Sex allocation conflict and sexual selection throughout the lifespan of eusocial colonies

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Abstract

Models of sex allocation conflict are central to evolutionary biology but have mostly assumed static decisions, where resource allocation strategies are constant over colony lifespan. Here, we develop a model to study how the evolution on dynamic resource allocation strategies is affected by the queen-worker conflict in annual eusocial insects. We demonstrate that the time of dispersal of sexuals affects the sex allocation ratio through sexual selection on males. Furthermore, our model provides three predictions that depart from established results of classic static allocation models. First, we find that the queen wins the sex allocation conflict, while the workers determine the maximum colony size and colony productivity. Second, male-biased sex allocation and protandry evolve if sexuals disperse directly after eclosion. Third, when workers are more related to new queens, then the proportional investment into queens is expected to be lower, which results from the interacting effect of sexual selection (selecting for protandry) and sex allocation conflict (selecting for earlier switch to producing sexuals). Overall, we find that colony ontogeny crucially affects the outcome of sex-allocation conflict because of the evolution of distinct colony growth phases, which decouples how queens and workers affect allocation decisions and can result in asymmetric control.

Keywords: life-history strategy, social insects, sex allocation, conflict, optimal resource allocation.

Introduction

Eusocial Hymenopteran colonies (e.g. ants, bees and wasps) may superficially appear to function as single organisms, where queens and workers could be viewed as the germinal and somatic tissues of multicellular organisms (Macevicz and Oster, 1976). However, individuals are usually not clonal in such colonies, whereby some genes, for instance those influencing sex allocation or reproductive ability of workers, can experience diverging selection pressures in different individuals (Haig, 2003; Ratnieks et al., 2006).

One of the most intensively studied genetic conflicts in eusocial Hymenoptera is the queen-worker conflict over sex allocation. In an outbred haplodiploid population where each colony is headed by a singly-mated queen, natural selection on resource allocation strategies favors alleles in queens that code for equal resource allocation to males and (sexual) females and alleles in workers that code for a 3:1 (sexual females to males) allocation ratio (Frank, 1998; Trivers and Hare, 1976; West, 2009). Factors such as multiple related queens per colony, multiple matings by the queen, and worker production of males, reduce the extent of the genetic conflict over sex allocation because they reduce the relatedness asymmetries between individuals within colonies (Ratnieks et al., 2006).

The long-term evolutionary "outcome" of the sex allocation conflict–the uninvadable resource allocation schedule–is determined by the mechanisms through which the two opposing "parties" can influence how colony resources are allocated into producing individuals of different types. These two parties are the genes in the workers and the genes in the colony-founding queen. The genetic control over the resource allocation decisions can be achieved through different genetic, behavioural, and physiological processes (Beekman and Ratnieks, 2003; Helanterä and Ratnieks, 2009; Mehdiabadi et al., 2003). Hereinafter, if one party fully determines a given resource allocation trait, then this party is said to be "in control" of that trait (here, "in control" has a related but more restricted meaning than "having power" as in e.g. Beekman and Ratnieks, 2003). In general, there are strong reasons to expect that the genes in the queen and the workers simultaneously control different resource allocation decisions (Bourke and Franks, 1995; Helanterä and Ratnieks, 2009; Trivers and Hare, 1976). Furthermore, it is often considered most likely that the genes in the queen determine the primary sex allocation

ratio (allocation of resources to females versus males) and the workers control the developmental fate of the female eggs (Bourke and Franks, 1995; Helanterä and Ratnieks, 2009; Trivers and Hare, 1976). Hereinafter, we refer to this scenario as "mixed control".

Theoretical models of resource allocation decisions with sex allocation conflict in eusocial insects provide three important insights into fundamental questions in evolutionary biology (e.g. Bourke and Chan, 1999; Bourke and Ratnieks, 1999; Pamilo, 1991a; Pen and Taylor, 2005; Reuter et al., 2004; Reuter and Keller, 2001). Firstly, they provide clear predictions that allow to test how relatedness affects selection on social traits (Crozier and Pamilo, 1996). Secondly, they allow to determine which party is in control of the underlying resource allocation decisions. Thirdly, they enable to predict to what extent the conflicts can be "resolved" (sensu Ratnieks et al., 2006, i.e. conflict outcome with modest colony-level costs) under various assumptions about the mechanisms of genetic control over the resource allocation decisions. However, all of the aforementioned models consider static allocation decisions without explicitly taking colony ontogeny into account. Nevertheless, it is known that many annual eusocial insect species (e.g. vespid wasps, bumble bees, and sweat bees) grow in two distinct phases (see references in Mitesser et al. (2007a), Crone and Williams (2016)). Such that, in the beginning of the season only workers are produced (the ergonomic phase) followed by a drastic shift into exclusive production of sexuals (the reproductive phase). This life-history schedule was shown to be the evolutionary outcome in annual eusocial colonies by Macevicz and Oster (1976) assuming clonal reproduction. However, only a few theoretical studies (Bulmer, 1981; Ohtsuki and Tsuji, 2009) have considered a sexually reproducing species (thereby including the possibility of genetic conflicts) and time-dependent resource allocation decisions in the context of colony life-history. The importance of colony ontogeny in studying within-colony conflict was demonstrated by Ohtsuki and Tsuji (2009) who showed (in the context of worker policing) that the extent of the potential conflict depends on the phase of colony ontogeny.

In his seminal work, Bulmer (1981) showed using a dynamic allocation model (i.e., time-dependent decisions) that the sex allocation conflict can have a detrimental effect on colony productivity (sexual biomass) under mixed control since relatively few resources are allocated into producing workers. Indeed, he predicted that the production of workers is expected to halt earlier under mixed control, but he did not consider the entire

colony ontogeny, since he only included two discrete generations of colony growth at the end of the season and his predictions relied on some additional restrictive assumptions. For example, he assumed that the worker generations do not overlap (workers only survive one generation) and that the sexuals can only mate at the very end of the season. Hence, the theoretical understanding of the life-history decisions of eusocial colonies has mostly relied on the assumption that the reproduction is clonal and genetic conflicts do not occur (Macevicz and Oster, 1976; Mitesser et al., 2007a).

The importance of considering dynamic resource allocation decisions for studying within-colony conflict is demonstrated by the fact that the static and dynamic resource allocation models can make contradicting predictions about which party wins the sex allocation conflict under mixed control (Bulmer, 1981; Reuter and Keller, 2001). Indeed, the static resource allocation model by Reuter and Keller (2001) predicts a sex allocation ratio under mixed control that is intermediate between the evolutionary prediction corresponding to full worker and full queen control. In contrast, Bulmer's (1981) dynamic model predicts that the queen wins the sex allocation conflict by laying only haploid eggs at the penultimate generation causing the colony to die one generation before the end of the season if the sex allocation ratio in the population is female-biased. However, the generality of Bulmer's predictions are limited due to the aforementioned restrictive assumptions of his model.

Furthermore, in another study assuming full queen control of resource allocation traits and the possibility of sexuals to mate before the end of the season, Bulmer (1983) showed that sexual selection on males will lead to protandry (males being produced before sexual females) if mating can occur over some period of time (i.e. nuptial flights are not highly synchronized). Indeed, sexual selection may thus play an important role for colony ontogeny, since protandry is ubiquitous among many annual eusocial insects, e.g. in paper wasps and bumble bees (Bourke, 1997; Strassmann and Hughes, 1986). Evolution of protandry however contradicts the earlier model by Bulmer (1981) for mixed control, since it predicted that males are produced in the very end of the season. Hence, there are no theoretical predictions for time-dependent colony resource allocation decisions and conflicts under mixed control, where individuals can mate over a finite period of time during the season with sexual selection occurring throughout.

In this paper, we address the limitations of previous studies by developing a dynamic resource allocation

model where we consider three alternative scenarios of genetic control of resource allocation decisions: full queen control, full worker control, and mixed control; and two alternative scenarios of dispersal of sexuals: delayed dispersal (all sexuals simultaneously disperse at the end of the season to mate) and direct dispersal (sexuals disperse immediately after eclosion to mate). In light of previous work, the purpose of this paper is to address the following questions: (i) How does conflict affect colony growth? (ii) How does sexual selection affect the order at which sexuals are produced? (iii) Which party wins the sex allocation conflict for different scenarios of dispersal of sexuals?

Model

Biological scenario

Life-cycle

We consider a seasonal population of haplodiploid eusocial insects consisting of a constant number (n) of colonies or breeding sites each occupied by a mated 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 the season of total length T, each queen occupying one of the n breeding sites initiates a colony that can grow throughout the season, and where workers, males, and new queens can be produced; we consider three scenarios of genetic control over the allocation decisions. (2) *Dispersal*: We assume that sexuals (juvenile queens and males) fully disperse out of their natal colony, such that no inbreeding, local mate competition, or local resource competition takes place, and consider two alternative scenarios of dispersal (to be detailed below). (3) *Mating*: random mating occurs and all queens mate exactly with $M \geq 1$ males. (4) *Regulation*: individuals of the parental generation and workers die and juvenile queens randomly compete for the n breeding slots to form the next generation of adults.

Dispersal and mating

The two scenarios of dispersal of the sexuals that we consider are as follows: (i) delayed dispersal, where sexuals all disperse at the same time at the end of the season (at time $t = T$), and (ii) direct dispersal, where sexuals disperse immediately after being produced. Females mate immediately with M males in the mating pool after which they will exit the mating pool. In contrast, males continue on mating until they die. Hence, the mating success of a male depends on his mortality rate and the availability of mating females. In order to gain fitness, females have to survive until the end of the season, while males have to inseminate females who survive until the end of the season.

Colony growth and production of sexuals

We model explicitly colony population dynamics during stage (1) of the life cycle. The size of a focal colony at time $t \in [0, T]$ is $y_{\mathrm{w}}(t)$, which gives the number of sterile workers (including the colony founding queen, who has been counted as a worker) in the colony at time t. In addition, by time t, the colony has produced $y_{\mathrm{q}}(t)$ surviving (juvenile) queens and $y_{\mathrm{m}}(t)$ surviving (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. We have resorted to this assumption for simplicity, since it allows to equate the investment allocation ratio to the numerical sex ratio and hence simplifies calculations. However, the assumption of equal production cost has no fundamental effect on the evolutionary process, since selection acts only on total investment in the sexes and not on their numbers and hence is independent of the production costs of different individuals (West, 2009).

Workers acquire resources from the environment to produce offspring. Let b denote the individual productivity rate of a worker (i.e. the net rate at which a worker acquires resources for the colony, measured in individuals produced per unit time). For simplicity, we assume that the availability of resources in the environment is constant over time and the rate at which resources are acquired scales linearly with the colony size (i.e. b is constant). The latter assumption implies that there are enough resources in the environment to sustain

constant per-worker rate of resource acquisition and the egg-laying rate of the queen is constrained only by the resources available to the colony.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 laying eggs.

The number $y_k(t)$ of type $k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$ individuals alive at time t that were produced in the focal colony is assumed to change according to

$$\frac{\mathrm{d}y_k(t)}{\mathrm{d}t} = ba_k(t)y_{\mathrm{w}}(t) - \mu_k y_k(t),\ y_k(0) = y_{k,0}, \tag{1}$$

where $a_k(t)$ 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 $y_{k,0}$ is the 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 $y_{\mathrm{w},0} = 1$ (since the colony founding queen is counted as a worker), $y_{\mathrm{q},0} = 0$ (no juvenile queens), and $y_{\mathrm{m},0} = 0$ (no juvenile males). Note that the number of juvenile queens $y_{\mathrm{q}}(t)$ and males $y_{\mathrm{m}}(t)$ are counted regardless if they have dispersed from the colony or not.

It will turn out to be useful to keep track of the number of queens that the males from a focal colony have inseminated. Let $y_{\mathrm{iq}}(t)$ be the expected number of females alive at time t, who have been inseminated by males from a focal colony, given that females mate only once (i.e. under a monandrous mating system, $M = 1$) and it changes according to

$$\frac{\mathrm{d}y_{\mathrm{iq}}(t)}{\mathrm{d}t} = \begin{cases} 0,\ \text{for } t < T,\ \text{with } y_{\mathrm{iq}}(T) = y_{\mathrm{m}}(T)\frac{y_{\mathrm{q}}(T)}{y_{\mathrm{m}}(T)} & \text{(delayed dispersal)}, \\ y_{\mathrm{m}}(t)\frac{ba_{\mathrm{q}}(t)y_{\mathrm{w}}(t)}{y_{\mathrm{m}}(t)} - \mu_{\mathrm{q}}y_{\mathrm{iq}}(t),\ y_{\mathrm{iq}}(0) = 0 & \text{(direct dispersal)}. \end{cases} \tag{2}$$

The number of females inseminated by sons in eq. (2) depends on the assumption about the time of dispersal of sexuals. Under delayed dispersal, all females are inseminated at time $t = T$, where a total number of $ny_{\mathrm{m}}(T)$ males compete for the $ny_{\mathrm{q}}(T)$ females. Hence the mating success of a male produced in a focal colony is $y_{\mathrm{q}}(T)/y_{\mathrm{m}}(T)$. Under direct dispersal, females are assumed to mate immediately after being produced. Hence,

at time t a total number of $nba_{\mathrm{q}}(t)y_{\mathrm{w}}(t)$ of females are available to mate, after which they will leave the mating pool. The males are assumed to stay in the mating pool, hence at time t, an average number of $ny_{\mathrm{m}}(t)$ males compete for the access to females. Hence, the mating success at time t of a male produced in a focal colony is $ba_{\mathrm{q}}(t)y_{\mathrm{q}}(t)/y_{\mathrm{m}}(t)$ and the last term in the second line of eq. (2) takes into account the mortality of the inseminated females. If females mate M times, then there are on average M times more matings available to males at any given time. Hence, the number of (surviving) females at time t, who have been inseminated by males from a focal colony is $My_{\mathrm{iq}}(t)$ in a population where females mate M times.

Evolving phenotypes

Here, we specify the evolving traits for which we will perform the evolutionary analysis. We assume that the allocation schedule, $a_k(t)$ ($k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$), that governs the dynamics of individuals produced in the focal colony (recall eq. 1), is determined by two underlying traits that are subject to evolution. The first trait $v_{\mathrm{f}}(t)$ is the proportion of resources allocated to producing females (individuals destined to become workers or queens) at time t. The second trait v_{q}, gives the proportion of resources allocated to producing queens from resources allocated to females at time t. Note that these resource allocation traits are functions of time and are defined over the entire season ($t \in [0, T]$). It follows that the quantity $(1 - v_{\mathrm{f}}(t))$ gives the proportional allocation to males at time t and $(1-v_{\mathrm{q}}(t))$ gives the proportional allocation of resources directed to producing workers from resources allocated to females at time t. The schematic description of these assumptions is illustrated in Fig. 1. Hence, the allocation schedules to individuals of type k ($k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$) that are produced in the focal colony can be written in terms of the evolving traits

$$a_{\mathrm{w}}(t) = v_{\mathrm{f}}(t)(1 - v_{\mathrm{q}}(t)), \qquad a_{\mathrm{q}}(t) = v_{\mathrm{f}}(t)v_{\mathrm{q}}(t), \qquad a_{\mathrm{m}}(t) = (1 - v_{\mathrm{f}}(t)). \tag{3}$$

In order for the traits v_{f} and v_{q} to be evolving traits, they have to be genetically determined. It is often assumed that the genes in the queen are in control of proportional investment into females v_{f}, if the workers are completely sterile (as also assumed here). However, the genes in the workers can ultimately determine the trait v_{f}, if they are able to redirect resources from male brood to female brood (Chapuisat et al., 1997; Sundström

et al., 1996). In many species, the genes in the workers control the developmental fate of the female larvae (trait v_{q}) by differential feeding, as the diet provided to the larvae by workers determines the caste of the female offspring (Berens et al., 2015; Ratnieks et al., 2006; Schwander et al., 2010). However, in some species, queens can also alter the caste determination of females by producing different types of diploid eggs (Wheeler, 1986). It is believed that in many eusocial insects, the queen and the workers are in control of different resource allocation decisions simultaneously and it is often considered most likely that the queen determines the primary sex ratio (ratio of female to male eggs), while the workers control the developmental fate of the female eggs (Bourke and Franks, 1995; Helanterä and Ratnieks, 2009; Trivers and Hare, 1976). Hence, in light of the empirical evidence of genetic control of resource allocation decisions, 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 (i.e. the genes in the queen fully determine how colony resources are allocated). Second, we consider the case where workers are in full genetic control over these traits (i.e. the genes in the workers fully determine how colony resources are allocated). Hence, full queen and full worker control represent a scenario where the genes in a one party fully determine the resource allocation schedule of the colony and we call this scenario a "single-party control". As a third case, we consider the scenario of "mixed control", where the genes in the queen control the proportional investment into females versus males v_{f} and the genes in the workers control the proportional investment into new queens versus workers v_{q}. 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 assumptions of the genetic control are in accordance with the corresponding assumptions of the static resource allocation model by Reuter and Keller (2001), where they also considered these three scenarios with the corresponding static traits.

Evolutionary analysis

Mutant-resident system

In order to analyse the long-term evolution of the resource allocation traits, we perform an evolutionary invasion analysis (e.g., Caswell, 2001; Charlesworth, 1994; Eshel and Feldman, 1984; Ferrière and Gatto, 1995; Fisher,

1930; Lehmann et al., 2016; McNamara et al., 2001; Metz, 2011; Otto and Day, 2007). That is, we consider the fate (invasion or extinction) of a single mutant allele introduced into a population of resident individuals, where the mutant allele determines an allocation schedule that is different from the resident allocation schedule throughout the entire season (i.e., the mutant allele determines a trajectory of a trait over $t \in [0, T]$ that is close to the trajectory determined by the resident allele). In our analysis, we assume that the traits are determined at separate single loci with two segregating alleles (resident and mutant) and the alleles at these different loci are in linkage equilibrium.

Let $v_\tau(t)$ and $u_\tau(t)$ denote the resident and mutant resource allocation phenotypes for a trait of type $\tau \in \{\mathrm{f}, \mathrm{q}\}$, respectively. It will turn out to be useful to define the mutant phenotype $u_\tau(t)$ as a trait expressed by a (hypothetical) colony where all the genes in control of the trait are mutant alleles (i.e. individuals whose genes are in control of the trait are homozygous for the mutant allele).

Since the fate (invasion or extinction) of a mutant allele is determined when it is rare in the population, then only one of the colony "founding" individuals is carrying a single copy of the mutant allele (heterozygous). 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. Furthermore, in haplodiploid systems, where females are diploid and males are haploid, the phenotypes of colonies founded by mutant individuals of opposite sexes will be different. The distinction between the phenotypes expressed in these two types of colonies will also turn out to be useful when describing these phenotypes under the various assumptions of genetic control that different parties have over the traits.

Thus, we will denote by $u_{\mathrm{f}}^{\mathrm{q}}(t)$ (and respectively, by $u_{\mathrm{f}}^{\mathrm{m}}(t)$) the proportion of resources allocated at time t to producing females in a colony founded by a focal mutant heterozygous female (haploid male) and by $u_{\mathrm{q}}^{\mathrm{q}}(t)$ (and respectively, by $u_{\mathrm{q}}^{\mathrm{m}}(t)$) the proportion of resources allocated to producing queens from resources allocated to females at time t in a colony founded by a focal mutant heterozygous female (haploid male). Let $u_\tau^s(t)$ denote the resource allocation phenotype for a trait of type $\tau \in \{\mathrm{f}, \mathrm{q}\}$ of a colony founded by a heterozygous individual

of type $s \in \{\mathrm{q}, \mathrm{m}\}$ and it can be expressed as (assuming additive genetic effects)

$$u_\tau^s(t) = p_c^s u_\tau(t) + (1 - p_c^s) v_\tau(t), \tag{4}$$

where $p_c^s > 0$ is the expected frequency of the mutant allele in party $c \in \{\mathrm{q}, \mathrm{w}\}$ in full control of the trait of type τ in a colony founded by a mutant individual of type s ($s \in \{\mathrm{q}, \mathrm{m}\}$). Hereinafter, the subscript $c = \mathrm{q}$ denotes a scenario of full queen control and $c = \mathrm{w}$ denotes a scenario of full worker control, and $c = \mathrm{mx}$ denotes a scenario of mixed control.

Under queen control of the trait, the expected colony phenotype $u_\tau^s(t)$ is determined from the 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 $p_\mathrm{q}^\mathrm{q} = 1/2$. Under queen control, mutant males who have mated with a colony-founding queen have no genetic influence on the resource allocation traits and thus $p_\mathrm{q}^\mathrm{m} = 0$. Hence, female mating frequency will also have no affect on the trait under queen control. Under worker control of the trait, the expected colony phenotype $u_\tau^s(t)$ is determined from the expected frequency of the mutant allele in workers. The expected frequency of the mutant allele in workers in a colony founded by a heterozygous mutant female is $p_\mathrm{w}^\mathrm{q} = 1/4$ and it is not affected by the mating frequency of the queen because a mutant female will only encounter resident males since the mutant allele is considered to be rare. The expected frequency of the mutant allele in workers in a colony founded by a mutant male is $p_\mathrm{w}^\mathrm{m} = 1/(2M)$, where M is the number of times the female has mated (when the mutant allele is rare, only one of the males is carrying the mutant allele).

Let $\mathbf{v} = \{v_\mathrm{f}(t), v_\mathrm{q}(t)\}_{t \in [0,T]}$ denote the full allocation schedule of a colony founded by resident individuals, i.e. it describes how colony resources are allocated throughout the entire season $t \in [0, T]$. Similarly, let $\mathbf{u} = \{u_\mathrm{f}(t), u_\mathrm{q}(t)\}_{t \in [0,T]}$ denote the full allocation schedule of a colony founded by individuals who carry only mutant alleles for both of the evolving traits. Similarly, let $\mathbf{u}^s = \{u_\mathrm{f}^s(t), u_\mathrm{q}^s(t)\}_{t \in [0,T]}$ denote the full allocation schedule of a colony founded by a heterozygous individual of type s for each of the evolving traits. This notation turns out to be useful for performing the invasion fitness analysis, but it does not imply that we are assuming pleiotropic effects.

Let $a^s_{k,\mathrm{u}}(t)$ be the proportion of resources allocated to producing type $k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$ individuals in a colony founded by a heterozygous individual of type $s \in \{\mathrm{q}, \mathrm{m}\}$, where the subscript "u" in $a^s_{s,\mathrm{u}}(t)$ emphasizes that it is the mutant allocation schedule, which, according to eq. (3) is

$$a^s_{\mathrm{w,u}}(t) = u^s_{\mathrm{f}}(t)(1 - u^s_{\mathrm{q}}(t)), \qquad a^s_{\mathrm{q,u}}(t) = u^s_{\mathrm{f}}(t)u^s_{\mathrm{q}}(t), \qquad a^s_{\mathrm{m,u}}(t) = (1 - u^s_{\mathrm{f}}(t)). \tag{5}$$

The rate of change in the number of type $k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$ individuals alive at time t, that have been produced in a colony founded by a mutant individual of type s, is given by the equation

$$\dot{x}^s_k(t) = ba^s_{k,\mathrm{u}}(t)x^s_{\mathrm{w}}(t) - \mu_k x^s_k(t),\ x^s_k(t_0) = y_{k0}, \tag{6}$$

where $x^s_k(t)$ denotes the number of individuals of type k alive at time t that have been produced in a colony founded a mutant individual of type s. The rate of change of females $x^s_{\mathrm{iq}}(t)$ alive at time t, who have been inseminated by the males produced in the focal colony (under a monandrous mating system) founded by a mutant individual of type s, is given by the equation

$$\frac{\mathrm{d}x^s_{\mathrm{iq}}(t)}{\mathrm{d}t} = \begin{cases} 0,\ \text{for } t < T,\ \text{with } x^s_{\mathrm{iq}}(T) = x^s_{\mathrm{m}}(T)\frac{y_{\mathrm{q}}(T)}{y_{\mathrm{m}}(T)} & \text{(delayed dispersal)}, \\ x^s_{\mathrm{m}}(t)\frac{ba_{\mathrm{q}}(t)y_{\mathrm{w}}(t)}{y_{\mathrm{m}}(t)} - \mu_{\mathrm{q}}x^s_{\mathrm{iq}}(t),\ x^s_{\mathrm{iq}}(0) = 0 & \text{(direct dispersal)}. \end{cases} \tag{7}$$

Note that the number of females alive at time t, who have been inseminated by the males produced in the focal colony founded by a mutant individual of type s in a mating system where females mate M times is $Mx^s_{\mathrm{iq}}(t)$.

The rate of change of individuals of type $k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$ produced in a resident colony and females inseminated by males from the resident colony are given by eq. (1) and eq. (2), respectively.

Fitness functions of mutant individuals

We will express the invasion fitness of the mutant allele in terms of gene transmission frequencies and fitness functions of mutant individual of type s ($s \in \{\mathrm{q}, \mathrm{m}\}$), who have founded colonies in the current season. The fitness is measured as the expected number of daughters and sons who become colony founders in the next

generation. Note that, since females mate with M males, a son can become a colony founder for multiple colonies. Hence, the number of sons who become colony founders in the next generation can be measured in the number of females inseminated by sons, who will become colony-founding queens in the next generation (Bulmer, 1994, p. 213). Hence, one fitness measurement cycle lasts from the beginning of the current season to the beginning of the following season and we keep track of the genes in mutant colony-founding individuals of type s.

Let $w_{s's}(\mathbf{u}^s, \mathbf{v})$ denote the expected number of mutant colony-founding individuals of type $s' \in \{\mathrm{q}, \mathrm{m}\}$ in the following season that descend from a current colony-founding mutant individual of type $s \in \{\mathrm{q}, \mathrm{m}\}$ in a resident population. The fitness function $w_{s's}(\mathbf{u}^s, \mathbf{v})$ is a function of the allocation schedule $\mathbf{u}^s$ of a colony founded by an individual of type s (by way of eqs. 5–7). Note that the fitness function $w_{s's}(\mathbf{u}^s, \mathbf{v})$ is ultimately a function of the mutant schedule $\mathbf{u}$, the frequency p_c^s of the mutant allele in the average individual in control of a resource allocation trait, and of the resident allocation schedule $\mathbf{v}$ (by way of eq. 4). However, since the mutant allele is considered to be rare for the invasion analysis and the population size is large, then the fitness function $w_{s's}(\mathbf{u}^s, \mathbf{v})$ is independent of the number (or frequency) of mutants in the population. The life cycle and our fitness accounting method are illustrated in Fig. 2.

For calculating the fitness functions, we only need to specify the number of individuals alive at the end of the season $t = T$. To that end it is useful to set

$$y_k(T) = y_k(\mathbf{v}) \quad \text{and} \quad x_k^s(T) = x_k(\mathbf{u}^s), \tag{8}$$

which gives the number of individuals of type $k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}, \mathrm{iq}\}$ at the end of the season $t = T$ associated with a resident colony and a colony founded by a mutant individual of type s, respectively (by way of eqs. 1–2 and 6–7). Note that type $k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$ individuals are individuals produced in a focal colony and type $k = \mathrm{iq}$ individuals are females inseminated by sons produced in the focal colony. In eq. (8) we have emphasized the functional dependence of the number of individuals at the end of the season on the allocation schedules, $\mathbf{u}^s$ and $\mathbf{v}$ (recall eqs. 5 and 3).

Next, we derive the fitness functions $w_{s's}(\mathbf{u}^s, \mathbf{v})$. A colony-founding female is expected to have $y_{\mathrm{q}}(\mathbf{u}^{\mathrm{q}})$

surviving daughters (juvenile queens) at the end of the breeding season and her sons are expected to have inseminated $My_{\mathrm{q}}(\mathbf{u}^{\mathrm{q}})$ surviving females at the end of the breeding season. The probability that a daughter or a female inseminated by a son will gain any one of the n breeding spots is $n/ny_{\mathrm{q}}(\mathbf{v})$, since there are total number of $ny_{\mathrm{q}}(\mathbf{v})$ juvenile queens competing for these spots. Hence, the number of mutant colony-founding individuals of type s' in the next generation that descend from a mutant colony-founding female can be written as

$$w_{\mathrm{qq}}(\mathbf{u}^{\mathrm{q}},\mathbf{v}) = \frac{x_{\mathrm{q}}(\mathbf{u}^{\mathrm{q}})}{y_{\mathrm{q}}(\mathbf{v})}, \qquad w_{\mathrm{mq}}(\mathbf{u}^{\mathrm{q}},\mathbf{v}) = \frac{Mx_{\mathrm{iq}}(\mathbf{u}^{\mathrm{q}})}{y_{\mathrm{q}}(\mathbf{v})}. \tag{9}$$

Since females mate with M males, each colony-founding male is expected to only father $1/M$ of the offspring (here we have not yet taken into account the transmission frequencies specific to different genetic systems). Hence, a colony-founding male is expected to father $x_{\mathrm{q}}(\mathbf{u}^{\mathrm{m}})/M$ surviving daughters at the end of the breeding season and his sons are expected to have inseminated $Mx_{\mathrm{iq}}(\mathbf{u}^{\mathrm{m}})$ surviving females at the end of the breeding season. The probability that the daughters and the females inseminated by sons will gain any one of the n breeding spots is $n/ny_{\mathrm{q}}(\mathbf{v})$. Hence, the number of colony-founding individuals of type s' in the next generation that descend from a colony-founding male can be written as

$$w_{\mathrm{qm}}(\mathbf{u}^{\mathrm{m}},\mathbf{v}) = \frac{1}{M}\frac{x_{\mathrm{q}}(\mathbf{u}^{\mathrm{m}})}{y_{\mathrm{q}}(\mathbf{v})}, \qquad w_{\mathrm{mm}}(\mathbf{u}^{\mathrm{m}},\mathbf{v}) = \frac{1}{M}\frac{Mx_{\mathrm{iq}}(\mathbf{u}^{\mathrm{m}})}{y_{\mathrm{q}}(\mathbf{v})}. \tag{10}$$

The number of individuals at the end of the season $y_{\mathrm{q}}(\mathbf{v})$, $x_{\mathrm{q}}(\mathbf{u}^{s})$ and $x_{\mathrm{iq}}(\mathbf{u}^{s})$ ($s \in \{\mathrm{q},\mathrm{m}\}$) in eqs. (9)–(10) are determined from eq. (1) (with eq. 3) and eqs. (6)–(7) (with eqs. 4 and 5), respectively.

The invasion fitness

We now have all the elements to obtain an expression for the invasion fitness, which allows to ascertain the fate of the mutant allele. Let us denote by $n_{\mathrm{q,u}}$ (and respectively, by $n_{\mathrm{m,u}}$) the number of mutant allele copies in females (males with whom the females have mated with), measured at time $t = T$ in the population. The change in the vector $\mathbf{n}_{\mathrm{u}} = (n_{\mathrm{q,u}}, n_{\mathrm{m,u}})^{\intercal}$ of number of gene copies from one generation to the next $\mathbf{n}'_{\mathrm{u}} = (n'_{\mathrm{q,u}}, n'_{\mathrm{m,u}})^{\intercal}$, when the mutant allele for a trait that is under genetic control of party $c \in \{\mathrm{q},\mathrm{w}\}$ is still rare in the population,

is given by the matrix

$$\mathbf{A}_c(\mathbf{u}^{\mathrm{q}}(\mathbf{u}), \mathbf{u}^{\mathrm{m}}(\mathbf{u}), \mathbf{v}) = \mathbf{A}_c(\mathbf{u}, \mathbf{v}) = \begin{bmatrix} \gamma_{\mathrm{qq}} w_{\mathrm{qq}}(\mathbf{u}^{\mathrm{q}}, \mathbf{v}) & \gamma_{\mathrm{qm}} w_{\mathrm{qm}}(\mathbf{u}^{\mathrm{m}}, \mathbf{v}) \\ \gamma_{\mathrm{mq}} w_{\mathrm{mq}}(\mathbf{u}^{\mathrm{q}}, \mathbf{v}) & \gamma_{\mathrm{mm}} w_{\mathrm{mm}}(\mathbf{u}^{\mathrm{m}}, \mathbf{v}) \end{bmatrix} \tag{11}$$

where $\gamma_{s's}$ is the probability that a gene sampled in an individual of type $s' \in \{\mathrm{q}, \mathrm{m}\}$ was contributed by an individual of type $s \in \{\mathrm{q}, \mathrm{m}\}$, i.e. a transmission frequency of type s to type s' (for haplodiploids $\gamma_{\mathrm{qq}} = 1/2$, $\gamma_{\mathrm{qm}} = 1/2$, $\gamma_{\mathrm{mq}} = 1$, $\gamma_{\mathrm{mm}} = 0$). Hence, elements $a_{s's}$ of matrix $\mathbf{A}_c(\mathbf{u}, \mathbf{v})$ give the expected number of mutant gene copies in a type $s' \in \{\mathrm{q}, \mathrm{m}\}$ individual that descends from an individual of type $s \in \{\mathrm{q}, \mathrm{m}\}$ carrying the mutant allele. Note that in eq. (11), the dependence on the party $c \in \{\mathrm{q}, \mathrm{w}\}$ who has the genetic control enters into the right-hand-side implicitly via the mutant schedules $\mathbf{u}^{\mathrm{q}}$ and $\mathbf{u}^{\mathrm{m}}$ (recall eq. 4).

The invasion fitness $W_c(\mathbf{u}, \mathbf{v})$ of the mutant allele is then given by the leading eigenvalue of the matrix $\mathbf{A}_c(\mathbf{u}, \mathbf{v})$, where the subscript $c \in \{\mathrm{q}, \mathrm{w}\}$ emphasizes the party in control of the focal trait. The invasion fitness can be interpreted here as the geometric growth rate (generational growth rate) of the mutant allele. This is the asymptotic per capita number of mutant copies produced by the mutant lineage descending from the initial mutation, when overall still rare in the population (see section 1 of Supporting Information (hereinafter S.I.) and (Lehmann et al., 2016) for more details and connections to different fitness measures used in evolutionary biology). Hence, 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, thus the unit of adaptation is the gene (Dawkins, 1978; Haig, 2012).

Uninvadable allocation schedule

An uninvadable schedule $\mathbf{u}^* = \{u^*_{\mathrm{f}}(t), u^*_{\mathrm{q}}(t)\}_{t\in[0,T]}$ is a resident schedule that is resistant to invasion by any mutant $\mathbf{u} \in \mathbb{U} = \mathbb{U}_{\mathrm{f}} \times \mathbb{U}_{\mathrm{q}}$ schedule. Here, $\mathbb{U}$ is a set of all possible allocation schedules, while $\mathbb{U}_{\mathrm{f}}$ and $\mathbb{U}_{\mathrm{q}}$ are sets of full trajectories of the traits $\mathbf{u}_{\mathrm{f}} = \{u_{\mathrm{f}}(t)\}_{t\in[0,T]}$ and $\mathbf{u}_{\mathrm{q}} = \{u_{\mathrm{q}}(t)\}_{t\in[0,T]}$ under consideration.

If party $c \in \{\mathrm{q}, \mathrm{w}\}$ is in full control of the two traits (i.e. single-party control), then the uninvadable schedule

$\mathbf{u}^*$ satisfies the condition

$$\mathbf{u}^* \in \arg\max_{\mathbf{u}\in\mathbb{U}} W_c(\mathbf{u}, \mathbf{u}^*), \tag{12}$$

that is, a mutant that adopts the resident schedule $\mathbf{u}^*$ has the highest invasion fitness from all possible strategies in a population, for a population expressing schedule $\mathbf{u}^*$. Hence, an uninvadable schedule $\mathbf{u}^*$ is a candidate endpoint of the evolutionary process.

Under mixed control, where the queen is in control of the trait u_f and the workers are in control of the trait u_q, the uninvadable schedule $\mathbf{u}^*$ satisfies condition

$$\mathbf{u}_\mathrm{f}^* \in \arg\max_{\mathbf{u}_\mathrm{f}\in\mathbb{U}_\mathrm{f}} W_\mathrm{q}\big((\mathbf{u}_\mathrm{f}, \mathbf{u}_\mathrm{q}^*), \mathbf{u}^*\big) \quad \text{and} \quad \mathbf{u}_\mathrm{q}^* \in \arg\max_{\mathbf{u}_\mathrm{q}\in\mathbb{U}_\mathrm{q}} W_\mathrm{w}((\mathbf{u}_\mathrm{f}^*, \mathbf{u}_\mathrm{q}), \mathbf{u}^*)\,. \tag{13}$$

Hence, the uninvadable allocation schedules to individuals of type k ($k \in \{\mathrm{w}, \mathrm{q}, \mathrm{m}\}$) can be written as follows

$$a_\mathrm{w}^*(t) = u_\mathrm{f}^*(t)(1 - u_\mathrm{q}^*(t)), \qquad a_\mathrm{q}^*(t) = u_\mathrm{f}^*(t)u_\mathrm{q}^*(t), \qquad a_\mathrm{m}^*(t) = (1 - u_\mathrm{f}^*(t)) \tag{14}$$

and we denote by $x_k^*(t)$ the resulting number of individuals at time t.

Results

In order to determine the (candidate) uninvadable allocation schedule $\mathbf{u}^*$, we use an analytic approach to derive the first-order condition by way of optimal control theory (see Kamien and Schwartz, 2012; Sydsæter et al., 2008 for general introductions and Day and Taylor, 2000; Perrin, 1992 for formalizations in the context of evolutionary biology). We verify these results by a numerical method called the iterative scheme of the best response map (Houston and McNamara, 1999, see section 9 in S.I.), combined with a general-purpose software for problems of optimal control theory called GPOPS–II (Patterson and Rao, 2014).

Marginal value and potential for conflict

Relatedness asymmetry

Consider an allocation schedule $\mathbf{u} = \{u_{\mathrm{f}}(t), u_{\mathrm{q}}(t)\}_{t\in[0,T]}$ that deviates slightly from a candidate uninvadable schedule $\mathbf{u}^*$, such that a trait $u_\tau(t)$ ($\tau \in \{\mathrm{f}, \mathrm{q}\}$) can be expressed as

$$u_\tau(t) = u^*_\tau(t) + \epsilon_\tau \eta_\tau(t), \tag{15}$$

where $\eta_\tau(t)$ is some (arbitrary) deviation from the resident trait $u^*_\tau(t)$ and the scale factor $\epsilon_\tau \ll 1$ gives the magnitude of the variation.

The first-order condition for a schedule $\mathbf{u}^*$ to be uninvadable when party c is in control of the trait of type τ can be written as

$$-\left.\frac{\mathrm{d}x_{\mathrm{iq}}(\mathbf{u})/\,\mathrm{d}\epsilon_\tau}{\mathrm{d}x_{\mathrm{q}}(\mathbf{u})/\,\mathrm{d}\epsilon_\tau}\right|_{\epsilon_{\mathrm{f}}=0,\epsilon_{\mathrm{q}}=0} = R_c \tag{16}$$

(see eqs. S14–S18 in section 2.2 of S.I. for derivation). Here, $\mathrm{d}x_k(\mathbf{u})/\,\mathrm{d}\epsilon_\tau$ is the functional (variational) derivative measuring the change in the number of individuals of type $k \in \{\mathrm{q}, \mathrm{iq}\}$ produced by the end of the season in a focal colony, due to the infinitesimal deviation $\epsilon_\tau \eta_\tau(t)$ of the trait of type τ throughout the entire season $t \in [0, T]$ (see more on functional derivatives from e.g., Troutman, 2012, p. 45–50, Luenberger, 1997, p. 171–178). Thus, the left-hand side in eq. (16) gives the ratio of the marginal change in the number of inseminated queens to the marginal change in the number of queens produced when the allocation schedule is varied. It measures the (invasion) fitness benefit obtained by allocating more resources to producing males in exchange for allocating less resources to queen production. Hence, the left-hand side in eq. (16) is a marginal substitution rate in fitness given explicitly by

$$R_c = \frac{\alpha^\circ_{\mathrm{q}} r^\circ_{\mathrm{q},c}}{\alpha^\circ_{\mathrm{m}} r^\circ_{\mathrm{m},c}}, \tag{17}$$

which is the so-called *relatedness asymmetry* (Boomsma and Grafen, 1991, p. 386). Here α°_s is the (neutral) reproductive value of all individuals of class $s \in \{\mathrm{q}, \mathrm{m}\}$, i.e., the probability that a gene taken in the distant future descends from an individual in class $s \in \{\mathrm{q}, \mathrm{m}\}$ and $r^\circ_{s,c}$ is the (neutral) coefficient relatedness between

an individual of type $s \in \{\mathrm{q}, \mathrm{m}\}$ and an average individual whose genes are in control of the resource allocation (see section 2.2 of S.I.). In section 2 of S.I. (eqs. S19–S20), we detail that the relatedness asymmetry can be interpreted as giving the ratio of sex-specific contributions, of genes in party c, to the gene pool in the distant future (under a neutral process). For haplodiploids, under full queen or worker control, the relatedness asymmetry simplifies to

$$R_{\mathrm{q}} = 1 \quad \text{(queen control)}, \qquad R_{\mathrm{w}} = \frac{2+M}{M} \quad \text{(worker control)}. \tag{18}$$

Eq. (16) is the dynamic version of the standard static marginal value result of sex allocation theory (e.g., Taylor and Frank, 1996, eq. 22). The novelty of eq. (16) is that it results from a time-dependent model, which shows that the relatedness asymmetry and marginal product determine the primary sex allocation regardless of the details of colony growth dynamics, and thus returns qualitatively the same results as under any static sex allocation model for the productivity at the end of the season. Furthermore, eq. (16) also shows that relatedness will play a pivotal role in determining selection on any characteristic of colony life-history, independently of the details of the life-cycle.

Proportional relatedness asymmetry

It follows from the first-order condition for uninvadability that the marginal value of allocating resources is given by the ratio of asymptotic contributions (recall eq. 16). However, it will turn out to be useful in the forthcoming analysis to consider the proportional contribution

$$P_c = \frac{R_c}{1+R_c} \tag{19}$$

of party c to contribute genes through queens to the future gene pool. This quantity can be thought of as a proportional relatedness asymmetry and it gives the uninvadable proportional allocation into females

$$P_{\mathrm{q}} = \frac{1}{2} \quad \text{(queen control)}, \qquad P_{\mathrm{w}} = \frac{2+M}{2(1+M)} \quad \text{(worker control)} \tag{20}$$

under single-party control ($c \in \{\mathrm{q}, \mathrm{w}\}$) in the framework of classical static models of sex allocation theory (Boomsma and Grafen, 1991; Trivers and Hare, 1976).

The conflict between workers and the queen is absent when the proportional relatedness asymmetries for queens and males are equal, i.e. $P_\mathrm{w}/P_\mathrm{q} = 1$. However, when $P_\mathrm{w}/P_\mathrm{q} > 1$, then future queens are more valuable to workers than to the queen in contributing genes to the future gene pool. Hence, the ratio

$$C = C(M) = \frac{P_\mathrm{w}}{P_\mathrm{q}} = \frac{2+M}{1+M}. \tag{21}$$

can be interpreted as the potential for conflict. In other words, whenever $C \neq 1$, then there is potential for conflict between the queen and the workers over sex allocation. The potential for conflict C decreases with the increase in polyandry M (Ratnieks and Boomsma, 1995), since the proportional relatedness asymmetry of workers approaches the proportional relatedness asymmetry of queens with polyandry ($P_\mathrm{w} \to P_\mathrm{q}$). Hence, the potential conflict is maximal when the queen mates only one, i.e. $C(1) = 1.5$. It turns out that the proportional relatedness asymmetry P_c and the potential for conflict C are key quantities describing the properties of the uninvadable allocation schedule $\mathbf{u}^*$, to which we next turn.

The candidate uninvadable resource allocation schedule

In order to determine how selection shapes the colony growth schedule, we need to determine the uninvadable allocation schedule $\mathbf{u}^*$ that satisfies the first-order condition for uninvadability (recall eq. 16). We now present this schedule assuming equal mortality in (juvenile) queens and males (i.e. $\mu_\mathrm{q} = \mu_\mathrm{m} = \mu_\mathrm{r}$) and later discuss the relaxation of this assumption.

The colony growth schedule

We find that the allocation schedule $\mathbf{u}^*$ consists of two phases: the ergonomic phase ($t \in [0, t^*_{c,1}]$) during which only workers are produced and the reproductive phase ($t \in [t^*_{c,1}, T]$) during which only sexual offspring are produced. Here, $t^*_{c,1}$ marks the switching time from the ergonomic phase to the reproductive phase and the subscript $c \in \{\mathrm{w}, \mathrm{q}, \mathrm{mx}\}$ emphasizes the scenario of genetic control. During the reproductive phase, males and

queens are produced simultaneously under delayed dispersal, while under direct dispersal, males are produced before queens.

Hence, under delayed dispersal of sexuals, the schedule $\mathbf{u}^*$ consists of the following phases of colony growth

$$\begin{array}{lll} \textbf{Production of workers:} & (u_{\mathrm{f}}^*(t), u_{\mathrm{q}}^*(t)) = (1, 0) & t \in \left[0, t_{c,1}^*\right], \\ \textbf{Production of males and queens:} & (u_{\mathrm{f}}^*(t), u_{\mathrm{q}}^*(t)) = (\hat{\bar{u}}_{\mathrm{f}}^*, 1) & t \in \left[t_{c,1}^*, T\right], \end{array} \tag{22}$$

where $\hat{\bar{u}}_{\mathrm{f}}^*$ denotes a constant singular arc that determines the proportional resource allocation into queens during the reproductive phase and is equal to the proportional relatedness asymmetry (see eqs. 25 and 19).

Under direct dispersal of sexuals, the allocation schedule $\mathbf{u}^*$ consists of the following phases

$$\begin{array}{lll} \textbf{Production of workers:} & (u_{\mathrm{f}}^*(t), u_{\mathrm{q}}^*(t)) = (1, 0) & t \in \left[0, t_{c,1}^*\right], \\ \textbf{Production of males:} & (u_{\mathrm{f}}^*(t), u_{\mathrm{q}}^*(t)) = (0, \tilde{u}_{\mathrm{q}}^*(t)) & t \in \left[t_{c,1}^*, t_{c,2}^*\right], \\ \textbf{Production of queens:} & (u_{\mathrm{f}}^*(t), u_{\mathrm{q}}^*(t)) = (1, 1) & t \in \left[t_{c,2}^*, T\right], \end{array} \tag{23}$$

where $t_{c,2}^*$ is the switching time from production of only males to production of only queens and $\tilde{u}_{\mathrm{q}}^*(t)$ denotes that $u_{\mathrm{q}}^*(t)$ is undetermined during that phase (reflecting the fact that if $\bar{u}_{\mathrm{f}}^* = 0$ then $u_{\mathrm{q}}^*(t)$ has no effect, since females are not being produced).

In Figs. 3–4 we have depicted the analytically and numerically determined uninvadable allocation schedules $\mathbf{u}^*$ in terms of proportional allocation to workers $a_{\mathrm{w}}^*(t) = u_{\mathrm{f}}^*(t)(1 - u_{\mathrm{q}}^*(t))$, queens $a_{\mathrm{q}}^*(t) = u_{\mathrm{f}}^*(t)u_{\mathrm{q}}^*(t)$, and males $a_{\mathrm{m}}^*(t) = (1-u_{\mathrm{f}}^*(t))$, under delayed dispersal and direct dispersal, respectively, assuming queen monandry ($M = 1$). In Figs. 5–6 we have depicted the number of (surviving) individuals of different types produced in the colonies following the uninvadable allocation schedule $\mathbf{u}^*$, under delayed dispersal and direct dispersal, respectively, assuming queen monandry ($M = 1$).

Production of workers in the ergonomic phase

The switching time $t_{c,1}^*$ from the ergonomic to the reproductive phase determines the overall amount of resources allocated to production of workers versus sexual offspring and it depends on the scenario of genetic control over

the resource allocation traits; namely,

$$t^*_{c,1} = \begin{cases} T - \dfrac{\ln\left(1 + \frac{\mu_\mathrm{r} - \mu_\mathrm{w}}{b}\right)}{\mu_\mathrm{r} - \mu_\mathrm{w}}, & \text{(single-party control, } c \in \{\mathrm{q}, \mathrm{w}\}\text{)}, \\ T - \dfrac{\ln\left(1 + C\frac{\mu_\mathrm{r} - \mu_\mathrm{w}}{b}\right)}{\mu_\mathrm{r} - \mu_\mathrm{w}}, & \text{(mixed control, } c = \mathrm{mx}\text{)}, \end{cases} \tag{24}$$

(see sections 5 and 6 of S.I. for derivation, especially see eqs. S85–S93, S95–S98, S109–S126, S116–S123). Under single–party control, this switching time is equal for queen and worker control (i.e. $t^*_{\mathrm{q},1} = t^*_{\mathrm{w},1}$). Furthermore, in this case it is identical to eq. (6) of Macevicz and Oster (1976), by setting $b = bR$, $\mu_\mathrm{w} = \mu$, and $\mu_\mathrm{r} = \nu$. The resource allocation model by Macevicz and Oster (1976) assumed clonal reproduction and two classes of individuals (sexuals and workers) and the total number of sexuals surviving until the end of the season was maximized (while we have a sexually reproducing haplodiploid population).

Eq. (24) shows that the switching time under mixed control $t^*_{\mathrm{mx},1}$ depends on the potential for conflict $C \geq 1$ (eq. 21). It follows from eq. (21) and eq. (24) and that the switch from the ergonomic to the reproductive phase under mixed control happens earlier in the season than under single-party control (i.e. $t^*_{\mathrm{mx},1} < t^*_{\mathrm{q},1} = t^*_{\mathrm{w},1}$, see also Fig. 3 for delayed dispersal and Fig. 4 for direct dispersal, assuming queen monandry, i.e. $C = 1.5$). More generally, the switching time $t^*_{\mathrm{mx},1}$ under mixed control happens earlier and, hence, the ergonomic phase is shorter if the potential for conflict C is larger. It turns out that the switching time $t^*_{\mathrm{mx},1}$ under mixed control is determined by the workers (see section 7.4 in S.I. for more detailed explanation).

Eq. (24) also implies 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 (b is small), but colony per-capita productivity still scales linearly as the colony grows (b is constant and does not depend on colony size). Increased mortality of workers (μ_w) and decreased mortality of sexuals (μ_r) also cause the time difference between optimal switching time and switching time under mixed control to be larger (see eq. 24).

Production of males and queens in the reproductive phase

Under delayed dispersal, both males and queens are produced simultaneously in the reproductive phase ($t \in [t^*_{c,1}, T]$) during which $u^*_\mathrm{f}(t) = \hat{\bar{u}}^*_\mathrm{f}$ and $\bar{u}^*_\mathrm{q} = 1$. In the reproductive phase a (constant) proportion $\hat{\bar{u}}^*_\mathrm{f}$ of

resources are allocated into producing queens and a (constant) proportion $(1 - \hat{\bar{u}}_{\mathrm{f}}^*)$ of resources are allocated into producing males. The (uninvadable) proportional allocation into production of queens in the reproductive phase is

$$a_{\mathrm{q}}^*(t) = \hat{\bar{u}}_{\mathrm{f}}^* = \begin{cases} P_{\mathrm{q}} & \text{(queen control \& mixed control)}, \\ P_{\mathrm{w}} & \text{(worker control)}. \end{cases} \tag{25}$$

Under direct dispersal, males are produced before queens. The switching time from the production of males to the production of queens under the scenario c of genetic control is

$$t_{c,2}^* = \begin{cases} T - \dfrac{1}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \ln\left(\dfrac{b + \mu_{\mathrm{r}} - \mu_{\mathrm{w}}}{b + (1 - P_{\mathrm{q}})(\mu_{\mathrm{r}} - \mu_{\mathrm{w}})}\right) & \text{(queen control, } c = \mathrm{q}), \\ T - \dfrac{1}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \ln\left(\dfrac{b + \mu_{\mathrm{r}} - \mu_{\mathrm{w}}}{b + (1 - P_{\mathrm{w}})(\mu_{\mathrm{r}} - \mu_{\mathrm{w}})}\right) & \text{(worker control, } c = \mathrm{w}), \\ T - \dfrac{1}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \ln\left(2 - \dfrac{b}{b + \frac{1}{2}C\,(\mu_{\mathrm{r}} - \mu_{\mathrm{w}})}\right) & \text{(mixed control, } c = \mathrm{mx}), \end{cases} \tag{26}$$

which shows that the switch to production of queens happens later under full queen control than under worker control ($t_{\mathrm{q},2}^* > t_{\mathrm{w},2}^*$), since $P_{\mathrm{q}} < P_{\mathrm{w}}$. This implies that more resources are expected to be allocated to queens under worker control than under queen control (since the length of the reproductive phase is the same under single-party control). The switching time $t_{\mathrm{mx},2}^*$ under mixed control increases as the potential conflict C increases. Equation (26) implies that the late switch to queen production under mixed control is more pronounced when per-worker productivity b is small (b is small), worker mortality rate μ_{w} is large (μ_{w}), mortality rate μ_{r} of sexuals is large.

In our model $(1/b)$ can be loosely interpreted as the time it takes for one worker to help produce one offspring, i.e. a generation time. We show in S.I. (see sections 5.1.3, 5.1.4, and 6.2) that if the mortality rate of sexuals is roughly equal to the mortality rate of workers, then the switching time from the ergonomic to the reproductive phase $t_{c,1}^*$ under single-party control ($c = \{\mathrm{q}, \mathrm{w}\}$) approaches to one generation time $(1/b)$ before the end of the season, i.e. only the last generation of brood is reproductive. However, under mixed control the switch happens C generations earlier. For example, when females mate only once (i.e. $M = 1$ and $C = 1.5$) the switch to reproductive phase happens one and a half generations before the end of the season.

Colony level traits

Colony size at maturity

During the ergonomic phase the number of workers in the colony grows exponentially until the switching time $t^*_{c,1}$ (see Fig. 5 for delayed dispersal and Fig. 6 for direct dispersal). At the time $t^*_{c,1}$ colony reaches its maximum size (owing to the mortality of workers) and starts to produce only sexuals. Hence, the number of workers at time $t^*_{c,1}$ gives the size of a colony at its maturity when the population is in an uninvadable state, which can be expressed as

$$x^*_{\mathrm{w}}(t^*_{c,1}) = \exp^{(b-\mu_{\mathrm{w}})t^*_{c,1}} \tag{27}$$

(see section 7.1 in S.I. for derivation). Since the ergonomic phase is shorter under mixed control than under single-party control ($t^*_{\mathrm{mx},1} < t^*_{\mathrm{q},1} = t^*_{\mathrm{w},1}$, recall eqs. 24 and 21), then the colony size at maturity is lower under mixed control than under single-party control (i.e. $x^*_{\mathrm{w}}(t^*_{\mathrm{mx},1}) < x^*_{\mathrm{w}}(t^*_{\mathrm{q},1}) = x^*_{\mathrm{w}}(t^*_{\mathrm{w},1})$, see also Figs. 5–6). Furthermore, both the colony size at maturity $x^*_{\mathrm{w}}(t^*_{\mathrm{mx},1})$ and the length of the ergonomic phase increase under mixed control as the potential for conflict C decreases and Fig. 7 depicts this effect. Since the potential for conflict C is a decreasing function of the mating frequency M of the queen (recall eq. 21), then it follows that the colony size at maturity $x^*_{\mathrm{w}}(t^*_{\mathrm{mx},1})$ increases as the mating frequency M of the queen increases under mixed control.

Colony productivity

We define colony productivity $B(t^*_{c,1})$ as the total number of males and females produced that have survived until the end of the season (i.e. $B(t^*_{c,1}) = y_{\mathrm{m}}(\mathbf{u}^*) + y_{\mathrm{q}}(\mathbf{u}^*)$). Since we have assumed that males and females are equally costly to produce, then it can also be interpreted as the total sexual biomass produced in a colony, which is a quantity often used as a fitness proxy in social insects (Wills et al., 2018). Colony productivity $B(t^*_{c,1})$ can be expressed as a function of the switching time $t^*_{c,1}$ as follows

$$B(t^*_{c,1}) = \frac{be^{bt^*_{c,1}}\left(e^{-\mu_{\mathrm{w}}T} - e^{-\mu_{\mathrm{r}}T+(\mu_{\mathrm{r}}-\mu_{\mathrm{w}})t^*_{c,1}}\right)}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \tag{28}$$

(see section 7.2 in S.I. for derivation). It turns out that the switching time $t^*_{c,1}$ under single-party control (given by eq. 24) maximizes the colony productivity (see section 7.2 in S.I. for proof). In Fig. 7, we have depicted the uninvadable colony productivity $B(t^*_{c,1})$ as a function of the potential for conflict C and it shows that the colony productivity can be significantly lower under mixed control than under single-party control if the potential conflict C is large. Since the potential conflict C is a decreasing function of the mating frequency M of the queen (recall eq. 21), it follows that the uninvadable colony productivity $B(t^*_{\mathrm{mx},1})$ under mixed control increases as the mating frequency M of the queen increases.

Sex allocation ratio

The overall sex allocation ratio at the evolutionary equilibrium, which we define as the proportion of the colony resources allocated to queens from the resources allocated to sexuals over the entire season (irrespective of whether they survive to reproduce) can be expressed as

$$S_c = \frac{\int_0^T b a^*_{\mathrm{q}}(t) x^*_{\mathrm{w}}(t)\,\mathrm{d}t}{\int_0^T b a^*_{\mathrm{q}}(t) x^*_{\mathrm{w}}(t)\,\mathrm{d}t + \int_0^T b a^*_{\mathrm{m}}(t) x^*_{\mathrm{w}}(t)\,\mathrm{d}t}. \tag{29}$$

Here, the subscript $c \in \{\mathrm{q}, \mathrm{w}, \mathrm{mx}\}$ emphasizes the dependence on the scenario of genetic control, which enters into eq. (29) implicitly via the uninvadable allocation schedule (given by eqs. 14, 22, and 23). Since we have assumed that males and queens are equally costly to produce, then in the context of our model S_c can also be interpreted as the overall proportion of queens among sexuals produced in the colony.

Under delayed dispersal, the overall sex allocation ratio can be expressed as (see section 7.3 of S.I., eqs. S148–S151 for derivation)

$$S_c = \hat{\bar{u}}^*_{\mathrm{f}} = \begin{cases} P_{\mathrm{q}} & \text{(queen control \& mixed control)}, \\ P_{\mathrm{w}} & \text{(worker control)}. \end{cases} \tag{30}$$

Hence, under delayed dispersal the overall sex allocation ratio is given by the proportional relatedness asymmetry (via eq. 25 and recall eqs. 19–20). It follows from eq. (30) that the prediction for the uninvadable overall sex allocation ratio under single-party control is equal to the corresponding prediction from the standard static

models of sex allocation theory (Boomsma and Grafen, 1991; Reuter and Keller, 2001; Trivers and Hare, 1976).

Under direct dispersal, the overall sex allocation ratio can be expressed as (see section 7.3 of S.I., eqs. S152–S154 for derivation)

$$S_c = \frac{e^{-\mu_{\mathrm{w}} t^*_{c,2}} - e^{-\mu_{\mathrm{w}} T}}{e^{-\mu_{\mathrm{w}} t^*_{c,1}} - e^{-\mu_{\mathrm{w}} T}}. \tag{31}$$

Note that the overall sex allocation ratio under direct dispersal, in contrast to delayed dispersal, depends also on other life-history characteristics of the species and not only on the proportional relatedness asymmetry in the colony (which enters into the equation via $t^*_{c,1}$ and $t^*_{c,2}$). For single party control, it follows from eq. (31) together with eqs. (24) and (26) (see Fig. 8) that for direct dispersal, the (uninvadable) overall sex allocation ratio is more male-biased than the static models of sex allocation theory predict (e.g. Boomsma and Grafen, 1991; Trivers and Hare, 1976) for biologically meaningful parameter values ($\mu_{\mathrm{w}} > 0$, $\mu_{\mathrm{r}} > 0$, $b > \mu_{\mathrm{w}}$, and $b > \mu_{\mathrm{r}}$).

We find that the overall sex allocation under direct dispersal is more male-biased under mixed control than under full queen control for the same parameter values (see Figs. 8 and 9). A more male-biased overall sex allocation under mixed control can be explained by observing that the reproductive phase is significantly longer under mixed control and males are produced before females. Hence, more males are produced to compensate for the increased loss of males due to mortality before the arrival of females. Indeed, if the mortality rate of the sexuals approaches to zero, then the overall sex allocation ratio under mixed control approaches to the overall sex allocation ratio under full queen control (see Fig. 8). Furthermore, a higher mortality rate of workers μ_{w} also results in a more male-biased overall sex allocation, because it causes the reproductive phase to be longer (see Figs. 9). Note that decreasing the productivity rate of a worker b has a qualitatively similar effect on the overall sex allocation for the same reason.

Surprisingly, we also find that under direct dispersal and mixed control the overall proportional allocation to queens is lower for higher values for the potential for conflict C (i.e. for lower values of queen mating frequency M, see Fig. 8–9). This means that the overall proportional investment into queens is expected to be lower if workers are more related to them and the overall proportional allocation to females should correlate negatively with the relatedness between the workers and the female brood.

Regardless of whether sexuals are produced simultaneously (like under delayed dispersal) or separately (like under direct dispersal) the primary sex allocation ratio $u_{\mathrm{f}}^{*}(t)$ during the reproductive phase ultimately determines the overall sex allocation ratio. Hence, the queen is in control of the overall sex allocation ratio under mixed control (see also section 7.4 in S.I. for more detailed explanation). Under delayed dispersal, this means that the overall proportional sex allocation under mixed control and full queen control are equal (recall eq. 30). Under direct dispersal, the overall sex allocation ratio is more male biased under mixed control than under full queen control (recall eq. 30 and see Figs. 8– 9). This additional male-bias arises because of the combined effects of protandry and a longer duration of the reproductive phase under mixed control which causes more males to die due to mortality before females emerge. For the same reason, this effect is absent when there is no mortality of sexuals (see Fig. 8) and more pronounced for a longer duration of the reproductive phase caused by higher worker mortality rate (see Fig. 9).

Unequal mortality rates of sexuals

We now discuss how relaxing the assumption of equal mortality ($\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = \mu_{\mathrm{r}}$) used in the derivation of the above results qualitatively affects these results. From further analysis (section 5.2 of S.I) and our numerical solutions, we find that under delayed dispersal, if the mortality rate of queens and males is not equal, then the sex with the lower mortality rate should be produced before, such that by the end of the season the sex ratio of queens to males would be given by R_c under single party control and R_{q} under mixed control (assuming that males and queens are equally costly to produce).

We also find that the main conclusions of our results under direct dispersal hold qualitatively if $R_c\mu_{\mathrm{q}} \geq \mu_{\mathrm{m}}$ under single-party control and $R_{\mathrm{q}}\mu_{\mathrm{q}} \geq \mu_{\mathrm{m}}$ under mixed control. Under direct dispersal, if $R_c\mu_{\mathrm{q}} < \mu_{\mathrm{m}}$ then the overall sex allocation under single-party control can be more female-biased than the static models of sex allocation theory predict (e.g. Boomsma and Grafen, 1991; Trivers and Hare, 1976). Similarly, if $R_{\mathrm{q}}\mu_{\mathrm{q}} < \mu_{\mathrm{m}}$ then the overall sex allocation under mixed control and direct dispersal can be female-biased. Furthermore, we find that under mixed control, if the mortality of queens is significantly smaller than that of males then males and queens are produced simultaneously after the switch to the reproductive phase until there is a switch to

producing only females (see section 6.3 of S.I.).

Discussion

Ontogenetic development of social insect colonies passes through different stages which causes behavioural trait expressions of individuals to be necessarily time-dependent (Oster and Wilson, 1979). In this paper, we formulated a mathematical model to analyse how sex allocation conflict affects the dynamic resource allocation to workers, queens, and males in annual eusocial monogynous species. We have considered three alternative scenarios of control of colony trait expression (full queen, full worker, and mixed control) and two alternative scenarios of dispersal of sexuals: direct dispersal after eclosion (common among many bees and wasps) and delayed dispersal by the end of the season, which resembles the life-history of species (more commonly found in ants) where nuptial flights appear to be highly synchronized (e.g. see Heinze, 2016 and references therein). Our model extends static allocation models with genetic conflict and dynamic allocation models without conflict and it allows to shed light on a number of questions about colony ontogeny, such as: how does sex allocation conflict affect colony growth? How does sexual selection affect the production of sexuals? Which party wins the sex allocation conflict?

From our dynamically and sexually explicit model, we find that the relatedness asymmetry (Boomsma and Grafen, 1991) quantitatively determines the sex allocation (expressed in terms of marginal substitution rate of inseminated queens by sons in exchange of daughter queens) and regardless of any details of colony life-cycle or growth dynamics, thereby generalizing the standard static marginal value result of sex allocation theory (e.g., Taylor and Frank, 1996) to any pattern of colony ontogeny. Solving the marginal value result under our specific life-cycle assumptions (a non-trivial task, see S.I.), we find that selection tends to favor a colony resource allocation schedule that consists of two qualitative phases. First, an ergonomic phase with production of only workers, which determines the colony size at maturity. Second, a reproductive phase with resource allocation to queens and males, which determines the colony productivity and overall sex-allocation ratio. Sexuals can be produced according to various schedules, possibly including switching between producing only males or females (or vice versa), depending on the assumptions about the life-cycle. Colony traits, such as the switching

times between different phases of colony growth, maximum colony size, colony productivity, and overall sex-allocation ratio are influenced by the assumptions about the genetic control of resource allocation traits and individual dispersal behaviour.

How does sex allocation conflict affect colony growth?

Our results confirm earlier predictions derived from dynamic resource allocation models (Macevicz and Oster, 1976; Ohtsuki and Tsuji, 2009) that colony resource allocation should consist of an ergonomic phase during which the colony grows exponentially to its maximal size $x^*_{\mathrm{w}}(t^*_{c,1})$ and a reproductive phrase during which the total number $B(t^*_{c,1})$ of sexuals are produced. During the ergonomic phase, the (invasion) fitness return of a (unit) investment into workers at a given point in time ("marginal return" for short) is higher than the return of investment into sexuals. Workers have a higher marginal return earlier in the season because colony productivity rate (by_{w}) increases linearly with colony size (hence exponentially during the ergonomic phase), allowing for the production of more sexuals later in the season. Sexuals have a lower marginal return earlier in the season, because they need to survive (queens need to survive until the end of the season and males need to survive until they can reproduce with the surviving queens). The colony switches from the ergonomic to the reproductive phase when producing workers no longer yields the highest marginal return.

We find that under mixed control, colonies evolve to switch to the reproductive phase earlier than under single-party control (i.e. $t^*_{\mathrm{mx},1} < t^*_{\mathrm{q},1} = t^*_{\mathrm{w},1}$). The early switch evolves, because the marginal return of queens becomes higher earlier in the season than that of workers from the perspective of the genes in workers. This is so because the overall sex allocation ratio is more male-biased under mixed control than under full worker control under both delayed and direct dispersal (i.e. $S_{\mathrm{mx}} < S_{\mathrm{w}}$, see Fig. 8) because the queen controls the overall sex allocation ratio (for why this is so, see section "Which party wins the sex-allocatin conflict and what is the overall sex allocation ratio?" below). Hence, to best-respond to the queens strategy, the workers start rearing female eggs into queens earlier, since too few resources are allocated to queens in the reproductive phase during which workers have no power over the resource allocation decisions. The asymmetric power then causes the switching time to the ergonomic phase to be controlled by the workers (see also section 7.4 of S.I. for more

technical explanation).

Colony size at maturity $x^*_{\mathrm{w}}(t^*_{c,1})$ and colony productivity $B(t^*_{c,1})$ are expected to be smaller under mixed control than under single party control. Under single-party control the colony productivity $B(t^*_{c,1})$ is maximized, but not under mixed control (see section 7.2 in S.I. for proof and Fig. 7). This is so, because in the latter case the switch to the reproductive phase occurs earlier causing the colony size at maturity $x^*_{\mathrm{w}}(t^*_{c,1})$ to be smaller (there is less time for worker numbers to increase exponentially during the ergonomic phase). Therefore, there are less workers to produce sexuals in the reproductive phase even though there is more time to produce sexuals under mixed control. The reduction in colony productivity $B(t^*_{\mathrm{mx},1})$ can be thought of as a colony-level cost of sex allocation conflict.

A loss in colony productivity due to sex allocation conflict was already predicted using a static allocation model (Reuter and Keller, 2001) and a dynamic allocation model assuming delayed dispersal (Bulmer, 1981), but for the latter model, the outcome of the resource allocation conflict is different from ours. Indeed, Bulmer (1981) concluded that colonies die one generation before the end of the season if the sex allocation at the population level is biased towards queens, since the queens are producing only males in the penultimate generation. His conclusion relied on the assumption that colony growth is divided into discrete generations, such that worker generations do not overlap and in his model he only considered two generations before the end of the season. Our analysis not only extends the results of Bulmer (1981) to less restrictive life-cycle assumptions and to direct dispersal of sexuals, but it also provides quantitative predictions for the the switching time from the ergonomic to the reproductive phase. Indeed, we predict that the premature switch from the ergonomic to the reproductive phase is more pronounced in species where the resource acquisition rate b is lower and the mortality rate of workers μ_{w} is higher and that of sexuals μ_{r} is lower. We also show that the switching time from the ergonomic to the reproductive phase under mixed control for delayed dispersal and direct dispersal are equal. This implies that sexual selection and the evolution of protandry do not have an effect on the cost of sex allocation conflict that manifests itself through loss of colony productivity.

We show that the switching time from the ergonomic to the reproductive phase under mixed control depends on the potential for conflict C, which is the ratio of party-specific proportional contribution of genes through

queens to the future of the gene pool (eq. 21), and a decreasing function of the mating number M of a queen. Our results imply that colonies with lower potential for conflict C are expected to grow larger and have higher colony productivity. 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). We have assumed monogyny, but allowing for multiple queens per colony should be a relatively straightforward extension to our model. Our analysis implies that polyandry is expected to evolve under mixed control, given that the workers are able to assess the mating frequency of the queen (Pamilo, 1991b). However, empirical evidence suggests that polyandry is generally less common in annual eusocial insects but has been found, for example, in *Polistes* (Seppä et al., 2011) and *Vespula* (Johnson et al., 2009).

The so-called "bang-bang" schedule of colony growth, such that allocation to workers and sexuals never occurs simultaneously, represents a general life-history principle of growth and reproduction in annual organisms for which productivity rate scales linearly with size and environmental fluctuations that can cause variations in the length of the season or food availability are small (Cohen, 1971; King and Roughgarden, 1982). A key result of our analysis is that the sex allocation conflict does not affect the overall shape of the colony growth curve, but only the time of the switch between growth and reproduction. This is not an obvious result, since trade-offs between producing different types of individuals are not linear. It has been shown before (assuming clonal reproduction) that selection favours a singular control (workers and sexuals are produced simultaneously and sometimes called a graded control) if the productivity rate (i.e. by_{w}) scales non-linearly with colony size, such that $b \equiv b(y_{\mathrm{w}})$ (Beekman et al., 1998; Poitrineau et al., 2009), but not for environmental fluctuations acting alone (Mitesser et al., 2007b). The properties of the relationship between productivity rate and colony size affects the way the marginal value of producing a worker changes over time, but not the marginal value of producing queens and males. In principle, this could affect the outcome of the sex-allocation conflict and it would be interesting to see how the results of our model change when the productivity rate would scale non-linearly with colony size.

Inherently, our model assumes that individuals in the colony possess some physiological mechanism that enables them to estimate the timing of the switch from the ergonomic phase to the reproductive phase. Currently,

the underlying mechanism behind the timing of the switch from the ergonomic to the reproductive phase is not known. However it has been shown that *Bombus terrestris* queens are able to control the switching time endogenously (Holland et al., 2013).

How does sexual selection affect the production of sexuals?

Our model predicts simultaneous production of queens and males under delayed dispersal and protandry (males produced before females) under direct dispersal. Protandry evolves because the reproductive success of males and queens depends asymmetrically on the time that they are produced under direct dispersal. On one hand, males that are produced early in the season have more mating opportunities than males produced late in the season (i.e. earlier males are alive over longer periods of higher female availability). Note that the highest number of females available to mate is realized shortly after the colony starts producing queens since colony productivity decreases exponentially during the reproductive phase due to the mortality of workers. On the other hand, females produced later in the season have higher chances of surviving until the end of the season. Under delayed dispersal, both males and queens have to survive until the end of the season to mate, so that their reproductive success depends symmetrically on the time that they are produced.

Our prediction about the evolution of protandry relies on the assumption that the females mate immediately and indiscriminately after dispersal with the males currently in the mating pool. However, there is some evidence of female choice in some social insects. For example, female bumble bees exhibit choosiness and may reject some males (Baer, 2003 and references therein). Furthermore, in many social insects, cryptic female choice can take place, since females can exert post-copulatory selection on the ejaculates (Baer, 2003). On the other hand, there is also evidence that earlier emergence of males can also give them an advantage in mating success through precopulatory sexual behaviours, such as searching and guarding of conspecific nest entrances and other strategic locations, leaving scent marks, and so forth (Baer, 2003, 2014; Foster, 1992). Furthermore, it has been shown that bumble bee (*B. terrestris*) males transfer a mating plug into the sexual tract of females, which optimizes sperm placement before the spermathecal duct and may also reduce female receptivity to other males (Baer et al., 2000).

Which party wins the sex allocation conflict and what is the overall sex allocation ratio?

We find that the queen wins (more accurately, the genes in queens win) the sex allocation conflict. The queen wins because the evolution of distinct phases of colony growth constrains the ability of workers to manipulate the overall sex allocation ratio. Indeed, during the reproductive phase the ratio at which the queen lays the female versus male eggs ($u_{\mathrm{f}}^{*}(t)$) determines the overall sex allocation ratio, because sexuals are only produced during the reproductive phase during which the workers rear all the female eggs into queens. Since workers can only influence the developmental fate of the female eggs, their only option to increase the overall allocation into queens is to switch to the reproductive phase earlier at the expense of reduced colony productivity. Furthermore, our model implies that the queen is always expected to win the sex allocation conflict, as long as workers and sexuals are produced during separate phases of colony growth and workers can only influence the developmental fate of the female eggs. The evolution of different phases of colony growth, decouples the trade-offs experienced by the queens. During the ergonomic phase, there is a latent trade-off between producing males versus workers (since workers rear all the female-eggs into workers), while during the reproductive phase there is a trade-off between producing queens versus males (since workers rear all the female-eggs into queens). The evolution of distinct phases also decouples how queens and workers can affect the allocation decisions in the colony. Impeding the ability of workers to influence the overall sex allocation during the reproductive phase and the ability of queens to influence the proportional allocation to workers versus sexuals (see also section 7.4 of S.I. for more detailed explanation).

Even though the queen wins the sex allocation conflict under mixed control, we find that the overall sex allocation ratio depends on the scenario of dispersal of sexuals. More precisely, under mixed control the overall sex allocation ratio is expected to be even under delayed dispersal and male-biased under direct dispersal (given that the mortality rate of males and queens is equal). Under single-party control and direct dispersal, our model predicts more male-biased overall sex allocation ratios than the static models of sex allocation theory predict (e.g. Boomsma and Grafen, 1991; Trivers and Hare, 1976), especially for higher mortality rates of sexuals (see Fig. 8) and lower mortality rates of workers (see Fig. 9). However, under single-party control and delayed dispersal, the overall sex allocation ratios predicted by our model are in accordance with the classical static

models of sex allocation theory (e.g. Boomsma and Grafen, 1991; Trivers and Hare, 1976) and do not depend on the life-history characteristics of the species (e.g. mortality rate of sexuals or workers).

More male-biased sex allocation ratios evolve under direct dispersal because of sexual selection on males. Indeed, it turns out that male-biased allocation results from the co-evolution of protandry (that evolves due to sexual selection on males) and sex allocation ratio, given that there is some mortality (of sexuals) during the reproductive phase. To see this, note that if males are produced before queens, then some males are expected to die due to mortality before queens emerge. Hence, more males should be produced to compensate for the loss of males due to mortality. This causes the sex allocation ratio to be more male-biased, especially if the mortality of sexuals is higher (see Fig. 8). Furthermore, since the length of reproductive phase is longer under mixed control than under single-party control, then proportionally more males are expected to die before the emergence of females. Therefore, the sex allocation should be more male-biased for mixed control than under queen control, because proportionally more resources should be allocated to males to compensate for the extra loss of males due to a longer reproductive phase under mixed control. This is exactly what we find, given that the mortality of sexuals is not negligible (see Figs. 8 and 9). For the same reason, this combined effect of protandry, mortality and a longer duration of the reproductive phase under mixed control is absent when there is no mortality of sexuals (see Fig. 8) and more pronounced for a longer duration of the reproductive phase caused by higher worker mortality rate (see Fig. 9). Hence, we find that in protandrous species, proportionally more resources are expected to be allocated into producing males, if workers have more power over the resource allocation decisions in the colony.

We predict that under direct dispersal and mixed control, the overall proportional investment to queens is lower if workers are more related to the female brood. Indeed, Fig. 9 illustrates that the overall sex allocation ratio S_{mx} becomes more male-biased as the workers become more related to the female brood (their sisters) (i.e. if the potential for conflict C increases or the queen mating frequency M decreases). This surprising prediction follows from the combined effect of protandry under direct dispersal and a longer duration of the reproductive phase under mixed control. If workers are more related to the female brood (e.g. for higher values of the potential conflict C), then the length of the reproductive phase is predicted to be longer (i.e. the switch

happens earlier) due to the sex allocation conflict. Hence, for higher relatedness between the workers and the female brood, more males are expected to die during the reproductive phase because it is longer, hence queens allocate proportionally more resources to males to compensate for this loss. For these reasons, in protandrous species, where resource allocation is under mixed control, worker relatedness to female brood is expected to correlate negatively with the proportional investment into queens.

Our prediction that for direct dispersal, the average worker relatedness to juvenile queens should correlate negatively with the overall proportional investment into queens under mixed control contradicts with the standard results from the static models of sex allocation theory (Boomsma and Grafen, 1991; Trivers and Hare, 1976) that predict the opposite correlation. We expect that other factors that reduce the queen-worker conflict over sex allocation have qualitatively similar effects on overall proportional allocation to queens.

Most comparative studies about population-wide sex allocation of eusocial Hymenoptera come from ants, where sex-allocation is mostly female-biased (Bourke and Franks, 1995; Ratnieks et al., 2006; Sundström et al., 1996), although it is not universal (Fjerdingstad et al., 2002; Helms, 1999; Helms et al., 2000; Passera et al., 2001). However, most ant species are perennial and their life-cycles diverge in many respects from the assumptions of our model. In bumble bees, who are annual and mostly monogynous species, the population-wide sex allocation tends to be overwhelmingly male-biased (Bourke, 1997). Indeed, Bourke (1997) found that the median proportional allocation to queens is only 0.32 (range 0.07–0.64) among 11 populations of seven bumble bee species. Interestingly, Johnson et al. (2009) found that in a social wasp (*V. maculifrons*) nestmate relatedness is negatively associated with overall investment into queens which would be in accordance with our model for mixed control under direct dispersal with male protandry (see Fig. 8). However, these results arise from a dataset where the queens have a relatively high mating frequency and the variation between mating frequencies is not very large (hence, the effect size is not very large) and male protandry in that species is not entirely clear (Johnson et al., 2009).

Static and dynamic approaches to resource allocation conflicts

The predictions of our dynamic model under delayed dispersal can be directly compared with the predictions of the static model by Reuter and Keller (2001). We followed their approach on modeling conflict within colony over resource allocation (with a slight difference only in the assumption of how colony productivity scales with colony size), but, contrarily to them, we find that under delayed dispersal and mixed control of the resource allocation traits, the queen is able to win the sex allocation conflict. Indeed, Reuter and Keller (2001) predict that under mixed control the sex allocation of sexuals is intermediate between the predicted uninvadable sex allocation strategies under full queen and full worker control (the exact values depending on the assumption about how colony productivity scales with colony size). However, as we argued in the previous section, the queen wins the sex allocation conflict in our model, because the sex allocation ratio is determined during the reproductive phase by the queen. However, in the model of Reuter and Keller (2001), behavioural decisions can not vary over time, meaning that the two parties make their decisions simultaneously for the whole season T. Hence, this way of modelling links all the allocation decisions together to happen simultaneously, which leads to the result that workers can influence the sex allocation ratio by rearing some worker destined female brood into queens. Pen and Taylor (2005) studied a static resource allocation model similar to the model of Reuter and Keller (2001), but they also looked at the effect of information exchange between the two parties. They concluded that the queen wins the sex allocation conflict if the queen is able to act first and the workers can observe the queen's strategy and respond; hence they studied the so-called Stackelberg equilibrium (Pen and Taylor, 2005). While they arrived at a conclusion similar to ours about the overall sex allocation ratio, our result implies that the workers do not have to have the information about the ratio at which the queen lays the male to female eggs.

Reuter and Keller (2001) argue that a complete control by a single party is not evolutionarily stable, since the conflict over sex allocation strongly selects for the other party to manipulate the sex allocation leading to a stable evolutionary equilibrium where the sex allocation is intermediate between the predicted evolutionary outcomes for full control of the two parties. However, under the dynamic model, we show that under the assumptions of mixed control, an intermediate sex allocation will not evolve. Hence, other mechanisms, such as higher queen

mating frequency, have to be involved for the sex allocation to be intermediate under mixed control.

Conclusion

We showed that when dynamic properties of resource allocation are considered, sex allocation conflict can substantially affect colony ontogeny, and thus overall patterns of growth and productivity. Helanterä (2016) has argued that life-history trade-offs may be easier traits to conceptualize as organismal traits (i.e. traits evolving like group-selected adaptations), as opposed to traits more heavily contingent on conflicts among genes in different individuals, such as traits involving sex allocation and dispersal behaviour. In contrast, our model suggests that colony life-history traits can generally not be viewed in isolation from traits that are influenced by genetic conflicts, and hence both, the "morphology" and "physiology" of a colony are likely to be affected by them, leading to a general breakdown of the "organismic" perspective of eusocial insect colonies.

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Figures and tables

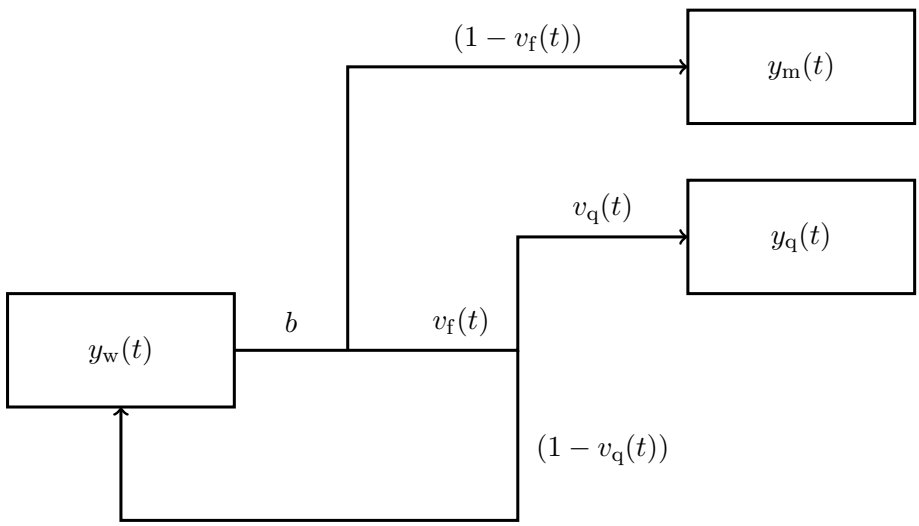

Figure 1: A schematic diagram that depicts how colony resource allocation gives rise to colony population dynamics. Workers (measured by $y_{\mathrm{w}}(t)$) acquire resources from the environment at a (constant) rate b. At time $t \in [0, T]$, a fraction $0 \leq v_{\mathrm{f}}(t) \leq 1$ of the resources is allocated to producing females (either new queens or workers), while the remaining fraction $(1 - v_{\mathrm{f}}(t))$ is allocated to males (measured by $y_{\mathrm{m}}(t)$). From the resources that are allocated to females, a fraction $0 \leq v_{\mathrm{q}}(t) \leq 1$ is allocated to sexual females (new queens, measured by $y_{\mathrm{q}}(t)$) and the remaining fraction $(1 - v_{\mathrm{q}}(t))$ is allocated to workers.

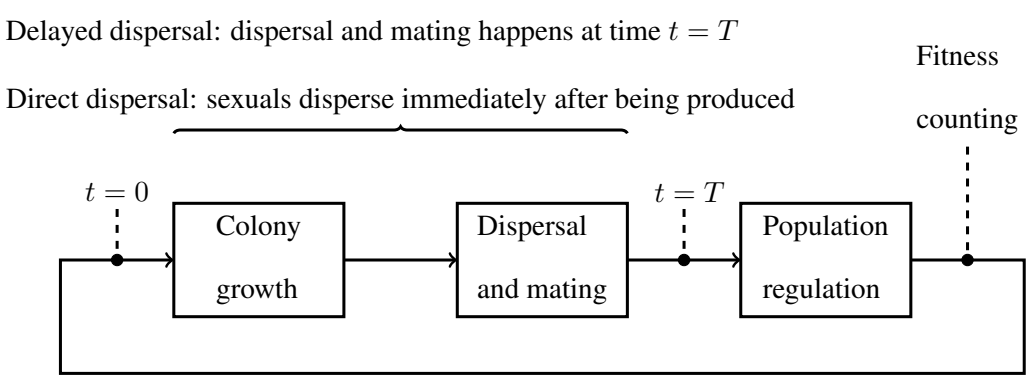

Figure 2: A schematic diagram of the life cycle of the the species. The fitness counting starts and ends at the beginning of the new season after population regulation (females compete for breeding spots).

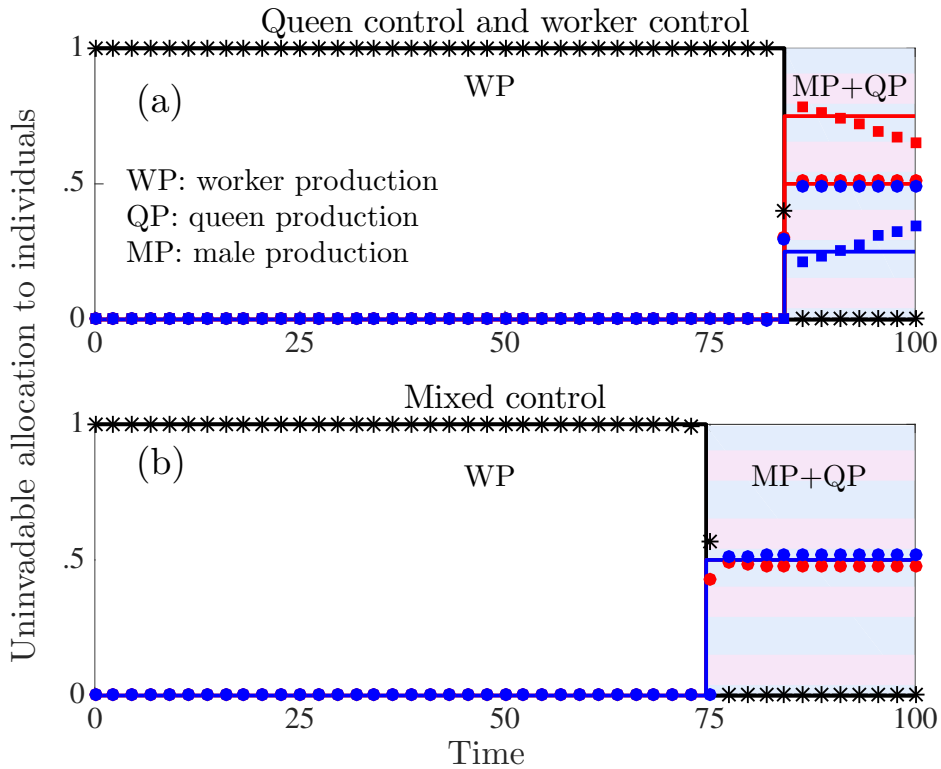

Figure 3: Uninvadable proportional allocation (under delayed dispersal) to workers $a_{\mathrm{w}}^*(t) = u_{\mathrm{f}}^*(t)(1 - u_{\mathrm{q}}^*(t))$ (black lines and asterisks), queens $a_{\mathrm{q}}^*(t) = u_{\mathrm{f}}^*(t)u_{\mathrm{q}}^*(t)$ (red lines, circles, and squares), and males $a_{\mathrm{m}}^*(t) = (1 - u_{\mathrm{f}}^*(t))$ (blue lines, circles, and squares). Ergonomic phase (white area), reproductive phase (area with pink and blue stripes, which represents simultaneous production of queens and males). Solid lines are analytically predicted results and the correspondingly colored circles, squares and asterisks represent the numerical results. Panel (a): single-party control, allocation to queens and males under queen control (circles) and under worker control (squares). Panel (b): mixed control. Parameter values: $M = 1$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

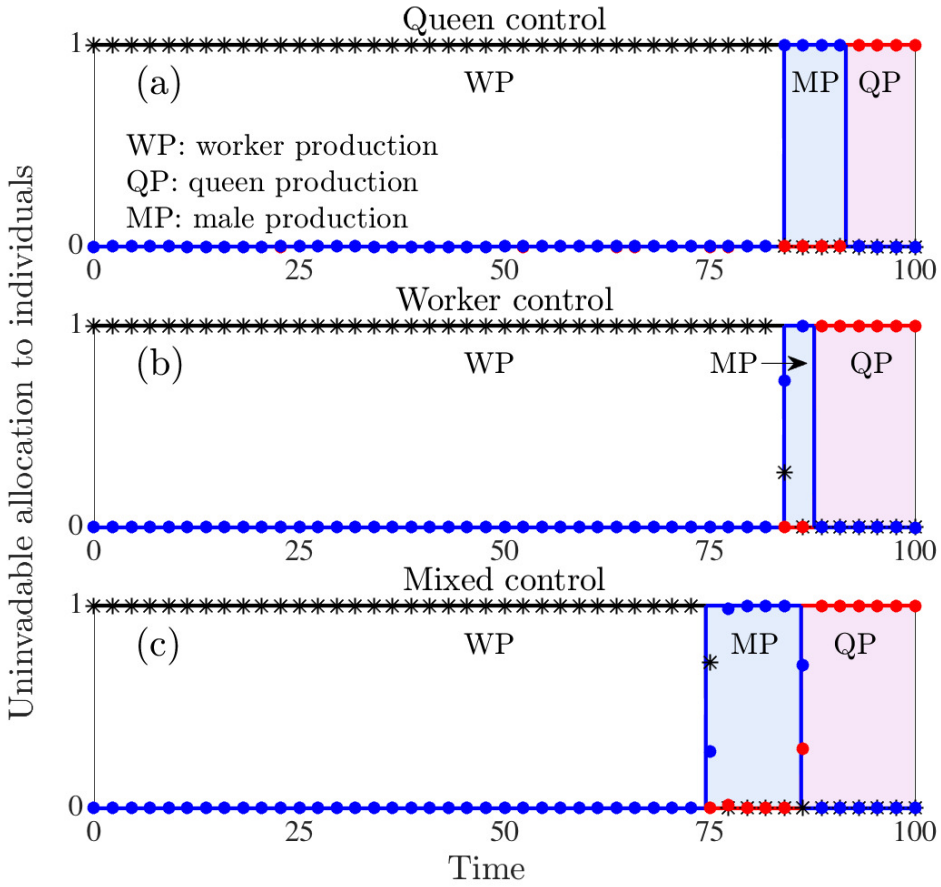

Figure 4: Uninvadable proportional allocation (under direct dispersal) to workers $a_{\mathrm{w}}^*(t) = u_{\mathrm{f}}^*(t)(1 - u_{\mathrm{q}}^*(t))$ (black lines and asterisks), queens $a_{\mathrm{q}}^*(t) = u_{\mathrm{f}}^*(t)u_{\mathrm{q}}^*(t)$ (red lines and circles), and males $a_{\mathrm{m}}^*(t) = (1 - u_{\mathrm{f}}^*(t))$ (blue lines and circles). Ergonomic phase (white area), reproductive phase: male production (blue area) and queen production (pink area). Solid lines are analytically predicted results and the correspondingly colored circles and asterisks represent the numerical results. Panel (a): queen control. Panel (b): worker control. Panel (c): mixed control. Parameter values: $M = 1$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

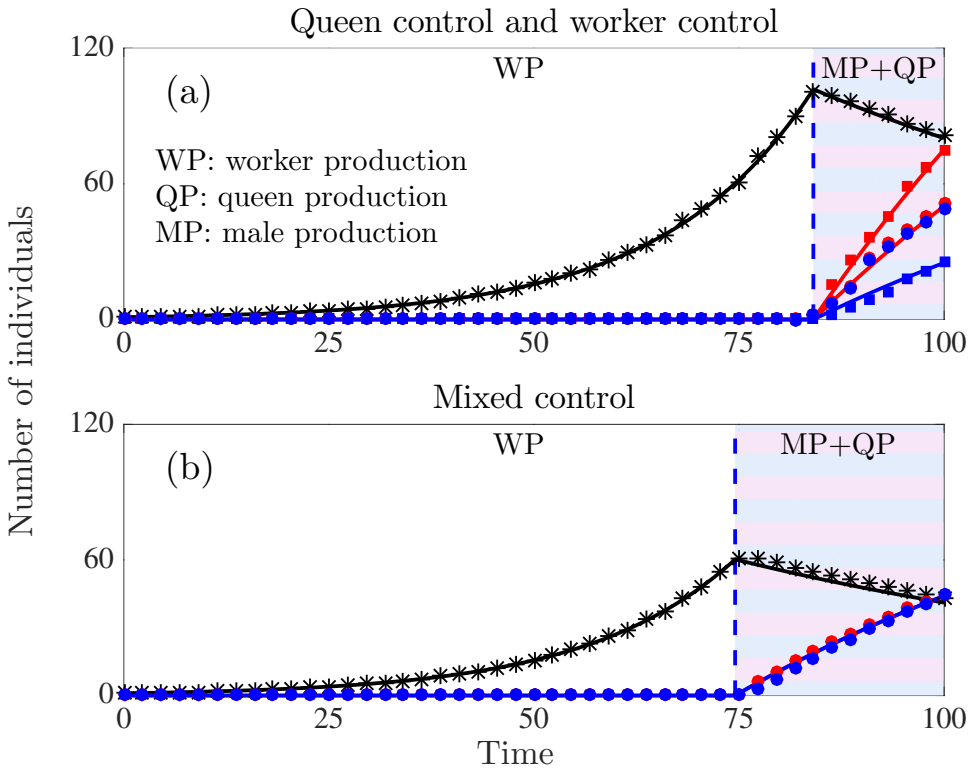

Figure 5: Number of individuals produced in a colony following the uninvadable resource allocation schedule $\mathbf{u}^*$ under delayed dispersal. Solid lines are analytically predicted results and the correspondingly colored circles, squares and asterisks represent the numerical results. Ergonomic phase (white area), reproductive phase (area with pink and blue stripes, which represents simultaneous production of queens and males). Panel (a): single-party control, the number of workers under full queen and full worker control (black), the number of juvenile queens under queen control (red circles) and worker control (red squares), the number of males under queen control (blue circles) and worker control (blue squares). Panel (b): mixed control, the number of workers (black), the number of juvenile queens (red), the number of males (blue). Parameter values: $M = 1$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

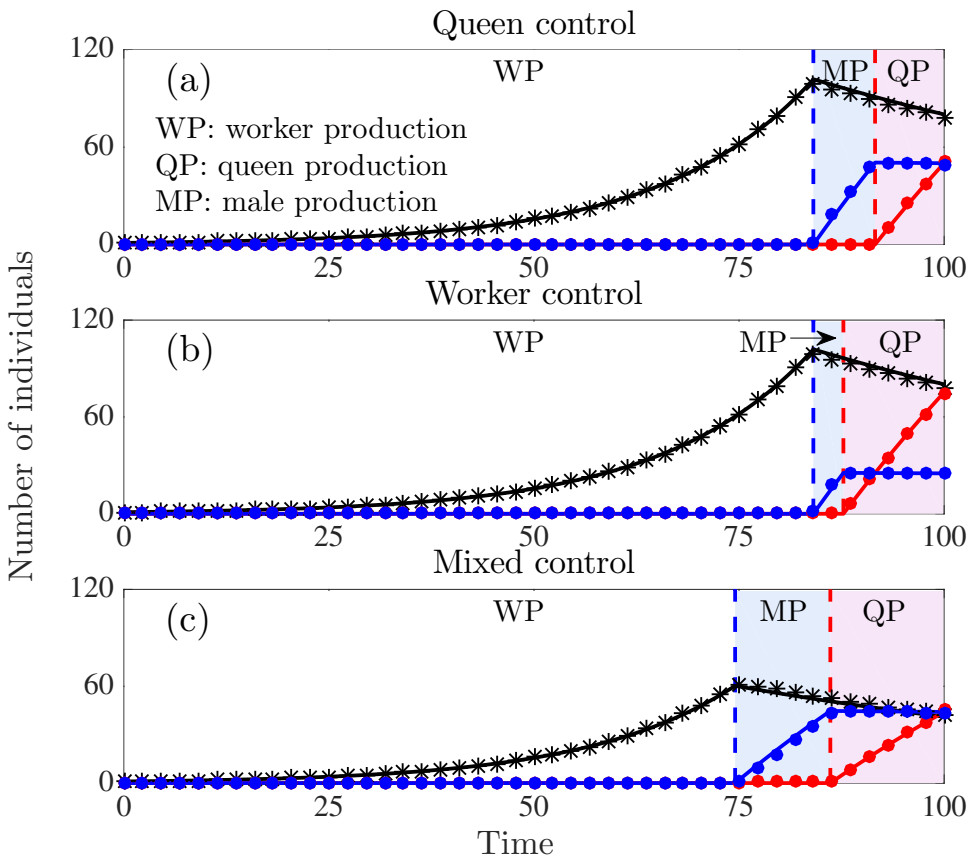

Figure 6: Number of individuals produced in a colony following the uninvadable resource allocation schedule $\mathbf{u}^*$ under direct dispersal. Solid lines are analytically predicted results and the correspondingly colored circles and asterisks represent the numerical results. Ergonomic phase (white area), reproductive phase: male production (blue area) and queen production (pink area). Panel (a): full queen control. Panel (b): full worker control. Panel (c): mixed control. Number of workers (black), number of juvenile queens (red), number of males (blue). Parameter values: $M = 1$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

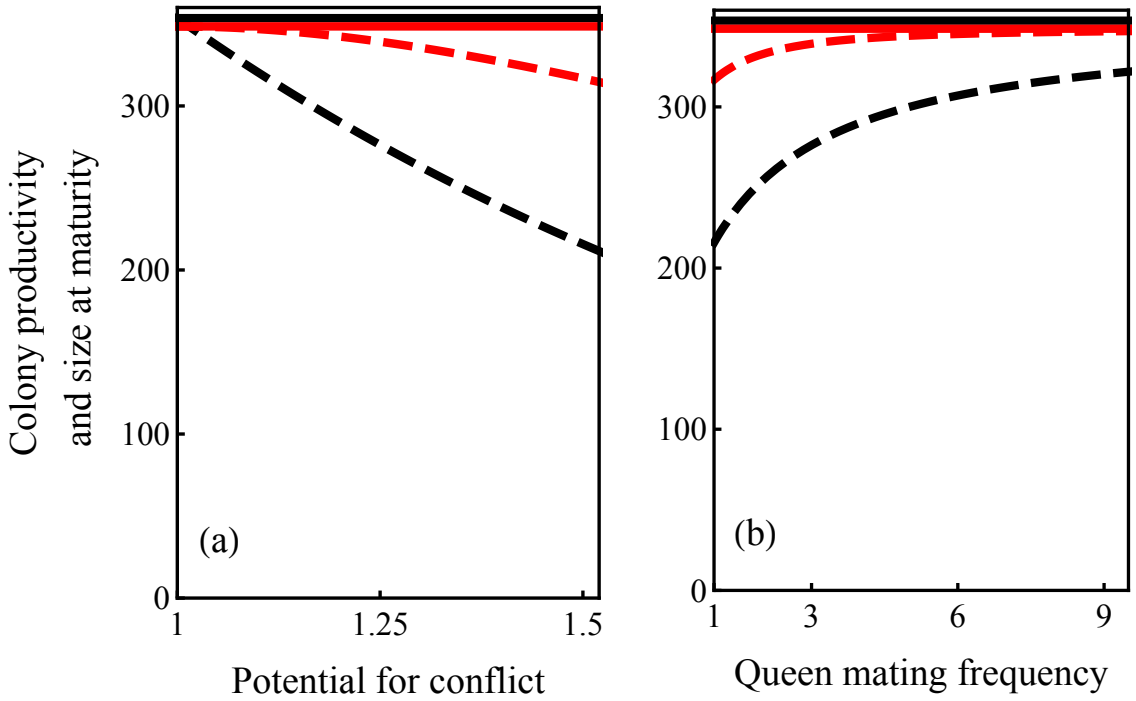

Figure 7: Colony productivity $B(t^*_{c,1})$ (red lines) and size at maturity $x^*_{\mathrm{w}}(t^*_{c,1})$ (black lines) under single-party (solid lines) and mixed control (dashed lines) as a function of the potential for conflict C (panel a) and as a function of queen mating frequeny (panel b) for the uninvadable resource allocation schedule $\mathbf{u}^*$. Parameter values: $b = 0.07$, $\mu_{\mathrm{w}} = 0.0015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

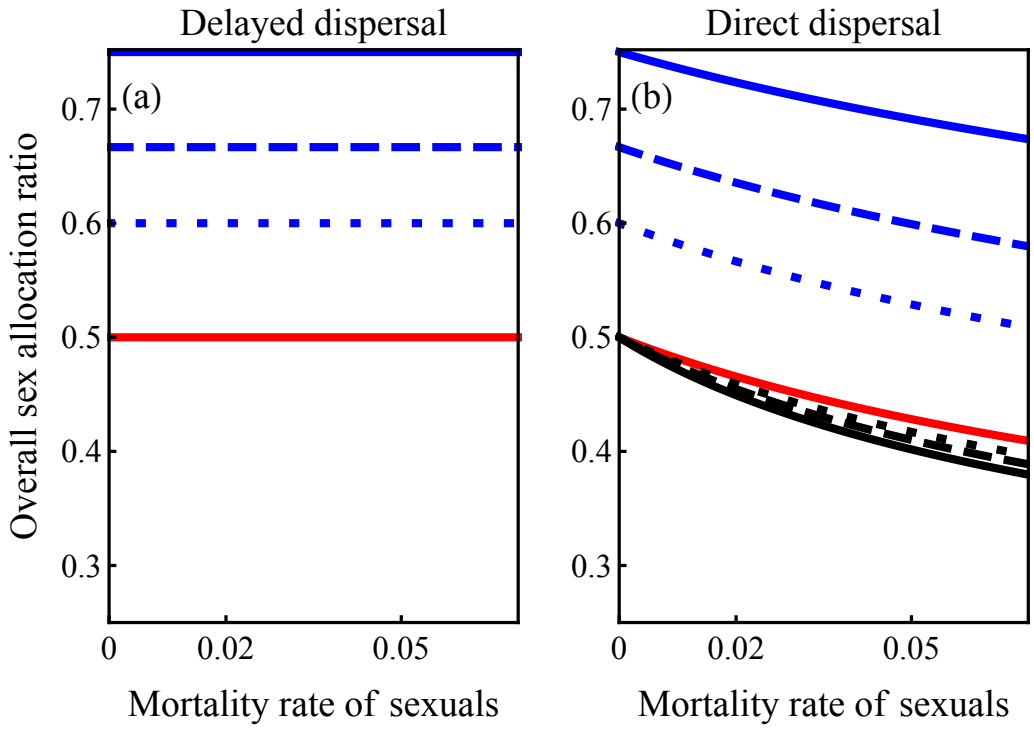

Figure 8: Overall proportional sex allocation ratio S_c as a function of mortality rate of the sexuals μ_{r} for different values of queen mating frequency M (or potential conflict $C = (2+M)/(1+M)$). Panel (a): delayed dispersal. Panel (b): direct dispersal. Queen control (red lines) for any value of queen mating frequency M; worker control (blue lines): $M = 1$ (solid blue), $M = 2$ (dashed blue), $M = 4$ (dotted blue); mixed control for delayed dispersal for any value of M (red line); mixed control for direct dispersal (black lines): $M = 1$ (solid black), $M = 2$ (dashed black), $M = 4$ (dotted black). Other parameter values: $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $T = 100$.

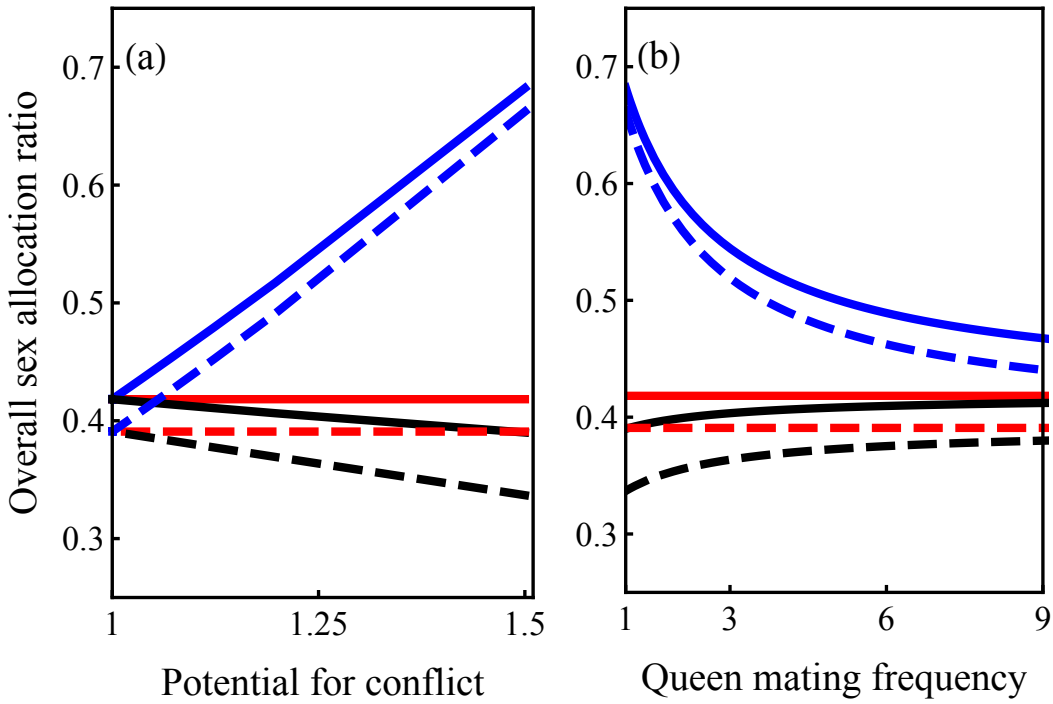

Figure 9: Overall proportional sex allocation ratio S_c under direct dispersal as a function of the potential for conflict C (panel a) and queen mating frequency M (panel b) for different values of mortality of workers μ_{w}. Queen control (red lines): $\mu_{\mathrm{w}} = 0.015$ (solid red), $\mu_{\mathrm{w}} = 0.065$ (dashed red); worker control (blue lines): $\mu_{\mathrm{w}} = 0.015$ (solid blue), $\mu_{\mathrm{w}} = 0.065$ (dashed blue); mixed control (black lines): $\mu_{\mathrm{w}} = 0.015$ (solid black), $\mu_{\mathrm{w}} = 0.065$ (dashed black). Parameter values: $b = 0.07$, $\mu_{\mathrm{r}} = 0.06$, $T = 100$.