way of applying optimal control theory, since formally uninvadable strategies are Nash equilibria and necessary conditions for Nash equilibria can be given in terms of Pontryagin's maximum principle (Mazalov 2014: p. 372, Theorem 10.8). We now provide the first-order conditions for uninvadability (see eq. 15), and do this by first providing a marginal condition that must be satisfied over the whole time schedule and then characterize the optimal schedule itself.

First-order condition 1: the critical sex-ratio

We here prove eq. (18). Because the functional derivative $\mathrm{d}W_{c}(\mathbf{u}, \mathbf{v}) / \mathrm{d}\epsilon_{\tau}$ determining the first order condition (eq. (15)) is an ordinary function in ϵ_{τ}, it follows from standard results of eigenvalue perturbation (Caswell 2000) that

$$\begin{aligned} \frac{\mathrm{d}W_{c}(\mathbf{u}, \mathbf{v})}{\mathrm{d}\epsilon_{\tau}} = & \left(v^{\circ}_{♀} \gamma_{♀♀} \frac{\mathrm{d}w_{♀♀}\big(\mathbf{u}^{♀}, \mathbf{v}\big)}{\mathrm{d}\epsilon_{\tau}} + v^{\circ}_{♂} \gamma_{♂♀} \frac{\mathrm{d}w_{♂♀}\big(\mathbf{u}^{♀}, \mathbf{v}\big)}{\mathrm{d}\epsilon_{\tau}} \right) q^{\circ}_{♀} \\ & + \left(v^{\circ}_{♀} \gamma_{♀♂} \frac{\mathrm{d}w_{♂♀}\big(\mathbf{u}^{♂}, \mathbf{v}\big)}{\mathrm{d}\epsilon_{\tau}} + v^{\circ}_{♂} \gamma_{♂♂} \frac{\mathrm{d}w_{♂♂}\big(\mathbf{u}^{♂}, \mathbf{v}\big)}{\mathrm{d}\epsilon_{\tau}} \right) q^{\circ}_{♂}. \end{aligned} \tag{B9}$$

Here, v°_{s} is the neutral reproductive value of an individual of sex s and q°_{s} is the neutral class frequency. Throughout the superscript $\circ$ will denote a quantity that is evaluated in the absence of natural selection, i.e., a process determined by the monomorphic resident population; that is, matrix

$$\mathbf{A}(\mathbf{v}, \mathbf{v}) = \begin{bmatrix} \gamma_{♀♀} & \gamma_{♀♂} \frac{x_{♀}(\mathbf{v})}{x_{♂}(\mathbf{v})} \\ \gamma_{♂♀} \frac{x_{♂}(\mathbf{v})}{x_{♀}(\mathbf{v})} & \gamma_{♂♂} \end{bmatrix} \tag{B10}$$

whose dominant eigenvalue is one. The reproductive values and class frequencies are, respectively, given by the left and right unit eigenvectors of $\mathbf{A}(\mathbf{v}, \mathbf{v})$, and we normalize these vectors such that the total reproductive value defined by

$$\alpha^{\circ}_{s} = v^{\circ}_{s} q^{\circ}_{s} \tag{B11}$$

(e.g., Taylor 1990, Taylor and Frank 1996, Rousset 2004) of all individuals of class i add up to one: $\alpha^{\circ}_{♂} + \alpha^{\circ}_{♀} = 1$. This normalization subtends the use of the perturbation formula eq. (B9) (e.g., Caswell 2000). With this, we obtain

$$\alpha^{\circ}_{♀} = \frac{1 - \gamma_{♂♂}}{2 - \gamma_{♂♂} - \gamma_{♂♂}} \quad \text{and} \quad q^{\circ}_{♀} = \frac{x_{♀}(\mathbf{v})}{x_{♀}(\mathbf{v}) + x_{♂}(\mathbf{v})}. \tag{B12}$$

In eq. (B9), the derivative $\mathrm{d}w_{s's}(\mathbf{u}^s, \mathbf{v})/\,\mathrm{d}\epsilon_\tau$ is the total variation of fitness with respect to mutant values, which acts on $\mathbf{u}^s$ (by way of eq. (3)). By the chain rule of functional derivatives, we can write this

$$\frac{\mathrm{d}w_{s's}(\mathbf{u}^s, \mathbf{v})}{\mathrm{d}\epsilon_\tau} = \frac{\mathrm{d}w_{s's}(\mathbf{z}, \mathbf{v})}{\mathrm{d}\epsilon_{\mathrm{z},\tau}} \frac{\mathrm{d}u^s_\tau(t)}{\eta(t)\,\mathrm{d}\epsilon_\tau}, \tag{B13}$$

where $\epsilon_{\mathrm{z},\tau}$ is the intensity of the direct variation of $z_\tau(t) = v_\tau(t) + \epsilon_{\mathrm{z},\tau}\eta(t)$ and $p^s_c = \mathrm{d}u^s_\tau(t)/(\eta(t)\,\mathrm{d}\epsilon_\tau)$ is the frequency of the mutant allele in the average phenotype of the individual c in control of the trait a the colony founded by a mutant of sex $s \in \{♀, ♂\}$. Indeed, by substituting eq. (14) of the main text into eq. (3), we have

$$u^s_\tau(t) = v_\tau(t) + \epsilon_\tau \eta(t) p^s_c, \tag{B14}$$

whereby $\mathrm{d}u^s_\tau(t)/(\eta(t)\,\mathrm{d}\epsilon_\tau) = p^s_c$.

Substituting eq. (B13) into eq. (B9), we have for control mode $c \in \{♀, \mathrm{w}\}$ that

$$\begin{aligned}\frac{\mathrm{d}W_c(\mathbf{u}, \mathbf{v})}{\mathrm{d}\epsilon_\tau} &= \left(v^\circ_{♀} \gamma_{♀♀} \frac{\mathrm{d}w_{♀♀}(\mathbf{z}, \mathbf{v})}{\mathrm{d}\epsilon_{\mathrm{z},\tau}} + v^\circ_{♂} \gamma_{♂♀} \frac{\mathrm{d}w_{♂♀}(\mathbf{z}, \mathbf{v})}{\mathrm{d}\epsilon_{\mathrm{z},\tau}} \right) p^{♀}_c q^\circ_{♀} \\ &\quad + \left(v^\circ_{♀} \gamma_{♀♂} \frac{\mathrm{d}w_{♂♀}(\mathbf{z}, \mathbf{v})}{\mathrm{d}\epsilon_{\mathrm{z},\tau}} + v^\circ_{♂} \gamma_{♂♂} \frac{\mathrm{d}w_{♂♂}(\mathbf{z}, \mathbf{v})}{\mathrm{d}\epsilon_{\mathrm{z},\tau}} \right) p^{♂}_c q^\circ_{♂},\end{aligned} \tag{B15}$$

where all derivative are evaluated at $\epsilon_{\mathrm{z},\tau} = 0$ and thus all controls are set to the resident schedule $\mathbf{v}$. Substituting the expressions for individual fitness (eqs. (7)–()), using eq. (B12), the equalities $\gamma_{♂♀} = 1 - \gamma_{♂♂}$ and $\gamma_{♀♂} = 1 - \gamma_{♀♀}$, we arrive by rearrangement at

$$\left.\frac{\mathrm{d}W_c(\mathbf{u}, \mathbf{v})}{\mathrm{d}\epsilon_\tau}\right|_{\epsilon_{\mathrm{f}}=0, \epsilon_{\mathrm{g}}=0} = 0 \qquad \Longrightarrow \qquad \frac{x_{♂}(\mathbf{v})}{x_{♀}(\mathbf{v})} = -\frac{\mathrm{d}x_{♂}(\mathbf{z})/\,\mathrm{d}\epsilon_\tau}{\mathrm{d}x_{♀}(\mathbf{z})/\,\mathrm{d}\epsilon_\tau} \times R_c, \tag{B16}$$

where

$$R_c = \frac{(1 - \gamma_{♀♀})}{(1 - \gamma_{♂♂})} \times \left(\frac{\gamma_{♂♀} p^{♀}_c + \gamma_{♂♂} p^{♂}_c}{\gamma_{♀♀} p^{♀}_c + \gamma_{♀♂} p^{♂}_c} \right), \tag{B17}$$

and using the explicit variable values for our model [$\gamma_{♂♀} = 1$, $\gamma_{♀♂} = 1/2$, $p^{♀}_{♀} = 1/2$, $p^{♂}_{♀} = 0$, $p^{♀}_{\mathrm{w}} = 1/4$, and $p^{♂}_{\mathrm{w}} = 1/(2M)$] we have

$$R_{♀} = 1 \quad \text{(queen control)} \qquad\qquad R_{\mathrm{w}} = \frac{M}{2 + M} \quad \text{(worker control).} \tag{B18}$$

This shows that R_c is the *relatedness asymmetry*, which is defined as the ratio of the relatedness weighted class reproductive values of an actor towards sex-specific recipients (Boomsma and Grafen 1991: p. 386). To see this we note that owing to eq. (B12), the first ratio in eq. (B17), $(1 - \gamma_{♀♀})/(1 - \gamma_{♂♂})$, is equal to the ratio $\alpha^\circ_{♂}/\alpha^\circ_{♀}$ of class reproductive values. Further, $\gamma_{♂♀} p^{♀}_c + \gamma_{♂♂} p^{♂}_c$ ($\gamma_{♀♀} p^{♀}_c + \gamma_{♀♂} p^{♂}_c$) is the probability that a gene randomly sampled in a recipient male (female) is identical-by-descent to a gene randomly sampled in an individual controlling trait expression (the actor); that is, the *coancestry* between a son (daughter) and its parent. Since a ratio of coancestry is equivalent to a ratio of relatedness, we can write the second ratio in eq. (B17) as $r^{\circ}_{\text{♂}}/r^{\circ}_{\text{♀}}$, where r°_{i} is the relatedness between recipients of sex i and the average actor affecting this class. With this we have

$$R_c = \frac{\alpha^{\circ}_{\text{♂}} r^{\circ}_{\text{♂}}}{\alpha^{\circ}_{\text{♀}} r^{\circ}_{\text{♀}}}, \tag{B19}$$

where the relatedness depends on who is control of the trait.

First-order condition 2: Hamiltonian and Pontryagin's maximum principle

We here characterize the optimal allocation schedule by way of applying optimal control theory (e.g., Sydsæter *et al.* 2008, Bryson and Ho 1975 for broad introductions and Iwasa and Roughgarden 1984, Macevicz and Oster 1976, Perrin 1992, Day and Taylor 2000 for previous application to evolutionary biology). Because the final values $\mathbf{x}_{\mathrm{u}}(T)$ determined by eq. (B4) are free and invasion fitness is entirely determined by them (by way of eq. (10)), it follows from standard results of optimal control theory results with terminal pay-offs (e.g, Mazalov 2014: p. 372, Theorem 10.8) that the first-order condition for uninvadability (eq. 15) can be expressed in term of point-wise marginal change:

$$\left.\frac{\mathrm{d}W_c(\mathbf{u},\mathbf{v})}{\mathrm{d}\epsilon_\tau}\right|_{\epsilon_{\mathrm{f}}=0,\epsilon_{\mathrm{g}}=0,\mathbf{u}=\mathbf{v}=\mathbf{u}^*} = 0 \qquad \Longrightarrow$$

$$\left.\frac{\partial H_c(\mathbf{x}^*,\mathbf{u},\boldsymbol{\lambda},t)}{\partial u_\tau}\right|_{\mathbf{u}=\mathbf{v}=\mathbf{u}^*} = 0 \quad \text{and} \tag{B20a}$$

$$\dot{\lambda}^s_{\mathrm{k}} = -\left.\frac{\partial H_c(\mathbf{x}_{\mathrm{u}},\mathbf{u}^*,\boldsymbol{\lambda},t)}{\partial x^s_{\mathrm{k,u}}}\right|_{\mathbf{x}_{\mathrm{u}}=\mathbf{x}=\mathbf{x}^*} \quad \text{for } \mathrm{k} \in \{\mathrm{w},\text{♀},\text{♂}\}. \tag{B20b}$$

Here,

$$H_c(\mathbf{x}_{\mathrm{u}},\mathbf{u},\boldsymbol{\lambda},t) = \sum_{\mathrm{k}\in\{\mathrm{w},\text{♀},\text{♂}\}} \lambda^{\text{♀}}_{\mathrm{k}} g^{\text{♀}}_{\mathrm{k,u}} + \mathbb{1}_c \sum_{\mathrm{k}\in\{\mathrm{w},\text{♀},\text{♂}\}} \lambda^{\text{♂}}_{\mathrm{k}} g^{\text{♂}}_{\mathrm{k,u}} \tag{B21}$$

is the so-called Hamiltonian function, where

$$\mathbb{1}_c = \begin{cases} 0 & \text{for } c = \text{♀}, \\ 1 & \text{for } c = \mathrm{w}, \end{cases} \tag{B22}$$

and $\lambda^s_{\mathrm{k}}(t)$ is a costate variable associated with the state variable $x^s_{\mathrm{k}}(t)$. A costate variable gives the marginal value of the corresponding state variable at time t, i.e., it gives the effect on invasion for a marginal change in the corresponding state variable at time t. Informally, the state equations represent constraints of the maximization problem, and the costate variables give the marginal cost of violating those constraints. Since $\mathbf{x}_{\mathrm{u}}(T)$ is free, the transversality condition for the co-state variable for $\mathrm{k} \in \{\mathrm{w}, \female, \male\}$ is

$$\lambda_{\mathrm{k}}^{s}(T) = \left. \frac{\partial W_c(\mathbf{u}, \mathbf{v})}{\partial x_{\mathrm{k,u}}^{s}(T)} \right|_{\mathbf{x}_{\mathrm{u}}=\mathbf{x}=\mathbf{x}^*} \tag{B23}$$

(e.g., Bryson and Ho 1975, Sydsæter *et al.* 2008).

When party $c \in \{\mathrm{w}, \female\}$ has full control over the traits, the first-order conditions for uninvadability is that the respective Hamiltonian H_c is maximized with respect to both of the controls

$$\left. \frac{\partial H_c(\mathbf{x}^*, \mathbf{u}, \boldsymbol{\lambda}, t)}{\partial u_\tau} \right|_{\mathbf{u}=\mathbf{v}=\mathbf{u}^*} = 0, \ \tau \in \{\mathrm{f}, \mathrm{g}\} \,. \tag{B24}$$

By contrast, the necessary first order condition for mixed control is given by

$$\left. \frac{\partial H_{\female}(\mathbf{x}^*, \mathbf{u}, \boldsymbol{\lambda}, t)}{\partial u_{\mathrm{f}}} \right|_{\mathbf{u}=\mathbf{v}=\mathbf{u}^*} = 0 \quad \text{and} \quad \left. \frac{\partial H_{\mathrm{w}}(\mathbf{x}^*, \mathbf{u}, \boldsymbol{\lambda}, t)}{\partial u_{\mathrm{g}}} \right|_{\mathbf{u}=\mathbf{v}=\mathbf{u}^*} = 0. \tag{B25}$$

Derivatives of the Hamiltonian

In order to compute the first-order conditions (eqs. B24-B25), we need the derivatives of the Hamiltonian with respect to controls u_τ. Substituting eq. (B8) into eq. (B21) produces

$$\left. \frac{\partial H_c(\mathbf{x}^*, \mathbf{u}, \boldsymbol{\lambda}, t)}{\partial u_\tau} \right|_{\mathbf{u}_{\mathrm{u}}=\mathbf{u}=\mathbf{u}^*} =$$

$$rx_{\mathrm{w}}^* \left[\lambda_{\mathrm{w}}^{\female} \frac{\partial a_{\mathrm{w,u}}^{\female}}{\partial u_\tau} + \lambda_{\female}^{\female} \frac{\partial a_{\female,\mathrm{u}}^{\female}}{\partial u_\tau} + \lambda_{\male}^{\female} \frac{\partial a_{\male,\mathrm{u}}^{\female}}{\partial u_\tau} + \mathbb{1}_c \left(\lambda_{\mathrm{w}}^{\male} \frac{\partial a_{\mathrm{w,u}}^{\male}}{\partial u_\tau} + \lambda_{\male}^{\male} \frac{\partial a_{\female,\mathrm{u}}^{\male}}{\partial u_\tau} + \lambda_{\male}^{\male} \frac{\partial a_{\male,\mathrm{u}}^{\male}}{\partial u_\tau} \right) \right]. \tag{B26}$$

For queen control ($c = \female$), we have

$$\frac{\partial a_{\mathrm{w,u}}^{\female}}{\partial u_{\mathrm{f}}} = (1 - u_g^*) p_c^{\female} \,, \ \frac{\partial a_{\female,\mathrm{u}}^{\female}}{\partial u_{\mathrm{f}}} = u_g^* p_c^{\female} \,, \ \frac{\partial a_{\male,\mathrm{u}}^{\female}}{\partial u_{\mathrm{f}}} = -p_c^{\female} \,,$$

$$\frac{\partial a_{\mathrm{w,u}}^{\male}}{\partial u_{\mathrm{f}}} = (1 - u_g^*) p_c^{\male} \,, \ \frac{\partial a_{\female,\mathrm{u}}^{\male}}{\partial u_{\mathrm{f}}} = u_g^* p_c^{\male} \,, \ \frac{\partial a_{\male,\mathrm{u}}^{\male}}{\partial u_{\mathrm{f}}} = -p_c^{\male} \,,$$

while for worker control ($c = \mathrm{w}$), we have

$$\frac{\partial a_{\mathrm{w,u}}^{\female}}{\partial u_{\mathrm{g}}} = -u_{\mathrm{f}}^* p_c^{\female} \,, \ \frac{\partial a_{\female,\mathrm{u}}^{\female}}{\partial u_{\mathrm{g}}} = u_{\mathrm{f}}^* p_c^{\female} \,, \ \frac{\partial a_{\male,\mathrm{u}}^{\female}}{\partial u_{\mathrm{g}}} = 0 \,, \ \frac{\partial a_{\mathrm{w,u}}^{\male}}{\partial u_{\mathrm{f}}} = -u_{\mathrm{f}}^* p_c^{\male} \,, \ \frac{\partial a_{\female,\mathrm{u}}^{\male}}{\partial u_{\mathrm{g}}} = u_{\mathrm{f}}^* p_c^{\male} \text{ and } \frac{\partial a_{\male,\mathrm{u}}^{\male}}{\partial u_{\mathrm{g}}} = 0. \tag{B27}$$

The derivatives of the Hamiltonian with respect to controls u_{f} and u_{g} can then be written as

$$\begin{aligned}\left.\frac{\partial H_c(\mathbf{x}^*,\mathbf{u},\boldsymbol{\lambda},t)}{\partial u_{\mathrm{f}}}\right|_{\mathbf{u}=\mathbf{u}^*} &= r x^*_{\mathrm{w}}\left(u^*_g \sigma^c_1 - \sigma^c_2\right)\\ \left.\frac{\partial H_c(\mathbf{x}^*,\mathbf{u},\boldsymbol{\lambda},t)}{\partial u_{\mathrm{g}}}\right|_{\mathbf{u}=\mathbf{u}^*} &= r x^*_{\mathrm{w}} u^*_{\mathrm{f}} \sigma^c_1,\end{aligned} \tag{B28}$$

where σ^p_1 and σ^p_2 are the so-called switching functions (e.g., Bryson and Ho 1975) and given by

$$\begin{aligned}\sigma^c_1 &= p^{\text{♀}}_c\left(\lambda^{\text{♀}}_{\text{♀}} - \lambda^{\text{♀}}_{\mathrm{w}}\right) + \mathbb{1}_c p^{\text{♂}}_c\left(\lambda^{\text{♂}}_{\text{♀}} - \lambda^{\text{♂}}_{\mathrm{w}}\right)\\ \sigma^c_2 &= p^{\text{♀}}_c\left(\lambda^{\text{♀}}_{\text{♂}} - \lambda^{\text{♀}}_{\mathrm{w}}\right) + \mathbb{1}_c p^{\text{♂}}_c\left(\lambda^{\text{♂}}_{\text{♂}} - \lambda^{\text{♂}}_{\mathrm{w}}\right).\end{aligned} \tag{B29}$$

Costate variables

The dynamical equations of the costate variables are

$$\begin{aligned}\dot{\lambda}^s_{\text{♀}} &= \mu_{\text{♀}}\lambda^s_{\text{♀}}\\ \dot{\lambda}^s_{\text{♂}} &= \mu_{\text{♂}}\lambda^s_{\text{♂}}\\ \dot{\lambda}^s_{\mathrm{w}} &= -\left[\lambda^s_{\mathrm{w}}(r a^*_{\mathrm{w}} - \mu_{\mathrm{w}}) + \lambda^s_{\text{♀}} r a^*_{\text{♀}} + \lambda^s_{\text{♂}} r a^*_{\text{♂}}\right],\end{aligned} \tag{B30}$$

where $a^*_{\mathrm{w}} = u^*_{\mathrm{f}}(1-u^*_{\mathrm{g}})$, $a^*_{\text{♀}} = u^*_{\mathrm{f}}u^*_{\mathrm{g}}$, and $a^*_{\text{♂}} = (1-u^*_{\mathrm{f}})$. The initial conditions for this system of equations depends on the transversality condition (B23). Because the number of workers does not appear in the expression of invasion fitness, we have, regardless of the mode of control of traits, that

$$\lambda^s_{\mathrm{w}}(T) = 0 \text{ for } s \in \{\text{♀},\text{♂}\}\,. \tag{B31}$$

Otherwise, we have from the perturbation formula for eigenvalues (eq. (B9)) that for $\mathrm{k} \in \{\text{♀},\text{♂}\}$

$$\lambda^s_{\mathrm{k}}(T) = v^\circ_{\mathrm{k}}\gamma_{\mathrm{ks}}\left.\frac{\partial w_{\mathrm{ks}}(\mathbf{u}^s,\mathbf{v})}{\partial x^s_{\mathrm{k,u}}(T)}\right|_{\mathbf{x}_{\mathrm{u}}=\mathbf{x}=\mathbf{x}^*} q^\circ_s, \tag{B32}$$

since in eq. (B9) ϵ_τ can be replaced by any scalar variable affecting invasion fitness $W(\mathbf{u},\mathbf{v})$, and x^s_{k} affects only component $w_{\mathrm{ks}}(\mathbf{u},\mathbf{v})$ of invasion fitness. Owing to eq. (B11) and the fitness functions (eqs. 7–), we have

$$\lambda^s_{\mathrm{k}}(T) = \frac{\alpha^\circ_{\mathrm{k}}\gamma_{\mathrm{ks}}}{x_k(\mathbf{u}^*)}. \tag{B33}$$

For queen control ($c = \text{♀}$), we have, the transversality conditions are

$$\begin{aligned}\lambda^{\text{♀}}_{\text{♀}}(T) &= \frac{1}{3x_{\text{♀}}(\mathbf{u}^*)},\\ \lambda^{\text{♀}}_{\text{♂}}(T) &= \frac{1}{3x_{\text{♂}}(\mathbf{u}^*)}.\end{aligned} \tag{B34}$$

while for worker control ($c = \mathrm{w}$), we have

$$\begin{aligned}
\lambda^{s}_{\female}(T) &= \frac{1}{3x_{\female}(\mathbf{u}^{*})}, s \in \{\female, \male\}, \\
\lambda^{\female}_{\male}(T) &= \frac{1}{3x_{\male}(\mathbf{u}^{*})}, \\
\lambda^{\male}_{\male}(T) &= 0.
\end{aligned} \tag{B35}$$

Solutions to the state and costate equations

For a constant allocation strategy $\mathbf{u}^{*}$ on a given time interval, we can derive the solutions to the state equations (B6). These will be useful to characterize the first-order conditions and are given by

$$\begin{aligned}
x^{*}_{\mathrm{w}}(t) &= x^{*}_{\mathrm{w}}(t_0)e^{t\left(ra^{*}_{\mathrm{w}}-\mu_{\mathrm{w}}\right)}, \\
x^{*}_{\female}(t) &= \frac{e^{-t\mu_{\female}}\left[ra^{*}_{\female}x^{*}_{\mathrm{w}}(t_0)\left(e^{t\left(ra^{*}_{\mathrm{w}}+\mu_{\female}-\mu_{\mathrm{w}}\right)}-1\right)+x^{*}_{\female}(t_0)\left(ra^{*}_{\mathrm{w}}+\mu_{\female}-\mu_{\mathrm{w}}\right)\right]}{ra^{*}_{\mathrm{w}}+\mu_{\female}-\mu_{\mathrm{w}}}, \\
x^{*}_{\male}(t) &= \frac{e^{-t\mu_{\male}}\left[ra^{*}_{\male}x^{*}_{\mathrm{w}}(t_0)\left(e^{t\left(ra^{*}_{\mathrm{w}}+\mu_{\male}-\mu_{\mathrm{w}}\right)}-1\right)+x^{*}_{\male}(t_0)\left(ra^{*}_{\mathrm{w}}+\mu_{\male}-\mu_{\mathrm{w}}\right)\right]}{ra^{*}_{\mathrm{w}}+\mu_{\male}-\mu_{\mathrm{w}}},
\end{aligned} \tag{B36}$$

where t_0 denotes beginning of a time interval. In the next section, we will show that we have two phases $[0, t^{*}_{c}]$ and $[t^{*}_{c}, T]$, during which $\mathbf{u}^{*}$ is constant. Hence, for the first phase $t_0 = 0$ and for the second phase $t_0 = t^{*}_{c}$.

The solutions to costate equations eq. (B30) for a time interval, where allocation strategy $\mathbf{u}^{*}$ is constant are

$$\begin{aligned}
\lambda^{s}_{\female}(t) &= \lambda^{s}_{\female}(t_f)e^{-\mu_{\female}(t_f-t)} \\
\lambda^{s}_{\male}(t) &= \lambda^{s}_{\male}(t_f)e^{-\mu_{\male}(t_f-t)} \\
\lambda^{s}_{\mathrm{w}}(t) &= \sum_{\mathrm{k}\in\{\female,\male\}} \lambda^{s}_{\mathrm{k}}(t_f)\frac{ra^{*}_{\mathrm{k}}}{ra^{*}_{\mathrm{w}}+\mu_{\mathrm{k}}-\mu_{\mathrm{w}}}\left(e^{(ra^{*}_{\mathrm{w}}-\mu_{\mathrm{w}})(t_f-t)}-e^{-\mu_{\mathrm{k}}(t_f-t)}\right),
\end{aligned} \tag{B37}$$

where t_f denotes the end of a time interval. Given the two phases of interest $[0, t^{*}_{c}]$ and $[t^{*}_{c}, T]$, during which $\mathbf{u}^{*}$ is constant, for the first phase $t_f = t^{*}_{c}$ and for the second phase $t_f = T$.

Note that eqs. (B35) and (B37) imply that $\lambda^{\male}_{\male}(t) = 0 \;\forall\, t \in [0, T]$. We can also see from equations eqs. (B35) and (B37) that $\lambda^{\female}_{\female}(t) = \lambda^{\male}_{\female}(t) \;\forall\, t \in [0, T]$.

Analysis of the optimal control problem

Conditions for candidate optimal controls

We now have all the elements to characterize the first-order conditions. When party c is in control of colony phenotype, we have from eq. (B20) that the candidate optimal controls are

$$u_{\mathrm{g}}^* = \begin{cases} 0 & \text{if } u_{\mathrm{f}} > 0 \text{ and } \sigma_1^c < 0 \\ 1 & \text{if } u_{\mathrm{f}} > 0 \text{ and } \sigma_1^c > 0 \\ \hat{u}_{\mathrm{g}} & \text{if } u_{\mathrm{f}} = 0 \text{ or } \big(u_{\mathrm{f}} > 0 \text{ and } \sigma_1^c = 0\big), \end{cases} \tag{B38}$$

$$u_{\mathrm{f}}^* = \begin{cases} 0 & \text{if } \big(u_{\mathrm{g}} = 0 \text{ and } \sigma_2^c > 0\big) \text{ or } \big(u_{\mathrm{g}} = 1 \text{ and } \sigma_1^c < \sigma_2^c\big) \text{ or } \big(u_{\mathrm{g}} = \hat{u}_{\mathrm{g}} \text{ and } \sigma_2^c > 0\big) \\ 1 & \text{if } \big(u_{\mathrm{g}} = 0 \text{ and } \sigma_2^c < 0\big) \text{ or } \big(u_{\mathrm{g}} = 1 \text{ and } \sigma_1^c > \sigma_2^c\big) \text{ or } \big(u_{\mathrm{g}} = \hat{u}_{\mathrm{g}} \text{ and } \sigma_2^c < 0\big) \\ \hat{u}_{\mathrm{f}} & \text{if } \big(u_{\mathrm{g}} = 0 \text{ and } \sigma_2^c = 0\big) \text{ or } \big(u_{\mathrm{g}} = 1 \text{ and } \sigma_1^c = \sigma_2^c\big) \\ & \text{or } \big(\sigma_1^c = \sigma_2^c = 0\big) \text{ or } \big(u_{\mathrm{g}} = \sigma_2^c/\sigma_1^c\big), \end{cases} \tag{B39}$$

where $\hat{u}_{\mathrm{f}}$ and $\hat{u}_{\mathrm{g}}$ denotes that the controls u_{f}^* and u_{g}^*, respectively, are singular arcs (Bryson and Ho 1975).

Realized allocation schedule

In this section we will determine from the possible candidate optimal controls given by eq. (B38) and eq. (B39), which allocation schedule will be realized during two phases of colony growth $t \in [0, t_c^*]$ (the ergonomic phase) and $t \in [t_c^*, T]$ (the reproductive phase), where t_c^* is the switching time from the ergonomic to the reproductive phase and the subscript $c \in \{♀, \mathrm{w}, m\}$ emphasizes the mode of control. In other words, the switching time t_c^* determines the time, where the controls $(u_{\mathrm{f}}^*, u_{\mathrm{g}}^*)$ change. We will later see that the root of $\sigma_1^c = 0$ determines this switching time. For now, we will use the constraints given in eq. (B38) and eq. (B39) and the results from our numerical simulations (see figs. 3, 4 and 7) to determine the properties of the allocation schedule $\mathbf{u}^*$ during the ergonomic and reproductive phases.

Eq. (B38) implies that the sign of the switching function σ_1^c determines $u_{\mathrm{g}}^*(t)$. The transversality conditions (B31), (B34), and (B35) yields that $\sigma_1^c > 0$ at $t = T$, since $\lambda_{\mathrm{w}}^s(T) < \lambda_{♀}^s(T)$ for all three modes of control. Hence, $u_{\mathrm{g}}^*(t) = 1$ in the reproductive phase, which is also supported by our numerical results that produce $u_{\mathrm{g}}^*(t) = 1$ in the reproductive phase $t \in [t_c^*, T]$ (see figs. 3, 4 and 7). In the next section, we show how we derive the switching time t_c^* from equation $\sigma_1^c = 0$ during which $u_{\mathrm{g}}^*(t)$ changes from 1 to 0. Hence, in the first phase $t \in [0, t_c^*]$ $u_{\mathrm{g}}^*(t) = 0$, which is also supported by our numerical results (see figs. 3, 4 and 7).

Eq. (B39) implies that given that $u_{\mathrm{g}}^*(t) = 1$, then the sign of $(\sigma_1^c - \sigma_2^c)$ determines $u_{\mathrm{f}}^*(t)$ in the reproductive phase. However, in order to determine the sign of $(\sigma_1^c - \sigma_2^c)$, we would need to know the values of (B34) and (B35), which depend on $u_{\mathrm{f}}^*(t)$. To get around this circular dependency, we can use the intuition from our numerical simulations which imply that $u_{\mathrm{f}}^*(t) = \hat{u}_{\mathrm{f}}(t)$ ($u_{\mathrm{f}}^*(t)$ is a singular arc) during the reproductive phase $(0 < u_{\mathrm{f}}^*(t) < 1)$ and $u_{\mathrm{f}}^*(t) = 1$ in the ergonomic phase $t \in [0, t_c^*]$ (see figs. 3, 4 and 7). Therefore, $(\sigma_1^c - \sigma_2^c) = 0$ and solving this equation for state variables, we get a condition that $u_{\mathrm{f}}^*(t) = \hat{u}_{\mathrm{f}}(t)$ has to satisfy in the final phase. To make the analysis tractable we assume hereinafter that the mortality rate of juvenile queens and males is equal, i.e. $\mu_{♀} = \mu_{♂} = \mu$.

For queen control of trait u_{f}, we then need $\sigma_1^{♀} - \sigma_2^{♀} = 0$ and substituting eq. (B29) along with eq. (B37) gives

$$\sigma_1^{♀} - \sigma_2^{♀} = \lambda_{♀}^{♀}(t) - \lambda_{♂}^{♀}(t) = \left[\lambda_{♀}^{♀}(T) - \lambda_{♂}^{♀}(T)\right] e^{-\mu(T-t)} = 0. \tag{B40}$$

Inserting the transversality condition eq. (B34) one then has

$$\frac{1}{3x_{♀}(\mathbf{u}^*)} - \frac{1}{3x_{♂}(\mathbf{u}^*)} = 0, \tag{B41}$$

whereby

$$\frac{x_{♂}(\mathbf{u}^*)}{x_{♀}(\mathbf{u}^*)} = R_{♀}, \tag{B42}$$

with $R_{♀} = 1$ being the relatedness asymmetry (see eq. (B18) or eq. (18) of the main text). Hence, we recover, as we should, eq. (B16), since for $\mu_{♀} = \mu_{♂} = \mu$, one has $-\,\mathrm{d}x_{♂}(\mathbf{z})/\,\mathrm{d}\epsilon_\tau/\,\mathrm{d}x_{♀}(\mathbf{z})/\,\mathrm{d}\epsilon_\tau = 1$.

Similarly, for worker control of trait u_{f}, we need $\sigma_1^{\mathrm{w}} - \sigma_2^{\mathrm{w}} = 0$ and substituting eq. (B29) along with eq. (B37) yields

$$\lambda_{♀}^{♀} + \frac{2}{M}\lambda_{♀}^{♂} - \lambda_{♂}^{♀} = (\lambda_{♀}^{♀}(T) + \frac{2}{M}\lambda_{♀}^{♂}(T) - \lambda_{♂}^{♀}(T))e^{-\mu(T-t)} = 0. \tag{B43}$$

Inserting the transversality condition eq. (B34) then produces

$$\frac{x_{♂}(\mathbf{u}^*)}{x_{♀}(\mathbf{u}^*)} = R_{\mathrm{w}}, \tag{B44}$$

where

$$R_{\mathrm{w}} = \frac{M}{2+M}, \tag{B45}$$

gives the relatedness asymmetry under worker control and is again consistent with eq. (B16)–(B18).

Given that $(u_{\mathrm{f}}^*(t) = 1, u_{\mathrm{g}}^*(t) = 0)$ in the ergonomic phase, then (B6) and (B7) imply that $x_{♀}(t_c^*) = x_{♂}(t_c^*) = 0$, i.e. only workers have been produced in the ergonomic phase and no new queens or males have been produced by time t_c^*. Hence, equations (B42) and (B44) give the conditions that $u_{\mathrm{f}} = \hat{u}_{\mathrm{f}}$ has to satisfy in the last phase. In other words, $u_{\mathrm{f}} = \hat{u}_{\mathrm{f}}$ that satisfies the condition (B42) (queen control of u_{f}) or (B44) (worker control of u_{f}) can be the candidate optimal control in the reproductive phase $t \in [t_c^*, T]$. The candidate optimal control has to satisfy the state equations (B36) for the reproductive phase $t \in [t_c^*, T]$, which can be simplified when we take $\mu_{♀} = \mu_{♂} = \mu$, $x_{♀}^*([t_c^*) = x_{♂}^*([t_c^*) = 0$, $u_{\mathrm{g}}^*(t) = 1$, as follows

$$\begin{aligned} x_{♀}^{s*}(T) &= \hat{u}_{\mathrm{f}}^*(t)\frac{rx_{\mathrm{w}}(t_c^*)\,(e^{-t\mu_{\mathrm{w}}} - e^{-t\mu})}{\mu - \mu_{\mathrm{w}}}, \\ x_{♂}^{s*}(T) &= (1 - \hat{u}_{\mathrm{f}}^*(t))\frac{rx_{\mathrm{w}}(t_c^*)\,(e^{-t\mu_{\mathrm{w}}} - e^{-t\mu})}{\mu - \mu_{\mathrm{w}}}. \end{aligned} \tag{B46}$$

It turns out that there are infinitely many such controls that satisfy (B42), (B44) and (B46), but we are interested in the most simple one, which is a constant function of time during the reproductive phase

$$u_{\mathrm{f}}^{*}(t)\Big|_{[t^{*},T]} = \hat{u}_{\mathrm{f}}(t)\Big|_{[t^{*},T]} = \frac{1}{R_{c}+1}. \tag{B47}$$

In conclusion, we have determined that in the candidate optimal control in the ergonomic phase is given by

$$\mathbf{u}^{*}\Big|_{[0,t^{*}]} = \left(u_{\mathrm{f}}^{*}(t) = 1, u_{\mathrm{g}}^{*}(t) = 0\right). \tag{B48}$$

and in the reproductive phase is given by

$$\mathbf{u}^{*}\Big|_{[t^{*},T]} = \left(u_{\mathrm{f}}^{*}(t) = \frac{1}{R_{c}+1}, u_{\mathrm{g}}^{*}(t) = 1\right). \tag{B49}$$

Hence, the allocation schedule of investment into different types of individuals in the ergonomic phase

$$a_{\mathrm{w,u}}^{*}(t)\Big|_{[0,t^{*}]} = 1, \qquad a_{♀,\mathrm{u}}^{s}(t)\Big|_{[0,t^{*}]} = 0, \qquad a_{♂,\mathrm{u}}^{s}(t)\Big|_{[0,t^{*}]} = 0 \tag{B50}$$

implies that all the resources are invested into producing workers. In the reproductive phase, the allocation schedule of investment into different types of individuals is

$$a_{\mathrm{w,u}}^{*}(t)\Big|_{[t^{*},T]} = 0, \qquad a_{♀,\mathrm{u}}^{s}(t)\Big|_{[t^{*},T]} = \frac{1}{R_{c}+1}, \qquad a_{♂,\mathrm{u}}^{s}(t)\Big|_{[t^{*},T]} = 1 - \frac{1}{R_{c}+1} \tag{B51}$$

and hence, all the resources are invested into producing sexuals. In terms of worker production versus production of sexuals, this strategy all-or-nothing strategy is called a "bang-bang" strategy (Bryson and Ho 1975, Macevicz and Oster 1976). In the reproductive phase, however, new queens and males are produced simultaneously. Hence, the $u_{\mathrm{f}}^{*}(t)$ is a singular control during the reproductive phase (Bryson and Ho 1975).

Switching time for single party control

We have determined the candidate optimal controls for the ergonomic $t \in [0, t_{c}^{*}]$ and the reproductive $t \in [t_{c}^{*}, T]$, and we are now going to determine the switching time t_{c}^{*} $c \in \{♀, \mathrm{w}\}$ (for single part control) that marks the time when the growth schedule switches from one phase to another. In the next section we will determine the switching time t_{m}^{*} for mixed control. We know from equation (B38) that when σ_{1}^{c} changes its sign then u_{g}^{*} switches its value from 1 to 0. Hence, solving the equation $\sigma_{1}^{c} = 0$ for t gives the time the switch in u_{g}^{*} happens, hence the switching time t_{c}^{*}.

For queen control of the trait u_{g}, $\sigma_1^{\female} = 0$ with eq. (B29) yields

$$\lambda_{\female}^{\female}(t_{\female}^*) - \lambda_{\mathrm{w}}^{\female}(t_{\female}^*) = 0, \tag{B52}$$

and with eq. (B37) and taking $\mu_{\female} = \mu_{\male} = \mu$ it leads to a following transcendental equation for finding $t_{\female}^*$

$$\lambda_{\female}^{\female}(T)e^{-\mu(T-t_{\female}^*)} - \frac{r\left(a_{\female}^*\lambda_{\female}^{\female}(T) + a_{\male}^*\lambda_{\male}^{\female}(T)\right)\left(e^{-\mu_{\mathrm{w}}\left(T-t_{\female}^*\right)} - e^{-\mu\left(T-t_{\female}^*\right)}\right)}{\mu - \mu_w} = 0. \tag{B53}$$

Similarly, for worker control of the trait u_{g}, $\sigma_1^{\mathrm{w}} = 0$ with eq. (B29) yields

$$\lambda_{\female}^{\female}(t_{\mathrm{w}}^*) - \lambda_{\mathrm{w}}^{\female}(t_{\mathrm{w}}^*) + \frac{2}{M}\left[\lambda_{\female}^{\male}(t_{\mathrm{w}}^*) - \lambda_{\mathrm{w}}^{\male}(t_{\mathrm{w}}^*)\right] = 0. \tag{B54}$$

and using eq. (B37) it leads to a following transcendental equation for finding t^*

$$\begin{aligned}\lambda_{\female}^{\female}(T)e^{-\mu(T-t_{\mathrm{w}}^*)} + \frac{2\lambda_{\female}^{\male}(T)}{M}\left(e^{-\mu(T-t_{\mathrm{w}}^*)} + e^{-\mu_{\mathrm{w}}\left(T-t_{\mathrm{w}}^*\right)} - e^{-\mu\left(T-t_{\mathrm{w}}^*\right)}\right)& \\ - \frac{a_{\female}^*\lambda_{\female}^{\female}(T) + a_{\male}^*\lambda_{\male}^{\female}(T)}{\mu - \mu_{\mathrm{w}}}\left(e^{-\mu_{\mathrm{w}}\left(T-t_{\mathrm{w}}^*\right)} - e^{-\mu\left(T-t_{\mathrm{w}}^*\right)}\right) &= 0.\end{aligned} \tag{B55}$$

By solving the transcendental equations (B53) for $t_{\female}^*$ and (B55) for t_{w}^* and taking $u_{\mathrm{g}}^*(t) = 1$, then we obtain the switching time when party $c \in \{\female, \mathrm{w}\}$ is in control

$$t_c^* = T - \frac{\ln\left(1 + \theta_c\frac{\mu-\mu_{\mathrm{w}}}{r}\right)}{\mu - \mu_{\mathrm{w}}}, \tag{B56}$$

where

$$\frac{1}{\theta_c} = \begin{cases} u_{\mathrm{f}}^* + (1 - u_{\mathrm{f}}^*)\frac{\lambda_{\male}^{\female}(T)}{\lambda_{\female}^{\female}(T)} & \text{for } c = \female, \\ u_{\mathrm{f}}^* + (1 - u_{\mathrm{f}}^*)\frac{\lambda_{\male}^{\female}(T)}{\lambda_{\female}^{\female}(T)+(2/M)\lambda_{\female}^{\male}(T)} & \text{for } c = \mathrm{w}. \end{cases} \tag{B57}$$

After substituting the control function u_{f}^* from equation (B47) for the respective case of control and using the transversality conditions (B34) and (B35) with conditions (B42) and (B44) we obtain that $\theta_c = 1$ for both cases of control. We have obtained that the switching time for single party control is

$$t_c^* = T - \frac{\ln\left(1 + \frac{\mu-\mu_{\mathrm{w}}}{r}\right)}{\mu - \mu_{\mathrm{w}}},\ c \in \{\female, \mathrm{w}\}. \tag{B58}$$

Switching time for mixed control

For mixed control, trait u_{g} is under worker control and trait u_{f} is under queen control. Hence, the switching time can be found by solving $\sigma_1^{\mathrm{w}} = 0$, which as we already showed leads to a transcendental equation (B55) with a solution

$$t_m^* = T - \frac{\ln\left(1 + \theta_m \frac{\mu - \mu_{\mathrm{w}}}{r}\right)}{\mu - \mu_{\mathrm{w}}}, \tag{B59}$$

where

$$\frac{1}{\theta_m} = u_{\mathrm{f}}^* + (1 - u_{\mathrm{f}}^*)\frac{\lambda^{♀}_{♂}(T)}{\lambda^{♀}_{♀}(T) + (2/M)\lambda^{♂}_{♀}(T)}.$$

Since the trait u_{f} is under queen control, we substitute u_{f}^* from eq. (B47) with transversality conditions (B34) for queen control with condition (B42) and obtain

$$\theta_m = \frac{2 + M}{1 + M}. \tag{B60}$$

We can easily see from equation (B59) that $t_m^* < t_c^*$ and as $M \to \infty$ so $t_m^* \to t_c^*$, where $c \in \{♀, \mathrm{w}\}$.

We should also mention that equations (B58) and (B59) hold if $\mu_{\mathrm{w}} < r/\theta_c + \mu$. It is not biologically restrictive, since the reproduction rate has to be be significantly higher than worker mortality otherwise the population will go extinct.

Pontryagin's maximum principle for the uninvadable resource allocation strategy

We can numerically check if the uninvadable strategies $\mathbf{u}^*$ found with iterative scheme of best response map satisfies the necessary first order condition given by eq. (B20). We have plotted the first order conditions in figs. B1- B3. Note that if evolutionarily stable value of the trait u_τ^* is on the boundary, i.e. equal to 0 or 1, then the first order condition does not have to be equal to 0. The first order condition can be positive if the control variable is on the upper boundary (equal to 1) and negative if the control variable is on its lower boundary (equal to 0). However, if evolutionarily stable value of the trait u_τ^* is not on the boundary (i.e. it is between 0 or 1), then the first order condition has to be equal to 0.

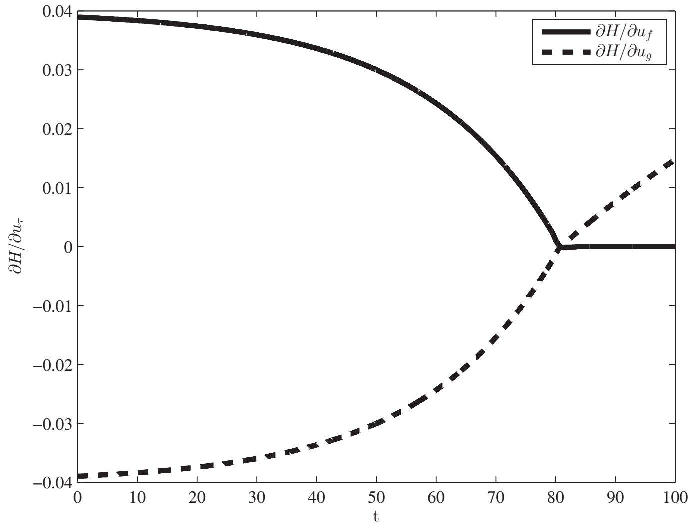

Figure B1: First order conditions as a function of time under full queen control and queen monandry ($M = 1$). Parameter values: $r = 0.06$, $\mu_\mathrm{w} = 0.02$, $\mu_♀ = \mu_♂ = 0.005$, $T = 100$.

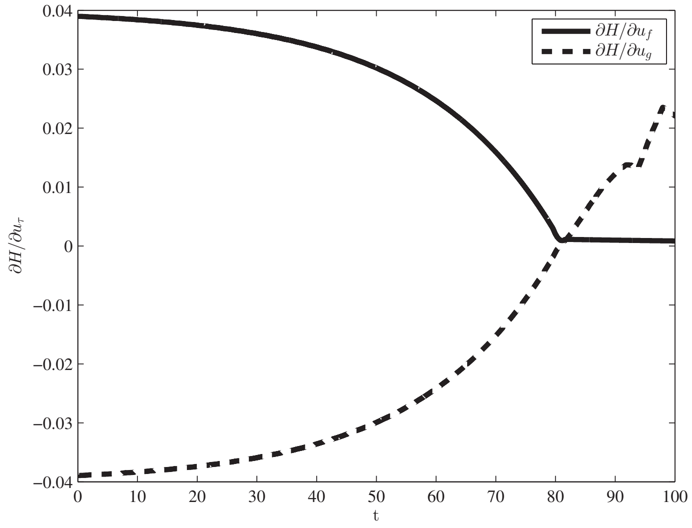

Figure B2: First order conditions as a function of time under full worker control and queen monandry ($M = 1$). Parameter values: $r = 0.06$, $\mu_\mathrm{w} = 0.02$, $\mu_♀ = \mu_♂ = 0.005$, $T = 100$.

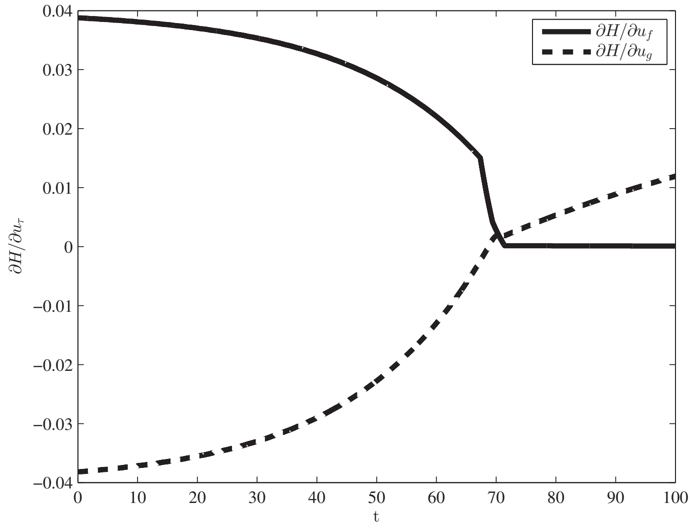

Figure B3: First order conditions as a function of time under mixed control and queen monandry ($M = 1$). Parameter values: $r = 0.06$, $\mu_{\mathrm{w}} = 0.02$, $\mu_{♀} = \mu_{♂} = 0.005$, $T = 100$.

APPENDIX C: ITERATIVE SCHEME OF THE BEST RESPONSE MAP

Here, we describe the computational technique for finding the uninvadable strategies for our optimal control problems. This method is known as the iterative scheme of the best response map (see p. 187 in (Houston and McNamara 1999)).

The strategy $\mathbf{u}$ that yields the highest invasion fitness of the mutant in an environment, where the resident strategy is $\mathbf{v}$ is said be the best response $\hat{b}(\mathbf{v})$ to the resident strategy, i.e.

$$W_c(\hat{b}(\mathbf{v}), \mathbf{v}) = \max_{\mathbf{u}} W_c(\mathbf{u}, \mathbf{v}), \tag{C1}$$

We start out from some initial resource allocation schedule for the resident population $\mathbf{u}^0$ and using GPOPS we find the mutant strategy that has the highest fitness $\mathbf{u}^1 = \hat{b}(\mathbf{u}^0)$. We then update the resident strategy for the next iteration

$$\mathbf{u}^i = \alpha\hat{b}(\mathbf{u}^{i-1}) + (1-\alpha)\mathbf{u}^{i-1} \tag{C2}$$

and repeat the process. Here, $0 > \alpha > 1$ is called the replacement factor. We can interpret this method biologically as replacing a proportion α of resident individuals at generation $i-1$ by mutant individuals with highest fitness for the next generation. From a mathematical point of view we can also interpret this new resident strategy as a polymorphism - each individual adopting a strategy $\hat{b}(\mathbf{u}^{i-1})$ with probability α and strategy $\mathbf{u}^{i-1}$ with probability $(1-\alpha)$ (Houston and McNamara 1999). To improve convergence after iterating from some while we can decrease α with further iterations (Houston and McNamara 1999, Krawczyk and Uryasev 2000).

This iterative scheme forms a sequence of strategies $(\mathbf{u}^0; \mathbf{u}^1; \mathbf{u}^2; ...)$ where each strategy is derived from the best response to the previous strategy according to equation (C2). If the difference between the best response and resident strategy approaches zero as the number of iterations increases, i.e.

$$\left|\mathbf{u}^i - \mathbf{u}^{i-1}\right| \rightarrow 0 \; as \; i \rightarrow \infty, \tag{C3}$$

then we have arrived at the uninvadable strategy (Nash equilibrium).

For single party control we use GPOPS to find the best response $\hat{b}(\mathbf{v})$ that maximizes the objective given by equation (11) of the party in control. For mixed control, the best response $\hat{b}(u_\mathrm{f})$ maximizes the the objective of the queen $W_♀(\mathbf{u},\mathbf{v})$ and $\hat{b}(u_\mathrm{g})$ maximizes the objective of the workers $W_\mathrm{w}(\mathbf{u},\mathbf{v})$.

Uninvadability is a necessary condition for evolutionary stability, but not sufficient. It does not guarantee stability against equally fit mutants or convergence back to $\mathbf{u}^*$ when the population is perturbed away from $\mathbf{u}^*$ (Smith 1982, Eshel 1983). However, since arriving at the uninvadable strategy is done through iteration, which is analogous to the evolutionary dynamics of the population, then we might regard this as giving support that the proper evolutionary dynamics would also converge to this uninvadable strategy. Under this heuristic approach, the iterative scheme of the best response map also implies stability of any uninvadable strategy found by it (Houston and McNamara 1999).

The software GPOPS uses a direct approach to find the best response $\hat{b}(\mathbf{u})$ for a given environment $\mathbf{u}$ in contrast to the indirect approach of Pontryagin's maximum principle (see Appendix B), which gives a necessary condition for optimality. We also show that all the uninvadable strategies found using this numerical approach also satisfies Pontryagin's maximum principle and we were able to show that our numerical solutions also satisfy the necessary first order condition of optimality (see Appendix B of the S.I.).

III

CO-FOUNDRESS ASSOCIATIONS IN PRIMITIVELY EUSOCIAL WASPS: A GAME THEORETICAL APPROACH

by

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Manuscript

CO-FOUNDRESS ASSOCIATIONS IN PRIMITEVELY EUSOCIAL WASPS: A GAME THEORETIC APPROACH

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ABSTRACT

Co-foundress associations have arisen numerous times in Hymenoptera, but the role of time- and context-dependent decision rules of cooperative breeding in wasps is still incompletely understood. We developed a dynamic optimization model to study the evolutionary stable nesting behaviour of a seasonal cooperatively breeding insect with alloparental care, in which foundresses must decide between founding a nest alone or joining an existing nest as a subordinate. We find that if foundresses have to invest a large amount of resources into the nest before producing sexual offspring then costly helping by subordinates is favoured by selection even without high average relatedness between co-foundresses. However, cooperation can be sustained in the reproductive phase only if the average relatedness between the co-foundresses is high or if subordinates are incapable of usurping the nest from the dominant female.

Keywords: Social wasps; cooperative breeding; inclusive fitness; dynamic optimization; game theory.

INTRODUCTION

The role of kin selection has been fundamental in understanding the evolution of specialized cooperative societies. Facultatively cooperative species, where individuals have retained the capacity to reproduce without the help of others, provide a unique opportunity for understanding how indirect and direct fitness benefits of helping relatives can shape the evolution of altruistic behaviour. While helping relatives can entail substantial indirect fitness benefits in some systems (Emlen, 1991), the relative importance of direct fitness benefits of helping should not be underestimated since helping is not restricted to family groups (Clutton-Brock, 2002, 2009; Field and Leadbeater, 2016; Gadagkar, 2016; Leadbeater *et al.*, 2011). The existence of unrelated helpers is well established in many species of cooperatively breeding vertebrates, but they are far less commonly known in the social insects. One example of unrelated helpers in social insects comes from the co-foundress associations that occurs in some ant (Bernasconi and Strassmann, 1999) and wasp species (Gadagkar, 2016; Field and Leadbeater, 2016; Liebert *et al.*, 2005).

Direct fitness benefits of helping have been shown to be especially important in paper wasps *Polistes dominulus*, where helping non-relatives is relatively common and the average within group relatedness is around ~ 0.3 (Zanette and Field, 2008). Leadbeater et al. (2011) showed that subordinate females are driven to help the dominant to gain direct fitness through nest inheritance even though it happens relatively rarely, as ~ 87% of dominant females retain their position throughout the entire season. Moreover, an average subordinate is expected to produced more own offspring per capita than an average solitary foundress. Nevertheless, indirect fitness benefits usually outweigh direct fitness benefits in this species (Leadbeater *et al.*, 2011), which makes it puzzling why the wasps do not associate with relatives more often. One possibility is that some wasps simply make kin recognition errors, but so far there is little evidence that suggests that wasps of these species are less able to detect kin from non-kin compared to the species where average co-foundress relatedness is high (Field and Leadbeater, 2016). The fundamental question of why the average relatedness between co-foundresses in some Polistes species is so much lower than in others where co-foundress associations happen mostly between close relatives has remained unclear (Field *et al.*, 1998; Reeve *et al.*, 2000; Seppä *et al.*, 2002).

While a large amount of empirical knowledge exists on co-foundress associations of social wasps, current accounts of explaining the variation of social behaviour in social wasps call for a re-evaluation from a formal theoretical perspective for several reasons. Firstly, in the beginning of the season, a large number of foundresses start initiating nests and switching between nests is common (Zanette and Field, 2008; Seppä *et al.*, 2012). Females that choose to nest solitarily have a chance that their nest will be joined by other females, which makes it less clear which of these options at a given time of the season offers higher direct fitness. Hence, comparing the success of behavioural outcomes (such as solitary nesting versus becoming a subordinate) provides no adequate measure of the success of the underlying strategies. Secondly, we have to account for the behavioural decisions made as a subordinate in the nest as separate from the decision to join the nest in the first place. If the main incentive of the subordinates is to inherit the nest, they should be less willing to forage and may even try to kill the dominant female to acquire the dominant position. Thirdly, there is variation in the value of the different nests depending on how much work effort has already been put into the nest. Females who join nests as subordinates should try to base their decision on the value of a particular nest and the number of females already in the nest. Fourthly, the success of a particular strategy depends on the strategy of other individuals in the population. It has been argued that context dependent helping may be key to the evolution of helping behaviour (Holman, 2014), because the cost and benefit ratio of helping may vary considerably depending on the time of the season or the type of nest that the female is associated with. When individuals can assess such variables, helping can evolve more easily.

In this paper we present a game theoretical time dependent model that follows a life cycle similar to seasonal species of social wasps. Our modelling approach allows wasps to make context dependent decisions, i.e. decisions depend on the time of the season and on what other individuals in the population are doing. Instead of measuring the success of behavioural outcomes, such as solitary versus cooperative nesting, our model allows to study the success of the underlying strategies of these behavioural outcomes. At the beginning of the season, females start initiating colonies using different options: (1) initiating nests alone, (2) cooperating with other females by building nests together, (3) usurping the nest of other females, (4) waiting around for other females to initiate their colonies and then take over the nest later in the season. We assume that there are two phases in the colony life cycle: (1) the pre-reproductive phase, where investment is made into building the colony structure and raising the non-reproductive worker caste and (2) the reproductive phase, where all effort is put into producing sexual offspring.

Assuming that individuals cannot directly assess relatedness to each other, we study to what extent elevated average relatedness between nest mates (above the population mean) is necessary to make such a system work. Our model allows us to study the evolutionarily stable level of helping by the subordinates in different phases of the life cycle of the nest over the course of the season.

MODEL

Biological scenario

We consider a seasonal population of facultatively cooperative insects. We are interested in the behaviour of the females in the population throughout the season of total length T. We assume that all females have a set of possible actions that depends on their state and the time of the season $t \in [0, 1, ...T-1]$. We assume that a female can be in different states: (i) a floater, who is not associated with any nest; (ii) a dominant female (breeder) in a nest, who lays all the eggs; (iii) a subordinate female (non-breeder) in a nest, which means that she can not lay any eggs herself. At the start of the season, all the females in the population are floaters. Floaters can initiate nests alone, or, alternatively, they can join the nests previously initiated by other females. When a floater initiates a nest, she will automatically become the dominant female in that nest. When a floater joins a nest initiated by an another female, she will initially become a subordinate in that nest. Subordinate females can inherit the dominant position if the dominant female dies.

We assume that the females in the nest have to invest some fixed amount of resources P into the nest before the dominant can start producing sexual offspring. This effort can be interpreted as investing into building the structure of the nest and into non-sexual (worker) offspring. The subordinates can stay in a nest as active helpers or passively stay in a nest without helping the dominant female to rear brood. Subordinates can also decide to leave the nest or behave aggressively towards the dominant female, to increase their chance of inheriting the nest and becoming a dominant themselves.

We assume that the decisions of the females depend on the time t of the season and on the type of nest that the female is associated with, or that she encounters as a floater. Nest type is characterized by two features: (i) the number of individuals in the nest $s \in [0, S]$ and (ii) the amount of effort that has already been invested into the nest (henceforth called nest phase) $p \in [0, P]$. We assume that there is a large constant number N of suitable nest sites in the population. At the start of the season, all nests are empty ($s = 0$) and in the initial phase ($p = 0$). Hereinafter, when we write that a nest is of type (s, p), it means that it is of size s and of phase p. At the end of the season, the whole adult generation dies, all nests are destroyed, and all juvenile females mate and start to hibernate.

While we do not model space explicitly, we make some assumptions that imply a certain spatial structure. Specifically, we assume that any given female interacts with only a subset of the total female population, being related to this subset by average relatedness r. This implies that female family members tend to live close to each other. This reflects an important behavioural component common in *Polistes*, which is that Polistes foundresses are philopatric, i.e. they tend to nest near the nest site where they were reared (West *et al.*, 2007; Hunt, 2007), however the average relatedness between the co-foundresses varies between species and in may cases the co-foundresses are not sisters (Strassmann, 1996) and can even be unrelated (Queller *et al.*, 2000; Leadbeater *et al.*, 2011; Field and Leadbeater, 2016). Moreover, we assume that the offspring of female nest mates are not related through their father's side. This implies that males disperse so widely that mating is random throughout the population. Finally, we assume that the reproductive value of sexual offspring (i.e., their contribution to future generations) is independent of the total number of sexual offspring produced in the same nest. This implies that there is sufficient dispersal to ensure that an individual's behaviour does not affect the local density faced by its descendants in the next generation. While we do not model sex allocation explicitly, our model is consistent with an even sex ratio of sexual offspring.

Behavioural traits

Nest formation and behaviour in the nest is governed by the behavioural traits $u_{k,\tau} = u_{k,\tau}(t)$ of females in state $k \in \{f(s,p), b(s,p), n(s,p)\}$ (floaters, dominants (breeders) in a nest of type (s,p), and subordinates (non-breeders) in a nest of type (s,p), respectively) that specify the probability of choosing an action τ that is available to a female in state k. We assume that these behavioural traits are under genetic control and therefore subject to selection. A female's behavioural options depends on her state $k \in \{f(s,p), b(s,p), n(s,p)\}$. For example, if a floater encounters a nest of type (s,p) at time t she will decide to join this nest with probability $u_{f(s,p),1} = u_{f(s,p),1}(t)$ and with probability $u_{f(s,p),2}(t) = 1 - u_{f(s,p),1}(t)$ she will decide to remain a floater. The dominant (breeder) can choose to stay in her nest with probability $u_{b(s,p),1} = u_{b(s,p),1}(t)$ and she will abandon the nest with probability $u_{b(s,p),2}(\mathbf{n},t) = 1 - u_{b(s,p),1}(s,p,t)$. For simplicity, we assume that dominant females who have at least one helper in the nest will not abandon it (i.e., $u_{b(s,p),1}(s,p,t) = 0$ for $s > 1$). This is a minor simplification because, if any nests exist with $s > 1$ in which leaving would benefit the dominant, then, leaving such nests will benefit the subordinates even more (since subordinates have less to lose from leaving than the dominant, while the fitness gain from leaving is the same for both). Hence, the dominant will be able to leave after a short time delay, after being abandoned by its subordinates. The non-breeding subordinate females can choose between 4 different actions at any given time: $u_{n(s,p),1} = u_{n(s,p),1}(t)$ is the probability that a given subordinate female will help the dominant female by foraging, $u_{n(s,p),2} = u_{n(s,p),2}(t)$ gives the probability that the subordinate will be aggressive towards the dominant female, which will increase the chances that the dominant will die, and $u_{n(s,p),3} = u_{n(s,p),3}(t)$ gives the probability that the subordinate will stay in a nest without helping the dominant female. The quantity $u_{n(s,p),4} = u_{n(s,p),4}(t) = 1 - u_{n(s,p),1}(t) - u_{n(s,p),2}(t) - u_{n(s,p),3}(t)$ gives the probability that the subordinate will leave the focal nest site. Note that out of the eight possible actions of females in different states, only five traits are independent traits. We define a vector of strategies $\mathbf{u} = \{u_{f(s,p),1}(t), u_{b(s,p),1}(t), u_{n(s,p),1}(t), u_{n(s,p),2}(t), u_{n(s,p),3}(t)\}$ that specifies the decision rules for all adult females in the population throughout the season. This strategy vector $\mathbf{u}$ specifies a rule of action for a female that can be in any state throughout the season.

Life-history characteristics

The behavioural traits $\mathbf{u}$ of the females determine all life-history events, such as mortality, joining or initiating nests and reproduction. We assume that all decisions made at time t are independent of each other, and their consequences take effect regardless of any deaths that might occur at time t. For example, if a subordinate helps its dominant yet also dies at time t, then this help still affects the dominant's reproduction at time t. Also, while decisions at time t are conditional on nest type (s, p) at time t, they cannot in turn affect these nest characteristics at time t; instead, decisions and deaths that occur at time t can only affect nest characteristics (s, p) at time $t + 1$.

Start of reproduction and fecundity

Let $r_{(s,p)}(\mathbf{u}, t)$ be the amount of resources foraged at time t in a nest of type (s, p) that has at least one individual. We assume that if the solitary foundress decides to stay at the nest, she is able to forage r_0 amount of resources. The amount of resources foraged in larger nests depends on the number of subordinates and the average amount of helping they do, i.e.

$$r_{(s,p)}(\mathbf{u}, t) = r_0 \left[1 + h u_{n,1}(s - 1)\right], \tag{1}$$

where h is the helping efficiency coefficient.

In nests whose nest phase is below the reproductive threshold ($p < P$), all foraging effort is directed into progressing the nest into the reproductive phase P and the increase of nest phase, at time t in nests of type (s, p), is given by

$$\triangle p_{(s,p)}(\mathbf{u}, t) = \begin{cases} \triangle p^1_{(s,p)}(\mathbf{u}, t) = \left\lceil r_{(s,p)}(\mathbf{u}, t) \right\rceil, \text{ if } (s > 0) \text{ with probability } \omega^1_{(s,p)} \\ \triangle p^2_{(s,p)}(\mathbf{u}, t) = \left\lfloor r_{(s,p)}(\mathbf{u}, t) \right\rfloor, \text{ if } (s > 0) \text{ with probability } \omega^2_{(s,p)} \end{cases} \tag{2}$$

where $\lceil\cdot\rceil$ and $\lfloor\cdot\rfloor$ stand for the ceiling and floor functions and $\omega^1_{(s,p)} = r_{(s,p)} - \left\lfloor r_{(s,p)} \right\rfloor$, $\omega^2_{(s,p)} = 1 - \omega^1_{(s,p)}$. Thus, nest phase progresses in discrete steps, and any contributions of foraging effort towards nest phase are rounded accordingly.

In nests whose nest phase has reached the reproductive threshold $p = P$, all foraging effort is directed into producing sexual offspring and the number of sexual offspring produced in a nest of type (s, p) at time t is given by

$$w_{(s,P)}(\mathbf{u}, t) = \epsilon r_{(s,P)}(\mathbf{u}, t), \tag{3}$$

where ϵ is the conversion efficiency of resources into offspring. Note that $w_{(s,p)}(\mathbf{u}, t) = 0$ if $p < P$.

Mortality

Let $\mu_{b(s,p)}(\mathbf{u},t)$, $\mu_{n(s,p)}(\mathbf{u},t)$, and μ_f be the mortality probability of dominants, subordinates and floaters at time t, respectively. The mortality probability of subordinates depends on their actions, weighted by the probability of choosing those actions:

$$\mu_{n(s,p)}(\mathbf{u},t) = \sum_{\tau=1}^{4} u_{n(s,p),\tau}(t)\mu_{n,\tau}, \tag{4}$$

where $\mu_{n,\tau}$ is the subordinate mortality probability associated with the action τ. The probability that a solitary foundress dies at time t is μ_s. The probability that the dominant dies in larger nests depends on the size of the colony and the aggression level $u_{n(s,p),2}$ of the subordinates in the nest at time t, i.e.

$$\mu_{b(s,p)}(\mathbf{u},t) = 1 - \left[(1-\mu_{b0})(1-a u_{n(s,p),2}(t))^{s-1}\right], \tag{5}$$

where μ_{b0} is the mortality of a dominant in a co-foundress nest without aggressive subordinates and a is the efficiency of usurping the nest.

Floaters joining the nest

We assume that the floaters find an empty nest site with constant probabilityα_0 if all nest sites are empty, and with proportionally lower probability if only a proportion $\frac{N_e}{N}$ of all nest sites are empty. Here, N is the number of all nest sites (sites suitable for building nests), and N_e is the number of empty nest sites. We assume that nests with at least one female attract more attention and thus they are found m-times as likely, i.e. $\alpha_s = m\alpha_0$, where $s > 0$. To ensure that probabilities sum to one, we must choose α_0 small enough to satisfy $\alpha_0 \frac{N_e}{N} + m\alpha_0 \frac{N_o}{N} \leq 1$, where N_o is the number of occupied nest sites. The number of floaters arriving to a nest site of type $i \in \{e, o\}$ follows a Poisson process with the respective means

$$\begin{array}{rcl} \alpha_e(t) & = & x_f(t)\alpha_0 \frac{N_e}{N}\frac{1}{N_e} \text{ (empty nest sites)}, \\ \alpha_o(t) & = & \alpha_o(t) = x_f(t) m\alpha_0 \frac{N_o}{N}\frac{1}{N_o} \text{ (occupied nest sites)}, \end{array} \tag{6}$$

where $x_f(t)$ is the density of floaters. Thus, the probability of at least one floater arriving to a given site is $1 - \exp(-\alpha_i)$. This follows directly from the definition of the Poisson probability distribution $f(x) = [(\alpha_i)^x/\alpha!]\exp(-\alpha_i)$, since $f(x \geq 1) = 1 - f(0) = 1 - \exp(-\alpha_i)$. For simplicity, we assume that in a given time step t only one floater can join a particular nest site. This constraint is insignificant as long as $m\alpha_0/N$ is small enough and we can adjust that by choosing the time interval t that is small enough. If multiple floaters arrive in the same time at a given nest site, only one of them (say, the first one to arrive) can choose to either join the nest site or leave. After floaters have arrived at the nest site, floater mortality is accounted for; so it can happen that the floater who has chosen to join a given nest site dies. Thus, the probability that a nest site of type (s, p) is joined by a floater at time t is

$$\eta_{(s,p)}(\mathbf{u},t) = [1-\exp(-\alpha_i)]\,(1-\mu_f)u_{f(s,p),1}(t). \tag{7}$$

Therefore, at time t, $\sum_s \sum_p \eta_{(s,p)}(\mathbf{u},t)x_{(s,p)}(t)$ is the number of females that find and join any nest site, either occupied or not, where $x_{(s,p)}(t)$ is the density of nest sites of type (s,p).

The probability that a focal floater will be the first one to find a nest of type (s,p) at time t (hence getting the opportunity to join) is

$$\phi_{(s,p)}(t) = \alpha_i \frac{x_{(s,p)}(t)}{N}\frac{N(1-\mathrm{e}^{-\alpha_i})}{\alpha_i x_f(t)}. \tag{8}$$

Thus, the probability that a floater is not the first one to find a nest site and therefore remains a floater is

$$\phi_f(t) = 1 - \frac{N_e(1-\mathrm{e}^{-\alpha_e})}{x_f(t)} - \frac{N_o(1-\mathrm{e}^{-\alpha_o})}{x_f(t)}. \tag{9}$$

Note that a nest's probability of being joined is linked to a floater's probability of joining as

$$\eta_{(s,p)}(\mathbf{u},t) = x_f(t)\phi_{(s,p)}(t)u_{f(s,p),1}(1-\mu_f)(t)\frac{1}{x_{(s,p)}(t)}. \tag{10}$$

Population dynamics

Let $x_f(t)$ and $x_{(s,p)}(t)$ be the number of floaters and nests of type (s,p) in the population, respectively.

The density of floaters in the population changes according to the equation

$$x_f(t+1) = x_f(t)(1-\mu_f) + \sum_{s=0}^{S}\sum_{p=0}^{P} x_{(s,p)}(t)\left[l_{(s,p)}(\mathbf{u},t) - \eta_{(s,p)}(\mathbf{u},t)\right], \tag{11}$$

where $l_{(s,p)}(\mathbf{u},t)$ is the average number of individuals who leave a nest of type (s,p) at time t and survive, i.e.

$$l_{(s,p)}(\mathbf{u},t) = \begin{cases} u_{b(1,p),2}(1,p,t)(1-\mu_0), (s=1), \\ \sum_{i=0}^{s-1}\sum_{j=0}^{s-1-i} jB, (s>1), \end{cases} \tag{12}$$

where

$$B = \mathrm{bin}(s-1, i, \mu_{n(s,p)}(\mathbf{u},t))\mathrm{bin}(s-1-i, j, u_{n(s,p),4}(\mathbf{u},t)).$$

Here

$$\text{bin}(n,k,p) = \left(\begin{array}{c} n \\ k \end{array}\right) p^k (1-p)^{n-k}$$

stands for the binomial probability. Here, the first summation goes through the number of subordinates i that may die during this time step, leaving $s-1-i$ survivors. The second summation goes through the number j of these survivors that may leave to become floaters. The change in the density of nests is given by

$$\begin{aligned} x_{s'p'}(t+1) &= \textstyle\sum_{s=0}^{S} \sum_{p=0}^{P} \gamma_{ss'pp'}(\mathbf{u},t) x_{(s,p)} \\ &+ \textstyle\sum_{s=0}^{S} \sum_{p=0}^{P} \eta_{(s,p)}(\mathbf{u}) x_{(s,p)} \left(\gamma_{s(s'-1)pp'}(\mathbf{u},t) - \gamma_{ss'pp'}(\mathbf{u},t) \right), \end{aligned} \tag{13}$$

where $\gamma_{ss'pp'}(\mathbf{u},t)$ gives the probability that a nest of type (s,p) will be of type (s',p') through the process of mortality and individuals in the nest deciding to leave. Note that $\gamma_{s(s'-1)pp'} = 0$ when $s' = 0$. We present the derivation of $\gamma_{ss'pp'}(\mathbf{u},t)$ in Appendix B.

The total number of individuals in the population at time t is given by

$$X(t) = x_f(t) + \sum_{s=0}^{S} \sum_{p=0}^{P} s x_{(s,p)}(t). \tag{14}$$

Mutant-resident system

We perform an evolutionary invasion analysis to study the evolution of the behavioural traits $\mathbf{u}$. That is, we consider the fate of a rare mutant in a population of resident individuals, where the phenotype of the mutant

$$\mathbf{u}^m = \{u^m_{f(s,p),1}(t), u^m_{b(s,p),1}(t), u^m_{n(s,p),1}(t), u^m_{n(s,p),2}(t), u^m_{n(s,p),3}(t)\} \tag{15}$$

can deviate from the resident throughout the season.

Invasion fitness

What quantity should be maximised by a female's optimal strategy (sequence of context-dependent decisions)? According to Hamilton (1963), the ultimate criterion that determines whether a gene G for a behaviour will spread is not whether the behaviour is to the benefit of the behaver, but whether it is to the benefit of the gene G. Hence, we consider how a rare gene G present in a focal female should shape the behaviour of that female, in order to maximise the number of G copies transmitted to the next generation. The focal female is related to her offspring by $1/2$, to her female nest mates by average relatedness r, and to the offspring of her female nest mates by average relatedness $r/2$. These relatedness coefficients can be interpreted as probabilities that a rare allele G, if present in the focal female, is also present in her relatives. Thus, measured in the currency of G copies transmitted to the next generation, nest mates' offspring are r times as valuable to the focal female as are her own offspring.

We adopt a dynamic kin selection approach according to which the quantity to be maximised by the focal female is the number of her own sexual offspring (i.e., her direct fitness) plus the net number of additional sexual offspring produced by her relatives due to her actions (i.e., her indirect fitness), where the indirect fitness component is weighted by r. The indirect fitness component can be either positive (due to the individual being a helpful subordinate) or negative (due to the individual being a dominant and holding the reproductive monopoly in the nest, thereby suppressing the reproduction of relatives). This measure of accounting fitness, is also known as the Wilson's definition of inclusive fitness (Grafen, 1982), since it was originally proposed by Wilson (1975). Wilson's definition of inclusive fitness departs from the classical definition of inclusive fitness by Hamilton (1964), in which the direct fitness component for a particular trait is "stripped of all components which can be considered as due to the individual's social environment". In our model, however, the fitness components are not additive, because, for example, under parameter settings where progressing a nest to the reproductive phase requires more than one individual, a breeder's direct fitness, stripped of the effect of the social environment, would be zero. Grafen (1982) argued that Wilson's definition leads to double-counting of fitness components. However, this problem only occurs when considering the spreading of a focal gene which is simultaneously being expressed in several interacting individuals. Next, we will explain how erroneous application and misunderstanding of Hamilton's definition of inclusive fitness may lead to a wrong conclusion (i.e., Creel's paradox) and outline the assumptions under which using Wilson's definition of inclusive fitness leads to the correct solution without double-counting of the fitness components.

A misunderstanding of the classical Hamilton's definition of inclusive fitness can lead to the 'Creel's paradox' (Creel, 1990; Lucas *et al.*, 1996; Queller, 1996). This paradox can arise in the context of obligatory cooperative breeding. In obligatory cooperatively breeding species dominant individuals have zero inclusive fitness according to the classical definition: their direct fitness component is zero, because they can not reproduce without their social environment and their indirect fitness component is also zero because they do not help anyone. Hence, when facing a choice between becoming a dominant or a subordinate (whose indirect fitness is positive, if $r > 0$), an individual trying to maximise the classical version of inclusive fitness should prefer to become a subordinate. This is clearly incorrect, however, since a rare gene influencing behaviour will leave more copies in the next generation if its carrier becomes a dominant. This apparent paradox arises from incorrect stripping apart of fitness components in systems with non-additive pay-offs.

The obvious way to bypass this difficulty is to consider the underlying genetics behind these traits (Queller, 1996). However, Queller (1996) argued that there are two ways that Creel's paradox disappears under the "phenotypic gambit" approach if one adopts the Wilson's definition of inclusive fitness that does not require the stripping away of the social environment. These two solutions depend upon the expression of the focal gene. Firstly, low penetrance (i.e., probability of being expressed in any given individual) of the focal gene ensures that the focal individual in which the rare mutant allele is expressed does not interact with other individuals with the same phenotype. Hence, the low penetrance assumption eliminates the effects of rare phenotypes interacting which each other and, accordingly, Wilson's definition of inclusive fitness gives the correct answer. Secondly, for conditional behaviours reflecting choices only available to the focal individual (but not simultaneously to its social partners), the quantity to be maximised the Wilson's definition of inclusive fitness.

The assumption of the conditional expression is also implicit in our model, since we do not constrain dominants and subordinates to behave similarly due to expression of the same genes. More generally, we avoid double-counting by holding constant the strategies of all other individuals, when calculating how alternative behaviours affect a focal individual's inclusive reproductive value. Biologically, this amounts to the implicit assumption that behaviour evolves gradually by the successive spreading of mutations with low penetrance (i.e., probability of being expressed in any given individual). This assumption is less restrictive than it might seem, since our model is a phenotypic one: our aim is not to model the spreading of specific alleles with specific effects. Rather, we want to find an individual's optimal strategy (phenotype), for a given strategy set used by others.

To conclude, we agree with Queller (1996) that the "phenotypic gambit" can be salvaged in inclusive fitness models with non-additive pay-offs; in other words: that we can learn something by studying phenotypes in such models even as we ignore the (often unknown) genetics underlying particular traits. Moreover, we believe that our method (based on Wilson's (1975) definition of inclusive fitness and the low penetrance assumption) can achieve this even beyond the scope of conditionally expressed traits as originally suggested by Queller (1996).

Hereinafter, by inclusive fitness, we mean Wilson's (1975) definition of an inclusive fitness of an individual. We define inclusive and direct reproductive values of females as the total amount of inclusive and direct fitness gained at time t and afterwards, respectively. Let $V_i(\mathbf{u}^m, \mathbf{u}, t)$ be the inclusive reproductive value of type $i \in \{f, b(s,p), n(s,p)\}$ individuals at time t. Calculating the inclusive reproductive values of individuals goes backwards in time. Inclusive reproductive value of a mutant floater at final time is

$$V_f(\mathbf{u}^m, \mathbf{u}, T-1) = (1-\mu_f) \sum_{s=0}^{S} \sum_{p=0}^{P} \phi_{(s,p)}(t) \sum_{\tau} u^m_{f(s,p),\tau} V_{f(s,p),\tau}(T-1), \qquad (16)$$

where $V_{f(s,p),\tau}(T-1)$ is the reproductive value gained at the final time if the floater chooses the action τ. This equation evaluates to zero (see table **2** in Appendix C), because in the last time step it is too late for a floater to reproduce or influence anyone else's reproduction. Inclusive reproductive value of a mutant floater at time $t < T-1$ is

$$\begin{aligned} V_f(\mathbf{u}^m, \mathbf{u}, t) &= (1-\mu_f)\Big[\textstyle\sum_{s=0}^{S}\sum_{p=0}^{P}\phi_{(s,p)}(t)\sum_\tau u^m_{f(s,p),\tau} V_{f(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t) \\ &+ \phi_f(t) V_f(\mathbf{u}^m, \mathbf{u}, t+1)\Big], \end{aligned} \tag{17}$$

where $V_{f(s,p),\tau}(\mathbf{u}, t)$ is the reproductive value gained at time t if the floater chooses the action τ.

Inclusive reproductive value of a dominant (subordinate) female at time t is

$$V_i(\mathbf{u}^m, \mathbf{u}, t) = \sum_\tau u^m_{i,\tau} V_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t),\ i \in \{b(s,p), n(s,p)\}, \tag{18}$$

where $V_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t), i \in \{b(s,p), n(s,p)\}$ is the inclusive reproductive value gained at time t of the season by choosing the action τ associated with a nest of type (s,p). We present the reproductive values gained with each action at the final time step $V_{i,\tau}(\mathbf{u}^m, \mathbf{u}, T-1)$ in table **2** in Appendix C. In previous time steps, the inclusive reproductive value that dominants (subordinates) gain with action τ is

$$V_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t) = V^\bullet_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t) + V^\circ_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t),\ t < T-1, \tag{19}$$

where $V^\circ_i(\mathbf{u}^m, \mathbf{u}, t)$ is the inclusive reproductive value gained by leaving the focal nest site either in the current time step or in the future (see Appendix C for its derivation) and

$$V^\bullet_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t) = v_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t) + \left[v^m_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t) - v_{(s-1,p)}(\mathbf{u}, t) - v_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t)\right] r \tag{20}$$

is the inclusive reproductive value gained within the focal nest site given that the focal female chooses the action τ. In eq. (20) $v_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t)$ is the direct reproductive value that the individual of type i gains from the focal nest, given that she chooses the action τ at time t; $v^m_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t)$ is the direct reproductive value of the focal nest with the mutant female who chooses the action τ; and $v_{(s-1,p)}(\mathbf{u}^m, \mathbf{u}, t)$ is the direct reproductive value of that nest if the focal female would be absent from that nest. The term in square brackets represents the net effect on the reproduction of relatives due to the female's presence in the focal nest and thus it is weighted by r. This net effect can be positive or negative, as it has two components: the first component, $v^m_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t) - v_{(s-1,p)}(\mathbf{u}, t)$, is positive and represents any extra offspring produced in this nest due to the presence of the focal individual; the second component, $-v_{i,\tau}(\mathbf{u}^m, \mathbf{u}, t)$, is negative and can be loosely interpreted as offspring lost by relatives due to the presence of the focal individual (in the sense that every offspring attributed to the focal female is one offspring less attributed to its nest mates).

The invasion fitness of the mutant is defined as the inclusive reproductive value of a mutant floater at the beginning of the season, i.e.

$$W(\mathbf{u}^m, \mathbf{u}) = V_f(\mathbf{u}^m, \mathbf{u}, 0). \tag{21}$$

Evolutionarily stable strategies

A mutant strategy $\hat{b}(\mathbf{u})$ that yields the highest invasion fitness in a population of resident individuals following the strategy $\mathbf{u}$ is said to be the best response to strategy $\mathbf{u}$, i.e.

$$W(\hat{b}(\mathbf{u}), \mathbf{u}) = \max_{\mathbf{u}^m \in U} W(\mathbf{u}^m, \mathbf{u}), \tag{22}$$

where $\hat{b}(\cdot)$ is called the best-response function and U is the domain of all possible strategies. A resident strategy

$$\mathbf{u}^* = \left\{ u^*_{f,1}(\mathbf{n}, t), u^*_{b(s,p),1}(\mathbf{n}, t), u^*_{n(s,p),1}(\mathbf{n}, t), u^*_{n(s,p),2}(\mathbf{n}, t), u^*_{n(s,p),3}(\mathbf{n}, t) \right\} \tag{23}$$

that can not be invaded by any mutant strategy $\mathbf{u}^m \in U$ is said to be the candidate endpoint of the evolutionary process and is said to be an evolutionarily stable strategy (ESS). Thus, a necessary condition for a strategy $\mathbf{u}^*$ to be evolutionarily stable is that it satisfies

$$\mathbf{u}^* \in \arg\max_{\mathbf{u}^m \in U} W(\mathbf{u}^m, \mathbf{u}^*). \tag{24}$$

Finding $\mathbf{u}^*$ is a problem of dynamic optimization (Mangel and Clark, 1988; Houston and McNamara, 1999) and we use an iterative scheme of the best response map (Houston and McNamara, 1999, p. 159) to solve this problem.

Iterative scheme of the best response map

It is important to note the best response $\hat{b}(\mathbf{u})$ to a particular environment $\mathbf{u}$ is a pure strategy (the values are either 0 or 1). This may introduce computational errors (Houston and McNamara, 1999) in finding the ESS through iteration. Therefore, instead of finding the best response, we will find the best response $\hat{b}_\delta(\mathbf{u})$ to the environment $\mathbf{u}$ with a degree of error $\delta > 0$, such that costlier errors occur less frequently than near-optimal actions (Houston and McNamara, 1999, p. 191-192).

For that we define

$$\lambda_{k,\tau}(\mathbf{u}^m, \mathbf{u}, t) = V_{k,\tau}(\hat{b}(\mathbf{u}), \mathbf{u}, t) - V_{k,\tau}(\mathbf{u}^m, \mathbf{u}, t) \tag{25}$$

as the cost on the inclusive reproductive value for the mutant following a strategy $\mathbf{u}^m$ for diverging from the best response strategy $\hat{b}(\mathbf{u})$ at time t in a population of residents following the strategy $\mathbf{u}$. Let $L(x) = \exp(-x/\delta)$ be the error function, where $\delta > 0$ controls the degree of error such that costlier errors occur less frequently than near-optimal actions (Houston and McNamara, 1999, p. 191-192). The elements of the best response vector $\hat{b}_\delta(\mathbf{u})$ are given by

$$\hat{b}_\delta(u_{k,\tau}(\mathbf{n}, t)) = \frac{L(\lambda_{k,\tau}(\mathbf{u}, \mathbf{v}, t))}{\sum_\tau L(\lambda_{k,\tau}(\mathbf{u}, \mathbf{v}, t))}. \tag{26}$$

Starting out with some initial resident strategy $\mathbf{u}^0$, we find the best response $\hat{b}_\delta(\mathbf{u}^0)$ to that strategy. Then we update the resident strategy for the next iteration with the replacement factor $0 > \beta > 1$ and repeat the process, using the iterative scheme

$$\mathbf{u}^i = \beta \hat{b}_\delta(\mathbf{u}^{i-1}) + (1-\beta)\mathbf{u}^{i-1}. \tag{27}$$

This iterative scheme produces a sequence of strategies $(\mathbf{u}^0, \mathbf{u}^1, \mathbf{u}^2, ...)$. If the absolute difference between the consecutive elements of the sequence converges to zero, i.e.

$$\left|\mathbf{u}^i - \mathbf{u}^{i-1}\right| \rightarrow 0 \text{ as } i \rightarrow \infty \tag{28}$$

then we have arrived at the evolutionary stable strategy (ESS) $\mathbf{u}^*$.

RESULTS

We consider an optimal nesting behaviour of females for a fixed level of average relatedness between the associating co-foundresses and for different species-specific life-history characteristics. We present the evolutionarily stable strategy $\mathbf{u}^*$ together with population dynamics (number of different individuals over the course of season) that this strategy entails. We started our dynamic optimisation with a completely solitary population, where floaters only join empty nest sites ($u^0_{f(s,p),1} = 1$ if $s = 0\ \forall p$ and $u^0_{f(s,p),1} = 0$ if $s > 0\ \forall p$), breeders never leave the nests ($u_{b(s,p),1} = 1 \forall s > 0, \forall p$) and subordinates are either aggressive or leave the nest ($u^0_{n(s,p),1} = 0$, $u^0_{n(s,p),2} = 0.5$, $u^0_{n(s,p),3} = 0, u^0_{n(s,p),4} = 0.5, \forall s > 1, \forall p$). However, note that our optimization approach does not explicitly model the evolutionary dynamics of the transition from a solitary population to a cooperatively breeding population. In all of our simulations we assumed that subordinates face a trade-off between helping and survival and between being aggressive and survival.

We compare three different scenarios of average relatedness between the associating co-foundresses: (i) co-foundresses are always full sisters ($r = 0.75$), (ii) co-foundresses have an average relatedness similar to *Polistes dominulus* ($r = 0.3$), and (iii) co-foundresses are completely unrelated ($r = 0$). We compare three different species-specific life-history settings: (i) the initial pre-reproductive investment into the nest is negligible $(P = 0)$ and the mortality of a solitary breeder is equal to the mortality of a dominant female and a helpful subordinate in a co-foundress nest, (ii) the initial pre-reproductive investment is substantial $(P = 5)$ (compared to the length of the season ($T = 51$) and foraging efficiency ($r_0 = 0.1$)) and the mortality of a solitary breeder is equal to the mortality of a dominant female and a helpful subordinate in a co-foundress nest (iii) the initial pre-reproductive investment is substantial $(P = 5)$ and a solitary breeder is three times less likely to survive compared to a dominant female and a helpful subordinate in a co-foundress nest (individuals survive better in co-foundress nests).

To simplify our analysis, we consider the results of the model for the smallest possible maximum nest size ($S = 2$), with one dominant female and one subordinate female. In appendix D, we show the results of our model for the same parameter values when we allow the formation of larger groups ($S = 3$), where we show that most of the co-foundress nests that are formed under these parameter settings are of size $s = 2$. However, considering small co-foundress associations is sufficient since the main focus of this work is on the conditions of how cooperative breeding can emerge as an optimal behaviour.

In interpreting our results, note that our optimization approach allows individuals to make some small degree of errors, such that costly errors are very rare and errors that have only a small effect on the inclusive reproductive value are more common. This property is important, since it eliminates some computational issues regarding complex problems of dynamic optimization and also takes into account that organisms make errors in their decision making process in a similar way (Houston and McNamara, 1999). Note that in the end of the season, some individuals might have very little opportunity to increase their reproductive value and hence the frequency of making errors becomes larger.

Result 1: cooperation in the pre-reproductive phase can evolve when average relatedness between co-foundresses is low, but high degree of relatedness is needed for alloparental care to evolve in the reproductive phase

We found that, if the required pre-reproductive investment P is sufficiently high, then co-founding becomes much more common in a population that follows the evolutionarily stable strategy $\mathbf{u}^*$(see fig. 1). Even when the average relatedness between the subordinate and the dominant individual is low and there are no survival benefits associated with larger groups, co-foundress associations become relatively common throughout the season.

We also found that for high pre-reproductive investment P, we observe a relatively high degree of costly helping (foraging) even in populations where the average relatedness between co-foundresses is low (see fig. 3). Moreover, in a population of high pre-reproductive investment requirement ($P = 5$) subordinates who are not full sisters of the dominant help the dominant only in the pre-reproductive phase (see fig. 4) and become more aggressive in the reproductive phase (see fig. 5), while subordinates who are full sisters of the dominant help the dominant throughout the season (see fig. 4) and show no aggression towards the dominant female.

In a population of high pre-reproductive investment requirement ($P = 5$), a high percentage of offspring produced come from co-foundress nests, even when the co-foundresses are unrelated (see fig. 2) and the subordinates are not helping the dominants to produce the reproductive offspring.

We conclude that high relatedness combined with high requirement for the pre-repoductive investment strongly facilitate cooperative breeding with alloparental care. We observe that cooperation takes place in the pre-reproductive phase when relatedness is low, but not in the reproductive phase. Hence, our simulations imply that for alloparental care of sexual offspring to evolve, a high degree of relatedness is required.

Result 2: increased survival in co-foundress nests facilitates co-foundress associations only if average relatedness between co-foundresses is high, but does not increase the tendency to help the dominant female

Empirical evidence suggests that individuals have higher survival in co-foundress nests (Tibbetts and Reeve, 2003). If the required pre-reproductive investment is sufficiently high ($P = 5$) and there is increased survival in co-foundress nests, we observed a higher percentage of co-foundress nests if the average relatedness between co-foundress nests is high, but we did not find this effect when the average relatedness is low (see fig. 1).

We also found that a survival benefit in co-foundress nests had negligible effect on subordinate behaviour for any average relatedness level between the subordinate and the dominant (see figs. 3, 4, and 5). This is also in accordance with the fact that significant increase of survival in co-foundress nests did not significantly increase the percentage of offspring produced in co-foundress nests (see fig. 2).

Result 3: co-foundress nests and costly helping as a secondary strategy in the absence of nest inheritance

Here, we consider a population where the dominant females always survive ($\mu_s = \mu_{b0} = 0$) and subordinates are completely incapable of usurping the nests through aggression ($a = 0$). In this population, dominant females always retain their positions and subordinates never inherit the nests.

We find that in the absence of pre-reproductive investment, almost no co-foundress nests are formed for any average relatedness level between subordinates (see fig. 6). In a population of substantial pre-reproductive investment ($P = 5$), we observe some degree of co-foundress nests and costly helping even in a population where the relatedness level between co-foundresses is relatively low ($r = 0.3$) (see fig. 6 and 8).

We find that co-foundress nests are mostly formed later in the season (see fig. 6). In the beginning of the season, there are no co-foundress nests. Females try to found nests solitarily and the formation of co-foundress nests tends to happen much later in the season compared to a population where subordinates can inherit the nest (see figs. 1 and 6). However, the formation of co-foundress nests in this population happens later in the season, where females who have failed to nest solitarily join other females as a secondary strategy.

If the average relatedness level is low ($r = 0.3$), the percentage of offspring produced in co-foundress nests is higher in a population with no nest inheritance compared to a population, where subordinates can usurp the nests (see figs. 2 and 7).

We conclude that the formation of co-foundress nests and costly helping can evolve as a secondary strategy if females have failed to nest solitarily, even if relatedness between co-foundresses is low. However, females would choose to be aggressive and usurp the nest in the reproductive phase if the relatedness between co-foundresses is low ($r = 0.3$).

DISCUSSION

Our model shows that high pre-reproductive investment requirement facilitates the formation of co-foundress associations and costly helping behaviour during the pre-reproductive phase even if the relatedness between co-foundresses is low. However, for costly helping to continue during the reproductive phase, co-foundresses have to have a high degree of relatedness or the subordinates have to be incapable of overturning the dominant female from her position.

We found that increased survival in co-foundress associations facilitates the formation of co-foundress associations only if relatedness between co-foundresses is high. Such a survival benefit does not, however, affect the behaviour of subordinates in the nest.

Our model predicts that costly investment into nest building (and producing the worker caste) can facilitate co-foundress associations of primitively eusocial wasps even when relatedness is low, since reaching the reproductive phase alone is relatively unlikely. Building the structure of a nest can be an expensive tasks for wasps and it requires a high amount of foraging. Polistes wasps mainly build their nests from fibres of dead wood, softened with water at collection, and they can mix this with oral secretions that may be proteinaceous and nutritionally expensive (Hunt, 2007). Secretions invested into nest structure can represent up to 20% of foraged protein in Polistes (Kudô *et al.*, 1998).

Gadagkar (2011) has argued that since relatedness between co-foundresses is low in *P. dominulus* then kin selection is unnecessary to explain the formation of social groups in *P. dominulus*. However, it is worth noting that the amount of pre-reproductive investment observed in primitively eusocial insects today may not be representative of the ancestral conditions under which co-foundress associations evolved. In particular, since the solitary ancestors of such species must have been reasonably capable of reaching the reproductive phase alone, it appears likely that high requirements of pre-reproductive investment may have evolved after cooperative nesting was already common. Thus, while high pre-reproductive investment requirement can have a stronger effect than relatedness on favouring the formation of co-foundress associations (fig. 1), this does not justify the conclusion that relatedness was unimportant at the origin of co-foundress associations. Moreover, our model implies that if subordinate females are able to inherit the nest (through nest usurpation) then costly helping during the reproductive phase can only evolve when the relatedness between co-foundresses is high.

Our model shows that the high cost of nest building and investing into the worker caste together with nest inheritance can explain how cooperative breeding and costly helping during the pre-reproductive phase can evolve with low average level of relatedness between co-foundresses. However, our model does not explicitly give to the focal individual a choice to join individuals with different relatedness levels. An extension of this model that would allow individuals to distinguish between relatives and unrelated individuals would allow us to theoretically test if *P. dominulus* foundresses are making kin recognition errors while joining the nests of unrelated females. This would allow to compare how important is relatedness to foundresses when they are associating together compared to the other factors, such as nest size and nest phase and time of the season. In fact, it has been observed that the average within-group relatedness varies from 0.189 to 0.491 for different stages of nesting cycles in *P. dominulus* (Zanette and Field, 2008). Current empirical evidence suggest that there are no clear differences between the subordinates that are differently related to the dominant wasp (Field and Leadbeater, 2016).

In our model the investment of pre-reproductive investment level P is a fixed quantity. Empirical studies suggest, however, that P is not fixed and depends on other factors such as amount of resources that are available to the colony. In fact, wasps actually invest more resources to the first non-reproductive brood and build bigger nests, when extra food is provided to the females in an experimental setting (Klahn, 1981). In addition, our model assumes that nest phase p cannot decrease in time, and hence investment cannot be lost. However, we know that predator attacks on Polistes wasps can sometimes destroy the whole nest structure (Hunt, 2007).

Another factor that we did not take into account is that subordinates can lay some small proportion of eggs that are destined to become reproductives (Leadbeater *et al.*, 2011). However, we believe that including this additional option would not profoundly change the results of our model, since egg-laying by subordinates is conceptually similar to other forms of selfish subordinate behaviour (namely, resting and being aggressive) that we did include.

In conclusion, our main findings show that the need to invest a high amount of resources into the nest before reproduction can be an essential factor in maintaining co-foundress associations and costly helping in social wasps, even when the average relatedness between co-foundresses is low. However, for helping to continue in the reproductive phase during the end of the season, high relatedness between cofoundresses is required. This work highlights the importance of considering time-dependent life-history factors in the evolution of social behaviour.

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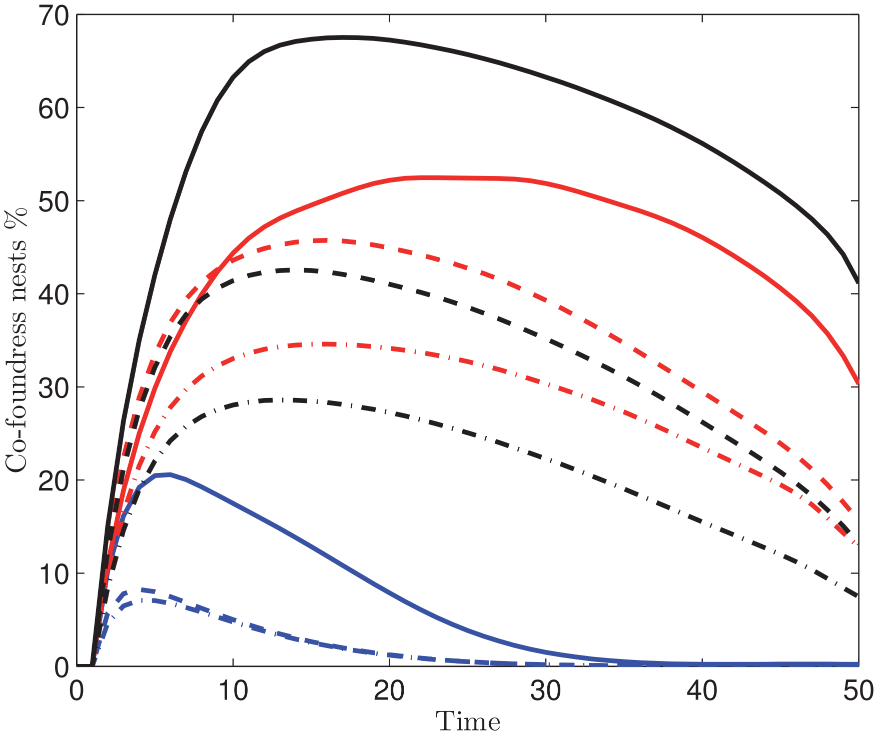

Figure 1: Percentage of co-foundress nests in three different populations for varying levels of average relatedness between co-foundresses. The subordinate and the dominant are full sisters $r = 0.75$ (solid line), the subordinate and the dominant have an average relatedness of $r = 0.3$ (dashed line), the subordinate and the dominant are not related $r = 0$ (dash-dotted line). We have modelled three types of populations: (i) negligible pre-reproductive investment ($P = 0$) and solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) (blue lines); (ii) substantial pre-reproductive investment ($P = 5$) and solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) (red lines); (iii) substantial pre-reproductive investment ($P = 5$) and solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$) (black lines). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

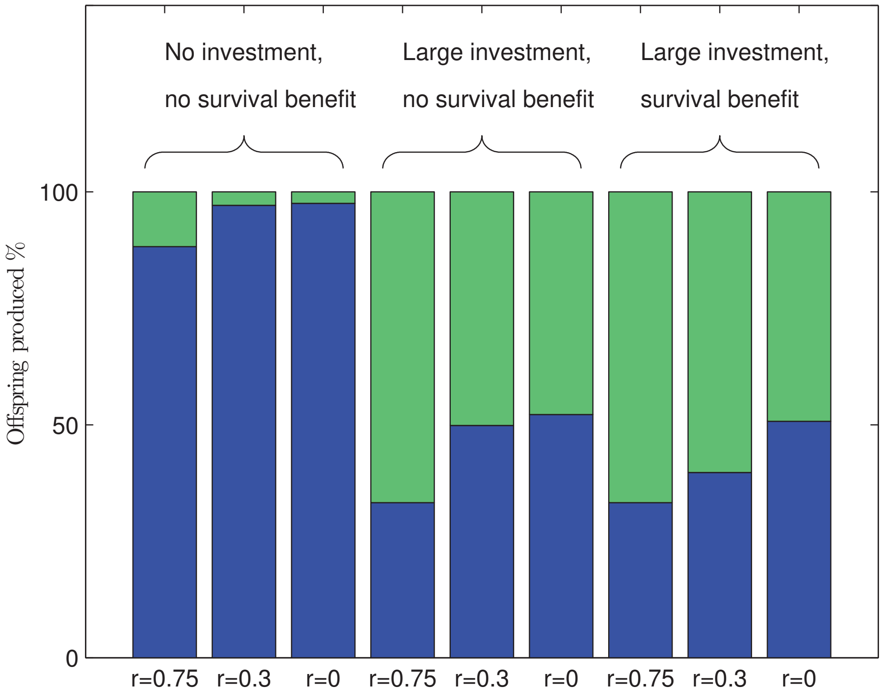

Figure 2: Percentage of offspring produced in nests of different size. Percentage of offspring produced in co-foundress nests (green), percentage of offspring produced in solitary nests (blue). The subordinate and the dominant are full sisters $r = 0.75$, subordinate and the dominant have an average relatedness of $r = 0.3$, the subordinate and the dominant are not related $r = 0$. We have modelled three types of populations: (i) negligible pre-reproductive investment ($P = 0$) and solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) (columns 1-3); (ii) substantial pre-reproductive investment ($P = 5$) and solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) (columns 3-6); (iii) substantial pre-reproductive investment ($P = 5$) and solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$) (columns 6-9). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$,$\delta = 0.05$.

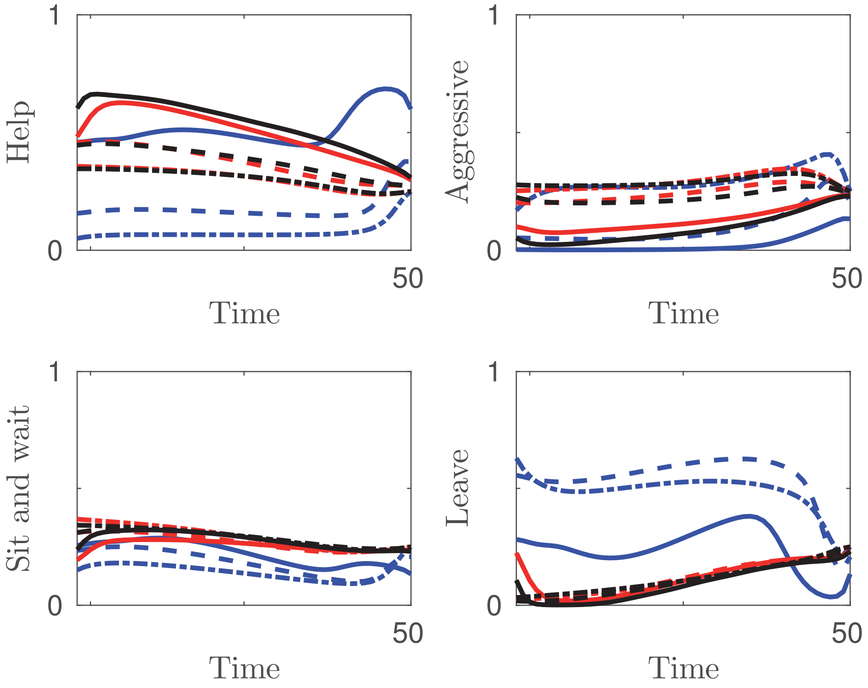

Figure 3: Evolutionarily stable probabilities of subordinates actions ($u^*_{n(s,p),\tau}(t)$) in nests of size $s = 2$. The probabilities have been averaged over different nest phases. The subordinate and the dominant are full sisters $r = 0.75$ (solid line), subordinate and the dominant have an average relatedness of $r = 0.3$ (dashed line), the subordinate and the dominant are not related $r = 0$ (dashed-dotted line).We have modelled three types of populations: (i) negligible pre-reproductive investment ($P = 0$) and solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) (blue lines); (ii) substantial pre-reproductive investment ($P = 5$) and solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) (red lines); (iii) substantial pre-reproductive investment ($P = 5$) and solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$) (black lines). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

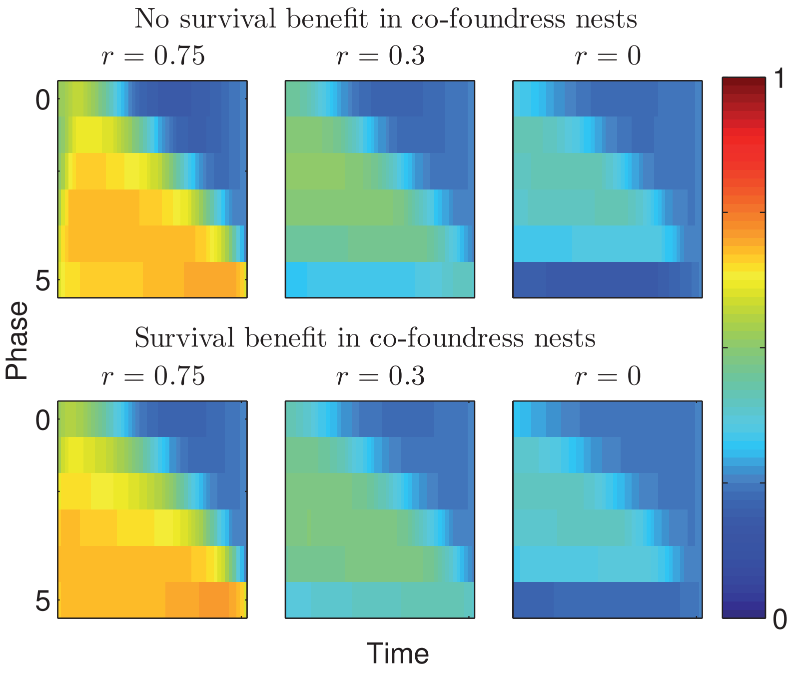

Figure 4: Evolutionarily stable probability for a subordinate to help ($u^*_{n(s,p),1}(t)$) in a nest of size $s = 2$ in different phases depending on the time of the season. The subordinate and the dominant are full sisters $r = 0.75$, the subordinate and the dominant are not related $r = 0$. We have presented the results for a population, where there is high pre-reproductive investment level $P = 5$ and (i) solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$), (ii) solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

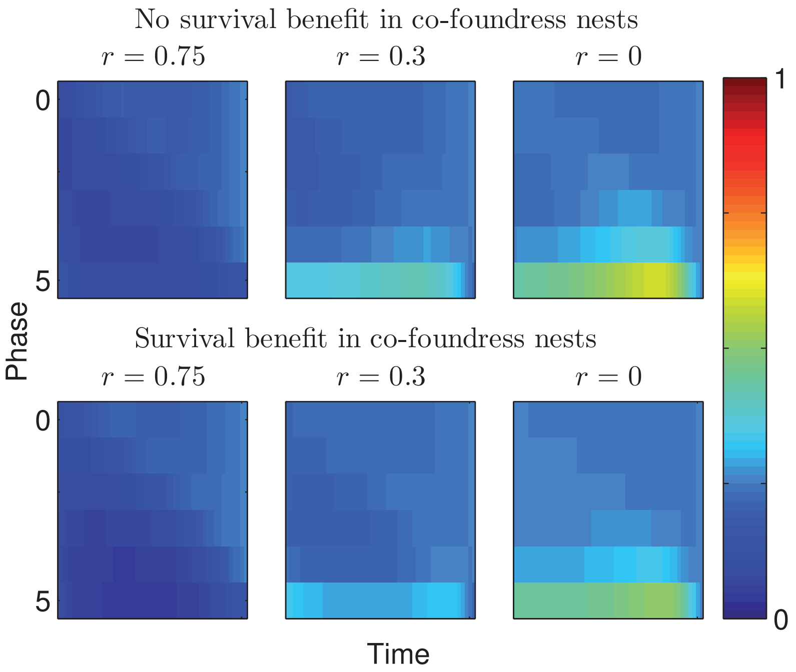

Figure 5: Evolutionarily stable probability for a subordinate to be aggressive ($u^*_{n(s,p),2}(t)$) in a nest of size $s = 2$ in different phases depending on the time of the season. The subordinate and the dominant are full sisters $r = 0.75$, the subordinate and the dominant are not related $r = 0$. We have presented the results for a population, where there is high pre-reproductive investment level ($P = 5$) and (i) solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$), (ii) solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

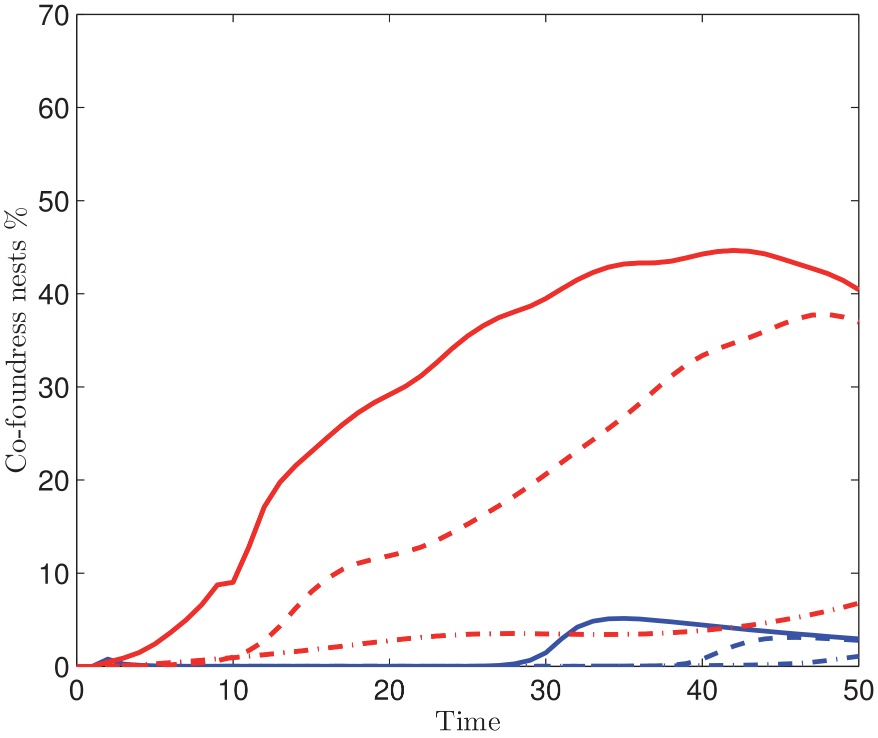

Figure 6: Percentage of co-foundress nests in two different populations for varying levels of average relatedness between co-foundresses, with no possibility of nest inheritance. The dominant females always survive ($\mu_s = \mu_{b0} = 0$) and subordinates are not able to usurp the nests through aggression ($a = 0$). The subordinate and the dominant are full sisters $r = 0.75$ (solid line), the subordinate and the dominant have an average relatedness of $r = 0.3$ (dashed line), the subordinate and the dominant are not related $r = 0$ (dash-dotted line). We have modelled two types of populations: (i) negligible pre-reproductive investment ($P = 0$) (blue lines); (ii) substantial pre-reproductive investment ($P = 5$) (red lines); (iii) substantial pre-reproductive investment ($P = 5$) and solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$) (black lines). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $\mu_f = 0.01$, $\mu_{n,1} = 0.04$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

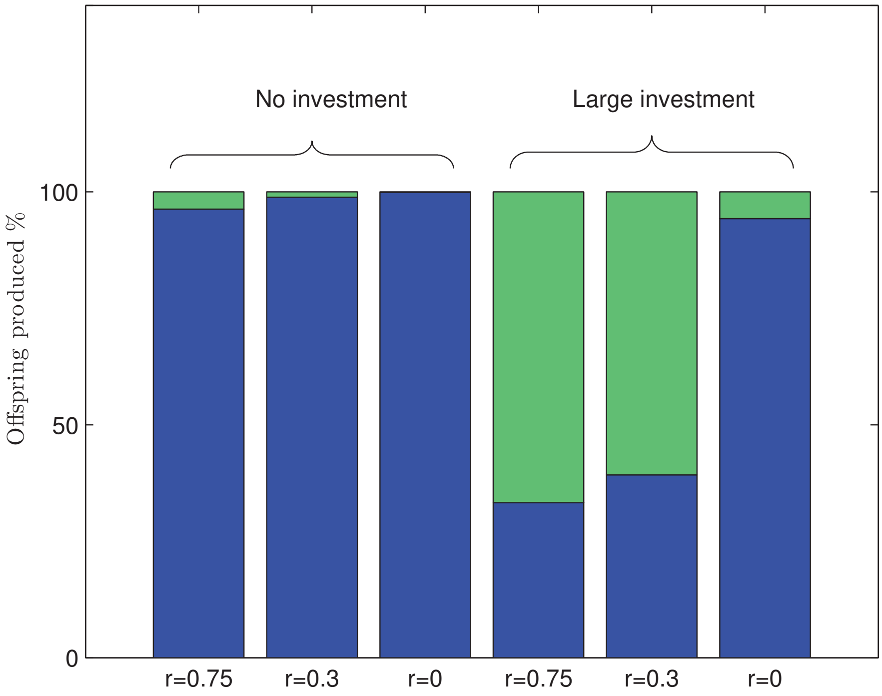

Figure 7: Percentage of offspring produced in nests of different size with no possibility of nest inheritance. Percentage of offspring produced in co-foundress nests (green), percentage of offspring produced in solitary nests (blue). The dominant females always survive ($\mu_s = \mu_{b0} = 0$) and subordinates are not able to usurp the nests through aggression ($a = 0$). The subordinate and the dominant are full sisters $r = 0.75$, the subordinate and the dominant have an average relatedness of $r = 0.3$, the subordinate and the dominant are not related $r = 0$. We have modelled two types of populations: (i) negligible pre-reproductive investment ($P = 0$) (columns 1-3); (ii) substantial pre-reproductive investment ($P = 5$) (columns 3-6). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $\mu_f = 0.01$, $\mu_{n,1} = 0.04$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

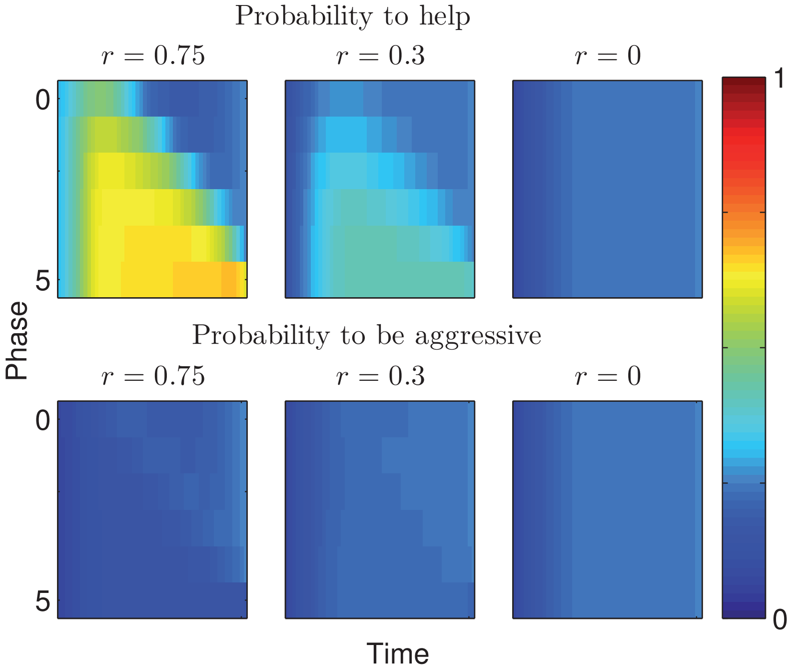

Figure 8: Evolutionarily stable probability for a subordinate to help ($u^*_{n(s,p),1}(t)$) and be aggressive ($u^*_{n(s,p),2}(t)$) in a nest of size $s = 2$ in different phases depending on the time of the season. The dominant females always survive ($\mu_s = \mu_{b0} = 0$) and subordinates are not able to usurp the nests through aggression ($a = 0$). The subordinate and the dominant are full sisters $r = 0.75$, the subordinate and the dominant have an average relatedness of $r = 0.3$, the subordinate and the dominant are not related $r = 0$. Other parameter values: $P = 5$, $r_0 = 0.01$, $S = 2$, $h = 1$, $\mu_f = 0.01$, $\mu_{n,1} = 0.04$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

APPENDIX A: LIST OF SYMBOLS

Symbol	Meaning
r_0	baseline species specific resource acquisition rate per unit time; resource acquisition rate of a solitary female
$r_{(s,p)}(\mathbf{u},t)$	resource acquisition rate at nests of type (s,p)
h	efficiency of helping
a	efficiency of usurping the nest
p	the amount the effort that has been invested into the nest (nest phase) ($p \in [0,P]$)
P	baseline amount of effort P that has to be invested into the nest before sexual reproduction can start.
s	size of the nest ($s \in [0,S]$)
S	maximum size of the nest S
t	time of the season $t \in [0,T-1]$
T	length of the season
$u_{f,\tau}$	probability that a floater that is the first floater to find a nest of type (s,p) at time t will: (i) join the nest $(\tau = 1)$, (ii) leave the nest $(\tau = 2)$
$u_{b,\tau}$	probability that the dominant in a nest of type (s,p) at time t will: (i) stay in the nest $(\tau = 1)$, (ii) leave the nest $(\tau = 2)$
$u_{n,\tau}$	probability that a subordinate in a nest of type (s,p) at time t will: (i) help the dominant $(\tau = 1)$, (ii) be aggressive towards the dominant $(\tau = 2)$, (iii) stay at the nest without helping or being aggressive $(\tau = 3)$, (iv) leave the nest $(\tau = 4)$
$\triangle p_{(s,p)}(\mathbf{u},t)$	nest progression rate from one phase to the next at the non-reproductive stage
$w_{(s,p)}(\mathbf{u},t)$	number of offspring produced at time t in a nest of type (s,p)
$z^i_{(s,p)}$	probability that in a nest of type (s,p) i subordinates survive and stay in the nest for the next time step
ϵ	conversion efficiency from resources to sexual offspring
$x_f(t)$	number of floaters in the population at time t
$x_{(s,p)}(t)$	number of nests of type (s,p) in the population at time t
$X(t)$	number of adult (sexual) females in the population at time t
$\eta_{(s,p)}(\mathbf{u},t)$	probability that a nest of type (s,p) will be joined by a floater at time t
$\gamma_{ss'pp'}$	probability that a nest of type (s,p) will be of type (s',p') at the next time step
$\phi_{(s,p)}(t)$	probability that a focal floater will be the first one to find a nest of type (s,p)
μ_f	mortality probability of a floater

$\mu_{i(s,p)}(\mathbf{u},t)$	average mortality probability of a dominant ($i = b$) / subordinate ($i = n$) female in a nest of type (s,p)
$\mu_{n,\tau}$	mortality probability of a subordinate female given that she chooses the action τ
$\omega^{i}_{(s,p)}(\mathbf{u},\mathrm{t})$	probability that nest phase will progress to a level $p + \triangle p^{i}_{(s,p)}(\mathbf{u},t)$, $i \in \{1,2\}$ for the nest time step

APPENDIX B: CALCULATING THE TRANSITION PROBABILITY $\gamma_{ss'pp'}(\mathbf{u}, t)$

We define the probability that in a nest of type (s, p) i subordinates survive and stay in the nest for the next time step, i.e.

$$z^{i}_{(s,p)}(\mathbf{u}, t) = \sum_{j=0}^{s-1-i} \mathrm{bin}(s-1, j, \mu_{n(s,p)}(\mathbf{u}, t))\mathrm{bin}(s-1-j, i, (1-u_{n(s,p),4}(s, p, t))), \quad \text{(B1)}$$

where $s > 0, \forall\, p$. Here, j stands for the number of subordinates that die and $\mathrm{bin}(n, k, p) = \begin{pmatrix} n \\ k \end{pmatrix} p^{k}(1-p)^{n-k}$ stands for the binomial probability. Moreover, let

$$\pi_{sps'} = \begin{cases} 1-u_{b,1}(s,p,t)(1-\mu_0), \text{ if } s = 1 \text{ and } s' = 0 \\ u_{b,1}(s,p,t)(1-\mu_0), \text{ if } s = s' = 1 \\ \mu_b z^{0}_{(s,p)}, \text{ if } s > 1 \text{ and } s' = 0 \\ \mu_b z^{s'}_{(s,p)} + (1-\mu_b) z^{s'-1}_{(s,p)}, \text{ if } s > 1 \text{ and } s > s' > 0 \\ (1-\mu_b) z^{s'-1}_{(s,p)}, \text{ if } s > 1 \text{ and } s = s' \\ 0, \text{ otherwise,} \end{cases} \quad \text{(B2)}$$

denote the probability that nests of size s at time t will be of size s' at time $t+1$, through the process of mortality and individuals deciding to leave the nest.

Next, we give the rules for calculating $\gamma_{ss'pp'}$ that gives the probability that a nest of type (s, p) will be of type (s', p') in the next time step through the effect of mortality, individuals deciding to leave the nest, and nest progression rate.

The probability that an empty nest of type $(s = 0, p)$ is of type (s', p') in the next time step is given by

$$\gamma_{0s'pp'} = \begin{cases} 1, \text{ if } s = s' = 0 \text{ and } p = p' \\ 0, \text{ otherwise.} \end{cases} \quad \text{(B3)}$$

The probability that a nest of type $(s > 0, p = P)$ is of type (s', p') in the next time step is given by

$$\gamma_{ss'pp'} = \begin{cases} \pi_{sps'}, \text{ if } p = p' = P \\ 0, \text{ otherwise.} \end{cases} \quad \text{(B4)}$$

The probability that a nest of type $(s = 1, p < P)$ is of type $(s', p' = p)$ in the next time step (i.e. nest phase stays the same) is

$$\gamma_{ss'pp'} = \begin{cases} \omega^{2}_{(s,p)}(\pi_{sps'} - u_{b,2}) + u_{b,2}, \text{ if } s' = 0 \text{ and } \triangle p^{2}_{(s,p)} = 0 \\ \omega^{2}_{(s,p)} \pi_{sps'}, \text{ if } s' = 1 \text{ and } \triangle p^{2}_{(s,p)} = 0 \\ u_{b,2}, \text{ if } \triangle p^{2}_{(s,p)} \neq 0. \end{cases} \quad \text{(B5)}$$

The probability that a nest of type $(s > 1, p < P)$ is of type $(s', p' = p)$ in the next time step (i.e. nest phase stays the same) is

$$\gamma_{ss'pp'} = \begin{cases} \omega^2_{(s,p)}\pi_{sps'}, \ \triangle p^2_{(s,p)} = 0 \\ 0, \ \text{otherwise.} \end{cases} \tag{B6}$$

The probability that a nest of type $(s = 1, p < P)$ is of type $(s', p' = P)$ in the next time step (i.e. nest phase reaches the reproductive treshold P) is

$$\gamma_{ss'pP} = \begin{cases} \pi_{sps'} - u_{b,2}, \ \text{if } \triangle p^2_{(s,p)} + p \geq P \text{ and } s' = 0 \\ \pi_{sps'}, \ \text{if } \triangle p^2_{(s,p)} + p \geq P \text{ and } s' = 1 \\ \omega^1_{(s,p)}(\pi_{sps'} - u_{b,2}), \ \text{if } \triangle p^1_{(s,p)} + p = P \text{ and } \omega^1_{(s,p)} \neq 0\text{and } s' = 0 \\ \omega^1_{(s,p)}\pi_{sps'}, \ \text{if } \triangle p^1_{(s,p)} + p = P \text{ and } \omega^1_{(s,p)} \neq 0 \text{ and } s' = 1 \\ 0, \ \text{otherwise.} \end{cases} \tag{B7}$$

The probability that a nest of type $(s > 1, p < P)$ is of type $(s', p' = P)$ in the next time step (i.e. nest phase reaches the reproductive treshold P) is

$$\gamma_{ss'pP} = \begin{cases} \pi_{sps'}, \ \text{if } \triangle p^2_{(s,p)} + p \geq P \\ \omega^1_{(s,p)}\pi_{sps'}, \ \text{if } \triangle p^1_{(s,p)} + p = P \text{ and } \omega^1_{(s,p)} \neq 0 \\ 0, \ \text{otherwise.} \end{cases} \tag{B8}$$

The probability that a nest of type $(s = 1, p < P)$ is of type $(s', p < p' < P)$ in the next time step (i.e. nest progression happens, but not to the reproductive treshold P) is

$$\gamma_{ss'pp'} = \begin{cases} \omega^1_{(s,p)}(\pi_{sps'} - u_{b,2}) \text{ if } \triangle p^1_{(s,p)} + p = p' \text{ and } \omega^1_{(s,p)} \neq 0 \text{ and } s' = 0 \\ \omega^1_{(s,p)}\pi_{sps'} \text{ if } \triangle p^1_{(s,p)} + p = p' \text{ and } \omega^1_{(s,p)} \neq 0 \text{ and } s' = 1 \\ \omega^2_{(s,p)}(\pi_{sps'} - u_{b,2}), \ \text{if } \triangle p^2_{(s,p)} + p = p' \text{ and } s' = 0 \\ \omega^2_{(s,p)}\pi_{sps'}, \ \text{if } \triangle p^2_{(s,p)} + p = p' \text{ and } s' = 1 \\ 0, \ \text{otherwise.} \end{cases} \tag{B9}$$

The probability that a nest of type $(s > 1, p < P)$ is of type $(s', p < p' < P)$ in the next time step (i.e. nest progression happens, but not to the reproductive treshold P) is

$$\gamma_{ss'pp'} = \begin{cases} \omega^1_{(s,p)}\pi_{sps'} \text{ if } \triangle p^1_{(s,p)} + p = p' \text{ and } \omega^1_{(s,p)} \neq 0 \\ \omega^2_{(s,p)}\pi_{sps'}, \ \text{if } \triangle p^2_{(s,p)} + p = p' \\ 0, \ \text{otherwise.} \end{cases} \tag{B10}$$

In addition, the probability that a nest of type (s, p) is of type $(s', p' < p)$ is 0, because we assume the nest phase can not regress.

APPENDIX C: REPRODUCTIVE VALUES

Average life-history characteristics of nests with a mutant subordinate female

In order to simplify our analysis, we define the average level of subordinate phenotype for action τ' in a nest, given that the mutant has chosen the action τ, as

$$\tilde{u}^{\tau}_{n(s,p),\tau'}(t) = \frac{1_{\tau'}(\tau) + u_{n(s,p),\tau'}(s,p,t)(s-2)}{s-1}, \tag{C1}$$

where $1_{\tau'}(\tau)$ is the indicator function, i.e.

$$1_{\tau'}(\tau) = \begin{cases} 1 \text{ if } \tau = \tau', \\ 0 \text{ if } \tau \neq \tau'. \end{cases} \tag{C2}$$

We define $\tilde{\mathbf{u}}^{\tau}_{n(s,p),\tau'} = \left\{\tilde{u}^{\tau}_{n(s,p),1}, \tilde{u}^{\tau}_{n(s,p),2}, \tilde{u}^{\tau}_{n(s,p),3}, \tilde{u}^{\tau}_{n(s,p),4}\right\}$ as a vector of average subordinate phenotype in a focal colony, where the focal mutant subordinate has chosen the action τ. Hence, in a colony with a mutant subordinate female, the mortality probability of the dominant is

$$\tilde{\mu}^{\tau}_{b(s,p)} = \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t) = 1 - \left[(1-\mu_0)(1 - c_2\mu_{n,2}\tilde{u}^{\tau}_{n(s,p),2}(t))^{s-1}\right] \tag{C3}$$

and the resource foraging rate is

$$\tilde{r}^{\tau}_{(s,p)} = \tilde{r}^{\tau}_{(s,p)}(\mathbf{u},t) = r_0\left[1 + c_1\tilde{u}^{\tau}_{n(s,p),1}(s-1)\right], \tag{C4}$$

which imply an average nest progression rate $\triangle\tilde{p}^{\tau}_{(s,p)}(\mathbf{u},t)$ with nest progression probabilities $\tilde{\omega}^{1\tau}_{(s,p)}$ and $\tilde{\omega}^{2\tau}_{(s,p)}$, and reproduction rate $\tilde{w}^{\tau}_{(s,p)}(\mathbf{u},t)$.

Terminal conditions

In table 2 we list the terminal conditions for different direct and indirect reproductive values in our model. For explanation of these expressions, see the treatment of the non-terminal conditions with $t < T-1$ below.

Reproductive value	Value at terminal time $T-1$
$V_{f(s,p),\tau}(\mathbf{u}, T-1)$ $\tau \in \{1,2\}$	0
$V_{b(s,p),1}(\mathbf{u}, T-1)$	$w_{(s,p)}(\mathbf{u}, T-1) - rw_{(s-1,p)}(\mathbf{u}, T-1)$
$V_{b(s,p),2}(\mathbf{u}, T-1)$	0
$V_{n(s,p),\tau}(\mathbf{u}, T-1)$ $\tau \in \{1,2,3\}$	$r[\tilde{w}^{\tau}_{(s,p)}(\mathbf{u}, T-1) - w_{(s-1,p)}(\mathbf{u}, T-1)]$
$V_{n(s,p),4}(\mathbf{u}, T-1)$	0
$v_{f(s,p),\tau}(\mathbf{u}, T-1)$ $\tau \in \{1,2\}$	0
$v_{b(s,p),1}(\mathbf{u}, T-1)$	$w_{(s,p)}(\mathbf{u}, T-1)$
$v_{b(s,p),2}(\mathbf{u}, T-1)$	0
$v_{n(s,p),\tau}(\mathbf{u}, T-1)$ $\tau \in \{1,2,3\}$	0
$v_{n(s,p),4}(\mathbf{u}, T-1)$	0

Table 2: Table of terminal conditions

Inclusive and direct reproductive value of floaters

The terminal condition for the inclusive and direct reproductive value of a floater is

$$V_f(\mathbf{u}^m, \mathbf{u}, T-1) = (1-\mu_f) \sum_{s=0}^{S} \sum_{p=0}^{P} \phi_{(s,p)}(t) \sum_{\tau} u^m_{f(s,p),\tau} V_{f(s,p),\tau}(T-1), \tag{C5a}$$

$$v_f(\mathbf{u}^m, \mathbf{u}, T-1) = (1-\mu_f) \sum_{s=0}^{S} \sum_{p=0}^{P} \phi_{(s,p)}(t) \sum_{\tau} u^m_{f(s,p),\tau} v_{f(s,p),\tau}(T-1), \tag{C5b}$$

where $V_{f(s,p),\tau}(\mathbf{u}, T-1)$ and $v_{f(s,p),\tau}(\mathbf{u}, T-1)$ are the inclusive and direct reproductive values of a floater that chooses the action τ, respectively. Since the season ends with the time step $T-1$, then $V_{f(s,p),\tau}(T-1) = v_{f(s,p),\tau}(T-1) = 0\ \forall s, p, \tau$.

The reproductive value of floater at time t is given by

$$\begin{aligned} V_f(\mathbf{u}^m, \mathbf{u}, t) &= (1-\mu_f) \Big[\textstyle\sum_{s=0}^{S} \sum_{p=0}^{P} \phi_{(s,p)}(t) \sum_{\tau} u^m_{f(s,p),\tau} V_{f(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t) \\ &+ \phi_f(t) V_f(\mathbf{u}^m, \mathbf{u}, t+1) \Big], \end{aligned} \tag{C6a}$$

$$\begin{aligned} v_f(\mathbf{u}^m, \mathbf{u}, t) &= (1-\mu_f) \Big[\textstyle\sum_{s=0}^{S} \sum_{p=0}^{P} \phi_{(s,p)}(t) \sum_{\tau} u^m_{f(s,p),\tau} v_{f(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t) \\ &+ \phi_f(t) v_f(\mathbf{u}^m, \mathbf{u}, t+1) \Big], \end{aligned} \tag{C6b}$$

where the quantity $V_{f(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t)$ and $v_{f(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t)$ are the respective inclusive and direct reproductive values of a floater after choosing the action τ at time t in relation to a nest of type (s, p). In eq. (C6), the first term is the reproductive value the floater gains from being the first floater to find a nest site of type (s, p); the second term is the reproductive value she gains by remaining a floater (by not finding any nest site, or by not being the first floater to find a given nest site at time t).

Reproductive values associated with floater decisions

The reproductive value gained by a floater when joining a nest of size $s = 0$ is given by

$$V_{f(0,p),1}(\mathbf{u}^m, \mathbf{u}, t) = V_{b(1,p)}(\mathbf{u}^m, \mathbf{u}, t+1), \tag{C7a}$$

$$v_{f(0,p),1}(\mathbf{u}^m, \mathbf{u}, t) = v_{b(1,p)}(\mathbf{u}^m, \mathbf{u}, t+1). \tag{C7b}$$

The reproductive value gained by the floater when joining a nest of size $s = 1$ is given by

$$\begin{aligned} V_{f(1,p),1}(\mathbf{u}^m, \mathbf{u}, t) &= u_{b(s,p),1}(t)(1-\mu_{b(1,p)}(\mathbf{u}, t)) V'_{n(2,p')}(\mathbf{u}^m, \mathbf{u}, t+1) \\ &+ u_{b(s,p),1}(t) \mu_{b(1,p)}(\mathbf{u}, t) V'_{b(1,p')}(\mathbf{u}^m, \mathbf{u}, t+1) \\ &+ u_{b(s,p),2}(t) V_{b(1,p)}(\mathbf{u}^m, \mathbf{u}, t+1), \end{aligned} \tag{C8a}$$

$$\begin{aligned} v_{f(1,p),1}(\mathbf{u}^m,\mathbf{u},t) &= u_{b(s,p),1}(t)(1-\mu_{b(1,p)}(\mathbf{u},t))v'_{n(2,p')}(\mathbf{u}^m,\mathbf{u},t+1) \\ &+ u_{b(s,p),1}(t)\mu_{b(1,p)}(\mathbf{u},t)v'_{b(1,p')}(\mathbf{u}^m,\mathbf{u},t+1) \\ &+ u_{b(s,p),2}(t)v_{b(1,p)}(\mathbf{u}^m,\mathbf{u},t+1), \end{aligned} \tag{C8b}$$

where

$$\begin{aligned} V'_{i(s',p')}(\mathbf{u}^m,\mathbf{u},t+1) &= \Big[\omega^1_{(s,p)}(t)V_{k(s',p+\triangle p^1_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1) \\ &+ \omega^2_{(s,p)}V_{k(s',p+\triangle p^2_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1)\Big], \end{aligned} \tag{C9a}$$

$$\begin{aligned} v'_{i(s',p')}(\mathbf{u}^m,\mathbf{u},t+1) &= \Big[\omega^1_{(s,p)}(t)v_{k(s',p+\triangle p^1_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1) \\ &+ \omega^2_{(s,p)}v_{k(s',p+\triangle p^2_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1)\Big], \end{aligned} \tag{C9b}$$

are the inclusive and direct reproductive values of a focal female by joining a nest of type (s,p) at time t, given that she will become a type i individual ($i \in \{n(s',p'), b(s',p')\}$) in a nest of size s' and phase $p+\triangle p^1_{(s,p)}$ with probability $\omega^1_{(s,p)}(t)$ and phase $p+\triangle p^2_{(s,p)}$ with probability $\omega^2_{(s,p)}(t)$. In equation (C8) the first term is the reproductive value gained by becoming a subordinate if the dominant stays and survives, the second term is the reproductive value gained by becoming the dominant if the dominant stays and dies and the third term is the reproductive value gained by becoming the dominant if the dominant leaves the nest.

The reproductive value gained by a floater when joining a nest of size $s > 1$ is given by

$$\begin{aligned} V_{f(s,p),1}(\mathbf{u}^m,\mathbf{u},t+1) &= \textstyle\sum_{i=0}^{s-1} z^i_{(s,p)}\Big[\mu_{b(s,p)}(\mathbf{u},t)\frac{i}{i+1}V'_{n(i+1,p')}(s,p,t) \\ &+ \mu_{b(s,p)}(\mathbf{u},t)\frac{1}{i+1}V'_{b(i+1,p')}(s,p,t) \\ &+ (1-\mu_{b(s,p)}(\mathbf{u},t))V'_{n(i+2,p')}(s,p,t)\Big], \end{aligned} \tag{C10a}$$

$$\begin{aligned} v_{f(s,p),1}(\mathbf{u}^m,\mathbf{u},t+1) &= \textstyle\sum_{i=0}^{s-1} z^i_{(s,p)}\Big[\mu_{b(s,p)}(\mathbf{u},t)\frac{i}{i+1}v'_{n(i+1,p')}(s,p,t) \\ &+ \mu_{b(s,p)}(\mathbf{u},t)\frac{1}{i+1}v'_{b(i+1,p')}(s,p,t) \\ &+ (1-\mu_{b(s,p)}(\mathbf{u},t))v'_{n(i+2,p')}(s,p,t)\Big], \end{aligned} \tag{C10b}$$

where the first term is the reproductive value gained by becoming a subordinate if the dominant dies, the second term is the reproductive value gained by becoming the dominant if the dominant dies, and the third term is the reproductive value gained by becoming a subordinate if the dominant survives.

The reproductive value gained by deciding not to join the nest is equal to the reproductive value of floaters in the next time step, i.e.

$$V_{f(s,p),2}(\mathbf{u}^m,\mathbf{u},t) = V_f(\mathbf{u}^m,\mathbf{u},t+1), \tag{C11a}$$

$$v_{f(s,p),2}(\mathbf{u}^m, \mathbf{u}, t) = v_f(\mathbf{u}^m, \mathbf{u}, t+1). \tag{C11b}$$

Direct reproductive value of nests

Direct reproductive value of nests with only resident individuals

The number of offspring produced at final time $T-1$ in a nest of type (s,p) is

$$v_{(s,p)}(\mathbf{u}, T-1) = u_{b(s,p),1}(T-1) w_{(s,p)}(\mathbf{u}, T-1). \tag{C12}$$

The reproductive value of a nest of type (s,p), where $s = 0$ at time t is given by

$$v_{(0,p)}(\mathbf{u}, t) = \eta_{(s,p)} v_{(1,p)}(\mathbf{u}, t+1) + (1-\eta_{(s,p)}) v_{(0,p)}(\mathbf{u}, t+1). \tag{C13}$$

The reproductive value of a nest of type (s,p), where $s > 0$ at time t is given by

$$v_{(s,p)}(\mathbf{u}, t) = \sum_{\tau} u_{b(s,p),\tau}(t) v_{(s,p),\tau}(\mathbf{u}, t) \tag{C14}$$

where $v_{(s,p),\tau}(\mathbf{u}, t)$ is the reproductive value of a focal nest, given that the dominant female has chosen the action τ. The reproductive value of a nest, given that the dominant female stays in the focal nest, is

$$\begin{aligned}
v_{(s,p),1}(\mathbf{u}, t) &= w_{(s,p)}(\mathbf{u}, t) + \textstyle\sum_{i=0}^{s-1} z^i_{(s,p)} \\
&\times \Big\{ \eta_{(s,p)}(\mathbf{u}, t) \Big[(1 - \mu_{b(s,p)}(\mathbf{u}, t)) v'_{(i+2,p')}(\mathbf{u}, t) \\
&+ \mu_{b(s,p)}(\mathbf{u}, t) v'_{(i+1,p')}(\mathbf{u}, t) \Big] \\
&+ (1 - \eta_{(s,p)}(\mathbf{u}, t)) \Big[(1 - \mu_{b(s,p)}(\mathbf{u}, t)) v'_{(i+1,p')}(\mathbf{u}, t+1) \\
&+ \mu_{b(s,p)}(\mathbf{u}, t)) v'_{(i,p')}(\mathbf{u}, t) \Big] \Big\}.
\end{aligned} \tag{C15}$$

where

$$\begin{aligned}
v'_{(s',p')}(\mathbf{u}, t+1) &= \Big[\omega^1_{(s,p)}(t) v_{(s',p+\triangle p^1_{(s,p)})}(\mathbf{u}^m, \mathbf{u}, t+1) \\
&+ \omega^2_{(s,p)} v_{(s',p+\triangle p^2_{(s,p)})}(\mathbf{u}^m, \mathbf{u}, t+1)) \Big].
\end{aligned} \tag{C16}$$

In eq. (C15), the first term gives the number of offspring produced at time t, the second term gives the number of offspring produced in the future given that a floater joins the nest and the dominant survives, the third term gives the number of offspring produced in the future, given that a floater joins the nest and the dominant dies, the fourth term gives the number of offspring produced in the future given that no floater joins the nest and the dominant survives, the fifth term gives the number of offspring produced in the future given that no floater joins the nest and the dominant dies.

Similarly, the reproductive value of a nest, given that the dominant female leaves the focal nest, is (keeping in mind that the dominant can leave the nest only when there are no subordinates in the nest)

$$v_{(s,p),2}(\mathbf{u},t) = \eta_{(s,p)}(\mathbf{u},t)v_{(1,p)}(\mathbf{u},t+1) + (1-\eta_{(s,p)}(\mathbf{u},t))v_{(0,p)}(\mathbf{u},t+1), \tag{C17}$$

where the first term gives the reproductive value in the next time step, given that a floater joins the nest, and the second term gives the reproductive value of a nest given that a floater joins.

Direct reproductive value of a nest with a mutant dominant female

Dominants only exist in non-empty colonies ($s > 0$), so $v^m_{b(s,p)}(\mathbf{u}^m,\mathbf{u},t) = v_{(s,p)}(\mathbf{u}^m,\mathbf{u},t)$ if $s < 1$ for any time t. The number of offspring produced at final time $T-1$ in a nest of type (s,p) is

$$v^m_{b(s,p)}(\mathbf{u}^m,\mathbf{u},T-1) = u^m_{b(s,p),1}(T-1)w_{(s,p)}(\mathbf{u},T-1). \tag{C18}$$

The reproductive value of a nest of type (s,p) at time t and afterwards if given by

$$v^m_{b(s,p)}(\mathbf{u}^m,\mathbf{u},t) = \sum_\tau u^m_{b(s,p),\tau}(s,p,t)v^m_{b(s,p),\tau}(\mathbf{u}^m,\mathbf{u},t), \tag{C19}$$

where $v^m_{b(s,p),\tau}(\mathbf{u},t)$ is the reproductive value of a focal nest, given that the (mutant) dominant female has chosen the action τ. The reproductive value of a nest, given that the dominant female stays in the focal nest, is

$$\begin{aligned}
v^m_{b(s,p),1}(\mathbf{u},t) &= w_{(s,p)}(\mathbf{u},t) + \textstyle\sum_{i=0}^{s-1} z^i_{(s,p)} \\
&\times \Big\{\eta_{(s,p)}(\mathbf{u},t)\Big[(1-\mu_{b(s,p)}(\mathbf{u},t))v^{m'}_{b(i+2,p')}(\mathbf{u}^m,\mathbf{u},t) \\
&+ \mu_{b(s,p)}(\mathbf{u},t)v'_{(i+1,p')}(\mathbf{u}^m,\mathbf{u},t)\Big] \\
&+ (1-\eta_{(s,p)}(\mathbf{u},t))\Big[(1-\mu_{b(s,p)}(\mathbf{u},t))v^{m'}_{b(i+1,p')}(\mathbf{u}^m,\mathbf{u},t+1) \\
&+ \mu_b(s,p,t)v'_{(i,p')}(\mathbf{u}^m,\mathbf{u},t)\Big]\Big\},
\end{aligned} \tag{C20}$$

where

$$\begin{aligned}
v'_{(s',p')}(\mathbf{u},t+1) &= \Big[\omega^1_{(s,p)}(t)v^m_{b(s',p+\triangle p^1_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1) \\
&+ \omega^2_{(s,p)}v^m_{b(s',p+\triangle p^2_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1)\Big].
\end{aligned} \tag{C21}$$

In eq. (C20), the first term gives the number of offspring produced at time t, the second term gives the number of offspring produced in the future given that a floater joins the nest and the dominant survives, the third term gives the number of offspring produced in the future given that a floater joins the nest and the dominant dies, the fourth term gives the number of offspring produced in the future given that no floater joins the nest and the dominant survives, the fifth term gives the number of offspring produced in the future given that no floater joins the nest and the dominant dies.

Similarly, the reproductive value of a nest given that the dominant female leaves the focal colony is

$$v^m_{b(s,p),2}(\mathbf{u}, t) = v_{(s,p),2}(\mathbf{u}, t). \tag{C22}$$

Thus, if the mutant dominant female leaves the nest, then the reproductive value of the nest will depend only on the resident strategy.

Direct reproductive value of a nest with a mutant subordinate female

Subordinates only exist in colonies of size $s > 1$, so $v^m_{n(s,p)}(\mathbf{u}^m, \mathbf{u}, t) = v_{(s,p)}(\mathbf{u}^m, \mathbf{u}, t)$ if $s < 2$ for any time t. Next, we derive $v^m_{n(s,p)}(\mathbf{u}^m, \mathbf{u}, t)$, when $s > 1$. Since we have assumed the the dominant never leaves such nests, we have simplified the equations below by setting $u_{b(s,p),1} = 1$ and $u_{b(s,p),2} = 0$. Number of offspring produced at final time $T - 1$ in a nest of type (s, p) is

$$v^m_{n(s,p)}(\mathbf{u}^m, \mathbf{u}, T-1) = \sum_{\tau} u^m_{n(s,p),\tau}(T-1)\tilde{w}^{\tau}_{sp}(\mathbf{u}, T-1). \tag{C23}$$

The reproductive value of a nest of type (s, p) at time $t < T - 1$ is given by

$$v^m_{n(s,p)}(\mathbf{u}^m, \mathbf{u}, t) = \sum_{\tau} u^m_{n(s,p),\tau}(t) v^m_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t), \tag{C24}$$

where $v^m_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t)$ is the reproductive value of a focal nest given that the (mutant) subordinate female has chosen the action τ. The reproductive value of a nest, given that the subordinate has chosen the action $\tau \in \{1, 2, 3\}$, is

$$\begin{aligned} v^m_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t) &= \tilde{w}^{\tau}_{(s,p)}(\mathbf{u}, t) + \mu_{n,\tau}(t) v^{m,1}_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t) \\ &+ (1 - \mu_{n,\tau}(t)) v^{m,2}_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t), \end{aligned} \tag{C25}$$

where $v^{m,1}_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t)$ is the reproductive value of a focal colony given that the (mutant) subordinate dies at time t and $v^{m,2}_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t)$ is the reproductive value of a focal colony given that the (mutant) subordinate survives at time t. The reproductive value of a focal colony, given that the (mutant) subordinate dies at time t , is

$$\begin{aligned} v^{m,1}_{n(s,p),\tau}(\mathbf{u}^m,\mathbf{u},t) &= \textstyle\sum_{i=0}^{s-2} z^i_{(s-1,p)} \\ &\times \Big\{\eta_{(s,p)}(\mathbf{u},t)\Big[(1-\tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t))v'_{(i+2,\tilde{p}^{\tau'})}(\mathbf{u},t+1) \\ &+ \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t)v'_{(i+1,\tilde{p}^{\tau'})}(\mathbf{u},t+1)\Big] \\ &+ (1-\eta_{(s,p)}(\mathbf{u},t))\Big[(1-\tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t))v'_{(i+1,\tilde{p}^{\tau'})}(\mathbf{u},t+1) \\ &+ \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t)v'_{(i,\tilde{p}^{\tau'})}(\mathbf{u},t+1)\Big]\Big\}. \end{aligned} \tag{C26}$$

where i is the number of subordinates that stay and survive in the focal nest at time t, and

$$\begin{aligned} v'_{(s',\tilde{p}^{\tau'})}(\mathbf{u},t+1) &= \Big[\omega^1_{(s,p)}(t)v_{(s',p+\triangle\tilde{p}^1_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1) \\ &+ \omega^2_{(s,p)}v_{(s',p+\triangle\tilde{p}^2_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1)\Big], \end{aligned} \tag{C27}$$

is the reproductive value of the nest in the next time step, given that the nest will be of size s' and phase $p+\triangle p^1_{(s,p)}$ with probability $\omega^1_{(s,p)}(t)$ and phase $p+\triangle p^2_{(s,p)}$ with probability $\omega^2_{(s,p)}(t)$.

In eq. (C26), the first term gives the number of offspring produced in the future given that a floater joins the nest and the dominant survives, the second term gives the number of offspring produced in the future given that a floater joins the nest and the dominant dies, the third term gives the number of offspring produced in the future given that no floater joins the nest and the dominant survives, the fourth term gives the number of offspring produced in the future given that no floater joins the nest and the dominant dies.

The reproductive value of a focal colony given that the (mutant) subordinate survives at time t is

$$\begin{aligned} v^{m,2}_{n(s,p),\tau}(\mathbf{u}^m,\mathbf{u},t) &= \textstyle\sum_{i=0}^{s-2} z^i_{(s-1,p)}\Big\{\eta_{(s,p)}(\mathbf{u},t) \\ &\times \Big\{(1-\tilde{\mu}^{\tau}_{d(s,p)}(\mathbf{u},t))v^{m'}_{n(i+3,\tilde{p}^{\tau'})}(\mathbf{u}^m,\mathbf{u},t) \\ &+ \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t) \\ &\times \Big[\tfrac{1}{i+2}v^{m'}_{b(i+2,\tilde{p}^{\tau'})}(\mathbf{u}^m,\mathbf{u},t)+\tfrac{i+1}{i+2}v^{m'}_{n(i+2,\tilde{p}^{\tau'})}(\mathbf{u}^m,\mathbf{u},t)\Big]\Big\} \\ &+ (1-\eta_{(s,p)}(\mathbf{u},t)) \\ &\times \Big\{(1-\tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t))v^{m'}_{n(i+2,\tilde{p}^{\tau'})}(\mathbf{u}^m,\mathbf{u},t+1) \\ &+ \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u},t) \\ &\times \Big[\tfrac{1}{i+1}v^{m'}_{b(i+1,\tilde{p}^{\tau'})}(\mathbf{u}^m,\mathbf{u},t)+\tfrac{i}{i+1}v^{m'}_{n(i+1,\tilde{p}^{\tau'})}(\mathbf{u}^m,\mathbf{u},t)\Big]\Big\}\Big\}. \end{aligned} \tag{C28}$$

where

$$
\begin{aligned}
v^{m'}_{i(s',\tilde{p}^{\tau'})}(\mathbf{u},t+1) &= \Big[\omega^1_{(s,p)}(t)v^m_{i(s',p+\triangle\tilde{p}^1_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1) \\
&+ \omega^2_{(s,p)}v^m_{i(s',p+\triangle\tilde{p}^2_{(s,p)})}(\mathbf{u}^m,\mathbf{u},t+1)\Big],
\end{aligned}
\tag{C29}
$$

is the reproductive value of the nest in the next time step, where the focal mutant female will be of type i ($i \in \{b,n\}$) in that nest and the nest will be of size s' and phase $p+\triangle p^1_{(s,p)}$ with probability $\omega^1_{(s,p)}(t)$ and phase $p+\triangle p^2_{(s,p)}$ with probability $\omega^2_{(s,p)}(t)$. In eq. (C28) the first term gives the number of offspring produced in the future given that a floater joins the nest and the dominant survives, the second term gives the number of offspring produced in the future given that a floater joins the nest and the dominant dies, the third term gives the number of offspring produced in the future given that no floater joins the nest and the dominant survives, the fourth term gives the number of offspring produced in the future given that no floater joins the nest and the dominant dies.

The reproductive value of a nest, given that the mutant subordinate female leaves the focal nest, is

$$
v^m_{n(s,p),4}(\mathbf{u},t) = v_{(s-1,p)}(\mathbf{u},t). \tag{C30}
$$

Note that if the mutant subordinate female leaves the nest, then the reproductive value of the nest will depend only on the resident strategy.

Direct reproductive value gained by a mutant dominant from the focal nest site

Note that, since dominants only exist in nests of size $s > 0$, we have $v_{b(0,p)}(\mathbf{u}^m,\mathbf{u},t) = 0$ for any $p \in [0,P]$ and $t \in [0,T-1]$. The direct reproductive value that the dominant gains in a nest of type (s,p) at time t is given by

$$
v_{b(s,p)}(\mathbf{u}^m,\mathbf{u},t) = \sum_{\tau} u^m_{b(s,p),\tau} v_{b(s,p),\tau}(\mathbf{u}^m,\mathbf{u},t), \tag{C31}
$$

where the direct reproductive value gained by choosing to stay at the nest is

$$
\begin{aligned}
v_{b(s,p),1}(\mathbf{u}^m,\mathbf{u},t) &= w_{(s,p)}(\mathbf{u},t) \\
&+ (1-\mu_{b(s,p)}(\mathbf{u},t))\textstyle\sum_{i=0}^{s-1} z^i_{(s,p)}\Big[\eta_{(s,p)}(t)v'_{b(i+2,p')}(\mathbf{u}^m,\mathbf{u},t+1) \\
&+ (1-\eta_{(s,p)}(t))v'_{b(i+1,p')}(\mathbf{u}^m,\mathbf{u},t+1)\Big],
\end{aligned}
\tag{C32}
$$

where the first term gives the direct fitness gained at time t, the second term gives the direct fitness gained in the future provided that that the dominant survives and a floater joins the nest, and the third term gives the direct fitness gained in the future provided that that the dominant survives and no floater joins.

The reproductive value gained by choosing to leave the nest is

$$v_{b(s,p),2}(\mathbf{u}^m, \mathbf{u}, t) = 0. \tag{C33}$$

Inclusive reproductive value of a mutant dominant female gained by leaving the focal nest site

At final time

$$V^{\circ}_{b(s,p)}(\mathbf{u}^m, \mathbf{u}, T-1) = 0. \tag{C34}$$

Similarly, as before, since dominants only exist in nests of size $s > 0$, we have $V^{\circ}_{b(s,p)}(\mathbf{u}^m, \mathbf{u}, t) = 0$ for any $p \in [0, P]$ and $t \in [0, T-1]$. Direct reproductive value that the dominant gains in a nest of type (s, p) at time t is given by

$$V^{\circ}_{b(s,p)}(\mathbf{u}^m, \mathbf{u}, t) = \sum_{\tau} u^m_{b(s,p),\tau} V^{\circ}_{b(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t), \tag{C35}$$

$$\begin{aligned} V^{\circ}_{b(s,p),1}(\mathbf{u}^m, \mathbf{u}, t) &= (1 - \mu_{b(s,p)}(t)) \textstyle\sum_{i=0}^{s-1} z^i_{(s,p)} \Big[\eta_{(s,p)}(t) V^{\circ\prime}_{b(i+2,p')}(\mathbf{u}^m, \mathbf{u}, t+1) \\ &+ (1 - \eta_{(s,p)}(t)) V^{\circ\prime}_{b(i+1,p')}(\mathbf{u}^m, \mathbf{u}, t+1)\Big], \end{aligned} \tag{C36}$$

$$V^{\circ}_{b(s,p),2}(\mathbf{u}^m, \mathbf{u}, t) = (1 - \mu_{b(s,p)}(\mathbf{u}, t)) V_f(\mathbf{u}^m, \mathbf{u}, t+1). \tag{C37}$$

Direct reproductive value gained by a mutant subordinate from the focal nest site

The number of offspring produced at final time $T-1$ by a subordinate female in a nest of type (s, p) is

$$v_{n(s,p)}(T-1) = 0. \tag{C38}$$

Note that, since subordinates only exist in nests of size $s > 1$, we define $v_{n(s,p)}(s \leq 1, p, t) = 0$ for any $p \in [0, P]$ and $t \in [0, T-1]$. The direct reproductive value of a subordinate in a nest of type $(s > 1, p)$ at time t is

$$v_{n(s,p)}(\mathbf{u}^m, \mathbf{u}, t) = \sum_{\tau} u_{n(s,p),\tau}(t) v_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t). \tag{C39}$$

The reproductive value gained by choosing an action $\tau \in \{1, 2, 3\}$ is given by

$$\begin{aligned} v_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t) &= (1 - \mu_{n,\tau}(\mathbf{u}, t)) \textstyle\sum_{i=0}^{s-2} z^i_{(s-1,p)}(\mathbf{u}, t) \\ &\times \Big\{ \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t) \eta_{(s,p)}(t) \\ &\times \Big[\tfrac{1}{i+2} v'_{b(i+2,\tilde{p}^{\tau'})}(\mathbf{u}^m, \mathbf{u}, t+1) + \tfrac{i+1}{i+2} v'_{n(i+2,\tilde{p}^{\tau'})}(\mathbf{u}^m, \mathbf{u}, t+1) \Big] \\ &+ \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t)(1 - \eta_{(s,p)}(t)) \\ &\times \Big[\tfrac{1}{i+1} v'_{b(i+1,\tilde{p}^{\tau'})}(\mathbf{u}^m, \mathbf{u}, t+1) + \tfrac{i}{i+1} v'_{n(i+1,\tilde{p}^{\tau'})}(\mathbf{u}^m, \mathbf{u}, t+1) \Big] \\ &+ (1 - \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t) \eta_{(s,p)}(t) v'_{n(i+1,\tilde{p}^{\tau'})}(\mathbf{u}^m, \mathbf{u}, t+1) \\ &+ (1 - \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t))(1 - \eta_{(s,p)}(t)) v'_{n(i,\tilde{p}^{\tau'})}(\mathbf{u}^m, \mathbf{u}, t+1) \Big\}, \end{aligned} \tag{C40}$$

where the first term (second and third line) gives the number of offspring produced in the future given that the dominant dies and a floater joins the nest and the subordinate either becomes the dominant or stays a subordinate,the second term (fourth and fifth line) gives the number of offspring produced in the future given that the dominant dies and no floater joins the nest and the subordinate either becomes the dominant or stays a subordinate, the third term (sixth line) gives the number of offspring produced in the future given that the dominant survives and a floater joins the nest and the subordinate stays a subordinate, the fourth term (seventh line) gives the number of offspring produced in the future given that the dominant survives and no floater joins the nest and the subordinate stays a subordinate.

The reproductive value gained by choosing to leave the nest is

$$v_{n(s,p),4}(\mathbf{u}^m, \mathbf{u}, t) = 0. \tag{C41}$$

Inclusive reproductive value of a mutant subordinate female gained by leaving the focal nest site

At final time

$$V^{\circ}_{n(s,p)}(\mathbf{u}^m, \mathbf{u}, T-1) = 0. \tag{C42}$$

Similarly as before, since subordinates only exist in nests of size $s > 1$, we define $V^{\circ}_{n(s,p)}(s \leq 1, p, t) = 0$ for any $p \in [0, P]$ and $t \in [0, T-1]$. The direct reproductive value that the subordinate gains in a nest of type (s, p) at time t is given by

$$V^{\circ}_{n(s,p)}(\mathbf{u}^m, \mathbf{u}, t) = \sum_{\tau} u^m_{n(s,p),\tau} V^{\circ}_{n(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t), \tag{C43}$$

where for $\tau \in \{1, 2, 3\}$

$$\begin{array}{rcl}
V^{\circ}_{b(s,p),\tau}(\mathbf{u}^m, \mathbf{u}, t) & = & (1 - \mu_{n,\tau}(\mathbf{u}, t)) \sum_{i=0}^{s-2} z^i_{(s-1,p)}(\mathbf{u}, t) \\
& \times & \Big\{ \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t) \eta_{(s,p)}(t) \\
& \times & \Big[\frac{1}{i+2} V^{\circ\prime}_{b(i+2,\tilde{p}^{\tau\prime})}(\mathbf{u}^m, \mathbf{u}, t+1) + \frac{i+1}{i+2} V^{\circ\prime}_{n(i+2,\tilde{p}^{\tau\prime})}(\mathbf{u}^m, \mathbf{u}, t+1) \Big] \\
& + & \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t)(1 - \eta_{(s,p)}(t)) \\
& \times & \Big[\frac{1}{i+1} V^{\circ\prime}_{b(i+1,\tilde{p}^{\tau\prime})}(\mathbf{u}^m, \mathbf{u}, t+1) \frac{i}{i+1} V^{\circ\prime}_{n(i+1,\tilde{p}^{\tau\prime})}(\mathbf{u}^m, \mathbf{u}, t+1) \Big] \\
& + & (1 - \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t) \eta_{(s,p)}(t) V^{\circ\prime}_{n(i+3,\tilde{p}^{\tau\prime})}(\mathbf{u}^m, \mathbf{u}, t+1) \\
& + & (1 - \tilde{\mu}^{\tau}_{b(s,p)}(\mathbf{u}, t))(1 - \eta_{(s,p)}(t)) V^{\circ\prime}_{n(i+2,\tilde{p}^{\tau\prime})}(\mathbf{u}^m, \mathbf{u}, t+1) \Big\},
\end{array} \tag{C44}$$

where the first term (second and third line) gives the inclusive reproductive value of leaving in the future given that the dominant dies and a floater joins the nest and the subordinate either becomes the dominant or stays a subordinate, the second term (fourth and fifth line) gives the inclusive reproductive value of leaving in the future given that the dominant dies and no floater joins the nest and the subordinate either becomes the dominant or stays a subordinate, the third term (sixth line) gives the inclusive reproductive value of leaving in the future given that the dominant survives and a floater joins the nest and the subordinate stays a subordinate, the fourth term (seventh line) gives the inclusive reproductive value of leaving in the future given that the dominant survives and no floater joins the nest and the subordinate stays a subordinate. If the subordinate chooses the action for $\tau = 4$ then

$$V^{\circ}_{n(s,p),4}(\mathbf{u}^m, \mathbf{u}, t) = (1 - \mu_{n,4}) V_f(\mathbf{u}^m, \mathbf{u}, t+1). \tag{C45}$$

APPENDIX D: RESULTS FOR MAXIMUM NEST SIZE OF *S*=*3*

Here, we show the results of our model if we allow the formation of larger nest sizes. We see from figs. D1 and D2 that co-foundress associations and helping can evolve also if we relax the condition for a small group size. We also observe that the behavioural tendencies (see figs. D2-D5) of the subordinates also depend on the group's size and the group size effect also depends on other factors, such as relatedness. The analysis of the group size effects needs to be studied in much more detail. The modelling approach presented here gives a basic framework to model state-dependent decision making of cooperatively breeding social systems and in this paper we have only begun to scratch the surface of what new insights this approach will give.

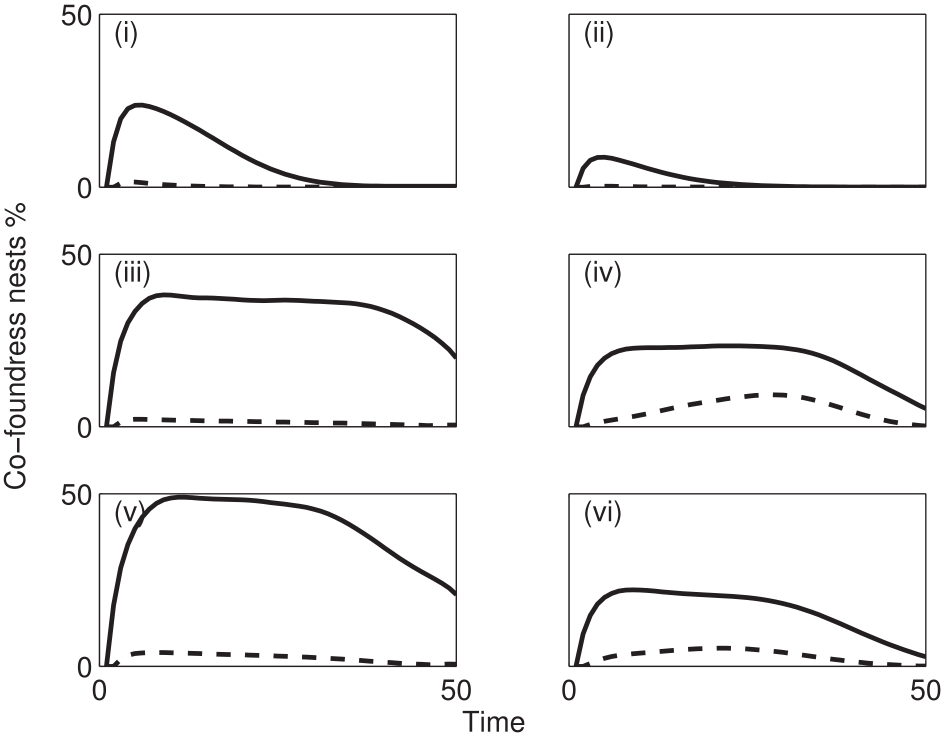

Figure D1: Percentage of co-foundress nests in three different populations for varying levels of average relatedness between co-foundresses. Nests of size $s = 2$ (solid lines), nests of size $s = 3$ (dashed lines). We have modelled three types of populations: (i) $r = 0.75$, $P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (ii) $r = 0$, $P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (iii) $r = 0.75$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) ; (iv) $r = 0$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (v) $r = 0.75$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$); (vi) $r = 0$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

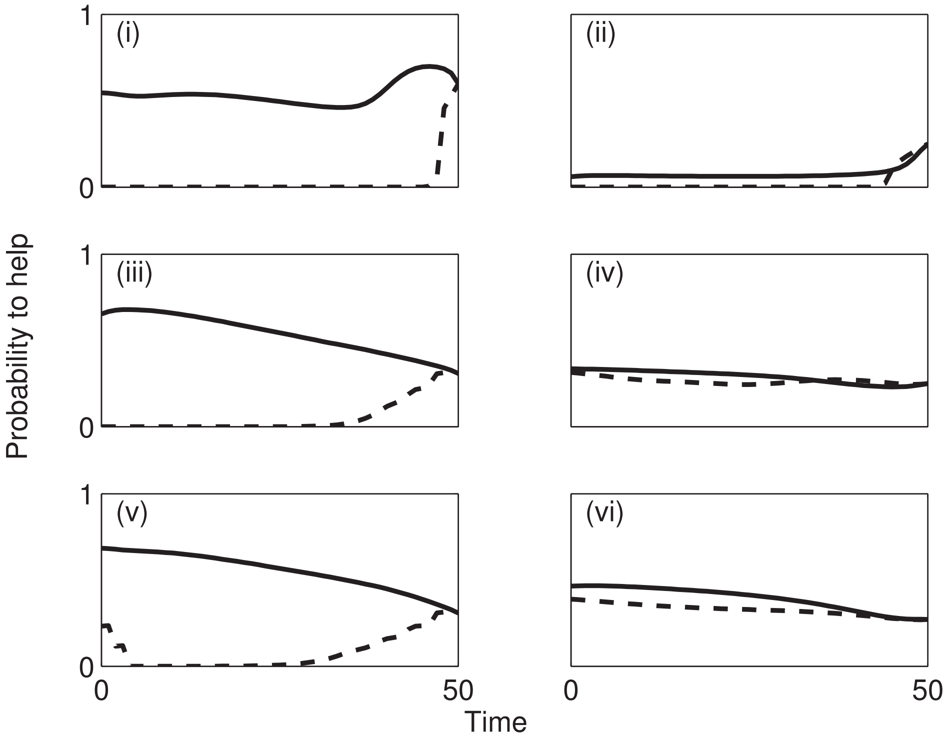

Figure D2: Evolutionarily stable probability of subordinates to help ($u^*_{n(s,p),1}(t)$). The probabilities have been averaged over different nest phases. Nests of size $s = 2$ (solid lines), nests of size $s = 3$ (dashed lines). We have modelled three types of populations: (i) $r = 0.75$, $P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (ii) $r = 0$, $P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (iii) $r = 0.75$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) ; (iv) $r = 0$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (v) $r = 0.75$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$); (vi) $r = 0$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

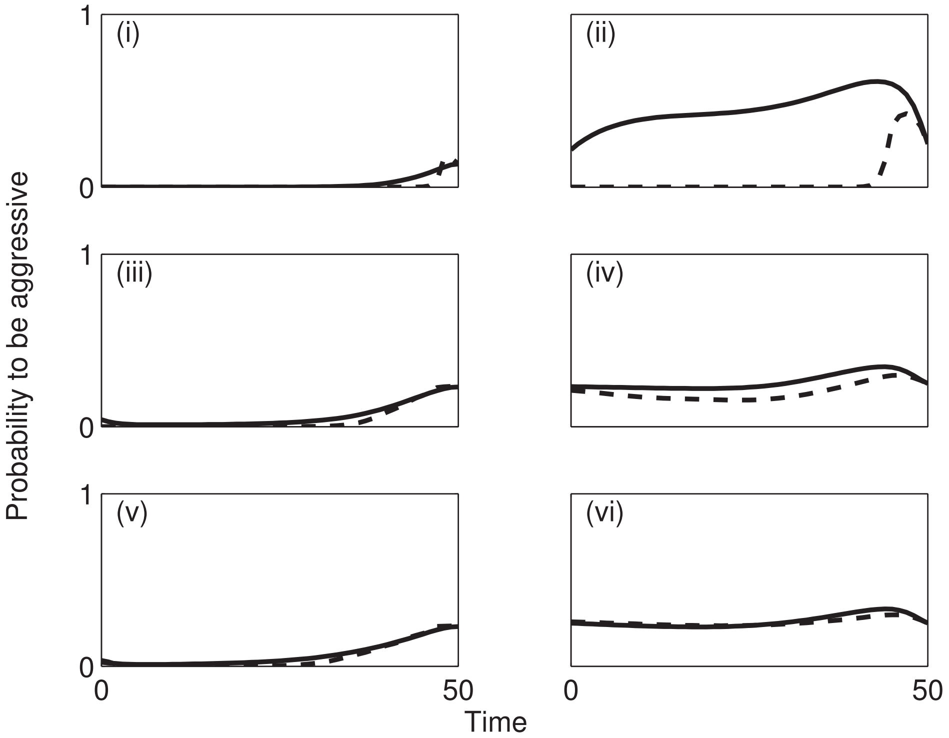

Figure D3: Evolutionarily stable probability of subordinates to be aggressive ($u^*_{n(s,p),2}(t)$). The probabilities have been averaged over different nest phases. Nests of size $s = 2$ (solid lines), nests of size $s = 3$ (dashed lines). We have modelled three types of populations: (i) $r = 0.75, P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (ii) $r = 0, P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (iii) $r = 0.75$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) ; (iv) $r = 0, P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (v) $r = 0.75$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$); (vi) $r = 0$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

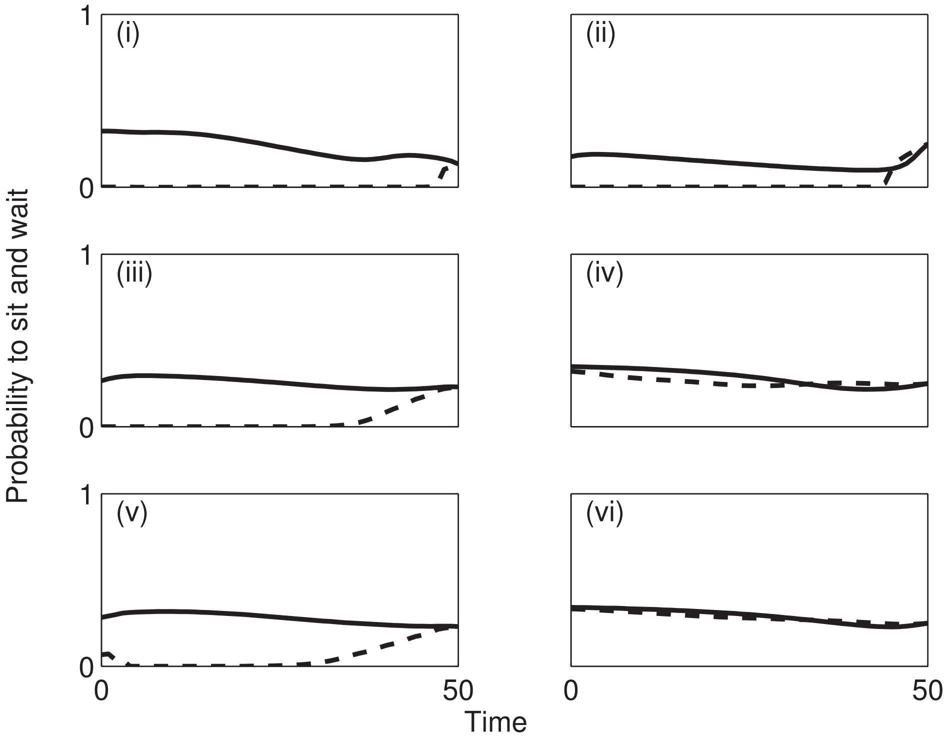

Figure D4: Evolutionarily stable probability of subordinates to sit and wait ($u^*_{n(s,p),3}(t)$). The probabilities have been averaged over different nest phases. Nests of size $s = 2$ (solid lines), nests of size $s = 3$ (dashed lines). We have modelled three types of populations: (i) $r = 0.75, P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (ii) $r = 0, P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (iii) $r = 0.75$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) ; (iv) $r = 0, P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (v) $r = 0.75$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$); (vi) $r = 0$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.

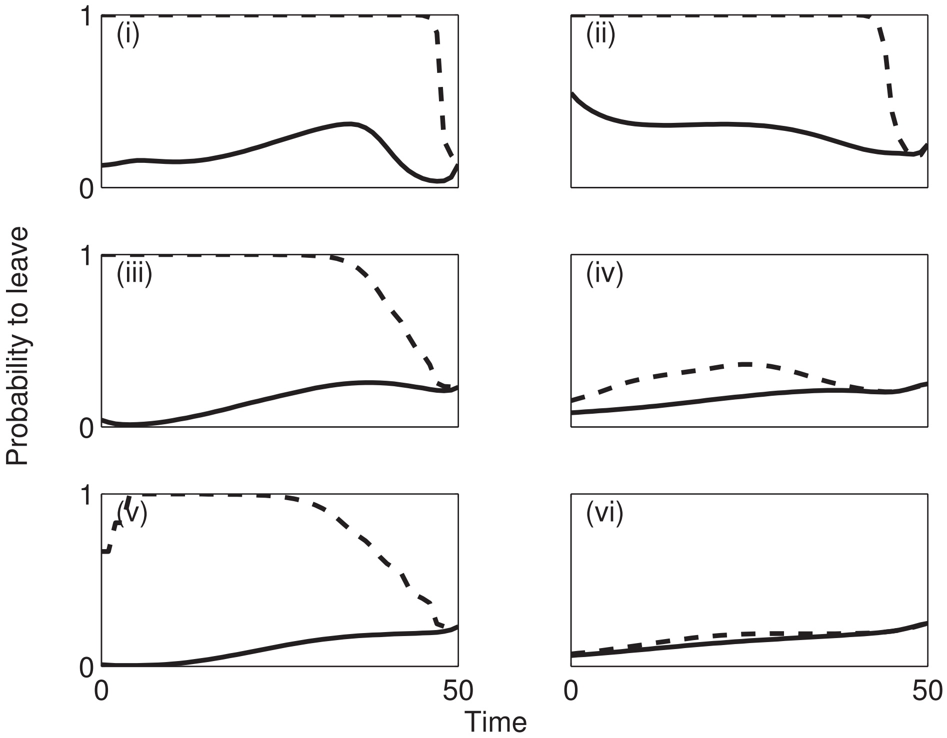

Figure D5: Evolutionarily stable probability of subordinates to leave ($u^*_{n(s,p),4}(t)$). The probabilities have been averaged over different nest phases. Nests of size $s = 2$ (solid lines), nests of size $s = 3$ (dashed lines). We have modelled three types of populations: (i) $r = 0.75$, $P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (ii) $r = 0$, $P = 0$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (iii) $r = 0.75$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$) ; (iv) $r = 0$, $P = 5$, solitary foundresses are just as likely to die as dominants and helpful subordinates in co-foundress nests ($\mu_s = \mu_{b0} = \mu_{n,1} = 0.04$); (v) $r = 0.75$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$); (vi) $r = 0$, $P = 5$, solitary foundresses are three times more likely to die than dominants and helpful subordinates in co-foundress nests ($\mu_s = 0.12$, $\mu_{b0} = \mu_{n,1} = 0.04$). Other parameter values: $r_0 = 0.01$, $S = 2$, $h = 1$, $a = 0.1$, $\mu_f = 0.01$, $\mu_{n,2} = 0.04$, $\mu_{n,3} = 0.01$, $\mu_{n,4} = 0.01$, $\alpha_0 = 0.3$, $M = 1.7$, $N = 1000$, $x_f(0) = 1000$, $\epsilon = 1$, $\delta = 0.05$.