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

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Short running title: Dynamic sex allocation conflict

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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 of 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.

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Introduction

Eusocial Hymenopteran colonies 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, such individuals are usually not clonal, whereby some genes, for instance those influencing sex allocation or reproductive ability of workers, can experience diverging selection pressures in different individuals (Haig, 2003; Hamilton, 1967; Ratnieks et al., 2006).

One of the most intensively studied genetic conflicts 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 and multiple matings by the queen, reduce the extent of the genetic conflict over sex allocation because they reduce relatedness asymmetries between individuals within colonies (Frank, 1998; 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 opposing "parties" can influence how colony resources are allocated into producing individuals of different types. If a colony is founded by a single queen, then there are two opposing parties, the genes in the workers and the genes in the colony-founding queen. The genetic control over 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 reasons to expect that the genes in the queen and workers simultaneously control different resource allocation decisions, because both parties are known to have means to control different resource allocation decisions and there can be strong selection for a party to seize control over a resource allocation decision if there are means to do so (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 sex allocation conflict 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 predict which party is in control of the underlying resource allocation decisions, given that one has sex-allocation data. 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

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references in Mitesser et al. (2007a), Crone and Williams (2016)). Such that, in the beginning of the season only workers are produced, i.e. the ergonomic phase followed by a drastic shift into exclusive production of sexuals (males and future queens), i.e. the reproductive phase. This life-history schedule is an 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 and his predictions relied on some additional restrictive assumptions. For example, he assumed that the worker generations do not overlap within a season (i.e. a colony grows in separate generation of workers within a season) 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 of clonal reproduction with no genetic conflicts (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 worker and 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 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: queen control, worker control, and mixed control; and two alternative scenarios of dispersal of sexuals: delayed disper-

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sal (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 future queens can be produced. (2) *Dispersal*: sexuals disperse out of their natal colony, such that no inbreeding, local mate competition, or local resource competition takes place; we consider two alternative scenarios for the timing of dispersal (to be detailed below). (3) *Mating*: random mating occurs and all queens mate exactly with $M \geq 1$ males. (4) *Regulation*: all individuals die at the end of the season, except (juvenile) queens who randomly compete for the n breeding slots to initiate colonies of the next generation.

Dispersal and mating

The two dispersal scenarios are as follows: (i) delayed dispersal, where sexuals all disperse at the same time at the end of the season, 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. To describe our model, we start by considering that the population is monomorphic for all phenotypes, and will later introduce variation and selection. The size of a focal colony at time $t \in [0, T]$ in the (monomorphic) population 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. For simplicity, we assume that all individuals are equally costly to produce, which allows to equate the investment allocation

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ratio to the numerical sex ratio. 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.

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 $y_{\mathrm{w},0} = 1$ (the colony founding queen is counted as a worker, since she can for example recover some resources from her body fat), $y_{\mathrm{q},0} = 0$ (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

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

Under delayed dispersal, all females are inseminated at time $t = T$, where a total number of $ny_\mathrm{m}(T)$ males compete for $ny_\mathrm{q}(T)$ females. Hence the mating success of a male produced in a focal colony is $y_\mathrm{q}(T)/y_\mathrm{m}(T)$, and the number of males in that colony at the end of the season is $y_\mathrm{m}(T)$. Under direct dispersal, females mate immediately after being produced, whereby at time t a total number of $nba_\mathrm{q}(t)y_\mathrm{w}(t)$ females are available to mate (after which they will leave the mating pool). In contrast, males stay in the mating pool, hence at time t, an average number of $ny_\mathrm{m}(t)$ males compete for the access to females. Therefore, the mating success of a male produced in a focal colony is $ba_\mathrm{q}(t)y_\mathrm{q}(t)/y_\mathrm{m}(t)$ at time 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.

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Resource allocation traits

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 controled by two traits

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

The first trait $0 \leq v_{\mathrm{f}}(t) \leq 1$ is the proportion of resources allocated to producing females (individuals destined to become workers or queens) at time t. The second trait $0 \leq v_{\mathrm{q}}(t) \leq 1$, gives the proportion of resources allocated to producing queens from resources allocated to females at time $t \in [0, T]$. Thus $(1 - v_{\mathrm{f}}(t))$ is the proportional allocation to males and $(1 - v_{\mathrm{q}}(t))$ is the proportional allocation of resources directed to producing workers from resources allocated to females.

Our aim is to investigate the evolution of the resource allocation schedule during the whole colony ontogeny, i.e., the evolution of $\mathbf{v} = \{v_{\mathrm{f}}(t), v_{\mathrm{q}}(t)\}_{t \in [0,T]}$. 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), but for simplicity we do not consider this scenario in our paper. 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: queen control (i.e. the genes in the queen determine resource allocation decisions), worker control (i.e. the genes in the queen determine resource allocation decisions) and mixed control, where the genes in the queen control v_{f} (the proportional investment into females versus males) and the genes in the workers control v_{q} (the proportional investment into new queens versus workers). 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.

In order to analyse the long-term evolution of the resource allocation traits, we perform an evolutionary invasion analysis (see section 1 of S.I. for more information). That is, we consider the fate (invasion or extinction) of a single mutant allele (an allele determines the entire allocation schedule, i.e., a trajectory of the trait over $t \in [0, T]$) introduced into a population of resident individuals and ask what is the (candidate) uninvadable allocation schedule $\mathbf{v}^* = \{v_{\mathrm{f}}^*(t), v_{\mathrm{q}}^*(t)\}_{t \in [0,T]}$; namely, the allocation schedule resistant to invasion by any mutant schedule that deviates from $\mathbf{v}^*$. We determine the (candidate) uninvadable allocation schedule $\mathbf{v}^*$ analytically using Pontryagin's maximum principle (see sections 3–6 of S.I.), which gives a necessary condition for optimality, and we confirm these results numerically using GPOPS–II (Patterson and Rao, 2014), which gives support

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to the attainability of the uninvadable schedules (see section 11 in S.I.).

Results

Marginal value, relatedness asymmetry, and potential for conflict

Dynamic marginal value result

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

$$u_\tau(t) = v^*_\tau(t) + \epsilon_\tau \eta_\tau(t), \tag{4}$$

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

Let us now denote by $y_k(\mathbf{u}) \equiv y_k(T)$ the number of type $k \in \{\mathrm{q}, \mathrm{iq}\}$ individuals at the end of the season where the resident allocation schedule $\mathbf{v}$ in eqs. (1) and (2) has been replaced by the mutant allocation schedule $\mathbf{u}$. Then, the first-order condition for a schedule $\mathbf{v}^*$ to be uninvadable when party $c \in \{\mathrm{q}, \mathrm{w}\}$ is in control of the trait of type $\tau \in \{\mathrm{f}, \mathrm{q}\}$ can be written as

$$-\left.\frac{\mathrm{d}y_{\mathrm{iq}}(\mathbf{u})/\,\mathrm{d}\epsilon_\tau}{\mathrm{d}y_{\mathrm{q}}(\mathbf{u})/\,\mathrm{d}\epsilon_\tau}\right|_{\epsilon_{\mathrm{f}}=0,\epsilon_{\mathrm{q}}=0} = R_c, \tag{5}$$

and for mixed control this equality holds simultaneously for each trait being under the control of the respective party (see eqs. S26–S31 in section 2 of S.I for a proof). Here, $\mathrm{d}y_k(\mathbf{u})/\,\mathrm{d}\epsilon_\tau$ is the functional (variational) derivative (e.g., Troutman, 2012, p. 45–50, Luenberger, 1997, p. 171–178) measuring the change in the number of individuals $y_k(\mathbf{u})$ of type $k \in \{\mathrm{q}, \mathrm{iq}\}$ produced by the end of the season in a mutant colony (and we here emphasized that this number depends on the whole allocation schedule, recall eqs. 1–2), due to the infinitesimal deviation $\epsilon_\tau \eta_\tau(t)$ of the trait of type τ throughout the entire season $t \in [0, T]$. Thus, the left-hand side in eq. (5) is minus 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. This can be thought of as measuring the amount of inseminated queens that needs to be gained by producing one male in exchange of a queen, while holding (replicator) fitness constant (i.e. "marginal substitution rate"), and is given by

$$R_c = \frac{\alpha^\circ_{\mathrm{q}} r^\circ_{\mathrm{q},c}}{\alpha^\circ_{\mathrm{m}} r^\circ_{\mathrm{m},c}}. \tag{6}$$

This turns out to be 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 of 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. S32–S34), we detail that the relatedness asymmetry

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can be interpreted as giving the ratio of sex-specific (queen/male) contributions, of genes in party c, to the gene pool in the distant future (under a neutral process). For haplodiploids the relatedness asymmetry is $R_{\mathrm{q}} = 1$ (queen control) and $R_{\mathrm{w}} = (2 + M)/M$ (worker control).

Eq. (5) is a generalised formulation of Fisher's (1930) theory of equal allocation (under queen control) and the standard static marginal value result of sex allocation theory (e.g., Taylor and Frank, 1996, eq. 22). The novelty of eq. (5) is that it results from a dynamic model, where the (gene) fitness return of a (unit) investment ("marginal return" for short) of producing an individual is time-dependent, and natural selection favours an allocation schedule that produces males and queens in such a way that the ratio of surviving inseminated queens and produced queens is equal to the relatedness asymmetry. Note that eq. (5) does not directly give the ratio of total amount of resources invested ("overall investment" ratio) in each sex, which depends on the characteristics of the life cycle. Furthermore, we show that the overall investment ratios can depart from classic static results of sex allocation theory under direct dispersal of our model.

Proportional relatedness asymmetry

It follows from the first-order condition that the marginal substitution rate is given by the relatedness asymmetry, i.e. the ratio of sex-specific asymptotic contributions to the gene-pool (eq. 5). However, it will turn out to be useful to define the proportional contribution of genes of party c through queens to the future gene pool, i.e.

$$P_c = \frac{R_c}{1 + R_c}, \tag{7}$$

which can be thought of as a proportional relatedness asymmetry. This quantity evaluates to $P_{\mathrm{q}} = 1/2$ (queen control) and $P_{\mathrm{w}} = (2+M)/(2(1+M))$ (worker control), and it is equal to the (overall) uninvadable proportional allocation into females according to the classical static models of sex allocation theory under single-party control (Boomsma and Grafen, 1991; Reuter and Keller, 2001; 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

$$C = \frac{P_{\mathrm{w}}}{P_{\mathrm{q}}}. \tag{8}$$

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. In haplodiploids, the potential for conflict $C = C(M) = (2 + M)/(1 + M)$ decreases with the increase in polyandry M (Ratnieks and Boomsma, 1995), since $P_{\mathrm{w}} \to P_{\mathrm{q}}$ with the increase in queen mating frequency. Hence, the potential conflict $C(1) = 1.5$ is maximal when the queen mates once. 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.

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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 $\mathbf{v}^*$ that satisfies the first-order condition (recall eq. 5). 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

The uninvadable allocation schedule $\mathbf{v}^*$ consists of two phases: the ergonomic phase ($t \in [0, t^*_{c,1}]$) during which workers are produced and the reproductive phase ($t \in [t^*_{c,1}, T]$) during which sexual offspring are produced (see sections 5 and 6 of SI for derivations). 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, resources should be allocated such that the sex allocation ratio at the end of the season is given by the relatedness asymmetry under delayed dispersal, while under direct dispersal, males are produced before queens and sex allocation ratio is more male-biased than under delayed dispersal.

Under delayed dispersal of sexuals, the schedule $\mathbf{v}^*$ consists of the following phases of colony growth

$$\begin{aligned} &\textbf{Production of workers:} && (v^*_{\mathrm{f}}(t), v^*_{\mathrm{q}}(t)) = (1, 0) && t \in \left[0, t^*_{c,1}\right], \\ &\textbf{Production of males and queens:} && (v^*_{\mathrm{f}}(t), v^*_{\mathrm{q}}(t)) = (\hat{\bar{v}}^*_{\mathrm{f}}, 1) && t \in \left[t^*_{c,1}, T\right], \end{aligned} \tag{9}$$

where $\hat{\bar{v}}^*_{\mathrm{f}}$ denotes a constant singular arc (simply put, singular arc in this context means that individuals of different types are produced simultaneously, see section 3.3 of SI for a formal definition) that determines the proportional resource allocation into queens during the reproductive phase and is equal to the proportional relatedness asymmetry (see eqs. 12 and 7).

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

$$\begin{aligned} &\textbf{Production of workers:} && (v^*_{\mathrm{f}}(t), v^*_{\mathrm{q}}(t)) = (1, 0) && t \in \left[0, t^*_{c,1}\right], \\ &\textbf{Production of males:} && (v^*_{\mathrm{f}}(t), v^*_{\mathrm{q}}(t)) = (0, \tilde{v}^*_{\mathrm{q}}(t)) && t \in \left[t^*_{c,1}, t^*_{c,2}\right], \\ &\textbf{Production of queens:} && (v^*_{\mathrm{f}}(t), v^*_{\mathrm{q}}(t)) = (1, 1) && t \in \left[t^*_{c,2}, T\right], \end{aligned} \tag{10}$$

where $t^*_{c,2}$ is the switching time from production of only males to production of only queens and $\tilde{v}^*_{\mathrm{q}}(t)$ denotes that allocation to queens versus workers is undetermined during male production.

In Figs. 1–2 we have depicted the analytically and numerically determined uninvadable allocation schedules $\mathbf{u}^*$ in terms of proportional allocation to workers $a^*_{\mathrm{w}}(t) = v^*_{\mathrm{f}}(t)(1 - v^*_{\mathrm{q}}(t))$, queens $a^*_{\mathrm{q}}(t) = v^*_{\mathrm{f}}(t)v^*_{\mathrm{q}}(t)$, and males $a^*_{\mathrm{m}}(t) = (1 - v^*_{\mathrm{f}}(t))$ and in Figs. 3–4 we have depicted the respective number of (surviving) individuals (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 workers versus sexuals and it depends on the scenario of genetic control over the resource allocation

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traits; namely,

$$t^*_{c,1} = \begin{cases} T - \dfrac{\ln\left(1 + \frac{\mu_\mathrm{r} - \mu_\mathrm{w}}{b}\right)}{\mu_\mathrm{r} - \mu_\mathrm{w}}, & \text{(single-party control, } c \in \{\mathrm{q}, \mathrm{w}\}), \\ T - \dfrac{\ln\left(1 + C\frac{\mu_\mathrm{r} - \mu_\mathrm{w}}{b}\right)}{\mu_\mathrm{r} - \mu_\mathrm{w}}, & \text{(mixed control, } c = \mathrm{mx}), \end{cases} \tag{11}$$

(see sections 5 and 6 of S.I. for derivation, especially see eqs. S100–S108, S110–S113, S124–S141, S131–S138). 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 the clonal model of Macevicz and Oster (1976), by setting $b = bR$, $\mu_\mathrm{w} = \mu$, and $\mu_\mathrm{r} = \nu$ (see section 13 of S.I. for an overview of how our model relates to previous work).

It follows from eq. (11) that the switch from the ergonomic to the reproductive phase under mixed control $t^*_{\mathrm{mx},1}$ depends on the potential for conflict $C \geq 1$. Furthermore, this switch happens earlier in the season under mixed control than under single-party control (i.e. $t^*_{\mathrm{mx},1} < t^*_{\mathrm{q},1} = t^*_{\mathrm{w},1}$, see also Fig. 1 for delayed dispersal and Fig. 2 for direct dispersal, assuming queen monandry, i.e. $C = 1.5$). 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 8 in S.I. for more detailed explanation). Eq. (11) 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. 11).

Production of males and queens in the reproductive phase

Under delayed dispersal, selection favors any allocation schedule that produces an allocation ratio of females and males at the end of the season which is equal to the relatedness asymmetry. There are several uninvadable strategies that can satisfy this condition, the most simple one being the constant allocation $v^*_\mathrm{f}(t) = \hat{\bar{v}}^*_\mathrm{f}$ and $\bar{v}_\mathrm{q} = 1$ during the reproductive phase ($t \in [t^*_{c,1}, T]$). The (candidate uninvadable) proportional allocation into production of queens in the reproductive phase is

$$a^*_\mathrm{q}(t) = \hat{\bar{v}}^*_\mathrm{f} = \begin{cases} P_\mathrm{q} & \text{(queen control \& mixed control)}, \\ P_\mathrm{w} & \text{(worker control)}. \end{cases} \tag{12}$$

Under direct dispersal, selection favours the production of males before queens (protandry). This is because the reproductive success of males and queens depends asymmetrically on the time they are produced. The switching time $t^*_{c,2}$ from male production to queen production happens for $M = 1$ when

$$\frac{F_c(t^*_{c,2})}{l_\mathrm{q}(t^*_{c,2})} = \begin{cases} R_\mathrm{q} = 1 & \text{(queen control \& mixed control)}, \\ R_\mathrm{w} = \dfrac{2+M}{M} & \text{(worker control)}, \end{cases} \tag{13}$$

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where the left hand side is the ratio of the cost to the benefit to (gene) fitness of producing a queen instead of a male at $t^*_{c,2}$ and the right hand side is the exchange rate between inseminated females and queens, which is given by the relatedness asymmetry (recall eq. 5). The cost of producing a queen instead of a male (at $t^*_{c,2}$) is equal to the potential mating success of a male (born at $t^*_{c,2}$), measured in the "currency" of expected number $F_c(t^*_{c,2})$ of inseminated queens who survive until the end of the season. The benefit of producing a queen (at $t^*_{c,2}$) is equal to the probability $l_{\mathrm{q}}(t^*_{c,2})$ that she survives until the end of the season. Note that in a population, where the queens mate M times, the expected number $MF_c(t^*_{c,2})$ of surviving queens inseminated by males alive at time $t^*_{c,2}$, has to divided by the the queen mating frequency M (since the focal male is expected to father only $1/M$ of the diploid offspring). Hence, eq. (13) holds under any queen mating frequency M (see section 9 of S.I.).

Queen is in control of the switch from male production to queen production under mixed control, since under both queen and mixed control the switch happens at the time when producing a male instead of a surviving queen yields one surviving inseminated queen (recall eq. 13). Note that this does not imply that the switching time under queen control $t^*_{\mathrm{q},2}$ and mixed control $t^*_{\mathrm{mx},2}$ is equal and it follows from eq. (13) that the switching time is

$$t^*_{c,2} = \begin{cases} T - \dfrac{1}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \ln\left(\dfrac{b + \mu_{\mathrm{r}} - \mu_{\mathrm{w}}}{b + (1 - P_{\mathrm{q}})(\mu_{\mathrm{r}} - \mu_{\mathrm{w}})}\right) & \text{(queen control, } c = \mathrm{q}), \\ T - \dfrac{1}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \ln\left(\dfrac{b + \mu_{\mathrm{r}} - \mu_{\mathrm{w}}}{b + (1 - P_{\mathrm{w}})(\mu_{\mathrm{r}} - \mu_{\mathrm{w}})}\right) & \text{(worker control, } c = \mathrm{w}), \\ T - \dfrac{1}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \ln\left(2 - \dfrac{b}{b + \frac{1}{2}C\,(\mu_{\mathrm{r}} - \mu_{\mathrm{w}})}\right) & \text{(mixed control, } c = \mathrm{mx}). \end{cases} \tag{14}$$

This shows that the switch to production of queens happens later under queen control than under worker control ($t^*_{\mathrm{q},2} > t^*_{\mathrm{w},2}$), because $P_{\mathrm{q}} < P_{\mathrm{w}}$ and it 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, i.e. $t^*_{\mathrm{q},1} = t^*_{\mathrm{w},1}$). The switch to production of queens happens later under mixed control for higher values of the potential conflict C. Furthermore, the switch to queen production happens later when per-worker productivity b is small, worker mortality rate μ_{w} is large, and the mortality rate μ_{r} of sexuals is large.

Switching times when the mortality rate of workers and sexuals is equal

In our model $(1/b)$ can be loosely interpreted as the time it takes for one worker to help produce one offspring. 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 the time $(1/b)$ it takes for a worker to help produce an offspring before the season end (i.e. $t^*_{\mathrm{q},1} = t^*_{\mathrm{w},1} = T - 1/b$); only the individuals produced at the end of the season are reproductive. However, under mixed control the switch happens C times earlier (i.e. $t^*_{\mathrm{mx},1} = T - C/b$). For example, when females mate only once (i.e. $M = 1$ and $C = 1.5$) then the switch to reproductive phase happens at time $T - 3/(2b)$.

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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. 3 for delayed dispersal and Fig. 4 for direct dispersal). At time $t^*_{c,1}$ the 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

$$y^*_{\mathrm{w}}(t^*_{c,1}) = e^{(b-\mu_{\mathrm{w}})t^*_{c,1}} \tag{15}$$

where $y^*_{\mathrm{w}}(t)$ is the number of workers alive at time t and produced in a colony following the uninvadable allocation schedule $\mathbf{v}^*$ (see section 7.1 and Table 1 for the summary of parameter dependence). The colony size at maturity is smaller under mixed control than under single-party control (i.e. $y^*_{\mathrm{w}}(t^*_{\mathrm{mx},1}) < y^*_{\mathrm{w}}(t^*_{\mathrm{q},1}) = y^*_{\mathrm{w}}(t^*_{\mathrm{w},1})$), especially for higher values of potential conflict C (see also Figs. 3–4, and 5). This is because the ergonomic phase is shorter under mixed control, especially for higher values of potential conflict C. Recall that the potential for conflict C is a decreasing function of the mating frequency M of the queen (eq. 8). Hence, under mixed control, the colony size at maturity $y^*_{\mathrm{w}}(t^*_{\mathrm{mx},1})$ is larger for higher queen mating frequency M.

Colony productivity

We define colony productivity $B(t^*_{c,1}) = y^*_{\mathrm{m}}(T) + y^*_{\mathrm{q}}(T)$ as the total number of males and queens produced that survive until the end of the season at the uninvadable state. Since we have assumed that males and females are equally costly to produce, 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

$$B(t^*_{c,1}) = \frac{be^{bt^*_{c,1}}\left(e^{-\mu_{\mathrm{w}}T} - e^{-\mu_{\mathrm{r}}T+(\mu_{\mathrm{r}}-\mu_{\mathrm{w}})t^*_{c,1}}\right)}{\mu_{\mathrm{r}} - \mu_{\mathrm{w}}} \tag{16}$$

(see section 7.2 in S.I. for derivation and Table 1 for the summary of parameter dependence). It turns out that the switching time $t^*_{c,1}$ under single-party control, $c \in \{\mathrm{q}, \mathrm{w}\}$ (given by eq. 11) maximizes the colony productivity (see section 7.2 in S.I. for proof). In Fig. 5, 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. Potential conflict C is a decreasing function of the mating frequency M of the queen (eq. 8). Hence, under mixed control, colony productivity $B(t^*_{\mathrm{mx},1})$ increases with the mating frequency M of the queen.

Sex allocation ratio

The overall sex allocation ratio at the evolutionary equilibrium, defined as the proportion of the colony resources allocated to queens from the resources allocated to sexuals over the entire season (irrespective of whether they

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survive to reproduce) can be expressed as

$$S_c = \frac{\int_0^T b a_{\mathrm{q}}^*(t) y_{\mathrm{w}}^*(t)\,\mathrm{d}t}{\int_0^T b a_{\mathrm{q}}^*(t) y_{\mathrm{w}}^*(t)\,\mathrm{d}t + \int_0^T b a_{\mathrm{m}}^*(t) y_{\mathrm{w}}^*(t)\,\mathrm{d}t}. \tag{17}$$

Here, the subscript $c \in \{\mathrm{q}, \mathrm{w}, \mathrm{mx}\}$ emphasizes the dependence on the scenario of genetic control, which enters into eq. (17) implicitly via the uninvadable allocation schedule (given by eqs. S14, 9, and 10). S_c can be interpreted as the overall proportion of queens among sexuals produced in the colony, since we assume that males and queens are equally costly to produce.

Under delayed dispersal, the overall sex allocation ratio is given by (section 7.3 of S.I., eqs. S163–S166)

$$S_c = \hat{\bar{u}}_{\mathrm{f}}^* = \begin{cases} P_{\mathrm{q}} & \text{(queen control \& mixed control)}, \\ P_{\mathrm{w}} & \text{(worker control)}. \end{cases} \tag{18}$$

Hence, under delayed dispersal the overall sex allocation ratio is given by the proportional relatedness asymmetry (via eq. 12 and recall eq. 7). It follows from eq. (18) 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 is given by (section 7.3 of S.I., eqs. S167– S169)

$$S_c = \frac{e^{-\mu_{\mathrm{w}} t_{c,2}^*} - e^{-\mu_{\mathrm{w}} T}}{e^{-\mu_{\mathrm{w}} t_{c,1}^*} - e^{-\mu_{\mathrm{w}} T}}. \tag{19}$$

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 $t_{c,2}^*$).

Under single party control, it follows from eq. (19) together with eqs. (11) and (14) (see Fig. 6) that for direct dispersal, the 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 $b > \mu_{\mathrm{r}}$). Under mixed control, the overall sex allocation ratio is more male-biased than under queen control for the same parameter values (see Fig. 6 and 7). The male-bias is more pronounced for higher mortality rates of sexuals (see Fig. 6) and workers (see Fig. 7). We illustrate in Figs. 6–7 that the male-bias can be substantial for higher values of mortality rates of sexuals and workers, e.g. $S_{\mathrm{mx}} \approx 0.35$ for mixed control under monandry, compared to $S_{\mathrm{mx}} = 0.5$ under delayed dispersal and $S_{\mathrm{mx}} \approx 0.56$ according to the corresponding static allocation model (see Table S3 in section 12 of S.I.). See also Table 1 for a summary of how S_c depends qualitatively on the parameters of the model.

In section 9 of S.I. we show that the switch from male production to queen production happens when producing a male yields R_c times as many surviving inseminated queens than producing a surviving queen (see eq. S183). Furthermore, we show that increased mortality of sexuals increases the reproductive success of (surviving) males produced before the emergence of queens, which delays the production of queens. This effect of increased mating success of males due to increased mortality is more pronounced under mixed-control when

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the reproductive phase is longer and proportionally more males are expected to die before the emergence of queens. Because of this, the sex allocation ratio is more male-biased for mixed control than under queen control (see Figs. 6 and 7). This combined effect of protandry, mortality and a longer duration of the reproductive phase under mixed control increases with the increase in the mortality of sexuals (see Fig. 6) and workers (see Fig. 7) and lower values of the productivity rate of a worker b.

Under mixed control and direct dispersal, the length of the reproductive phase is longer for higher values of the potential for conflict C. Because of this, proportionally more males die before the emergence of queens. Hence, under mixed control and direct dispersal, 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. 6–7). 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 the order in which sexuals are produced, the primary sex allocation ratio $u_{\mathrm{f}}^{*}(t)$ during the reproductive phase determines the overall sex allocation ratio. Hence, the queen is in control of the overall sex allocation ratio under mixed control (see also section 8 in S.I. for more detailed explanation).

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 earlier, 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 lower 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

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scenarios of dispersal of sexuals: direct dispersal after eclosion (common among many bees and wasps) and delayed dispersal at the end of the season, which resembles the life-history of species, where nuptial flights appear to be highly synchronized (more commonly found in ants, 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?

The results from our model suggest 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 using optimal control theory (a non-trivial task, see S.I. sections 5 and 6), 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 to its maximal size $y^*_{\mathrm{w}}(t^*_{c,1})$ and a reproductive phrase during which the total number $B(t^*_{c,1})$ of sexuals are produced. During the ergonomic phase, the marginal return of workers is higher than the return of investment into sexuals. Workers have a higher early marginal return 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 early marginal return 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 switch 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 under mixed control the queen controls the sex allocation ratio (for why this is so, see section "Which party wins the sex allocation conflict?" below), meaning that workers can not increase allocation to queens during the reproductive phase, even though producing more queens would increase the fitness of genes residing in workers. Hence, workers start rearing female eggs (destined to become workers under single-party control) into queens earlier, in order to increase the allocation to queens. This asymmetric

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control over the sex allocation ratio causes the switching time to the reproductive phase to be controlled by the workers (see also section 8 of S.I. for more technical explanation).

Colony size at maturity $y^*_{\mathrm{w}}(t^*_{c,1})$ 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. 5). This is so because in the latter case the switch to the reproductive phase occurs earlier, causing the colony size at maturity $y^*_{\mathrm{w}}(t^*_{c,1})$ to be smaller (there is less time for worker numbers to increase exponentially during the ergonomic phase). Therefore, there are fewer workers to produce sexuals in the reproductive phase, which results with a decline in colony productivity $B(t^*_{\mathrm{mx},1})$ (colony-level cost of sex allocation conflict).

A loss in colony productivity due to sex allocation conflict was already predicted using a static (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 within a season 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 earlier in species where the resource acquisition rate b is low, the mortality rate of workers μ_{w} is high and that of sexuals μ_{r} low. 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.

The switching time 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. 8), 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

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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 (sometimes called a graded control; i.e. workers and sexuals are produced simultaneously) 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 (but it has been shown that *Bombus terrestris* queens are able to control the switching time endogenously, Holland et al., 2013). Nevertheless, the framework of our model can be used to also study the evolution of eusociality, when we allow for the brood to have control over their own developmental fate. Current models that study the emergence of eusociality that explicitly track colony growth usually fix the switch from ergonomic to reproductive phase to happen at arbitrary size of the colony (e.g. **?**). Hence, extending our model to study evolution of eusociality could explain how life-history interacts with other mechanisms that are known to drive the evolution of eusociality.

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. 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. Under direct dispersal, reproductive success of males and queens depends asymmetrically on the time that they are produced. 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). On the other hand, females produced later in the season have higher chances of surviving until the end of the season. This asymmetry leads to protandry.

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

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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?

Our model shows that the queen wins (more accurately, the genes in queens win) the sex allocation conflict, and this obtains because the distinct phases of colony growth constrain 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 ($v_{\mathrm{f}}^{*}(t)$) determines the overall sex allocation ratio, since workers can only influence the developmental fate of the female eggs. The workers' only option to increase the overall allocation into queens, therefore, is to switch to the reproductive phase earlier at the expense of reduced colony productivity, while queens, regardless of the workers' allocation, can always further affect the sex-ratio without disturbing colony productivity.

The evolution of different phases of colony growth is thus crucial as it 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 distinct phases of colony growth 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 8 of S.I. for more detailed explanation). Our results thus suggest 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 overall sex allocation ratio

In our model, the overall sex allocation ratio depends on the scenario of dispersal of sexuals. 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 delayed dispersal, the overall sex allocation ratios predicted by our model are in accordance with the classical static models (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). However, under direct dispersal, we observe more male-biased overall sex allocation ratios than occur in the static models of sex allocation theory (e.g. Boomsma and Grafen, 1991; Trivers and Hare, 1976), especially for higher mortality rates of sexuals (see Fig. 6) and lower mortality rates of workers (see Fig. 7).

More male-biased sex allocation ratios evolve under direct dispersal because of the co-evolution of protandry (that evolves due to sexual selection on males) and sex allocation ratio due to mortality of sexuals. The sex allocation ratio is determined by the switching time $t_{c,2}^{*}$ from male production to queen production (which happens when producing a male yields R_c times as many surviving inseminated queens as producing a queen yields surviving queens). Hence, the mating success of males produced later in the season determines the switching time from male production to queen production. Males produced later in the season (just before

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the emergence of queens) have a higher mating success for higher values of mortality of sexuals, since there are fewer surviving males to compete with. Hence, higher mortality of sexuals delays the switch to queen production because it increases the mating success of males. Note that the increased mortality of a focal male does not cancel out here with increased mortality of competing males. This is because mortality affects equally (since we assumed that males and queens have equal mortality rates) the focal male, the queens he inseminates, and the focal queen, and these survival costs cancel each other out, when deciding to produce either a male (to gain surviving inseminated queens) or a queen (to gain surviving queens). However, independently of this, mortality affects the number of males available to mate. Hence, the overall sex allocation ratio is more male-biased under direct dispersal for higher values of mortality since males produced just before the emergence of queens have higher reproductive success (see section 9 for a more detailed analysis).

Under direct dispersal, the overall sex allocation ratio is more male-biased for mixed control than for queen control, even though for both queen and worker control, the switch from male production to queen production happens when producing a male instead of a surviving queen yields one surviving inseminated queen. This is because, for mixed control, the reproductive phase is longer during which proportionally more males die before they can mate, which increases the mating success of males produced later. This is why the overall allocation is more male-biased under mixed control for higher values of mortality of sexuals (see Fig. 6) and for other life history characteristics that cause the reproductive phase to be longer, such as higher values of the mortality rate of workers μ_{w} (see Fig. 7). Hence, we find that in protandrous species, proportionally more resources are expected to be allocated into producing males.

Surprisingly, under direct dispersal and mixed control 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, see Fig. 7). This 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, worker relatedness to female brood is expected to correlate negatively with the proportional investment into queens when resource allocation is under mixed control. This prediction contradicts 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

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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. 6). 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

Corresponding static and dynamic models can make completely different predictions for the outcome of the conflict. This can be seen when comparing the predictions of our model under delayed dispersal with the predictions of a corresponding static model by Reuter and Keller (2001). See section 12 of S.I., for a proof that our models are indeed comparable, even though there is a slight deviation in the assumption about how productivity scales with colony size (since this assumption does not affect qualitatively their results). We followed their approach on modeling conflict, but our result that queen wins the sex allocation conflict contradicts with theirs that the sex allocation ratio under mixed control is intermediate between sex allocation ratios predicted for queen and worker control (the exact values depending on the assumption about how productivity scales with colony size). This is so because in our dynamic model 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.

It has been shown by Pen and Taylor (2005) that if the two parties make their allocation decisions sequentially (the so-called Stackelberg equilibrium, such that the queen acts first and workers respond), then the queen is expected to win the sex allocation conflict even assuming static resource allocation decisions. 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. 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) also generally argue that 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.

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

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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

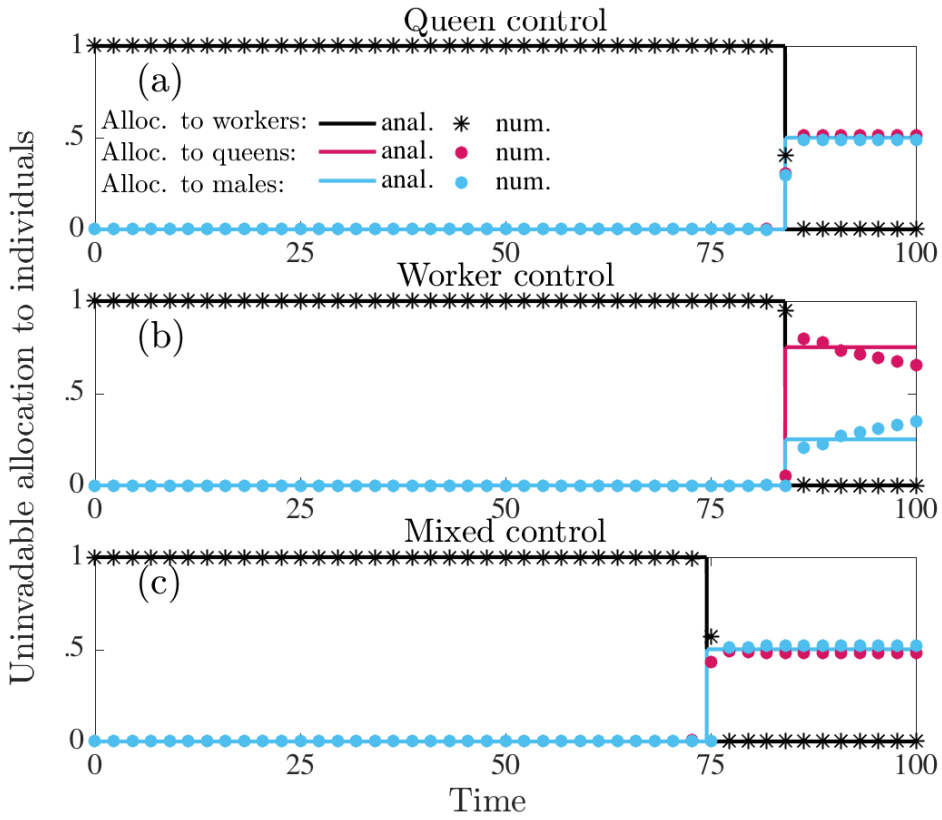

Figure 1: Uninvadable proportional allocation (under delayed dispersal) to workers $a^*_{\mathrm{w}}(t) = v^*_{\mathrm{f}}(t)(1 - v^*_{\mathrm{q}}(t))$ (black), queens $a^*_{\mathrm{q}}(t) = v^*_{\mathrm{f}}(t)v^*_{\mathrm{q}}(t)$ (red), and males $a^*_{\mathrm{m}}(t) = (1 - v^*_{\mathrm{f}}(t))$ (blue). Solid lines are analytically predicted results and the correspondingly colored symbols represent the numerical results. Panel (a): queen control. Panel (b): worker control. Panel (c): mixed control. Proportional allocation to queens and males exactly match for queen and mixed control, which is why red lines do not appear in the corresponding panels. Notice that the numerical results slightly deviate from the analytical results, since any strategy that gives the sex ratio (queens to males) at the end of the season, equal to relatedness asymmetry R_c of the party in control of $v_{\mathrm{f}}(t)$ has equal invasion fitness (see Fig. 3). Parameter values: $M = 1$, i.e. $C = 1.5$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

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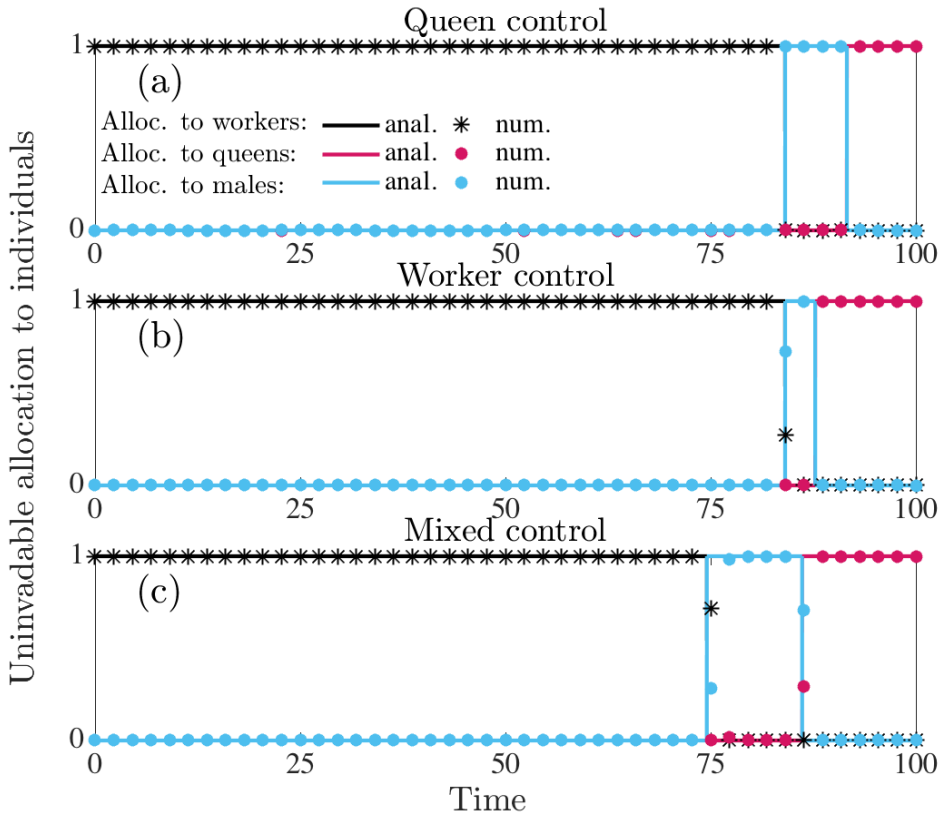

Figure 2: Uninvadable proportional allocation (under direct dispersal) to workers $a_{\mathrm{w}}^*(t) = v_{\mathrm{f}}^*(t)(1 - v_{\mathrm{q}}^*(t))$ (black), queens $a_{\mathrm{q}}^*(t) = v_{\mathrm{f}}^*(t)v_{\mathrm{q}}^*(t)$ (red), and males $a_{\mathrm{m}}^*(t) = (1 - v_{\mathrm{f}}^*(t))$ (blue). Solid lines are analytically predicted results and the correspondingly colored symbols represent the numerical results. Panel (a): queen control. Panel (b): worker control. Panel (c): mixed control. Parameter values: $M = 1$, i.e. $C = 1.5$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

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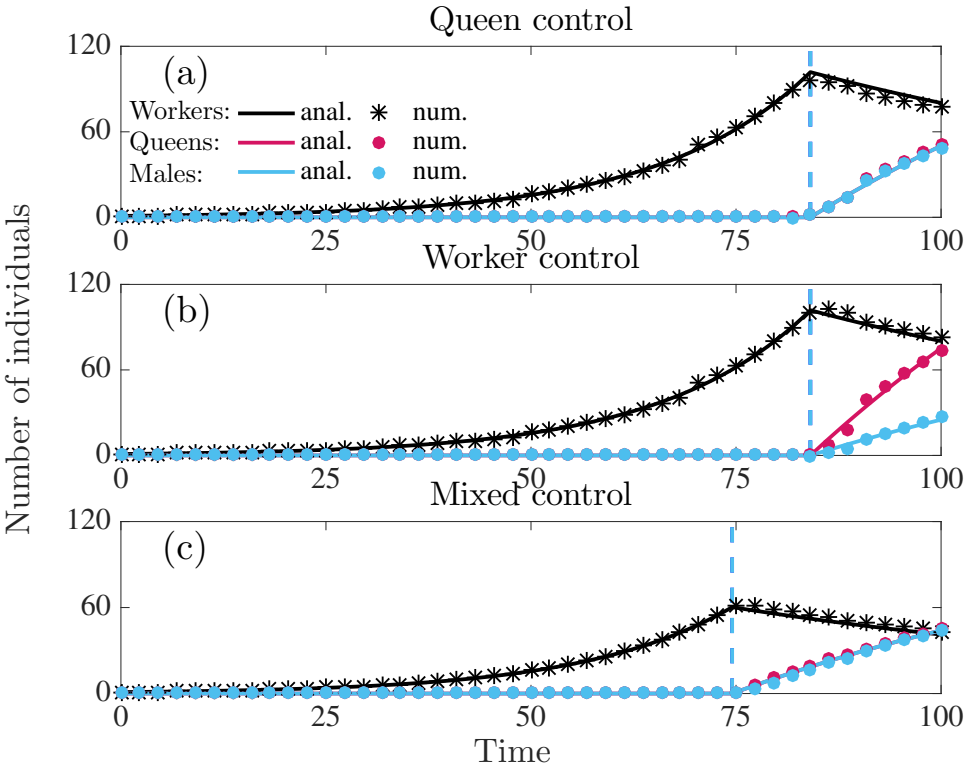

Figure 3: Number of individuals produced in a colony following the uninvadable resource allocation schedule $\mathbf{v}^*$ under delayed dispersal. Number of workers (black), queens (red), males (blue). Solid lines are analytically predicted results and the correspondingly colored symbols represent the numerical results. Panel (a): queen control. Panel (b): worker control. Panel (c): mixed control. Parameter values: $M = 1$, i.e. $C = 1.5$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

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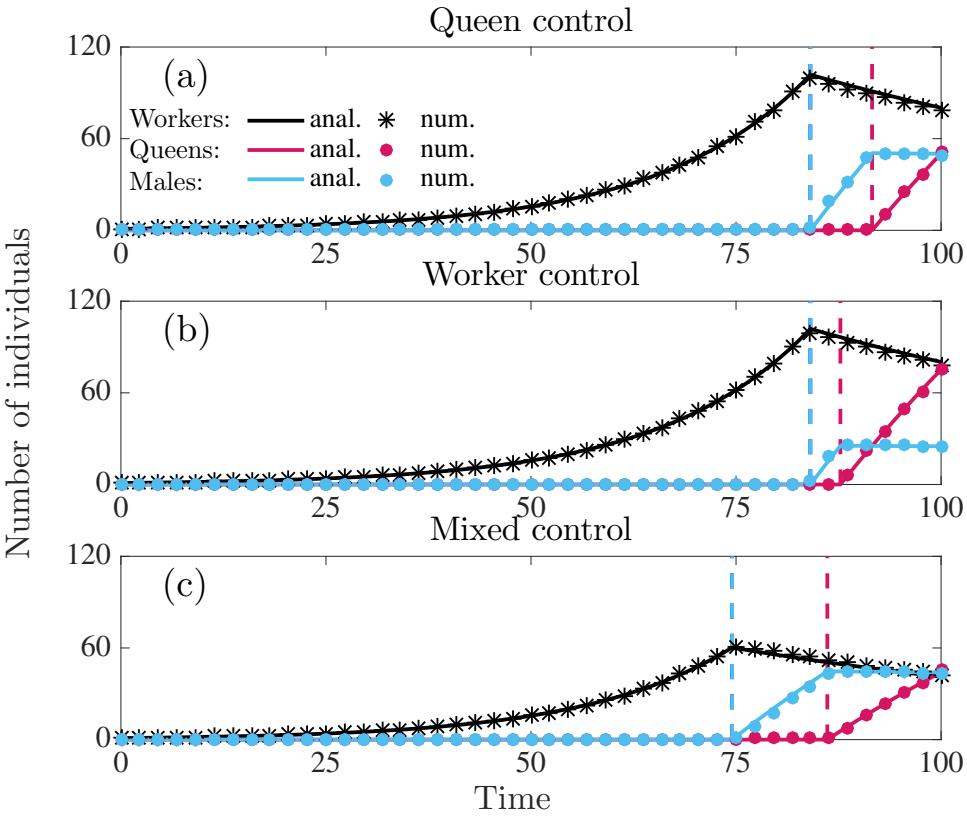

Figure 4: Number of individuals produced in a colony following the uninvadable resource allocation schedule $\mathbf{v}^*$ under direct dispersal. Number of workers (black), queens (red), males (blue). Solid lines are analytically predicted results and the correspondingly colored symbols represent the numerical results. Panel (a): queen control. Panel (b): worker control. Panel (c): mixed control. Parameter values: $M = 1$, i.e. $C = 1.5$ (queen monandry), $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

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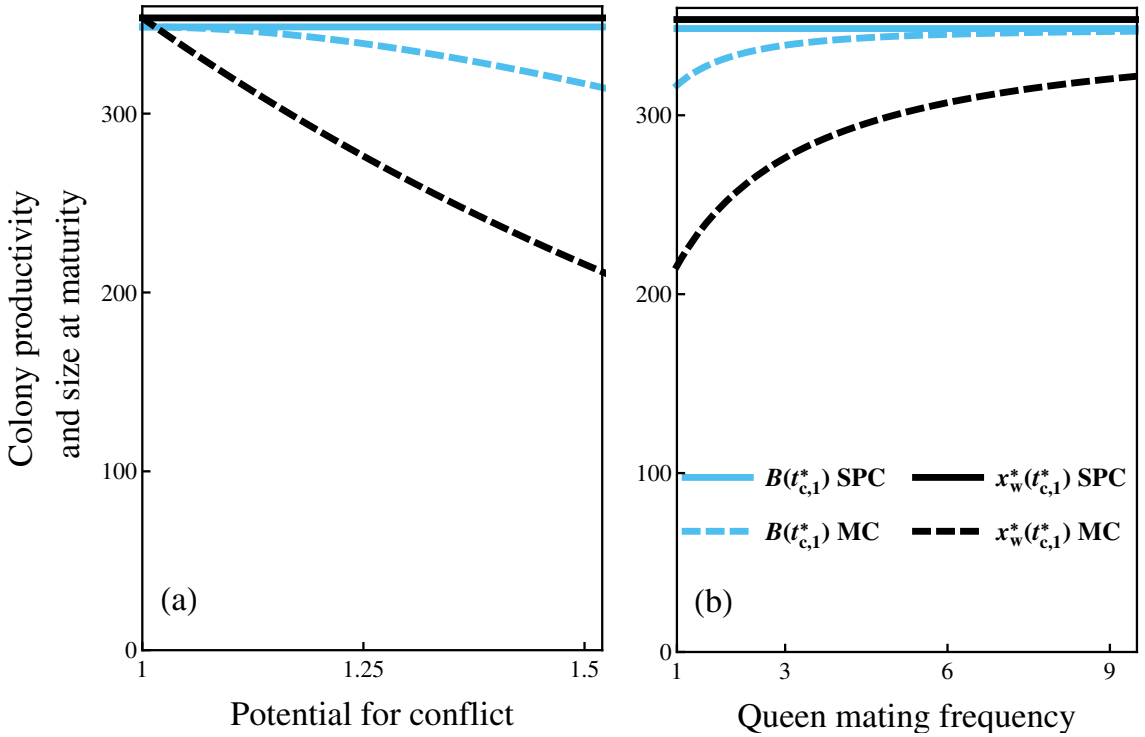

Figure 5: Colony productivity $B(t^*_{c,1})$ (blue lines) and size at maturity $x^*_{\mathrm{w}}(t^*_{c,1})$ (black lines) under single-party (SPC, solid lines) and mixed control (MC, dashed lines) as a function of the potential for conflict C (panel a) and as a function of queen mating frequeny M (panel b) for the uninvadable resource allocation schedule $\mathbf{u}^*$. Recall that $C = (2 + M)/(1 + M)$. Parameter values: $b = 0.07$, $\mu_{\mathrm{w}} = 0.0015$, $\mu_{\mathrm{q}} = \mu_{\mathrm{m}} = 0.001$, $T = 100$.

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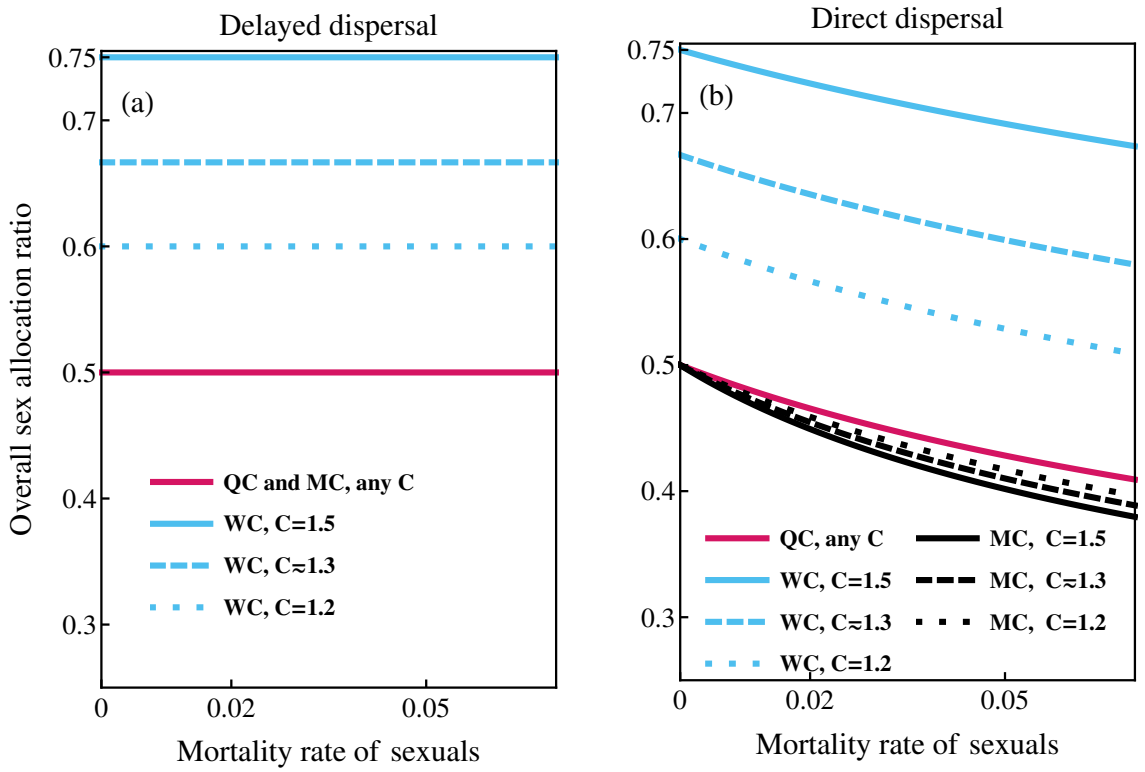

Figure 6: Overall proportional sex allocation ratio S_c (proportional investment into queens) as a function of mortality rate of the sexuals μ_{r} for different values of potential for conflict C. Panel (a): delayed dispersal; queen and mixed control (QC and MC, red lines), worker control (WC, blue lines). Panel (b): direct dispersal; queen control (QC, red lines), worker control (WC, blue lines), mixed control (MC, black lines). Other parameter values: $b = 0.07$, $\mu_{\mathrm{w}} = 0.015$, $T = 100$. Note that classical results from static models (e.g Reuter and Keller, 2001) only coincide with these results under delayed dispersal and single-party control.

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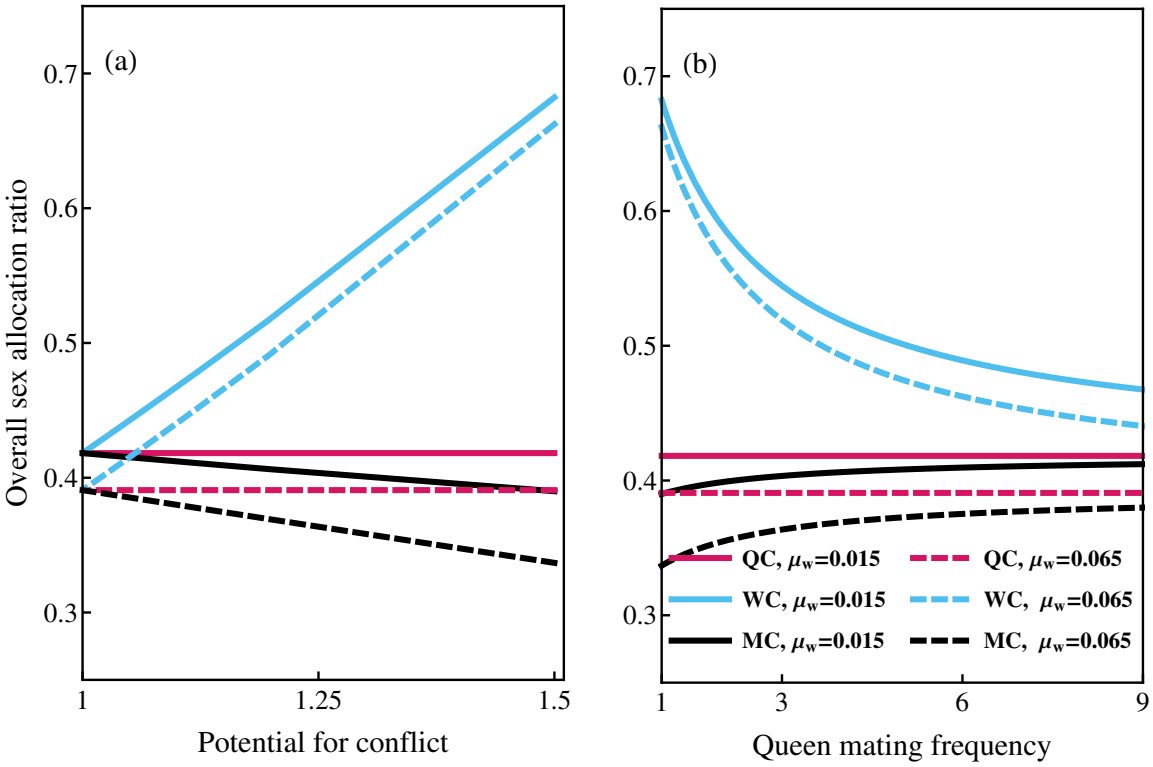

Figure 7: Overall proportional sex allocation ratio S_c (proportional investment into queens) under direct dispersal as a function of the potential for conflict C (panel a) and queen mating frequency M (panel b) for different values of mortality of workers μ_{w}. Queen control (QC, red lines); worker control (WC, blue lines); mixed control (MC, black lines). Parameter values: $b = 0.07$, $\mu_{\mathrm{r}} = 0.06$, $T = 100$.

Parameter dependence of allocation characteristics		
Allocation characteristics	Positive	Negative
Switching times, $t^*_{c,1}$ and $t^*_{c,2}$	M (MC), b, μ_{r}	C (MC), μ_{w}
Colony size at maturity, $y^*_{\mathrm{w}}(t^*_{c,1})$	M (MC), b	C (MC), μ_{w}
Colony productivity, $B(t^*_{c,1})$	M (MC), b, μ_{r}	C (MC), μ_{w}
Sex allocation ratio for delayed disp., S_c (prop. alloc. to queens)	C (WC)	M (WC)
Sex allocation ratio for direct disp., S_c (prop. alloc. to queens)	C (WC), M (MC)	M (WC), C (MC), μ_{r}, μ_{w}, b

Table 1: Parameter dependence of colony resource allocation characteristics for biologically meaningful parameter values ($\mu_{\mathrm{w}} > 0$, $\mu_{\mathrm{r}} > 0$, $b > \mu_{\mathrm{w}}$, and $b > \mu_{\mathrm{r}}$). We predict positive relationship between the allocation characteristics and the parameters listed under "Positive" column and negative dependence between the allocation characteristics and the parameters listed under "Negative" column. Here, "(MC)" and "(WC)" that follows after the parameter, emphasizes that this relations only holds for mixed or worker control, respectively.